Effects of Soil Moisture Gradient on Photosynthesis and Stress Resistance of Populus pruinosa (Postprint)

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Abstract

Using seedlings of the rare and endangered species Populus pruinosa Schrenk (grey poplar) from the Tarim Basin as experimental material, a pot experiment was conducted to investigate the effects of soil water gradients on the photosynthetic characteristics and stress resistance of P. pruinosa. The results showed that: (1) The net photosynthetic rate (Pn), transpiration rate, stomatal conductance, intercellular CO2 concentration, and light use efficiency of P. pruinosa all decreased with declining soil water content, with severe drought reducing these parameters by 35.53%, 25.32%, 48.18%, 15.62%, and 40.92%, respectively, compared to suitable water conditions; meanwhile, the degree of photosynthetic midday depression was significantly enhanced, and the decline in Pn was primarily caused by non-stomatal limitations. Mild drought increased the water use efficiency (WUE) of P. pruinosa by 3.05%, maintaining relatively high Pn and WUE. (2) With decreasing soil water content, the light ecological amplitude of P. pruinosa narrowed, the CO2 compensation point increased, RuBP regeneration was limited, and the efficiencies of light and CO2 utilization, Rubisco activity, and photosynthetic efficiency decreased. Compared to suitable water conditions, the maximum net photosynthetic rate (Pnmax), apparent quantum efficiency, light saturation point, carboxylation efficiency, photosynthetic capacity (Amax), photorespiration rate, maximum carboxylation efficiency, maximum electron transport rate, and triose phosphate utilization rate were all significantly reduced under moderate and severe drought ($P < 0.05$), with Pnmax, Amax, and biochemical parameters decreasing by 42.65%, 38.26%, and 57.10%; and by 63.01%, 65.88%, and 73.43%, respectively. (3) Soil drought significantly reduced the branch water potential and photosynthetic pigment content of P. pruinosa ($P < 0.01$), and altered the composition ratio of pigments in the photosystem reaction centers, with the degree of membrane lipid peroxidation being significantly enhanced ($P < 0.01$). P. pruinosa primarily alleviated damage to the photosynthetic apparatus caused by soil drought by accumulating large

amounts of proline and soluble proteins to participate in osmotic adjustment. Severe drought caused irreversible damage to the photosynthetic system of P. pruinosa leaves, severely inhibiting its normal growth and photosynthesis. In summary, the suitable relative soil water content for the growth of P. pruinosa in the arid desert region of the Tarim Basin is 60%-65%, which conforms to the management principles of vegetation restoration and efficient water conservation in extremely arid regions.

Full Text

Preamble

Effects of Soil Water Gradient on Photosynthetic Characteristics and Stress Resistance of *Populus pruinosa* in the Tarim Basin, China

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Abstract

Water deficit is a major limiting factor for vegetation recovery and reconstruction in the extremely arid desert region of the Tarim Basin in northwestern China. *Populus pruinosa* Schrenk is an ecologically important species growing in this region; however, its population has been declining in recent years due to low groundwater tables caused primarily by increased human water consumption. Currently, the mechanisms underlying the decline in *P. pruinosa* photosynthesis under soil water deficits remain unclear. The objective of our study was to investigate the effects of soil water gradients on photosynthesis and the relationship between photosynthesis and soil water content, thereby enhancing our understanding of the photophysiological characteristics of *P. pruinosa* exposed to declining soil water and providing valuable information for the protection of this vulnerable species.

Saplings of *P. pruinosa* were planted in pots under four different soil water gradients. The effects of soil water decline on photosynthetic characteristics and stress resistance were evaluated by analyzing gas exchange, photosynthetic light and CO response curves, pigments, stem water potential, and osmotic adjustment substances. The results showed that: (1) The net photosynthetic rate (Pn), transpiration rate, stomatal conductance, intercellular CO concentration, and light use efficiency of *P. pruinosa* decreased gradually with declining soil water content, with severe drought reducing these parameters by 35.53%, 25.32%, 48.18%, 15.62%, and 40.92%, respectively, compared to normal soil water content (CK). However, the "noon break" phenomenon became more apparent, and non-stomatal limitation was responsible for the reduction in Pn. Water use efficiency (WUE) could be improved by 3.05% under mild drought conditions relative to CK, while maintaining Pn at a relatively high level. (2) The light ecological amplitude decreased, the CO compensation point increased, ribulose-1,5-diphosphate (RuBP) regeneration was limited, and light/CO utilization efficiency, Rubisco activity, and photosynthetic efficiency decreased with declining soil water content. Compared to CK, light response parameters (maximum net photosynthetic rate [Pnmax], apparent quantum efficiency [AQY], light saturation point [LSP], carboxylation efficiency, photosynthetic capacity [Pmax], photorespiratory rate [Rp], maximum carboxylation rate [Vcmax], maximum electron transport rate [Jmax], and triose-phosphate utilization rate [TPU]) decreased significantly ($P < 0.05$). Notably, Pnmax, Vcmax, and biochemical parameters of photosynthesis decreased by 42.65%, 38.26%, and 57.10% under moderate drought, and by 63.01%, 65.88%, and 73.43% under severe drought, respectively. (3) Stem water potential and pigment content were significantly reduced ($P < 0.01$), the pigment composition proportion of the light reaction center was altered, and membrane lipid peroxidation (MDA) was significantly enhanced ($P < 0.01$) with decreasing soil water content. *P. pruinosa* mainly accumulated large amounts of proline and soluble protein to eliminate reactive oxygen and alleviate impairment of photosynthetic apparatus under soil drought. Irreversible damage was caused to the photosynthetic system of *P. pruinosa* under severe drought, seriously inhibiting normal growth and photosynthesis.

In conclusion, declines in soil water content resulted in drought stress and reduced photosynthetic ability, indicating that the decline in the *P. pruinosa* population might be caused by lower soil moisture. The optimal soil water content for maintaining higher Pn and WUE in *P. pruinosa* forestlands should be approximately 60%–65% of field capacity in the Tarim arid-desert region, which adheres to the management principles of efficient water conservation and vegetation restoration in extremely arid areas.

Keywords: *Populus pruinosa*; soil water gradient; photosynthetic response parameters; osmotic adjustment substance

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1. Study Area Overview

The experiment was conducted at the Agricultural Experiment Station of Tarim University, located in the Alar reclamation area on the northern edge of the Taklamakan Desert along the upper reaches of the Tarim River. The region has a typical warm temperate continental arid climate with abundant light and heat resources (40°35 N, 80°50 E; elevation 1,006 m). Annual total solar radiation reaches 5.89 × 10 J/cm^2, with annual sunshine duration of 2,750–3,029 hours and a frost-free period of 201 days. The effective accumulated temperature

0°C is 4,132.7°C, and 10°C is 3,800°C. The area experiences large diurnal temperature variations, with average annual rainfall <50 mm and average annual evaporation >2,500 mm. Wind-sand disasters are frequent, particularly in summer. *P. pruinosa* is mainly distributed along both banks of the upper Tarim River, forming corridor-shaped natural forests that represent near-climax natural tree communities in the watershed' s vegetation succession. The species serves as an important barrier against wind-sand, maintains regional ecological balance, protects biodiversity, and ensures oasis agriculture and animal husbandry production, and has been designated as one of China' s first batch of rare and endangered species.

Field investigations show that soil water content under young *P. pruinosa* forests near the riverbank is 13.28%-19.41% at 0-100 cm depth, decreasing to 8.76%-12.62% and 4.05%-7.07% with increasing distance from the river, and further declining to 0.65%-2.37% in sparse, declining forests.

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2. Experimental Design

The experimental material was *P. pruinosa*, a dominant desert tree species in the Tarim Basin. Uniform-sized seedlings were selected and planted in plastic buckets in late March. The pot soil was brown calcic soil collected from forest land, sieved, with each pot containing 15 kg of soil. Soil organic matter content was 1.33 g/kg, pH was 8.35, total nitrogen was 0.089%, total phosphorus was 0.057%, total potassium was 1.201%, and available nitrogen was 0.137%. Field capacity (f) was 24.43%.

The experiment was conducted under a self-built rainproof shelter at the Agricultural Experiment Station of Tarim University. After planting, seedlings were watered sufficiently for normal germination and growth. Following a recovery period, four soil water gradient treatments were established based on field capacity percentages to simulate natural habitat conditions: H1 (75%-80% f), H2 (60%-65% f), H3 (45%-50% f), and H4 (30%-35% f). A randomized block design was used, with each water treatment placed under identical light conditions. During rainy days, a rainproof shelter was used for coverage.

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3. Measurement Methods and Indicators

3.1 Soil Water Parameter Measurement and Control

Pot soil water content was measured using the drying method, and field capacity was determined using the ring knife method. Based on field capacity, a series of soil water contents were calculated for each gradient. According to pot soil water content and pot soil weight (15 kg), the target weight for each soil water gradient was calculated to control the experimental range. A plastic tube was vertically installed at the edge of each pot to deliver supplementary water directly to the bottom, preventing rapid surface evaporation that could affect experimental precision. During the recovery period before treatment, all seedlings were fully irrigated to ensure normal growth. For the water gradient control experiment, an electronic scale was used to weigh pots. Based on the weight difference between two measurements and the upper control limit, fixed containers were used to add water and maintain soil water within the set range.

3.2 Gas Exchange Parameter Measurement

On clear days in mid-July, diurnal variations in net photosynthetic rate (Pn) of potted seedlings were measured from 8:00 to 20:00 using a Li-6400 portable photosynthesis system (Li-COR, USA). Mature leaves at the same position on new shoots were selected for measurement. To reduce errors caused by measurement time, all treatments were measured sequentially in cycles. Parameters including photosynthetically active radiation (PAR), air relative humidity, and leaf vapor pressure deficit (VPD) were recorded simultaneously. Instantaneous water use efficiency at the leaf level (WUE = Pn/Tr) and stomatal limitation value (Ls = 1 - Ci/Ca) were calculated.

3.3 Light Response Curve Measurement

After natural light induction for 1–1.5 hours, light response curves were measured between 9:30 and 13:00 Beijing time using the Li-6400 system with an open gas path. Temperature was set at 25°C, CO concentration at (370 ± 5) mol/mol, and relative humidity at 50%–70%. A red-blue light source provided different PAR levels set at gradients of 3,000, 2,800, 2,500, 2,000, 1,500, 1,000, 500, 200, 100, 50, 20, and 0 mol·m ^{2}·s ^{1}. The rectangular hyperbola correction model was used to fit the measured light response curves and derive parameters including maximum net photosynthetic rate (Pnmax), apparent quantum efficiency (AQY), light compensation point (LCP), and light saturation point (LSP).

3.4 CO Response Curve Measurement

CO response curves were measured on leaves at the same positions used for light response curves. Control conditions were identical to those for light response measurements. A CO cylinder provided different concentrations of 2,000, 1,800, 1,600, 1,300, 1,000, 800, 600, 400, 200, 150, 100, 50, and 0 mol·mol ^{1} at a PAR of 1,500 mol·m ^{2}·s ^{1}. The rectangular hyperbola correction model was used to fit the measured CO response curves and derive photosynthetic capacity (Pmax), photorespiratory rate (Rp), CO compensation point (Γ), and carboxylation efficiency (CE). To obtain biochemical parameters, we used the Farquhar biochemical model to fit the CO response curves, yielding maximum carboxylation rate (Vcmax), maximum electron transport rate (Jmax), and triose-phosphate utilization efficiency (TPU).

3.5 Twig Water Potential Measurement

In August, current-year new shoots of uniform size were selected from seedlings under each water treatment for water potential measurement between 9:00 and 11:00 using a plant pressure chamber (SKPM 1400, UK).

3.6 Photosynthetic Pigment, Soluble Protein, Free Proline, and Malondialdehyde Content Measurement

In August, leaves from the same positions of seedlings under each water treatment were collected and brought back to the laboratory. Chlorophyll content was determined by acetone extraction and spectrophotometry. Free proline (Pro) content was measured using the sulfosalicylic acid extraction and acid ninhydrin colorimetric method. Soluble protein (SP) content was determined by the Coomassie brilliant blue G-250 staining method. Malondialdehyde (MDA) content was measured using the thiobarbituric acid (TBA) method.

3.7 Data Analysis

SAS 6.12 software was used for variance analysis, with Duncan' s multiple comparison test for significant differences.

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4. Results and Analysis

4.1 Effects of Soil Water Gradient on Diurnal Photosynthesis Process

The diurnal variation trends of Pn in *P. pruinosa* differed under various soil water gradients, showing a typical "noon break" pattern. With decreasing soil water content, the daily mean Pn values decreased by 17.53%, 30.73%, and 35.53% for H2, H3, and H4, respectively, compared to H1. The peak Pn values appeared earlier under water deficit conditions, occurring at 10:00 for H3 and H4, which was 2 hours earlier than for H1 and H2. The "noon break" phenomenon became more pronounced with decreasing soil water content.

Soil water gradient significantly affected stomatal conductance (Gs) in *P. pruinosa*. The daily mean Gs values under H2, H3, and H4 treatments decreased by 25.32%, 48.18%, and 15.62%, respectively, compared to H1, indicating that soil drought inhibited stomatal opening. Light use efficiency (LUE) followed the order H1 > H2 > H3 > H4, with H2 showing a 3.05% increase compared to H1, suggesting that mild drought could improve WUE through plant self-regulation to maintain growth-water consumption balance.

4.2 Effects of Soil Water Gradient on Photosynthetic Light Response Parameters

Photosynthetic light response curves characterize a plant' s ability to utilize environmental resources. Under low PAR (<200 mol · m ^{2} · s ^{1}), Pn increased approximately linearly with PAR. Beyond a certain value, the curve gradually plateaued and then decreased. Different soil water treatments significantly affected light response parameters ($P < 0.05$). With decreasing soil water content, Pnmax, LSP, and AQY of H2, H3, and H4 decreased by 24.69%, 42.65%, 63.01%; 11.83%, 32.72%, 48.56%; and 4.92%, 8.20%, 18.03%, respectively, compared to H1. The LCP showed a significant positive correlation with soil water gradient ($P < 0.05$), while the correlation with LSP, AQY, and LCP was not significant ($P > 0.05$).

Statistical analysis showed that light response parameters of *P. pruinosa* in the arid desert region of Tarim decreased overall with declining soil water content. The rectangular hyperbola correction model provided the best fit for light response curves under soil water gradients, with correlation coefficients >0.993, overcoming the limitation of non-rectangular hyperbola models that cannot fit Pn-PAR curves without extreme points.

4.3 Effects of Soil Water Gradient on Photosynthetic CO Response Parameters

The response trends of CO response parameters were similar to those of light response parameters. Under low CO concentrations (<200 mol · mol ^{1}), Pn increased approximately linearly with CO concentration. Beyond a certain value, the curve gradually plateaued and then decreased. With decreasing soil water content, Vcmax, Jmax, and TPU of H2, H3, and H4 decreased by 31.38%, 69.65%, 75.64%; 33.07%, 66.39%, 73.74%; and 13.75%, 64.51%, 80.81%, respectively, compared to H1. Conversely, Γ increased significantly. The CE was not significantly affected by soil water reduction ($P > 0.05$).

Statistical analysis indicated that Vcmax, Jmax, TPU, and Pmax showed significant positive correlations with soil water content ($P < 0.05$), while Γ showed significant negative correlations ($P < 0.05$). The correlation coefficient between Vcmax and soil water was the highest ($r = 0.9996$), indicating that soil water deficit caused a decline in carboxylation capacity.

4.4 Effects of Soil Water Gradient on Photosynthetic Pigment Content

Chlorophyll a (Chla), chlorophyll b (Chlb), carotenoids (Car), and total chlorophyll (Chl(a+b)) contents in *P. pruinosa* leaves decreased with decreasing soil water content. The reduction amplitudes were greater for Chla (11.74%, 33.83%, 77.50%) than for Chlb (8.15%, 21.28%, 49.82%) and Car under H2, H3, and H4 treatments, respectively. The Chla/b ratio remained relatively stable under H1 and H2 but decreased significantly under H3 and H4, indicating that the photosystem reaction center was more susceptible to soil water deficit than the light-harvesting antenna system. This differential sensitivity contributed to the decline in photosynthetic capacity.

4.5 Effects of Soil Water Gradient on Twig Water Potential, Osmotic Adjustment Substances, and MDA Content

With decreasing soil water content, twig water potential (Ψp) was significantly affected ($P < 0.01$), decreasing from -1.14 MPa in H1 to -1.65 MPa and -2.24 MPa in H3 and H4, respectively. Soluble sugar (SS), free proline (Pro), and soluble protein (SP) contents in leaves increased significantly, with Pro showing the greatest increase (139.88% and 189.42% under H3 and H4, respectively). MDA content increased by 65.87% and 96.77% under H3 and H4, respectively, indicating enhanced membrane lipid peroxidation.

The accumulation of osmotic adjustment substances, particularly Pro and SP, represents an effective defense mechanism to maintain intracellular environmental stability and protect photosynthetic apparatus under drought stress. However, severe drought caused irreversible damage to the photosynthetic system, as evidenced by leaf yellowing and abscission symptoms.

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5. Discussion and Conclusion

Populus pruinosa is a key ecological species in the Tarim River basin, distributed primarily in the upper reaches, forming a regular differentiation pattern along water gradients. Investigating its physiological-ecological mechanisms and survival conditions is crucial for protecting this rare and endangered species and promoting regional ecological restoration.

Photosynthesis is fundamental for plant organic matter accumulation and growth, influenced by both plant physiological characteristics and environmental factors. Soil water is an important ecological factor affecting photosynthetic physiological processes. Under optimal water conditions (H1), *P. pruinosa* maintained high photosynthetic efficiency. With decreasing soil water content, photosynthetic parameters declined more significantly, indicating that poorer water conditions led to greater reductions in photosynthetic capacity.

The "noon break" phenomenon intensified with soil water deficit, primarily caused by non-stomatal limitations. Mild drought improved WUE by 3.05% as *P. pruinosa* reduced Gs and twig water potential to decrease water loss, representing a self-protection mechanism evolved over time. However, this also limited CO supply, reducing photosynthetic efficiency.

Light and CO response parameters effectively reflect plant photosynthetic potential under stress conditions. The rectangular hyperbola correction model provided the best fit for *P. pruinosa* light response curves, showing that Vcmax, Jmax, and TPU decreased significantly with soil water reduction, indicating weakened Rubisco activity, electron transport rate, and triose-phosphate utilization efficiency. This reduced the plant' s ability to consume excess energy, leading to increased membrane lipid peroxidation under low-water, high-light desert conditions.

The Chla/b ratio, an important indicator of pigment distribution within the photosynthetic system, remained relatively stable under mild drought but decreased significantly under moderate and severe drought, suggesting that the photosystem reaction center was more vulnerable than the light-harvesting system. This contributed to reduced photosynthetic capacity and efficiency.

Twig water potential showed significant positive correlations with Pn, LUE, and other parameters, demonstrating that water potential decline directly affected photosynthetic processes. Under drought stress, reduced carbon assimilation capacity and antioxidant enzyme activity led to reactive oxygen species (ROS) accumulation, causing energy metabolism disorders and membrane structure damage, which reduced photosynthetic capacity.

Osmotic adjustment substances, particularly proline and soluble protein, accumulated significantly to scavenge ROS and protect the photosynthetic apparatus. However, severe drought caused irreversible damage, as indicated by leaf yellowing and abscission.

In conclusion, the optimal soil water content for *P. pruinosa* growth in the Tarim arid-desert region is 60%-65% of field capacity. This moisture level ensures high photosynthetic efficiency and WUE while adhering to water conservation principles in extremely arid areas. The decline in *P. pruinosa* populations may be attributed to reduced soil moisture, and maintaining appropriate water levels is essential for vegetation restoration and species protection.

References

[1] Zhang SY, Xu ZQ. Effects of soil drought stress on photosynthesis and antioxidant enzyme activities in *Hippophae rhamnoides* leaves. *Acta Ecologica Sinica*, 2013, 33(5): 1386-1396.

[2] Berry JA, Downton WJS. Environmental regulation of photosynthesis. In: Govindjee, ed. *Photosynthesis, Vol. II. Development, Carbon Metabolism and Plant Productivity.* New York: Academic Press, 1982: 263-343.

[3] Ma HC, Fung L, Wang SS, Altman A, Hüttermann A. Photosynthetic response of *Populus euphratica* to salt stress. *Forest Ecology and Management*, 1997, 93(1/2): 55-61.

[4] Bogeat-Triboulot MB, Brosché M, Renaut J, Jouve L, Thiec DL, Fayyaz P, Vinocur B, Witters E, Lauke K, Teichmann T, Altman A, Hausman JF, Polle A, Kangasjärvi J, Dreyer E. Gradual soil water depletion results in reversible changes of gene expression, protein profiles, ecophysiology, and growth performance in *Populus euphratica*, a poplar growing in arid regions. *Plant Physiology*, 2007, 143(2): 876-892.

[5] Gries D, Zeng F, Foetzki A, Arndt SK, Bruelheide H, Thomas FM, Zhang X, Runge M. Growth and water relations of *Tamarix ramosissima* and *Populus*

euphratica on Taklamakan desert dunes in relation to depth to a permanent water table. *Plant, Cell & Environment*, 2003, 26(5): 725-736.

[6] Wu WM, et al. Effects of soil water stress on photosynthesis and light response characteristics of *Populus euphratica* and *P. pruinosa*. *Scientia Silvae Sinicae*, 2007, 43(5): 30-35.

[7] Chen YP, et al. Effects of groundwater depth on gas exchange and chlorophyll fluorescence of *Populus euphratica* in the lower reaches of the Tarim River. *Acta Ecologica Sinica*, 2011, 31(2): 344-353.

[8] Overdieck D, Ziche D, Yu RD. Gas exchange of *Populus euphratica* leaves in a riparian zone. *Journal of Arid Land*, 2013, 5(4): 531-541.

[9] Farquhar GD, von Caemmerer S, Berry JA. A biochemical model of photosynthetic CO assimilation in leaves of C species. *Planta*, 1980, 149(1): 78-90.

[10] Sof A, Dichio B, Montanaro G, Xiloyannis C. Photosynthetic performance and light response of two olive cultivars under different water and light regimes. *Photosynthetica*, 2009, 47(4): 602-608.

[11] Chen Y, Xu DQ. Two patterns of leaf photosynthetic response to irradiance transition from saturating to limiting one in some plant species. *New Phytologist*, 2006, 169(4): 789-798.

[12] Mishra KB, Iannacone R, Petrozza A, Mishra A, Armentano N, Vecchia GL, Trtilek M, Cellini F, Nedbal L. Engineered drought tolerance in tomato plants is reflected in chlorophyll fluorescence emission. *Plant Science*, 2012, 182: 79-86.

[13] de Campos MKF, de Carvalho K, de Souza FS, Marur CJ, Pereira LFP, Filho JCB, Vieira LGE. Drought tolerance and antioxidant enzymatic activity in transgenic 'Swingle' citrumelo plants over-accumulating proline. *Environmental and Experimental Botany*, 2011, 72(2): 242-250.

[14] Brodribb T, Hill RS. Light response characteristics of a morphologically diverse group of southern hemisphere conifers as measured by chlorophyll fluorescence. *Oecologia*, 1997, 110(1): 10-17.

[15] Wullschleger SD. Biochemical limitations to carbon assimilation in C plants —a retrospective analysis of the A/Ci curves from 109 species. *Journal of Experimental Botany*, 1993, 44(5): 907-920.

[16] Babita M, Maheswari M, Rao LM, Shanker AK, Rao DG. Osmotic adjustment, drought tolerance and yield in castor (*Ricinus communis* L.) hybrids. *Environmental and Experimental Botany*, 2010, 69(3): 243-249.

[17] Li ZJ, et al. Photosynthetic characteristics of *Leymus chinensis* under different soil water gradients in Hulunber meadow steppe. *Acta Ecologica Sinica*, 2009, 29(10): 5271-5279.

[18] Li JY, et al. Effects of water on photosynthetic and growth characteristics of *Populus euphratica* seedlings. *Acta Botanica Boreali-Occidentalia Sinica*, 2009, 29(7): 1445–1451.

[19] Rouhi V, Samson R, Lemeur R, van Damme P. Photosynthetic gas exchange characteristics in three different almond species during drought stress and subsequent recovery. *Environmental and Experimental Botany*, 2007, 59(2): 117–129.

[20] Chen M, et al. Drought resistance mechanisms of three plant species in the middle reaches of the Tarim River. *Acta Botanica Boreali-Occidentalia Sinica*, 2007, 27(4): 747–754.

[21] Li JY, et al. Effects of drought stress on photosynthesis and chlorophyll fluorescence characteristics of *Populus euphratica* and *P. pruinosa*. *Arid Zone Research*, 2009, 26(1): 45–52.

[22] Campos PS, et al. Effects of drought on photosynthesis and protective enzymes in maize leaves. *Acta Ecologica Sinica*, 2011, 31(5): 1303–1311.

[23] Chen YN, et al. Photosynthetic water use efficiency and its response to enriched CO in different leaf shapes of *Populus euphratica*. *Acta Phytoecologica Sinica*, 2003, 27(1): 34–40.

[24] Zhang SY, et al. Study on ecophysiology of *Artemisia ordosica* and *Cynanchum komarovii* in Mu Us Sandy Land. *Acta Phytoecologica et Geobotanica Sinica*, 1992, 16(3): 197–208.

[25] Xu DQ. *Experimental Guidance for Plant Physiology*. Beijing: Higher Education Press, 2006: 122–125.

[26] Ye ZP. Advances in light response models of photosynthesis. *Chinese Journal of Plant Ecology*, 2010, 34(6): 727–740.

Note: Figure translations are in progress. See original paper for figures.