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Effect of leaf position and age on anatomical structure, photosynthesis, stomatal conductance and transpiration of Asian pear

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Abstract. The effects of leaf position and leaf age on gas exchange, transpiration, stomatal resistance, and anatomical structure of seven-year-old trees of Asian pear cv. Huanghua and Jingshiu II (*Pyrus serotina* Rehd. cv. *culta* rehd.) were examined under field conditions. Individual leaves were monitored from unfolding to maturation, and detailed measurements were made on leaves at various node positions and leaf ages. The anatomical structure varied according to the node position of the leaf, with palisade thickness increasing and the thickness of spongy mesophyll decreasing from the base to the apex of the branch. Intercellular space fraction of leaves decreased from the apex to the base of a shoot. "Huanghua" leaves took 20 days for full expansion while "Jingshiu II" required 25 days. Net photosynthesis (Pn) and stomatal conductance (Gs) of both genotypes increased with leaf age, particularly in the early stage. Pn reached a maximum value when the leaf was completely expanded. Leaves at different developmental stages from the apical position to the base performed differently. The transpiration rate and the vapor pressure deficit of older leaves on the base of the branch were higher than those of the younger leaves at the apex of the branch. Leaves at node 3 to 16 had higher saturation vapor pressure and transpiration rates. Both the apical and basal leaves had higher stomatal resistance and lower net photosynthesis than leaves in an intermediate position.

Keywords: Anatomical structure; Leaf position; Leaf age; Photosynthesis; Stomatal resistance; Transpiration.

Abbreviations: Pn, net photosynthesis; **Gs,** stomatal conductance; **Ci,** intercellular CO_2 concentration; **Rs,** stomatal resistance; **Rh,** relative humidity; **Cc,** CO_2 concentration in photosynthetic chamber; **Tf,** leaf temperature.

Introduction

Asian pear (*Pyrus serotina* Rehd. cv. *culta* rehd.) is one of the most prevalent tree crops in southern China. The subtropical climate of this region provides for cloudy, rainy conditions with low temperatures in the spring, when pears produce new shoots, expand leaves, flower and set fruit, increasing the demand for organic and inorganic nutrients. Plants meet these nutritional requirements three ways: (1) nutrient storage, (2) uptake of inorganic nutrients from the soil through the root system, and (3) synthesis of carbohydrate through leaves. Under unfavorable conditions, leaves have a stronger photosynthetic capacity to supply sufficient carbohydrates and organic nutrients to assure pears can finish various biochemical and physiological processes. Hancock and Flore (1989) reported the regression coefficient of net photosynthetic rates was significantly correlated with yield. Determining the leaf photosynthetic characteristics of pear is therefore important to maintaining yield and improving fruit quality.

Many studies have shown how environmental preconditioning such as temperature, light intensity, CO_2 concentration, and soil water deficit affect stomatal response, gas exchange and photosynthesis (Mooney and Harrison, 1970; Berry and Bjorkman, 1980; Lieth and Pasian, 1990; Xie et al., 1996; Moriana et al., 2002). Based on changes during the day or between days, Heinicke and Childers (1937) concluded that light was the major factor affecting whole-canopy NCER of apple trees, and temperature was second most important, although Sirois and Cooper (1964) concluded CO_2 was second. A recent study (Corelli-Grappadelli and Magnanini, 1993) reported short-term whole-canopy NCER measurements declined with gradually declining light levels for one apple tree. Photosynthesis and transpiration were greatly influenced by stomatal behavior. Stomatal opening is affected by CO_2 concentration, vapor pressure gradient (VPG), light, turgor pressure caused by change in potassium and organic acids, and by abscisic acid (ABA) (Raschke, 1970; Schulze and Hall, 1982). Berry and Bjorkman (1980) found light intensity, CO_2 concentration, temperature, and soil water deficit may have affected gas exchange of plants in a greenhouse. Bunce (1984) reported photosynthesis increased when humidity was increased in the environment. Transpiration at noon under a high temperature after 48 h of acclimation was 400% higher than under a moderate temperature. Stomatal resistance reached a minimum at noon, in accordance with the transpiration rate. Leaf wa-

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ter potential (ψ_L) reached minima of -1.01 and -0.72 mPa at noon under high and moderate temperatures, respectively (Hall and Kaufman, 1975).

Leaf photosynthesis can be influenced by many plant factors such as leaf age, leaf position, sink effects, and mutual shading, as well as environmental factors such as light, temperature, nutrition, and water availability (Constable and Rawson, 1980; Field and Mooney, 1983; Leech and Baker, 1983; Lieth and Pasian, 1990). Constable and Rawson (1980) suggested that leaf position and age influence leaf area, gas exchange, leaf conductance, and saturated net photosynthetic rate. Lieth and Pasian (1990) also found young, expanding leaves had low net photosynthesis. Leaf age and structure affected the number of mesophyll cells and subsequently influenced photosynthesis (Araus et al., 1997). However, only a few studies have focused on plant leaf position and age influencing photosynthesis, and no published reports were found on Asia pear.

This paper will examine the effect of leaf position and leaf age on the gas exchange of field-grown pear trees. Individual pear leaves were monitored from the unfolding to mature stages, and detailed measurements were made at various node positions and leaf age. The aim of the studies was to uncover general patterns of gas exchange, stomatal resistance, photosynthesis, vapor pressure deficit, and transpiration of Asian pear.

Materials and Methods

Plant Materials and Growth Conditions

All trials were performed on two cultivars of Asian pear (*Pyrus serotina* Rehd) Huanghua and Jingshiu II in 1997 to 1998. The trees were 7 years old, grown on *Pyrus betulaeflia Bunge* rootstock in red-clay-loam soil, pH 4.8 ~5.5, on the Hunan Agricultural University experimental farm in Changsha, Hunan, in southern China. Tree spacing was 4.5 m between rows and 2.5 m within rows with a north-south orientation. Standard fertilization, pest control, and irrigation practices were used to assure that the trees were in good health, with no serious disease or insect problems.

Experimental Design

Five similar trees were randomly selected from the experimental orchard to account for any possible differences between individual trees. On each tree four branches were tagged, one per quadrant (east, south, west and north). Leaves 3, 7 and 12 (from the base of the branch) of each branch were tagged for leaf age measurements. Leaf age was determined as the number of days after the leaflet unfolded. Leaf length and photosynthesis were measured at different ages.

Another five trees were randomly selected in the same orchard. Two healthy branches with disease-free leaves in the southeast and northwest quadrants were tagged and numbered from the apex to the base of each branch on 20 June 1997 to measure photosynthesis and anatomical structure as a function of leaf development.

Gas Exchange Measurement

Leaf photosynthesis was measured using the LI-6200 portable photosynthesis system (LI-COR, Lincoln, Nebraska 68504, USA) on attached leaves in the field between 10:00 a.m. and 2:00 p.m. (Beijing time) on sunny days. Air temperature (Ta), leaf temperature (Tf), relative humidity (Rh), net photosynthesis (Pn), stomatal conductance (Gs), intercellular CO_2 concentration (Ci), stomatal resistance (Rs), and stomatal conductance (Cs) were measured or calculated. Leaf gas exchange readings were taken by quadrants (i.e., readings were taken from the eastern, southern, western, and northern quadrants of each tree) to minimize any potential environmental impacts.

Leaf Structure

Following Pn measurements, some leaves were collected to estimate leaf area, anatomical structure and stomatal density. After determining their area (LI-3100 leaf area meter, LICOR, Lincoln, Nebraska 68504, USA), some leaves were sprayed with collodion using an airbrush. The epidermis was then removed, and stomates were counted under a light transmission microscope (Shanghai Instrument Cooperative, Shanghai, China). Other leaves were also sliced (Shanghai Instrument Cooperative, Shanghai, China). The thickness of the palisade layer, the spongy mesophyll, and the intercellular space fraction were measured under a light transmission microscope (Shanghai Instrument Cooperative, Shanghai, China).

Statistics and Data Analysis

All data were the average of multiple replicated measurments. Statistical analyses were conducted via SAS and Microsoft Excel.

Results

The Relationship Between Leaf Expansion and Age

The leaf expansion rates of the two cultivars of Asian pear in southern China were different (Figure 1), with “Huanghua” leaves completely expanding to a length of 7.67 cm after 20 days, whereas “Jingshiu II” required 25 days to reach its maximum length of 9.01 cm. Leaves of both cultivars had similar growth patterns, with leaves expanding quickly in the first 10 days, after which the expansion rate slowed.

Leaf Structure

After Pn measurements, some “Huanghua” pear leaves were collected to evaluate leaf area, anatomical structure, and stomatal density (Table 1). The anatomical structure varied according to the node position of the leaf, with palisade thickness increasing and the thickness of spongy mesophyll decreasing from the base to the apex of the

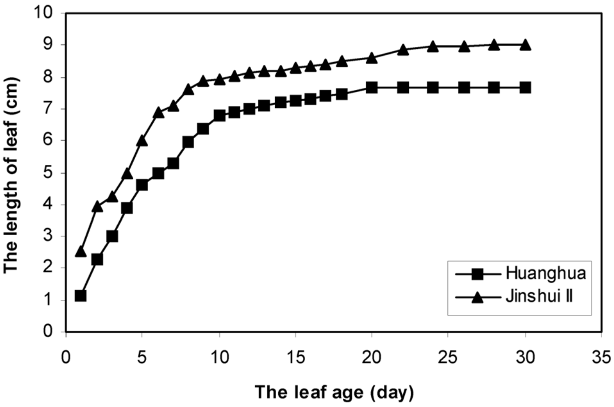

Figure 1. The leaf growth and developmental curves of Asian pear cv. Huanghua and Jinshiu II. Leaf age was determined as the number of days from the date on which the leaflet unfolded.

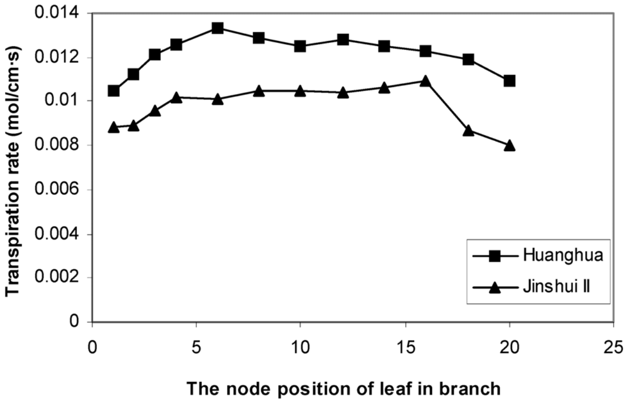

Figure 2. The relationship between transpiration rate and the leaf position in the branch of Asian pear cv. Huanghua and Jinshiu II. The leaf position was counted from top to base of branch. The measured leaves are fully expanded.

branch. The intercellular space of the more apical leaves was less than that of the leaves in the basal positions. However, the trend was reversed for stomatal density and the ratio of the palisade to spongy mesophyll tissue, with greater values for apical position leaves than leaves in the basal positions. The largest leaves on the branch were at nodes 9 to12.

Transpiration and Leaf Position

The transpiration rate varied with the node position of the leaf on the branch (Figure 2). The transpiration rate and vapor pressure deficit of old leaves at the base of branch, as well as the young leaves at the apex of the branch, were low. Leaves at nodes 3 to 16 had a higher transpiration rate. Both cultivars followed a similar pattern. However, the transpiration rate of "Huanghua" were greater than those of "Jingshui II." The maximum transpiration rate of "Huanghua" was 13.2 mmol $m^{-2}s^{-1}$, whereas that of "Jingshiu II" was 10.8 mmol $m^{-2}s^{-1}$.

Photosynthesis and Leaf Age

Net photosynthesis and stomatal conductance of Asian pear cv. Huanghua and Jingshiu II increased rapidly during the first 11 days after leaf unfolding (Table 2), followed by continued, but relatively slow leaf expansion. Net photosynthesis reached a maximum value when the leaf was completely expanded and then gradually declined. In contrast, the stomatal resistance of the leaf decreased with leaf age. During leaf expansion, young (apical) and old (basal) leaves had greater stomatal resistance. CO_2 concentration in intercellular spaces and leaf age shared no statistically significant relationship although a negative trend was observed.

There were differences between the photosynthetic characters of the two varieties. The stomatal conductance and net photosynthesis were, respectively, 0.39 µmol CO_2 $m^{-2}s^{-1}$ and 4.6 µmol CO_2 $m^{-2}s^{-1}$ for leaves of "Jingshiu II" 3 days after unfolding. Leaves of "Huanghua" at the same leaf age had greater net photosynthesis, 5.6 µmol CO_2 $m^{-2}s^{-1}$. Net photosynthesis peaked when the leaf age was 25 days for "Jingshiu II" and 20 days for "Huanghua."

Photosynthesis and Leaf Position

Gas exchange was measured from leaves at different node positions on healthy branches of Asian pear cv. "Huanghua" and "Jingshiu II." Leaves were different due to differences in the stage of development from the apex to the base of the shoot. Both apical position leaves and basal position leaves had lower stomatal conductance and lower net photosynthesis. Intermediate position leaves had higher photosynthesis and higher conductance (Figures 3 and 4). Net photosynthesis peaked, 11.75 µmol

Table 1. The relationship between leaf position and leaf anatomical structure of *Asian pear* cv. Huanghua.

Leaf of position*	Thickness of palisade layer (µm)	Thickness of spongy mesphyll (µm)	Intercellular space %	Area leaf (cm^2)	Stomatal density No./mm^2
3	97±8	118±9	26±2	10.75±0.91	207±20
6	104±11	102±10	23±4	17.43±1.10	267±18
9	109±6	91±5	20±3	35.74±1.73	254±21
12	115±10	88±5	18±1	35.17±2.35	408±27
15	121±13	83±6	15±2	23.47±1.65	498±31

*Leaf position was numbered from the base leaves to the top leaves on the branch. Data were the mean value ± s.d.

Table 2. The effect of leaf age on photosynthetic character of Asian pear cv. Jinshiu II and Huanghua. Leaf age was determined as the number of days from the date on which the leaflet unfolded.

Varieties	Age of leaf (day)	Cc (Mgkg^{-1})	Ci (Mgkg^{-1})	Gs (μmolm^{-2}s^{-1})	Pn (μmolm^{-2}s^{-1})
Jinshiu II	1	368.5	352.7	0.22	-0.19
	3	372.9	338.4	0.39	4.65
	7	356.2	323.5	0.54	6.30
	11	353.0	312.8	0.56	9.19
	15	345.1	306.2	0.56	10.87
	20	342.0	292.1	0.45	11.87
	25	359.7	290.8	0.42	12.58
	30	347.1	293.8	0.41	11.67
	35	350.6	289.5	0.37	11.43
Huanghua	1	248.3	321.4	0.40	3.52
	3	343.9	308.8	0.47	5.61
	7	338.1	309.4	0.67	6.47
	11	344.9	307.5	0.72	8.85
	15	339.2	303.5	0.74	10.06
	20	342.1	302.1	0.74	11.62
	25	343.1	301.5	0.73	10.96
	30	336.5	291.2	0.65	10.72
	35	336.1	298.2	0.58	10.51

Cc: CO_2 concentration in photosynthetic chamber; Ci: intercellular CO_2 concentration; Gs: stomatal conductance; Pn: net photosynthesis.

CO_2 m^{-2}s^{-1}, at the seventh leaf (numbered from the apex to the base) on the branch of "Huanghua." The maximum value for "Jingshiu II" was 12.64 μmol CO_2 m^{-2}s^{-1}, measured at the eleventh leaf on the branch. Stomatal conductance of top position leaves of Huanghua was significantly greater than that of Jingshiu II leaves at the same position. However, intermediate position leaves showed no significant difference in stomatal conductance.

Discussion

Leaf area determines light interception and thus influences dry matter production of plants. Similarly, it plays an important role in determining plant CO_2 uptake and photosynthesis (Liu and Stütze, 2002). The different genotypes of Asian pear varied in the time required to reach maximum leaf area, with "Huanghua" leaves completely expanded after 20 days and "Jingshiu II" only after 25 days (Figure 1). The leaf growth patterns are basically similar. These growth curves have two phases: a rapid phase, probably reflecting cell division and a slow phase, reflecting cell expansion. For the cell division phase, due to the faster cell division and greater quantity of cells, there is clear difference in rate of leaf expansion, with "Jingshiu II" expanding at a higher rate than "Huanghua." A large leaf area also results in "Jingshiu II." The cultivars in phase 2 seem to have no differences as cell expansion rates are similar. Our data also showed differences in stomatal conductance in fully expanded leaves and across all nodes between the cultivars but no strong differences in photosynthesis (Table 2, Figures 3, 4). Thus differences in leaf growth patterns between the two cultivars are not related to the sup-

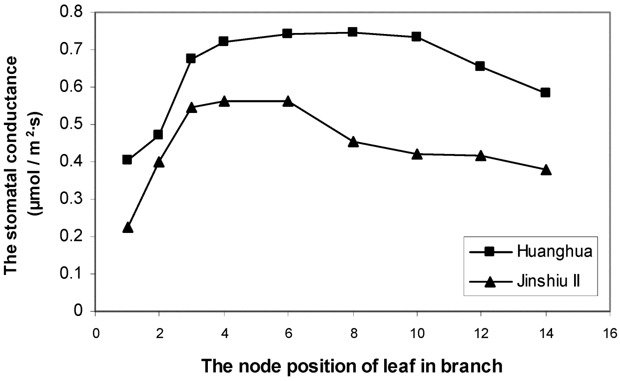

Figure 3. The relationship between stomatal conductance and leaf position on the branch of Asian pear cv. Huanghua and Jinshiu II. The leaf position was counted from top to base of branch. The measured leaves are fully expanded.

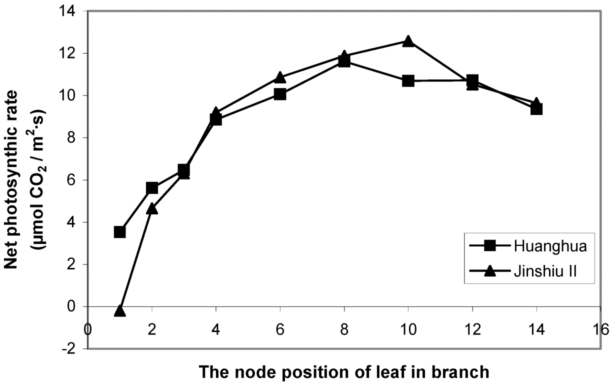

Figure 4. The relationship between net photosynthetic rate and leaf position on the branch of Asian pear cv. Huanghua and Jinshiu II. The leaf position was counted from top to base of branch. The measured leaves are fully expanded.

ply of carbon. Instead, "Huanghua" may possibly lose water more easily and hence may be slightly water stressed. This may affect cell division and hence the slower expansion rate and smaller leaf area of this cultivar compared with "Jingshiu II."

The Pn and stomatal conductance of both genotypes changed with leaf age, increasing rapidly in the beginning. Pn peaked when the leaf had completely expanded. After this, it gradually declined. Leech and Baker (1983) observed that Pn was low for young, rapidly expanding leaves and maximum at some intermediate age, followed by a gradual decline as leaves aged. Field and Mooney (1983) reported leaf age had an impact on saturated net photosynthetic rate. Using potted kiwifruit, Greer (1999) demonstrated maximum rates of photosynthesis coincided with, or shortly followed, full leaf expansion, and photosynthetic development was dependent on the environmental history of the leaves. Young expanding leaves were characterized by low efficiency of photochemistry and photosynthesis, low capacity for both electron transport through photosystem II, low CO_2 fixation, high respiration, and a high capacity for non-radiative thermal dissipation (Greer and Halligan, 2001). When the leaves had fully expanded, there were marked shifts towards higher photon yields, ETR and Pmax, and low respiration and NPQ. The increase for young, completely expanded leaves has been attributed to biochemical changes in the production of fully developed chloroplasts, including synthesis of a variety of molecules and increases in the total number of chloroplasts (Constable and Rawson, 1980; Leech and Baker, 1983; Lieth and Pasian, 1990). Reductions in photosynthetic rate as leaves age have been attributed to reductions in concentrations of enzymes involved in the various photosynthetic reactions (Zima and Sestak, 1979) and chloroplast membrane composition (Novitskaya et al., 1977).

Photosynthesis and transpiration are greatly influenced by stomatal behavior. The stomatal opening is affected by CO_2 concentration, vapor pressure gradient (VPG), light, turgor pressure caused by changes in potassium and organic acids, and by ABA (Raschke, 1970; Schulze and Hall, 1982). Stomatal and internal conductances, either independently or together, have been proposed as the cause of changes in Pn with leaf age. Most studies have shown that the decline in Pn is associated with a reduction in stomatal conductance (Begg and Jarvis, 1968; Buttery, and Buzzel 1977; Constable and Rawson, 1980). Hodgkinson (1974) reported the internal conductance of lucerne leaves had marked reductions as they aged beyond 40 days. Salih (1977) found that stomatal conductance of bean began to decline even while internal conductance was still increasing. Bhatti et al. (1998) pointed out the reduction in photosynthesis was probably caused in part by an increase in stomatal resistance. Constable and Rawson (1980) observed similar results with cotton. Our data gave indications that Asian pear cv. Huanghua and Jingshiu II had the same relationship between stomatal CO_2 conductance and leaf age as reported for other plant species. Wunsche et al. (2000) demonstrated that photosynthesis was highly correlated with stomatal conductance. From our data (Table 2), "Huanghua" showed a similar trend between Pn and stomatal conductance while "Jingshiu II" did not. Additional research is required to determine the cause for this difference.

Leaves at different positions on the branch had different leaf areas and stomatal densities and were at different developmental stages. Leaves with the larger leaf area were located at intermediate positions (nodes) along the branch with more apical and basal node positions having smaller leaves. The largest leaves on the branch were at nodes 9 to12. The stomatal density of the basal leaves was lower than that of leaves in apical positions. The thickness of the palisade layer increased with the node position of the leaf from the base to apex of the branch while the thickness of the spongy mesophyll decreased. Since photosynthesis occurs within the palisade cells, the increase in thickness of the palisade tissue provides for greater production of carbohydrates. Greer (1996) observed that kiwifruit vines produced 0.5 leaves per day, with the earliest expanding leaves taking about 40 days and later emerging leaves up to 70 days to expand fully. Maximum leaf area increased up to leaf 9 then declined with later emerging leaves. Photosynthesis and photochemical efficiency depended on node position, but were both highest in the earliest emerging leaves. Maximum photosynthetic capacity of individual leaves generally occurred in concert with leaves reaching full expansion. Apical leaves were immature while basal position leaves were old. Both apical leaves and basal leaves had higher stomatal resistance and lower net photosynthesis. Intermediate position leaves of Asian pear trees had higher photosynthesis and lower resistance (Figures 3 and 4). The apical leaves of "Huanghua" branches had a net photosynthesis rate greater than "Jingshiu II"; this was reversed for intermediate position leaves. The transpiration rate and the difference of water pressure had the same trend as Pn (Figures 2 and 3). Transpiration rates of "Huanghua" leaves across all nodes are higher than those for "Jingshiu II", and in fully expanded leaves (Table 2), stomatal conductance of "Huanghua" is higher (0.65 $\mu mol/m^2/s$) than "Jingshiu II" (0.4 $\mu mol/m^2/s$). Thus, the high transpiration losses of "Huanghua" can be attributed to more open stomata. Rawson and Hackett (1974) found the leaf position on the stem of tobacco affected gas exchange and transpiration rate, with intermediate position leaves having higher net photosynthesis and transpiration. The photosynthesis and transpiration rate per unit area of cotton leaves at intermediate nodes of branch tended to be higher than those of immature leaves at the apex and old leaves at the basal nodes (Constable and Rawson, 1980). However, Greer and Halligan (2001) found that fully expanded kiwifruit leaves had low respiration rates. Further research is required to make a more precise evaluation.

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亞洲梨葉位元和葉齡對解剖結構、光合作用、氣孔導度及蒸散作用的影響

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在田間條件下，研究了 7 年生亞洲梨－黃花、金水二號（*Pyrus serotina* Rehd. cv. *culta* rehd.）不同葉位元和葉齡對解剖結構、光合作用、氣孔導度及蒸散作用的影響。葉片解剖結構隨葉位元不同而異，從枝條基部葉到頂部葉，柵欄組織厚度增加、海綿組織厚度減少。從頂部葉到基部葉，葉肉細胞空隙逐漸減少。金水二號完全展葉需要 25 天，黃花只需要 20 天。兩品種的淨光合作用（Pn）和氣孔導度（Gs）隨葉齡的增加而增加，在葉片生長初期這種趨勢更加明顯。當葉片完全展後，淨光合作用達到最大值。枝條基部老葉的蒸散作用、蒸氣壓差比頂部新葉的強。枝條上第 3片葉到第 16片葉的蒸散率、蒸氣壓飽和差較高。枝條基部老葉及頂部新葉的氣孔阻力較大，淨光合率較低。

關鍵詞：亞洲梨；解剖結構；葉位；葉齡；光合作用；氣孔導度；蒸散作用。