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A DISSERTATION FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

Photosynthesis Enhancement in Greenhouse-grown ‘Irwin’ Mango Trees Using Vertical CO₂ Enrichment System Based on Ray-tracing Simulation

광추적 시뮬레이션에 기반한 수직적 CO₂ 시비 시스템에 의한 온실 재배 ‘어윈’ 망고의 광합성 증진

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Photosynthesis Enhancement in Greenhouse-grown ‘Irwin’ Mango Trees Using Vertical CO₂ Enrichment System Based on Ray-tracing Simulation

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ABSTRACT

Mango (Mangifera indica L.) is one of the 30 major crops in the world and grown mainly in tropical or subtropical regions. In order to increase the production of fruit crops, their photosynthesis must be increased. To estimate the whole plant photosynthetic rate accurately, how light interception by crops changes with environmental and morphological factors is needed to be investigated. The whole plant photosynthetic rates could be efficiently estimated by combining the measurement and simulation methods with leaf photosynthetic rate models in determining procedures for CO₂ enrichment in greenhouses. CO₂, as a material for photosynthesis, is needed to be enriched sufficiently. Most of commercialized CO₂ enrichment devices are not considering the distribution of photosynthetic rate. The objectives of this study were to determine the precise photosynthetic rate model, to analyze accurate light intensity using a 3D plant model and
ray-tracing method, to calculate the spatial distributions of the photosynthetic rate, and to optimize the efficient CO₂ enrichment position for ‘Irwin’ mango trees grown in greenhouses. Regression analyses for three different leaf photosynthetic rate models such as simple multiplication, rectangular hyperbola, and Farquhar, von Caemmerer, and Berry (FvCB) models were conducted. The determination coefficient (R²) value was highest in the simple multiplication model at 0.79, and the rectangular hyperbola model had the lowest value of 0.68. The vertical leaf photosynthetic rate models established in this study will help determine environmental conditions that can maximize photosynthesis of ‘Irwin’ mango trees grown in greenhouses. Under artificial light, the estimated photosynthetic rate increased from 2.0 to 2.9 μmol CO₂·m⁻²·s⁻¹ with increasing CO₂ concentration. On the other hand, under natural light, the photosynthetic rate increased from 0.2 μmol CO₂·m⁻²·s⁻¹ at 06:00 to a maximum of 7.3 μmol CO₂·m⁻²·s⁻¹ at 09:00, and then gradually decreased to −1.0 μmol CO₂·m⁻²·s⁻¹ at 18:00. In validation, simulation results were in good agreement with the measured results with R² and root mean square error were 0.79 and 0.263, respectively. This method could accurately estimate the whole plant photosynthetic rate and be useful for determining the levels of pruning and CO₂ enrichment. The accumulated CO₂ consumption calculated by simulation was found to be the highest value of 5.63 ± 0.02 g·plant⁻¹ when the CO₂ was enriched at 1.2 m height. When CO₂ was enriched at 1.2 m height, the accumulated CO₂ consumption was 12.9% higher than at 0.5 m height. Therefore, the CO₂ enrichment to the middle to top of the crop canopy, where photosynthesis mainly occur, can increase photosynthesis compared with the conventional CO₂ enrichment method to the lower part of the crop. From the results, it is confirmed that...
this method will enhance crop photosynthesis and CO₂ utilization efficiency in greenhouses.

Additional keywords: assimilation, carbon dioxide enrichment, precision agriculture, three-dimensional plant model, ventilation

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GENERAL INTRODUCTION

Photosynthesis reactions must be performed for the life activities of plants. In greenhouses, light intensity is changed by meteorological factors or by the structure and covering materials, and by the architecture of the crops (Buck-Sorlin et al., 2011; Kim et al., 2016). When CO$_2$ at high concentration is supplied, it is used for the growth of leaves and stems of crops and affect the photosynthesis of the crops (Hu et al., 2011; Son et al., 1999). The crop production is determined by the synthesis and distribution of assimilation products (Heuvelink, 1996; Marcelis et al., 1998). To hold carbon through photosynthesis, lignification is required and crops must be cultivated in long-term (Xu et al., 2007). In order to increase the yield of fruit crops, the assimilation by photosynthesis must be increased, so it is important to know exactly the whole plant photosynthetic rate.

In order to calculate whole plant photosynthetic rate, leaf photosynthetic rate should be accurately measured, quantified, and expressed to a mathematical model. Thus, modeling techniques have recently come into the spotlight as a way to quantify environmental factors affecting photosynthesis (Medina-Ruíz et al., 2011; Noe and Giersch, 2004). While many models expressing photosynthesis as affected by single environmental factor are simple in form, models representing the photosynthesis changes caused by various environmental factors are often complex in form. Although simple multiplication models with easy form have long been used, rectangular hyperbola model and Farquhar, von Caemmerer, and Berry (FvCB) model reflecting the physiological characteristics of plants have also been developed (Farquhar et al., 1980; Jones et al., 1991; Kaitala et al., 1982).
Mango trees growing greenhouses with heating system have a highly sealed thermal insulation structures to prevent heat loss, and large amounts of steel structures to prevent damage from frequent typhoons. Due to such spatial constraints within the greenhouse, mango trees are grown in a vase shape through artificial training and pruning (Yonemoto, 2006). When a mango tree grows higher than 2 m in a vase-shape, the light intensities at the top and bottom leaves in the canopy are different. However, actual light interception of the canopy is difficult to be measured due to technical limitations.

From this aspect, three-dimensional (3D) plant model should be constructed to reflect the exact physical characteristics of the plant architecture. Ray-tracing is a reasonable approach to integrate optical characteristics such as reflectance and transmittance of leaves and other structures into light simulations. Many attempts have recently been made to investigate light distribution in crop leaves using 3D plant models and ray-tracing techniques (Buck-Sorlin et al., 2011; De Visser et al., 2014; Der Zande et al., 2011; Kim et al., 2016). Although various studies are underway to accurately represent the photosynthesis rate of crops, most of commercialized CO₂ enrichment devices are not considering the distribution of photosynthesis rate. Most of the devices for enriching CO₂ are in the form of spraying CO₂ upward from the floor of the greenhouse (Takeya et al., 2017). Furthermore, vertical CO₂ enrichment at the each position of dense canopy-forming or complex-formed crops has not been conducted. Since CO₂ enrichment is generally recommended from sunrise until sunset as long as the greenhouse is not ventilated on sunny days (Mortensen, 1987), this study was conducted in the morning when the roof and side windows of the greenhouse were closed, with high CO₂ consumption efficiency.
The objectives of this study were to determine the precise photosynthetic rate model, to analyze accurate light intensity using a 3D plant model and ray-tracing method, to calculate the spatial distributions of the photosynthetic rate, and to optimize the efficient CO₂ enrichment position for mango trees grown in greenhouses.
LITERATURE REVIEW

Mango cultivation in non-tropical regions

Mango (*Mangifera indica* L.) is one of the 30 major crops in the world and grown mainly in tropical or subtropical regions. ‘Carabao’ mango of the yellow fruit skin, has a slight sour taste (Naef et al., 2006), While ‘Irwin’ mango, also called apple mango, has red fruit skin. ‘Irwin’ mangoes are high in sugar contents and juicy, and have a strong fragrance. Demand for ‘Irwin’ mango has recently been increasing. The cultivation areas of ‘Irwin’ mango trees in Korea, including Jeju Island, Yeosu, and Tongyeong, are growing at around 25 ha (An et al., 2015; Park et al., 2014). In Japan, mango trees have been cultivated in greenhouses in Okinawa for commercial purposes since 1984 (Akinaga and Hasbullah, 2002). However, Korea has unsuitable climate characteristics for the growth and development of mangoes, especially in winter, cold damage can happen easily. Therefore, mangoes have to be grown in greenhouses with heating systems (Honsho et al., 2012). For saving the heating cost, geothermal heat pumps or waste heat from thermal power plants as a form of hot water have been used for growing several subtropical fruit crops (Lee et al., 2006; Ryou et al., 2012). The mango growing greenhouse with heating system, has a highly sealed thermal insulation structure to prevent heat loss. Also, greenhouses in Jeju Island use large amounts of steel structures to prevent damage from frequent typhoons. Due to such spatial constraints within the greenhouse, mango trees are grown in a vase shape through artificial training and pruning (Yonemoto, 2006). Even when growing as a vase shape, mango trees grow higher than 2 m, the light intensities reaching the top and
bottom leaves are different. In order to hold carbon through photosynthesis of plants, it must be a long-term growing crop, and lignification is required (Xu et al., 2007). Mangoes are suitable crops in terms of carbon sequestration. To date, however, no systematic research has been conducted to determine the physiological responses such as photosynthesis of the mango trees under the characteristic environment of greenhouses.

**Models for expressing leaf photosynthetic rate of mango trees**

In order to increase the production of fruit crops, the photosynthesis must be increased, and it is very important to know the photosynthetic rate accurately. Thus, modeling techniques have recently come into the spotlight as a way to quantify environmental factors affecting photosynthesis (Medina-Ruíz et al., 2011; Noe and Giersch, 2004). While many models expressing the changes in photosynthesis caused by single environmental factor are simple in form, models representing the photosynthetic rate for various environmental factors are often complex in form. Traditionally, simple multiplication models have been used to multiply simple equations that quantify photosynthetic rate for a single environmental factor by one another (Jones et al., 1991; Park et al., 2016). However, the simple multiplication model does not reflect the physiological characteristics of the crop. Rectangular hyperbola or negative exponential models are mainly used to express photosynthetic rates for light intensity and CO₂ concentrations (Baker and Allen, 1993; Valladares et al., 1997). Thornley (1974) developed a simple chemical reaction model for the chemical reactions that take place in light and dark reactions of photosynthesis. This chemical reaction model, expressed in the form of differential equations, makes it possible
to express photosynthetic rate in a rectangular hyperbola model (Acock et al., 1976; Kaitala et al., 1982; Thornley, 2002). The most widely used models in recent years are the FvCB models developed by Farquhar, von Caemmerer, and Berry (Farquhar et al., 1980; Yin et al., 2009). The FvCB model is constructed by selecting a region that is a limiting factor in the process of photosynthetic reaction and applying different models to each region. Each coefficient included in the FvCB model has a disadvantage in that it has a complicated shape because it is composed of a form corresponding to the physiological response of the plant, but it is known as the most suitable model for expressing the photosynthetic rates changed by various environmental factors (Qian et al., 2012).

In the case of ‘Kensington’ mango exposed to high CO₂ concentration for a short period, the photosynthetic rate was reported to increases with increasing CO₂ concentration (Schaffer et al., 1997). However, photosynthetic rate with 1,200 μmol·m⁻²·s⁻¹ of light intensity showed a saturation point, which was interpreted as the maximum level of biochemical reaction of photosynthesis (Whiley and Schaffer, 1997). In addition, Chamchaiyaporn et al. (2013) expressed changes in photosynthetic rate with increasing light intensity using a rectangular hyperbola model, but the photosynthetic rate measured once at 37°C, which was low about 3.5 μmol CO₂·m⁻²·s⁻¹. ‘Nam Dok Mai’ mango trees were grown with different temperature differences between day and night, the diurnal photosynthetic rates varied from 1.7 to 7.8 μmol CO₂·m⁻²·s⁻¹ (Pongsomboon et al., 1991).
**Photosynthetic rate with various environmental and morphological factors**

The photosynthetic rate of crops can be used for predicting crop production (Monteith, 1956) and determining CO$_2$ supply (Hu et al., 2011; Jung et al., 2016; Son et al., 1999). In general, the photosynthesis of crops grown in greenhouses depends on environmental factors such as light intensity, temperature, CO$_2$ concentration, and relative humidity inside the greenhouse. These environmental factors are closely related to the structural characteristics of the greenhouse and the meteorological conditions outside the greenhouse. In particular, the light intensity on leaves is dependent not only on the environmental factors but also on the morphological characteristics of the crops (Chen et al., 1999; Vos et al., 2010). Other environmental variables, such as light direction, ratio of diffuse light, plant growth stage, and plant density, also affect light interception inside the crop canopy (Buck-Sorlin et al., 2011; Leith and Pasian, 1990; Stirling et al., 1994). Therefore, in order to estimate the whole plant photosynthetic rate of crops, it is important to investigate the light interception of crops related with these environmental and morphological factors.

**3D ray-tracing simulation for complex canopy plants**

The FvCB model represents leaf-level biochemical mechanisms, which are the most well-known reactions for photosynthesis, and has been used consistently in various studies (Zhu et al., 2012). The main assumption of the FvCB model is that the absorbed photosynthetic active radiation affects the photosynthetic capacity of each canopy position and contributes to the overall canopy photosynthesis (De Pury and Farquhar, 1997; Johnson et al., 2010). In addition, to simplify the calculation, the models assume that the
vertical distribution of light interception has a negative exponential pattern from the top to the bottom of the canopy (Monsi and Saeki, 1953; Norman, 1980). However, in these models, the spatial and temporal heterogeneity of light interception are not considered. Many models of canopy photosynthesis have been devoted to reflect the structural characteristics of crops and the scattering of light within the crop canopy (Hikosaka, 2014; Kim et al., 2010; Tang et al., 2015). However, photosynthesis models that explain canopy photosynthesis have a disadvantage in that the model formulas are complicated because of sunlit and shaded leaves. Moreover, while the FvCB model has been used for the analysis of carbon fluxes in an ecosystem, it has rarely been used for the analysis of light intensity and photosynthesis of a greenhouse crop canopy (Yin and Struik, 2009). Therefore, using a simple leaf photosynthesis model and reflecting the changes along the leaf position are suitable for expressing the whole plant photosynthetic rate of the crop (Jung et al., 2015; Schaffer et al., 1997). Thus, it is necessary to study the method of using specific values for light intensity in the canopy for simple leaf photosynthesis models.

Preconditions for analyzing accurate light distribution, spatial leaf photosynthetic rate, and whole plant photosynthetic rate of crop canopy are required (Chen et al., 2015). From this aspect, 3D plant model should reflect the exact physical characteristics of the plant architecture. Ray-tracing is a reasonable approach to integrate optical characteristics such as reflectance and transmittance of leaves and other structures into light simulations. Recently, there have been many studies investigating light distribution in crop leaves using 3D plant models and ray-tracing techniques (Buck-Sorlin et al., 2011; De Visser et al., 2014; Der Zande et al., 2011; Kim et al., 2016).
Limitations of commercialized CO_2 enrichment methods

Although various studies are underway to accurately represent the photosynthesis rate of crops, most of commercialized CO_2 enrichment devices are not considering the distribution of photosynthesis rate. Most of the devices for enriching CO_2 are in the form of spraying CO_2 upward from the floor of the greenhouse (Takeya et al., 2017). However, majority of soil releases CO_2 resulting from the respiration of internal microorganisms, and naturally increases the CO_2 concentration near the floor even in the greenhouse (Fernandez and Bailey, 1994; Muñoz et al., 2010). In addition, the vertical CO_2 enrichment at each position of dense canopy-forming or complex-formed crops has not been conducted.
LITERATURE CITED


Park IG, Yoon HJ, Kim MA, Lee KY, Park HC, Kim SH (2014) Effect on pollinating activities on mango flower by bumblebee (Bombus terrestris), honeybee (Apis mellifera), and oriental latrine fly (Chrysomyia megacephala) in greenhouse. J Apic 29:235–243


CHAPTER 1

Evaluation of Vertical Leaf Photosynthetic Rate Models for Greenhouse-grown ‘Irwin’ Mango Trees

ABSTRACT

Mango (Mangifera indica L.) is one of the 30 major crops in the world and grown mainly in tropical or subtropical regions. In order to increase the production of fruit crops, their photosynthetic rates must be increased based on quantitative analysis. The objective of this study was to measure and quantify the photosynthetic rate of ‘Irwin’ mango leaves according to the leaf position and to determine the precise photosynthetic rate model including light intensity, CO₂ concentration, and leaf temperature. Leaf photosynthetic rates were measured at different light intensities of 0, 50, 100, 200, 300, 400, 600, and 800 μmol·m⁻²·s⁻¹ and CO₂ concentrations of 100, 400, 800, 1,200, and 1,600 μmol·mol⁻¹, at three different leaf positions. Measurements were taken in triplicates of the top (4-6 nodes), the middle (2-4 nodes), and the bottom (1-2 nodes) of the tree, based on the number of nodes. Regression analyses for three different multi-variable leaf photosynthetic rate models such as simple multiplication, rectangular hyperbola, and FvCB models were conducted. As the validation results, the R² value was highest in the simple multiplication model at 0.79, and the rectangular hyperbola model had the lowest result of 0.68. The vertical leaf photosynthetic rate models established in this study will help determine
environmental conditions that can maximize photosynthesis of ‘Irwin’ mango trees grown in greenhouses.

Additional keywords: assimilation, carbon dioxide, environment, leaf position, regression analysis
INTRODUCTION

Mango (*Mangifera indica* L.) is one of the 30 major crops in the world and grown mainly in tropical or subtropical regions. ‘Irwin’ mango, which is also called as apple mango, is high in sugar contents and juicy, and has a strong fragrance. Korea has unsuitable climate characteristics for the growth and development of mango trees, especially in winter, cold damage can happen easily. Therefore, most mango cultivating farmers have to prepare heating systems in greenhouses (Honsho et al., 2012). Due to spatial constraints inside greenhouses, mango trees are trained in a vase shape (Yonemoto, 2006). Even as a vase shape, mango trees grow higher than 2 m, the light intensities reaching the top and bottom leaves are varied. To date, however, no systematic research has been conducted to determine the physiological responses of mango trees such as photosynthesis under the characteristic environment the greenhouses. In order to increase the production of fruit crops, the photosynthesis must be increased based on quantitative analysis. Thus, modeling techniques have recently come into the spotlight as a way to quantify environmental factors affecting photosynthesis (Medina-Ruíz et al., 2011; Noe and Giersch, 2004).

Although many models express the changes in photosynthesis caused by single environmental factor are simple in their forms, models representing the photosynthetic rate for various environmental factors are often complex. Traditionally, simple multiplication models have been used to multiply simple equations that quantify photosynthetic rate for a single environmental factor by one another (Jones et al., 1991; Park et al., 2016). However, the models do not reflect the physiological characteristics of the crop.
Rectangular hyperbola or negative exponential models have mainly been used to express photosynthetic rates for light intensity and CO₂ concentrations (Baker and Allen, 1993; Valladares et al., 1997). Thornley (1974) developed a simple chemical reaction model for the chemical reactions that take place in light and dark reactions of photosynthesis. FvCB model is the most widely used in recent years developed by Farquhar, von Caemmerer and Berry (Farquhar et al., 1980; Yin et al., 2009). Each coefficient included in the FvCB model has a complicated shape because it is composed of a form corresponding to the physiological response of the plant, but it is known as the most suitable for expressing the photosynthetic rates changed by various environmental factors (Qian et al., 2012).

In the case of 'Kensington' mango exposed to high CO₂ concentration for a short period, the photosynthetic rate has been reported to increase with increasing CO₂ concentration. However, photosynthetic rate with 1,200 μmol·m⁻²·s⁻¹ of light intensity showed a saturation point, which was interpreted as the maximum level of biochemical reaction of photosynthesis (Schaffer et al., 1997; Whiley and Schaffer, 1997). In addition, Chamchaiyaporn et al. (2013) expressed changes in photosynthetic rate with increasing light intensity using a rectangular hyperbola model, but the photosynthetic rate measured once at 37°C, which was low about 3.5 μmol CO₂·m⁻²·s⁻¹. ‘Nam Dok Mai’ mangoes were grown with different temperature differences between day and night, the diurnal photosynthetic rates varied from 1.7 to 7.8 μmol CO₂·m⁻²·s⁻¹ (Pongsomboon et al., 1991). However, these results of photosynthesis measurements on certain mango tree leaves are difficult to be used as values representing photosynthetic rate of the complex trees. For reflecting the photosynthetic rate of the trees, which varies by vertical position of leaves
on the trees, the accurate model reflecting the changes in photosynthetic rate according to environmental factors is required.

The objective of this study was to quantify the photosynthetic rate of ‘Irwin’ mango leaves according to the leaf position and to determine the precise photosynthetic rate model including light intensity, CO₂ concentration, and temperature.
MATERIALS AND METHODS

Cultivation conditions

To investigate the leaf photosynthetic rate of ‘Irwin’ mango trees, experiments were conducted in the Hangboknanum Farm Association’s plastic greenhouse of 2,640 m² area which located in Seogwipo, Korea (33.304°N, 126.626°E). 6-year-old ‘Irwin’ mango trees used for measurement were grown in large plastic containers (40 × 80 cm, height × diameter). The trees were irrigated once every 4-5 days for 15 min a day with 30 L of water. Tempering curtains with polyethylene foam and nonwoven fabric were installed in the plastic greenhouse. The temperature and relative humidity inside the greenhouse were maintained at 25-30°C and 55-60%, respectively. The trees were insect-pollinated during their flowering season in January to early February, and the fruits were harvested around May. Once a year, a newly grown branch was hedged out at the top to generate three branches, and the branches were trained to the greenhouse steel structure using the training strip.

Measurement of leaf photosynthetic rates

Leaf photosynthetic rates were measured twice for model establishment and verification. The first measurement was conducted from 10:00 to 17:00 on February 23-24, 2015. This period corresponds to a fruit enlargement phase which has the greatest influence of CO₂ enrichment on fruit growth. Light intensities were set to 0, 50, 100, 200, 300, 400, 600, and 800 μmol·m⁻²·s⁻¹ and CO₂ concentrations were set to 100, 400, 800,
1,200, and 1,600 μmol·mol⁻¹ as previously employed by Schaffer et al. (1997). Measurements were made for 8 levels of light intensities and 5 levels of CO₂ concentrations (totally 40 conditions) for each position of the leaves. Measurements were taken in triplicate of the top (4-6 nodes), the middle (2-4 nodes), and the bottom (1-2 nodes) of the tree, based on the number of nodes shown in Fig. 1-1. Leaf photosynthetic rates were measured using portable photosynthesis measuring devices (LI-6400, LI-Cor. Inc., Lincoln, NE, USA).

The second measurement was conducted from 15:00 to 18:00 on April 3, 2015, and the leaf photosynthetic rate was obtained to verify the model established in the first measurement. Light intensities were set to 50, 200, 400, and 600 μmol·m⁻²·s⁻¹ and CO₂ concentrations were set to 100, 800, and 1,600 μmol·mol⁻¹. The measurement method was the same as the first, and measurements were made on four levels of light intensities and three levels of CO₂ concentrations (totally 12 conditions) for each position of the leaves. Each measurement was triplicated.

**Estimation of intercellular CO₂ concentrations**

In order to express the $A/C_i$ curve (where $A$ is the net CO₂ assimilation rate and $C_i$ is intercellular CO₂ concentration) and to calculate leaf photosynthetic rate with FvCB model using the measured atmospheric CO₂ concentration, the relationship between the atmospheric and intercellular CO₂ concentrations were regressed. Eight models are available express the CO₂ exchange between the atmosphere and the leaves of plants. In
Fig. 1-1. Leaf positions by stem node of greenhouse-grown 6-year-old ‘Irwin’ mango tree.
this study, the widely-used Ball-Berry model was selected because of its simple equation (Katul et al., 2000):

\[
\frac{C_i}{C_a} = 1 - \frac{1}{m} \times \frac{1}{RH}
\]  
(Eqn. 1-1)

where \( C_i \) and \( C_a \) are the intercellular and atmospheric CO\(_2\) concentrations (\(\mu\)mol\(\cdot\)mol\(^{-1}\)), respectively. \( m \) is an empirical parameter and \( RH \) is the relative humidity. In other plant species \( m \) ranges from 3-10, but it has not been reported for mango (Leuning, 1995). To estimate the \( m \) value for mango, \( C_i \), \( C_a \), and \( RH \) values were measured using a portable photosynthesis measuring devices (LI-6400, LI-Cor. Inc.) and regression analysis was conducted with Eqn. 1-1.

Models for expressing leaf photosynthetic rates

Empirical equations (Eqn. 1-2, 1-3, and 1-4) representing the form of a saturated curve were chosen as models for expressing leaf photosynthesis rates with varying light intensity, CO\(_2\) concentrations, and leaf temperatures:

\[
P = a \times (1 - e^{-b \times PPFD}) + c
\]  
(Eqn. 1-2)

\[
P = a \times (1 - e^{-b \times C_i}) + c
\]  
(Eqn. 1-3)

\[
P = a \times T_l^2 + b \times T_l + c
\]  
(Eqn. 1-4)
where \( P \) is leaf photosynthetic rate (\( \mu \text{mol CO}_2\cdot \text{m}^{-2}\cdot \text{s}^{-1} \)), \( PPFD \) is photosynthetic photon flux density (\( \mu \text{mol} \cdot \text{m}^{-2}\cdot \text{s}^{-1} \)), \( C_i \) is intercellular CO\(_2\) concentration (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( T_l \) is leaf temperature (\(^\circ \text{C}\)), and \( a-c \) are regression coefficients. These three expressions were simply multiplied to form a three-parameter model (Eqn. 1-5) with light intensity, CO\(_2\) concentration, and leaf temperature. The simple multiplication model used in the analysis was expressed in the following equation:

\[
P = a \times (1 - e^{-b \times PPFD}) \times (1 - e^{-c \times C_i}) \times (T_l^2 + d \times T_l + e) + f \quad \text{(Eqn. 1-5)}
\]

where \( P \) is leaf photosynthetic rate (\( \mu \text{mol CO}_2\cdot \text{m}^{-2}\cdot \text{s}^{-1} \)), \( PPFD \) is photosynthetic photon flux density (\( \mu \text{mol} \cdot \text{m}^{-2}\cdot \text{s}^{-1} \)), \( C_i \) is intercellular CO\(_2\) concentration (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( T_l \) is leaf temperature (\(^\circ \text{C}\)), and \( a-f \) are regression coefficients.

The second model for expressing leaf photosynthetic with varying light intensity and CO\(_2\) concentration, a rectangular hyperbola model established by Kaitala et al. (1982), was used. The rectangular hyperbola model used in the analysis was expressed in the following equation:

\[
P = \left( \frac{\alpha \times PPFD \times \beta \times C_i}{\alpha \times PPFD + \beta \times C_i} \right) - R \quad \text{(Eqn. 1-6)}
\]

where \( P \) is leaf photosynthetic rate (\( \mu \text{mol CO}_2\cdot \text{m}^{-2}\cdot \text{s}^{-1} \)), \( \alpha \) is photochemical efficiency (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( PPFD \) is photosynthetic photon flux density (\( \mu \text{mol} \cdot \text{m}^{-2}\cdot \text{s}^{-1} \)), \( \beta \) is carboxylation conductance (\( \text{s}^{-1} \)), \( C_i \) is intercellular CO\(_2\) concentration (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), and
$R$ is respiration ($\mu$mol CO$_2$·m$^{-2}$·s$^{-1}$). The rectangular hyperbola model is difficult to reflect the leaf photosynthetic rate according to changes in temperature. A modified rectangular hyperbola model with temperature variables has been developed, but it was used on the basis of empirical equations to express the change in photochemical efficiency and carboxylation conductance (Jung et al., 2017). The photochemical efficiency and carboxylation conductance used in the rectangular hyperbola model were expressed in the following equation:

$$\alpha = a_1 * T_l^2 + b_1 * T_l + c_1 \quad \text{(Eqn. 1-7)}$$

$$\beta = a_2 * T_l^2 + b_2 * T_l + c_2 \quad \text{(Eqn. 1-8)}$$

where $\alpha$ is photochemical efficiency ($\mu$mol·mol$^{-1}$), $T_l$ is leaf temperature (°C), $\beta$ is carboxylation conductance (s$^{-1}$), and $a_1$-$c_2$ are regression coefficients.

The FvCB model, reflecting of the physiological response of the plant, was expressed in the following expressions:

$$P = \min(A_c, A_j) \quad \text{(Eqn. 1-9)}$$

$$A_c = \left( \frac{\nu_c(C_l - R')}{C_l + K_c(1 + \frac{\nu_c}{R'})} \right) - R \quad \text{(Eqn. 1-10)}$$
\[ V_c = V_{cmax} \left( \frac{31 + \left( \frac{1}{1 + e^{-0.0099(PPFD - 500)}} \right)^{6.9}}{100} \right) \]  
(Eqn. 1-11)

\[ A_j = \left( \frac{I^*(C_i - \Gamma^*)}{4C_i + 8I^*} \right) - R \]  
(Eqn. 1-12)

\[ J = \left( \frac{\alpha*PPFD + J_{max} - \sqrt{(\alpha*PPFD + J_{max})^2 - 4\theta*J_{max}\alpha*PPFD}}{2\theta} \right) \]  
(Eqn. 1-13)

where \( P \) is leaf photosynthetic rate (\( \mu \text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( A_c \) is ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) carboxylation limited photosynthesis rate (\( \mu \text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( A_j \) is ribulose-1,5-bisphosphate (RuBP) regeneration limited photosynthesis rate (\( \mu \text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( V_c \) is carboxylation capacity at certain light intensity (\( \mu \text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( C_i \) is intercellular CO\(_2\) concentration (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( \Gamma^* \) is CO\(_2\) compensation point (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( K_c \) is Michaelis-Menten constant of Rubisco for CO\(_2\) (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( O \) is O\(_2\) concentration (210 mmol\cdot mol\(^{-1} \)), \( K_O \) is Michaelis-Menten constant of Rubisco for O\(_2\) (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), \( R \) is respiration (\( \mu \text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( V_{cmax} \) is maximum carboxylation capacity (\( \mu \text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( PPFD \) is photosynthetic photon flux density (\( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( J \) is electron transport rate at certain light intensity (\( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( \alpha \) is efficiency of light energy conversion on an incident light basis (mol\cdot mol\(^{-1} \)), \( J_{max} \) is maximum electron transport rate (\( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), and \( \theta \) is curvature of the light response of \( J \) (dimensionless) (Qian et al., 2012). Regression analysis was performed on each models using a SPSS statistical package (IBM, New York, NY, USA).
Validation of leaf photosynthetic rate models

In the leaf photosynthetic rate model determined by regression analysis, the calculated leaf photosynthetic rate was compared with the actual measured leaf photosynthetic rate in the secondary measurement under the specific light intensity and CO₂ concentration. A regression analysis was performed on an 1:1 line using the SPSS statistical package (IBM) and a graph of the model was drawn using Sigmaplot (Systat Software, San Jose, CA, USA).
RESULTS

Intercellular CO\textsubscript{2} concentration

The intercellular CO\textsubscript{2} concentration increased linearly with increasing the atmospheric CO\textsubscript{2} concentration (Fig. 1-2). As the atmospheric CO\textsubscript{2} concentration increased from 100 to 1,600 μmol·mol\textsuperscript{-1}, the intercellular CO\textsubscript{2} concentration increased from 100 to 900 μmol·mol\textsuperscript{-1}. The \( m \) value in Eqn. 1-1 was estimated to be 3.44 at RH of 67%. The R\textsuperscript{2} and root mean square error (RMSE) values in the Ball-Berry model were estimated to be 0.97 and 0.352, respectively.

Regression analysis of simple multiplication model

The regression coefficients \( a-f \) included in Eqn. 1-5 were analyzed (Table 1-1). The R\textsuperscript{2} values were high at 0.76 in middle leaves, but regressed coefficients did not increase or decrease according to the leaf position. The results were substituted for Eqn. 1-5 showing the leaf photosynthetic rate in three-dimensional space with light intensity and CO\textsubscript{2} concentration in X and Y axes (Fig. 1-3). The leaf photosynthetic rates in top leaves increased in the form of saturation curves with increasing light intensity and CO\textsubscript{2} concentration, and similar trends were observed in middle leaves. However, the photosynthetic rate in bottom leaves linearly increased with increasing CO\textsubscript{2} concentrations.

Regression analysis of rectangular hyperbola model

The photochemical efficiency (\( \alpha \)), carboxylation conductance (\( \beta \)), and respiration (\( R \))
Fig. 1-2. Relationship between atmospheric ($C_a$) and intercellular ($C_i$) CO$_2$ concentrations using Ball-Berry model in greenhouse-grown ‘Irwin’ mango tree leaves.
Table 1-1. Regression parameters, $R^2$, and RMSE values of simple multiplication model.

<table>
<thead>
<tr>
<th>Leaf position</th>
<th>$a$</th>
<th>$b$</th>
<th>$c$</th>
<th>$d$</th>
<th>$e$</th>
<th>$f$</th>
<th>$R^2$</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top</td>
<td>0.001</td>
<td>0.011</td>
<td>0.001</td>
<td>-5.24*10^3</td>
<td>1.83*10^3</td>
<td>-0.252</td>
<td>0.76</td>
<td>4.985</td>
</tr>
<tr>
<td>Middle</td>
<td>1.002</td>
<td>0.029</td>
<td>2.04*10^-7</td>
<td>1.49*10^3</td>
<td>-7.55*10^3</td>
<td>-0.546</td>
<td>0.79</td>
<td>1.173</td>
</tr>
<tr>
<td>Bottom</td>
<td>1.980</td>
<td>0.038</td>
<td>1.95*10^-7</td>
<td>-1.33*10^3</td>
<td>5.33*10^4</td>
<td>-0.582</td>
<td>0.76</td>
<td>1.491</td>
</tr>
</tbody>
</table>
Fig. 1-3. Leaf photosynthetic rates of greenhouse-grown ‘Irwin’ mango trees expressed with the simple multiplication model according to light intensities and CO₂ concentrations at top (A), middle (B), and bottom positions (C). Leaf temperature was constant at 27°C. White dots mean actually measured leaf photosynthetic rates and curved meshes mean regressed simple multiplication model.
included in Eqn. 1-6 were analyzed (Table 1-2). The photochemical efficiency increased from the top to bottom leaves, and the carboxylation conductance decreased from the top to bottom leaves. The photochemical efficiency increased quadratically with increasing leaf temperature and the carboxylation conductance decreased quadratically with increasing leaf temperature. The results were substituted for Eqn. 1-6 showing the leaf photosynthetic rate in three-dimensional space with light intensity and CO$_2$ concentration in X and Y axes (Fig. 1-4). The photosynthetic rates in top leaves increased in the form of saturation curves with increasing light intensity and CO$_2$ concentrations, the photosynthetic rates in middle and bottom leaves increased in the form of saturation curves with increasing light intensity. With increasing CO$_2$ concentration, however, the leaf photosynthetic rates increased linearly, without showing the form of saturation curve.

**Regression analysis of FvCB model**

The maximum carboxylation capacity ($V_{c,max}$) and maximum electron transport rate ($J_{max}$) included in Eqn. 1-11 and 1-13 were analyzed (Table 1-3). From top to bottom leaves, maximum carboxylation capacity and maximum electron transport rate showed a decreasing tendency, with higher accuracy in regression analysis at the top leaves. The results were substituted for Eqn. 1-9 to 1-13 showing the leaf photosynthetic rate in three-dimensional space with light intensity and CO$_2$ concentration in X and Y axes (Fig. 1-5). In the top leaves, the whole light intensity conditions were shown to be the RuBP regeneration limited zone under the low CO$_2$ concentration conditions, and in the high CO$_2$ concentration conditions, the light intensity within 200 to 600 μmol·m$^{-2}$·s$^{-1}$ was found to
Table 1-2. Regression coefficients, $R^2$, and RMSE values of photochemical efficiency and carboxylation conductance of rectangular hyperbola model.

<table>
<thead>
<tr>
<th>Regression coefficient</th>
<th>Leaf position</th>
<th>$a$</th>
<th>$b$</th>
<th>$c$</th>
<th>$R^2$</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Photochemical efficiency</td>
<td>Top</td>
<td>–0.001</td>
<td>0.023</td>
<td>0.563</td>
<td>0.88</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>–0.044</td>
<td>2.379</td>
<td>–31.8</td>
<td>0.62</td>
<td>0.023</td>
</tr>
<tr>
<td></td>
<td>Bottom</td>
<td>–0.583</td>
<td>3.236</td>
<td>–47.3</td>
<td>0.66</td>
<td>0.946</td>
</tr>
<tr>
<td>Carboxylation conductance (s$^{-1}$)</td>
<td>Top</td>
<td>0.001</td>
<td>0.071</td>
<td>0.956</td>
<td>0.76</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>0.001</td>
<td>0.041</td>
<td>0.550</td>
<td>0.78</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Bottom</td>
<td>0.001</td>
<td>0.053</td>
<td>0.688</td>
<td>0.84</td>
<td>0.001</td>
</tr>
</tbody>
</table>
Fig. 1-4. Leaf photosynthetic rates of greenhouse-grown ‘Irwin’ mango tree expressed with the rectangular hyperbola model according to light intensities and CO₂ concentrations at top (A), middle (B), and bottom positions (C). Leaf temperature was constant at 27°C. White dots mean actually measured leaf photosynthetic rates and curved meshes mean regressed rectangular hyperbola model.
Table 1-3. Maximum carboxylation capacity ($V_{cmax}$) and maximum electron transport rate ($J_{max}$), $R^2$, and RMSE values of FvCB model.

<table>
<thead>
<tr>
<th>Leaf position</th>
<th>$V_{cmax}$</th>
<th>$R^2$</th>
<th>RMSE</th>
<th>$J_{max}$</th>
<th>$R^2$</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top</td>
<td>23.449</td>
<td>0.71</td>
<td>3.936</td>
<td>40.033</td>
<td>0.71</td>
<td>10.343</td>
</tr>
<tr>
<td>Middle</td>
<td>20.267</td>
<td>0.75</td>
<td>0.894</td>
<td>25.332</td>
<td>0.70</td>
<td>2.791</td>
</tr>
<tr>
<td>Bottom</td>
<td>12.862</td>
<td>0.67</td>
<td>0.492</td>
<td>17.826</td>
<td>0.54</td>
<td>4.129</td>
</tr>
</tbody>
</table>
Fig. 1-5. Leaf photosynthetic rates of greenhouse-grown ‘Irwin’ mango tree expressed with the FvCB model according to light intensities and CO$_2$ concentrations at top (A), middle (B), and bottom positions (C). Leaf temperature was constant at 27°C. White dots mean actually measured leaf photosynthetic rates and curved meshes mean regressed FvCB model.
be the RuBP regeneration limited zone. Similar forms were observed in the middle and bottom leaves, but the Rubisco carboxylation limited zone was found to be wider than the RuBP regeneration limited zone.

**Validation of leaf photosynthetic rate models**

Regression analysis on an 1:1 line was performed against the calculated leaf photosynthetic rates according to the leaf position using the simple multiplication, rectangular hyperbola and FvCB models, and the actually measured photosynthetic rate obtained by secondary measurement (Fig. 1-6). The $R^2$ values were highest (0.79) and lowest (0.68) in the simple multiplication model and the rectangular hyperbola model, respectively.
Fig. 1-6. Validation results of leaf photosynthetic rates in greenhouse-grown ‘Irwin’ mango trees estimated by the simple multiplication, rectangular hyperbola, and FvCB leaf photosynthetic models.
DISCUSSION

For the simple multiplication model, the regression coefficients used to represent the leaf photosynthetic rate of ‘Irwin’ mango trees did not reflect the physiological characteristics of plants. The regression coefficients shown in Table 1-1 did not show tendency between the regressed coefficients, because they were found by statistical methods to best describe the actual data. Thus, the simple multiplication model could be used for expressing the leaf photosynthetic rate concisely only for a particular plant.

For the rectangular hyperbola model, the photochemical efficiency and carboxylation conductance were used to express plant physiological reactions as factors in the model. The photochemical efficiency increased toward the bottom leaves of the tree, implying that the bottom leaves use light efficiently, but not show high leaf photosynthetic rates. Shaded leaves at the bottom of the tree have low photosynthesis capacity and nitrogen content, resulting in insufficient photosynthesis even with increased CO₂ concentrations (Del Pozo et al., 2007). Photochemical efficiency and carboxylation conductance were 0.00028 μmol⁻¹·m² and 0.001053 (kg CO₂·m⁻³)·s⁻¹, respectively, in willow trees (Kaitala et al., 1982). In addition, the photochemical efficiency measured in orache plants was known as 0.177 μmol CO₂·mol⁻¹ (Marshall and Biscoe, 1980). This value was similar to the photochemical efficiency in the top leaves estimated in the rectangular hyperbola model for mango tree. A modified rectangular hyperbola model with temperature variables has also been developed, but it was used on the basis of empirical equations to express the change in photochemical efficiency and carboxylation conductance (Jung et al., 2017).
addition, studies on how photochemical efficiency and carboxylation conductance differ depending on leaf position are not sufficient.

On the other hand, for FvCB models, the Michaelis-Menten constants for CO$_2$ and O$_2$ concentrations were used to express photosynthetic reactions that vary with temperature (Qian et al., 2012). Therefore, the FvCB model can more accurately represent the leaf photosynthetic rate compared to the previously used simple multiplication or rectangular hyperbola model, and the actual verification results show the highest R$^2$ value with the FvCB model (Fig. 1-6). For shaded leaves at the bottom of canopy in various crops, the Rubisco content and RuBP regeneration capacity have been reported to tend to decrease (Baker and McKiernan, 1988; Evans, 1993; Osborne et al., 1998). From top to bottom leaves, maximum carboxylation capacity and maximum electron transport rate tended to decrease (Table 1-3). The validation results that the leaf photosynthetic rates are different for each position of the plant can be also predicted more accurately in the FvCB model than in the simple multiplication or the rectangular hyperbola model (Fig. 1-6). Therefore, the FvCB model was considered to be most appropriate, as it sufficiently accurately reflected physiological reactions.

The regression using measured leaf photosynthetic rates was often inaccurate in the middle and bottom leaves of the plant. Using 3D plant model and simulations, Sinoquet et al. (1998) reported that the light intensity on the middle leaves of plant varied significantly. Therefore, different leaf photosynthetic rate models should be applied to the outer leaves with high light intensity and the inner leaves with low light intensity, by subdividing leaves located in the middle of the plant. The bottom leaves show smaller difference in the light
distribution according to position compared to the middle leaves. However, the leaf photosynthetic rate was not changed largely with changing environmental factors in the bottom leaves with low absolute amount of light (Léchaudel et al., 2013). Photosynthesis varies depending on the leaf position, due to the changes of physiological and anatomical characteristics such as leaf cell structure and chlorophyll contents according to the environmental condition (Larbi et al., 2015). Therefore, anatomical structures and physiological indicators of the leaves are needed to be identified according to the leaf position.

Environmental factors are not uniformly maintained throughout the greenhouse. Since the leaves of the plant are subjected to different environmental conditions, depending on their position, environmental management accordingly must be precisely conducted to increase the crop yield. The vertical leaf photosynthetic rate models established in this study will help determine environmental conditions that can maximize photosynthesis of ‘Irwin’ mango trees grown in greenhouses.
LITERATURE CITED


CHAPTER 2

Estimation of Whole Plant Photosynthetic Rate of ‘Irwin’ Mango Trees Using a Three-dimensional Plant Model and Ray-tracing

ABSTRACT

Photosynthesis is an important physiological response for determination of CO₂ enrichment in greenhouses and estimation of crop growth. In order to estimate the whole plant photosynthetic rate, it is necessary to investigate how light interception by crops changes with environmental and morphological factors. The objectives of this study were to analyze plant light interception using a three-dimensional (3D) plant model and ray-tracing, to determine the spatial distribution of the photosynthetic rate, and to estimate the whole plant photosynthetic rate of mango (Mangifera indica L. cv. Irwin) trees grown in greenhouses. Actual light interceptions of the mango trees were difficult to be measured at the canopy level due to their vase shape. A 2-year-old ‘Irwin’ mango trees were used to measure the whole plant photosynthetic rate. Light interception and whole plant photosynthetic rate were measured under artificial and natural light conditions in a closed polycarbonate chamber (1 × 1 × 2 m, length × width × height). A 3D plant model was constructed and ray-tracing simulation was conducted for calculating the photosynthetic rate with a two-variable leaf photosynthetic rate model of the tree. Under artificial light,
the estimated photosynthetic rate increased from 2.0 to 2.9 μmol CO₂·m⁻²·s⁻¹ with increasing CO₂ concentration. On the other hand, under natural light, the photosynthetic rate increased from 0.2 μmol CO₂·m⁻²·s⁻¹ at 06:00 to a maximum of 7.3 μmol CO₂·m⁻²·s⁻¹ at 09:00, then gradually decreased to −1.0 μmol CO₂·m⁻²·s⁻¹ at 18:00. In validation, the simulation results were consistent with the measured results with R² and RMSE of 0.79 and 0.263, respectively. This method could accurately estimate the whole plant photosynthetic rate and be useful for determining the levels of pruning and CO₂ enrichment.

Additional keywords: CO₂ consumption, leakage, light interception, measurement chambers, three-dimensional plant model
INTRODUCTION

Photosynthesis of crops grown in greenhouses is an important physiological indicator that determines CO$_2$ enrichment and estimates crop growth. The cumulative amount of assimilation products produced as a result of photosynthesis is closely related to crop yield. Thus, the photosynthetic rate of crops can be used for predicting crop production (Monteith, 1956) and determining CO$_2$ supply (Hu et al., 2011; Jung et al., 2016b; Son et al., 1999).

In general, the photosynthesis of crops grown in greenhouses depends on environmental factors such as light intensity, temperature, CO$_2$ concentration, and relative humidity inside the greenhouse. These environmental factors are closely related to the structural characteristics of the greenhouse and the meteorological conditions outside the greenhouse. In particular, the light intensity on leaves is dependent not only on the environmental factors but also on the morphological characteristics of the crops (Chen et al., 1999; Vos et al., 2010). Other environmental variables, such as light direction, ratio of diffused light, plant growth stage, and plant density, also affect light interception inside the crop canopy (Buck-Sorlin et al., 2011; Leith and Pasian, 1990; Stirling et al., 1994). Therefore, in order to estimate the whole plant photosynthetic rate of crops, it is important to investigate the light interception of the crops related with these environmental and morphological factors.

Mango (*Mangifera indica* L.) is one of the 30 most important crops in the world and grown mainly in tropical or subtropical regions. Recently, mango cultivation in greenhouses has been started in Northeast Asia including Korea and Japan. Due to the spatial constraints within a greenhouse, mango trees are cultivated in a vase shape with a
low height through pruning of branches (Yonemoto, 2006). When cultivated in a vase-shape, a mango tree grows higher than 2 m and thus the light intensities at the top and bottom leaves in the canopy are different. However, actual light interception of a plant canopy is difficult to be measured due to technical limitations.

Whole plant photosynthesis has been estimated by various modeling approaches. The Farquhar, von Caemmerer, and Berry (FvCB) model has widely been used as a single-leaf model because it can express leaf photosynthesis, which is affected by various environmental factors (Farquhar et al., 1980). The FvCB model represents leaf-level biochemical mechanisms, which are the most well-known reactions for photosynthesis, and has been used consistently in previous studies (Zhu et al., 2012). The main assumption of the FvCB model is that the absorbed photosynthetic active radiation affects the photosynthetic capacity of each canopy position and contributes to the overall canopy photosynthesis (De Pury and Farquhar, 1997; Johnson et al., 2010). To simplify the calculation, the models also assume that the vertical distribution of light interception has a negative exponential pattern from the top to the bottom of the canopy (Monsi and Saeki, 1953; Norman, 1980). In these models, however, the spatial and temporal heterogeneity of light interception were not considered. Many models of canopy photosynthesis have been devoted to reflect the structural characteristics of crops and the light scattering within the crop canopy (Hikosaka, 2014; Kim et al., 2010; Tang et al., 2015). However, photosynthesis models that explain canopy photosynthesis have a disadvantage in that the model formulas are complicated because of sunlit and shaded leaves. Moreover, while the FvCB model has been used for the analysis of carbon fluxes in an ecosystem, it has rarely
been used for the analysis of light intensity and photosynthesis of a greenhouse crop canopy (Yin and Struik, 2009). Using a simple leaf photosynthesis model and reflecting the changes along the leaf position are suitable for expressing the whole plant photosynthetic rate of the crop (Jung et al., 2015; Schaffer et al., 1997). Thus, the method of using specific values for light intensity should be studied in the canopy for developing simple leaf photosynthesis models.

Preconditions for analyzing accurate light distribution, spatial leaf photosynthetic rate and whole plant photosynthetic rate of crop canopy are required (Chen et al., 2015). From this aspect, construction of the three-dimensional (3D) plant model should reflect the exact physical characteristics of the plant architecture. Ray-tracing is a reasonable approach to integrate optical characteristics such as reflectance and transmittance of leaves and architectural structures into light simulations. The phenomenon of varying diffuse light due to weather changes also has an important role in the light environment analysis (Yeom et al., 2012). Ray-tracing simulations can represent changes in light according to weather conditions. Recently, light distribution in crop leaves has been investigated using 3D plant models and ray-tracing techniques (Buck-Sorlin et al., 2011; De Visser et al., 2014; Der Zande et al., 2011; Kim et al., 2016).

To investigate the whole plant photosynthetic rate of mango trees under the conditions of controlled light intensity, the changes in light interception under artificial and natural lights should be determined. Estimating canopy photosynthetic rates by combining the above methods and photosynthesis models is useful in determining production strategies for greenhouse crops. The objectives of this study were to analyze accurate intercepted
light intensity using a 3D plant model and ray-tracing method, to determine the spatial distributions of the photosynthetic rate, and to estimate and validate the whole plant photosynthetic rate of mango trees under artificial and natural lights in greenhouses.
**MATERIALS AND METHODS**

**Measurement of photosynthetic rates of ‘Irwin’ mango tree**

Whole plant photosynthetic rates were measured in a closed polycarbonate chamber (1 × 1 × 2 m, length × width × height) at the experimental farm of the Seoul National University, Suwon, Korea (37°27′N, 126°98′E). A 2-year-old mango (*M. indica* L. cv. Irwin) cultivated in a cylindrical pot (40 cm height and 30 cm diameter) was placed in the center of the chamber floor (Fig. 2-1). The temperature inside the closed chamber was maintained at 32°C and the relative humidity was maintained at 60 to 70%. Two radiators circulating cold water were placed along sidewalls to maintain the internal temperature. Two fans were used to mix the internal air. Light intensities at five points of the mango canopy were measured using five quantum sensors (SQ-110, Apogee Instr., Logan, UT, USA). Two sensors were placed at both the top and middle of the tree canopy, and one sensor was placed at the bottom. Sensors were arranged vertically, separated by 15 cm. Changes in CO₂ concentration inside the chamber were measured using an infrared gas analyzer (LI-840A, LI-Cor. Inc., Lincoln, NE, USA). Light intensity and CO₂ concentration were collected by using a data logger (GL840, Graphtec, Yokohama, Japan). To measure the chamber leakage, CO₂ concentration change was monitored over an initial CO₂ concentration of 1,300 μmol·mol⁻¹ for 48 h.

To measure the whole plant photosynthetic rate under artificial light, a plasma lamp (PLS, G3, LG electronics Inc., Seoul, Korea) was installed inside the chamber (Fig. 2-1). The lamp position was 1.5 m above the tree canopy. A black cloth was wrapped around
Fig. 2-1. Schematic diagram of closed chamber for measuring CO$_2$ consumption of ‘Irwin’ mango trees. Under artificial light condition, a plasma lamp was used with a black cloth installed outside the chamber.
the outside of the chamber to block external light. The initial CO₂ concentration was injected at 1,000 μmol·mol⁻¹. Changes in light intensity and CO₂ concentration inside the chamber were measured for 12 h on July 15, 2016. Similarly, the whole plant photosynthetic rate under natural light was measured for 12 h on July 21, 2016. The artificial light and black cloth were not installed when measuring the whole plant photosynthetic rate under natural light. The initial CO₂ concentration under natural light conditions was set at 1,000 μmol·mol⁻¹. Changes in light intensity and CO₂ concentration in the chamber were collected on every second. The decrease in CO₂ concentration was used as an estimate for the calculation of whole plant photosynthetic rate. At a situation where CO₂ concentration was decreasing in the chamber, a whole plant photosynthetic rate at a specific CO₂ concentration was calculated using an average decrease in CO₂ concentration for 3 min.

**Construction of 3D plant model**

A 3D plant model was constructed in the same shape as the mango tree to measure the photosynthetic rate. Considerations before making the 3D plant model were as follows: (i) leaf area and petiole length; (ii) phyllotaxis of the leaves; and (iii) branch pattern, stem length, and diameter. Since the mango leaves used in the experiment were not destroyed, leaf area (LA) was calculated using a model consisting of leaf length (L) and width (W):

\[ LA = -14.623 + 8.074W + 0.085L^2 + 0.452W^2 \ (R^2 = 0.971) \]  
(Jung et al., 2016a). The leaf length, leaf width, and petiole length were measured for all leaves using a ruler (H-101C, Shinwa, Niigata, Japan). The total LA of the mango tree used in the experiment was 4,194
To determine the phyllotaxis of the mango leaves, photographs were taken vertically at the apex of the stem and the angle between adjacent leaves were measured using protractor (Fig. 2-2A, Table 2-1). In order to create a 3D plant model, the leaves were arranged in the same order as verticillation using the average adjacent leaf angle shown in Table 2-1. The shape of a 2-year-old mango branch had a simple form with a new branch growing at the top of the main stem in a large Y-shape. The stem length, stem diameter, and number of leaves attached to each branch were measured using a digital vernier caliper (500-182-30, Mitutoyo, Kanagawa, Japan) and they were reflected in the 3D model. The 3D plant model was constructed using measured leaf length and width, phyllotaxis, branch pattern, stem length, and stem diameter. The 3D plant model was developed using 3D CAD software (SolidWorks, Dassault Systemes, Velizy-Villacoublay, France).

**Simulation of intercepted light intensity**

Using the 3D plant model, light interception was simulated with ray-tracing software (OptisWorks, OPTIS Inc., Toulon, France). The chamber was designed with the 3D CAD software and assembled with the 3D plant model. Using simulation software, microclimate parameters such as sun direction (coordinates, date, time, zenith, and north direction) and sunlight properties (ratio of direct and diffuse lights), and material parameters such as optical properties of the mango leaves, closed chamber, and greenhouse structure were entered. Optical properties such as absorbance, transmittance, and reflectance of the mango leaves and branches were measured using an integrating sphere (IC2, StellarNet Inc., Tampa, FL, USA) with a spectrometer (BLUE-Wave, StellarNet Inc.) and light source (SL1
Fig. 2-2. Angle between adjacent 2-year-old ‘Irwin’ mango leaves for estimating phyllotaxis (A) and the actual mango tree shape (B), and a constructed 3D plant model (C).
Table 2-1. Angles between the adjacent leaves of 2-year-old ‘Irwin’ mango trees.

<table>
<thead>
<tr>
<th>Leaf number from the bottom</th>
<th>Angle (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-2</td>
<td>151.5 ± 4.75²</td>
</tr>
<tr>
<td>2-3</td>
<td>133.2 ± 5.20</td>
</tr>
<tr>
<td>3-4</td>
<td>141.5 ± 11.80</td>
</tr>
<tr>
<td>4-5</td>
<td>157.6 ± 7.05</td>
</tr>
<tr>
<td>5-6</td>
<td>129.9 ± 0.25</td>
</tr>
<tr>
<td>6-7</td>
<td>122.1 ± 0.50</td>
</tr>
<tr>
<td>7-8</td>
<td>138.0 ± 6.75</td>
</tr>
<tr>
<td>8-9</td>
<td>138.8 ± 3.00</td>
</tr>
<tr>
<td>9-10</td>
<td>124.4 ± 10.25</td>
</tr>
<tr>
<td>10-11</td>
<td>150.9 ± 2.15</td>
</tr>
<tr>
<td>11-12</td>
<td>125.9 ± 18.40</td>
</tr>
<tr>
<td>Average</td>
<td>137.6 ± 13.38</td>
</tr>
</tbody>
</table>

²Mean ± SD (n = 3)
Fig. A-1 to A-4 showed the absorbance, transmittance, and reflectance of the mango leaves and branches. These values were entered in the preferences section for the leaves in the simulation software. The optical properties of the mango leaves showed little difference in the vertical position within the mango. Ray-tracing simulations were conducted with 1 giga rays and the number of max impacts was set to 10 for all conditions. Light detectors were set at 5 mm intervals on all leaf surfaces of the 3D plant model. The intercepted light intensity, transmittance, and reflectance at the detector position on the leaf were calculated through simulation. To simulate the distribution of light interception under artificial light, a modeled artificial lamp was assembled with the 3D plant model in the same position as the actual measurement. The transmittance and reflectance of the closed chamber were set at 0% as the chamber was covered with a black cloth. Similarly, the distribution of light intensity under natural light was simulated for 12 h on July 21, 2016. Unlike under artificial light, the black cloth around the chamber was not installed for natural light. The intercepted light intensity was simulated at the top, middle, and bottom of the plant under artificial and natural light. Each position was determined to be the same as where the actual quantum sensors were installed.

**Calculation of whole plant photosynthetic rate**

Since the photosynthetic rate according to the CO$_2$ concentration and light intensity was shown as a saturation curve, a simple saturation curve equation was used to determine the photosynthesis model. In the case of 'Kensington' mangoes, photosynthetic rate increased with increasing CO$_2$ concentration and saturated at a light intensity of 1,200 μmol·m$^{-2}$·s$^{-1}$.
(Schaffer et al., 1997; Whiley and Schaffer, 1997). In addition, Chamchaiyaporn et al. (2013) used the rectangular hyperbola equation to express the photosynthetic rate that increase with increasing light intensity. Therefore, the two most widely used empirical equations for saturation were summarized as follows. Eqn. 2-1 and 2-2 showed the rectangular hyperbola and negative exponential models, respectively.

\[
P = \frac{a \cdot X}{X + b} + c \quad \text{(Eqn. 2-1)}
\]

\[
P = a \cdot (1 - e^{-b \cdot X}) + c \quad \text{(Eqn. 2-2)}
\]

where \( P \) is the net leaf photosynthetic rate (\( \mu \text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( X \) is the photosynthetic photon flux density (PPFD; \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)) or the CO\(_2\) concentration (\( \mu \text{mol} \cdot \text{mol}^{-1} \)), and \( a-c \) are regression parameters. The two-variable model expressed as the product of the two models is easy to use because of its simple form (Jones et al., 1991). According to Jung et al. (2015), a negative exponential model equation was more suitable for expressing the leaf photosynthetic rates of ‘Irwin’ mango trees. In this study, a leaf photosynthetic rate model for ‘Irwin’ mango trees suggested by the previous study (Jung et al., 2015) was used as in Eqn. 2-3.

\[
P = 12.928 \cdot (1 - e^{-0.014 \cdot PPFD}) \cdot (1 - e^{-0.001 \cdot Ci}) - 0.889 \quad \text{(Eqn. 2-3)}
\]
where $P$ is the net leaf photosynthetic rate ($\mu$mol CO$_2$·m$^{-2}$·s$^{-1}$), $PPFD$ is the photosynthetic photon flux density ($\mu$mol·m$^{-2}$·s$^{-1}$), and $C_i$ is the intercellular CO$_2$ concentration ($\mu$mol·mol$^{-1}$). The light intensity obtained from the ray-tracing simulation and CO$_2$ concentration was substituted into the above equation to calculate the photosynthetic rate distribution in the whole plant.

**Validation of light intensity and whole plant photosynthetic rate**

The validation process was performed in two steps. First, the measured light interception at each position in the mango was compared with the estimated interception. Unlike artificial light, natural light intensity changes with time; therefore, the simulated light intensities were compared with the measured intensities with time. Secondly, the measured whole plant photosynthetic rates in the closed chamber were compared with the calculated ones using the leaf photosynthetic rate model and simulated light intensity. A work flow for the construction of the 3D plant model, calculation, and validation of the whole plant photosynthetic rate was described in Fig. 2-3.
Fig. 2-3. A workflow for the construction of 3D plant model, calculation, and validation of a whole plant photosynthetic rate of greenhouse-grown ‘Irwin’ mango trees.
RESULTS

Actual distribution of light intensity and measured whole plant photosynthetic rate

Under the artificial light, the light intensity at the top of the mango tree was higher than twice as large as the middle and bottom positions (Fig. 2-4A). Specifically, the measured light intensities were 833.1 ± 5.10, 373.0 ± 2.73, and 33.7 ± 0.46 μmol·m⁻²·s⁻¹ at the top, middle, and bottom, respectively. Fine noise was generated, but the light intensity was kept at a substantially constant level during the measurement period. The CO₂ concentrations in the closed chamber exponentially decreased from an initial 1,000 μmol·mol⁻¹ concentration to 600 μmol·mol⁻¹ after 12 h. The decrease in CO₂ concentration over time was calculated, and the whole plant photosynthetic rate of mango was estimated according to CO₂ concentration (Fig. 2-5). When the CO₂ concentration inside the chamber was 600 μmol·mol⁻¹, the whole plant photosynthetic rate was around 2.0 μmol CO₂·m⁻²·s⁻¹. The whole plant photosynthetic rate did not increase at the CO₂ concentrations of 800 to 900 μmol·mol⁻¹, but gradually increased at the other CO₂ concentrations examined.

Under natural light, the light intensities at the top, middle, and bottom were rapidly changed during the measurement period and showed a maximum value at around 13:00 (Fig. 2-4B, 2-6). The maximum light intensities were 1,143.9, 548.9, and 57.2 μmol·m⁻²·s⁻¹ at the top, middle, and bottom, respectively. The CO₂ concentration in the closed chamber decreased resembling a sigmoidal curve from 1,000 to 200 μmol·mol⁻¹ after 12 h. The decrease in CO₂ concentration over time was calculated, and the whole plant photosynthetic rate of the tree was estimated (Fig. 2-7). The whole plant photosynthetic
Fig. 2-4. Changes in measured CO$_2$ concentration in the closed chamber and light intensity at top, middle and bottom leaves of greenhouse-grown ‘Irwin’ mango trees on July 15, 2016 under artificial light (A) and July 21, 2016 under natural light (B) for 12 h.
Fig. 2-5. Measured and estimated whole plant photosynthetic rates of greenhouse-grown ‘Irwin’ mango trees according to CO₂ concentration under artificial light for 12 h.
Fig. 2-6. Measured and simulated light intensity at top, middle, and bottom leaves of greenhouse-grown 'Irwin' mango trees under natural light on July 21, 2016.
Fig. 2-7. Measured and estimated whole plant photosynthetic rate of greenhouse-grown ‘Irwin’ mango trees under natural light on July 21, 2016.
rate started at -0.2 μmol CO₂·m⁻²·s⁻¹ at 06:00, reached its maximum of 7.0 μmol CO₂·m⁻²·s⁻¹ around 10:00, and then gradually decreased to -1.0 μmol CO₂·m⁻²·s⁻¹ at 18:00.

**Simulated distribution of intercepted light intensity and estimated whole plant photosynthetic rate**

The average simulated light intensities under the artificial light were 820, 375, and 40 μmol·m⁻²·s⁻¹ at the top, middle, and bottom, respectively. When the light distribution of the entire plant was simulated, the intercepted light intensity appear to be different on each leaf (Fig. 2-8A, 2-8B). The maximum light intensity at the top leaves was 1,200 μmol·m⁻²·s⁻¹, while the bottom intensity was almost 0 μmol·m⁻²·s⁻¹. The distribution of the whole plant photosynthetic rate under the artificial light was expressed in 3D space using the simulated light intensity and the leaf photosynthetic rate model at a CO₂ concentration of 500 μmol·mol⁻¹ (Fig. 2-9A, 2-9B). The photosynthetic rates of the top and middle leaves were about 4 μmol CO₂·m⁻²·s⁻¹ by the light intensity above the saturation point. Photosynthetic rates below 0 μmol CO₂·m⁻²·s⁻¹ were observed in some leaves at the bottom. The whole plant photosynthetic rate showed an increasing tendency at CO₂ concentrations from 600 to 1,000 μmol·mol⁻¹, which was similar to the actual results (Fig. 2-5). The estimated whole plant photosynthetic rate under the artificial light increased from 2.0 to 2.9 μmol CO₂·m⁻²·s⁻¹ with increasing CO₂ concentration.

Similarly, the simulated light intensities at the top, middle, and bottom of the tree under natural light fluctuated like the actual measurements (Fig. 2-6). At 06:00, the light intensities at the leaves in the top, middle, and bottom began at 0 μmol·m⁻²·s⁻¹, but they
Fig. 2-8. Estimated spatial distributions of light interceptions of greenhouse-grown ‘Irwin’ mango trees under artificial light (A, top view; B, front view) and under natural light on July 21, 2016 (C, top view; D, front view).
Fig. 2-9. Estimated spatial leaf photosynthetic rates of greenhouse-grown ‘Irwin’ mango trees under artificial light (A, top view; B, front view) and under natural light on July 21, 2016 (C, top view; D, front view).
became different among the positions as time passed. At all positions, the simulated light intensity reached maximum at 13:00, and changed similarly to the measured one. Using the 3D plant model, the distribution of the intercepted light intensity under natural light was expressed in 3D space at 12:00 on July 21, 2016 (Fig. 2-8C, 2-8D). The maximum light intensities at the top and bottom leaves were 600 and near 0 μmol·m$^{-2}$·s$^{-1}$, respectively. The distribution of the whole plant photosynthetic rate under the natural light at 12:00 on July 21, 2016 was expressed in 3D space using the simulated light intensity, measured CO$_2$ concentration, and leaf photosynthetic rate model (Fig. 2-9C, 2-9D). In most of the top leaves, the photosynthetic rate was 4 μmol CO$_2$·m$^{-2}$·s$^{-1}$, and the light intensity on these leaves exceeded the saturation point. Unlike under the artificial light, however, discontinuous sections were observed where the photosynthetic rate was 0 μmol CO$_2$·m$^{-2}$·s$^{-1}$ at the middle and bottom leaves. For comparing to the actual results, whole plant photosynthetic rates were calculated at 1 h intervals on July 21, 2016 using the simulated light intensities, CO$_2$ concentrations inside the chamber, and the leaf photosynthetic rate model (Fig. 2-7). The whole plant photosynthetic rate started at 0.2 μmol CO$_2$·m$^{-2}$·s$^{-1}$ at 06:00, reached the maximum of 7.3 μmol CO$_2$·m$^{-2}$·s$^{-1}$ at 09:00, and then gradually decreased to −1.0 μmol CO$_2$·m$^{-2}$·s$^{-1}$ at 18:00.

Validation of light intensity and whole plant photosynthetic rate

The validation results revealed that the measured and estimated whole plant photosynthesis rates under both artificial light and natural light conditions were linearly correlated (Fig. 2-10). The coefficient of determination ($R^2$) and root mean square error
Fig. 2-10. Validation of the measured and estimated whole plant photosynthetic rates of the greenhouse-grown ‘Irwin’ mango tree under the artificial and natural lights.
(RMSE) were 0.73 and 0.020 under the artificial light and were 0.72 and 0.447 under the natural light, respectively. Under combined light conditions, $R^2$ was 0.79 and RMSE was 0.263.
Plant photosynthesis is a complicated physiological phenomenon in response to various environmental factors. Despite a number of photosynthesis studies conducted at the leaf level, a few studies have estimated the photosynthetic rate at the whole plant or canopy level. At the whole plant level, various factors affecting photosynthetic capacity such as leaf age, leaf acclimation to light, and nitrogen distribution should be considered (Kim et al., 2016). In particular, intercepted light intensity is sensitively affected by leaf shape, leaf angle, and plant position inside the canopy architecture (Gonzalez-Real and Baille, 2000; Sarlikioti et al., 2011). Therefore, light intensity reaching the leaf surface of a plant is technically difficult to be measured and estimated accurately. However, the ray-tracing simulation technique might be appropriate to predict the intercepted light intensity at crop leaves on the whole plant level. This technique can also be of great help in estimating whole plant photosynthetic rates.

The ray-tracing simulation predicted a similar level of light intensity to the actual light intensity measured using sensors mounted on the mango tree (Fig. 2-2). This result implies that ray-tracing simulation is suitable for predicting the intercepted light intensity over the crop canopy. However, there was a larger difference between the measured and predicted light intensities under the natural light condition than under the artificial light condition. This is probably due to the influence of the black cloth used in the artificial light condition. Compared to the artificial light condition, there were some effects of scattered light by the greenhouse and chamber under natural light condition. The light intensity measured under
natural light appeared more homogeneous throughout the crop (Fig. 2-8C, 2-8D). As scattered light easily penetrates into the crop canopy (De Pury and Farquhar, 1997), scattered light in the greenhouse structure should be considered in simulations for accurate estimation.

Simulation results showed that the whole plant photosynthetic rate increased in the form of a saturation curve with increasing CO$_2$ concentration under the artificial light, since the increase in whole plant photosynthetic rate by high CO$_2$ concentration followed the increase in leaf photosynthetic rate even with different light intensities on individual leaves. However, the measured whole plant photosynthetic rate did not appear as a saturation curve (Fig. 2-5). In order to measure the whole plant photosynthetic rate under the artificial light condition, the changes in CO$_2$ concentration were measured in the chamber for 12 h (Fig. 2-2A). In this case, the CO$_2$ concentration was between 700 and 1,000 μmol·mol$^{-1}$ during the nighttime from 19:00 to 05:00. The crop adapts according to the photoperiod and performs photosynthesis in the daytime and translocation of assimilates in the daytime or respiration at night (Miao et al., 2007). Therefore, the measured whole plant photosynthetic rate at night may differ from the actual value.

To precisely determine the photosynthetic rate in a closed photosynthetic measurement system, air distribution should be uniform without leakage (Bugbee, 1992; Takahashi et al., 2008). Moreover, the 3D crop model should be similar to the actual crop shape (Fig. 2-3). The crop shape was constructed in the present study by examining the leaf form and phyllotaxis of the mango; L-system can be another choice for constructing 3D models (Prusinkiewicz, 2004). In addition, there are considerations regarding the model equations.
for calculating whole plant photosynthetic rates. A simple form of Eqn. 2-3, which includes light intensity and CO₂ concentration was used. Stomatal opening varies with time in a day and leaf temperature (Flanagan and Ehleringer, 1991; Prior et al., 1997), Photosynthetic rate cannot be accurately calculated with a model that does not reflect stomatal conductivity or leaf temperature. Since the mango trees used in the present study were two years old, the photosynthetic rate model for a newly developed leaves on shoots was used (Jung et al., 2015). However, leaves in the lower part of the canopy have been reported to have decreased Rubisco content and RuBP reproduction capacity in various crops (Evans, 1993; Osborne et al., 1998). For this reason, leaves at the lower part of the canopy decreased photosynthetic ability and nitrogen content inside the tissue. As a result, leaves in shaded areas cannot perform enough photosynthesis even at elevated CO₂ concentration (Del Pozo et al., 2007). Although photosynthetic models related to nitrogen distribution have been developed (Thornley, 2004), they are needed to be improved for predicting more accurate whole plant photosynthetic rates.

Fruit-bearing vegetables or fruit trees, like mangoes, are often pruned to improve fruit quality. The simulation performed in this study could be useful to evaluate the effect of pruning on photosynthesis, because the distributions of light intensity and leaf photosynthetic rate vary over the canopy. Since the photosynthetic rate affects fruit yield, photosynthesis distribution over the crop canopy should be managed for improving crop yield and quality (Marcelis et al., 1998). Both the actual measurement and simulation results showed that the whole plant photosynthetic rates were at their maximum around 09:00 (Fig. 2-7). Therefore, CO₂ enrichment is recommended to be applied when the whole
plant photosynthetic rates of the mango trees are maximized after sunrise. Efficient CO$_2$ enrichment can be also considered that the leaf photosynthetic rate varies depending on leaf position in the plant. Therefore, this study will contribute to the development of efficient cultivation methods for various fruit crops including mango.


LITERATURE CITED


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CHAPTER 3

Analysis of photosynthesis enhancement in greenhouse-grown ‘Irwin’ mango by vertical CO₂ enrichment based on 3D plant modeling and ray-tracing simulation

ABSTRACT

Since photosynthesis closely affects the quality and yield of crops, environmental factors related to photosynthesis should be efficiently managed. In general, CO₂ is supplied to the bottom of crops in greenhouses for convenience of installation, however, optimum positions for CO₂ enrichment might be different depending on plant shape, light distributions, and various environmental factors. The objectives of this study were to calculate the whole plant photosynthetic rates of mango trees using 3D plant model and ray-tracing simulation, and to analyze the photosynthesis enhancement of by vertical CO₂ enrichment in greenhouses. Totally 27 CO₂ sensors were installed at each vertex of the grid around 4-year-old mango tree to measure distribution of the CO₂ concentration at different CO₂ enrichment conditions. Intercepted light intensity was simulated with 3D plant model and ray-tracing method, and the leaf photosynthetic rate was calculated with Faquhar, von Caemmerer, and Berry (FvCB) model. The CO₂ consumption rate of mango tree every 30 min and the accumulated CO₂ consumption from 08:00 to 10:30 were
calculated by enriching CO₂ between 0.5 to 1.5 m high in 0.1 m intervals. When CO₂ was enriched at 0.5, 1.0, and 1.5 m high, the CO₂ concentrations increased by 45.6%, 48.4%, and 153.6% at that height, respectively. The accumulated CO₂ consumption obtained by ray-tracing simulation with the 3D plant mode was found to be highest of 5.63 ± 0.02 g·plant⁻¹ when the CO₂ was enriched at 1.2 m high. The accumulated CO₂ consumptions from 08:00 to 10:30 when windows were closed for CO₂ enrichment were improved by 12.9% at the CO₂ enrichment at 1.2 m high compared to 0.5 m high. From the results, it is confirmed that this method will enhance crop photosynthesis and CO₂ utilization efficiency in greenhouses.

Additional keywords: carbon dioxide enrichment, light interception, nozzle, precision agriculture, ventilation
INTRODUCTION

Photosynthesis is physiological reactions required for the life activities of plants. In fruit crops, increasing photosynthesis is needed to increase fruit quality and yield, and environmental factors involved in photosynthesis should be managed precisely. Light intensity and CO$_2$ concentration are two environmental factors having the greatest effect on photosynthesis. The light intensity in greenhouses is changed by meteorological factors, by greenhouse structures and covering materials, and by the architecture of the crops (Buck-Sorlin et al., 2011; Kim et al., 2016). The CO$_2$ are used for the growth of leaves and stems of crops and its concentration affects the photosynthetic rate of crops (Hu et al., 2011; Son et al., 1999). In order to increase the yield of fruit crops, photosynthesis must be increased, so it is important to know exactly the whole plant photosynthetic rate.

Mango (*Mangifera indica* L.) is one of the globally important fruit crops, which is grown mainly in tropical and subtropical regions. ‘Irwin’ mango fruit is unique in color and flavor, gaining popularity among consumers. ‘Irwin’ mango trees are also grown in some areas in Korea and their cultivation area is gradually increasing (An et al., 2015; Park et al., 2014). When mango trees are grown in greenhouses to avoid the cold in winter, artificial training and pruning are used to make the tree form a vase shape (Yonemoto 2006). Since a mango tree has many leaves and stems, whole plant photosynthesis is difficult to be identified. For analysis of the plant photosynthetic rate, accurate light distribution and leaf photosynthetic rates are prerequisite (Chen et al., 2015). Therefore, a method to indirectly predict the photosynthesis of mango trees by using 3D plant model
and ray-tracing simulation might be useful (Kim et al., 2010; De Visser et al., 2014; Der Zande et al., 2011; Tang et al., 2015).

A simple model of the equation have been used to express the rate of photosynthetic rate in the mango trees (Farquhar et al., 1980; Zhu et al., 2012). In the case of ‘Kensington’ mango, leaf photosynthetic rate increased with increasing CO$_2$ concentration and saturated at a light intensity of 1,200 μmol·m$^{-2}·$s$^{-1}$ (Schaffer et al., 1997). A negative exponential model equation was found to be suitable for expressing the leaf photosynthetic rate of ‘Irwin’ mango trees (Jung et al., 2015). Although various studies are underway to accurately represent the photosynthesis rate of crops, most of commercialized CO$_2$ enrichment devices are not consider the distribution of photosynthesis rate. Most of the devices for enriching CO$_2$ are in the form of spraying CO$_2$ upward from the floor of the greenhouse (Takeya et al., 2017). In practical, CO$_2$ enrichment is generally recommended from sunrise until sunset as long as the greenhouse is not ventilated on sunny days (Mortensen, 1987).

Vertical CO$_2$ enrichment at a specific position for dense canopy-forming or complex-formed crops like mango have not been studied. Using 3D plant model and ray-tracing simulation, the intercepted light intensity on dense canopy-forming crops can be analyzed accurately. Enriching CO$_2$ at positions where photosynthesis occurs mainly can increase photosynthesis efficiently. Therefore, finding the precise position to enriching CO$_2$, and predicting the increase in photosynthesis when using the new CO$_2$ enrichment system are necessary.
The objectives of this study were to calculate the whole plant photosynthetic rates of mango trees using 3D plant model and ray-tracing simulation, and to analyze the photosynthesis enhancement of by vertical CO\textsubscript{2} enrichment in greenhouses.
MATERIALS AND METHODS

Plant materials and growth conditions

Mango trees (*Mangifera indica* L. cv. Irwin) were cultivated in a double-span plastic greenhouse (374 m²) located at Boryeong, Korea (36°23'34"N 126°29'12"E) for the experiment. One hundred 4-year-old mangoes cultivated in cylindrical plastic pots (0.5 × 0.8 m, height × diameter) were placed in the equidistant intervals in the greenhouse. Planting density was 0.27 plants·m⁻². Stems of the trees were trained and pruned periodically to lead vegetative growth and to determine tree structure in a vase shape. The greenhouse was covered with polyolefin (PO) films with a light transmittance of 92% and thickness of 0.15 mm. The inside temperature of the greenhouse was controlled at 32 ± 1°C using three hot-water heat exchange systems. The ventilation system was automatically operated at a set point of 40°C and ventilation windows opened sequentially. Water was irrigated daily for 10 min using a drip irrigation system. Water has been sufficiently irrigated to prevent it becoming a limiting factor. CO₂ was not enriched during cultivation before the experiment.

Measurement of spatial CO₂ concentration according to vertical CO₂ enrichment

On April 2, 2019, distribution of CO₂ concentration around a mango tree was measured. The day of the experiment was clear without clouds. This period was a fruit enlargement phase which has the greatest influence on fruit growth when CO₂ enrichment was employed. For measurement purposes, a tree in the center of the greenhouse was selected.
and an 1.0 × 1.0 × 1.0 m aluminum grid was installed around the tree at intervals of 0.5 m (Fig. 3-1A). Totally 27 CO₂ sensors (DS-GC-0023-MISIR, CO2meter.com, Ormond Beach, FL, USA) was installed at each vertex of the grid (Fig. 3-1A) and the measured CO₂ concentration was recorded as an analogue voltage. The CO₂ sensors had a measurement range of 0 to 5,000 μmol·mol⁻¹ and its accuracy was within ± 3% of reading. For measurement of light intensity at 0.5, 1.0, and 1.5 m height, three quantum sensors (SQ-110, Apogee Instruments, Logan, UT, USA), a data logger (GL-840, Graphtec, Yokohama, Japan) were used for data logging. Environmental changes in greenhouse gases were recorded by measuring changes in the diurnal light intensity and the CO₂ concentration.

On April 3, 2019, four spherical nozzles for enriching CO₂ were placed around the center axis of the tree at intervals of 0.5 m (Fig. 3-1B). Liquefied CO₂ gas for food and beverage was used in the tank, and the injection pressure was 2 kgf·cm⁻². This injection pressure allowed to maintain a maximum CO₂ concentration of 1,000 μmol·mol⁻¹. The control group was set to a situation where CO₂ was not enriched and the three treatment groups were set to three situations where CO₂ was enriched at 0.5, 1.0, and 1.5 m high at every 30 min. For the treatment groups, CO₂ was enriched for 20 min and the CO₂ concentrations were measured and recorded every 1 second. Leaf temperature at each condition was measured using an infrared thermal imaging camera (i7, FLIR, Wilsonville, OR, USA). Leaf temperature values were selected randomly at three locations of the image taken and averaged. The day of the experiment was also clear without clouds. Wind direction and wind speed were measured using a weather station installed outside the
Fig. 3-1. Aluminum grids and CO$_2$ sensors installed at 0.5, 1.0, and 1.5 m high (A) installed in greenhouse-grown 4-year-old ‘Irwin’ mango tree, a schematic diagram of the placement of CO$_2$ sensors and nozzles at each height (B), and a constructed 3D plant model (C).
greenhouse roof (Vintage Pro 2, Davis instruments, Hayward, CA, USA). The experiment was conducted on the conditions under which all roof and side windows were closed. On July 18, 2018, distribution of CO$_2$ concentration was measured again on the conditions under which all roof and side windows were opened. The mean and standard deviation of CO$_2$ concentrations measured over 20 min were calculated. The CO$_2$ behavior when enriching CO$_2$ compared with condition of the roof and side windows closed was analyzed.

**Construction of 3D plant model and ray-tracing simulation conditions**

A 3D plant model was constructed in the same architecture of a 4-year-old mango tree (Fig. 3-1C). Leaf area ($LA$), petiole length, phyllotaxis, branch pattern, stem length, and stem diameter were measured using a digital vernier caliper (500-182-30, Mitutoyo, Kanagawa, Japan) and they were reflected in the 3D model. Since the mango tree used in the experiment could not be destroyed to growth survey, $LA$ was calculated using the existing model: $LA = -14.623 + 8.074W + 0.085L^2 + 0.452W^2$, $R^2 = 0.97$ (Jung et al., 2016). The total $LA$ of the mango used in the experiment was 47,654.8 cm$^2$. The vertical $LA$ distribution of the 3D plant model used in this study showed the highest value around 1.2 m height (Fig. 3-2). In order to construct a 3D plant model, the leaves were arranged in the same order as in actual verticillation (Jung et al., 2018). The 3D plant model was constructed using 3D CAD software (SolidWorks, Dassault Systemes, Velizy-Villacoublay, France).
Fig. 3-2. Calculated leaf area of greenhouse-grown 4-year-old ‘Irwin’ mango trees by using the 3D model according to the tree height.
Using the constructed 3D plant model, intercepted light intensity was simulated with ray-tracing software (OptisWorks, OPTIS Inc., Toulon, France). Optical properties such as transmittance and reflectance of the mango leaves and branches were measured using an integrating sphere (IC2, StellarNet Inc., Tampa, FL, USA) with a spectrometer (BLUE-Wave, StellarNet Inc.) and light source (SL1 Tungsten Halogen, StellarNet Inc.). Fig. A-1 to A-4 showed the absorbance, transmittance, and reflectance of the mango leaves and branches. Ray-tracing simulations were conducted with 1 giga rays and the number of max impacts was set to 10 for all conditions. Detectors were set at 5 mm intervals on all leaf surfaces of the 3D plant model. The light intensity at the detector position on each leaves were calculated through simulation. On April 3, 2019, the 3D mango model was used to simulate light intensity at a 30 min interval from 10:00 to 11:30. The light intensity was simulated at 0.5, 1.0, and 1.5 m high of the tree and each position was determined to be the same as where the actual quantum sensors were installed. To represent the simulation results statistically, the 3D plant model was rotated by 120° about the center axis and simulated three times (n = 3).

**Calculation of whole plant photosynthetic rate**

Since the photosynthetic rate of plant according to light intensity and intercellular CO₂ concentration was expressed as a saturation response, simple saturation curve equations were used to determine the plant photosynthetic rate model. In the case of ‘Kensington’ mango, photosynthetic rate increased with increasing CO₂ concentration and saturated at a light intensity of 1,200 μmol·m⁻²·s⁻¹ (Schaffer et al., 1997). In addition, Chamchaiyaporn
et al. (2013) used a rectangular hyperbola equation to express the photosynthetic rates of mango leaves that increase with increasing light intensity. Therefore, rectangular hyperbola and negative exponential models have widely been used as empirical equations for saturation. According to Jung et al. (2015), a negative exponential model equation was more suitable for expressing the photosynthetic rate of ‘Irwin’ mango trees. In this study, however, Faquhar, von Caemmerer, and Berry (FvCB) photosynthetic rate models for ‘Irwin’ mango trees according to each leaf position were used as following equations:

\[ P = \min(A_c, A_j) \]  
(Eqn. 3-1)

\[ A_c = \left( \frac{V_c(C_l - \Gamma^*)}{C_l + K_c(1 + \frac{0}{K_o})} \right) - R \]  
(Eqn. 3-2)

\[ V_c = V_{cmax} * \left( 31 + \frac{69}{1 + e^{-0.009*(PPFD - 500)/100}} \right) \]  
(Eqn. 3-3)

\[ A_j = \left( \frac{J^*(C_l - \Gamma^*)}{4C_l + 8\Gamma^*} \right) - R \]  
(Eqn. 3-4)

\[ J = \left( \frac{a*PPFD + I_{max} - \sqrt{(a*PPFD + I_{max})^2 - 4\theta*I_{max} + a*PPFD}}{2\theta} \right) \]  
(Eqn. 3-5)

where \( P \) is leaf photosynthetic rate (\( \mu \text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( A_c \) is ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) carboxylation limited photosynthesis rate (\( \mu \text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)).
$A_j$ is ribulose-1,5-bisphosphate (RuBP) regeneration limited photosynthesis rate (μmol CO$_2$·m$^{-2}$·s$^{-1}$), $V_c$ is carboxylation capacity at certain light intensity (μmol CO$_2$·m$^{-2}$·s$^{-1}$), $C_i$ is intercellular CO$_2$ concentration (μmol·mol$^{-1}$), $Γ^\ast$ is CO$_2$ compensation point (μmol·mol$^{-1}$), $K_c$ is Michaelis-Menten constant of Rubisco for CO$_2$ (μmol·mol$^{-1}$), $Θ$ is O$_2$ concentration (210 mmol·mol$^{-1}$), $K_O$ is Michaelis-Menten constant of Rubisco for O$_2$ (μmol·mol$^{-1}$), $R$ is respiration (μmol CO$_2$·m$^{-2}$·s$^{-1}$), $V_{emax}$ is maximum carboxylation capacity (μmol CO$_2$·m$^{-2}$·s$^{-1}$), $PPFD$ is photosynthetic photon flux density (μmol·m$^{-2}$·s$^{-1}$), $J$ is electron transport rate at certain light intensity (μmol·m$^{-2}$·s$^{-1}$), $α$ is efficiency of light energy conversion on an incident light basis (mol·mol$^{-1}$), $J_{max}$ is maximum electron transport rate (μmol·m$^{-2}$·s$^{-1}$), and $θ$ is curvature of the light response of $J$ (dimensionless) (Qian et al., 2012). The values of the various variables required for the FvCB model were determined, using the results obtained from Table 1-3.

The light intensity obtained from the ray-tracing simulation and CO$_2$ concentration was substituted into the above equations to calculate the whole plant photosynthetic rate distribution. When CO$_2$ was enriched differently by each height, the actual measured CO$_2$ concentrations were substituted for the equations to calculate whole plant photosynthetic rate in each treatment. The leaf photosynthetic rates of mango trees at each height were calculated to determine the position where photosynthesis increased. The CO$_2$ consumption rate of the whole plant was calculated to compare the effects of photosynthesis enhancement between the control group (no CO$_2$ enrichment) and the CO$_2$ treatment groups.
Simulations for optimizing CO$_2$ enrichment position

During the CO$_2$ enriched at each height, an empirical equation was described to express the CO$_2$ concentration at each height. The empirical equation was expressed in the following form:

$$C_p = a \times H^2 \times P^2 + b \quad \text{(Eqn. 3-6)}$$

where, $C_p$ is CO$_2$ concentration at $P$ m height (μmol·mol$^{-1}$), $H$ is CO$_2$ enrichment height (m), $P$ is vertical position (m), and $a$ and $b$ are regression coefficients.

Since the CO$_2$ concentration around mango trees could not be measured at the same time, the light conditions had to be simulated at each time. The light intensity was expressed using the simulation results of the 3D mango model at every 30 min interval from 10:00 to 11:30 on April 3, 2019. The CO$_2$ concentrations in each location were calculated using Eqn. 3-6 under different CO$_2$ enrichment height every 0.1 m interval. The leaf photosynthetic rate was calculated by applying the FvCB model, reflecting the measured temperature over time. The accumulated CO$_2$ consumption of mango tree were calculated during experimental periods, when CO$_2$ was enriched between 0.5 and 1.5 m height at intervals of 0.1 m. Then, optimal enrichment height showing the maximum accumulated CO$_2$ consumption was found.

After finding the optimal enrichment height, the light intensity was expressed using the simulation results of the 3D mango model at every 30 min interval from 08:00 to 10:30 on April 3, 2019. Since photosynthesis increased after sunrise and the windows of the
greenhouse were closed, this period was generally known as a time zone suitable for the CO₂ enrichment. The leaf photosynthetic rate was calculated by applying the FvCB model. Then, the CO₂ consumption rates of mango tree were calculated without CO₂ enrichment and with CO₂ enrichment at the 0.5 and 1.2 m height. Then, the CO₂ consumption rates under different CO₂ enrichment conditions were analyzed by calculating cumulative CO₂ consumption rate from 08:00 to 10:30.
RESULTS

Measured daily light intensity and CO₂ concentration change

The daily light intensity on April 2, 2019, increased from 08:00 to indicate the maximum value of 800 μmol·m⁻²·s⁻¹ around 12:00 and decreased to 0 μmol·m⁻²·s⁻¹ around 18:00 (Fig. 3-3A). The light intensity tended to decrease from the top to the bottom of the tree, and the maximum light intensity at the height of 0.5 m was about 160 μmol·m⁻²·s⁻¹. The CO₂ concentration tended to increase until sunrise and then decreased by photosynthesis after sunrise (Fig. 3-3B). As the ventilation window opened for temperature control at 10:30, the CO₂ concentration decreased sharply and showed a similar value to the CO₂ concentration outside the greenhouse. The CO₂ concentration showed the highest value of 1,050 μmol·mol⁻¹ at 1.5 m high at night and the highest value of 550 μmol·mol⁻¹ at 0.5 m high during the day.

Measured CO₂ concentration at each position under different CO₂ enrichment conditions

The CO₂ concentration around the mango tree was logged for 20 min which averaged the nine sensors installed according to each height when the roof and side windows of greenhouse were closed (Fig. 3-4, A-5, Table 3-1). The CO₂ concentration increased at the height where CO₂ was enriched, but the amount of CO₂ moving down was small and that moving up was not shown. When CO₂ was enriched at of 0.5, 1.0, and 1.5 m high, the CO₂
Fig. 3-3. Changes in measured light intensity (A) and CO₂ concentration (B) in greenhouse-grown 4-year-old ‘Irwin’ mango tree leaves for 24 h on April 2, 2019 at 0.5, 1.0, and 1.5 m high.
Fig. 3-4. Vertical changes in average CO₂ concentration measured in greenhouse-grown 4-year-old ‘Irwin’ mango tree leaves using nine CO₂ sensors for 20 min according to CO₂ enriched height when the greenhouse windows open and closed. A, B, C, and D mean no CO₂ enrichment (control), CO₂ enriched at 0.5, 1.0, and 1.5 m high, respectively. Bars represent means ± SD (n = 9).
Table 3-1. Measured average light intensity, leaf temperature, and CO₂ concentration in a greenhouse for growing 4-year-old ‘Irwin’ mango trees according to CO₂ enriched and measured heights.

<table>
<thead>
<tr>
<th>CO₂ Enrichment height (m)</th>
<th>Time (hh:mm)</th>
<th>Measured height (m)</th>
<th>Light intensity (μmol·m⁻²·s⁻¹)</th>
<th>Leaf temperature (°C)</th>
<th>CO₂ concentration (μmol·mol⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No</td>
<td>10:00-0.5</td>
<td>0.5</td>
<td>68.1 ± 12.65z</td>
<td>29.3 ± 0.67y</td>
<td>544.6 ± 9.45z</td>
</tr>
<tr>
<td></td>
<td>10:20-1.0</td>
<td>1.0</td>
<td>111.0 ± 14.34</td>
<td>32.5 ± 0.83</td>
<td>455.8 ± 9.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.5</td>
<td>316.9 ± 128.43</td>
<td>34.7 ± 0.65</td>
<td>406.3 ± 13.89</td>
</tr>
<tr>
<td>0.5</td>
<td>10:30-0.5</td>
<td>0.5</td>
<td>94.8 ± 8.97</td>
<td>29.1 ± 0.47</td>
<td>792.8 ± 19.03</td>
</tr>
<tr>
<td></td>
<td>10:50-1.0</td>
<td>1.0</td>
<td>145.0 ± 19.67</td>
<td>32.6 ± 0.91</td>
<td>454.7 ± 9.76</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.5</td>
<td>343.8 ± 44.93</td>
<td>35.7 ± 0.71</td>
<td>399.7 ± 12.99</td>
</tr>
<tr>
<td>1.0</td>
<td>11:00-0.5</td>
<td>0.5</td>
<td>96.8 ± 13.92</td>
<td>29.7 ± 0.64</td>
<td>589.3 ± 35.49</td>
</tr>
<tr>
<td></td>
<td>11:20-1.0</td>
<td>1.0</td>
<td>158.6 ± 21.18</td>
<td>34.1 ± 1.88</td>
<td>675.0 ± 40.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.5</td>
<td>340.9 ± 46.51</td>
<td>37.4 ± 2.74</td>
<td>411.1 ± 15.77</td>
</tr>
<tr>
<td>1.5</td>
<td>11:30-0.5</td>
<td>0.5</td>
<td>114.5 ± 9.90</td>
<td>31.6 ± 0.31</td>
<td>531.0 ± 54.44</td>
</tr>
<tr>
<td></td>
<td>11:50-1.0</td>
<td>1.0</td>
<td>184.4 ± 19.30</td>
<td>35.5 ± 1.45</td>
<td>586.3 ± 73.92</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.5</td>
<td>525.7 ± 59.86</td>
<td>40.7 ± 6.33</td>
<td>1042.6 ± 65.87</td>
</tr>
</tbody>
</table>

zMean ± SD (n = 1,200); yMean ± SD (n = 4)
concentrations increased by 45.6, 48.4, and 153.6% at those heights, respectively (Fig. 3-4, Table 3-1). The CO₂ concentration around the mango tree was logged for 20 min which averaged the nine sensors installed according to each height when the roof and side windows of greenhouse were open (Fig. 3-4, A-6). The CO₂ concentration increased at the height where CO₂ was enriched. When CO₂ was enriched at 0.5, 1.0, and 1.5 m high, the CO₂ concentrations increased by 56.7, 39.1, and 109.7% at those heights, respectively.

A regression analysis based on the actually measured CO₂ concentrations resulted in the regression coefficients $a$ and $b$ included in the Eqn. 3-6 showing values of 75.288 and 506.696, respectively (Fig. A-7). The $R^2$ and RMSE for this equation were 0.65 and 3.696, respectively.

**Measured spatial distribution of CO₂ concentration under different CO₂ enrichment conditions**

The CO₂ concentration around the mango tree was logged during 20 min which the 27 sensors installed according to each vertex of the grid (Fig. 3-5). When CO₂ was not enriched as control, the averaged CO₂ concentration around mango trees was uniform at around 464.1 μmol·mol⁻¹ (Fig. 3-5A). The CO₂ concentrations measured at 1.5 m high were lower than those measured at 0.5 m high. When CO₂ was enriched at 0.5 m high, a gradient of CO₂ concentration was observed between 0.5 to 1.5 m high (Fig. 3-5B). Even with the differences in height, there was no difference in CO₂ concentration distribution depending on the direction. When CO₂ was enriched at 1.0 m high, the CO₂ concentration increased at 1.0 m high and slightly higher in the south than in the north direction, but CO₂
Fig. 3-5. Distribution of CO$_2$ concentration measured in greenhouse-grown 4-year-old ‘Irwin’ mango tree leaves using 27 CO$_2$ sensors at each vertex of grid. A, B, C, and D mean no CO$_2$ enrichment (control), CO$_2$ enriched at 0.5, 1.0, and 1.5 m high, respectively.
concentration distributions depending on the direction were not different (Fig. 3-5C). When CO₂ was enriched at 1.5 m high, the CO₂ concentration increased around 1,200 μmol·mol⁻¹ at 1.5 m high and slightly higher in the south than in the north direction, but differences in CO₂ concentration distribution depending on the direction were small (Fig. 3-5D). During the measurements, the wind direction and average wind speed were northeast and 3.2 m·s⁻¹, respectively.

**Calculated photosynthetic rate distribution under different CO₂ enrichment conditions**

The intercepted light intensity distribution of mango trees was obtained through ray-tracing simulation at each measurement time (Fig. 3-6, Table 3-2). The photosynthetic rate distribution of the trees was calculated using the simulation results and the spatial CO₂ concentration distribution obtained through the actual enrichment (Fig. 3-7, Table 3-2). The CO₂ consumption rates per plant were listed according to the CO₂ enrichment conditions (Fig. 3-8). When CO₂ was not enriched as control, CO₂ consumption rate was 1.76 ± 0.02 g·h⁻¹·plant⁻¹. When CO₂ was enriched at each height, average leaf photosynthetic rate were 2.64 ± 0.05, 2.88 ± 0.03, and 2.46 ± 0.01 g·h⁻¹·plant⁻¹. With increasing the CO₂ enrichment height, the CO₂ consumption rate per plant increased to 1.0 m high and decreased slightly from 1.5 m high. However, the increased ratio of the CO₂ consumption rate could not be calculated directly, because the CO₂ enrichment conditions were different according to the measured time.
Fig. 3-6. Distribution of light interception in greenhouse-grown 4-year-old ‘Irwin’ mango tree calculated using actually measured leaf temperature and CO₂ concentration at each leaf position. A, B, C, and D mean no CO₂ enrichment (control), CO₂ enriched at 0.5, 1.0, and 1.5 m high, respectively.
Table 3-2. Calculated average light intensity and leaf photosynthetic rate of greenhouse-grown 4-year-old ‘Irwin’ mango trees according to CO₂ enriched and measured heights.

<table>
<thead>
<tr>
<th>CO₂ enrichment height (m)</th>
<th>Measured height (m)</th>
<th>Light intensity (μmol·m⁻²·s⁻¹)</th>
<th>Leaf photosynthetic rate (μmol CO₂·m⁻²·s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No enrichment 0.5</td>
<td>0.5</td>
<td>67.5 ± 3.06</td>
<td>1.78 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>1.0</td>
<td>114.0 ± 2.04</td>
<td>1.92 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>1.5</td>
<td>318.5 ± 4.50</td>
<td>4.98 ± 0.04</td>
</tr>
<tr>
<td>0.5</td>
<td>0.5</td>
<td>92.8 ± 3.30</td>
<td>1.92 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>1.0</td>
<td>145.9 ± 0.92</td>
<td>2.06 ± 0.07</td>
</tr>
<tr>
<td></td>
<td>1.5</td>
<td>343.0 ± 3.17</td>
<td>5.37 ± 0.05</td>
</tr>
<tr>
<td>1.0</td>
<td>0.5</td>
<td>90.4 ± 3.38</td>
<td>2.00 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>1.0</td>
<td>161.7 ± 4.65</td>
<td>2.86 ± 0.07</td>
</tr>
<tr>
<td></td>
<td>1.5</td>
<td>341.3 ± 3.37</td>
<td>5.58 ± 0.09</td>
</tr>
<tr>
<td>1.5</td>
<td>0.5</td>
<td>114.2 ± 0.88</td>
<td>2.17 ± 0.06</td>
</tr>
<tr>
<td></td>
<td>1.0</td>
<td>184.0 ± 0.78</td>
<td>2.54 ± 0.06</td>
</tr>
<tr>
<td></td>
<td>1.5</td>
<td>528.9 ± 4.33</td>
<td>6.18 ± 0.01</td>
</tr>
</tbody>
</table>

*Mean ± SD (n = 3)
Fig. 3-7. Distribution of leaf photosynthetic rate in greenhouse-grown 4-year-old ‘Irwin’ mango tree calculated using actually measured leaf temperature and CO$_2$ concentration at each leaf position. A, B, C, and D mean no CO$_2$ enrichment (control), CO$_2$ enriched at 0.5, 1.0, and 1.5 m high, respectively.
Fig. 3-8. CO₂ consumption rate per plant calculated using actually measured leaf temperature and CO₂ concentration in greenhouse-grown 4-year-old ‘Irwin’ mango tree leaves at each leaf position and simulated light intensity according to CO₂ enrichment height. Bars represent means ± SD, and simulation was performed three times with 120° rotated 3D plant models (n = 3).
**Optimized position for CO₂ enrichment**

The accumulated CO₂ consumption calculated by simulation was found to be the highest value of $5.63 \pm 0.02$ g plant$^{-1}$, when the CO₂ was enriched at 1.2 m high (Fig. 3-9). The accumulated CO₂ consumption increased from 0.5 to 1.2 m high, and gradually decreased over 1.2 m high. The accumulated CO₂ consumption was shown to increase by 11.9% when the CO₂ was enriched at 1.2 m high than 0.5 m high. The optimal enrichment height was determined at the 80% of the plant height with highest CO₂ enrichment efficiency.

From 08:00 to 10:30 the calculated CO₂ consumption rates decreased (Fig. A-8). Regardless of whether CO₂ was enriched or not, when the roof and side windows opened at 10:30, the calculated CO₂ consumption rates showed a sharp decrease until 1.91 g h$^{-1}$ plant$^{-1}$. When CO₂ was enriched at 1.2 m high, the CO₂ consumption rates were always higher than those under the other conditions during enrichment period. When CO₂ was not enriched as control, accumulated CO₂ consumption was $7.43 \pm 0.28$ g plant$^{-1}$ during 08:00 to 10:30 (Fig. 3-10). When CO₂ was enriched at 0.5 and 1.2 m high, accumulated CO₂ consumption was $7.81 \pm 0.17$ and $8.82 \pm 0.16$ g plant$^{-1}$, respectively, during 08:00 to 10:30. The accumulated CO₂ consumptions were shown to increase by 5.2 and 18.8% when the CO₂ was enriched at 0.5 and 1.2 m high, respectively, than those under no enrichment condition. In addition, the accumulated CO₂ consumptions were shown to increase by 12.9% when the CO₂ was enriched at 1.2 m high than those at 0.5 m high.
Fig. 3-9. Accumulated CO$_2$ consumption in greenhouse-grown 4-year-old ‘Irwin’ mango tree leaves calculated using actually measured leaf temperature and CO$_2$ concentration at each leaf position and simulated light intensity during 10:00 to 11:30 according to CO$_2$ enrichment height. Bars represent means ± SD, and simulation was performed three times with 120° rotated 3D plant models (n = 3).
Fig. 3-10. Comparison of accumulated CO$_2$ consumptions per plant in greenhouse-grown 4-year-old ‘Irwin’ mango tree leaves among no CO$_2$ enrichment, CO$_2$ enriched at 0.5 and 1.2 m high during 08:00 to 10:30. Bars represent means ± SD, and simulation was performed three times with 120° rotated 3D plant models (n = 3). Different letters indicate significant differences by Duncan’s multiple range test at $P < 0.05$. 
DISCUSSION

Photosynthesis is an essential physiological response to carry out the various activities of plants for maintaining their life. The crop production is determined by the synthesis and distribution of assimilates (Marcelis et al., 1998). Plants accept light energy to create assimilation products in the form of carbon compounds and store in their bodies in metabolically usable form (Lawlor, 2002). Researches about light, which becomes an energy source of photosynthesis reaction, are being conducted in a variety of ways, such as in the light intensity and the light quality, and these are being studied at the level of genes and enzymes that drive physiological reactions within plants (Hihara et al., 2001; Jeong et al., 2004). However, photosynthesis studies have rarely been conducted at the level of the whole plant, and most studies have been conducted from a plant physiology perspective. From the point of view of food production, researches are needed to improve the photosynthesis of crops on whole plant or higher level (Cohen et al., 2005; Raines, 2011). In addition, to fix the carbon in the body, cultivation period of the target crops should be longer than that of vegetables. And they should be conduct lignification (Xu et al., 2007). Mangoes are suitable crops in terms of carbon sequestration. This study would be useful in terms of increasing crop yields and carbon control, because it was intended to confirm the increase in photosynthesis by CO₂ enrichment at the whole plant level.

A number of studies have been conducted to increase the photosynthesis of crops by supplying CO₂ and consequently increase the yield (Leakey et al., 2006; Schaffer et al., 1999). In earlier studies, CO₂ was supplied to increase the crop production within a semi-
closed system such as greenhouses (Phillips et al., 1996). The most active recent topic of study with CO₂ that called free-air CO₂ enrichment (FACE) is predicting crop yields due to climate change (Ainsworth et al., 2008; Maheshwari et al., 2017; Parry et al., 2004). The purpose of the FACE study is to monitor the productivity change of field plants according to environmental changes such as elevated CO₂, drought, and high temperature. For field studies, however, the FACE is costly, and should be employed differently from the greenhouse study, which provides active CO₂ supply with an aim to increase productivity. When using the technology to supply CO₂ to a greenhouse, CO₂ leakage of the greenhouse should be considered (Kuroyanagi et al., 2014). Enriching the exact amount of CO₂ that a crop needs, or increasing the amount of CO₂ that a crop consumes through photosynthesis, can compensate the amount of CO₂ leaking out of the greenhouse. Although, there are studies about the CO₂ enrichment during ventilation of greenhouse, the CO₂ enrichment was generally recommended from sunrise until sunset as long as the greenhouse was not ventilated on sunny days (Mortensen, 1987). Analyzing from the fact that there is a large variation in CO₂ concentration when windows were open and CO₂ was enriched, CO₂ will easily escape from the greenhouse (Fig. 3-4). In this study, CO₂ consumption rate was confirmed to increase when CO₂ was enriched during the window closed period (Fig. 3-10), and the optimal CO₂ enrichment position was 1.2 m height (Fig. 3-9). Enriching CO₂ at this height will increase the photosynthesis of the plant and reduce the amount of CO₂ that escape from the greenhouse. If the technology was used to supply the exact amount of CO₂ consumed by the crop photosynthesis, CO₂ released outside of the greenhouse could be reduced (Ohyama et al., 2005). Precise CO₂ enrichment technology can increase crop
production while reducing the amount of CO\textsubscript{2} leaking the atmosphere to save cost and is also effective in reducing the emission of greenhouse gases.

When growing small crops such as leaf vegetables in greenhouses, little consideration is given to the effect of CO\textsubscript{2} concentration gradient. However, when growing fruit vegetables such as paprika and tomato and fruit trees such as mango and citrus in greenhouses, the spatial distribution of CO\textsubscript{2} concentration and photosynthesis should be considered (Jung et al., 2015). In the case of paprika grown to form dense canopy, or mango where canopy is formed in complex form due to the large number of branches and leaves, the exact photosynthesis distribution is difficult to be found out (Jung et al., 2018; Kim et al., 2016). In such cases, the ray-tracing simulation technique will allow accurate light distribution to be monitored for each position of the crop. Quantum sensors were installed in this study to measure the light intensity in each height of the crop, but the exact light intensity could not be measured because sensors could not be placed throughout the entire mango tree (Fig. 3-1A). Although there is a difficulty in reflecting the structural and optical characteristics of crops to accurately calculate the light intensity reaching the whole leaf of the crop, the ray-tracing technique is considered to be efficient for the research of photosynthesis in fruit crops. The vertical leaf area distribution of the 3D plant model used in this study showed the highest value around 1.2 m height (Fig. 3-2). Therefore, if the leaf distribution of the crop such as phyllotaxis changes, the position of maximum photosynthesis might be different, and further researches on the architecture of the plants are needed.
For CO₂ measurements, the CO₂ concentration was measured by placing the CO₂ sensor at intervals of 0.5 m. When comparing Figs. 3-5 and 3-7, there was a difficulties in measuring the CO₂ concentration of the foreground surrounding the crop. In addition, predicting whole plant photosynthetic rate using leaf photosynthetic rate models was consistent with the actually observed whole plant photosynthetic rate (Jung et al., 2018). However, the whole plant photosynthetic rate is likely to be incorrectly predicted. This may be because the variables used in the models were incorrectly predicted, or there were differences between the environmental factors applied to make the model and the environmental factors used to cultivate the actual crops. Photosynthesis could be predicted more accurately, if various physiological indicators such as stomatal response and anatomical characteristics of leaf involved in leaf photosynthetic rate were identified (Larbi et al., 2015; Léchaudel et al., 2013). Several chamber systems have been designed to measure the accurate whole plant photosynthetic rate (Bugbee, 1992; Takahashi et al., 2008), but they are difficult to be used in large crops like mango.

For increasing the crop production, CO₂ should be enriched precisely. CO₂ enrichment has often increase LAI, an indicator for crop growth (Hartz-Rubin and de Lucia, 2001). Commercialized CO₂ enrichment equipments are mostly supplying CO₂ to the bottom of the crop. However, given the existing studies and the results measured in this experiment (Fernandez and Bailey 1994), CO₂ is recommended to be enriched at the top of the crop where photosynthesis is active. According to the method analyzed in this study, when CO₂ is enriched at a position where photosynthesis mainly occurs, the quality and yield of fruit
will increase. And the CO$_2$ utilization efficiency will increase, the economic burden of mango growing farmers will ease.
LITERATURE CITED


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CONCLUSIONS

Although various studies are underway to accurately represent the photosynthesis rate of crops, most of commercialized CO\textsubscript{2} enrichment devices are not considering the distribution of photosynthetic rate. Most of the devices for enriching CO\textsubscript{2} are in the form of spraying CO\textsubscript{2} upward from the floor of the greenhouse. Moreover, the vertical CO\textsubscript{2} enrichment at the each position of dense canopy-forming or complex-formed crops have not been conducted.

It is necessary to reflect the photosynthetic rate, which varies by vertical position of leaves on mango tree, and the accurate model of the changes in photosynthetic rate according to environmental factors is required. The calculated leaf photosynthetic rate according to leaf position using the simple multiplication, rectangular hyperbola, and FvCB models, showed their R\textsuperscript{2} values of 0.79, 0.68, and 0.77, respectively. The vertical leaf photosynthetic rate models established in this study will help determine environmental conditions that can maximize photosynthesis of greenhouse-grown ‘Irwin’ mango trees.

In the case of fruit crops in which the canopy develops in complicated forms, the analysis of light intensity inside the canopy is difficult but possible through 3D plant modeling and ray-tracing simulation. The light distributions in the canopy estimated by the simulation were similar to those actually measured by using quantum sensors. The photosynthetic rates of the whole mango tree calculated using the leaf photosynthetic model with ray-traced light intensities were in good agreement with the measured ones. Through estimating the leaf photosynthetic rates at each position of the tree, pruning and
training practices as well as CO$_2$ enrichment could efficiently be performed, improving the productivity and quality of crops grown in greenhouses.

The adequate CO$_2$ enrichment position was investigated and the enhanced photosynthesis was quantified. The actual CO$_2$ concentration distribution was measured to enrich CO$_2$ at different positions of 4-year-old ‘Irwin’ mango tree with 1.5 m height. Light interception and photosynthetic rate were analyzed through the 3D model of the plant and ray-tracing simulation. CO$_2$ concentrations around the plant were different when CO$_2$ was enriched at different positions. The accumulated CO$_2$ consumptions from 08:00 to 10:30 when windows were closed for CO$_2$ enrichment were improved by 12.9% at the CO$_2$ enrichment at 1.2 m high compared to 0.5 m high, which is the conventional position. Enriching CO$_2$ at an adequate height could increase the photosynthesis of the crops compared to the commercialized method. From the results, it is confirmed that this method will enhance crop photosynthesis and CO$_2$ utilization efficiency in greenhouses.
ABSTRACT IN KOREAN

망고(Mangifera indica L.)는 열대와 아열대 지역에서 주로 재배되는 세계 30대 주요 과수 중 하나이다. 과수 작물의 생산량을 증대시키기 위해서는 광합성이 우선적으로 증대되어야 하며, 광합성 속도를 정확하게 예측하는 것은 매우 중요하다. 작물 개체의 광합성을 정확하게 예측하기 위해서는 광합성에 영향을 미치는 환경 요인과 작물의 형태적 요인을 모두 고려해야 한다. 실험과 시뮬레이션을 동시에 진행하여 작물의 개체 광합성을 추정하는 기술은 작물 재배 시 CO₂ 관리를 위한 기술로 기능할 수 있다. CO₂는 광합성의 재료로 사용되므로 충분한 시비를 실시할 필요가 있으나, 많은 양을 시비할 경우 온실 밖으로 빠져나가 소실이 생길 우려가 있다. 대부분의 상용 CO₂ 시비 장치들은 광합성 분포를 고려하지 않은 형태로 설계되어 있다. 본 연구에서는 정확한 엽 광합성 속도 모델을 확립하고, 3차원 작물 모델과 광추적 시뮬레이션을 활용하여 작물 수광량을 분석함으로써, 공간적 광합성 분포를 계산하고, CO₂ 시비 시 효율적인 위치를 최적화 하는 것을 목표로 한다. 이를 위하여 단순곱 모델과 직각쌍곡선 모델, FvCB 모델에 대하여 회귀 분석을 실시하였다. 회귀 분석 결과 R² 값은 단순곱 모델에서 0.79로 가장 높은 정확도를 보였으며, 직각쌍곡선 모델에서 0.68로 가장 낮은 정확도를 보였다. 수직적 엽 광합성 속도 모델을 활용하면 망고 재배 시 광합성을 최대화 할 수 있는 환경 조건을 찾는 데 유용할 것이다. 인공광 하에서 2년생
망고의 개체 광합성 속도는 CO\(_2\) 농도가 증가함에 따라 2.0에서 2.9\(\mu\)mol CO\(_2\)\(\cdot\)m\(^{-2}\)\(\cdot\)s\(^{-1}\)로 증가하였다. 반면, 자연광 하에서 2년생 망고의 광합성 속도는 오전 6시에 0.2\(\mu\)mol CO\(_2\)\(\cdot\)m\(^{-2}\)\(\cdot\)s\(^{-1}\)로 나타났으며, 점차 증가하여 오전 9시에 7.3\(\mu\)mol CO\(_2\)\(\cdot\)m\(^{-2}\)\(\cdot\)s\(^{-1}\)으로 최대 광합성 속도를 나타낸 뒤, 점차 감소하여 오후 6시에 -1.0\(\mu\)mol CO\(_2\)\(\cdot\)m\(^{-2}\)\(\cdot\)s\(^{-1}\)으로 나타났다. 검증 절차를 통해 시뮬레이션을 통한 개체 광합성 속도 예측값은 \(R^2\)가 0.79로, RMSE가 0.263으로 나타났다. 이러한 결과를 통해 개체 광합성 속도의 분포를 확인하는 것은 광환경 개선을 위한 전정이나, 적절한 CO\(_2\) 시비를 위해 중요함을 확인할 수 있었다.

CO\(_2\) 시비 위치를 다르게 했을 때, 실험을 수행한 기간 동안 망고 개체의 적산 CO\(_2\) 소비량을 계산한 결과, 최대값은 1.2m 높이에 시비했을 때 5.63 ± 0.02g\(\cdot\)plant\(^{-1}\)로 나타났다. 망고의 과실 비대기를 기준으로, CO\(_2\) 시비가 주로 이루어지는 08시부터 10시 30분까지의 기간 동안 0.5m 높이에 CO\(_2\)를 시비했을 경우에 비해 1.2m 높이에 시비하는 경우 적산 CO\(_2\) 소비량이 12.9% 증가하는 것으로 나타났다. 따라서 본 연구를 통해 작물의 하단부에 CO\(_2\)를 시비하는 관행 방식에 비해 광합성이 주로 일어나는 작물의 중상단에 CO\(_2\)를 시비하는 것이 광합성을 증대시킬 수 있음을 확인하였다. 이 결과를 통해 새로 개발한 방식으로 CO\(_2\)를 시비하면 작물의 광합성이 증대되고 온실에서의 CO\(_2\) 이용 효율 또한 증대될 것이다.
추가 주요어: 3차원 작물 모델, 동화작용, 정밀 농업, 탄소 시비, 환기

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APPENDIX

SUPPORTING INFORMATION ON SIMULATION ANALYSIS
Supporting Information Section 1. Optical characteristics of ‘Irwin’ mango tree leaves and branches (Chapter 2)

Optical properties such as absorbance, transmittance, and reflectance of the mango leaves and branches were measured using an integrating sphere (IC2, StellarNet Inc., Tampa, FL, USA) with a spectrometer (BLUE-Wave, StellarNet Inc.) and light source (SL1 Tungsten Halogen, StellarNet Inc.). Fig. A-1 to A-4 showed the absorbance, transmittance, and reflectance of the mango leaves and branches. These values were entered in the preferences section for the leaves in the simulation software. The optical properties of the mango leaves showed little difference in the vertical position within the mango.
Fig. A-1. Measured reflectance of ‘Irwin’ mango tree leaves on adaxial (A) and abaxial side (B).
Fig. A-2. Measured transmittance of ‘Irwin’ mango tree leaves.
Fig. A-3. Measured absorbance of ‘Irwin’ mango tree leaves.
Fig. A-4. Measured reflectance and absorbance of ‘Irwin’ mango tree branches.
Supporting Information Section 2. Measured CO$_2$ concentration at each position under different CO$_2$ enrichment conditions, calculated photosynthetic rate distribution under different CO$_2$ enrichment conditions, and the distribution of leaf area with plant height (Chapter 3)

The CO$_2$ concentration around the mango tree was logged for 20 min which averaged the nine sensors installed according to each height when the roof and side windows of greenhouse were closed and open (Fig. A-5, A-6).

And a regression analysis based on the actually measured CO$_2$ concentrations resulted in the regression coefficients $a$ and $b$ included in the Eqn. 3-6 showing values of 75.288 and 506.696, respectively (Fig. A-7). The $R^2$ and RMSE for this equation were 0.65 and 3.696, respectively. This result was used to standardize the CO$_2$ enrichment conditions for different time periods using the ray-tracing simulation method.

After finding the optimal enrichment height, the light intensity was expressed using the simulation results of the 3D mango model at every 30 min interval from 08:00 to 10:30 on April 3, 2019 (Fig. A-8). This result was used to calculate the accumulated CO$_2$ consumption of mango tree under no enrichment condition and CO$_2$ enriched at the 0.5 and 1.2 m height conditions.

A 3D plant model was constructed in the same architecture of a 4-year-old mango tree. Leaf area, petiole length, phyllotaxis, branch pattern, stem length, and stem diameter were measured. The vertical leaf area distribution of the 3D plant model used in this study showed the highest value around 1.2 m height (Fig. A-9).
Fig. A-5. Changes in average measured CO$_2$ concentration in greenhouse-grown 4-year-old ‘Irwin’ mango tree leaves using nine CO$_2$ sensors for 20 min according to the height when roof and side windows closed. No enrichment as control group (A), CO$_2$ enriched at the 0.5 (B), 1.0 (C), and 1.5 m (D) high.
Fig. A-6. Changes in average measured CO$_2$ concentration in greenhouse-grown 4-year-old ‘Irwin’ mango tree leaves using nine CO$_2$ sensors for 20 min according to the height when roof and side windows open. No enrichment as control group (A), CO$_2$ enriched at the 0.5 (B), 1.0 (C), and 1.5 m (D) high.
Fig. A-7. Regression result of CO$_2$ concentration in greenhouse-grown 4-year-old ‘Irwin’ mango tree leaves at each measurement height according to CO$_2$ enrichment height. White dots mean actually measured CO$_2$ concentrations and curved mesh means regressed empirical model.
Fig. A-8. Changes in calculated CO₂ consumption rate per plant based on optimal CO₂ enrichment height in greenhouse-grown 4-year-old ‘Irwin’ mango tree leaves for no enrichment condition and conditions that were enriched at 0.5 and 1.2 m high during 08:00 to 10:30 at 30 min intervals. Bars represent means ± SD, and simulation was performed three times with 120° rotated 3D plant models (n = 3).