Critical responses of photosynthetic efficiency of goldspur apple tree to soil water variation in semiarid loess hilly area

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Abstract

Goldspur apple (*Malus pumila* cv. Goldspur) is one of the main fruit trees planted in semiarid loess hilly areas. The photosynthetic efficiency in leaves of eight-year-old trees were studied under different soil water conditions with a *Li-6400* portable photosynthesis system and a *Li-Cor1600* portable steady state porometer in order to explore the effects of soil water stress on photosynthesis and the suitable soil water content (SWC) for water-saving irrigation of apple orchards. The results showed that the leaf net photosynthetic rate (P_N), transpiration rate (E), water-use efficiency (WUE), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and stomatal limiting value (L_s) displayed different threshold responses to soil water variation. When SWC was within a range of about 60%–86% of field capacity (FC), P_N and E were maintained in a relative steady state. At an elevated level but below 60% of FC, both P_N and E decreased evidently with decreasing soil moisture. The SWC needed to support WUE in a relatively steady state and at a high level was in the range of about 50%–71% of FC. When SWC was less than 48% of FC, g_s and L_s declined with decreasing soil moisture, while C_i increased rapidly. Based on the analysis of the stomatal limitation of photosynthesis using two criteria (C_i and L_s) suggested by Farquhar and Sharkey, it was implied that the predominant cause of restricting P_N had changed from stomatal limitation to nonstomatal one under severe water stress. In terms of water-saving irrigation for enhancing water-use efficiency, it was concluded that in semiarid loess hilly areas, the suitable range of SWC for water-saving irrigation in goldspur apple orchards is in the range of about 50%–71% of FC, and the most severe degree of soil water stress tolerated for photosynthesis is about 48% of FC.

Additional key words: critical efficiency; goldspur apple tree; loess hilly area; photosynthetic efficiency; soil water content.

Introduction

In extensive areas of north China, drought and water shortage are the most critical ecological factors restricting vegetation restoration and agricultural production. The uses of water-saving agricultural models are becoming increasingly important along with the continual sharpening of water-resource crises and drying hazards. How to fully raise the available utilizations and production efficiency of limited water resources and create an ecological environment boosting agricultural sustainable development are the key objectives in a water-saving agriculture (Li 2001, Kang *et al*. 2007, Zhang *et al*. 2007). The significant theories on which water-saving agriculture and water-saving irrigation are based are photosynthesis, water metabolism and its mechanisms of ecophysiology, and soil regulation with regard to the enhancement of plant yield and water-use efficiency in an optimal combination (Shan and Xu 1991, Liu 1998). Many researchers of water-saving irrigation and its

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Abbreviations: C_i – intercellular CO_2 concentration; E – transpiration rate; FC – field capacity; g_s – stomatal conductance; L_s – stomatal limiting value; P_N – net photosynthetic rate; RWC – relative soil water content; SWC – soil water content; WUE – water-use efficiency.
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mechanisms of ecophysiology concentrate on crops (Kicheva *et al.* 1994, Tang *et al.* 2005, 2008; Xue *et al.* 2006, Grzesiak *et al.* 2006, Huang *et al.* 2008) and in-depth research on the effects of water stress on photosynthesis and water-use efficiency and its mechanisms (Chandrasekar *et al.* 2000, Souza *et al.* 2004, Miyashit *et al.* 2005, Thiagarajan and Lada 2007, Blum 2009). Researchers assumed that crops had a certain adaptability and resistivity to limited water shortages (Jalota *et al.* 2006). Under moderate water stress, photosynthesis was not influenced, and even higher than that under abundant water, the crop yield might not fall but water-use efficiency increased remarkably (Zhang *et al.* 2000, Wei *et al.* 2000). When a crop endures drought, the main cause of restrained photosynthesis changes from stomatal factors under slight and moderate water stress to nonstomatal factors under severe water stress, but the time of transition depends on crop drought-resistant capability, drought degree and application ways, among others (Farquhar and Sharkey 1982, Kicheva *et al.* 1994, Xu 1997, Lhomme and Monteny 2000, Li *et al.* 2004).

The apple is the most widespread fruit in northern China and occupies an important place in agricultural development and fruit production. In recent years, research on dry-farming technology, water-saving cultivation, growth effects and physiology achieved some results (Xu and Ma 2000, Zhang and Zhao 2001). However, compared with crops, the research on the mechanisms of ecophysiology in water-saving irrigation, especially the connection between photosynthesis and soil moisture, was still in beginning stages (Xu and Ma 2000). Most existing research, which reported potting experimental results and lacked observations under multilevel water stress (Jie *et al.* 2001, Wang *et al.* 2003, Li *et al.* 2005, Kang *et al.* 2007), was restricted heavily when applied to supervising practical production. In the management of soil moisture for apple production, the ideas of water-saving irrigation emphasized the promotion of growth in preliminary stage and then control vegetative growth, combine promotion with control, but it still did not come to the quantification and indexing level (Xu and Ma 2000). Thus, we explored the rules of soil moisture on apple photosynthesis in a field environment and ascertained the soil water supply level (moderate water stress) that was good for promoting photosynthesis and boosting water-use efficiency. Eight-year-old *Malus pumila* cv. Goldspur in an apple orchard in the semiarid loess hilly area was used to study the regularity of photosynthesis and water-use efficiency with continuous soil water variation in order to provide a scientific basis and technical standard for field water management of dry-farming culture and water-saving irrigation of apple trees.

Materials and methods

Study area: The experimental site is located in the Tuqiaogou watersheds, Yukou town, Fangshan county, Shanxi Province, China, a part of the gully-hilly area of the Loess Plateau in the middle reaches of the Yellow River. It lies at north latitude 37° 36′ 58″, east longitude 110°02′ 55″, with an average altitude of about 1,200 m and a maximum of 1,446 m. The average annual precipitation is 416.0 mm, and the precipitation in June, July, August and September is more than 70%. The annual potential evaporation is 1,857.7 mm, and the greatest evaporation appears from April to June. The soil is classified as a medium and lossal soil. The average soil bulk density is about 1.2 g cm^{-3}, and the mean of field capacity (FC) is roughly 21.0%.

Study material and disposal: In the study on the responses of gas-exchange parameters to soil water, eighteen eight-year-old apple trees were selected as experimental samples and divided into six groups (three trees per group and denoted by I, II, III, IV, V, and VI). The average height of apple trees was about 2.3 ± 0.4 m and the average diameter at breast height was about 10.3 ± 0.3 cm. A one-meter-long aluminum tube of *LNW-50A* neutron probes (*CAS*, Nanjing, Jiangsu, CHN) was buried about 0.5 m away from the apple trees. In order to avoid soil water infiltration**,** the ditches of about one meter in depth and 0.2 m in width were dug between different disposals. The soil water gradient was obtained in six groups by providing water supply and natural water consumption**.** The detailed method we used was as follows. First, we graded the soil surface into a slope, which was low inside and high outside, around the experimental plant within a radius of 0.5 m. Then we built a 0.2-m high bulwark against water. Two days before the experimental observation (June 10, 2008), we provided different water supplies to six groups, and then monitored the change of soil water content (SWC) by the neutron probes. Two days later (June 12, 2008), we obtained the early soil water gradient and carried out the first observation, with SWC measured with a *LNW-50A* neutron probe (*CAS*, Nanjing, Jiangsu, CHN) in six groups as follows (average of three trees): group I (22.4%), II (20.1%), III (18.2%), IV (15.9%), V (11.7%) and VI (6.2%). After producing a continuous degree of soil water stress by evapotranspiration every three days, the second and third observations were carried out (June 16 and June 20, respectively). At this point, SWC for the six groups were as follows: group I (18.7% and 16.7%), II (17.4% and 16.2%), III (16.7% and 14.8%), IV (13.6% and 11.9%), V (10.5% and 9.6%) and VI (5.6% and 5.0%). One group was chosen for contrast, and this group was not supplied with water. For this group, the SWC measured with the *LNW-50A* neutron probe (*CAS*, Nanjing, Jiangsu, CHN) on June 12, June 16, and

June 20 were 5.0%, 4.8% and 4.7%, respectively.

Measurement method: A portable photosynthesis system (*Li-6400*, *Li-COR Inc*., Lincoln, NE, USA) was used to measure the photosynthetic parameters including P_N, g_s, and C_i, and at the same time. E was measured with a portable steady-state porometer (*Li-Cor1600*, *Li-COR Inc*., Lincoln, NE, USA) and revised mildly by the weighing method (Liu 1997) because the natural transpiration rate was higher than the observed value, and the better the water condition was, the larger was the error. WUE and L_s were calculated according to the formula WUE = P_N/E and $L_s = 1 - C_i/C_a$ (Farquhar and Sharkey 1982).

Five fully developed mature leaves were selected from the center of the crowns in the east, south, west, and north, respectively, and denoted carefully, so that twenty leaves were measured for every tree and sixty in every group. The same leaf was measured with three repeated observations on June 12, 16, and 20. The water disposal and observation period was from June 10 to 20, and the first observation was carried out on June 12, the second day after giving the water supply. Then, the second and third observations were carried out (June 16 and 20, respectively) every three days, respectively. The duration of observation was between 09:00–11:00 h on a sunny day every time. In the measurements, CO_2 concentration was controlled at 370 μmol mol^{-1} with *LI-COR* CO_2 injection system (*Li-COR Inc*., Lincoln, NE, USA), and a saturating photosynthetic photon flux density of 1,400 μmol m^{-2} s^{-1} from a *LI-COR* LED (*Li-COR Inc*., Lincoln, NE, USA) irradiation source was supplied. Air temperature of leaf chamber was maintained at about 32ºC, a relative humidity was maintained at 41% and the flow rate of air in the measuring chamber was 200 μmol s^{-1}. Before recording of data, the measured leaves were kept in the leaf chamber for at least 5 min to reach a steady state of photosynthesis.

SWC was observed with *LNW-50A* neutron probes (*CAS*, Nanjing, Jiangsu, CHN) on the same day when the photosynthetic parameters were measured. The measurement depth was 1 m, and every 20 cm a soil horizon. The average of SWC was then found. In this paper, the SWC is the mass soil water content, and the relative soil water content (RWC) is the ratio of SWC to FC.

Data processing: The data, including SWC and leaf gas-exchange parameters under different water disposal and observation periods, were investigated intensively. The *Statistical Program for Social Science* (*SPSS*, Chicago, IL, USA) software and *Excel 2003 for Windows* were applied for statistical evaluation and regression analysis, and the response rules of leaf gas-exchange parameters (P_N, E, WUE, g_s, C_i, and L_s) to SWC were obtained.

Results

P_N and E rose faster with increasing SWC. When SWC reached a certain critical value, the P_N and E changed from increasing to decreasing ones and showed an obvious threshold value for soil water (Fig. 1*A*,*B*). When the SWC was in the range of 12.5–18.0% (equal to the 60–86% of FC, namely RWC), the P_N and E were stable at higher levels and did not change evidently with the increase of SWC, indicating that the threshold value of SWC had a considerably large effect on P_N and E. The rating curve of P_N and SWC followed a quadratic equation (Fig. 1*A*); therefore, the critical value of SWC, maintaining the highest P_N, was obtained at about 16.0% (RWC was about 76%), indicating that SWC of about 16.0% had maximum effectiveness on photosynthesis. The rating curve of E and SWC agreed with a cubic equation (Fig. 1*B*); therefore, the critical value of SWC, maintaining the highest E, was obtained at about 17.0% (RWC was about 81%), indicating that this SWC had maximum effectiveness on transpiration.

WUE displayed the rule of "S" type with the increase of SWC (Fig. 1*C*), namely WUE increased faster when SWC was less than approximately 10.5%. When the SWC was in the range of 10.5–15.0% (RWC was 50–71%), WUE maintained a higher level and varied a little, indicating that the threshold value of SWC had a considerably large effect on WUE. When SWC was higher than 15.0%, WUE fell in contrast with the increase of SWC, and when SWC was about 17% (RWC was 81%), WUE had a minimum value.

g_s, C_i, and L_s displayed different response rules to different soil water thresholds (Fig. 2). When SWC was in the range of 10.0–16.0% (RWC was between 48–76%), g_s and C_i fell evidently (Fig. 2*AC*), but L_s rose evidently (Fig. 2*B*) with the decrease of SWC. When SWC was less than 10.0%, g_s and L_s fell (Fig. 2*A,B*), but C_i rose evidently (Fig. 2*C*) with the decrease of SWC. The above analysis indicated that along with the increase of water-stress levels, the main reason behind the P_N decline was relevant to the transformation from a stomatal factor to the nonstomatal one (Farquhar and Sharkey 1982, Xu 1997), and the soil water threshold for visible change was about 10.0% (RWC about 48%).

Discussion

Plant growth, development state, and various physiological activities had significant relationship with SWC. The impact of soil water on plant growth has a highest, optimal and lowest basic point. When SWC is less than the lowest basic point, the plant will stop growing, wither and die. If SWC is more than the highest basic points, the lack of oxygen will dwarf the plant root and cause the whole plant to die. Only a plant growing in the optimal range of SWC can maintain plant moisture equilibrium and show plant growth in a good state (Li 2001).

The responses of various physiological activities to soil water did not agree. For most vegetation, the threshold of soil water content for plant growth was higher than that for plant transpiration, while the threshold of soil water content for plant's assimilation of carbon dioxide was the lowest. Some results indicated that some physiological activities related to yield formation were influenced by water deficit along with the decline of soil effective water. The growth was affected firstly, followed by transpiration, photosynthesis, and transportation (Shan and Chen 1998). The effect of water deficit on plant growth, mainly displayed in the diminution of cell dilation, first caused the diminution of the photosynthetic green area. Transpiration is a physiological phenomenon along with the process of crop water uptake and growth and had no direct relation to crop yield. Only the effect of water deficit on photosynthesis and transportation was substantial because photosynthesis is the only process for forming organic matter in crops in which water is the significant material. The effect of

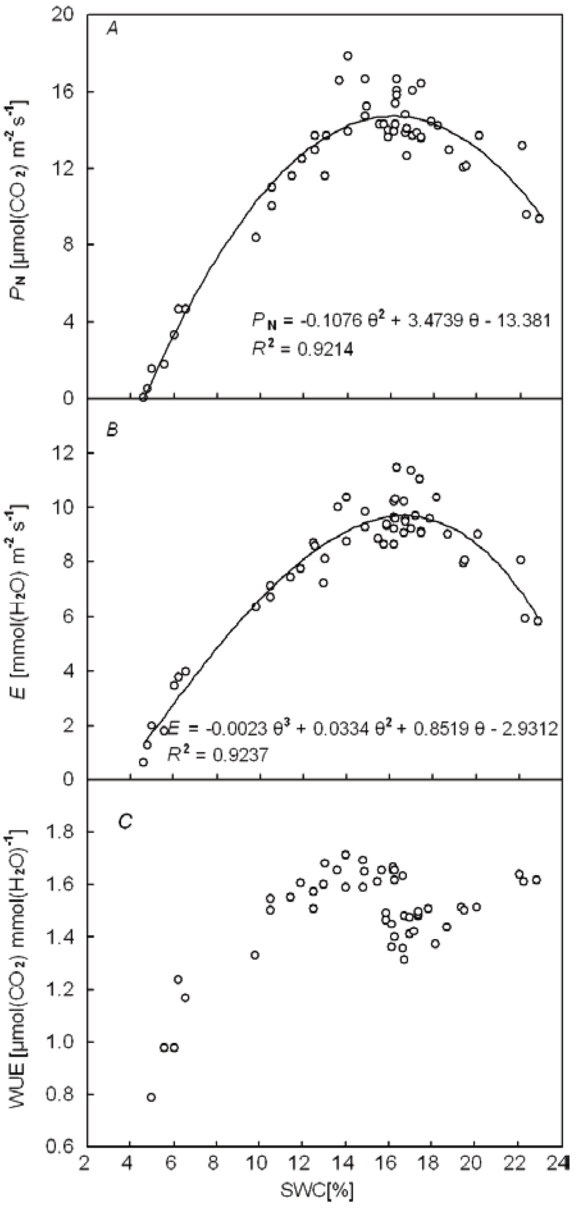

Fig. 1. Responses of *A*: net photosynthetic rate (P_N), *B*: transpiration rate (E), and *C*: water-use efficiency (WUE) in apple leaves to soil water content (SWC).

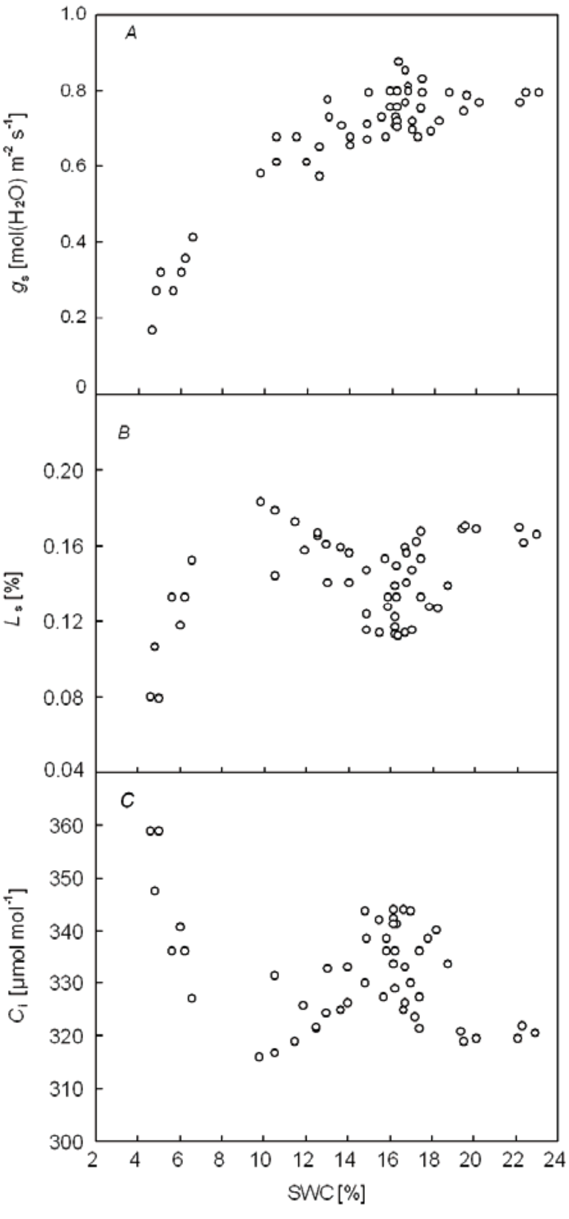

Fig. 2. Responses of *A*: stomatal conductance (g_s), *B*: stomatal limitation (L_s) and *C*: intercellular CO_2 concentration (C_i) in apple leaves to soil water content (SWC).

water on photosynthesis and yield formation determined whether the crop had a yield or not. The effects of crop growth, transpiration and transportation process on yield determined how great the yield was. Evidently, the effect of water deficit on photosynthesis and transportation was more significant and direct, and thus, the reasonable soil water index constantly relied mainly on the soil water index influencing photosynthesis, which was called the photosynthetic soil water index (Chen *et al.* 1997). Using the results of the yielded crop, the optimal RWC threshold values of corn and winter wheat, which are good for photosynthesis, were in the range of about 60%–80% (Yang *et al.* 1997), which is a little lower than what is good for plant growth and transpiration, indicating that the RWC threshold value maintaining an apple leaf at a higher P_N was in the range of about 60%–86% (SWC about 12.5%–18%), and the optimum RWC for photosynthesis was about 76% (SWC about 16%), which was roughly the same for varying crop soil water indices. In the same soil water range, the E of the apple leaves also maintained a higher level (Fig. 1*B*), and RWC with the highest E was about 81% (SWC about 17.0%). Thus, the WUE of apple leaves did not always maintain a higher level in the same soil water range (Fig. 1*C*). Usually when RWC was higher than 71% (SWC 15.0%), WUE fell along with the increase of soil water and the increase of E. WUE appeared as a valley value when RWC was about 81% (SWC about 17%), and it was the same SWC where E had the highest value, indicating that the higher SWC improved the apple photosynthetic rate and yield and led to a higher E, which consumed more soil water and was not good for the improvement of the WUE. It did not conform to the standards of soil water management on agriculture in arid zones with the aim of high efficient utilization of limited water resources.

The aim of field water management in water-saving agriculture is to improve the water-use efficiency of rainfall and irrigation water and also obtain a greater yield (Shan and Chen 1998, Zhang *et al.* 2000). The research on the relationship between crop and soil water indicated that the crop had a certain adaptability and resistivity to limited water shortage (Jalota *et al.* 2006). Under moderate water stress, P_N and E fell with a moderate decrease of g_s, but WUE rose instead because the response of transpiration to SWC was more sensitive than that of photosynthesis. Thus, the transpiration fell earlier than photosynthesis, and the decreased rate of E was greater than that of P_N. Because P_N did not fall evidently, the crop still obtained higher or more than moderate yields; therefore, this moderate water stress is called the soil water such that WUE and yield are in concert (Chen *et al.* 1997). The optimal RWC threshold value in the crop was in the range of about 40%–60% (Huang 1998). This study indicated that the RWC threshold value maintaining apple higher WUE was in the range of about 50%–71% (SWC about 10.5%–15.0%), and if SWC was higher or lower than this range, WUE fell evidently (Fig. 1*C*).

In the discussion above, we assumed that the optimal RWC of water-saving irrigation in the apple yard should be controlled in the range of about 60%–71% (SWC about 12.5–15.0%) in the semiarid loess hilly area. This soil water threshold value had the lowest SWC maintaining a higher P_N as the lower limit, and the highest SWC maintaining a higher WUE as the upper limit. It made apple leaves have the highest WUE and higher P_N, and it was the soil water threshold value or economy water threshold value leading to the WUE and yield being in concert (Shan and Xu 1991). Compared with other studies that had different results for the condition of potted plants, the optimal RWC of water-saving irrigation in two-year-old apples was in the range of about 55%–75% (Wang and Wang 2002). Other varietal apple RWCs were in the range of about 60%–80%, which made the fruit yield the highest and the quality the best (Wang 1988). As was indicated, the optimal soil water index of water-saving irrigation is related to apple variety and age. Otherwise, the soil water threshold of apple water-saving irrigation would be higher than that of crops (RWC was 40%–60%). It had some characteristics in common with apples because the apple is a woody plant and fruit tree with moderate drought resistance and has a special biological habit and physio-ecological characteristics relative to crops (Xu and Ma 2000).

Given the physio-ecological characteristics of plant, photosynthesis and transpiration are the exchange processes, inside and outside, in which CO_2 and water molecules are transported, respectively, and the main channels are the stomata. Stomatal movement controls mesophyll cells water, CO_2 exchange, and WUE (Liang *et al.* 1999). CO_2 exchange is influenced by stomatal and mesophyll cell factors at the same time; therefore, stomatal limiting theory (Farquhar and Sharkey 1982) assumes that the effect of water stress on photosynthesis is divided into a stomatal- and nonstomatal limit. The stomatal limit is the water stress that causes stomata to close, g_s to fall and the CO_2 supply to be obstructed. The nonstomatal limit is the water stress that results in a damage to the photosynthetic apparatus and a decrease of mesophyll cell photosynthesis ability, including the increase of gas-phase space in the intercellular region between mesophyll cells, CO_2 diffusion resistance, the decline of phosphorylation activity of PSII and photosynthesis, a decrease of Rubisco and FBPase activities, the suffocation of Rubisco regeneration, among others. The changing direction of C_i and L_s are the standards to judge the stomatal- and nonstomatal limits. When P_N and g_s fall, C_i falls and L_s rises, and thus, a stomatal limit is found out. When C_i rises and L_s falls, the nonstomatal limit is found. This paper indicates that the main reason for decreasing photosynthesis is the stomatal limit in gentle and moderate water stress and the nonstomatal limit in more than moderate and severe water stress.

When a plant suffered from drought, the main reason was that photosynthesis was restrained, with the process changing from the stomatal limit to the nonstomatal one due to the aggravation of water stress. The changing time varied with plant species, drought-resistant capability, and water stress degree, among others. For various plant species, the exact soil water threshold value causing this changes is not clear (Xu and Ma 2000). The results in this paper showed that in the conditions of yield soil water, natural drought, and the aggravation of water stress, RWC was lower than 48% (SWC about 10.0%) and P_N and g_s of apple leaves all fell noticeably (Fig. 1*A,* 2*A*). The L_s fell and C_i rose evidently (Fig. 2*B,C*), which indicated that the main reason causing the decrease in P_N was the change from stomatal- to nonstomatal factors, and the photosynthetic apparatus was damaged. If SWC descended further, the leaf turned yellow and even withered, and WUE and photosynthetic capability decreased severely. Therefore, we considered that RWC lower than 48% (SWC about 10.0%) was the soil water maximum deficit level. With the water-saving irrigation allowed in the semiarid loess hilly area for apples, this SWC is consistent with the soil water lower limit (RWC 50%) for maintaining a higher WUE (Fig. 1*C*).

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