

## THREE-DIMENSIONAL DYNAMIC VARIATION OF APPLE CANOPY FOR PHOTOSYNTHESIS IN MICROCLIMATIC FACTORS

ZHAOQUAN GAO\*, ZHIQIANG LI AND CHEN JIHU<sup>1</sup>

*Beijing Vocational College of Agriculture, Beijing 102442, P. R. China*

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### Abstract

A photosynthesis coupling model for the simulation of the effects of three-dimensional apple (*Malus domestica* Borkh. cv. 'Fuji') canopies on microclimatic factors is presented. The coupled model was developed on the basis of a biochemical model of C3 photosynthesis and a 3-D distribution of canopy radiation as determined by direct measurement. An experimental equation was used to describe the foliage photosynthetic capacity at different canopy positions. Then, the model was systematically assessed for sensitivity to microclimatic factors. The net photosynthetic rate ( $P_n$ ) of the apple leaves was highly sensitive to variations in the carbon dioxide ( $CO_2$ ) concentration at the leaf surface and was a function of photosynthetically active radiation. The experimental results showed that the 3-D distribution of  $P_n$  was similar to that of the relative radiation. These models were tested against observation data in an apple orchard (latitude 40°13' north, longitude 116°13' east, altitude 79 m). According to the model, in a given day an apple tree would fix 9 - 11 mol of  $CO_2$  on clear days and 2 - 4 mol of  $CO_2$  on cloudy days (assuming leaf area of 37.95 m<sup>2</sup> per tree).

### Introduction

Photosynthesis is the primary physiological activity of plants, and also a main factor affecting the yield and quality of fruit trees (Wagenmakers and Callesen 199, Louarn *et al.* 2008). This process depends on the photosynthesis distribution in three-dimensional canopy. How to improve the fruit tree photosynthesis has always been the core of fruit tree production. Simulation models that estimate photosynthesis are very important tools in the study of crop production and crop characteristics (González-Talice *et al.* 2013). First, light interception depends on the leaf area index (LAI) and the spatial distribution of the leaves. LAI and shoot number can be improved by increasing planting density, which can also improve the canopy radiant interception of the fruit orchard and fruit yield. However, the fruit yield often decreases in orchards that develop under dense canopies or in very dense planting systems (Lakso and Grappadalli 1993). Thus, the crucial influence of photosynthesis should be considered in any 3-D model. Differences in light exposure during the development of single leaves may modify their photosynthetic apparatus and alter the capacity for photosynthesis during leaf development (Rodríguez-Calcerrada *et al.* 2008, Williams *et al.* 2014, Janka *et al.* 2016). Leaf morphology and physiology are likely to change continuously as incident photosynthetically active radiation (PAR) decreases (Meir *et al.* 2002). If the distribution of the photosynthetic capacity among leaves is proportional to the profile of the absorbed irradiance, the equation describing leaf photosynthesis will also represent canopy photosynthesis (Sellers *et al.* 1992, Ethier and Livingston 2004). Thus, the majority of research on canopy assimilation has focused on foliage photosynthetic capacity (Amax). In this paper, leaf-scale measurements and parameterisations of the C3 model for apple leaves at different light intensities are described.

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\*Author for correspondence: < 72009@bvca.edu.cn >. <sup>1</sup>Comprehensive Business Bureau, Ministry of Water Resources, Beijing 100053, China.

### Materials and Methods

Leaf photosynthetic rate ( $A$ ) is simulated by the biochemical model of C3 photosynthesis proposed by Farquhar *et al.* (1980) and modified by others (Leuning *et al.* 1995, Bernacchi *et al.* 2003). The following equation represents net photosynthesis ( $A$ ):

$$A = \min\{A_c, A_q\} - R_d, \quad (1)$$

where  $A_c$  is the gross rate of photosynthesis limited by Rubisco activity,  $A_q$  is the gross rate of ribulose 1,5-bisphosphate (RuBP) regeneration through electron transport and  $R_d$  is dark respiration. This paper uses the model given by Leuning (1990) to describe  $g_{sc}$ .

To determine the distribution of light, a four vertical plane grid (grid section:  $0.5 \text{ m} \times 0.5 \text{ m} \times 0.5 \text{ m}$ ) was placed through the centre of the tree canopy. PAR was recorded by quantum sensors (Quantum light meter; Spectrum Technologies, East Plainfield, IL, USA) on top of the grids between 07:00 and 17:00 under a clear sky. An experiential equation was used to describe the  $A_{max}$  relationship between the top, mature, and sunlit leaves, among others in the canopy:

$$A_{\max(n)} = A_{\max} (0.083 + 0.01634x - 7.49184x^2 / 100000) \quad (2)$$

where  $A_{\max(n)}$  is the maximal rate of photosynthesis limited by Rubisco activity or RuBP regeneration of the  $i$ th grid in the canopy and  $x$  is the average relative radiation. Based on the average PAR in every grid section and the above models, it is possible to calculate the net photosynthetic rate ( $P_n$ ) in the 3-D canopy. The gross canopy photosynthetic rate of the grid ( $P_{n-c}$ ) was calculated based on the  $A_n$  and leaf area ( $L$ ) in every grid section:

$$P_{n-c} = A_n L \quad (3)$$

The diurnal variations in photosynthesis in the whole-tree canopy ( $P_n$ ) per unit ground can be calculated based on the  $P_{n-c}$  and PAR in every cell, which can be determined using the average relative radiation (%) and the radiation recorder at the meteorological station (Gao and Li 2016).

The experiment was carried out from 2014 to 2015 in Zhongri Farm of Changping District, Beijing (latitude  $40^{\circ}13'$ , longitude  $116^{\circ}14'$ , altitude 87 m). Twenty years old Fuji apple trees were used as the test materials (*Malus domestica* Borkh. cv. 'Fuji'). The planting spacing was  $5 \text{ m} \times 3 \text{ m}$ , and each tree was trained as an open-centre system. The soil of the orchard was loam soil and the soil water potential was controlled to constantly be greater than  $-10 \text{ kPa}$ .

The net photosynthetic rate ( $P_n$ ) of the leaves was measured by the portable photosynthetic system LI 6400 (LI-COR, US). The stomatal conductance ( $G_s$ ) of the leaves was measured by an AP4 porosity meter (Delta-T, UK). All of the measured samples were from the canopy, and the relevant model parameters were estimated according to the least squares method or from the predecessor data. At the end of the experiment, the total leaf area was measured in every cell of five apple trees by removing the leaves and measuring the leaf area of 3% (by weight) of the leaves. A leaf area meter (Li-3100; LI-COR) was used to measure this area from scanned images. The canopy extinction coefficient was measured with the CI-110 Canopy Analyser (CID Inc., Vancouver, WA, USA).

### Results and Discussion

The response of  $P_n$  to microclimatic factors is shown in Fig. 1. When PAR was below the light saturation point, the  $P_n$  consistently increased as the PAR increased. After the light saturation point, the  $P_n$  remained relatively static (Fig. 1A, D, E). However, the light saturation point of photosynthesis also increased with the increase in  $\text{CO}_2$  concentration (Fig. 1A) and optimum temperature ( $T_a$ ) until the light saturation point was approximately  $27^{\circ}\text{C}$  under natural conditions (Fig. 1C, D). Because the leaf  $P_n$  increased with the increase of  $\text{CO}_2$  concentration,  $P_n$  and  $\text{CO}_2$

concentrations had a significantly positive correlation (Fig. 1A, C). Initially,  $P_n$  increased rapidly with an accompanied increase in  $\text{CO}_2$  concentration, then started to become saturated when the limitation transitioned from RuBP carboxylation to RuBP regeneration (Fig. 1A, C, F). The saturation points of the  $\text{CO}_2$  concentration were smaller under the lower  $T_a$  and PAR conditions (Fig. 1A, C). The  $P_n$  response to canopy temperature was successfully simulated by the models described herein over the entire range of temperatures at various PAR, RH and  $\text{CO}_2$  concentrations (Fig. 1B, C, D). Note that the optimal temperature of the  $P_n$  shifted to a higher temperature as PAR

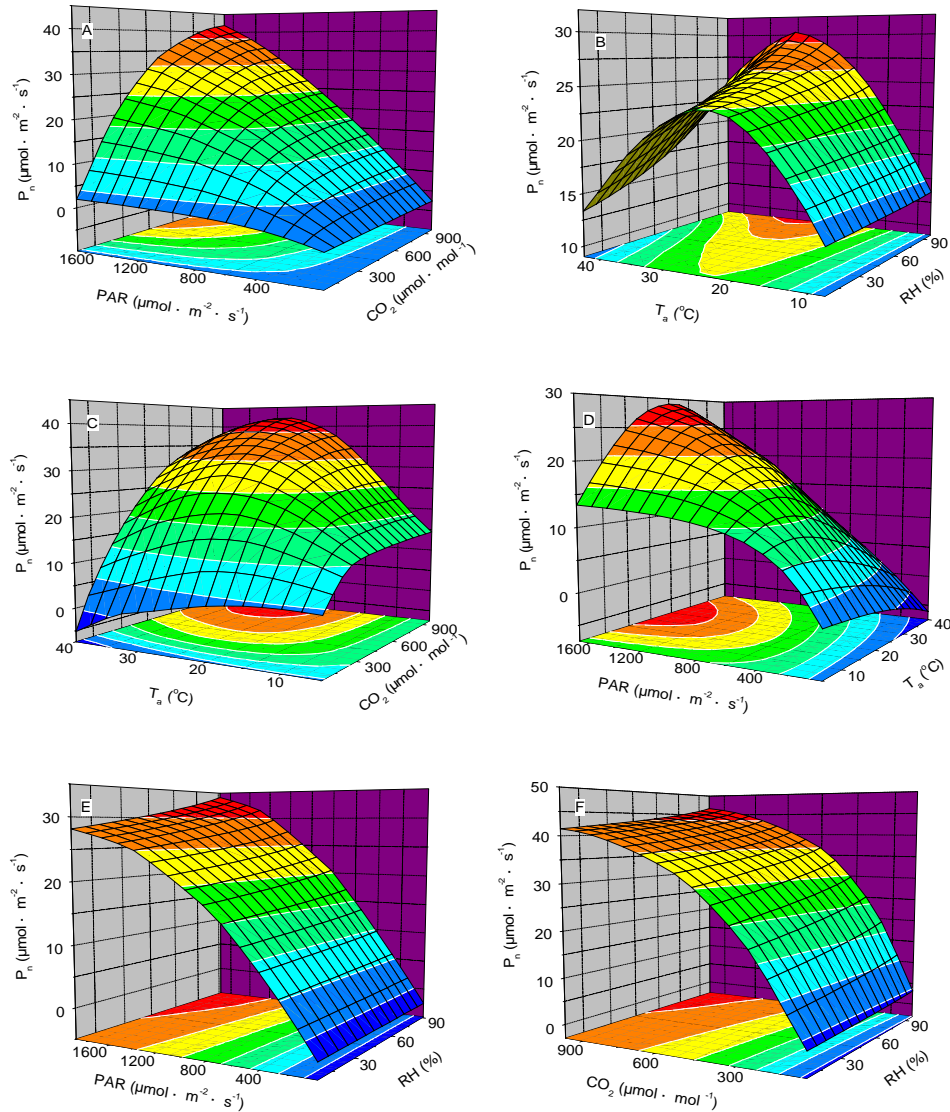


Fig. 1. Average photosynthesis rate ( $P_n$ ) responses of apple canopy under different photosynthetic active radiation, air relative humidity (RH), air temperature ( $T_a$ ) and  $\text{CO}_2$  concentration.

or  $\text{CO}_2$  increased (Fig. 1C, D). The influence of RH on  $P_n$  occurred through the stomata, which closed as the RH decreased (Fig. 1F). The data recorded in this study indicated only slight effects of RH on  $P_n$ .

One of the purposes of this study was to simulate the responses of the  $P_n$  model to microclimatic factors in real-world environments. The dynamics of the diurnal variation in photosynthesis of the 3-D canopy in an apple orchard was calculated according to the above model (Fig. 2). In addition, throughout the day,  $P_n$  showed a unimodal curve with the maximum peak occurring at about 11:00 with a gradual change at noon, indicating the “noon break” phenomenon (Fig. 2). The peak of  $P_n$  occurred later than the peak of  $G_s$  and showed an insignificant “noon break” phenomenon, which can be explained by enhanced photosynthesis due to enhanced radiation and increased temperatures at noon. Calculations indicated that the maximum  $P_n$  of the average canopy leaves throughout the day was  $12.4 \mu\text{mol}/\text{m}^2/\text{s}$ . Throughout this period, the average total diurnal photosynthesis of the experimental apple trees was about 9 - 11 mol per tree in a clear day and 2 - 4 mol in a cloudy day.

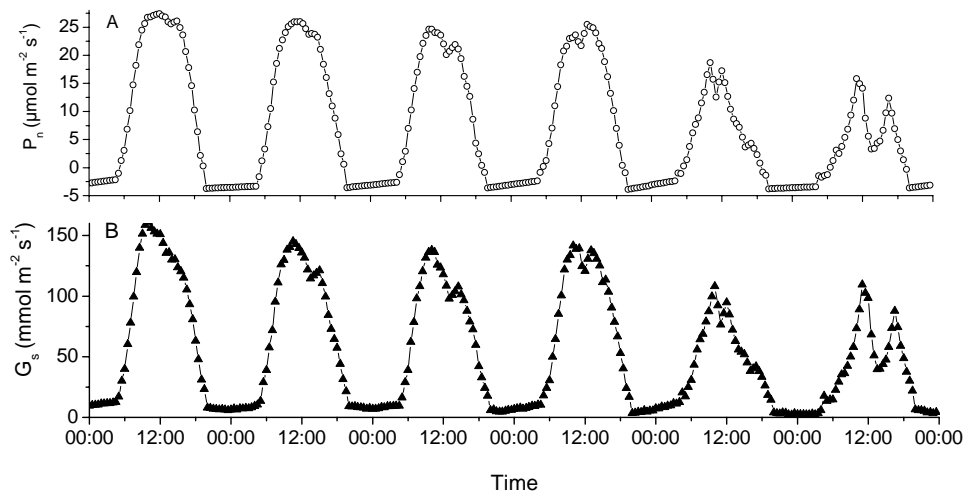


Fig. 2. Diurnal variation of average photosynthetic rate and stomatal conductance in apple canopy from June 14 - 20, 2014.

Photosynthesis is a major factor that affects crop yield and quantity. This process depends on the interception of light energy by plants. The primary finding of this study was that the leaf area and relative radiation distribution were the most important factors that influenced photosynthetic distribution. However, these parameters are very difficult to accurately simulate using mathematical models because orchards are complex agricultural systems in which the main difficulties in modelling the leaf area distribution and the light interception are linked to spatial inhomogeneity (Génard *et al.* 2000, Massonet *et al.* 2008). Inconsistencies include different shapes and heights of the trees, species, training system and rootstock. Additionally, different row-orientation and spacing give a wide range of orchard types (Nerozzi *et al.* 1997). Thus, in this study, the distribution of leaves and relative radiation were directly determined, and photosynthesis and stomatal conductance were subsequently calculated. The experimental trees were pruned in an open centre system with a smaller LAI ranging from 0.0 to  $1.2 \text{ m}^2 \text{ leaves m}^{-3}$ .

The results of this study were similar to those reported by Cohen *et al.* (1995) in a young hedgerow apple orchard.

The leaf model of photosynthesis presented by Farquhar *et al.* (1980) has been extensively used to describe carbon uptake from leaves to canopies (Sellers *et al.* 1992, Bernacchi *et al.* 2003). The disadvantage of the C3 model is that it requires rather extensive calibration of several parameters (Cannell and Thornley 1998). Fortunately, the recent development of highly sophisticated gas-exchange systems has simplified the process of estimating model parameters. To test the effect of variations in environmental factors on modelled  $P_n$ , the relationship between the simulated  $P_n$  and different PAR,  $T_a$ , RH and  $CO_2$  concentrations was plotted (Fig. 1). It was found that PAR and  $CO_2$  concentration were the main driving factors. Below the light saturation point,  $P_n$  was mainly limited by light. In contrast, above the light saturation point,  $P_n$  was mainly limited by  $CO_2$  concentration (Fig. 1). Assimilation was dependent on enzyme activities, and changes in temperature of a few degrees Celsius may have a considerable impact over the entire photosynthetic process (Bernacchi *et al.* 2003, Sage and Kubien 2007). The optimum temperature of  $P_n$  was found to be approximately 27°C under natural conditions, and it shifted to a higher temperature as the PAR or  $CO_2$  concentration increased (Fig. 2). Similar results were reported by Kattge and Knorr (2007). The model proposed in this paper requires only a few parameters which can be easily obtained by gas exchange. Therefore, it is an effective approach for studying the three-dimensional dynamic variation of apple canopies for photosynthesis in real microclimatic factors.

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