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LIGHT USE EFFICIENCY DISTRIBUTION AS A FUNCTION OF DIFFERENT TREE SHAPES IN APPLE

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ABSTRACT

Light use efficiency (*LUE*) is the single, most influencing factor on fruit yield and quality. The three-dimensional (3-D) distribution and diurnal variation of the *LUE* of the fruit tree canopy can be simulated by establishing the coupled model of the net photosynthetic rate (P_n) and the 3-d canopy's photo synthetically-active radiation (*PAR*). The 3-D distribution of the P_n of the canopy was determined by the C_3 photosynthesis model and the 3-D distribution of *PAR* and leaf area. *LUE* was expressed as the ratio of P_n to *PAR*. The diurnal variations and 3-D distributions of four apple tree shapes *LUEs* (I: small-sparse shape, II: disperse-stratified shape, III: spindle shape, and IV: open-center shape) were simulated through the coupled model. The results of the simulation demonstrated that, under high radiation conditions (*PAR*=1500 μmol·m^{-2}·s^{-1}), the *LUEs* of the four tree shapes were 0.0186 μmol·mol^{-1}, 0.0199 μmol·mol^{-1}, 0.0187 μmol·mol^{-1}, and 0.0150 μmol·mol^{-1}, in treatment I to IV, respectively. On clear days, the apple tree canopy's *LUE* displayed a bimodal curve. The *LUEs* of the four tree shapes' canopies per unit of ground for a day were 0.0127 mol·mol^{-1}, 0.0151 mol·mol^{-1}, 0.0144 mol·mol^{-1}, and 0.0115 mol·mol^{-1}, in treatment I to IV, respectively. Of the four tree shapes, the average *LUE* of the open-center shape was the highest, being 0.0175 mol·mol^{-1}, and it was respectively 8.3%, 5.9%, and 5.7% higher than that of the small-sparse shape, the stratified-disperse shape, and the spindle shape. The study indicated that the 3-D distributions and diurnal variations of the *LUEs* of the different apple tree shapes' 3-D canopies can be simulated through the coupled model. The results also showed that, of the four apple tree shapes, the *LUE* of the open- center shape was the highest, which could improve fruit quality. Also, the other three tree shapes' canopies had high total amounts of *LUE*, which could raise fruit yield.

Keywords: Apple; Tree shape; Light use efficiency; Photosynthetically active radiation; Model; Photosynthesis; Distribution.

INTRODUCTION

Fruit yield relies largely on the light use efficiency (*LUE*) of canopies (Robinson *et al*., 1991; Buler and Mika 2009; Balan and Cimpoies 2009), whereas fruit quality is primarily related to the light distribution among the canopies. This is because fruit quality (such as the weight of a single fruit, soluble solids, hardness, and color) is primarily related to the carbohydrate fixation and the supply of surrounding leaves as well as depends upon the light use of the canopies' leaves (Louarn *et al*., 2008; Buler and Mika 2009; Hassan *et al*., 2010; González-Talice *et al*., 2013). Therefore, studying the *LUE* distribution and difference of different tree shapes in an effort to improve canopies' *LUE* is of extreme significance to the improvement of fruit yield and quality. *LUE* is generally expressed as the dry matter accumulation when crops consume a unit amount of light, and can be physiologically described as the ratio of the net photosynthetic rate (P_n) of canopies (leaves) to photosynthetically-active radiation (*PAR*) (Anderson *et al*., 2000). Currently, studies conducted over the *LUE* of China's different apple tree shapes have rarely been reported. Using the photosynthesis model of the three-dimensional tree canopy (Gao *et al*., 2012a), this paper systematically studied the *LUE* distribution and difference of the four apple tree shapes in China's production (Gao *et al*., 2012b), with a goal of providing a theoretical basis for the shape selection as well as providing a routine pruning of fruit trees.

MATERIALS AND METHODS

Material Processing: Long-branch "Fuji" apple trees (*Malusdomestica* Borkh. cv. 'Fuji') were selected as the experimental material. All of the trees in the experimental plot were both uniform and strong, with a controlled yield of approximately37 tons per hectare. The orchard soil was sandy loam and was treated according to consistent standards in terms of production management; it also contained the proper water quantity. The experiment consisted of four treatments:

Treatment I (small-sparse shape) The experimental material was obtained from the experimental orchard of Yantai Muping Forestry Bureau, Shandong (37º23′North Latitude, 121º35′East Longitude, and11m altitude). The stocks were *M.micromalus* Makino, pollinated by *M. Domestica* Borkh. 'Delicious' and planted in 1994, with spacing between trees and rows of 2 m×3 m and rows oriented north/south. The trunk height was 40~60 cm, the tree height was 2.5~3 m, and the canopy diameter was approximately 2.5 m. Each tree had three tiers of three boughs, two boughs, and one bough, respectively, with spacing of about 60 cm. After winter pruning, 200×10^4~250×10^4 branches were retained per hectare. All canopy parameters and radiation distributions were determined from July to August from 2008 to 2010;

Treatment II (stratified-disperse shape) The experimental material was obtained from Shisanling farm, Changping District, Beijing (40º13′North Latitude, 116º13′East Longitude, and79 m altitude). The stocks were *M. micromalus* Makino, pollinated by *M. Domestica* Borkh. ‘Orin’ and planted in 1985, with spacing between trees and rows of 3 m×5 m and rows oriented north/south. The trunk height was generally 40~60 cm, and the tree height was 4~5 m. After winter pruning, 180×10^4~240×10^4 branches were retained per hectare. Each tree generally had 12~15 boughs. All canopy parameters and radiation distributions were determined from July to August from 2008 to 2010;

Treatment III (spindle shape)The experimental material was obtained from the experimental orchard of Guojia Town, Qin’an County, Tianshui City, Gansu (35°11′North Latitude, 105°21′East Longitude, and1,530m altitude). The stocks were *M. micromalus* Makino, pollinated by *M. domestica* Borkh. ‘Delicious’ and planted in 1990, with spacing between trees and rows of 3 m×4 m and rows oriented north/south. The trunk height was generally 40~60 cm, the tree height was 4.5~5 m. After winter pruning, 160×10^4~210×10^4 branches were retained per hectare. Each tree generally had about 15~20 boughs without large twigs and was pruned through uniaxial extension. All canopy parameters and radiation distributions were determined from July to August from 2009 to 2012;

Treatment IV (open-center shape) The experimental material received Treatment II. From 2001, the original stratified-disperse shape was transformed to the open-center shape. In 2007, the average trunk height was above 1.5 m, the tree height was 3.5~4 m, there was no trunk heads, and each tree had 3~5 boughs arranged in a spiral way and distributed in open-center shape. After winter pruning, 75×10^4~105×10^4 branches were retained per hectare. All canopy parameters and radiation distributions were determined from July to August from 2009 to 2012.

Measurement of Radiation and Photosynthetic Rate: During the radiation measurement, the canopy was first divided into 0.5×0.5×0.5 m cells. After this division, a light quantum meter (LQF5) was used to measure the *PAR* and each cell’s total solar radiation. And average extinction coefficient (k) was measured by digital plant canopy imager (CI-110). Then, Beer's law was used to calculate (Johnson *et al*., 1989) the average *PAR* and average radiation received by the leaves in each cell. A LI 6400 photosynthesis system (LI-COR) was used to measure P_n, and an AP4 porometer (Delta-T Devices) was used to measure G_s. Additionally, the parameters of leaves G_s and P_n were fitted using the morning data for sunny days. Microclimatic factors were obtained from both the photosynthesis system and the small meteorological station in the orchard. The meteorological data for Beijing (2012) was used to simulate the diurnal variation of *LUE*. Finally, the least square method was used to estimate model parameters, and some parameters were also derived from previous research data (Farquhar *et al*., 1980; Leuning *et al*., 1995; Gao, *et al*., 2012a).

In order to validate the simulation effect of the net photosynthetic rate of the three-dimensional canopy, typical sunny days were selected to randomly measure the P_n of leaves in different parts of different tree shapes in the experimental plot from July to August during 2008-2012. During measurement, the leaves’ orientation and angle were not changed, and the measurement was repeated for 15 days. The diurnal variation of the canopy’s overall net photosynthetic rate for each period was calculated based on the average of this meteorological data (measured using the photosynthesis system). The simulation was carried out from 5:00~19:00 with 30 minute intervals. After the experiment, the weighing method was used to obtain the distribution of the leaf areas of 15 experimental trees for each treatment in the three-dimensional cell.

Model Building: The Leaf Photosynthetic Model—Farquhar (Farquhar *et al*., 1980) proposed the biochemical simulation model of the P_n of simple leaves based upon the biochemical mechanism of photosynthesis in C_3 plants, and some scholars have since improved upon the original model (Leuning *et al*., 1995). The formula 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 ribulose-1,5-bisphosphate carboxylase (RuBisCO), A_qi the photosynthetic rate restricted by the regeneration rate of ribulose-1,5-bisphosphate (RuBP), and R_d is the dark respiration rate of leaves. It is required that the stomatal conductance to CO2 (G_{sc}) be determined before this formula is used to calculate P_n(Farquhar *et al*., 1980). In this paper, the semi-mechanistic model of stomatal conductance, improved by Leuning (Leuning *et al*., 1995), was used to calculate G_{sc}.

The Three-dimensional Model of Canopy Photosynthesis- The photosynthesis model of the large sun leaves in the upper canopy was determined according to Formula 1. The A_c relationship between the leaves in the different parts of the three-dimensional canopy and the large sun leaves was described using the following quadratic equation (Gao, *et al*., 2012c):

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

where $A_{c(i)}$ is the maximum photosynthetic rate of the i^{th} cell of the canopy restricted by the activity of Rubisco, and x is the relative photosynthetically-active radiation (*RPAR*) of this cell. According to the above model and to each cell's average *RPAR*, the distribution of the net photosynthetic rate $P_n$of simple leaves in the different parts of the entire canopy can be simulated. The gross canopy photosynthetic rate of the i^{th} cell (P_{n-c}) was calculated based on the P_n and leaf area (L) in every cell section:

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

The total photosynthesis in the whole -tree canopy (P_{n-t}) can be calculated based on the P_n and PAR in every cell.

The *LUE* Model—The *LUE* of leaves in the different parts of the three-dimensional apple tree canopy is defined as the ratio of P_n to *PAR* in this part (Anderson *et al*., 2000):

$$LUE = \frac{P_n}{PAR} \quad (4)$$

The canopy's overall *LUE* was calculated according to the ratio of its net photosynthetic rate to the *PAR* reaching its top.

RESULTS

Three-dimensional Distribution of the Light Use Efficiency (LUE) of Leaves of Different Tree Shapes: The *LUE* distribution of leaves in the three-dimensional canopy space of the four different tree shapes is shown in Fig. 1. Generally, the *LUE* of the lower canopy and the canopy chamber was high because the leaves' *LUE* reached its maximum when the radiation reached about 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. For the small-sparse shape and the spindle shape, the upper layer's leaves were too dense, and the radiation in the lowest layer could not reach 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ even under high radiation conditions, so the lowest layer's *LUE* was low. However, the entire canopy's overall *LUE* primarily depends upon the leaf area size and the canopy light interception. Calculations indicated that the average *LUEs* of the four tree shapes' canopies under high radiation conditions were 0.0186 $\mu mol \cdot mol^{-1}$ (small-sparse shape), 0.0199 $\mu mol \cdot mol^{-1}$ (stratified-disperse shape), 0.0187 $\mu mol \cdot mol^{-1}$ (spindle shape), and 0.0150 $\mu mol \cdot mol^{-1}$ (open-center shape), respectively. The *LUE* of the open-center shape was the lowest because it had the smallest leaf area, and consequently, the corresponding intercepted light was also low. However, the leaf area index of the small-sparse shape was 64% greater than that of the open-center shape, but the canopy's overall *LUE* under high radiation conditions only increased by 22.1%. The leaf area indexes of the stratified-disperse shape and the spindle shape were respectively 57% and 53% greater than that of the open-center shape but the canopies' overall *LUEs* under high radiation conditions only increased by 32.6% and 24.9%, respectively. This was possibly because the light in these tree shapes' lower canopies was too limited, thus resulting in insufficient photosynthesis in the leaves. Under low radiation conditions, the *LUE* of closed canopies will be lower. Therefore, when the canopy is closed, a large number of branches and leaves do not always increase the canopy's *LUE*. This means that canopies have an optimum structure parameter.

Diurnal Variations of Canopy LUEs of Different Tree Shapes: Formula 3 shows that canopy *LUE* is determined by P_n and *PAR*. The diurnal variation of the overall *LUE* of the three-dimensional canopy for each treatment is shown in Fig. 2. It was cloudy on June 14 and 15, clear from June 16 to 18, and overcast on June 19 (Fig.2A). Because the *LUE* reached its maximum under low radiation conditions, it sharply declined at noon (Fig. 2B and 2C). Because the *LUE* of both the lower canopy and the canopy chamber reached its peak late, the canopy's overall *LUE* reached its peak one or two hours later than the leaves in the upper layer. From June 14 to 19, the average canopy *LUEs* of the four tree shapes were 0.0128 $mol \cdot mol^{-1}$, 0.0153 $mol \cdot mol^{-1}$, 0.0144 $mol \cdot mol^{-1}$, and 0.0120 $mol \cdot mol^{-1}$, respectively. The *LUE* of the stratified-disperse shape was the highest, followed by that of the spindle shape and the small-sparse shape, and they were respectively 27.7%, 20.7%, and 6.7% higher than the open-center shape's *LUE*. The all-day average *LUEs* of the four tree shapes per unit orchard area for the clear days were 0.0127 $mol \cdot mol^{-1}$, 0.0151 $mol \cdot mol^{-1}$, 0.0144 $mol \cdot mol^{-1}$, and 0.0115 $mol \cdot mol^{-1}$, respectively; those for the cloudy days were 0.0145 $mol \cdot mol^{-1}$, 0.0173 $mol \cdot mol^{-1}$, 0.0163 $mol \cdot mol^{-1}$, and 0.0155 $mol \cdot mol^{-1}$, respectively; and those for the overcast day were 0.0079 $mol \cdot mol^{-1}$, 0.0095 $mol \cdot mol^{-1}$, 0.0086 $mol \cdot mol^{-1}$, and 0.0094 $mol \cdot mol^{-1}$, respectively. For the overcast day, because insufficient light reached the lower layer and the chamber, the all-day *LUEs* of the small-sparse shape (*LAI*=4.14) and the spindle shape (*LAI*=3.88) were respectively 15% and 8% lower than that of the open-center shape (*LAI*=2.53), and the all-day *LUE* of the stratified-disperse shape was also only 2% higher than that of the open-center shape.

The average diurnal variations of the *LUEs* of simple leaves of the different tree shapes could be calculated according to the radiation received by the canopy's leaves as well as the P_n of the leaves, as shown in Fig.2C. Because the light conditions in the canopy of the open-center shape were the best and the photosynthetic capacity of the leaves was the strongest, accordingly its *LUE* of simple leaves was also the highest. From June 14 to 19, the average *LUE* of simple leaves in the canopy of the open-center shape was 0.0175 mol·mol^{-1}, being respectively 8.3%, 5.9%, and 5.7% higher than that of the small-sparse shape, the stratified-disperse shape, and the spindle shape. Fruit quality primarily depends on the output of the surrounding leaves' photosynthetic products. Therefore, the increase in the simple leaves' *LUE* could help improve fruit quality.

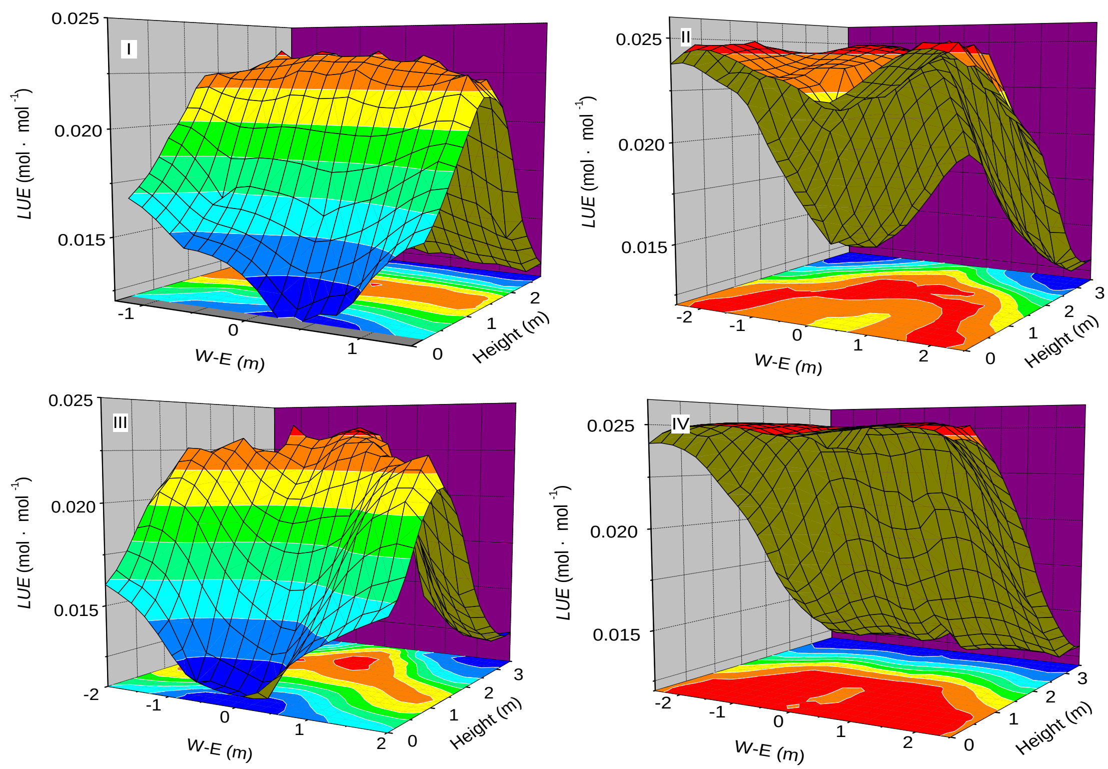

Figure 1 Three-dimensional distribution of light use efficiency (*LUE*) in different apple tree systems
Note: The standard conditions were *PAR*=1500 μmol·m^{-2}·s^{-1}, *RH*=50%, T_a=25℃, [CO_2]=360 μmol·mol^{-1}. I, small and sparse canopy system; II, disperasal stratified system; III, spindle system; IV, open center system.

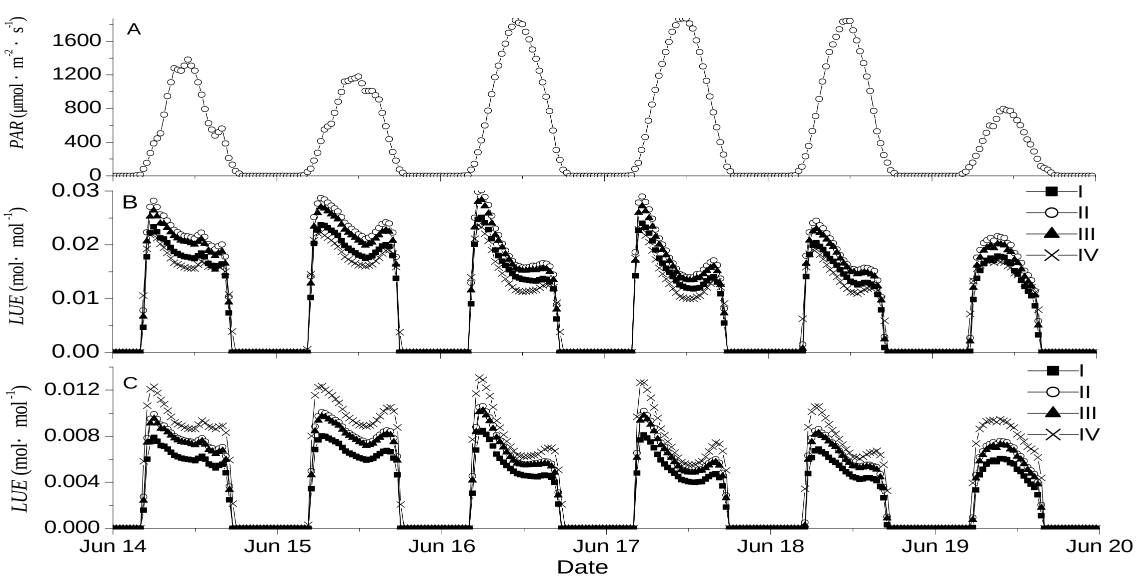

Figure 2. The diurnal average variations of canopy *LUE*(B) on per unit orchard and leaf *LUE*(C), and the diurnal variations of orchard radiation from Jun 14 to 20 in 2012

Model Validation: This study validated the model's effect on the photosynthesis simulation of the entire three-dimensional canopy by randomly sampling the leaves in the different parts of the four different apple tree canopies in order to measure their diurnal variations of photosynthesis (Fig. 3). Fig. 3 shows that the simulated value and measured value of the canopy's P_n were relatively consistent. The *P* test reached a significant level, indicating that this model can be used to simulate the net photosynthetic rate of the three-dimensional apple tree canopy and then to study the overall *LUE* change of the three-dimensional canopy.

DISCUSSION

The canopy structure of the different tree shapes has a decisive effect on both the light use efficiency and the light distribution (Louarn *et al*, 2008; Balan and Cimpoies 2009; Liu *et al*, 2012). First, an excellent fruit tree shape is necessary for intercepting as much light as possible in order to obtain maximum light use efficiency, and then, it is necessary to improve the canopy's light distribution as much as possible in order to improve fruit quality (Costes *et al*, 2006; Louarn *et al*, 2008; Cherbiy-Hoffmann *et al*, 2013). These two aspects, however, are contradictory. Therefore, in-depth research is required on the canopy's light use. In this paper, the photosynthesis model of the three-dimensional canopy was used to systematically study the *LUE* distribution and difference of the four apple tree shapes in China's production. It needs to be pointed out that the *LUE*

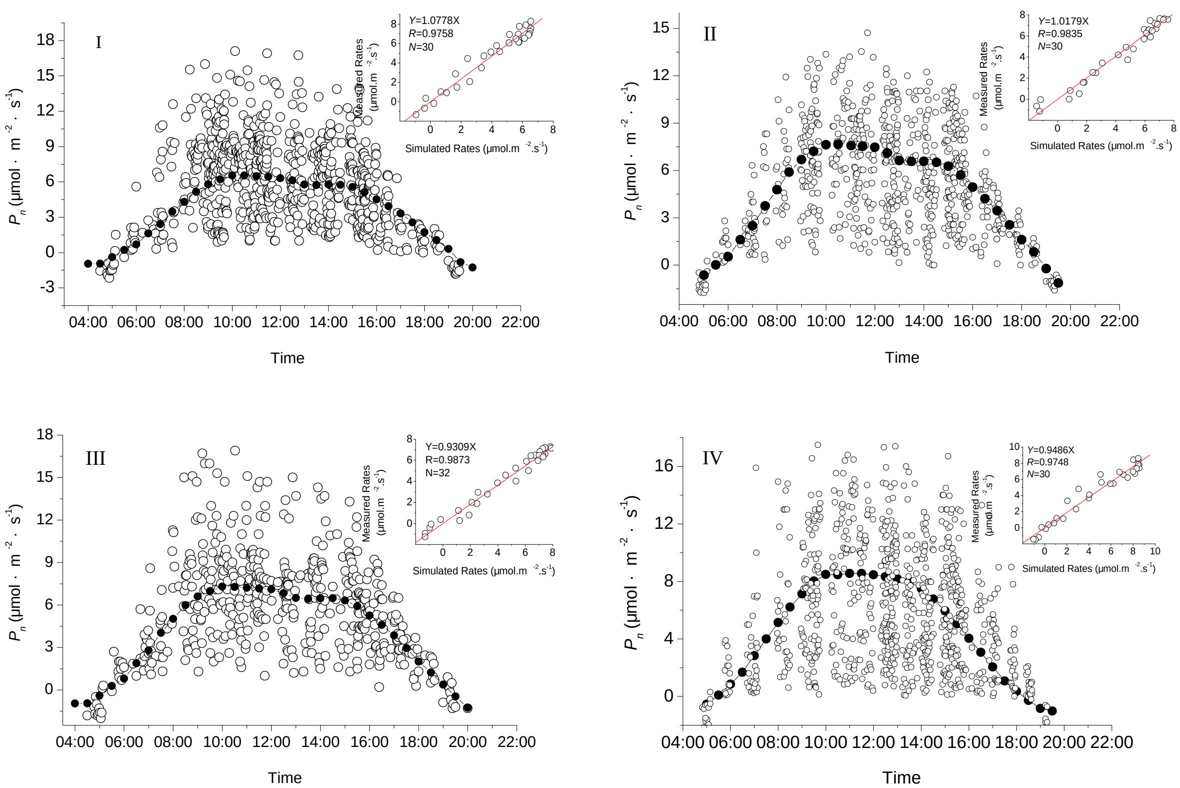

Figure3. The diurnal variation of measured (○) and simulated (●) photosynthetic rates of different apple system in clear days.

of leaves in the three-dimensional canopy in this paper was calculated using the P_n of leaves and the *PAR* at this location, while the *LUE* of the whole canopy is equal to the ratio of the total photosynthetic rate to the PAR intercepted by the canopy. The former can be used to analyze the use of light at different locations in the three-dimensional canopy, and the latter is primarily used to analyze the total light use of the canopy. It can be seen that the *LUE* distribution (Fig. 1) differed greatly from the relative radiation distribution (Gao, *et al*., 2012b).Results showed that the overall *LUEs* of both the spindle shape and the stratified-disperse shape were relatively high, which could improve fruit yield. Results also indicated that both the radiation obtained by the open-center shape's leaves as well as its *LUE* were high (Gao, *et al*., 2012b), which could lead to better fruit quality.

Canopy light interception is determined by tree structure (Duursma *et al*, 2011), but different tree shapes may have similar amounts of light interception and similar *LUEs* (Valladares *et al*, 2002). This study also found that the *LUEs* of both the stratified-disperse shape and the spindle shape were basically consistent (Fig. 1), which may be related to their similar total amounts of light interception. However, the small-sparse shape's *LUE* was lower than that of the stratified-disperse shape and the spindle shape, which may be caused by the numerous branches and leaves as well as the poor light in the lower layer of the small-sparse shape. In addition, although the overall *LUEs* of both the stratified-disperse shape and the spindle shape were similar, their canopy *LUE* distributions were not consistent (Fig. 1), which was primarily due to their different light distributions. Although the open-center apple tree can improve fruit quality, the canopy's overall *LUE* was low, so consequently the fruit yield was restricted. During production, many fruit growers fail to realize this and still retain fruits according to the standards for the stratified-disperse shape and the spindle shape in traditional management, thus preventing apple trees from fruiting stably and growing strong. Through a survey, it has been discovered that, under China's general water and fertilizer conditions, it is appropriate to control the yield of an open-center apple tree orchard within 30-37.5 tons per hectare, and for an orchard with high water and fertilizer conditions, the yield can be controlled within 40-45 tons per hectare.

LUE is the primary limiting factor on crop yield (Costes *et al*, 2006; Liu *et al*, 2012). Values of *LUE* depend on definitions of output and input and their units (Hirose and Bazzaz, 1998). Here LUE was defined as the ration between photosynthetic rate and *PAR* absorbed in the canopy or leaves, which can be to describe the distribution and difference of LUE in different apple tree shapes. Selecting reasonable tree shapes in order to ensure sufficient canopy light distribution is a precondition for realizing high fruit quality and fruit yield. When the canopy's overall *LUE* increases, more leaves in the canopy will shadow one another, thus resulting in a reduction in the photosynthesis in the canopy's leaves and in the local carbohydrate export. For example, the canopy *LUE* of the stratified-disperse apple tree was 27.7% higher than that of the open-center apple tree, whereas the average radiation obtained by the leaves in its canopy was reduced by 8.4% (Gao, *et al*., 2012b), and its leaves' average photosynthetic rate was also 20.3% smaller than that of the leaves of the open-center apple tree (material to be published). Therefore, in evaluating a tree shape, consideration should not only be given to *LUE* but also to the photosynthetic capacity, yield, quality, and so on.

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