

## THREE-DIMENSIONAL SIMULATION OF CANOPY PHOTOSYNTHESIS IN AN APPLE ORCHARD

ZHAOQUAN GAO\* AND ZHIQIANG LI

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

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### Abstract

A coupled model was developed to simulate the three-dimensional (3-D) distribution and the diurnal variations in canopy photosynthesis in an apple (*Malus domestica* Borkh. cv. 'Fuji') orchard (40°13' N, 116°13' E, altitude 79 m). The coupled model was developed on the basis of a biochemical model of C<sub>3</sub> photosynthesis and 3-D distribution of canopy radiation as determined by direct measurement. Foliage photosynthetic capacity at different canopy positions was described by an experiential equation. A flat step in the top canopy of the 3-D P<sub>n</sub> distribution was observed, which decreased rapidly with the decreasing PAR caused by leaf interception. However, the 3-D distribution of the total photosynthetic rate in a unit cell was mainly depended on the pattern of the leaf area density. The diurnal variations of the P<sub>n</sub> mostly depended on net radiation, represented by double-peak curves. The values of the canopy photosynthesis increased in the morning and reached a maximum level at about 11:00, then decreased to lower values by midday. These values recovered to the second maximum level at about 15:00 and decreased again in the late afternoon, creating an asymmetrical diurnal pattern on a sunny day. The midday depressions of P<sub>n</sub> in the top canopy were expressed more strongly than those in the middle and bottom canopy regions. During a whole day (24 hrs), an apple tree (leaf area = 37.95 m<sup>2</sup>) was fixed at 9 - 11 mol of CO<sub>2</sub> on a clear day and 2 - 4 mol of CO<sub>2</sub> on a cloudy day.

### Introduction

Photosynthesis is usually the most important factor influencing the growth and development of plants. The distribution of photosynthesis within the canopy determines the productivity and quality in a fruit orchard (Cohen and Fuchs 1987, González-Talice *et al.* 2013), and the yield per area in fruit is determined from the amount of radiant energy intercepted by the tree canopy (Annandale *et al.* 2004). In fruit trees, the variability of the fruit growth and quality is related strongly to local source-sink relationships (Génard *et al.* 2000, Raphael 2015). The source leaves provide the photosynthetic carbon to fruits, and the assimilation of carbon depends on the distribution of photosynthesis within the individual fruit trees (Urban *et al.* 2003). This factor can affect fruit size, fruit colour, soluble solid content, firmness and other fruit-quality factors (Wagenmakers and Callesen 1995, Green *et al.* 2001). To accurately estimate orchard yield and quality, researchers must model the three-dimensional (3-D) distribution of photosynthesis in hedgerow tree crops using hourly time steps based on real data and sound modelling technologies. Thus, the leaf photosynthetic model and the distribution of light within the tree canopy should be determined to develop a canopy photosynthesis model in a fruit orchard. The 3-D distribution of the canopy radiation was determined by taking direct measurements in this study to facilitate its extrapolation and utility in any kind of fruit orchard.

The principal objective of this study was to develop a coupled model to simulate the 3-D distribution and the diurnal variations in canopy photosynthesis under various conditions in an apple orchard. This objective did not require the modelling of a tree canopy structure (such as leaf clumping, transmission and reflection coefficients of the leaves) or the radiation variations in the

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\*Author for correspondence.

canopy (such as latitude and position of the sun). Rather, the model was envisaged to simulate the 3-D distribution of plants within a relatively large and dense stand; this is why the calculations and measurements of the parameters were maintained as simply as possible and why more sophisticated models have not been widely used.

### Materials and Methods

The experiment was conducted in a 'Fuji' apple (*Malus domestica* Borkh. cv. 'Fuji') orchard during the 2014 - 2015 growing seasons. The orchard is on the farm of the Zhongriguoyuan (40° 13' N, 116° 13' E, altitude 80 m) in Changping County of Beijing. The 'Fuji' apple trees were planted in 1994 in north-south rows at a density of 667 plants per hectare. The planting spacing was 5 m × 3 m, and each tree was trained as an open-centre system. The framework structure of the traditional open-centre tree and principles underlying its training and pruning were reported by Kikuchi and Shiozaki (1992). To determine the distribution of light, a four vertical plane grid (grid section: 0.5 m × 0.5 m) was placed through the centre of the tree canopy. PAR was recorded with 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. From 2014 to 2015, five typical trees were measured every year; every tree was measured beyond 3 clear days between June and August and five times every day. The reference level PAR was recorded on the top of the canopy. The relative radiation (%) was calculated by incident PAR recorder and the reference level PAR. The average leaf PAR in each grid section was calculated following Johnson *et al.* (1989).

The leaf photosynthesis model is based on the mechanistic understanding of C<sub>3</sub> photosynthesis encapsulated in the description of Farquhar *et al.* (1980) and modified by others (Leuning *et al.* 1995, Urban *et al.* 2003). The equations describing net photosynthesis (*A*) were given as follows:

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

where *A<sub>c</sub>* is the gross rate of photosynthesis limited by Rubisco activity, *A<sub>q</sub>* is the gross rate of ribulose 1,5-bisphosphate (RuBP) regeneration through electron transport and *R<sub>d</sub>* is dark respiration.

An experiential equation was used to describe the relationship of *A<sub>max</sub>* between the top, mature, sunlit leaves, and others in the canopy:

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

where *A<sub>max</sub>(i)* is the maximal rate of photosynthesis limited by Rubisco activity or RuBP regeneration of the *i*th grid in the canopy and *x* is average relative radiation. Based on the average PAR in every grid section, and the above models, the net photosynthetic rate (*P<sub>n</sub>*) in the 3-D canopy could be calculated. The gross canopy photosynthetic rate of the grid (*P<sub>n</sub> - c*) was calculated based on the *P<sub>n</sub>* and leaf area (*L*) in every grid section:

$$P_n - c = P_n \cdot L \quad (3)$$

The diurnal variations in photosynthesis in the whole - tree canopy (*P<sub>n</sub> - t*) can be calculated based on the *P<sub>n</sub> - c* and PAR in every cell, which can be determined using the average relative radiation (%) and the radiation recorder at the meteorological station.

The parameters of the leaf photosynthesis model, that is, the maximum carboxylation rate, potential rate of electron transport, the rate of triose phosphate utilisation and their CO<sub>2</sub> and temperature dependence, were determined using gas-exchange data of fully expanded, mature, sunlit leaves. Randomly sampled leaves in the canopy were used to measure the stomatal conductance (*G<sub>s</sub>*) and *P<sub>n</sub>* for testing these models in the whole-tree canopy. *G<sub>s</sub>* was measured with

an AP4 Porometer (AP4; Delta-T Devices, Cambridge, UK). The  $P_n$  was measured using the Li-6400 Portable Photosynthesis System (LI 6400; LI-COR, Lincoln, NE, USA). A meteorological station was installed close to the trees that recorded the 30-min averages of incoming radiation, wind speed, air temperature ( $T_a$ ), RH and  $CO_2$  concentration. The instruments were mounted in the middle of the canopy at a height of about 1.5 m above the ground except for the wind sensor at 2.0 m above ground.

## Results and Discussion

The row cross section and horizontal projection distribution of the leaf area is shown in Fig. 1a and b. The leaf area density (leaf area per unit volume of canopy) in a 3-D plot varied from 0 to 1.2  $m^2$  leaves per  $m^{-3}$  (Fig. 1a). The vertical distribution of the leaf area indicated that the distribution mode was in the range of 0.0 to 4.0 m (high), and mostly between 1.0 and 3.0 m. The highest density of the leaf area was located within 1.5 to 2.0 m of the canopy (Fig. 1a). Below this level, the leaf area density dropped as the canopy height decreased. In the whole canopy, about 50.25% of the leaves were 1.0 - 2.0 m from the canopy, 35.67% were 2.0 - 3.0 m and 14.07% were at other distances from the canopy. No obvious difference in leaf area distribution was seen in the north-south orientation, and a basin foliage distribution was concentrated around the trunk (Fig. 1b). Therefore, a considerable amount of direct or diffuse light could penetrate through the canopy to the lower exposed leaves and fruit, which represents the distinct advantage of an open-centre system.

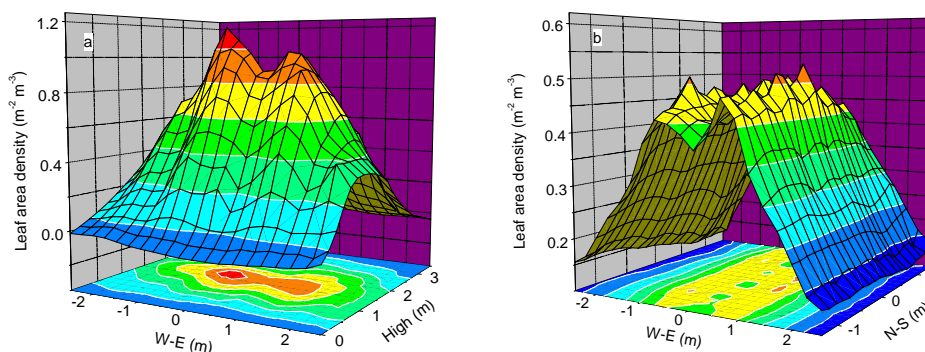


Fig. 1. Three-dimensional distribution of leaf area density in apple tree canopy.

The 3-D distribution of the relative radiation of the apple canopy is shown in Fig. 2a and b. In the vertical section, the relative radiation decreased with increasing canopy depth. The rapid depression of the relative radiation was concentrated in the middle of the canopy where the leaf area density was highest (Fig. 2a). The decline in radiation at the middle of the tree canopy was steeper, which may have been related to the north-south orientation of the rows and their smaller self-shading spatial area. Only a slight fluctuation in light distribution was observed in the north-south orientation, and less than a 5% difference was seen in the relative radiation between the two sides of the hedgerow (Fig. 2b). However, more than 36% of the relative radiation was on the sides compared to near the trunk. The distribution of the relative radiation in the apple tree canopy was highly skewed, with 24% of all grids less than 20, 51% grids less than 40 and 15.7% grids more than 80%.

A predicted 3-D distribution of the  $P_n$  in the apple canopy is shown in Fig. 3 a and b, with PAR equal to 1500  $\mu\text{mol}/m^2/s$  on the top canopy. The simulations ignored the finitude of the

boundary-layer conductance effects, and changes in the  $T_a$ , RH and leaf surface  $\text{CO}_2$  concentration. The  $T_a$ , RH and  $\text{CO}_2$  concentrations were stipulated as  $25^\circ\text{C}$ , 50% and  $380 \mu\text{mol/mol}$ , respectively. The 3-D distribution of Pn patterns was similar to that of the relative radiation (Fig. 2). A flat step was observed in the top canopy ( $> 2.5 \text{ m}$ ), and these leaves began to be saturated as the radiation exceeded the saturation point. The Pn values in the top canopy and the sunlit leaves were generally about four times greater than those in the bottom and the shaded leaves.

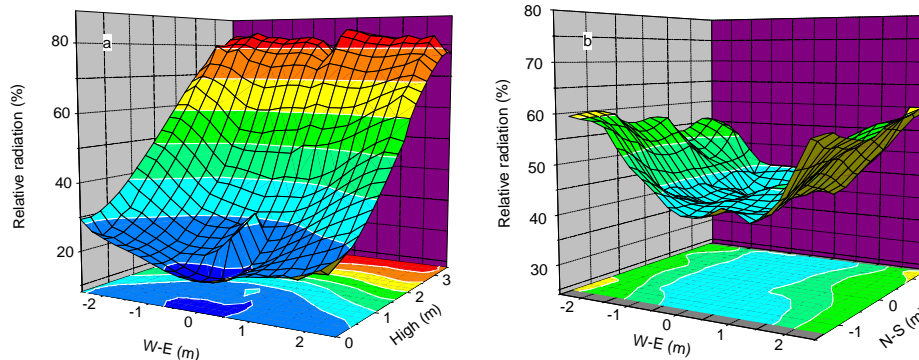


Fig. 2. Three-dimensional distribution of relative radiation in apple tree canopy.

The 3-D plot showed that Pn decreased rapidly with the decrease in radiation interception by the leaves (Fig. 3a). When the canopy height decreased from 3.0 m to 1.0 m, the average relative radiation and Pn decreased by 73 to 22.82% and by 53 to  $7.78 \mu\text{mol/m}^2/\text{s}$ , respectively. A “U” pattern of Pn was shown in a vertical section with a west-east orientation. By plotting Pn as an independent variable in the 3-D spatial distribution, we could see a more complete picture of Pn, which was very important in fruit tree pruning. The main aim of tree pruning is to remove useless shoots and leaves, and identification of these parts can be conveniently determined in a 3-D plot. Overall, the coupled model performed well in predicting instantaneous photosynthetic rates for different leaf area distribution patterns.

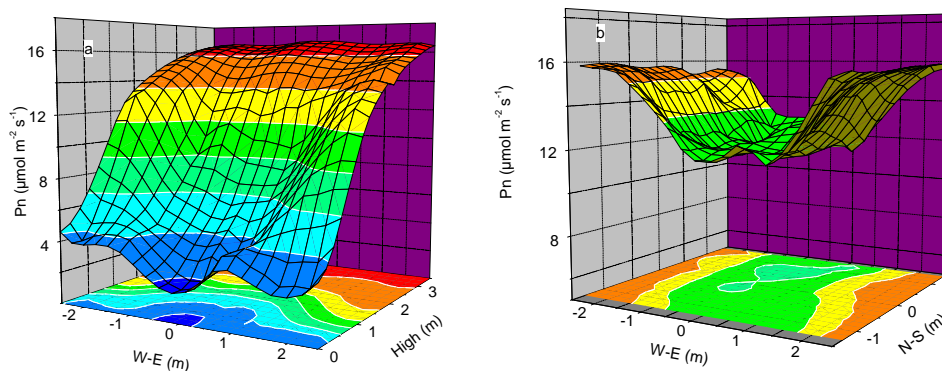


Fig. 3. Three-dimensional distribution of average leaf photosynthesis (Pn) in apple tree canopy. The standard conditions were  $\text{PAR} = 1500 \mu\text{mol/m}^2/\text{s}$ ,  $\text{RH} = 50\%$ ,  $T_a = 25$ ,  $[\text{CO}_2] = 360 \mu\text{mol/mol}$ .

One goal of this study was to examine the responses of the models of the 3-D canopy to microclimatic factors in a real environment. The simulated responses of Pn and Gs in the different canopy layers and Pn-t (the total photosynthesis of a whole tree) to the daily march of microclimatic

conditions are shown in Fig. 4. The microclimatic data used in this study were recorded by a meteorological station in an experimental orchard (LAI = 2.53) from 14 - 20 June 2014; 14 - 17 June had clear conditions and 18 - 20 June had cloudy conditions. The peak values for Ra and Ta were about  $800 \text{ W/m}^2$  and  $32^\circ\text{C}$  on clear days, respectively. On cloudy days, the Ra fluctuation was primarily caused by clouds.

The diurnal variations in Pn and Pn-t depended mostly on Ra, represented as double-peak curves (Fig. 4a, b). The values of photosynthesis increased in the morning, reached a maximum at about 11:00, decreased to lower values at midday, recovered to a second maximum at about 15:00 and decreased to early morning values in the late afternoon, creating an asymmetrical diurnal pattern on a sunny day. As shown in Fig. 4b, Pn-t varied with Ra, and showed a rough linear relationship on clear days. The diurnal course of Gs (Fig. 4c) was simulated by means of Eq. (9) and meteorological data and showed a double-peak-type curve on clear days. Gs peaked midmorning at about 9:30 and midafternoon at about 15:00. The decline in Gs at noon was caused by the RH and Ta.

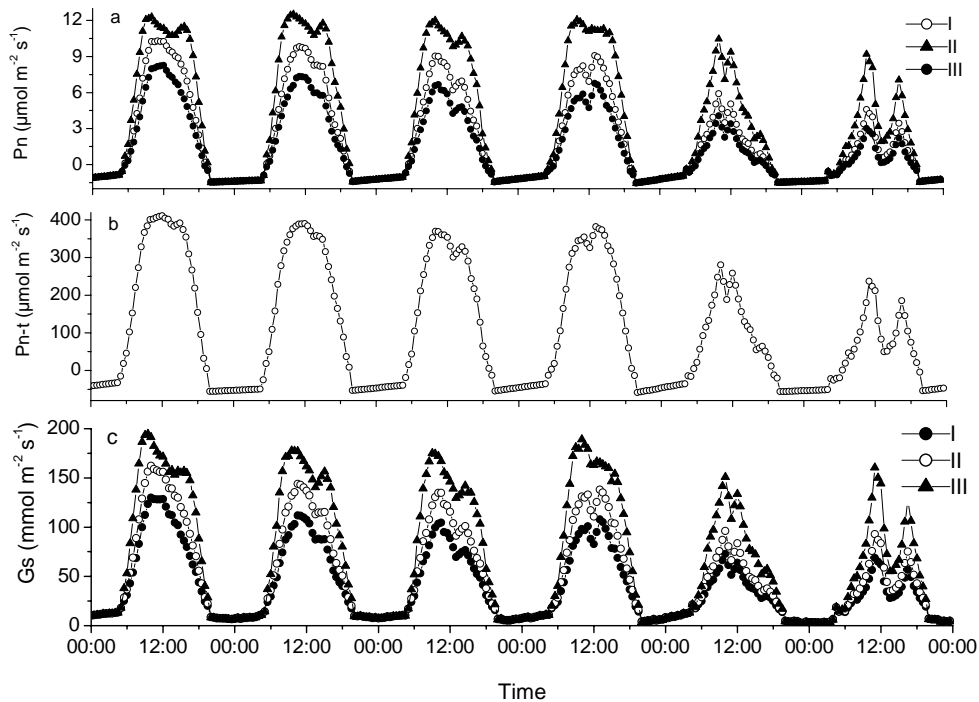


Fig. 4. The diurnal variation of average leaf photosynthetic rate (Pn), photosynthetic rate of per apple tree (Pn-t, Leaf area =  $38.23 \text{ m}^2$ ), stomatal conductance (Gs) in apple canopy from June 14th to 20th in 2014 (I, bottom canopy from 0 to 1 m; II, middle canopy from 1 to 2 m; III, upper canopy >2 m).

Midday slight depressions of Pn and Pn-t (Fig. 4a, b) may have been related to the depression of Gs (Fig. 4c), and the midday depressions in Gs were stronger than Pn. The depressions of Pn and Gs at the top canopy were more strongly expressed than at the middle and the bottom of the canopies (Fig. 4a, c). In natural canopies, both temperature and water VPD generally increase with increasing light availability from the bottom to the top of the canopy. Thus, leaves in the upper canopy are often exposed to greater heat stress and may suffer from greater water stress.

During a whole day (24 hrs), an apple tree (leaf area = 37.95 m<sup>2</sup>) fixed 9 - 11 mol of CO<sub>2</sub> on clear days and 2 - 4 mol of CO<sub>2</sub> on cloudy days. On the cloudy days of 18 - 20 June, lower Ra and Ta caused by less sunshine and more clouds led to a decrease in photosynthesis and stomatal conductance by about 70 and 55%, respectively, compared to the values on clear days. In the daytime, average stomatal conductance of the whole canopy was about 116 mmol/m<sup>2</sup>/s on clear days and 68 mmol/m<sup>2</sup>/s on cloudy days.

The correlations between measured and simulated values of Gs and Pn are shown in Fig. 5. The diurnal variations in the Pn in different layers of the apple tree canopy compared to the model predictions showed generally good agreement (Fig. 5b-d). Only a slight overestimation of Pn was found in the top canopy, which might have been caused by shading leaves and the nonlinear relationship between Pn and PAR. Pn correlation coefficients of the linear regression equations between measured and simulated values were all close to 1.0 (Fig. 5b-d). The r values for the regressions were also high. These results showed that the coupled model has the ability to predict Pn in a 3-D apple canopy. The relationship between measured (Y) and estimated (X) values of Gs (Fig. 5a) in the canopy was expressed as follows:  $Y = 1.0839 \times X$  ( $R^2 = 0.5360$ ,  $n = 232$ ).

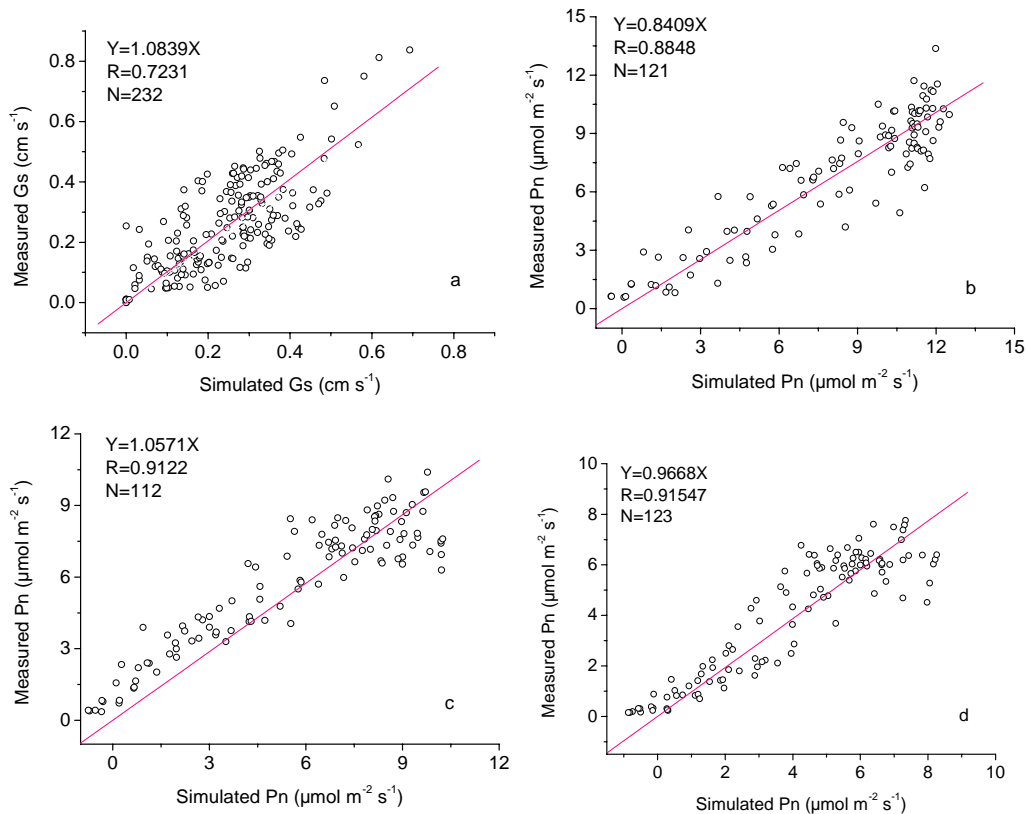


Fig. 5. The relationship between measured and simulated values of stomatal conductance (Gs) (a) and photosynthetic rates (Pn) in upper (b), middle (c) and bottom (d) canopy during clear day.

The 3-D distribution of Pn was determined by direct measurement of the 3-D distribution of PAR, leaf area and C<sub>3</sub> photosynthesis models in an apple orchard. The Gs was determined by the Pn and VPD. The parameters of the model were maintained as simply as possible to facilitate their wide

use in canopy photosynthesis simulations, especially for studying the effects of shape and pruning in fruit trees. A few models have described a 3-D distribution of photosynthesis in a fruit canopy (Cohen and Fuchs 1987, Génard *et al.* 2000, Massonnet *et al.* 2008). The present model considered the actual distribution of foliage and PAR in the canopy rather than using values from simulations; thus, the model can be applied to any kind of fruit orchard.

Fruit development essentially depends on the current photosynthesis, especially with the effects of light exposure on local leaf photosynthetic characteristics (González-Talice *et al.* 2013). In natural canopies, the photosynthetic rate generally decreases with decreasing PAR from the top to the bottom of the canopy. The parameter most critical to the performance of the photosynthesis sub-model is  $A_{\max}$ , the maximum Rubisco activity per unit leaf area, which usually must be estimated in every laboratory measurement series (e.g., PAR, CO<sub>2</sub>, Ta, RH) to obtain reasonable estimates of the other model parameters (Dang *et al.* 1998). Typically,  $A_{\max}$  increases two to four-folds from the bottom to the top of the canopy (Meir *et al.* 2002). The relationship between photosynthetic capacity and PAR was described by the experiential equation in this study. When canopy height decreased from the top to the bottom, relative radiation and  $A_{\max}$  decreased by 80% to 15%, and by 70% to 5  $\mu\text{mol}/\text{m}^2/\text{s}$ , respectively (Fig. 3a). Further, important interactions can occur between environmental factors within canopies, which can significantly modify the profiles of  $A_{\max}$  such as simultaneous acclimation to multiple stresses like heat, water, light (Baldochi *et al.* 2002).

Midday depressions of Gs and Pn have been observed in many plants (Muraoka and Koizumi 2005), and several studies have reported that lower VPD and higher temperature exposed plants to greater stress in the upper canopy, which led to stomatal closure in the upper canopy leaves (Niinemets 2007). The photosynthesis models used in the present simulations did not include any direct effects of the rate of transpiration or leaf water potential, which have often been invoked to explain the midday depression of Pn observed in the field (Niinemets 2007, Ega *et al.* 2011, Gao *et al.* 2015). In this paper, using the above models authors obtained similar results. Note that stomatal closure may be caused by a reduction in RH and Pn, which should have a positive feedback effect on stomata. The humidity-induced decrease in Gs leads to a reduction in Pn that causes a further decrease in Gs (Cottlatz *et al.* 1991, Lawson *et al.* 2014). In conclusion, the present coupled gas exchange model for the investigated apple tree canopy was capable of predicting photosynthesis in a 3-D spatial distribution, along with the diurnal variations. However, predictions of stomatal conductance were less satisfactory. The model has simple input and output parameters and can be widely used as a module in a crop simulation model.

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