

## DYNAMIC SIMULATION OF PHOTOSYNTHETIC RATES IN POTTED APPLE TREES UNDER DROUGHT STRESS

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### Abstract

Predicting photosynthetic rates ( $P_n$ ) during drought is a very important factor in fruit production. A coupled model of photosynthesis, stomatal conductance and transpiration was designed for the simulation of photosynthetic rates of apple trees under water stress. The parameters of this model were estimated using potted apple trees (*Malus domestica* Borkh. cv. 'Fuji') under gradual experimental drought stress. The results showed that  $P_n$  was driven mainly by carbon dioxide ( $CO_2$ ) concentration and stomatal conductance ( $G_s$ ) and strong interactions among various microclimatic factors and soil water potential.  $P_n$  consistently decreased with the decrease in soil water potential and decreased rapidly when soil water potential was below  $-0.6$  MPa. The diurnal course of  $P_n$  reached its peak around 10:00 and the maximum was about  $14.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  in a clear day. Based on this model, it was apparent that during a whole day, a potted apple tree with a leaf area of  $0.26 \text{ m}^2$  would fix  $115.8 \text{ mmol}$  of  $CO_2$  when soil water is not limited and fix  $21.3 \text{ mmol}$  of  $CO_2$  when soil water potential is around  $-1.5$  MPa. Comparison among simulated and measured values indicated that the coupled model was able to simulate the changes in soil water contents as well as the changes in  $P_n$  of potted apple tree under drought stress.

### Introduction

Soil moisture is one of the major factors constraining agricultural production (Boutraa 2010, Naithani *et al.* 2012). Rain water is an especially serious problem in China due to the uneven spatial and temporal distribution of rainfall. Mathematical simulation models are valuable tools for examining the dynamic changes in the photosynthetic rates ( $P_n$ ) of crops in order to understand the moisture conditions of crops, improve crop yield and quality drought-resistance and water-saving irrigation (Gao *et al.* 2009, Li *et al.* 2013). The biochemical model of  $C_3$  photosynthesis proposed by Farquhar *et al.* (1980) has been widely applied to models that range in scope from single leaf to global climate simulations (Li *et al.* 2013, Bonan *et al.* 2014). Further, this model can respond to many microclimatic factors, such as light, temperature, carbon dioxide ( $CO_2$ ) concentration and relative humidity (RH). Leaf stomatal conductance is crucial to the calculation of photosynthetic rates (Bonan *et al.* 2014, Lawson *et al.* 2014) and can be calculated using the semi-theoretical equation proposed by Leuning (1990). However, this equation cannot respond to changes in soil moisture. A number of coupled photosynthesis models were established in recent years that can respond to soil moisture changes (Yang *et al.* 2009, Gao *et al.* 2010, Keenana *et al.* 2010, Li *et al.* 2013). But these models have not been extensively used in fruit trees. This study simulates the dynamics of photosynthetic rates in potted apple trees under different soil moisture conditions by establishing a coupled model of photosynthesis, stomata conductance and transpiration that can respond to soil moisture conditions.

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### Materials and Methods

The experiment was carried out using the biennial potted apple, *Malus domestica* (Borkh. cv. 'Fuji'), planted in the Shisanling Farm, Changping District, Beijing (40° 13' N, 116° 13' E, 79 m in altitude) from 2011 - 2012. The upper and lower diameters and height of the pots were 25, 35 and 45 cm, respectively. The soil was a mixture of fine sandy soil, fermented organic fertilizer, and fertile orchard soil in a ratio of 1 : 2 : 3. Forty apple trees with the same thick and large bottom stem were selected from one hundred and twenty experimental trees and subjected to gradual drought stress from May 11 to 24 in 2011. One hundred and twenty apple trees were established in rows, with 60 cm spacing between each individual and 100 cm spacing between the rows. Before each treatment, the apple trees were sufficiently watered, and then reflective films were used to seal the pots in order to prevent water loss. A rainproof shelter was built in order to prevent rainfall from affecting the experiment. The gradual drought condition was applied from May 11 to 24 in 2011 without irrigation.

The net photosynthetic rate ( $P_n$ ) of the leaves was measured using a LI-6400 portable photosynthesis system (LI-COR, USA). The stomatal conductance of the leaves was measured using an AP4 porometer (Delta-T, the United Kingdom). The leaf water potential ( $\Psi_1$ ) was determined using a Scholander pressure chamber. The sap flow at the base of the trunk was determined using a sap flow gauge (Probe 12) (Gao *et al.* 2009). The moisture content and whole-day transpiration of the soil were weighed using a scale (ACS-S) at night. The transpiration per fruit tree was determined according to the results of the sap flow gauge and the scale. The relevant model parameters were estimated using the least square method or obtained from previous data (Farquhar *et al.* 1980, Leuning 1995).

Farquhar *et al.* (1980) proposed a biochemical model for simulating the  $P_n$  of single leaves according to the biochemical mechanism for photosynthesis of  $C_3$  plants, and other researchers have improved upon this model (Leuning 1995). The equation for calculating  $P_n$  is:

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

where  $A_c$  is the photosynthetic rate restricted by the activity of Rubisco,  $A_q$  is the photosynthetic rate restricted by the regeneration rate of RuBP, and  $R_d$  is the dark respiration rate of leaves. The stomatal conductance for carbon dioxide ( $G_{sc}$ ) must be determined to simulate  $P_n$  (Farquhar *et al.* 1980).

The semi-mechanism model for  $G_{sc}$  was improved by Leuning (Leuning 1995) and was used to calculate  $G_{sc}$  in this paper.

$$G_{sc} = G_0 + \frac{a_1 P_n}{(c_s - \Gamma)(1 - D/D_0)} \quad (2)$$

where  $G_{sc}$  is the stomatal conductance for  $CO_2$ ,  $a_1$  and  $D_0$  are constants,  $D$  is the vapor pressure deficit and  $\Gamma$  is the carbon dioxide compensation point. It was assumed that  $G_s = 1.56 G_{sc}$  where  $G_s$  is the stomatal conductance for water vapor.

In order to account for the effects of  $\Psi_1$  and soil water potential ( $\Psi_s$ ) on  $G_s$ , Eq. 1 was revised and two restriction equations were added:

$$G_s = 1.56 G_{sc} \cdot G(\Psi_1) \cdot G(\Psi_s) \quad (3)$$

where  $G(\Psi)$  is described by the following equation (Jones 1992):

$$G(\Psi) = 1 - \left| \frac{\Psi}{b_1} \right|^{b_2} \quad (4)$$

where  $b_1$  and  $b_2$  are empirical constants.  $\Psi_1$  was calculated according to the Penman-Monteith equation for transpiration (1965) and the resistance model for water transport (Monteith 1965, Jones and Tardieu 1998), and  $G(\Psi_s)$  was simulated using the empirical equation fitted by the experimental results:

$$G(\Psi_s) = a + b \exp(\Psi_s), \quad (5)$$

where  $a$  and  $b$  are constants.

The photosynthesis model was validated according to the measured and simulated values of the photosynthetic rates of the leaves of the potted apple trees subjected to gradual drought stress (Gao *et al.* 2009). The soil water potential was determined by the leaf water potential of the slips on the roots (Kavanagh *et al.* 2007). The leaves were tightly packed using plastic bags during night before measurement in order to ensure the consistency between the leaf water-and the soil water potential; the leaf water potential was measured at 13:00 for each day.

### Results and Discussion

Under different soil moisture conditions, the average  $P_n$  of the apple leaves decreased as the soil water potential decreased (Fig. 1A-D). When the soil water potential was higher than  $-0.6$  MPa,  $P_n$  changed slightly as the soil water potential changed; when the soil water potential decreased from  $-0.6$  to  $-1.6$  MPa,  $P_n$  decreased almost linearly; after the soil water potential dropped below  $-1.5$  MPa,  $P_n$  gradually approached zero. The  $P_n$  could reach  $12 - 14 \mu\text{mol m}^{-2} \text{s}^{-1}$  and was  $10 - 12 \mu\text{mol m}^{-2} \text{s}^{-1}$  under mild drought.  $P_n$  increased as radiation increased (Fig. 1A). This was because the efficiency of electron transfer in photosynthesis increased as radiation increased. Under sufficient soil moisture conditions,  $P_n$  increased as radiation increased without the occurrence of the light saturation point. However, when the soil moisture content decreased,  $P_n$  increased at a slower rate as the radiation increased and light saturation gradually increased (Fig. 1A).  $\text{CO}_2$  concentration is the driving factor for photosynthesis and when  $\text{CO}_2$  concentration was lower than  $600 \mu\text{mol/mol}^{-1}$ ,  $P_n$  increased linearly as  $\text{CO}_2$  concentration increased, and increased at a slower rate after exceeding  $600 \mu\text{mol/mol}$  (Fig. 1B).

Because the effect of stomatal humidity on photosynthesis is transmitted via stomatal conductance, and its effect on stomata is not very intense, the effect of humidity on photosynthesis was not very significant (Fig. 1C). However, temperature affects the activity of enzymes in photosynthesis and has a significant effect on photosynthesis. As soil draught increased, the optimum temperature decreased constantly (Fig. 1D).  $\Psi_s$  had strong interactions with different microclimatic factors, and as the soil water potential increased, these interactions became stronger (Fig. 1). This indicates that not only the effect of drought on the photosynthesis of apple trees but also the interactions of microclimatic factors, should be taken into consideration.

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 potted apple trees (the leaf area per tree was  $0.26 \text{ m}^2$ ) under gradual drought conditions (Fig. 3) was calculated according to the above model. The changes in radiation, temperature, and humidity in the entire period of drought are shown in Fig. 2. The simulation of the soil water potential indicated that, as the soil moisture content gradually decreased, the soil water potential declined at a relatively constant rate as the moisture content decreased (Fig. 3A). The leaf water potential also decreased as the soil moisture content decreased, but the range of the amplitude of the diurnal variation gradually decreased (Fig. 3A) which resulted from the decline in diurnal transpiration.

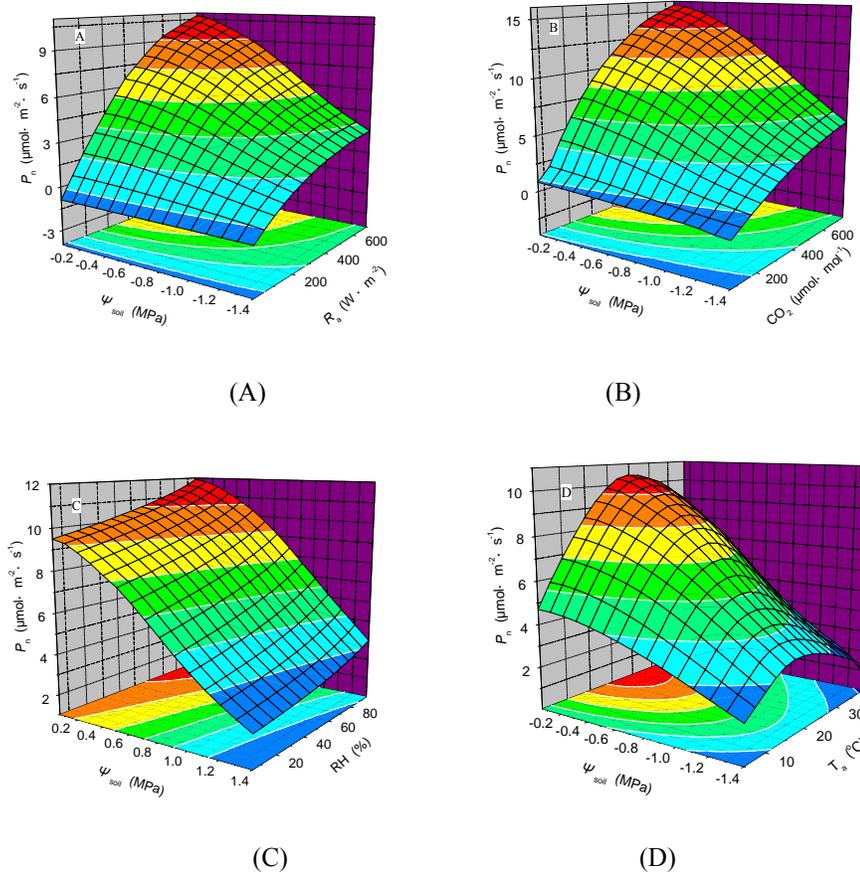


Fig. 1. The responses of leaf photosynthesis ( $P_n$ ) to (A) net radiation ( $R_a$ ), (B) air  $\text{CO}_2$  concentration ( $\text{CO}_2$ ), (C) air relative humidity (RH) and (D) air temperature ( $T_a$ ) under drought. The range of  $R_a$  was from 0 to  $700 \text{ W m}^{-2}$ , RH from 5 to 95,  $T_a$  from 5 to  $40^\circ\text{C}$ ,  $\text{CO}_2$  concentration from 50 to  $1000 \mu\text{mol mol}^{-1}$  and leaf water potential ( $\Psi_l$ ) from 0 to  $-1.6 \text{ MPa}$ . The standard conditions were  $R_a = 600 \text{ W m}^{-2}$ , RH = 50%,  $T_a = 25^\circ\text{C}$ ,  $[\text{CO}_2] = 360 \mu\text{mol mol}^{-1}$ ,  $\Psi_l$  being calculated by transpiration and water transport models.

$P_n$  decreased as the soil moisture content declined but not significantly under mild drought (Fig. 3B). In addition, throughout the day,  $P_n$  showed a unimodal curve with the maximum peak occurring at about 10:00 a.m. with a gradual change at noon indicating a “noon break” phenomenon. The peak of  $P_n$  occurred later than the peak of  $G_s$ , and showed an “noon break” phenomenon which was primarily due to the fact that the enhanced radiation and higher temperature at noon could cause reductions in photosynthesis (Fig. 2). Calculations indicated that the maximum  $P_n$  of the leaves throughout the day was  $14.6 \mu\text{mol.m}^{-2} \text{ s}^{-1}$  and throughout the period of drought, the average total diurnal photosynthesis of the experimental apple trees decreased from  $115.8 \text{ mmol}$  per tree to  $21.3 \text{ mmol}$  per tree.

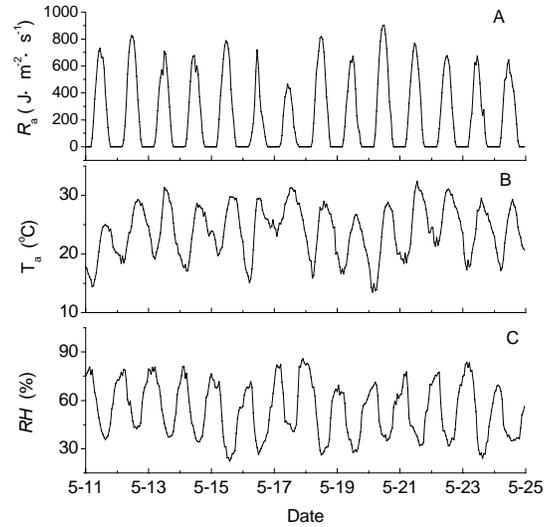


Fig. 2. The diurnal variations of (A) radiation ( $R_a$ ), (B) air temperature ( $T_a$ ) and (C) relative humidity ( $RH$ ) in the apple orchard from May 11 to 24 in 2011.

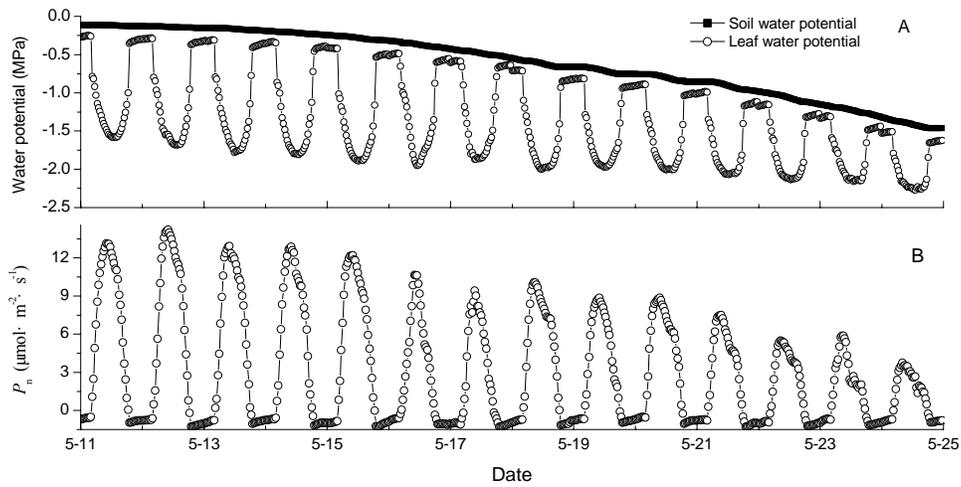


Fig. 3. The simulation of diurnal variation of (A) soil water potential, leaf water potential, (B) leaf photosynthetic rates ( $P_n$ ) for potted apple trees.

The measured and simulated values of the soil water potential and the leaf water potential were highly consistent under gradual drought stress ( $R = 0.9657$  and  $0.9263$ ) indicating that this model can be used to simulate the overall water loss by transpiration and leaf moisture conditions of the potted apple trees (Fig. 4A-B). The overall trends and dynamic diurnal variations in the simulated and measured values of the photosynthesis of the potted apple trees were consistent ( $R = 0.94$ ) under gradual drought stress indicating that this model can be used to accurately simulate the effect of different soil moisture conditions on the dynamics of photosynthesis of the experimental trees (Fig. 5). However, the maximum values of the measured photosynthesis generally occurred around 9:00 a. m., about one hour earlier than those of the simulated photosynthesis and the “noon break” phenomenon was also very obvious (Fig. 5) which was possibly caused by the negative feedback of photosynthetic products. In addition, the actual  $P_n$  was lower than the simulated values under later drought stress (Fig. 5), possibly because the photosynthetic systems of the leaves were destroyed due to increased drought.

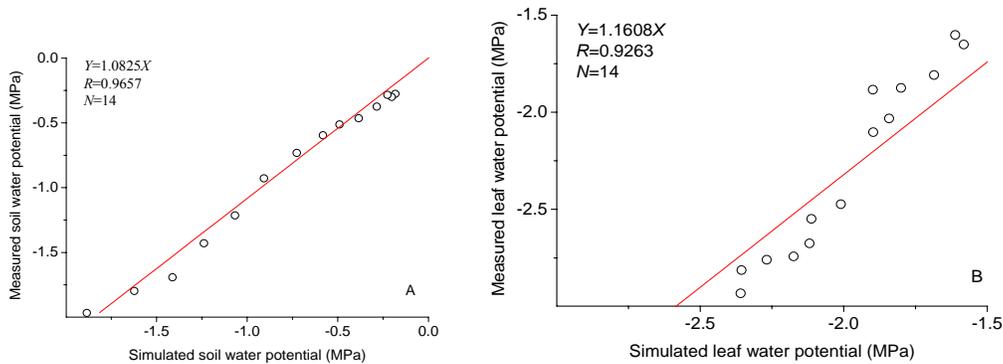


Fig. 4. The relationship between measured and simulated soil water potential (A) and leaf water potential (B) of potted apple tree with gradually drought.

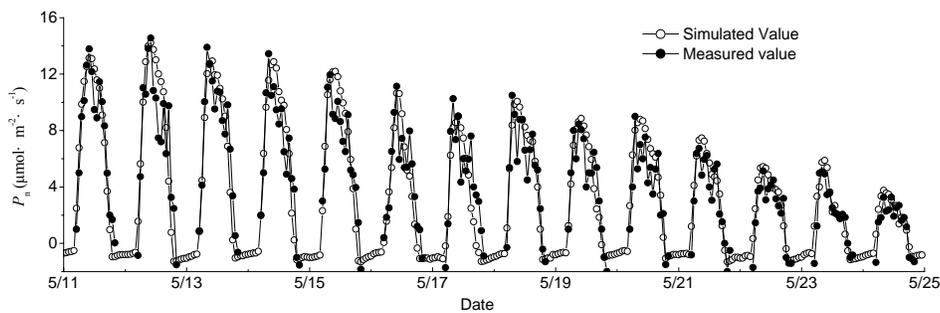


Fig. 5. The diurnal variation measured and simulated photosynthetic rate of potted apple tree under gradual drought.

Photosynthesis and transpiration are the major physiological processes affecting crop yield and quality. These two processes depend on the interception of light energy by plants (Green *et al.* 2003, Pieruschka *et al.* 2010) and are regulated by the size of stomata (Boutraa 2010, Naithani *et al.* 2012, Damour 2010, Bonan *et al.* 2014, Lawson *et al.* 2014). Building a coupled model of photosynthesis, stomata, and transpiration under different moisture conditions cannot only accurately simulate the gas exchange dynamics of plants but also provide information for water-saving irrigation. Generally, after plant leaves receive a certain amount of light, the stomata will open and photosynthesis begins and water vapor diffuses (Pieruschka *et al.* 2010). As transpiration intensifies, the leaf water potential will decline, thus decreasing photosynthesis (Ega *et al.* 2011). In this study, the feedback regulation of  $G_s$  by photosynthesis was simulated using the semi-mechanism model (Eq. 2) proposed by Leuning (1995) and the feedback regulation of  $T_r$  was realized by the steady-state flow model and the regulation module for leaf water potential (Eq. 3) (Jones and Tardieu 1998). The coupled model cannot always respond to the effect of drought stress on gas exchange (Green *et al.* 2003, Tuzet *et al.* 2003, Gao *et al.* 2010, Li *et al.* 2014) and this problem was solved by adding the modules for regulation of stomatal conductance by soil and leaf water potential (Eq. 3) in this paper. Although the model proposed in this paper also used the Penman-Monteith equation to calculate transpiration, the simulation was carried out using leaves as units. It also incorporates a photosynthesis module. The simulation results are more accurate than using canopies as units (Gao *et al.* 2009). The model can also be used to compare the water use efficiencies of different parts of canopies. Calculations indicated that the model established in this paper adequately simulated the dynamic changes in the photosynthetic rates of the potted apple trees under different moisture conditions (Fig. 5). This model is defined by a few parameters that can be easily obtained by gas exchange and water potential measurements providing an effective technical means for the photosynthetic dynamics and water-saving irrigation of fruit trees under drought stress. It needs to be noted that field fruit trees respond differently to the content of water from potted fruit trees. First, both the root growth and nutrient absorption of potted fruit trees are limited. This limitation has negative effects on the photosynthesis of leaves which would amplify over the years. Secondly, field fruit trees are often threatened by droughts which typically start from surface roots and gradually extended downward (Yang *et al.* 2009).

The stomata plays a vital role in regulating  $\text{CO}_2$  exchange and can respond to changes in environmental conditions such as radiation, temperature, humidity,  $\text{CO}_2$  concentration and soil moisture (Naithani *et al.* 2012, Hetherington and Woodward 2003, Ega *et al.* 2011, Lawson *et al.* 2014). A good number of reports have indicated that when soil moisture is deficient, the roots will produce significant amounts of ABA. When ABA enters the leaves along the transpiration stream partial stomatal closure and reduced transpiration, and mild drought can produce a significant effect on stomata (Hetherington and Woodward 2003). In this study, this regulatory mechanism was simulated using the empirical equation for  $G_s$  and soil water potential. Moreover, the decline in soil water potential could also result in a decline in leaf water potential and a further decline in  $G_s$  (Eq. 4). The validation results indicated that the measured and simulated values of  $P_n$  of the potted apple trees under different moisture conditions were highly consistent (Fig. 5) demonstrating that the model design and parameter estimation in this paper were reasonable. Because the parameters for this model can be easily obtained using conventional parameters for gas exchange and equipment for moisture studies, this model can be easily used to study the effect of soil moisture on the photosynthesis of other crops. However, Fig. 5 also indicated that the peaks of the simulated diurnal variations occurred about one hour later than those of the measured diurnal variations. One possible explanation is that the roots of the apple trees absorbed some water at night and stored it in the trunks, branches and roots, thus easing the deficiency in leaf moisture in the morning (Jones and Tardieu 1998). In addition, the “noon break” phenomenon of the diurnal variation in the measured

$P_n$  was more significant than that in the simulated values, possibly because the accumulation of the photosynthetic products of the leaves resulted in a negative feedback effect which failed to be considered in this paper.

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