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RESEARCH ARTICLE

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Comparison of stomatal characteristics and photosynthesis of polymorphic *Populus euphratica* leaves

Abstract The leaf shapes of adult *Populus euphratica* vary from lanceolate to dentate broad-ovate. In order to find the mechanism regarding the ecological adaptation of the polymorphic leaves, the dentate broad-ovate, broad-ovate, and lanceolate leaves were chosen to study their stomatal and photosynthetic characteristics. It is observed that the stomas on the adaxial and abaxial epidermis of the same leaves open non-uniformly with similar densities. The stomatal densities are different among the three typical leaves, which decrease from broad-ovate to lanceolate leaves. Their stomatal sunken degree varied obviously, decreasing from broad-ovate to lanceolate leaves. The changes of the diurnal photosynthetic rate of the three typical leaves follow a single peak curve. The mean diurnal photosynthetic rates of these leaves rank from high to low as broad-ovate > dentate broad-ovate > lanceolate leaves. The light compensation points are similar in the three typical leaves, while the light saturation points vary obviously. The efficiency of solar energy conversion and potential activity of the PSII in the leaves differ significantly, with the dentate broad-ovate leaves the highest. The results suggest that their leaf shapes, anatomic structures, and photosynthetic characteristics change during the leaf development.

Keywords *Populus euphratica*, polymorphic leaves, stomas, photosynthetic characteristics, chlorophyll fluorescence

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1 Introduction

Populus euphratica is one of the deciduous arbor belonging to family Salicaceae and genus *Populus*, mainly distributed in arid and desert regions of middle and west Asia, north Africa, and south Europe as a typical drought-mesophyte and mesophyte plant. It is also an important species for desert riverbank afforestation with a strong adaptability to a wide temperature range (Wang, 1995). The shape of the leaves vary from linear lanceolate, narrow lanceolate to lanceolate on the seedlings, young trees and the sprouts at the bottom of the adult trees due to the long-term adaptation to the extremely dry continental climate. In the adult trees there are not only lanceolate leaves, but also rhombus broad-ovate leaves, broad-ovate leaves, dentate broad-ovate leaves, and kidney-shaped leaves (Su, 2003). The leaf shapes show regular changes from lanceolate to dentate broad ovate for both *P. euphratica* transplanted to the Beijing area or the ones growing in the Dunhuang area which is located in the desert of west China. The change is related to the ecological adaptation (Li and Zheng, 2005).

Extensive studies were taken on the resistance of *P. euphratica* in morphology, cytology, physiological ecology, biochemistry, genetics, and molecular biology in recent years (Li et al., 1996; Ma et al., 1998; Fay et al., 1999; Rottenberg et al., 2000; Watanabe et al., 2000; Saito et al., 2002, Chen et al., 2003; Ma et al., 2003; Gu et al., 2004; Zeng et al., 2004; Zhang et al., 2004). But the research on the characteristics of the polymorphic leaves is insufficient, including the comparison of the microscopic structure of the lanceolate and the broad ovate leaves (Chen, 1961), anatomic structure, $\Delta^{13}C$, stomatal, and photosynthetic characteristics of lanceolate and broad-ovate leaves (Wang, 1997), water utilization efficiency and the response to CO_2 enrichment of lanceolate and broad-ovate leaves (Su, 2003), the ability of the osmoregulation of lanceolate and broad-ovate leaves (Yang, 2004), discussion of the anatomic structure and ecological adaptation of the three kinds of typical leaves, dentate broad ovate lanceolate, and broad-ovate leaves (Li and Zheng, 2005). In order to reveal the ecological adaptation mechanism of the polymorphic leaves, the characteristics of leaf stomas, photosynthetic rate, and fluorescent dynamic parameters of chlorophylls were analyzed using the typical leaves as materials like dentate broad-ovate, lanceolate and broad-ovate on the seedlings and adult trees of *P. euphratica* transplanted to Beijing in this study.

2 Materials and methods

2.1 Materials

The adult *P. euphratica* trees were from the nursery of Beijing Forestry University. The two-year-old *P. euphratica* seedlings were transplanted from Yulin cavity, Dunhuang, west China's Gansu Province. The seedlings were cultured and watered in 20-L pots. The measurements were finished during the growing period. *P. canadensis* with dentate broad-ovate leaves and *Salix matsudana* with lanceolate leaves were selected to compare the stomatal density.

2.2 Methods

2.2.1 The test of stomatal density

The stomatal density was observed with an optical microscope mainly referring to Li et al. (1994).

2.2.2 The test of stomatal opening rate, size, and index

The sampling time was in accordance with the test of diurnal changes of photosynthetic rate. The material was fixed as Cao (1995), and observed by scanning electron microscopy (FEI QUANTA 200) at the Institute of Microbiology, Chinese Academy of Sciences. Pictures of at least three different visual fields were taken for each sample, and three of them were selected for statistical analysis. The stomatal opening rate and the epidermis structure were observed from the pictures. The stomatal size was expressed by the length of guard cell. Stomatal index $SI = [S/(E+S)] \times 100$, here S is the number of stomata in a given leaf area, and E is the number of the epidermal cells in the area.

2.2.3 The test of photosynthetic rate

Photosynthetic rate was measured with Ciras-2 photosynthesis apparatus (PP-SYSTERM Company, England). The daily changes of photosynthetic rate were measured in a sunny day during the growing season, and the data was collected every two hours from 5:00 to 19:00. Three pieces of functional leaves in different shapes were chosen at the same side to test, keeping them at the same height for each test. Each leaf was measured three times. Light response curve and CO_2 response curve were made by the given procedures of the apparatus. The light intensity for light response curve was 0, 20, 40, 60, 80, 100, 200, 300, 400, 500, 600, 700, 800, 900, 1,000, 1,200, 1,400, 1,500 μmol/($m^2 \cdot s$), respectively. The fixed light intensity for CO_2 response curve was 800 μmol/($m^2 \cdot s$), and CO_2 concentration was 0, 20, 40, 60, 80, 100, 200, 300, 400, 500, 600, 700, 800, 900, 1,000, 1,100, 1,200, 1,300, 1,400, 1,500 μL/L, respectively.

2.2.4 The test of fluorescent dynamics parameters of chlorophyll *a*

The fluorescent dynamics parameters were measured in a sunny day during the growing season from 9:00 to 10:00 with PAM 2100 modulatory fluorescent apparatus. The leaves were chosen in the same way as Section 2.2.3.

3 Results

3.1 Variation rule of polymorphic leaves

The leaf shape of adult *P. euphratica* in Beijing had similar changes with those in Dunhuang, which showed the regular transition from lanceolate leaf, broad-ovate leaf to dentate broad-ovate leaf (Fig. 1). The shape of lanceolate leaf (Fig. 1A-I) was similar to willow leaf, dentate broad-ovate leaf (Fig. 1A-III) was similar to poplar leaf and broad-ovate leaf shape (Fig. 1A-II) was a transitional type from lanceolate leaf to dentate broad-ovate leaf. All of the *P. euphratica* leaves were lanceolate on seedlings and branches that sprouted from the bottom of the adult trees. With the increase of tree height and branch development, the shape of the leaves transited from lanceolate to dentate broad-ovate. The result was similar to previous researches (Chen et al., 1961; Wang et al., 1997; Su et al., 2003; Yang et al., 2004; Li and Zheng, 2005) in the natural distribution area of *P. euphratica*.

3.2 Changes of stomatal density

As the statistics show in Table 1, the stomatal density of *P. euphratica* was obviously lower than *P. canadensis* and *S. matsudana*, and the difference was significant between adaxial and abaxial epidermis. The leaves of *P. euphratica* seedlings were similar to those of *S. matsudana,* with fewer stomas, and the stomatal density in adaxial epidermis was almost equal to that of *S. matsudana.* The stomatal intensity of dentate broad-ovate leaves was the highest, while that of lanceolate leaves was the lowest on adult *P. euphratica*, showing the transitional characteristics towards xerophytic. The conclusion was consistent with Wang (1995).

3.3 Changes of stomatal size, index and the sinking degree

The stomatal size, stomatal index, and the stomatal sinking degree are able to reflect plant ecological characteristics. The stomatal size and index of the three typical leaves were tested and analyzed according to the picture from the SEM

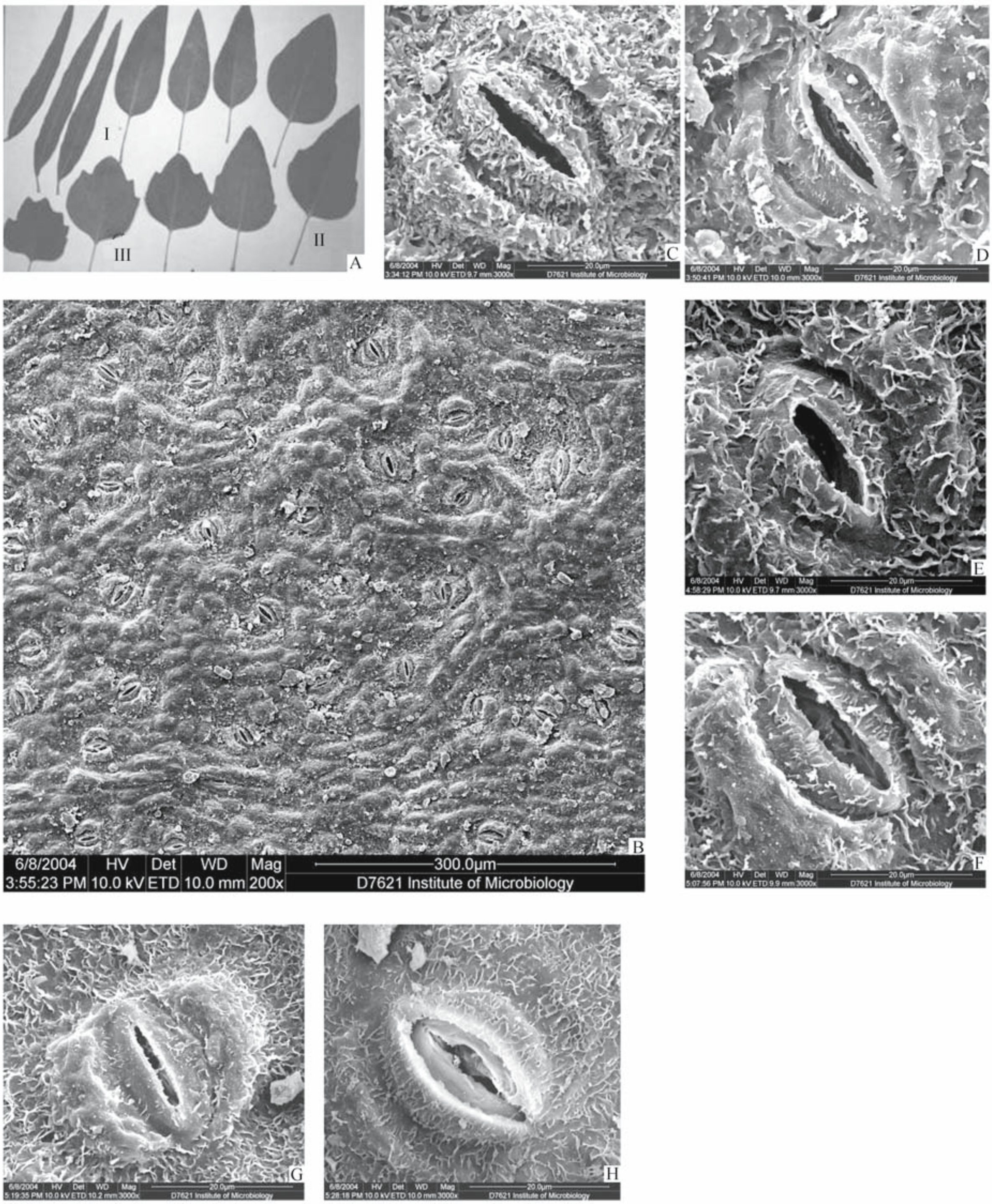

Fig. 1 Comparison of the characteristics of stomas and photosynthesis of *Populus euphratica* polymorphic leaves
A. Polymorphic leaves of *P. euphratica*; B. The view of the adaxial leaf surface of *P. euphratica* by SEM (× 200); C–H. The stomas of adaxial and abaxial dentate broad-ovate leaves, adaxial and abaxial broad-ovate leaves, adaxial and abaxial lanceolate leaves of *P. euphratica* by SEM (× 3,000), lanceolate leave of *P. euphratica* by SEM.

(Table 2). It indicated that there were distinct differences in the stomatal size and index of the three typical leaves. The stomatal size of dentate broad-ovate and broad-ovate leaves was larger than that of lanceolate leaves. The stomatal index of dentate-broad ovate leaves was larger than the others.

It can be deduced that all the leaves had substomatal chambers according to the cell structures under the stoma in the microscopic images. The darker color and invisible structure of the mesophyll cells through the stomas showed that the gap between the cells was broad (Fig. 1D). The darker color and

Table 1 Comparison of stomatal density (unit: stoma · mm^{-2})

Tree species	Adult *Populus euphratica*			Leaves of *Populus euphratica* seedlings	Leaves of *Populus canadensis*	Leaves of *Salix matsudana*
	Dentate broad-ovate leaf	Broad-ovate leaf	Lanceolate leaf			
Adaxial	110.9 (1.3)	98.1 (3.1)	93.7 (1.5)	97.3 (4.7)	418.3 (6.2)	97.7 (3.3)
Abaxial	103.1 (0.9)	95.4 (0.4)	90.1 (0.8)	97.3 (2.9)	781.4 (5.7)	315.2 (4.6)

Note: The number in the bracket is standard deviation, the same as below.

Table 2 Comparison of stomatal size and index

	Dentate broad-ovate leaves	Broad-ovate leaves	Lanceolate leaves
Stoma size /μm	30.4 (0.5)	30.6 (0.9)	28.4 (1.2)
Stomatal index	14.5 (2.1)	11.5 (0.8)	11.5 (1.1)

visible structure of the mesophyll cells through the stomas indicated a narrow gap between the cells (Fig. 1F). Inferred from above, the substomatal chamber sizes of the three typical leaves increased from dentate broad-ovate leaf, broad-ovate leaf to lanceolate leaf. The stomatal sinking degree presented regularly changes, which was observed clearly on the wide visual field (Fig. 1B) and guard cell images (Fig. 1C–H). The stomatal sinking of the abaxial epidermis was deeper than that of the adaxial epidermis. The stomatal sinking of dentate broad ovate and broad ovate leaf was deeper than that of lanceolate leaf on the same surface. The result coincides with the anatomic observation from Li and Zheng (2005). The stoma sinking, substomatal chamber (Li et al., 1996; Huang et al., 1995), and the change of stoma size (Li, 1994) were all drought-tolerant characteristics of plants. The anatomy of cell and tissues shows that *P. euphratica* polymorphic leaves approach the characteristics of common arid desert plants. It was the reflection of long-term adaptation to the environment.

3.4 Changes of stomatal opening rate

The stomatal opening rate of adaxial and abaxial epidermis of the leaves of *P. euphratica* planted in Beijing was analyzed according to the pictures and the mean value shown in Table 3. The result indicated that the stomas of *P. euphratica* belonged to non-uniform opening and closure (Xu, 1995), i.e., part of the stomas opened and part closed in the daytime. The stomatal opening rate of the three typical leaves was larger at noon than in the morning and night. There exists a difference in variation range among the three typical leaves: the range of dentate broad-ovate and broad-ovate leaves was lower, while the range of lanceolate leaf was higher. The stomatal opening rate of the broad-ovate leaves was higher than others, while that of the lanceolate leaves was the lowest according to the diurnal mean value. Xu (1995) considered that many factors, such as water deficiency, low humidity, intense light and high CO_2 concentration, could cause the stomatal nonuniform opening and closure. The variation of the stomatal opening rate of *P. euphratica* polymorphic leaves reflected the adaption to drought and intense light.

Table 3 The diurnal changes in stomatal opening rate of polymorphic leaves (unit: %)

Time of data collection	Dentate broad-ovate leaves	Broad-ovate leaves	Lanceolate leaves
7:00	73.6 (2.3)	76.9 (0.9)	65.6 (1.3)
13:00	74.6 (5.9)	88.9 (3.7)	84.7 (2.0)
17:00	63.1 (0.6)	78.0 (0.1)	38.0 (0.7)
Daily average	70.4	81.3	68.7

3.5 Changes of photosynthetic rate

The changes of daily photosynthetic rate of the polymorphic leaves of *P. euphratica* growing in Beijing were measured from 2002 to 2004, and the result agrees with Ma et al. (1998). The daily changes of photosynthetic rate of the three typical leaves all presented a single peak curve. As shown in Table 4, there were differences in the mean value of the diurnal photosynthetic rate of the polymorphic leaves in the three-year research. The mean value of the diurnal photosynthetic rate of the dentate broad-ovate and broad-ovate leaves was higher than that of the lanceolate leaves. It implied that the dentate broad-ovate and broad-ovate leaves have strong survival ability with high light utilization efficiency.

Table 4 The average value of the diurnal photosynthetic rate of polymorphic leaves (unit: μmol · m^{-2} · s^{-1})

Leaf type	2002	2003	2004	Total average
Dentate broad-ovate	8.1 (0.2)	8.4 (0.5)	7.9 (2.5)	8.1
Broad-ovate	8.6 (0.5)	8.9 (0.3)	9.1 (0.9)	8.9
Lanceolate	6.3 (0.9)	6.4 (1.4)	6.2 (0.4)	6.3

3.6 Responses of photosynthetic rate to light intensity and CO_2 concentration

The response curve of photosynthetic rate to light intensity and CO_2 concentration is shown in Fig. 2. It indicates that the CO_2 saturation point is high in *P. euphratica*. In the same condition, there were differences in light saturation point among the three polymorphic leaves, which are 932 (dentate broad-ovate), 1,025 (broad-ovate), and 881 (lanceolate) μmol/(m^2 · s), respectively. Otherwise, the light compensation point was about 50 μmol/(m^2 · s) with no obvious difference among them. Under the same light intensity and CO_2 concentration, the photosynthetic rate of broad-ovate leaves was higher than that of the others, which was consistent with the change of stomatal opening rate. It indicated that the broad-ovate leaves have higher light utilization efficiency and a stronger adaptation.

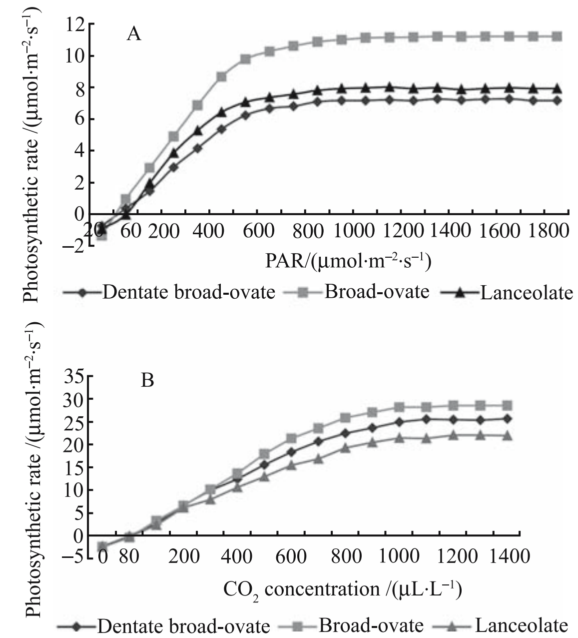

Fig. 2 The trend of photosynthetic rate of polymorphic leaves of *Populus euphratica* in different light intensities (A) and CO_2 concentrations (B)

3.7 Chlorophyll *a* fluorescent parameters

The chlorophyll *a* fluorescent parameters of polymorphic leaves were measured by PAM2100 (Table 5). There were differences in the chlorophyll *a* fluorescent parameters among the polymorphic leaves, in which the F_0, F_m, F_v of the dentate broad-ovate leaves were maximum, the *ETR* of the broad-ovate leaves was the largest, while that of lanceolate leaves was minimum. It showed that the photosynthetic biochemical mechanism varies in *P. euphratica* polymorphic leaves.

4 Discussion

4.1 The shape change of *Populus euphratica* leaves and its ecological adaptability

The phenomena of polymorphic leaf appears commonly in plants, such as *Gossypium hirsutum*, *Ginkgo biloba*, *Eucalyptus*, *Sabina chinensis*, *Sabina vulgaris*, *Broussonetia papyrifera* and so on. It is a result of the temporo-spatial gene regulation and expression, which is correlated with environmental exchanges. For example, a dandelion's leaves change into serration under drought stress. *Trapa*'s leaves in some special environment mutate into submerged leaves and floating leaves separately. *P. euphratica*, as a kind of river-bank afforestation species, originates from places with limited water supply, and its assimilative organs reshape due to the environment changes like drought and desertification, and diversiform leaves appear in the same tree. The leaf shape of *P. euphratica* planted in Beijing, like the ones in the natural distribution areas, turns from lanceolate in seedlings or stump-sprouts to dentate broad-ovate in adult trees (Fig. 1A). This transition is directly correlated to the water supply to leaves. The leaves of seedlings and stump-sprouts of adult trees develop into lanceolate leaves due to the better water supply. The shape of the upper leaves on the tree usually develops into broad-ovate and dentate broad-ovate with better drought resistance, which is caused by the strong light irradiation and insufficient water supply due to evapotranspiration. It has been proven that from lanceolate, broad-ovate to dentate broad-ovate, the leaf structure tends to be more drought-resistant (Li and Zheng, 2005). For example, the palisade tissue is more developed, spongy tissue is decreased, cuticula becomes thicker, stomas sink more, the number of mitochondria increases, and the chloroplast shape changes from regular spindle to irregular rotundity or ellipse. It is reported that the osmoregulation ability of broad-ovate leaves is stronger than lanceolate leaves (Yang, 2004), which shows that its drought-resistance is stronger than the lanceolate leaves. Although the overall water situation of *P. euphratica* growing in Beijing is better than those in the western region, it is still worse than the original conditions. The high temperatures in summer in Beijing causes drought stress for upper leaves of the trees, so the adult *P. euphratica* still retains the polymorphic leaf shapes.

4.2 Stomatal characteristics and ecological adaptation of the polymorphic leaves

Currently, the mesophyte leaves are arranged in the same direction and the stomatal density on the abaxial epidermis is higher than that on the adaxial epidermis. To avoid injury from strong light or to make full use of the scattered light, the leaves of *P. euphratica* are arranged in different directions. Their stomatal density is similar on both leaf sides, and the stomas in abaxial epidermis sink deeper than in adaxial epidermis. That implies that the leaf area for photosynthesis increases, and the photosynthesis can be finished efficiently on both leaf sides, while the transpiration rate decreases and

Table 5 The chlorophyll fluorescence parameters of polymorphic leaves

Leaf type	F_0	F_m	F_v	*ETR*	F_v/F_0	F_v/F_m
Dentate broad-ovate	0.23 (1.21)	1.36 (0.17)	1.13 (0.78)	85 (7.7)	4.88 (2.42)	0.83 (0.54)
Broad-ovate	0.26 (0.64)	1.07 (0.61)	0.81 (0.42)	142 (7.6)	3.07 (0.11)	0.75 (0.53)
Lanceolate	0.27 (0.98)	1.26 (2.36)	0.99 (1.32)	51 (3.5)	3.62 (1.87)	0.78 (1.77)

F_0: initial fluorescence, F_m: maximum fluorescence, F_v (variable fluorescence) $= F_m - F_0$, *ETR*: apparent photosynthetic electric transferable rate (Zhang, 1999).

the water utilization efficiency increases. This is another ability of *P. euphratica* that allows it to exist in drought and high light intensity environments.

From lanceolate to dentate broad-ovate leaf, the stomatal density becomes higher, which also shows a characteristic of drought resistance. Sunken stomata and the bigger substomatal chamber is also an adaptation of plants under drought stress. The bigger substomatal chamber can result in wet environments, which consequently reduces the water loss through transpiration. The sunken stomata also take an active role in reducing light radiation and water loss (Huang, 1997). Compared with the lanceolate leaves, the dentate broad-ovate and the broad-ovate leaves have a higher stomatal density, sinking degree, and larger substomatal chamber. The anatomic differences cause the stronger ability of the dentate broad--ovate and the broad-ovate leaves to tolerate drought and high light intensity. So it is beneficial for *P. euphratica* to survive in the drought environment. The result is the same as the morphologic leaf change of *Sabina vulgaris* (He and Zhang, 2001).

Stomata opening of *P. euphratica* are nonuniform, which is relevant to growth under the stress of drought and light in a long time (Xu, 1995). There are differences in stomatal opening rate among the three typical leaves. The rate of broad-ovate leaves is higher, and that of the lanceolate leaves is lower. The phenomenon is also an adaptation to drought and high light intensity.

4.3 Photosynthetic characteristics of polymorphic leaves and ecological adaptability

Photosynthetic rates of the three typical leaves of *P. euphratica* increase from lanceolate, dentate broad-ovate to broad-ovate leaf. The dentate broad-ovate and broad-ovate leaves at a more advantageous position, with a larger leaf surface for photosynthesis, have a stronger possibility to survive. Lanceolate leaves are in a state of maintaining growth because of the low photosynthetic rate. Generally, since small leaves can reduce water transpiration, sandy or xeric plants hold water by reducing the leaf area, such as *Haloxylon ammodendron* (Huang, 1995, 1997), except *P. euphratica*. With the further growth of *P. euphratica*, it is hard to survive by nutrition from lanceolate leaves, thus broad-ovate and dentate broad-ovate leaves appear with structures to resist severe drought or to retain water and with larger photosynthetic leaf surface. It is useful to improve the photosynthetic rate and water use efficiency of a plant, and it is also beneficial for plant growth and propagation under environmental stress.

Feng et al. (2002) considered that compared with gas exchange index, the chlorophyll fluorescence dynamic parameter is more able to reflect intrinsic trait. For example, water stress can cause F_0 rise and F_v decline, and the extent of this change can be used to identify the ability of the plant to resist or tolerate drought. The result of this paper shows that among the three typical leaves, the dentate broad-ovate leaves have the strongest ability to resist drought with the smallest F_0 and the largest F_v. The measured result of photosynthetic rate and ETR of the three typical leaves shows that the photosynthetic rate follows the order broad-ovate > dentate broad-ovate > lanceolate leaves. Usually, F_v/F_m indicates primary solar energy transition efficiency of PS II and F_v/F_0 indicates potential activity of PS II (Zhang, 1999). The F_v/F_m and F_m/F_0 of dentate broad-ovate leaves are higher than those of the other two types in this paper. It implies that the primary solar energy transition efficiency of PS II and the potential activity of PS II are all higher in the dentate broad-ovate leaves.

In conclusion, the shape of *P. euphratica* leaf varies in morphology, anatomy and photosynthesis during its development to adapt to the desertification of the environment.

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