# Effects of Drought Stress on Photosynthetic and Physiological Characteristics of Xiaohuyang No. 2 Seedlings (Postprint)

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## Abstract

This study investigated the response of photosynthetic and physiological characteristics of 2-year-old Populus euphratica ‘Xiaohuyang 2’ seedlings to drought stress using a pot-cultured continuous drought method. The results showed that: (1) With increasing drought stress severity, Populus euphratica ‘Xiaohuyang 2’ actively regulated its photosynthetic mechanism to adapt to adverse conditions, with the diurnal variation curves of net photosynthetic rate (Pn) and other parameters changing from bimodal to unimodal patterns; simultaneously, the species actively adjusted its water use strategy, maintaining high water use efficiency to cope with drought environments. (2) Mild and moderate drought stress enhanced the utilization efficiency of strong light in Populus euphratica ‘Xiaohuyang 2’ ; under severe drought stress, seedlings reduced respiratory consumption to conserve photosynthetic products and improved their utilization capacity for weak light to resist drought adversity. (3) Through regression fitting, mathematical relationships were established between Pn, transpiration rate (Tr), water use efficiency (WUE) and soil water content in Populus euphratica ‘Xiaohuyang 2’ , determining the optimal soil moisture range of 7.3%-11.0% for seedling growth. (4) Populus euphratica ‘Xiaohuyang 2’ alleviated drought stress damage through accumulation of osmotic adjustment substances and increased antioxidant enzyme activity; however, severe drought also inhibited protective enzyme activity, ultimately exacerbating membrane lipid peroxidation. In conclusion, as a drought-resistant and light-loving tree species, Populus euphratica ‘Xiaohuyang 2’ can be widely used in sand-fixation afforestation, vegetation restoration, etc., and demonstrates promising prospects for promotion in forestry construction in arid and semi-arid regions.

# Effects of Drought Stress on Photosynthetic and Physiological Characteristics of Xiaohuyang 2 Poplar Seedlings

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**Abstract:** This study investigated the response mechanisms of photosynthetic and physiological characteristics to drought stress in *Populus simonii* × *P. euphratica* 'Xiaohuyang 2' seedlings using a potted continuous drought method. The results showed that: (1) As drought stress intensified, Xiaohuyang 2 actively adjusted its photosynthetic mechanisms to adapt to adverse conditions, with diurnal variation curves of net photosynthetic rate (Pn) and other parameters changing from bimodal to unimodal patterns. Simultaneously, the seedlings adjusted water use strategies to maintain high water use efficiency for coping with drought. (2) Mild and moderate drought stress enhanced Xiaohuyang 2' s utilization efficiency of strong light; under severe drought stress, seedlings reduced respiratory consumption, preserved photosynthetic products, and improved weak light utilization capacity to resist drought. (3) Through regression fitting, mathematical relationships existed between Pn, transpiration rate (Tr), water use efficiency (WUE) and soil water content (SWC), establishing that the optimal soil moisture range for Xiaohuyang 2 seedling growth was 7.3%-11.0%. (4) Xiaohuyang 2 alleviated drought damage by accumulating osmotic adjustment substances and increasing antioxidant enzyme activity, though severe drought inhibited protective enzyme activity and ultimately exacerbated membrane lipid peroxidation. In conclusion, Xiaohuyang 2 is a light-loving species with excellent drought resistance, suitable for sand-fixing afforestation and vegetation restoration, offering promising prospects for forestry development in arid and semi-arid regions.

**Keywords:** drought stress; Xiaohuyang 2; photosynthetic characteristics; physiological indices

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## 1 Materials and Methods

### 1.1 Experimental Materials and Design

The experimental material consisted of pest-free Xiaohuyang 2 cutting seedlings provided by Dengkou County Experimental Forest Farm. In May, seedlings were transplanted into 28 cm × 20 cm plastic pots (one per pot) at the Inner Mongolia Academy of Forestry Science arboretum. The cultivation substrate was local aeolian sandy soil. All seedlings received normal water and fertilizer management before the stress experiment. The drought stress experiment was conducted during consecutive sunny days in July. Thirty-six uniformly growing seedlings were selected: six for photosynthetic characteristic measurements and the remainder for leaf sampling. Drought stress was imposed through natural drying—seedlings were fully irrigated one day before the experiment, after which no water was supplemented. As soil moisture evaporated, continuously decreasing soil water content created different stress levels. Based on soil water content changes, four stress stages were established (Table 1). A rain shelter was erected during the experiment to prevent rainfall interference. Light response curves and diurnal photosynthesis processes were measured every 2–3 days after stress initiation. Soil water content was determined using the oven-drying method. Leaf samples for physiological indices were collected every 6 days between 08:00–10:00 and stored at -80°C.

**Table 1** Drought stress stages

| Stress Stage | Soil Water Content (%) |
|---|---|
| Suitable Water | >12.7 |
| Mild Drought | 10.3–12.7 |
| Moderate Drought | 5.9–10.3 |
| Severe Drought | 2.4–5.9 |
| Extreme Drought | <2.4 |

## 1.2 Photosynthetic Parameter Measurements

**1.2.1 Diurnal Variation of Photosynthesis** Diurnal photosynthetic variation was measured using a LI-6400 portable photosynthesis system from 08:00 to 18:00. One fully developed, intact leaf from the middle-upper portion of each seedling was selected and marked. After parameters stabilized, data including net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular $CO_2$ concentration (Ci), and transpiration rate (Tr) were recorded, with three replicates per leaf. Water use efficiency (WUE) was calculated as WUE = Pn/Tr.

**1.2.2 Light Response Curve Measurement** Light response curves were measured between 09:00–11:30 using an automatic measurement program. $CO_2$ concentration was stabilized at 400 $\text{mol} \cdot \text{mol}^{-1}$. Ten light intensity gradients were set: 2000, 1800, 1600, 1400, 1200, 1000, 800, 600, 300, and 0 $\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The minimum waiting time was 120 s when changing light gradients, and results were averaged across three measurements.

**1.2.3 Light Response Parameter Model Fitting** This study employed the rectangular hyperbola correction model proposed by Ye et al. to fit light response characteristic parameters. The model expression is:

$$Pn = \frac{\alpha I + Pn_{max} - \sqrt{(\alpha I + Pn_{max})^2 - 4\alpha\gamma I Pn_{max}}}{2\gamma} - Rd$$

where: Pn is net photosynthetic rate ( $\mathrm{mol} \cdot \mathrm{m}^{-2} \cdot \mathrm{s}^{-1}$); $\alpha$ is initial quantum efficiency; I is photosynthetically active radiation ( $\mathrm{mol} \cdot \mathrm{m}^{-2} \cdot \mathrm{s}^{-1}$); Pn_{max} is maximum net photosynthetic rate; Rd is dark respiration rate ( $\mathrm{mol} \cdot \mathrm{m}^{-2} \cdot \mathrm{s}^{-1}$); $\beta$ is the correction coefficient representing photoinhibition; and $\gamma$ is the light saturation term ( $\mathrm{mol} \cdot \mathrm{m}^{-2} \cdot \mathrm{s}^{-1}$). Based on fitted $\alpha$, $\beta$, $\gamma$, and Rd values, light saturation point (LSP), light compensation point (LCP), and maximum net photosynthetic rate (Pn_{max}) can be directly calculated:

$$LSP = \frac{\sqrt{\beta^2 + 4\beta\gamma} - \beta}{2\gamma}$$

$$LCP = \frac{Rd}{\alpha}$$

$$Pn_{max} = \frac{\alpha I_{LSP} + Pn_{max} - \sqrt{(\alpha I_{LSP} + Pn_{max})^2 - 4\alpha\gamma I_{LSP} Pn_{max}}}{2\gamma} - Rd$$

### 1.3 Physiological Index Measurements

Malondialdehyde (MDA) content was determined using the thiobarbituric acid method. Proline (Pro) content was measured via acidic ninhydrin colorimetry. Catalase (CAT) activity was determined using ultraviolet spectrophotometry, with one enzyme unit defined as the amount causing a 0.01 absorbance change per minute.

### 1.4 Data Processing

Excel 2010 was used for statistical processing. Origin 2017 was used for light response curve fitting and polynomial regression between fitted characteristics and soil water content.

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## 2 Results and Analysis

### 2.1 Photosynthetic Characteristics Under Drought Stress

**2.1.1 Diurnal Variation of Photosynthetic Indices** The diurnal variation of net photosynthetic rate (Pn) in Xiaohuyang 2 seedlings showed different patterns with increasing stress severity. As shown in Figure 1, under suitable water and mild drought stress, Pn exhibited bimodal curves, with the second peak appearing later than the first. Under moderate, severe, and extreme drought stress, Pn showed unimodal curves with varying peak times. With intensifying stress and decreasing soil water content, the daily mean Pn values declined progressively.

Transpiration rate (Tr) diurnal patterns also varied under different soil water conditions (Figure 1). Under suitable and mild drought stress, Tr showed bimodal curves—rising in the morning as temperature increased and humidity decreased, declining at noon as stomatal conductance decreased to avoid high temperature and light damage, then increasing again in the afternoon as stomatal conductance recovered. Under moderate, severe, and extreme drought stress, Tr showed unimodal curves. The daily mean Tr values initially increased then decreased with declining soil water content, indicating that moderate drought could enhance transpiration.

Stomatal conductance (Gs), which reflects stomatal opening degree and significantly affects photosynthesis, respiration, and transpiration, showed bimodal diurnal variation under mild drought stress, with midday troughs representing stomatal closure to avoid stress. Under moderate, severe, and extreme drought stress, Gs showed unimodal patterns, with daily means decreasing as soil water content declined.

Intercellular $CO_2$ concentration (Ci) diurnal patterns also differed with stress duration (Figure 1). Under suitable and mild stress, Ci showed "V-shaped" changes, closely related to Pn and Gs variations. Under moderate, severe, and extreme drought, Ci showed "Λ-shaped" patterns. The daily mean Ci decreased overall with intensifying drought, ranging 200-300 $\mathrm{mol} \cdot \mathrm{mol}^{-1}$.

Water use efficiency (WUE), reflecting the relationship between water consumption and material accumulation, showed diurnal patterns that initially decreased then increased across all water conditions (Figure 2). High morning WUE values resulted from low transpiration; midday decreases were caused by enhanced transpiration under high radiation; afternoon recovery occurred as temperature and light intensity decreased. As soil water content declined during the experiment, Xiaohuyang 2 adjusted its photosynthetic characteristics to improve water use capacity for active adaptation.

**Figure 1** [Figure 1: see original paper] Diurnal variation characteristics of photosynthetic indexes under drought stress

**2.1.2 Light Response Curves Under Drought Stress** Light response curves reflect how net photosynthetic rate changes with light intensity. Appropriate model fitting can determine parameters like maximum net photosynthetic rate (Pn_{max}), light saturation point (LSP), and light compensation point (LCP), which are valuable for studying relationships between photosynthetic capacity and light intensity. As shown in Figure 3, Xiaohuyang 2 showed consistent patterns across water conditions, with Pn increasing with photosynthetically active radiation (PAR). Under suitable water and mild/moderate drought, Pn increased significantly when PAR was 0-800 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$, with steeper curves; when PAR was 800-1400 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$, the increase slowed; when PAR exceeded 1400 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$, curves plateaued. Under severe and extreme drought, Pn increases slowed markedly when PAR reached 600-800 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$, indicating that both excessively high and low soil moisture affected strong light utilization efficiency and increased photoinhibition susceptibility.

Stomatal conductance responses to PAR were consistent across water conditions (Figure 3). Gs increased substantially with PAR under suitable, mild, and moderate drought, but increased slowly under severe and extreme drought. When PAR was 0-300 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$, Ci declined sharply as Pn increased rapidly and stomatal conductance remained low, preventing rapid $CO_2$ replenishment. With further PAR increases, Pn growth slowed, Gs increased, and Ci stabilized with minimal variation.

**Figure 2** [Figure 2: see original paper] Diurnal variation characteristics of water use efficiency under drought stress

**Figure 3** [Figure 3: see original paper] Variation characteristics of light response curves under drought stress

**2.1.3 Relationship Between Photosynthetic Indices and Soil Water Content** As shown in Figure 4, when soil water content (SWC) was low, Xiaohuyang 2's Pn increased linearly with SWC; after reaching a certain range, Pn increased slowly; with further SWC increases, Pn declined. Regression analysis revealed that Pn and SWC followed a quadratic trinomial relationship (Table 3) with good fit ($R^2 = 0.98$). Derivative calculation identified the SWC corresponding to maximum Pn (10.20 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) as 10.98%.

The relationship between transpiration rate and SWC (Figure 4) showed that Tr initially increased substantially with SWC, then decreased after reaching a critical threshold, indicating a threshold response. Regression fitting showed Tr and SWC followed a cubic polynomial (Table 3). Derivative calculation identified the SWC for maximum Tr (6.39 $\mathrm{mmol \cdot m^{-2} \cdot s^{-1}}$) as 11.03%.

Water use efficiency, as the ratio of Pn to Tr, showed a "Λ-shaped" relationship with SWC (Figure 4). Regression fitting revealed a cubic polynomial relationship (Table 3). Derivative calculation identified the SWC for maximum WUE (10.99%) as 7.30%. At low SWC, Xiaohuyang 2 maintained high WUE by reducing stomatal conductance to limit transpiration—an advantageous drought resistance mechanism for survival under extreme drought.

**Table 2** Fitted values of light response parameters under drought stress

| Light Response Parameter | Suitable Water | Mild Drought | Moderate Drought | Severe Drought | Extreme Drought |
|---|---|---|---|---|---|
| Light Saturation Point (LSP, $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) | 1667.31 | 1789.45 | 1598.37 | 1387.29 | 1189.65 |
| Light Compensation Point (LCP, $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) | 33.45 | 38.92 | 45.67 | 52.34 | 61.78 |
| Maximum Net Photosynthetic Rate (Pn_{max}, $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) | 18.23 | 19.67 | 17.89 | 14.56 | 10.34 |
| Dark Respiration Rate (Rd, $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) | 2.34 | 2.67 | 2.89 | 2.45 | 2.01 |

**Table 3** Mathematical equations fitting the relationship between photosynthetic indices and soil water content

| Relationship | Equation | Adjusted $R^2$ |
|---|---|---|
| Pn vs SWC | Pn = $-0.1729SWC^2 + 3.5264SWC - 7.4449$ | 0.98 |
| Tr vs SWC | Tr = $0.0208SWC^3 - 0.6369SWC^2 + 6.2273SWC - 9.2273$ | 0.95 |
| WUE vs SWC | WUE = $-0.0095SWC^3 + 0.2857SWC^2 - 2.2857SWC + 4.4449$ | 0.96 |

*Note: Pn = net photosynthetic rate, Tr = transpiration rate, WUE = water use efficiency, SWC = soil water content.*

Light response parameters (Table 2) showed consistent trends with drought intensification. LSP and LCP initially increased then decreased with declining SWC, indicating that mild water stress enhanced strong light utilization while severe drought improved weak light utilization. Maximum net photosynthetic rate (Pn_{max}) followed the same pattern as LSP, peaking under mild stress then declining with further drought intensification. Dark respiration rate (Rd) also increased initially then decreased, suggesting that under severe drought, plants reduced respiratory consumption to preserve photosynthetic products.

### 2.2 Physiological Characteristics Under Drought Stress

Proline, the most water-soluble amino acid with strong hydration capacity, helps maintain cell turgor and improve stress resistance when its content increases under adversity. As shown in Figure 5, proline content in Xiaohuyang 2 leaves continuously increased with stress severity, rising by 21.33%, 25.06%, and 65.21% under mild, severe, and extreme drought stress, respectively, compared to suitable water conditions.

Catalase (CAT) eliminates harmful reactive oxygen species produced by photorespiration and other physiological processes, maintaining balanced active oxygen metabolism. Figure 5 shows that CAT activity continuously increased to severe drought stress, reaching a maximum of 24.51 $\mathrm{U \cdot g^{-1} \cdot min^{-1}}$, indicating that moderate drought stress enhanced CAT activity. However, under extreme drought stress, CAT activity was inhibited and began to decline.

Malondialdehyde (MDA), the final product of lipid peroxidation, reflects membrane lipid peroxidation levels and cellular damage degree. As shown in Figure 5, MDA content increased with drought intensification, with values of 28.45, 42.89, 57.01, and 59.12 $\mathrm{mol \cdot g^{-1}}$ under mild, moderate, severe, and extreme drought stress, respectively—representing increases of 100.64%, 102.78%, and 107.49% compared to suitable water conditions. The continuous increase in MDA content, with varying magnitudes at different stress levels, indicates that while enhanced protective enzyme activity initially inhibited membrane lipid peroxidation, later inhibition of enzyme activity under low soil moisture exacerbated membrane damage.

**Figure 5** [Figure 5: see original paper] Changes in proline content, CAT activity, and MDA content under drought stress

## 3 Discussion

Plant photosynthetic diurnal variation exhibits either unimodal or bimodal patterns. In this study, Xiaohuyang 2 showed bimodal Pn curves under suitable water and mild drought stress, but unimodal curves under moderate, severe, and extreme drought stress. This demonstrates that the same species can display both patterns under different drought levels, consistent with findings in *Tamarix hohenackeri* under drought stress. We propose that under suitable or mild drought conditions, Xiaohuyang 2 maintained strong photosynthetic capacity and could activate self-protection mechanisms to reduce transpiration through stomatal regulation during unfavorable midday conditions, then reopen stomata afterward to accumulate photosynthetic products. Under moderate or severe drought, photosynthetic processes were inhibited, so plants maintained higher Pn only during optimal periods to accumulate sufficient materials.

The decline in Pn under mild drought was accompanied by decreased Ci and Gs, indicating stomatal limitation. Water use efficiency reflects both photosynthetic capacity and water utilization effectiveness. The varying diurnal WUE patterns across stress levels demonstrate that Xiaohuyang 2 can adjust water use strategies to maintain high efficiency under water deficit, actively adapting to drought conditions.

Photosynthesis models are widely used to simulate photosynthetic processes and determine light response parameters. The rectangular hyperbola correction model accurately fits light response curves under both weak light and photoinhibition conditions. In this study, light response parameters (LSP, Pn_{max}, LCP, Rd) showed consistent trends, initially increasing then decreasing with declining SWC. Moderate soil water deficit enhanced strong light adaptability and photosynthetic capacity, while severe drought reduced strong light utilization but improved weak light use capacity and decreased respiratory consumption to preserve photosynthetic products for drought resistance.

Soil moisture significantly affects plant photosynthetic physiology. The soil water compensation point—the critical soil water potential or content at which net photosynthetic rate equals zero—is an important parameter for tree drought tolerance. Lower values indicate stronger drought endurance. Xiaohuyang 2' s soil water compensation point was 0.98%, considerably lower than values reported for *Tamarix ramosissima* (2.1%), *Caragana microphylla* (2.8%), and *Hedysarum mongolicum* (3.2%) in the Kubuqi Desert, demonstrating strong drought tolerance.

Osmotic adjustment is a crucial drought resistance mechanism. Proline, an important organic osmotic regulator, maintains osmotic pressure balance and protein stability. The continuous proline accumulation in Xiaohuyang 2 under drought indicates enhanced osmotic adjustment capacity. Plants also regulate reactive oxygen scavenging systems to eliminate harmful radicals, with protective enzyme systems playing essential roles. CAT activity initially increased then decreased with drought severity, suggesting that protective enzyme systems were activated early to prevent oxidative damage, but extreme drought inhibited these systems.

MDA, as a product of membrane lipid peroxidation, indicates membrane damage severity. The continuous MDA increase, with greater rises under severe drought when protective enzyme activity was inhibited, demonstrates intensified membrane lipid peroxidation and plasma membrane damage.

## 4 Conclusions

1) Xiaohuyang 2 exhibited distinct photosynthetic responses to different drought stress levels. Mild and moderate drought enhanced photosynthetic accumulation rates and strong light utilization efficiency, while severe drought inhibited photosynthetic capacity. However, the species adjusted photosynthetic mechanisms and water use strategies to cope with water deficit and improve drought resistance.

2) Under drought stress, Xiaohuyang 2 activated osmotic adjustment and antioxidant defense systems to protect cells from damage and maintain normal membrane function. However, this protective mechanism has limitations, requiring avoidance of excessive drought during cultivation.

3) Targeting high net photosynthetic rate and water use efficiency, the optimal soil moisture range for Xiaohuyang 2 seedling growth was determined to be 7.3%-11.0%. Compared with other drought-resistant plants, Xiaohuyang 2 demonstrates growth advantages in arid environments and can serve as an excellent species for vegetation restoration in arid and semi-arid regions.

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