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Research Article

Dynamic Simulation of Transpiration and Water Use Efficiency in Apple Tree Canopies

Zhaoquan Gao, Shezhang Feng and Zhiqiang Li
Beijing Vocational College of Agriculture, Beijing 102442, P.R. China

Abstract: We developed a model that couples canopy stomatal conductance, transpiration and canopy Water Use Efficiency (WUE) in an apple orchard (*Malus pumila* Mill. 'Fuji'). The model used the Penman-Monteith equation to compute effects of the interaction between canopy transpiration rate (T_r) and microclimatic factors. For convenience, WUE was expressed as the ratio of photosynthesis to transpiration rate; we simulated the relationship between WUE and microclimatic factors. Models developed were tested against observational data from an apple orchard (latitude 40° 13' N, longitude 116° 13' E, altitude 79 m). The models and parameters well simulated T_r and WUE in apple trees. The mathematical simulation showed strong interactions among various microclimatic factors and indicated that transpiration was driven mainly by Vapor Pressure Deficit (VPD) and stomatal conductance. During the course of 1 day, transpiration increased (decreased) as net radiation and stomatal conductance increased (decreased). Maximum transpiration rates of experimental trees (leaf area index, LAI = 2.53) were about 8 mmol/m^2/s on clear days and about 3 mmol/m^2/s on cloudy days. Over 24 h, an apple tree (leaf area = 37.95 m^{-2}) lost 50 to 70 L of water in clear weather and about 15 L in cloudy weather. On clear days, the peak of WUE was reached early after sunrise; it then decreased to a stable level maintained through most of the day until falling to zero at sunset.

Keywords: Apple, canopy, model, PAR, transpiration, water use efficiency

INTRODUCTION

Water vapor exchange between plant surfaces and the atmosphere is the most important component to agricultural production (Naithani *et al*., 2012). The Penman-Monteith equation has been widely used to estimate plant transpiration from intercellular to canopy (Green *et al*., 2003; Pereira *et al*., 2006; Teixeira *et al*., 2008). This equation is based on net radiation and the resistance from cell to air. The parameters of canopy resistance and stomatal resistance needed for the Penman-Monteith equation are difficult to acquire. For convenience, WUE is expressed as the ratio of photosynthesis to transpiration rate, based on fundamentals underlying leaf gas exchange (Hsiao and Xu, 2000). Although the equation is simple, many factors in the equation have major impacts on WUE, such as soil water moisture, air relative humidity, light interception, leaf temperature and canopy characteristics (Alarcón *et al*., 2006).

Apples are very important economic crops, with orchards covering nearly 5,000,000 ha worldwide. Many orchards are in arid or semiarid areas. Modeling studies of regional water balance in dry regions can assess the importance of orchards in water exchange. Transpiration in fruit trees has been modeled many times, especially for predicting diurnal variation in water exchange (Green *et al*., 2003; Pereira *et al*., 2006). Little literature is available on the fluxes of water loss for apple trees exposed to varying microclimate factors.

The objective of this study was to develop a coupled model to simulate the variation of canopy transpiration (T_r) and WUE in a natural environment including the interaction between T_r, WUE and microclimatic factors, such as net radiation flux density (R_a), air Relative Humidity (RH), air temperature (T_a), air CO_2 concentration (CO_2) in order to simulate diurnal variations of T_r and WUE in an apple canopy under different weather conditions.

Models and methods:

Transpiration model: Evaporation of water from a plant can be effectively modeled using the Penman-Monteith equation (Monteith, 1965):

$$\lambda E = \frac{sR_n + 0.93\rho c_p D_a / r_a}{s + 0.93\gamma(2 + r_s / r_a)} \quad (1)$$

Corresponding Author: Zhaoquan Gao, Beijing Vocational College of Agriculture, Beijing 102442, P.R. China, Tel.: 13810459871

where, E is the transpiration rate per unit leaf area, R_n is the net radiation flux density absorbed by the leaf, ρ is air density, c_p is specific heat capacity of air, λ is the latent heat of evaporation of water, γ is the psychrometer constant, s is the slope of the curve relating saturation vapor pressure to temperature, D_a is the vapor pressure deficit of the air, r_a is the leaf boundary layer resistance and r_s is stomatal resistance. Use of the factor 0.93 is based on the assumption that boundary layer resistance for vapor is 0.93 times that of sensible heat (Caspari *et al*., 1993). Leaf boundary layer resistance (r_a) was calculated from the empirical relation, derived by Perrier (1975).

Darcy's law was used to simulate sap flow within an apple tree, which was described by following equation (Jones and Tardieu, 1998; Dauzat *et al*., 2001):

$$E = \frac{\Psi_s - \Psi_l}{R_{sp}} \tag{2}$$

where, Ψ_s and Ψ_l are soil and leaf water potential, R_{sp} is the resistance of the whole soil-plant pathway. Maximum soil water potential under optimal conditions is zero, so that:

$$\Psi_l = -E \times R_{sp}$$

Water use efficiency model: At the physiological level, WUE may be defined as the ratio of photosynthesis and transpiration rate, which is difficult to monitor over long periods and is sensitive to changes in environmental factors. Canopy WUE is defined as the ratio of canopy photosynthetic rate (P_n) to canopy transpiration rate (Warren and Adams, 2006):

$$WUE = \frac{P_n}{T_r} \tag{3}$$

The canopy photosynthesis is simulated by C_3 photosynthesis model (Farquhar *et al*., 1980; Gao *et al*., 2012), Using the above models, we can calculate effects of environmental factors on WUE.

MATERIALS AND METHODS

The experiment was carried out in a 'Fuji' apple (*Malus domestica* Borkh. cv. 'Fuji') orchard from 2004 to 2007. The orchard is in the farm of The Ming Tombs (latitude 40° 13′ north, longitude 116° 13′ east, altitude 79 m) in Changping county of Beijing. The 'Fuji' apple trees were planted in 1985 in south-north rows at a density of 667 plants/ha. The planting spacing was 5×3 m. Each tree was trained as an open-center system. The framework structure of the traditional open-center tree and principles underlying its training and pruning were reported by Kikuchi and Shiozaki (1992). The soil of the orchard was loam soil and soil water potential was always controlled greater than -10 kPa.

Leaf stomatal conductance was measured by an AP4 Porometer (AP4, Delta-T, Cambridge, UK). Leaf net photosynthetic rate was measured by the Li-6400 Portable Photosynthesis System (LI 6400; LI-COR, Inc., Lincoln, NE, USA). Canopy was simulated by the model of Gao *et al*. (2012) In order to test the transpiration models the sap flow at the base of the tree stem was measured routinely using the Compensation Heat-pulse Technique (Swanson and Whitfield, 1981). In the trunk 2 sets of probes were installed into parallel holes drilled radially into the tree stem at heights of about 0.6 m above the ground. Sap velocity was measured at radial depths of 10 and 30 mm following the procedure given by Green and Clothier (1988) and using the theoretical calibrations of Swanson and Whitfield (1981) to account for the probe-induced effects of wounding. Volume sap flow rates were calculated in the tree stem by integrating the radial profile of sap velocity over the sapwood cross-section. The total leaf area of 10 apple trees was measured at the end of the experiment by removing all the leaves and measuring the leaf area of 3% (by weight) of the leaves using the scanned images with Optimas software (v6.5, Media Cybernetics, Silver Spring, MD).

A meteorological station was installed close to the trees recording 30 min averages of incoming radiation, wind speed, air temperature, relative humidity 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 m above the ground. The canopy radiant interception was simulated by a multi-layer canopy model. The radiant flux density absorbed in canopy was assumed to be 65% of the top canopy radiant flux density, with 10% reflected to the atmosphere and 25% on the ground. The leaves in any given layer were regarded as being exposed to the same air temperature, relative humidity, CO_2 concentration and wind speed. Leaf temperature was assumed equal to air temperature. Radiation was the only variable.

We presented 3D plots to describe the effects of microclimatic factors and their interaction. All the parameters were estimated with a nonlinear optimization technique or from previous reports.

RESULTS

When R_a was <200 W/m^2, T_r increased sharply with increasing R_a, which is connected to the increase in G_s (Fig. 1B and C). A higher leaf temperature results in more dramatic canopy transpiration. However, after optimum leaf temperature was exceeded, G_s decreased with increasing leaf temperature. The optimum T_a for T_r was higher than that for G_s due to the increase in

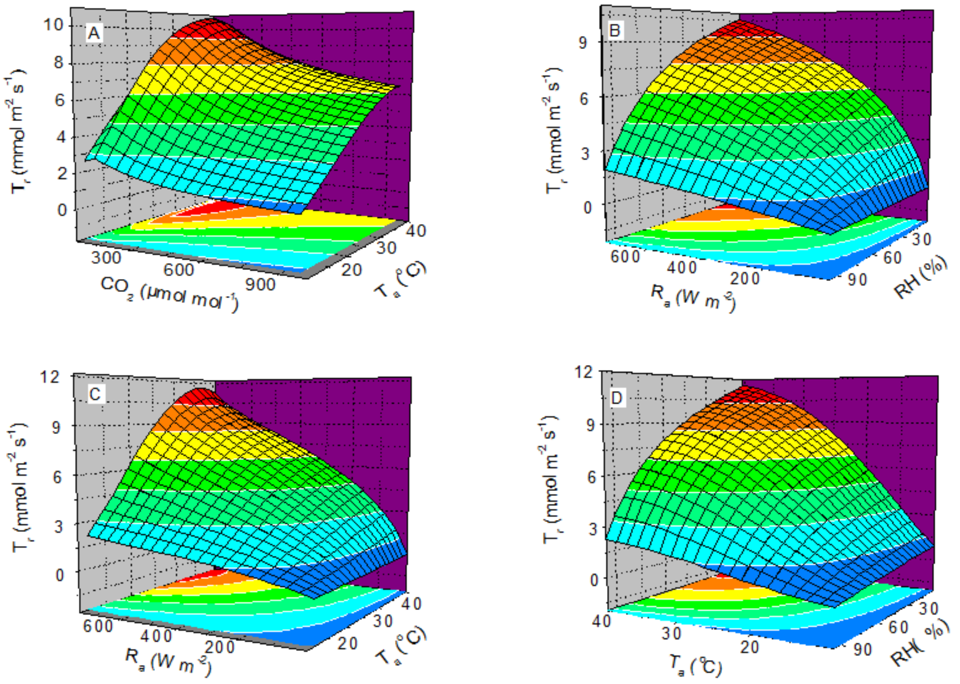

Fig. 1: The response of transpiration rate (T_r) per unit ground in apple orchard to net radiation flux density (R_a), air Relative Humidity (RH), air temperature (T_a) and air CO_2 concentration (CO_2)

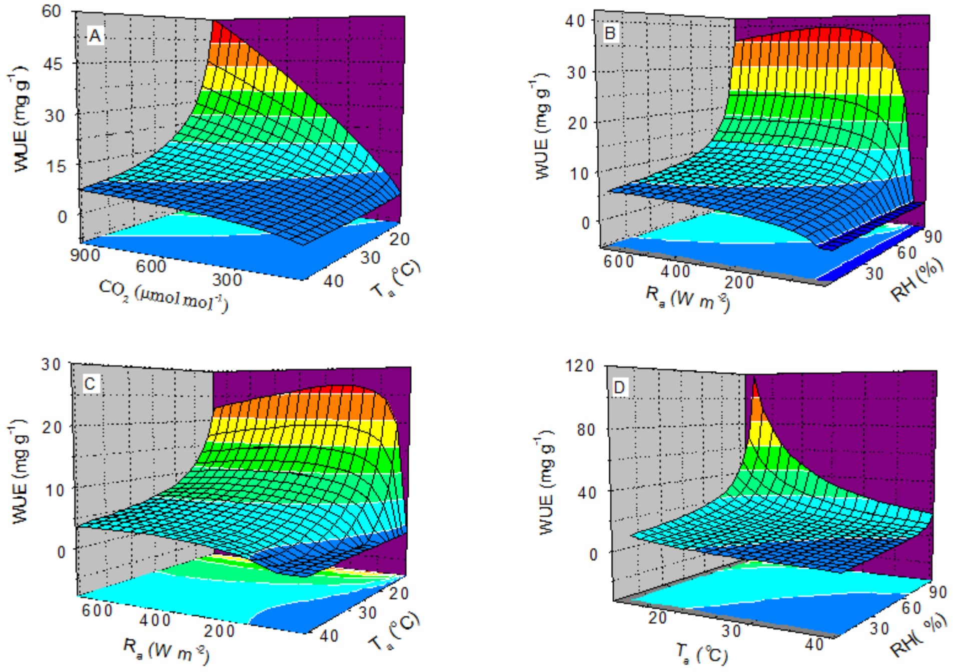

Fig. 2: The response of Water Use Efficiency (WUE) per unit ground in apple orchard to net radiation flux density (R_a), air Relative Humidity (RH), air temperature (T_a) and air CO_2 concentration (CO_2)

Vapor Pressure Deficit (VPD). The optimum T_a for T_r was >40°C under low radiation conditions and 37°C under high radiation conditions (Fig. 1B and C). This difference was caused by the feedback from photosynthesis to stomatal conductance.

T_r increased rapidly when CO_2 concentration decreased from 350 to 100 μmol/mol (Fig. 1A). However, T_r decreased when CO_2 concentration decreased from 100 to 0 μmol/mol because of the feedback from photosynthesis to stomatal conductance.

When CO_2 concentration was >400 μmol/mol, T_r became slightly reduced with increasing CO_2 concentration. VPD was the driving factor for T_r, which increased linearly as RH decreased from 100 to 0 (Fig. 1B and D).

From Eq. (3), canopy WUE was completely determined by canopy photosynthesis (P_n) and transpiration (T_r). As a result, WUE and CO_2 concentration showed a nearly linear relationship (Fig. 2). As shown in Fig. 2B and D, WUE was highly sensitive to RH, especially when RH was in the range of 50-95%. RH affects WUE both through the physical process of evaporation from the canopy and by acting upon stomatal resistance to CO_2 exchange. These effects produce the non-linear relationship depicted in Fig. 2B and D. Both P_n and T_r increased with increasing R_a; when R_a was >200 W/m^2 (Fig. 2B and C), P_n increased exponentially as R_a increased from 0 to 200 W/m^2. As a result, WUE had a linear relationship with R_a only when R_a increased from 0 to 200 W/m^2. Due to the feedback of T_r to P_n, there was a slight decrease in WUE when R_a was >600 W/m^2.

Figure 2A, B and D shows the effect of T_a on WUE when T_a varied from 10 to 40°C. It was apparent that the effect of T_a became stronger when T_a, CO_2 concentration and RH were all high. Although there were optimum temperatures for G_s, T_r and P_n, WUE was linearly related to T_a. An increase in T_a caused a linear decrease in WUE because the increase in T_r was steeper than that of P_n with increasing T_a.

Diurnal variations in canopy transpiration (T_r) were simulated in Fig. 3 (LAI = 2.53). The diurnal change in T_r was similar to those of R_a and P_n, following monotonic curves on clear days. The microclimatic data used were from 14 to 20 June 2007; conditions were clear from June 14th to 17th and cloudy June 18th to 20th. The maximum T_r values for experimental trees (LAI = 2.53) were about 8 $mmol/m^2/s$ on clear days and about 3 $mmol/m^2/s$ on cloudy days. Over 24 h, one apple tree (leaf area = 37.95 m^2) lost 50 to 70 L of water on clear days and about 15 L on cloudy days. In general, over 1 day, T_r was 300% higher under clear conditions than under clouds.

The pattern of variation in WUE from June 14th to 17 th in 2007 is shown in Fig. 4. On clear days, a typical WUE pattern was found in most measurements. The peak of WUE was reached early after sunrise, decreasing to a stable level and maintaining this during most of the day, until finally decreasing to zero at sunset. RH was much larger and T_a smaller in the early morning than during the remainder of the day, so that there was a peak of WUE in the early morning. Both P_n and T_r increased with R_a, so that a stable level existed across almost the whole day. On the cloudy days of 19 and 20 June, lower R_a and T_a due to reduced sunshine and increased cloudiness led to a decrease in photosynthesis and water loss by about 70 and 60%, respectively, compared to values on clear days. Thus the WUE on clear days was >25% higher than on cloudy days.

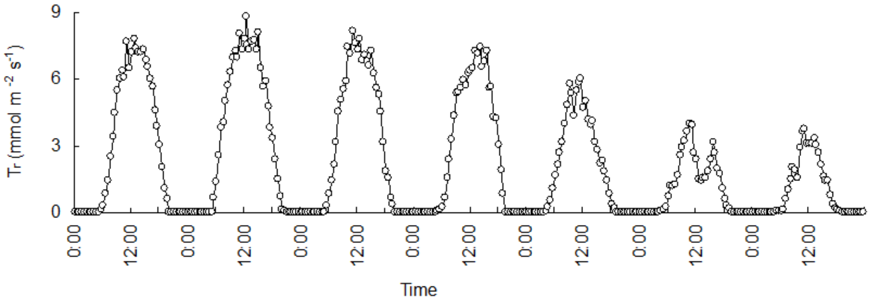

Fig. 3: The diurnal variation of transpiration rate (T_r) per unit ground in apple orchard from June 14th to 20th (LAI = 2.53)

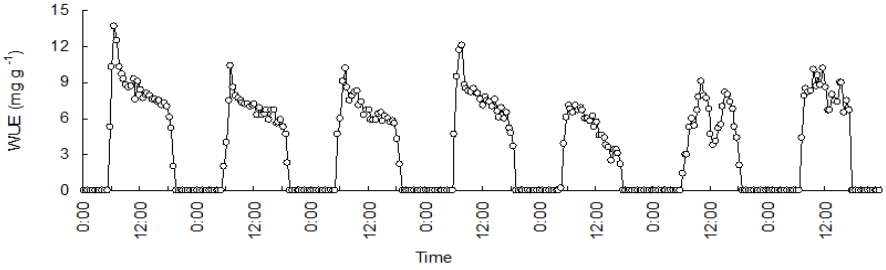

Fig. 4: The diurnal variation of Water Use Efficiency (WUE) per unit ground in apple orchard from June 14th to 20th (LAI = 2.53)

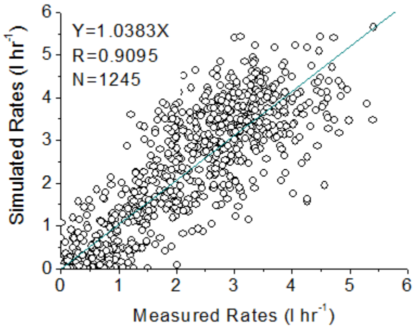

Fig. 5: The relationship between measured sapflow and simulated transpiration values in apple canopy

There is a satisfactory correspondence between measured and simulated values of transpiration in Fig. 5. The relationship between estimated transpiration (T_r) and measured Sapflow (S) is expressed as follows: S = 1.038 T_r ($r^2 = 0.9095$, n = 1245). The p value for the regressions was very high. Hence, the models and parameters we used were good enough to predict T_r in apple tree canopies.

DISCUSSION

A coupled model was developed to incorporate apple tree G_s and T_r for assessing effects of the interaction between tree canopy and microclimatic factors on T_r and the interactions between themselves. The models can be applied at different validation scales from leaf to orchard. We have demonstrated that these models were also of value in estimating diurnal variations under different weather conditions.

The Penman-Monteith equation was successful in simulating plant water use in our study and in others (Teixeira *et al*., 2008). It is based on the energy balance using the "big-leaf" approach and requires micrometeorologial and canopy variables to estimate evaporative losses from plant communities (Irmak *et al*., 2008). However, canopy variables, such as stomatal resistance (r_l) and canopy resistance (r_c) are difficult to measure. Some studies have evaluated different methods of scale-up as a function of different microclimatic, soil and crop characteristics.

WUE is defined as the amount of dry matter produced by a crop per unit of water transpired over a season (Ma *et al*., 2008). However, WUE can also be understood in terms of physiological and biochemical processes that determine the state of the plant canopy (Kumar *et al*., 1996), including microclimate and stomatal conductance. WUE is related to individual weather parameters, such as interception of radiation, relative humidity, soil moisture, temperature and wind velocity. The diurnal course of WUE was simulated by using our models and the microclimatic data from the canopy. WUE was sensitive to RH, T_a and CO_2 concentration (Fig. 2). However, it was not sensitive to R_a, because both transpiration and photosynthesis increased linearly with increasing R_a (Fig. 2). Moreover, peak WUE was reached in early morning, followed by decreases to a stable level over most of the day. The results were similar to those of Testi *et al*. (2008).

The stomatal conductance was the key factor to simulate water evaporation and assimilation (Naithani *et al*., 2012). But the regulation of photosynthesis and transpiration by stomatal conductance was different. This difference could maximize the assimilation and avoid excessive loss of water in the plant. Upadhyaya *et al*. (1983) reported that transpiration rate is directly correlated with stomatal diameter when stomatal diameters are <10 μm, but photosynthesis rate is directly correlated with stomatal diameter only when stomatal diameter is <2 μm. Our simulation also showed the different influence of stomata on CO_2 and water vapor fluxes.

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