Effect of soil water availability on photosynthesis in *Ziziphus jujuba* var. *spinosus* in a sand habitat formed from seashells: Comparison of four models

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Abstract

The photosynthetic and chlorophyll fluorescence parameters were studied in *Ziziphus jujuba* var. *spinosus* under different soil water gradients obtained by irrigation and natural water consumption. We used the rectangular hyperbola model, the nonrectangular hyperbola model, the exponential model, and the modified rectangular hyperbola model to fit our data and evaluate them quantitatively. Based on the relationship among the parameters, the effects of the availability of soil water on photosynthesis were elucidated. The results showed that: (*1*) The relationship between water content and photosynthetic parameters were fitted best by the modified rectangular hyperbola model, followed by the nonrectangular hyperbola model, the exponential model, and the rectangular hyperbola model. The modified rectangular hyperbola model fitted best the maximum net photosynthetic rate (P_{Nmax}) and the light-saturation point (LSP), while the nonrectangular hyperbola model fitted best the dark respiration rate (R_D), the apparent quantum yield (AQY), and the light-compensation point (LCP). (*2*) The main reason for the net photosynthetic rate (P_N) decline was that it reached a stomatal limit when the soil relative water content (RWC) was greater than 25% and it reached a nonstomatal limit when the RWC was lesser than 25%. Under these conditions, the photosynthetic apparatus of *Z. jujuba* was irreversibly damaged. (*3*) P_{max}, R_D, AQY, and LSP increased first and then decreased, while LCP increased contrary to the RWC. The P_N light-response parameters reached optimum when the RWC was 56–73%. (*4*) The quantum yield of PSII photochemistry reached a maximum when RWC was 80%. Nonphotochemical quenching decreased rapidly, and the minimum fluorescence in the dark-adapted state increased rapidly when RWC was lesser than 25%. Under these conditions, PSII was irreversibly damaged. (5) The RWC range of 11–25% resulted in low productivity and low water use efficiency (WUE). The RWC range of 25–56% resulted in moderate productivity and moderate WUE, and the RWC range of 56–80% resulted in high productivity and high WUE. The RWC range of 80–95% resulted in moderate productivity and low WUE. In summary, photosynthesis of *Z. jujuba* was physiologically adaptable in response to water stress in sand formed from seashells. The photosynthetic and physiological activity was maintained relatively high when the RWC was between 56 and 80%; *Z. jujuba* seedlings grew well under these conditions.

Additional key words: chlorophyll fluorescence, light-response model; photosynthetic productivity; relative water content.

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Received 5 October 2013, *accepted* 11 March 2014.
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Abbreviations: AQY – apparent quantum yield; C_i – intercellular CO_2 concentration; E – transpiration rate; EM – exponential model FC – field capacity; F_m – maximum fluorescence of the dark-adapted state; F_m' – maximuml fluorescence yield; F_0 – minimum fluorescence yield of the dark-adapted state; F_s – steady-state fluorescence; F_v/F_m – maximum quantum yield of PSII photochemistry; g_s – stomatal conductance; GWC – gravitational water content; LCP – light-compensation point; L_s – stomatal limiting value; LSP – light-saturation point; MRHM – modified rectangular hyperbola model; NPQ – nonphotochemical quenching; NRHM – nonrectangular hyperbola model P_{Nmax} – maximum net photosynthetic rate; P_N – net photosynthetic rate; R^2 – determination coefficient; R_D – dark respiration rate; RE – relative error; RHM – rectangular hyperbola model; RWC – relative water content; WUE – water-use efficiency; Φ_{PSII} – effective quantum yield of PSII photochemistry.
Acknowledgements: This study was supported by the National Natural Science Foundation of China (No. 31100468 and No. 31100196), the promotive research fund for excellent young and middle-aged scientists of Shandong Province (BS2013NY010), and the Major State Basic Research Development Program (No. 2012CB416904/zgc).
J.B. Xia and G.C. Zhang contributed equally to this work.

Introduction

Photosynthetic efficiency is a critical factor in plant productivity and crop yield (Peng 2000). Soil water availability strongly limits plant photosynthesis, growth, and yield. This is especially true now due to water shortages and droughts across the world (Chaves *et al.* 2003, Islam *et al.* 2008, Varela *et al.* 2010). The key objective of water-saving agroforestry is using limited water resources productively in the field (Deng *et al.* 2006, Kang *et al.* 2007). Much research focused on the effects of soil water content on photosynthetic and water-use efficiency (Galmés *et al.* 2007, Zhang *et al.* 2007a, Xia *et al.* 2011b, Wang *et al.* 2012). However, many of these studies were limited to fewer than eight water gradients and ignored variations in water availability. These limitations resulted in unclear quantitative relationships between photosynthetic parameters and soil water content.

Measuring P_N and fitting these data to a model is important to understand photosynthesis. It allows to determine parameters, such as AQY, R_D, LCP, LSP, and P_{max}. These parameters can reflect photosynthetic efficiency (Robert *et al.* 1984) and have been used to generate light-response models (Webb *et al.* 1974, Ye 2010, Lang *et al.* 2013). Thus, the commonly used models include the rectangular hyperbola model (Lewis *et al.* 1999), the nonrectangular hyperbola model (Thornley 1998), the exponential model (Prado and deMoraes 1997), and the modified rectangular hyperbola model (Ye 2007), all of which have certain advantages and disadvantages. These models are usually evaluated qualitatively (Duan and Zhang 2009, Lang *et al.* 2013), which restricts their accuracy in determining how well the data fit the models.

The shell ridge island of Yellow River Delta in China is a special ecological system formed by seashells and their debris, which accumulate near the high tide line. The soil salinity was the main factor to the seaside of shell ridge island land side, where the vegetation mainly included halophytes. The shell sand/soil does not retain water well due to its high altitude, low groundwater level, large soil porosity, and high content of coarse sand. Together with a high evaporation to precipitation ratio and serious seasonal water shortages in this region, these properties inhibit a growth of vegetation. Therefore the vegetation includes mainly xerophytic shrubs and herbs, and the ecological environment is very fragile. *Z. jujuba* var. *spinosus*, which conserves soil nutrients and water, benefits from the shell ridge island and is a preferred species for restoring vegetation and ecological reconstruction efforts. Much of the previous research on this species has focused on its chemical, medicinal, and economic value (Cheng *et al.* 2000, Peng *et al.* 2000, Outlaw *et al.* 2002). The applicability of the light-response models and the quantitative relationships between the main photosynthetic parameters and the soil water content remain unclear. Therefore, studies on the physiological characteristics of drought resistance in *Z. jujuba* var. *spinosus* are limited in their application to other species and site conditions.

In this study, four models describing the effects of soil water content on photosynthesis in *Z. jujuba* var. *spinosus* leaves were evaluated by using a gradient of water levels and measuring the main photosynthetic parameters and chlorophyll fluorescence. The light-response parameter, P_N, was fitted to these models to provide a theoretical standard for site selection for *Z. jujuba* var. *spinosus*.

Materials and methods

Plants: The experimental site was located in the research greenhouse of the Shandong Key Laboratory of Eco-Environmental Science for the Yellow River Delta in the Shandong Province. In the greenhouse, the light intensity was approximately 85% of that of the natural light in the area. The temperature was 18–30°C, the CO_2 concentration 345–365 μmol mol^{-1} and the relative humidity 41–65%. The experimental substrate was shell sand/soil (Table 1) collected from the wild jujube community in October of 2011; the sand grains with a diameter greater than 2 mm were removed with a sieve. The average soil density was 1.3 g cm^{-3}; the average field capacity (FC) was 24%. The experimental samples were selected from 3-year-old *Z. jujuba* var. *spinosus* plants in the shell ridge island of Yellow River Delta, China. Nine plants were planted in plastic pots (80 cm long × 40 cm wide × 80 cm high) in the greenhouse; this volume was sufficient for unrestricted root growth. The mean root diameter on the ground was 0.8 ± 0.1 cm and the mean plant height was 0.7 ± 0.08 m; 5 best-growing plants were selected for the experiments after 120 days.

Table 1. The physical characteristics of the shell sand soil.

Sample	Soil particle-size fractions [%]				Bulk density	Total porosity	Capillary	Noncapillary	Void ratio
	Gravel	Coarse sand	Fine sand	Silt-clay	[g cm^{-3}]	[%]	porosity [%]	porosity [%]	
Shell sand	17.33	61.31	19.97	1.39	1.25	47.42%	45.14%	2.28%	0.91

The design of the water gradient: A water gradient was generated in the sand by providing water first and then allowing the plants to transpire. The soil in the pots of 5 sample plants was sufficiently watered for 2 days before the examination period (July 12–13, 2012). Then, the soil water was gradually reduced by plant transpiration from July 14, 2012, until the end of the experiment (August 11, 2012). Meanwhile, the soil surface was covered with a plastic film to prevent soil water evaporation. The soil gravitational water content (GWC) of the 5 samples was measured by the oven-drying method on every sunny day (1–2 d intervals). Three samples from each pot were measured. The average relative soil water content (RWC) was calculated on each sunny day as RWC = GWC/FC. Eighteen water gradients were obtained and varied from 11.2 to 94.6% during the experiment.

Experimental methods: The main gas-exchange parameters, including P_N, transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were measured in 5 mature leaves at the center of each plant in response to light. The same leaf was measured 3 times. This was performed using a portable photosynthesis system (*LI-COR 6400*, *LI-COR Inc*., Lincoln, NE, USA) between 9:00–11:30 h on the same days when the GWC was measured. A relative humidity was maintained at 45%, air temperature of leaf chamber was maintained at about 33ºC, and the flow rate of air in the measuring chamber was 200 µmol m^{-2}. WUE and the stomatal limiting value (L_s) in response to light were calculated according to the formulas WUE = P_N/E (Frank *et al*. 1987) and $L_s = 1 - C_i/C_a$ (Farquhar and Sharkey 1982), where C_a is the atmospheric CO_2 concentration. The PPFD was held constant at 1,600; 1,400; 1,200; 1,000; 800, 600, 400, 200, 150, 100, 80, 40 or 20 µmol m^{-2} s^{-1}, with an interval of 120 s by *LI-COR* LED (*LI-COR Inc*., Lincoln, NE, USA) irradiation source.

The main chlorophyll fluorescence parameters were measured in 3 mature leaves at the center of each plant using a portable fluorometer (*FMS-2, Hansatech*, Kings Lynn, UK) at the same time as the gas-exchange parameters. Different leaves were used for these 2 types of measurements. The minimum fluorescence of the dark-adapted state (F_0) and the maximum fluorescence of the dark-adapted state (F_m) were determined after the leaf samples were dark-adapted for 1 h. Then the steady-state fluorescence (F_s) and the maximum fluorescence yield (F_m') were determined in response to 1 h of natural light. The maximum quantum yield of PSII photochemistry (F_v/F_m), the effective quantum yield of PSII photochemistry (Φ_{PSII}), and the nonphotochemical quenching (NPQ) were calculated according to the formula $F_v/F_m = (F_m - F_0)/F_m$, where $\Phi_{PSII} = (F_m' - F_s)/F_m'$ and $NPQ = (F_m - F_m')/F_m'$ (Genty *et al*. 1989, Gilmore and Yamamoto 1991).

Data processing: The P_N curves were drawn, and P_{max}, R_D, AQY, LCP, and LSP were estimated from the curves (Ye 2010). These data were fitted to the rectangular hyperbola model (RHM), the nonrectangular hyperbola model (NRHM), the exponential model (EM), and the modified rectangular hyperbola model (MRHM) (Lang *et al*. 2013) using *SPSS 18.0* (Chicago, IL, USA). Two dimensional contour line maps of gas-exchange parameters showing the RWC and the PPFD were generated using *Origin 8.0* (Easthampton, MA, USA). The quantitative relationships between the soil water content and the light-response parameters or the main chlorophyll fluorescence parameters were identified by polynomial regression analysis and integral solutions using *Origin 8.0* systematic cluster analysis. The analysis of the soil water content was carried out using *SPSS 18.0*. Significant differences between the treatments at a 0.05 significance level were determined using the *Student*'s *t*-test function in *SPSS 18.0*.

Results

Fitting the light responses to the models: The light-response curves of *Z. jujuba* var. *spinosus* leaves under different water conditions were fitted to 4 models, such as the RHM, the NRHM, the EM, and the MRHM. All 4 models fitted the light-response curves well, as shown by the determination coefficients ($R^2 \geq 97.5\%$), although there were some differences (Table 2). The average R^2 value from the MRHM (99.983%) was greater than that for the EM (99.867%). These values were followed by those of the NRHM (99.861%) and the RHM (99.250%) (Table 2). To evaluate the accuracy of the 4 models, the relative error (RE) was calculated according to the formula: $RE = |(y_t - \hat{y}_t) / y_t| \times 100\%$, where $\hat{y}_t$ is the measured value and y_t is the fitted value; neither of these values can be 0.

The greater the RE, the greater the deviation of the measured value from the fitted value. The smaller the RE, the better is the fit of the model to the data. When the RWC was 31.94%, the PPFD was 40 µmol m^{-2} s^{-1}, the P_N was 0 µmol m^{-2} s^{-1}, and the fitted values of the RHM, the NRHM, the EM, and the MRHM were –0.17, –0.05, –0.09, and –0.08 µmol m^{-2} s^{-1}, respectively. Therefore, the RHM provided the worst fit to the data. Under other soil water and light intensity conditions, the mean RE of the P_N light-response curve was 3.86% for the MRHM, 4.13% for the NRHM, 5.47% for the EM, and 11.99% for the RHM (Table 2). These data indicated that the MRHM fitted best the P_N curves. The NRHM provided the second-best fit; it was followed by the EM and then by the RHM. The mean RE of the P_N light-response parameters was 18.93% for the RHM, 24.68% for the NRHM, 37.91% for the EM, and 64.55% for the RHM (Table 2). This order was consistent with that for the P_N light-response curves, while the mean RE of the P_N light-response parameters was greater than that for the P_N light-response curves for every model. This

Table 2. Fitting four models to the net photosynthetic rate (P_N)-light response curves and parameters in *Ziziphus jujuba* var. *spinosus* leaves. Each value of P_N is the mean of 15 replicates. R^2 – determination coefficient; R_D – respiration rate; AQY – apparent quantum yield; LCP – light compensation point; P_{max} – maximum net photosynthetic rate; LSP – light saturation point. RHM – rectangular hyperbola model; NRHM – nonrectangular hyperbola model; EM – exponential model; MRHM – modified rectangular hyperbola model.

Light-response model	Average R^2 [%]	Average relative error [%]						
		Light-response curve	Light-response parameter	R_D	AQY	LCP	P_{max}	LSP
RHM	99.250	11.990	64.547	79.619	115.142	2.386	48.658	76.932
NRHM	99.861	4.130	24.679	14.861	18.056	1.553	22.680	66.247
EM	99.867	5.473	37.908	35.191	46.014	7.441	18.598	82.294
MRHM	99.983	3.859	18.933	36.523	51.921	1.631	0.461	4.128

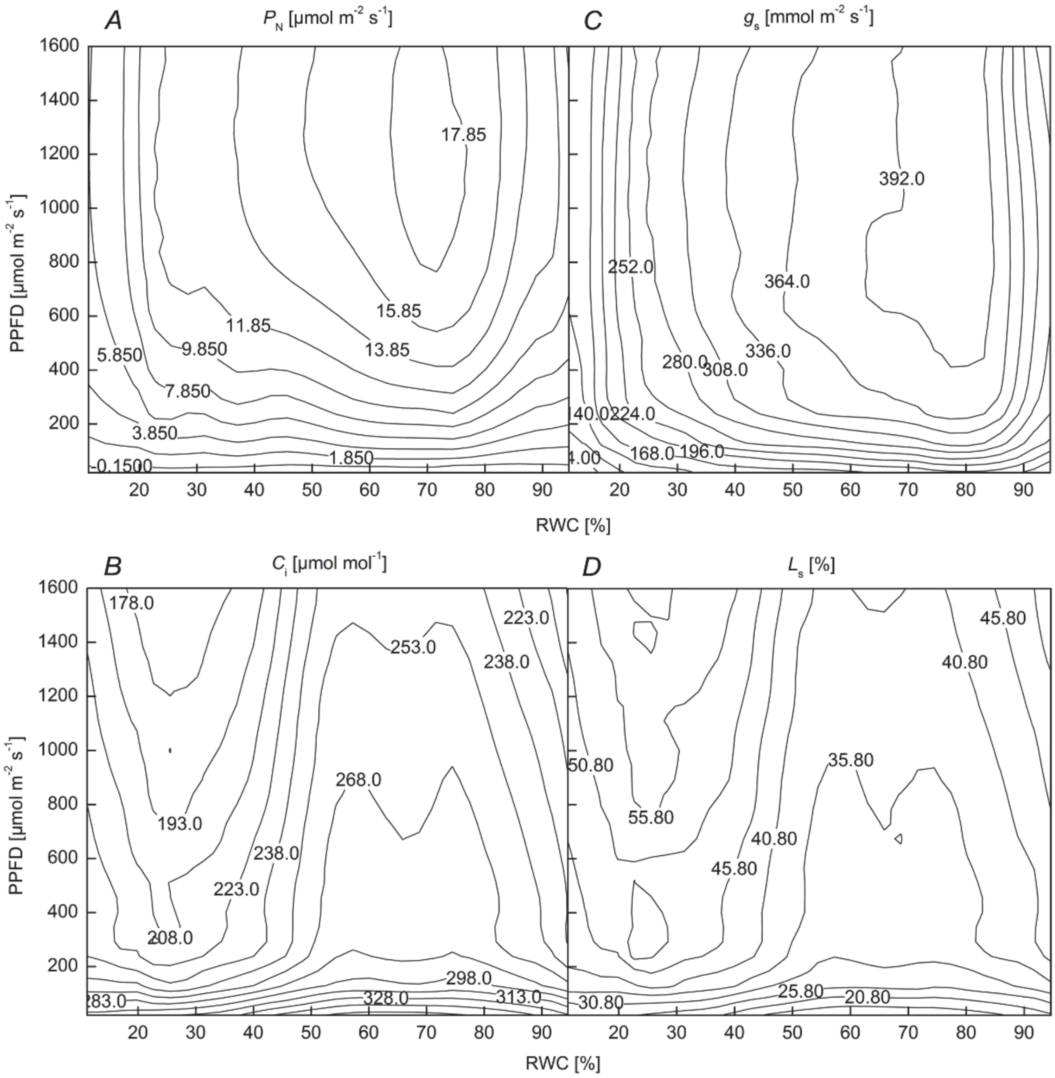

Fig. 1. The response to light and soil water of the net photosynthetic rate (P_N), the stomatal conductance (g_s), the intercellular CO_2 concentration (C_i), and the stomatal limitation values (L_s) for *Ziziphus jujuba* var. *spinosus*. Each value of P_N is the mean of 15 replicates fitted to the modified rectangular hyperbola model, and the other parameter values are the means of 15 replicates. RWC – relative water content.

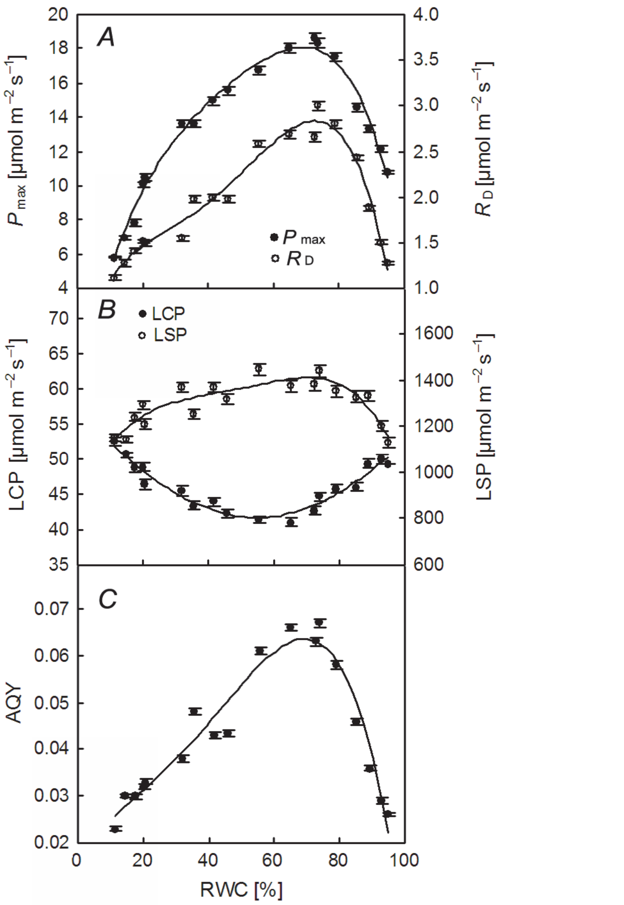

Fig. 2.The values of the maximum net photosynthetic rate (P_{max}) and the light saturation point (LSP) as determined by the modified rectangular hyperbola model. The respiration rate (R_D), light compensation point (LCP), and apparent quantum yield (AQY) were fitted to the nonrectangular hyperbola model for various water content levels. Each value is the mean ± SE (n = 15). RWC – relative water content.

result showed that the models fitted the P_N light-response curves better than the P_N light-response parameters. The NRHM fitted the R_D the best because the average RE of the R_D from this model was the lesser than those from the other models. Therefore, the NRHM also provided the best fit for the AQY and the LCP, and the MRHM provided the best fit for the P_{max} and the LSP (Table 2).

Light response of gas-exchange parameters: The MRHM best fitted the P_N light-response curves and therefore the estimated P_N value from this model was used instead of the measured P_N value. Photosynthesis was mainly inhibited by light intensity when PPFD ≤ 400 µmol m^{-2} s^{-1}. Photosynthesis was not substantially affected by soil water, and the main gas-exchange parameters were consistent at high light intensities (Fig. 1). P_N increased first quickly and then slowly as PPFD and RWC increased (Fig. 1*A*). P_N reached its maximum when the RWC was 72% (Fig. 1*A*), indicating that P_N was affected by drought and waterlogging stress. The response pattern of g_s to the soil water content and light intensity was similar to that of P_N. g_s reached a maximum when the RWC was 74% (Fig. 1*C*). This result might be related to the ability of *Z. jujuba* var. *spinosus* to control carbon assimilation by stomata opening and closing. C_i decreased with the increase in PPFD (Fig. 1*B*), indicating a trend of "decrease – increase – stationary – decrease" with the increase of the RWC. The response pattern of L_s to soil water content and light intensity was essentially the opposite to that of C_i (Fig. 1*D*).

P_N, g_s, and L_s decreased and C_i increased when the RWC was 11–25% (Fig. 1), indicating that photosynthesis was mainly restrained by the nonstomatal limitation under severe drought stress. P_N, g_s, and L_s increased and C_i decreased when the RWC was 25–55% or 80–95% (Fig. 1), suggesting that photosynthesis was mainly restrained by the stomatal limitation under light, drought or waterlogging stress. P_N and g_s were high and C_i and L_s were constant when the RWC was 55–80%, showing that the photosynthetic activity was higher under suitable water conditions.

***P*N light-response parameters**: R_D, AQY, and LCP were studied fitting the data to the NRHM. P_{max} and LSP were studied fitting the data to the MRHM. The quantitative relationships between P_{max}, R_D, AQY, LCP, or LSP and the soil water content were determined using a quartic equation. The fit precision was relatively high; R^2 was

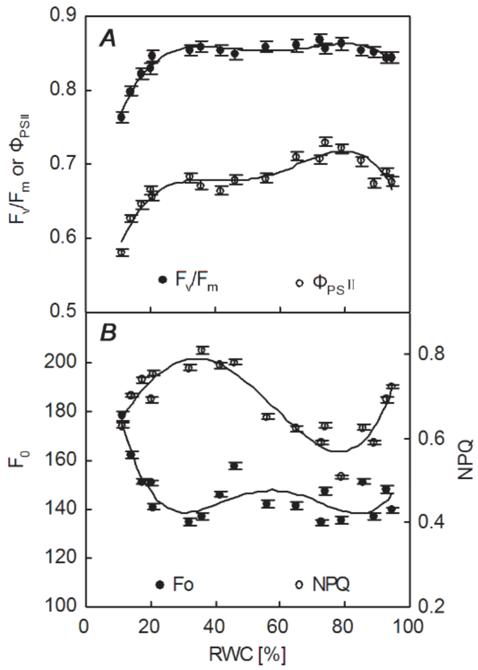

Fig. 3. The maximum quantum yield of PSII photochemistry (F_v/F_m), the effective quantum yield of PSII photochemistry (Φ_{PSII}), the minimum fluorescence of the dark-adapted state (F_0), and the nonphotochemical quenching (NPQ) for *Ziziphus jujuba* var. *spinosus* under different water content levels. Each value represents the mean ± SE (n = 15). RWC – relative water content.

Table 3. The soil water productivity for *Ziziphus jujuba* var. *spinosus* in response to different relative water content (RWC). *Different letters* indicate significant differences (P<0.05). P_N – net photosynthetic rate; WUE – water-use efficiency.

RWC [%]	Cluster mean ± SE P_N [µmol m^{-2} s^{-1}]	WUE [µmol mmol^{-1}]	Soil water productivity and WUE	RWC predictive threshold [%]
11, 15, 17, 20, 21	8.32 ± 0.866^c	3.08 ± 0.134^c	Low productivity, low WUE	11–25
32, 36, 42, 46, 56	14.22 ± 0.536^b	3.80 ± 0.030^b	Middle productivity, middle WUE	25–56
65, 73, 74, 79	18.40 ± 0.268^a	4.13 ± 0.048^a	High productivity, high WUE	56–80
85, 89, 93, 95	14.22 ± 0.536^b	3.08 ± 0.134^c	Middle productivity, low WUE	80–95

Table 4. The results of researchers about grading criterion of soil water productivity and availability. RWC – relative water content.

Grading of soil water productivity and availability	Range of RWC [%] *Robinia pseudoacacia* (Zhang *et al*. 2012)	*Platycladus orientalis* (Zhang *et al*. 2012)	*Prunus sibirica* (Xia *et al*. 2011a)
Non-productivity and non-efficiency water	<21.5	<19.0	-
Low productivity and middle efficiency water	-	-	>81.8% and <33.5%
Low productivity and low efficiency water	21.5～47.5 and >90.5	19.0～40.5 and >90.5	-
Middle productivity and high efficiency water	47.5～64.0	40.5～52.0	-
Middle productivity and middle efficiency water	-	-	33.5%～46.9%
High productivity and middle efficiency water	64.0～81.0	52.0～76.0	-
High productivity and high efficiency water	-	-	46.9%～74.5%
Middle productivity and low efficiency water	81.0～90.5	76.0～90.5	74.5%～81.8%

0.8299–0.9848. P_{max}, R_D, AQY, and LSP first increased and then decreased (Fig. 2); LCP first decreased and then increased with the increasing RWC (Fig. 2*B*). The response thresholds of different parameters varied (Fig. 2). P_{max} reached a maximum of 18.1 µmol m^{-2} s^{-1} when the RWC was 69% and an average of 14.6 µmol m^{-2} s^{-1} when the RWC was 39 and 88% (Fig. 2*A*). This result was based on extremum and integral solutions of the quartic equation and indicated that P_{max} was maintained at a higher lever when the RWC was 38–88% (Fig. 2*A*). P_{max} decreased with water stress. R_D, AQY, and LSP reached maxima of 2.8, 0.064, and 1,410 µmol m^{-2} s^{-1}, when the RWC was 73, 69, and 71%, respectively (Fig. 2). All of these parameters decreased with drought stress (RWC<40%) and waterlogging stress (RWC>90%). LCP decreased to a minimum of 42 µmol m^{-2} s^{-1}, when the RWC was 56%, and it increased, when the RWC was less than 30% or greater than 80% (Fig. 2*B*). All of the P_N light-response parameters reached their optimum levels when the RWC was 56–73% (Fig. 2). Adequate water conditions improved light-use efficiency and photosynthetic activity, while water stress reduced these parameters.

Chlorophyll fluorescence parameters: The quantitative relationships between F_v/F_m, Φ_{PSII}, F_0, or NPQ and the soil water content were also fitted to a quartic equation (Fig. 3). R^2 was 0.689–0.952, and F_v/F_m was larger than Φ_{PSII} (Fig. 3*A*). All of these parameters reached their maxima when the RWC was 80%. The PSII photochemistry efficiency was also the highest at this RWC (Fig. 3*A*). F_v/F_m and AQY were used as key indices of photoinhibition (Demmig-Adams and Adams 1992). All chlorophyll fluorescence parameters decreased upon drought stress when the RWC was lesser than 30% (Fig. 3), indicating substantial photoinhibition. The NPQ increased upon drought stress (RWC of 30–80%) and waterlogging stress (RWC of 80–95%) (Fig. 3*B*), indicating that PSII can dissipate heat to protect the photosynthetic apparatus from damage when the RWC is 30–95% (Gilmore and Yamamoto 1991). The NPQ decreased and the F_0 increased when the RWC was lesser than 25% (Fig. 3*B*), indicating that PSII was irreversibly damaged (Demmig and Björkman 1987, Krause 1988). This water threshold was consistent with that of the photosynthetic nonstomatal limit.

Grading criterion of soil water productivity: Systematic cluster analysis was used to analyze the effect of water content on the P_N and the WUE under saturated light intensity. The number of clusters was set to 3, and P_N and WUE were designated the "productivity" and "efficiency" of photosynthesis, respectively (Zhang *et al*. 2012). The RWC was divided into bins of 11–21%, 32–56%, 85–95%, and 65–79% (Table 3); the corresponding clusters had low, middle, and high productivity. The RWC was divided into 11–21% and 85–95%, 32–56% and 65–79% bins based on the WUE; the WUE in the corresponding clusters was designated as low, middle, or high (Table 3). The photosynthetic and fluorescence parameters reached optimum levels, when the RWC was 56–80%, and the main limit on photosynthesis changed from the stomatal to the nonstomatal limitation, when the RWC was reduced to 25% (Table 3). Therefore, 25, 56, and 80% were used as key critical points in dividing the soil water levels into bins. The range of the RWC from 11.2 to 25% resulted in low productivity and low WUE (Table 3). From 25 to 56%, the range of the RWC resulted in moderate productivity and moderate WUE. From 56 to 80%, the range of the RWC resulted in high productivity and high WUE. From 80 to 94.6%, the range of the RWC resulted in moderate productivity and low WUE.

Discussion

Fitting the data to the P_N light-response models is important in studying photosynthesis. Recently, a number of models have been quantitatively evaluated by calculating the mean absolute error, the mean square error, or the root mean square error (Chen *et al.* 2011, Li *et al.* 2011). However, these evaluation indices have limitations in evaluating the fit of different parameters. In this study, the RE was used to address this difficulty. The result showed that the MRHM fitted best the P_N light-response curves and parameters and the NRHM provided the next best fit. It was followed by the EM and the RHM. The MRHM fitted the P_N and other parameters at high light intensities (Ye 2007), and the NRHM fitted under other conditions because it introduced another parameter to the RHM (Lu *et al.* 2001). The order of the models from best to worst fit was consistent with the results of studies on winter wheat (Li *et al.* 2011) and *Populus szechuanica* Schneid (Wang *et al.* 2011). The MRHM fitted the P_{max} and the LSP well, and the NRHM fitted the R_D, the AQY, and the LCP. These data indicated that the MRHM is suitable for light-response parameters at high light intensities and the NRHM is suitable for response parameters at low light intensities.

The stomatal limitation theory (Farquhar and Sharkey 1982, Zhang *et al.* 2010) states that the effect of soil water stress on photosynthesis is divided into the stomatal and the nonstomatal limit. The former comes from stomata closure and reduced gas exchange, which reversibly affect photosynthesis. The latter comes from damage to the photosynthetic apparatus, which has an irreversible effect on photosynthesis. Plants regulate photosynthesis by the stomatal limit to respond to drought stress, and the nonstomatal limit affects photosynthetic potential and drought resistance (Wang *et al.* 2012). The turning point from the stomatal to the nonstomatal limit determines the soil water maximum deficit that the plant can tolerate. We found that the main reason for the P_N decline in *Z. jujuba* var. *spinosus* was the change from the stomatal to the nonstomatal limitation when the RWC was reduced to 25%. The turning point for *Malus pumila* cv. Goldspur (Zhang *et al.* 2010) and *Hippophae rhamnoides* Linn. (Pei *et al.* 2013) occurred when the RWCs were 48% and 39%, respectively. Therefore, the turning points of different species varied, while the turning point of *Z. jujuba* var. *spinosus* occurred under severe drought stress. This result indicated that the photosynthetic apparatus of *Z. jujuba* var. *spinosus* adapted well to drought stress.

Intricate relationship between fluorescence kinetics and photosynthesis underlies photosynthetic biophysical processes. Chlorophyll fluorescence techniques have been used extensively to assess quickly and harmlessly plant responses to environmental stress (Sayed 2003). The responses of photosynthesis and fluorescence parameters to the soil water content indicated that *Z. jujuba* var. *spinosus* grown in sand formed from seashells had strong photosynthetic capacity and it showed also great physiological adaptability. The range of RWC from 11.2 to 25% resulted in low productivity and low WUE; it also reduced seedling growth. This finding might indicate that the photosynthetic apparatus, mainly the PSII reaction centers, was irreversibly damaged. The range of RWC from 25 to 56% resulted in moderate productivity and moderate WUE; the range of RWC from 80 to 94.6% resulted in moderate productivity and low WUE. Between these 2 ranges, photosynthetic productivity was kept at a moderate level, because it was restrained by the stomatal limitations in a reversible manner. The WUE was restrained to different degrees depending on drought or waterlogging stress. The range of the RWC from 56 to 80% resulted in high productivity and high WUE, and the photosynthesis and fluorescence parameters reached all optimum levels, resulting in the robust plant growth.

The parameters P_N and WUE indicate "productivity" and "efficiency" and are useful for describing moisture availability. Soil water productivity measurements were only recently standardized. Zhang *et al.* (2012) and Chen *et al.* (2008) determined first the quantitative relationships between the photosynthetic parameters (P_N, WUE, E, and L_s) and the soil water content. They also determined the critical points (extremum, average, compensation point, and turning point) of those parameters by a nonlinear regression analysis and integral solution, and then divided the soil water content into different productivity levels based on those critical points. Extremum means the critical point, *e.g.*, the water saturation point of P_N, water saturation point of WUE; average included the mean value point of P_N and WUE; the compensation point means the water compensation point of P_N; the turning point means the turning point from stomatal limitation to nonstomatal limitation of P_N. Xia *et al.* (2011b) and Zhang *et al.* (2007b) classified the soil water content by cluster analysis based on the main photosynthetic parameters (P_N, WUE, and E). This study performed a cluster analysis on the RWC using the P_N and the WUE separately, which resulted in a more detailed cluster analysis than using all of the photosynthetic parameters. Our analysis combined the threshold effects of photosynthesis and the fluorescence parameters with soil water content and used the mathematical intersection calculation principle to establish water grading criteria. However, it needs to be determined, which grading method applies best to experimental results.

In areas suffering from drought, the soil water threshold of high productivity and high WUE or moderate productivity and high WUE was designated as a suitable water condition for plant growth (Table 4). However, high productivity and moderate WUE were also considered suitable, *e.g*., in the RWC range of 48 to 64% in *Robinia pseudoacacia* and of 41 to 52% in *Platycladus orientalis* (Zhang *et al*. 2012). The suitable RWC for other plants was: 60–71% for the goldspur apple tree (Zhang *et al*. 2010), 47–75% for *Prunus sibirica* (Xia *et al*. 2011a), 44–85% for *Aralia elata* (Chen *et al*. 2008), and 44–72% for *Euonymus fortunei* var. *radicans* (Zhang *et al*. 2007). The water ecological amplitudes of arbor trees (*Robinia pseudoacacia* and *Platycladus orientalis*) and a fruit tree (goldspur apple) were relatively narrow. *Robinia pseudoacacia* and *Platycladus orientalis* are adapted to a mild drought habitat, and the goldspur apple tree is adapted to a moderate water content habitat. The water ecological amplitudes of shrub trees (*Z. jujuba* var. *spinosus*, *Prunus sibirica*, and *Aralia elata*) and liana (*Euonymus fortunei* var. *radicans*) were relatively high, and these species are adapted to different water habitats. Therefore, the suitable water conditions for various plants depend on the plant species and the habitat.

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