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Accepted author version posted online: 08 Jan 2014. Published online: 31 Mar 2014.


To link to this article: http://dx.doi.org/10.1080/11263504.2013.878407

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Photosynthetic and water use characteristics in three natural secondary shrubs on Shell Islands, Shandong, China

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Abstract
Ziziphus jujuba var. spinosa Hu, Periploca sepium Bunge, and Securinega suffruticosa (Pall.) Rehd are mainly natural secondary shrubs on Shell Islands of the Yellow River Delta. The physiological characteristics of leaves of the 3-year-old shrub species, including photosynthesis, apparent quantum yield (AQY), dark respiration rate (R₀), light compensation point (LCP), light saturation point (LSP), transpiration rate (E), and water use efficiency (WUE) and so on, were studied by using a Li-Cor6400 portable photosynthesis system. The results showed that the modified rectangular hyperbola model could simulate the photosynthesis–light response curves better, with a compound correlation coefficient (R²) greater than 0.996. There were significant differences in the photosynthetic capacity, AQY, R₀, LCP, LSP, E, and WUE among the three shrub species. The three shrub species displayed different photosynthetic ability in the same environment; the photosynthetic capacity of Z. jujuba was 1.49 times that of S. suffruticosa. Z. jujuba had the highest ability to use low light, and its AQY was 0.058, and that of other two species was among ordinary species. The consumption of photosynthetic products of S. suffruticosa was highest and it had the most active physiological metabolism. Z. jujuba had higher shade tolerance, while these three species were photophilous. The sequence of water-consuming ability by transpiration was in the order of Z. jujuba > P. sepium > S. suffruticosa. The water-consuming ability of P. sepium and S. suffruticosa did not show significant correlation with meteorological factors. P. sepium had the highest WUE, followed by Z. jujuba, and S. suffruticosa had the least. The net photosynthetic rate (Pn) and WUE had evident threshold responses to the variations of soil moisture to maintain high efficient water use. The relative moisture content (Wᵣ) of Z. jujuba, P. sepium, and S. suffruticosa was within the range of 36.18–68.89%, 42.31–81.76%, and 46.87–91.62%, respectively, in which three natural secondary shrubs had higher levels of Pn and WUE. In summary, P. sepium had higher development potential, and Z. jujuba had physiological characteristics of higher photosynthetic ability, transpiration, and WUE, and is the most suitable shrub species for afforestation.

Keywords: Photosynthetic characteristics, water use efficiency, soil water, shrub, Shell Island

Introduction
Shell ridges are distinctive shell sand deposits lying on the upper surface of tidal flats where shellfish and fresh water discharge are minimal. The shell ridge, formed over thousands of years in the Yellow River Delta, is one of the three old shell ridges in the world, and has a very important role and value in the study of the marine geology and biodiversity species. In the recent 20 years, the fragile ecological system in the Shell Island has been severely damaged, and the area of the Shell Island and the biodiversity species reduced sharply because of the increase of human activities, including sand digging, illegal requisitioning, and occupation of forest land, and destructive lumbering. Therefore, the ecological restoration technology with vegetation reconstruction was one of the important measures to recover vegetation and
ecology (Weinstein 2007; Dowarah et al. 2009; Tsonev et al. 2011; Fenu et al. 2012). The selection of shrub species is critical for vegetation restoration, and constructing soil and water conservation plantation with combination of shrubs, grasses, and arbors, mainly with shrubs, has significance for accelerating afforestation and soil and water conservation (Chen et al. 2008; Cano et al. 2011; Xia et al. 2011a,b; Marchetti et al. 2012). However, some problems such as single shrub specie, unreasonable disposition, and selection of shrub species still exist in some areas. Currently people know little about some local shrub species and there is little research about water relationship of plant varieties (Namirembe et al. 2009; Gaitán et al. 2011; Encina et al. 2012; Promis et al. 2012). So, comparing their discrepancy of photosynthesis, transpiration, and zoology adjustability was the basis for providing a scientific basis for vegetation selection and reasonable disposal aiming at local land condition in the process of vegetation construction.

Photosynthesis is the most important physiological process of plants, and one of the criterions in evaluating plant primary productivity (Rascher & Pieruschka 2008; McMinn et al. 2010; Encina et al. 2012; Rahman et al. 2012; Redha et al. 2012; Vashistha et al. 2012). The plant photosynthesis is closely related to its existent ecological environment, and the research on plant photosynthetic characteristics is one of the effective ways to reveal the ecological adaptability of different plants to its existent environment. In recent years, research on crop photosynthesis and its impact factors of microenvironment achieved some results (Stutte et al. 2005; Hegedűșová & Senko 2011; Manolaki & Papastergiadou 2012; Pippo et al. 2012). However, the research on the connection between photosynthesis and soil moisture of shrub species in different sand conditions in vegetation construction, management and reasonable disposal in the process of matching sites with trees, and the techniques of the culture and management under different sand conditions in vegetation construction, this paper systematically compared physiological parameter characteristics of three shrub species, such as photosynthesis, transpiration, and water utility, in order to provide a scientific basis for water management and reasonable disposal in the process of vegetation construction on the Shell Island in the Yellow River Delta.

### Materials and methods

#### Materials

Three-year-old shrub species of *Z. jujuba*, *P. sepium*, and *S. suffruticosa*, which were growing in the full light, were selected, respectively, from natural secondary forests as experimental materials. In March 2012, we selected six seedlings of each species with similar growth from the nursery, and planted each seedling in a pot in the greenhouse where the temperature is 27–32°C, the air humidity is 43–56%, and the concentration of CO₂ is 360–380 μmol mol⁻¹. The soil type is typical of shell sand, and the field moisture capacity (FC) and average soil bulk density are 29.01% and 1.31 g cm⁻³, respectively. The soil organic matter, available nitrogen, available phosphorus, available potassium content in Shell Islands are 1.0%, 5.4%, 5.9%, and 32.5 mg kg⁻¹, respectively. The general growth situation and soil physical properties of the three shrub species in the experiment are shown in Table I. In order to avoid influencing the growth of the root system and the nutrients uptake, self-made containers were designed to a larger size of 1.0 m length × 1.0 m width × 1.5 m depth. The buckets were buried in the shell sand in order to achieve the same conditions as the field environment. Two
Table II. Soil water gradient of the three shrub species.

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>Soil water</th>
<th>Soil water gradient (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Z. jujuba</td>
<td>$W_m$ 5.77</td>
<td>14.01 15.86 19.07 21.03 22.21 24.22</td>
</tr>
<tr>
<td></td>
<td>$W_r$ 20.07</td>
<td>48.73 55.17 66.33 73.15 77.25 84.24</td>
</tr>
<tr>
<td>P. sepium</td>
<td>$W_m$ 6.55</td>
<td>13.42 15.06 17.12 19.66 21.72 23.77</td>
</tr>
<tr>
<td></td>
<td>$W_r$ 22.58</td>
<td>46.26 51.91 59.01 67.77 74.87 81.94</td>
</tr>
<tr>
<td>S. suffruticosa</td>
<td>$W_m$ 7.01</td>
<td>14.12 15.87 18.01 19.87 22.89 24.36</td>
</tr>
<tr>
<td></td>
<td>$W_r$ 23.94</td>
<td>48.22 54.20 61.51 67.86 78.18 83.20</td>
</tr>
</tbody>
</table>

months later, in the middle of June 2012, we selected from these potted seedlings three seedlings of each species with similar growth. We thus had a total of nine experimental seedlings.

Measurement of soil water content

The soil water gradient was achieved by an artificial water supply and the plants’ natural water consumption was measured during June 2012. Two days before measuring photosynthetic efficiency, we provided sufficient water to each seedling to saturate the soil, and then monitored the change in volumetric water content using a Soil Moisture Meter (Delta-T, Cambridge, England, UK). Two days later, the gravitational water content ($W_m$) of the soil was measured for the nine seedlings, using the oven-drying method. For each seedling, five records were taken at 20 cm depth intervals in a 0–100 cm soil layer, the average of $W_m$ was then found. As soil water content decreases continuously by evapotranspiration, every 2 or 3 days, soil water content and photosynthetic efficiency were measured, until the seedling withered. The relative moisture content ($W_r$) is the ratio of $W_m$ to FC. Data points under nine different soil water content situations (Table II) were obtained for each of the tree species.

Observation of light response process

Three fully developed mature leaves were selected from the center of the crowns, and denoted carefully, so nine leaves were measured for each shrub species and the same leaf was selected for the three repeated observations. A portable photosynthesis system (Li-Cor6400, Li-COR Inc., Lincoln, NE, USA) was used to measure the photosynthesis parameters, including net photosynthetic rate ($P_n$) and transpiration rate ($E$). The water use efficiency (WUE) was calculated according to the formula $WUE = P_n/E$.

In order to reduce the effect of light fluctuation, the time of observation was always between 09:00–11:00 am on a sunny day. For the measurements, 12 gradients photosynthetic photon flux density (PAR) of 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 300, 150, 100, 50, 20 μmol m$^{-2}$s$^{-1}$ from a LI-COR LED (Li-COR Inc.) irradiation source was supplied, and CO$_2$ concentration was controlled at 365 μmol mol$^{-1}$ with a LI-COR CO$_2$ injection system (Li-COR Inc.). Air temperature of the leaf chamber was maintained at about 30°C, relative humidity was maintained at 41% and the flow rate of air in the measuring chamber was 200 μmol m$^{-2}$ s$^{-1}$. Before recording of data, the leaves for measurement were kept in the leaf chamber for at least 5 min to reach a steady state of photosynthesis.

Data processing

The water condition keeping $P_n$, $E$ and WUE at the maximal level was regarded as the optimal water environment. Light response curves ($P_n$–PAR curve) were simulated according to the modified rectangular hyperbola model (Ye 2007), and then the maximal $P_n$, namely photosynthetic capacity, was worked out. And the light saturation points (LSPs), the light compensation points (LCPs), the dark respiration rate ($R_D$), and the apparent quantum yield (AQY) were evaluated according to this model. All data, including soil water content 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.

Results

Photosynthetic capacity

The observed and simulated values of $P_n$ to light intensity are shown in Figure 1. The trend of simulated values was uniform to that of the observed value, and the model could accurately simulate $P_n$ to light intensity with the compound correlation coefficient ($R^2$) being above 0.996. The results showed that the response rules of $P_n$ to light intensity of the three shrub species were basically similar. Namely, in the low light intensity (PAR was less than 300 μmol m$^{-2}$ s$^{-1}$), $P_n$ rose in positive proportion with increasing light intensity, indicating that light
intensity was a major limiting factor on photosynthesis. When the light intensity reached a certain value, $P_n$ ascended slowly, indicating that the leaves could not absorb and utilize high light intensity, meanwhile, a series of enzyme’s reaction speeding in the process of CO2 assimilation dropped behind. The $P_n$ of *Z. jujuba* exhibited obviously decreased trend after LSP, while that of the other two shrub species decreased inconspicuously. However, $P_n$ of *Z. jujuba* had the highest level in the same light intensity before LSP. There was considerable discrepancy in the photosynthetic capacity among the three shrub species (Table III), the photosynthetic capacity of *Z. jujuba* was higher with 22.23 $\mu$mol m$^{-2}$s$^{-1}$, and that of *S. suffruticosa* was the lowest with 14.89 $\mu$mol m$^{-2}$s$^{-1}$. The photosynthetic capacity of *Z. jujuba* was 1.49 times as much as that of *Z. jujuba*, indicating that *Z. jujuba* had the physiological characteristic of high photosynthetic capacity.

### Parameters of light response curves to net photosynthesis rate

The parameters for using the modified rectangular hyperbola model to simulate light response curves are shown in Table IV. The compound correlation coefficient ($R^2$) of the three shrub species was all more than 0.996, indicating that the curves could more accurately simulate the light response rules of $P_n$ in low-light intensity. The AQY of *Z. jujuba* was the highest with 0.058, indicating that *Z. jujuba* had the highest assimilation potential and kept the higher photosynthetic ability under low-light conditions. The AQY of *S. suffruticosa* was the lowest with 0.041. Therefore, it was concluded from the above results that *Z. jujuba* was obviously superior to the other two shrub species, both in photosynthetic capacity and in the ability to utilize low light.

There was considerable discrepancy in $R_D$ among the three shrub species. The $R_D$ of *S. suffruticosa* was the highest with about 1.506 $\mu$mol m$^{-2}$s$^{-1}$ and that of *Z. jujuba* and *P. sepium* two shrub species was 1.301 and 1.194 $\mu$mol m$^{-2}$s$^{-1}$, respectively, indicating that various shrub species had different ability to consume photosynthetic products under suitable water conditions. In this study, *S. suffruticosa* had higher ability to consume photosynthetic products than the other two; however, lower $R_D$ of *Z. jujuba* and *P. sepium* could decrease the consumption of photosynthetic products by respiration and was contributed to the accumulation of dry materials, which established well basis on advancing biomass.

The leaf LSP and LCP, reflecting the vegetable photosynthetic requirement to light conditions, were important indexes to judge whether plants had shade endurance or not. The results showed that *S. suffruticosa* had the highest LCP with 38.3 $\mu$mol m$^{-2}$s$^{-1}$, *P. sepium* followed, and the LCP of *Z. jujuba* was 23.0 $\mu$mol m$^{-2}$s$^{-1}$, indicating that *Z. jujuba* had higher shade endurance and abilities than *P. sepium* and *S. suffruticosa* to utilize low light on the appropriate water conditions. *S. suffruticosa* has the lowest ability to utilize low light, which was consistent with the previous results. The LSPs of three shrub species were all greater than 1082 $\mu$mol m$^{-2}$s$^{-1}$ and that of *P. sepium* and *S. suffruticosa* reached above 1300 $\mu$mol m$^{-2}$s$^{-1}$, indicating that the three shrub species relatively adapted to high-light intensity.

### Transpiration rate

Figure 2 showed the transpiration rates decreasing from left to right in optimal water conditions, with shrub species following in the order of *Z. jujuba*, *S. suffruticosa*, *P. sepium*, and *Z. jujuba*.

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**Table III.** Photosynthetic and physiological parameters of the three shrub species in optimal water condition.

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>Photosynthetic capacity ($\mu$mol m$^{-2}$s$^{-1}$)</th>
<th>Maximal water consumption capacity ($\mu$mol m$^{-2}$s$^{-1}$)</th>
<th>Maximal WUE ($\mu$mol mmol$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Z. jujuba</em></td>
<td>22.23</td>
<td>13.5</td>
<td>2.36</td>
</tr>
<tr>
<td><em>P. sepium</em></td>
<td>20.67</td>
<td>8.7</td>
<td>3.28</td>
</tr>
<tr>
<td><em>S. suffruticosa</em></td>
<td>14.89</td>
<td>5.8</td>
<td>1.80</td>
</tr>
</tbody>
</table>

**Table IV.** Simulated values of characteristic parameters from light response curves of the three shrub species.

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>$R_D$ ($\mu$mol m$^{-2}$s$^{-1}$)</th>
<th>LCP ($\mu$mol m$^{-2}$s$^{-1}$)</th>
<th>LSP ($\mu$mol m$^{-2}$s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Z. jujuba</em></td>
<td>0.058</td>
<td>23.0</td>
<td>1082.0</td>
</tr>
<tr>
<td><em>P. sepium</em></td>
<td>0.050</td>
<td>24.6</td>
<td>1385.4</td>
</tr>
<tr>
<td><em>S. suffruticosa</em></td>
<td>0.041</td>
<td>38.3</td>
<td>1428.9</td>
</tr>
</tbody>
</table>

---

**Figure 1.** Observed and simulated light response curves of $P_n$ of three shrub species.
Photosynthetic and water use characteristics

and *P. sepium*. Under the same light conditions (PAR was 1400 µmol m$^{-2}$ s$^{-1}$), the values of $E$ increased from 6.44 ± 0.24 mmol m$^{-2}$ s$^{-1}$ (*P. sepium*) to 10.42 ± 0.32 mmol m$^{-2}$ s$^{-1}$ (*Z. jujuba*), and the increased range was more than 1.60 times, indicating that there was significant discrepancy in $E$ between *P. sepium* and *Z. jujuba*. There was discrepancy in the response rules of $E$ to light intensity among the three shrub species. The $E$ of *Z. jujuba* increased with the increase of light intensity, and could reach 12.5 mmol m$^{-2}$ s$^{-1}$ in the range of measured light intensity. However, the $E$ of the other two shrub species increased inconspicuously with the increase of light intensity. That is, sufficient soil moisture could help plants maintain certain $E$, the opening of the stomata would not enlarge any more and moisture could help plants maintain certain metabolic factors was inconspicuous. These might have something to do with plants’ characteristics and the reason for this still needs further study.

**Water use efficiency**

The soil water that *Z. jujuba*, *P. sepium*, and *S. suffruticosa* had the highest WUE with 55.17%, 51.91%, and 67.86%, respectively. As shown in Figure 3, the light response rules of WUE of the three shrub species were basically similar in low-light intensity (the PAR was less than 400 µmol m$^{-2}$ s$^{-1}$). When the light intensity was higher than LSP, the response curves of *Z. jujuba* and *P. sepium* descended rapidly, and that of *S. suffruticosa* inconspicuously changed. Namely, in suitable water conditions, *S. suffruticosa* was little influenced by light intensity, and adapted to a wider range of light intensity. Under the same light conditions, there was considerable discrepancy in WUE among the three shrub species. *P. sepium* had the highest WUE, that of *Z. jujuba* followed and that of *S. suffruticosa* was last. Compared with WUE of *P. sepium*, WUE of *Z. jujuba* and *S. suffruticosa* was more than 1.60 times, indicating that there was considerable discrepancy in WUE among the three shrub species.

**The soil moisture threshold of $P_n$ and WUE**

The response of $P_n$ to soil moisture was that, in saturated light intensity, the response of $P_n$ was similar to the changes in the soil moisture. Namely, $P_n$ increased with increasing soil moisture. When the $P_n$ reached $P_{n_{max}}$, $P_n$ decreased slowly with increasing soil moisture. Namely, the response of $P_n$ was consistent with the quadratic equation (Figure 4), and the quadratic equation of $P_n$ of *Z. jujuba*, *P. sepium*, and *S. suffruticosa* is given below, respectively:

$$P_n = -0.143W_m^2 + 4.525W_m - 15.89, \quad R^2 = 0.883,$$
$$P_n = -0.1187W_m^2 + 4.2722W_m - 21.014, \quad R^2 = 0.876,$$
$$P_n = -0.0838W_m^2 + 3.3737W_m - 18.694, \quad R^2 = 0.957.$$
The soil moisture that maintained Z. jujuba the maximum \( P_n \) calculated by the quadratic equation was 15.79%, and when \( P_n \) was zero, the corresponding soil moistures were 4.02% and 27.56%, respectively. The soil moisture that maintained P. sepium and S. suffruticosa the maximum \( P_n \) was 18.00% and 20.13%, respectively, and when \( P_n \) was zero, the corresponding soil moistures of P. sepium were 5.88% and 30.11%, respectively, and those of S. suffruticosa were 6.63% and 33.62%, respectively. According to the integration of the regression equations:

\[
\frac{1}{24.22 - 5.77} \left( \sqrt{5.77} \right)^{24.22} (0.143x^2 + 4.525x - 15.89) dx.
\]

The average value of \( P_n \) in the measured range of 5.77–24.22% was calculated and found to be 15.68 \( \mu \)mol m\(^{-2}\)s\(^{-1}\), and the corresponding soil moistures were 10.40% and 21.18%, respectively. Using a similar approach, the average \( P_n \) value of P. sepium and S. suffruticosa was 13.54 and 11.50 \( \mu \)mol m\(^{-2}\)s\(^{-1}\), respectively, the corresponding soil moistures of P. sepium were 12.27% and 23.72%, respectively, and those of S. suffruticosa were 13.43% and 26.83%, respectively. Therefore, the range of \( W_m \)s that maintained higher \( P_n \) values in Z. jujuba, P. sepium, and S. suffruticosa was 10.40–21.18%, 12.27–23.72%, and 44.5–87.5%, respectively, when \( W_m \) was less than 4.02%, 5.88%, and 6.63%, respectively, \( P_n \) decreased significantly, and the normal growth of Z. jujuba, P. sepium, and S. suffruticosa was restricted.

During the saturated light intensity corresponding to photosynthesis, the response of WUE to soil moisture was consistent with the quadratic equation (Figure 5), and the WUE increased and decreased with increasing soil moisture, but the soil moisture that maintained highest WUE was different. The quadratic equation of WUE of Z. jujuba, P. sepium, and S. suffruticosa is as follows, respectively.

\[
\text{WUE} = -0.008W_m^2 + 0.240W_m - 0.147, \quad R^2 = 0.895, \\
\text{WUE} = -0.01W_m^2 + 0.346W_m - 0.842, \quad R^2 = 0.993, \\
\text{WUE} = -0.005W_m^2 + 0.228W_m - 0.961, \quad R^2 = 0.944.
\]

According to the solving methods for photosynthesis, the soil moisture that maintained Z. jujuba, P. sepium, and S. suffruticosa the maximum WUE was 14.45%, 15.72%, and 21.10%, respectively. The average value of WUE in Z. jujuba, P. sepium, and S. suffruticosa in the measured range of 5.77–24.22% was calculated and found to be 1.35, 1.60, and 1.15 mol mol\(^{-1}\), respectively, and the corresponding soil moistures were 9.10% and 19.81%, 2.66% and 28.78%, and 13.72% and 28.48%, respectively.

Namely, the range of \( W_m \)s that maintained higher WUE values in Z. jujuba, P. sepium, and S. suffruticosa was 9.10–19.81%, 2.66–28.78%, and 13.72–28.48%, respectively.

**Discussions**

Photosynthesis was an important physiological index for representing different plants or crop species (Xia et al. 2011a,b; Mojaddam et al. 2012; Zhang et al. 2012). The maximal photosynthetic rate of the leaf expressed the maximal photosynthetic capacity under the optimal environment conditions (Tartachnyk & Blanke 2004; Yuan et al. 2012). Researches indicated that there was considerable discrepancy in the leaf maximal photosynthetic rate among various plants under the conditions of non-adversity, saturated light intensity and optimum temperature. As shown in this research, the photosynthetic capacity of the three shrub species was intermediate between arbors (Iryna & Michael 2004; Kitaoka & Koike 2004) and C3 plants (Chandrasekar et al. 2000), and had little difference from C3 herbage plants (Yiruhan et al. 2005). The reason for causing different photosynthetic capacities of plants might be the plants’ self-adjustment capacities or be influenced by environmental factors (Meir et al. 2002). Some researchers found that the leaf adapted to the change outside the light environment by regulating the photosynthetic capacity in many ways (Warren & Adama 2001; Walcroft et al. 2002), which was a major reason leading to the discrepancy of photosynthetic capacity among species. Meanwhile, as economical shrubs, they attained higher photosynthetic capacity by adequately utilizing solar energy absorbed by the light-harvesting pigment, thereby, improving light use efficiency to accumulate more ATP and NADPH for carbon assimilation and settle the foundation for accumulating more photosynthetic products and high yield.

![Figure 5. WUE of three shrub species under different soil water conditions.](image-url)
In a certain environment condition, AQY reflected the utilization of light, especially the low light (Llusia et al. 2005; Pessarakli et al. 2011). In this research, the modified rectangular hyperbola model simulated light response curves of three shrub species better. Results showed that the AQY of *S. suffruticosa* and *P. sepium* was close to the lower and larger limit values (0.03–0.05) of general plants, respectively. And the AQY of *Z. jujuba* was basically close to that of C3 plant (about 0.055) reported in the literature. The AQY of *Z. jujuba* was highest with 0.058, indicating that *Z. jujuba* had higher ability to use low light than the other two species, and various plants had different abilities to use low light in optimal water conditions. Meanwhile, water stress or water logging decreased the AQY of three shrub species, which was in accord with the study of Centritto et al. (2001). Therefore, the plants’ AQY could be improved in optimal water conditions to some extent.

Respiration is a process that ATP, CO$_2$, and water are generated by oxidizing carbohydrate, fat, and protein, etc., and is adverse to the process of photosynthesis. Dark respiration consumed most of the carbon and energy fixed during photosynthesis, and is essential for plants’ growth. Therefore, dark respiration is regarded as the resources of materials and energy for normal growth of plants, and holds important status in plants’ eco-physiological research (Pessarakli et al. 2011; Xia et al. 2011a,b). In the optimal water and light conditions, there is considerable discrepancy in consuming photosynthetic products among various species, when they obtained maximal $P_n$. The results showed that the $R_D$ of the three shrub species was between 1.194 and 1.506 mmol m$^{-2}$ s$^{-1}$, less than that of economical arbors (Romero & Botía 2006) and obviously higher than that of general arbors (Warren & Adama 2001), indicating that there is considerable discrepancy in adaptability in consuming photosynthetic products among various species, when they obtained maximal $P_n$. The results showed that the $R_D$ of the three shrub species was between 1.194 and 1.506 mmol m$^{-2}$ s$^{-1}$, less than that of economical arbors (Romero & Botía 2006) and obviously higher than that of general arbors (Warren & Adama 2001), indicating that there is considerable discrepancy in adaptability to the environment and physiological adaptability to low light among various plant. Plants, whose LCP is less than 20 mmol m$^{-2}$ s$^{-1}$ and LSP less than 500 mmol m$^{-2}$ s$^{-1}$, are generally regarded as typical shade-demanding plants, whereas plants whose LCP is greater than 50 mmol m$^{-2}$ s$^{-1}$ and LSP greater than 800 mmol m$^{-2}$ s$^{-1}$ are generally regarded as typical light-demanding plants. Compared with other researches (Wen et al. 2000; Yiruhan et al. 2005), the LCP and LSP of the three shrub species indicated that *S. suffruticosa* has certain characteristics of light demand, and *Z. jujuba* and *P. sepium* have powerful adaptability to low light. *S. suffruticosa* and *P. sepium* have wider light ecological amplitude, and *Z. jujuba* has a narrow range to adapt to light environment in an optimal water condition.

Transpiration mainly depended on available water in the soil, essential energy and water potential gradient inside and outside the leaf, namely, it was affected not only by outside factors, but also by the regulation of the plant interior structure and physiological status (Iryna & Michael 2004). Water consumption by transpiration increased with the increase of soil water supply, which was the key factor determining transpiration (Rodriguez-García et al. 2007). $E$ reflected momentary water consumption of unit leaf area, and also reflected the ability to regulate water consumption of shrub species and adapt to drought environment. When the soil water was not a restraining factor, the discrepancy of $E$ reflected the water consumption potential of various shrub species. The results showed that the water consumption potential of *Z. jujuba* was the highest and its momentary water consumption rate was $11.2 \pm 1.12$ mmol m$^{-2}$ s$^{-1}$ on average, performing the characteristic to take root deeply and higher ability to utilize soil moisture by keeping high $P_n$ and $E$ whether in drought seasons or in humid seasons. When the water supply is sufficient, the water consumption potential of *S. suffruticosa* and *P. sepium*, which was determined by their species characteristics and influenced unapparently by the outside environment, was obviously less than that of arbors and herbs (Guo et al. 2003; Romero & Botía 2006) and is close to that of some sand shrub species (Rodriguez-García et al. 2007). It was concluded that the three shrub species had powerful drought-avoiding ability and could resist drought stress by lower water consumption.

WUE was not only a comprehensive ecophysiological index for evaluating plants’ adaptability to the environment, but also one of the significant indexes for confirming essential water supply for plants’ growth (Chen et al. 2008; Pessarakli et al. 2011). The purpose of economical irrigation was to utilize water resources most efficiently. As an effective irrigation index, the WUE of crops could be improved by the following measures: CO$_2$ concentration, decreasing atmospheric humidity (Romero & Botía 2006), controlling soil water supply and so on. Therefore, moderate water shortage could contribute to increase in crop yield. In fact, mild water shortage could improve leaf WUE as well, as shown in Figure 3; the WUE of the three shrub species could reach maximum in moderate water stress, which was in accord with the research of Romero et al. In mild water shortage, the growth of leaf was restrained and $E$ decreased, but photosynthetic enzyme activity and carboxylation efficiency of chloroplast had unapparent change, $P_n$ declined slightly, and so WUE was higher. The relationship between plants and moisture has shown that plants have some adaptability and resistance to soil moisture deficit, and various physiological functions are active under moderate...
moisture deficit (Redha et al. 2012; Zhang et al. 2012). This moisture range varies by plant species and physiological processes. This study showed that the $W_f$ that produced high $P_n$ in Z. jujuba, P. sepium, and S. suffruticosa was in the range of 36.18–73.66%, 42.31–81.76%, and 45.88–91.62%, respectively, and the most suitable $W_f$ was 54.92%, 62.03%, and 68.75% (Figure 4), respectively. Because the leaf WUE is influenced by both $P_n$ and $E$, the suitable $W_f$ was different from that of $P_n$. The $W_f$ that maintained high WUE in Z. jujuba, P. sepium, and S. suffruticosa was in the range of 31.65–68.89%, 9.16–99.20%, and 46.87–97.27%, respectively, and the most suitable $W_f$ was 50.27%, 54.18%, and 72.27% (Figure 5), respectively. From the above results, we conclude that the $W_f$ that maintained efficient water use in Z. jujuba, P. sepium, and S. suffruticosa was in the range of 36.18–68.89%, 42.31–81.76%, and 46.87–91.62%, respectively, which shows that the three shrubs have higher photosynthesis and normal growth, and prevented a higher $E$ to consume more soil water, so that the shrubs could maintain higher WUE. Compared with other studies on shrubs that had different suitable $W_f$ deficits, the optimal $W_f$ of Prunus sibirica was in the range of about 46.9–74.5% (Xia et al. 2011a,b), the optimal $W_f$ of Syringa oblata was in the range of about 59–76% (Chen et al. 2004), and that of Aralia elata was in the range of about 44–79% (Chen et al. 2008), indicating that the Z. jujuba, which had higher drought assistance and did not suffer high soil moisture, adapted to shell sand with deficient soil moisture; S. suffruticosa had no resistant to drought and needed high soil moisture; P. sepium had a wider range to adapt to soil moisture, which could maintain higher $P_n$ and WUE in a wide range of soil moisture.

To summarize the above-mentioned results, it was concluded that S. suffruticosa had a wider range to adapt to light environment, but it had lower photosynthetic capacity and WUE, and it was not suitable for vegetation in the Shell Island. P. sepium had intermediate $P_n$ and $E$, but it had the highest WUE in drought stress. Furthermore, it had been found that moderate water shortage impacted well on both accelerating flower bud differentiation and improving fruits quality. Z. jujuba, which had physiological characteristics of higher photosynthetic capacity and middle WUE, and had higher ability of being anti-drought, was one of the most suitable shrub species for afforestation in the Shell Island area.

Fundings

This work was financially supported by the National Natural Science Foundation of China [grant number 31100468], [grant number 31100196], [grant number 41201023]; by Important National Basic Research Program of China [grant number 2012CB416904/zgc], [grant number 2013CB430403]; by Science and Technology Plan of Universities in Shandong Province [grant number J13LC03]; by the National Key Science and Technology Item in “11th Five Year” period [grant number 2009BADB2B0502]; the Strategic Priority Research Program of the Chinese Academy of Sciences (CAS) [grant number XDA05030404]; One Hundred-Talent Plan of the Chinese Academy of Sciences (CAS); the CAS/SAFEA International Partnership Program for Creative Research Teams; the Chinese Academy of Sciences (CAS) Visiting Professorship for Senior International Scientists [grant number 2012T1IZ0010]; the Science & Technology Development Plan of Shandong Province [grant number 2010GSF10208]; the Science & Technology Development Plan of Yantai City [grant number 2011016]; Yantai Double—hundred High—end Talent Plan [grant number XY—003—02]; and 135 Development Plan of YIC—CAS.

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