Empirical Model for the Estimation of Whole-plant Photosynthetic Rate of Cherry Tomato Grown in a Commercial Greenhouse

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The objective of this study was to develop an empirical model for whole-plant net photosynthetic rate ($P_n$, µmol s⁻¹ per plant) as a function of four essential environmental factors: photosynthetically active radiation (PAR) above the canopy (I, W m⁻²), air temperature ($T_a$, °C), CO₂ concentration ($C$, µmol mol⁻¹), and vapor pressure deficit (VPD, kPa) by using the dataset of $P_n$ and corresponding environmental factors. To prepare the dataset, we monitored the photosynthesis of mature cherry tomato plants grown in a commercial greenhouse for 15 days in summer with a non-contact, non-intrusive photosynthesis real-time monitoring chamber. Four linear models, namely the general linear model (G-model), linear interaction model (I-model), linear squared model (S-model), and linear interaction-squared model (IS-model), were developed and validated their accuracy. The results suggest that the proposed models successfully simulated the cherry tomato plant’s photosynthesis grown in a commercial greenhouse, and IS-model kept relatively higher accuracy regardless of weather conditions. However, to achieve the most accurate $P_n$ estimation is to apply S-model for a sunny day and I-model for a rainy day. These models are prospective for a model-based plant diagnosis to make a judgment whether the current photosynthesis is normal or not.

Keywords: aerial factor, cherry tomato, PAR, photosynthesis chamber, Regression Learner

INTRODUCTION

There have been many works to improve productivity of greenhouse-grown tomato. One effort is to analyze the photosynthetic rate as it influences productivity (Hisaeda et al., 2007; Takayama et al., 2010). Thus, quantifying photosynthetic rates is essential to diagnose the plant condition as well as to achieve the optimum cultivation condition in the greenhouse in the speaking plant approach concept (Hashimoto, 1989; Udink ten Cate et al., 1978). To bridge the plant’s photosynthesis and greenhouse climate control, many researchers developed various kinds of mathematical models of the environmental response of photosynthesis. The models were used as research tools or analytical means, for forecasting, or to be implemented in a computerized system for climate control (Nederhoff and Vegter, 1994). Thornley’s model (Thornley, 1976), Acck’s model (Acck et al., 1978), TOMGRO (Dayan et al., 1993), and TOMSIM (Heuvelink, 1996) are some established models. Some studies used photosynthesis measurements of single-leaf (Thornley, 1976; Acck et al., 1978; Xin et al., 2019), other studies used canopy-level measurements in a closed chamber (Acck et al., 1978), or whole-greenhouse (Nederhoff and Vegter, 1994; Tsafaras and de Koning, 2017). However, these studies could not provide a real-time response of the photosynthesis of a full-size plant, as part of a community under greenhouse condition, to its environment. Furthermore, the variables used in the photosynthesis models vary among the models. The Thornley’s model used incident light flux density, ambient CO₂ concentration, and dark respiration rate with three other parameters to calculate net photosynthesis of single leaf (Acck et al., 1978). The model was then constructed by Acck et al. (1978) for canopy photosynthesis in tomato. Nederhoff and Vegter (1994) used variables of photosynthetically active radiation (PAR, i.e., light flux, 400–700 nm), CO₂ concentration, and leaf area index (LAI) in an empirical photosynthesis model. However, other environmental factors may also contribute to photosynthesis activity. Based on previous literature, photosynthesis activity has an apparent response to temperature (Castilla, 2013), and is affected by vapor pressure deficit (Acck et al., 1976; Shamshiri et al., 2018).

The objective of the present study was to develop an empirical model for the estimation of the whole-plant net photosynthetic rate ($P_n$) of cherry tomato as a function of relevant greenhouse environmental factors. We used data of $P_n$ at the whole-plant level as a real-time response to instantaneous PAR, air temperature, vapor pressure deficit,
and CO₂ concentration under a commercial greenhouse during summer in Japan. The data were measured in 5-minute intervals by the photosynthesis real-time monitoring chamber of Shimomoto et al. (2020), a much higher time resolution compared to previous studies of photosynthesis measurements (Acock et al., 1978; Nederhoff and Vegter, 1994; 10-minute and 30-minute intervals, respectively). We used 10-day data to estimate the next day data by using the regression model.

MATERIAL AND METHODS

Plant materials grown in a semi-commercial greenhouse

The plant materials were two mature cherry tomato plants (S. lycopersicum var. cerasiforme; cv. Scarlet) planted on 24th August in 2017. The plants were grown hydroponically and maintained as a commercial crop under a venlo-type semi-commercial greenhouse (65 m [W] × 32 m [D] × 11003 32 m [H]) in Mie Prefecture, Japan (Romdhonah et al., 2021). A commercial microcomputer (HortiMaX; Hortisystem Co., UK) controlled the greenhouse climate, irrigation, and fertigation at a commercially optimum condition. CO₂ was supplied to maintain a set point of 500 μmol mol⁻¹. Also, the shade screen was closed to avoid the excessive-high air temperature, especially on sunny days. The plants had 15 leaves, and the planting density was 4.2 plants m⁻² when we conducted the photosynthesis measurement.

Measurements of net photosynthetic rate and environmental factors

Net photosynthetic rate of two adjacent cherry tomato plants enclosed by the chamber, PAR at the top of the canopy (I, W m⁻²), air temperature (T, °C), CO₂ concentration of greenhouse air (C, μmol mol⁻¹), and vapor pressure deficit (VPD, kPa) were measured at an interval of 5 minutes for consecutive 15 days from 13th to 27th June in 2018 by using the aforementioned photosynthetic chamber system developed in our previous study (Shimomoto et al., 2020; Fig.1). The system was composed of a transparent open-bottom chamber, which is similar to that of Takayama et al. (2012), and a sensing unit to measure CO₂ concentration of the inflow and outflow air of the chamber and the above-mentioned environmental factors. The detail of measurements is described in Romdhonah et al. (2021). To obtain the net photosynthetic rate of a single plant (Pn, μmol s⁻¹ per plant), we divided the measured photosynthetic rate by two, which is the number of the plants in the chamber.

Dataset for net photosynthesis estimation model

For the model development and validation, we used the above-mentioned four essential environmental factors of I, T, C, and VPD. To omit error data, we cleaned the measured data (n = 2,730) in the same way as Romdhonah et al. (2021) and 17 numbers of data, which is 0.62 % of the measured data, were regarded as error data and removed. After that, the 5-point moving average filter was applied to the cleansed data based on the findings of our previous study (Romdhonah et al., 2021), i.e., the 30-minute moving (or simple) average dramatically increased the R² and decreased the Root Mean Squared Error (RMSE) of the simple linear regression model for the cherry tomato plants’ photosynthesis, and prepared the dataset for model development.

Figure 2 shows the time course of Pn, and Fig. 3 shows the time courses of I, T, C, and VPD of the dataset, which is used for the model development. The dataset was divided into two groups, i.e., training data (data from 13th to 22nd June 2018 of the time period in grey of Fig. 2, 3; n = 1,804) and test data (data from 23rd to 27th June 2018 of the time period in white of Fig. 2, 3; n = 909). The training data were used for the supervised machine learn-
NET PHOTOSYNTHESIS MODEL

Akaike’s Information Criterion (AIC) for model comparison (Akaike, 1974). AIC measures the trade-off between model fit and complexity of a model. A better fit model is the one with lower AIC among the other models (Mohamed et al. 2015).

Development of linear regression models of net photosynthetic rate

As mentioned above, the Regression Learner application of MATLAB® R2019a was used for the model development. We explored four different types of linear regression to take account of the 2-factor interactions such as $I \times T \times I$, $T \times C \times T$, and $I \times C \times I$, etc. and squared components such as $I^2$, $T^2$, $C^2$, and $VPD^2$. The stepwise method was used to judge whether the component should be kept in the model or removed from the model, i.e., the component was kept in the model if the $p$-value of the component is less than 0.05 and vice versa.

The following equations correspond to the four models, namely the general linear model ($G$-model) (Eq. 1), linear interaction model ($I$-model) (Eq. 2), linear squared model ($S$-model) (Eq. 3), and linear interaction-squared model ($IS$-model) (Eq. 4).

$$P_n = \alpha_0 + \alpha_1 T + \alpha_2 C + \alpha_3 VPD$$ (1)

$$P_n = \beta_0 + \beta_1 T + \beta_2 C + \beta_3 VPD + \beta_4 I + \beta_5 T \times I + \beta_6 C \times I + \beta_7 VPD$$ (2)

$$P_n = \gamma_0 + \gamma_1 I + \gamma_2 T + \gamma_3 C + \gamma_4 VPD + \gamma_5 I^2 + \gamma_6 T^2 + \gamma_7 C^2 + \gamma_8 VPD^2$$ (3)

$$P_n = \delta_0 + \delta_1 I + \delta_2 T + \delta_3 C + \delta_4 VPD + \delta_5 I \times T + \delta_6 I \times C + \delta_7 T \times C + \delta_8 VPD + \delta_9 I^2 + \delta_{10} T^2 + \delta_{11} C^2 + \delta_{12} VPD^2$$ (4)

where $P_n$ ($\mu$mol s$^{-1}$ per plant) is the photosynthetic rate of a cherry tomato plant, $I$ (W m$^{-2}$) is PAR, $T$ (°C) is the air temperature, $C$ (μmol mol$^{-1}$) is the CO$_2$ concentration, $VPD$ (kPa) is the vapor pressure deficit, and $\alpha$, $\beta$, $\gamma$, and $\delta$ are the regression coefficients. Therefore, $G$-model (Eq. 1) only accounts for original predictors in their linear form. $I$-model (Eq. 2) accounts for the linear form and interaction between two predictors. $S$-model (Eq. 3) accounts for the linear and squared forms of the predictors, while $IS$-model (Eq. 4) accounts for the linear, 2-factor interactions and squared form of the predictors. After developing the models by using the training data, we investigated the accuracy of the model by using the test data.

RESULTS AND DISCUSSIONS

Features of dataset

The conditions of rainy and sunny days were included in the dataset (Fig. 3). The average value of $C$ during daytime was 379 μmol mol$^{-1}$, while $I$, $T$, and $VPD$ were 149.21 W m$^{-2}$, 23.4°C, 0.46 kPa, respectively. The maximum value of $P_n$ was 15.0 μmol s$^{-1}$ per plant, which equals 24.2 μmol m$^{-2}$ s$^{-1}$ per unit leaf area, recorded at 15:09 on 16th June 2018. At that time, $T$ was 27.2°C, $I$ was...
The continuous measurement established diurnal patterns of $P_{n}$ (Fig. 2). The rates during nighttime (light intensity is 0 W m$^{-2}$) were negative for the dark respiration ($R_d$), then the $P_{n}$ increased promptly after sunrise. Furthermore, the $P_{n}$ showed a slight decrease at midday, which might be caused by the sudden drop of $I$ by closing the shade-screen and then decreased during the afternoon until the sunset.

Outline of four linear regression models

Table 1 shows the $R^2$, RMSE, and AIC and the calculated regression coefficients of the variables for the four models developed by the training data. In the IS-model, a square of $T$ ($T^2$) was deleted from the model because the $F$-value of this variable was more than 0.1 in the stepwise method. The deletion implies that the variable $T$ provides enough contribution to the IS-model as the linear ($T$) and interaction ($T \times T$, $T \times C$, $T \times C^T$, and $T \times VPD$) components. The four models gave high $R^2$’s ranging from 0.82 to 0.92. IS-model showed the highest $R^2$ of 0.92, which was slightly higher than that of the $I$-model (0.91). Furthermore, the RMSE value of IS-model was the lowest among the four models. This result probably because IS-model has a larger number of components compared with other models. A similar discussion had been done in several previous studies (Jiao et al., 1991; Leonards et al., 1994; Percival et al., 1996; Lootens and VendeCASTEEL, 1998). In these models, the regression coefficients were rounded to four decimal digits, the coefficients were rounded to four decimal digits, the RMSE of IS-model increased to 2.369 from 1.449, and the $R^2$ decreased to 0.75 from 0.89 (Table 2).

Figure 4 shows the time course of the measured and estimated $P_{n}$ of G-model (Eq. 1), $I$-model (Eq. 2), $S$-model (Eq. 3), and IS-model (Eq. 4) on a typical sunny day (24th June 2018), i.e., the day had high total solar radiation (24.29 MJ m$^{-2}$ d$^{-1}$) with no rainfall events. From 5:20 until 9:30, G-model slightly underestimated the $P_{n}$ in spite of the other models accurately estimated the $P_{n}$. From 9:30 to 14:00, G-model showed underestimation at around 10:00 and 13:30, and an obvious overestimation at around 12:30. S-model showed slight underestimation at around 10:00, 12:30, and 13:30, on the other hand, $I$- and IS-models showed better estimation during this time period. From 14:00 to 19:00, $S$-model showed good estimation throughout the time period, however, G-model overestimated after 17:30, and $I$- and IS-models showed constant overestimation throughout this time period. These results suggest that the components of squared environmental factors such as $I^2$, $T^2$, and $C^2$ (Table 1), which are used in the $S$- and $IS$-models, are important for the $P_{n}$ estimation on a sunny day. Figure 5 shows the time course of the measured and model-estimated $P_{n}$ on a typical rainy day (23rd June 2018), i.e., the day had low total solar radiation (5.71 MJ m$^{-2}$ d$^{-1}$) with rainfall events (11:00–18:00). From 4:00 to 10:00, all the models tended to underestimate the $P_{n}$. Especially, G-model apparently underestimated the $P_{n}$, and the estimated $P_{n}$ kept at about −1.35 μmol s$^{-1}$ per plant until 7:30. From 10:00 to 16:00, all the models more or less overestimated the $P_{n}$. However, the extent of the overestimation was much smaller in the $I$- and IS-models compared with other models and limited at the time period from 13:00 to 14:00. After 16:00, $I$-, $S$-, and IS-models showed good estimation, but only G-model kept the overestimation. These results

Table 1 Summary and coefficients of the linear empirical models derived from the Regression Learner MATLAB® R2019a using the training dataset from 13th to 22nd June 2018 ($n = 1,804$). $R^2$ is the coefficient of determination, RMSE is Root Mean Squared Error, and AIC is Akaike’s Information Criterion.

| Model       | General ($\beta_0$) | Interaction ($\beta_1$) | Squared ($\beta_2$) | Interaction-squared ($\beta_3$) |
|-------------|---------------------|-------------------------|---------------------|---------------------------------|
| $R^2$       | 0.82                | 0.91                    | 0.90                | 0.92                            |
| RMSE        | 1.755               | 1.220                   | 1.286               | 1.180                           |
| AIC         | 7.154               | 5.848                   | 6.037               | 5.732                           |
| Regression coefficients | | | | |
| Intercept   | 21.568543226        | 30.397694796            | 67.849712610        | 83.192052126                    |
| $I$         | 0.014438811         | 0.006249509             | 0.045484796         | 0.027068085                     |
| $T$         | 0.127484169         | −1.402852991            | 0.655722967         | −1.681326211                    |
| $C$         | −0.050808105        | −0.69541362             | −0.348380378        | −0.317867269                    |
| VPD         | 1.079146866         | 46.084567946            | −1.792831605        | 29.427053425                    |
| $IT$        | −0.002045443        | −0.001326529            | −0.000146429        | −0.000305578                     |
| $IC$        | 0.000233875         | 0.000446129             | 0.000446129         | −0.000305578                     |
| $IVPD$      | −0.031713733        | −0.025305578            | −0.025305578        | −0.025305578                     |
| $IC^T$      | 0.003204569         | 0.004090373             | 0.004090373         | 0.004090373                     |
| $CVPD$      | 1.035827097         | 0.579150195             | 0.579150195         | 0.579150195                     |
| $I^2$       | −0.3177226612       | −0.000055460            | −0.000055460        | −0.000055460                     |
| $T^2$       | −0.015699075        | Removed                 | −0.015699075        | Removed                         |
| $C^2$       | 0.000403450         | 0.000281020             | 0.000281020         | 0.000281020                     |
| VPD$^2$     | 3.077339476         | 3.798660781             | 3.798660781         | 3.798660781                     |
imply that the interaction components such as I_T, T_C, and T_VPD (Table 1), which are used in I- and IS-models, are important for the \( P_n \) estimation on a rainy day. Figures 6 and 7 show the residuals (measured \( P_n \) minus estimated \( P_n \)) of \( P_n \) estimations of the models against the measured data on a typical sunny day (24th June 2018) and a typical rainy day (23rd June 2018), respectively. According to Reed et al. (1976), there should be an equal number of positive and negative residuals for an appropriate model. Figure 6 shows that the residuals of the \( S \)-model were distributed about zero, except for the higher \( P_n \) range, indicating a suitable model for a sunny day, whereas, for a rainy day, the \( I \)-model is a suitable model. Furthermore, the residual plots of all the models on a sunny day do not show any specific patterns or skew. However, the skewed shapes of the residuals were obviously seen in \( G \)-model and \( S \)-model on a rainy day (Fig. 7), suggesting needed changes in the models (Reed et al., 1976). A linear-only or with a squared form in the model may not be able to estimate the \( P_n \) accurately for a rainy day.

Table 2 summarizes RMSEs and \( R^2 \)s derived from the validations of the developed four models for the 5-consecutive days from 23rd to 27th June, a typical sunny day (24th June, Fig. 4), and a typical rainy day (23rd June, Fig. 5). The models gave \( R^2 \)s ranging from 0.78 to 0.89 for 5-consecutive days (\( n = 909 \)). Most of the models performed better for the typical sunny day (\( n = 183 \)) and worse for the
Fig. 6  Residuals (measured $P_n$ minus estimated $P_n$) of $P_n$ estimations of the models on a typical sunny day (24th June 2018).

Fig. 7  Residuals (measured $P_n$ minus estimated $P_n$) of $P_n$ estimations of the models on a typical rainy day (23rd June 2018).

Table 2  Validation of $G$-, $I$-, $S$-, and $IS$-models using test data

| Model | 5-consecutive days | Typical sunny day | Typical rainy day |
|-------|-------------------|------------------|------------------|
|       | 23rd-27th June    | 24th June        | 23rd June        |
|       | ($n = 909$)       | ($n = 183$)      | ($n = 181$)      |
|       | RMSE   | $R^2$ | RMSE   | $R^2$ | RMSE   | $R^2$ |
| $G$   | 3.264  | 0.78  | 3.841  | 0.79  | 2.386  | 0.42  |
| $I$   | 1.990  | 0.87  | 2.605  | 0.86  | 0.816  | 0.71  |
| $S$   | 1.891  | 0.88  | 1.618  | 0.92  | 1.218  | 0.55  |
| $IS$  | 1.449  | 0.89  | 1.665  | 0.90  | 0.894  | 0.67  |
typical rainy day (n = 181) compared with the 5-consecutive days. The worse estimation for the rainy day might be caused by limited days with rainfall events in the training data. G-model was the least accurate in all cases. On a typical sunny day, S- and IS-model that including squared components such as \( I^2, T^2 \) and \( C^2 \) (Table 1) showed relatively higher accuracy compared with G- and I-models. While on a typical rainy day, I- and IS-models, which account for interaction components such as \( I.T, T.C \) and \( T.VPD \) (Table 1), had better accuracy than G- and S-models. These results suggest that the squared components \( (I^2, T^2, \) and \( C^2) \) play an important role to increase the accuracy of the \( P_n \) estimation on a sunny day, on the other hand, the interaction components \( (I.T, T.C, \) and \( T.VPD) \) may have a significant effect to keep the \( P_n \) estimation accuracy at a relatively higher level on a rainy day. Therefore, IS-model keeps relatively higher accuracy regardless of weather conditions, although the best way to achieve the most accurate \( P_n \) estimation is to apply S-model for a sunny day and I-model for a rainy day. The stable higher accuracy of IS-model seems normal because this model consists of most environmental factors, including interaction and squared components. In addition, IS-model has the smallest AIC (Table 1), which means that this model is considered having a better fit compared with the other models to estimate future values (Akaike, 1974; Mohammad et al. 2015). However, the reason of that the highest accuracies of S-model for a sunny day and I-model for a rainy day cannot be clarified in this study.

This study proposed that the conventional linear regression models developed by using the high time-resolution photosynthesis data measured with the photosynthesis real-time monitoring chamber successfully simulated the cherry tomato plant’s photosynthesis grown in a commercial greenhouse. The comparison of the developed four models, which consist of different variables, proved that the interaction components such as \( I.T, T.C, \) and \( T.VPD \) (Table 1) and the squared components such as \( I^2, T^2 \) and \( C^2 \) (Table 1) dramatically increases the accuracy of the \( P_n \) estimation. Furthermore, we pointed out that the model (I-model) consist of the interaction components, but not having the squared components showed the highest accuracy for the rainy day and the model (S-model) consisting of the squared components, but not the interaction components showed the highest accuracy for the sunny day. To increase the accuracy of the \( P_n \) estimation model, the plant growth information such as an increase in LAI and stem length, etc. and some kinds of worker’s operations such as leaf removal and harvesting, etc. should be taken account into the model because these physical changes in the plant body can alter the environmental response of photosynthesis. In addition, the coefficients of the model should be updated by using the latest photosynthesis data measured with the photosynthesis real-time monitoring chamber to keep the higher accuracy of the models. Through further improvement as mentioned above, the model-based plant diagnosis, i.e., making a judgment whether the current photosynthesis is normal or not, might be possible in the near future.

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