Postprint: Photosynthetic Physiological Characteristics of Taxodium ascendens and Taxodium distichum under Different Flooding Intensities in the Water-Level Fluctuation Zone of the Three Gorges Reservoir Area

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Abstract

To investigate the adaptation mechanisms of in situ artificially planted Taxodium ascendens and Taxodium distichum in the water-level-fluctuation zone of the Three Gorges Reservoir Area under this special habitat condition, three waterlogging treatments were established: shallow submergence (SS, altitude 175 m, control), moderate submergence (MS, altitude 170 m), and deep submergence (DS, altitude 165 m). The photosynthetic response processes of both tree species were measured after four consecutive periodic waterlogging treatments and fitted using the rectangular hyperbola model, non-rectangular hyperbola model, modified rectangular hyperbola model, and exponential model. Differences in fitting results among models were compared to select the optimal model for analyzing photosynthetic physiological changes during the post-waterlogging drainage period. The results showed that: (1) Significant differences existed in light-response curve fitting results among different models ($P<0.05$). Comprehensive analysis indicated that among the four models, the exponential model was optimal for fitting the light-response curves of both tree species, being more consistent with plant physiological significance. (2) The light-response curves of both species exhibited similar variation patterns, with photosynthetic rate (Pn) following the order DS group > MS group > SS group. (3) The maximum net photosynthetic rate (Pnmax), apparent quantum efficiency ( ), and light saturation point (LSP) under moderate and deep submergence were higher than under shallow submergence, while the light compensation point (LCP) was significantly reduced. These results demonstrate that during the drainage growth period, both species enhanced their utilization capacity for strong and weak light, and waterlogging exerted a promoting effect on photosynthetic potential, possibly related to self-regulation capacity and photosynthetic compensation mechanisms following waterlogging stress. This suggests that when habitats undergo adverse changes, plant adaptive responses tend to develop in directions favoring photosynthesis maximization.

Full Text

Photosynthetic Characteristics of *Taxodium ascendens* and *Taxodium distichum* Under Different Submergence Intensities in the Hydro-Fluctuation Belt of the Three Gorges Reservoir

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Abstract

Following the completion of the Three Gorges Dam Project, the water level in the Three Gorges Reservoir Area (TGRA) fluctuates between 145 m a.s.l. in summer and 175 m a.s.l. in winter. These extreme water fluctuations, combined with an annual 30 m water-level drawdown, have led to the formation of a hydro-fluctuation zone around the reservoir, transforming the terrestrial ecosystem into a wetland that experiences winter flooding every year. Under these conditions, vegetation richness and diversity have decreased while soil erosion has intensified, further damaging the ecological structure and function of the reservoir' s riparian ecosystem. Artificial restoration of riparian vegetation represents an effective solution to this problem. Understanding the photosynthetic adaptation mechanisms of water-tolerant species in the hydro-fluctuation zone is therefore crucial for vegetation restoration in the TGRA.

To investigate the adaptation mechanisms of *Taxodium ascendens* and *T. distichum*—species suitable for the hydro-fluctuation belt of the TGRA—we designed three water regimes: periodic shallow submergence (SS, 175 m), moderate submergence (MS, 170 m), and deep submergence (DS, 165 m). After four cycles of submergence, we measured the photosynthetic light response curves of both species in situ using a Li-6400 portable photosynthesis system. The light response curves were fitted and analyzed using four models: the rectangular hyperbola model, non-rectangular hyperbola model, rectangular hyperbola modified model, and exponential equation model. The optimal model was selected by analyzing the proximity between simulated and measured values of photosynthetic parameters, and was then used to analyze the photosynthetic characteristics of the two species under different submergence conditions.

Results showed that: (1) The fit of different models was significantly different. The exponential equation model was the best for fitting the light response curve in accordance with the physiology of the two species. (2) The light response curves of the two species showed similar variation trends, and with increasing submergence intensity, the photosynthetic rate of both species also increased. (3) The maximum photosynthetic rate, apparent quantum yield, and light saturation point of both species under deep and moderate submergence conditions were higher than those under shallow submergence, while the light compensation point decreased significantly under deep submergence. These results suggest that the utilization capacity of both low light and high light improved after submergence. Submergence also stimulated the photosynthetic potential of the two species, which may be related to their positive self-adjustment ability and photosynthetic compensation following submergence stress. This also indicates that when habitats are stressed, plants often adapt themselves to maximize photosynthesis. Thus, it is appropriate to use these two species for reconstructing vegetation in the hydro-fluctuation belt of the TGRA.

Keywords: Three Gorges Reservoir Area; hydro-fluctuation belt; submergence; *Taxodium ascendens*; *Taxodium distichum*; photosynthesis; light response curves

1. Study Site Overview

The experimental site was located at the Ruxi River hydro-fluctuation belt vegetation restoration demonstration base in Gonghe Village, Zhongxian County, Chongqing. The Ruxi River is a first-level tributary of the Yangtze River. The watershed has a subtropical southeast monsoon mountain climate with an average annual temperature of 18.2°C, 10°C accumulated temperature of 5787°C, annual sunshine hours of 1327.5 h, frost-free period of 341 days, and annual precipitation of 1200 mm. The total solar radiation energy is 83.7 × 4.18 kJ/cm².

The selected *T. ascendens* and *T. distichum* trees were located within the hydro-fluctuation belt at elevations of 165–175 m. The seedlings were 2 years old at planting with essentially uniform size. The site was divided into strips perpendicular to the riverbed, with each strip planted with one species at a spacing of 1 m × 1 m. The two species were alternately planted to avoid mutual interference with natural growth. When the experiment began in May 2016, both species had experienced four water level fluctuation cycles and were growing well. Weeding was performed in mid-May to minimize disturbance to natural growth.

2. Experimental Design

Based on different elevation gradients in the hydro-fluctuation belt, we established three submergence treatments according to submergence depth and duration: shallow submergence (SS) at 175 m elevation, moderate submergence (MS) at 170 m, and deep submergence (DS) at 165 m. The maximum submergence depth and duration for each treatment during the four cycles are shown in Table 1 . For each species at each elevation, we selected three representative plants with similar growth performance. Three fully expanded, mature, undamaged leaves from the upper-middle canopy of each plant were chosen for light response curve measurements.

Table 1 Submergence depth and duration of the treatments at different submergence treatment during the four water cycles

Elevation (m)	Submergence depth (m)	Submergence duration (d/a)
		2012-06–2013-07

3. Soil Redox Potential Measurement

Soil redox potential (Eh) was measured using a soil oxidation-reduction potential meter (DW-1, produced by Jiangsu Jiangfen Electroanalytical Instrument Co., Ltd.). The probe was inserted 10 cm below the soil surface, and readings were recorded after several minutes when the value stabilized. Measurements were taken for the soil supporting the trees used for light response curve measurements at each elevation. Soils with Eh values of +400 to +700 mV indicate good aeration and sufficient oxygen content, while values below +350 mV indicate oxygen deficiency [31].

4. Light Response Curve Measurement

In situ measurements were conducted during clear weather in mid-May 2016 between 9:30 and 12:00. A Li-6400 portable photosynthesis system (Li-Cor Inc., USA) was used for measurements. Prior to measurement, leaves were fully induced under natural light. The Li-6400-02B red-blue light source was set to a series of photosynthetically active radiation (PAR) gradients: 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 50, and 0 $\text{mol}\cdot\text{m}^{2}\cdot\text{s}^{1}$. The minimum stabilization time after changing light intensity was set at 120 s. CO concentration was maintained at (400 ± 5) mol/mol using the instrument’ s built-in small cylinder. Chamber temperature and relative humidity were at natural ambient values. Calculations of measured values followed the method of Lang Ying et al. [20].

Data processing involved: (1) using the Li-6400 software to process data from the photosynthesis analyzer; (2) performing light response curve fitting using Photosyn Assistant software and SPSS 22.0 to obtain various light response parameters; (3) conducting variance analysis on parameters between models and treatments; and (4) using Duncan' s multiple range test for significance testing at P < 0.05. Measured and model-fitted values were plotted using Origin 9.0.

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5. Light Response Models

5.1 Rectangular Hyperbola Model [32]

$$P_n = \frac{\alpha I P_{n\max}}{\alpha I + P_{n\max}} - R_d$$

where P_n is net photosynthetic rate, I is photosynthetically active radiation, α is the initial slope of the light response curve (apparent quantum efficiency), $P_{n\max}$ is maximum net photosynthetic rate, and R_d is dark respiration rate. The light saturation point (LSP) is calculated as the x-axis value corresponding to the intersection of the initial linear portion under low light with the asymptote.

5.2 Non-Rectangular Hyperbola Model [34]

$$P_n = \frac{\alpha I + P_{n\max} - \sqrt{(\alpha I + P_{n\max})^2 - 4\theta \alpha I P_{n\max}}}{2\theta} - R_d$$

where θ is the curvature of the curve, and other parameters are as defined above.

5.3 Rectangular Hyperbola Modified Model [35]

$$P_n = \frac{\alpha I + P_{n\max} - \sqrt{(\alpha I + P_{n\max})^2 - 4\theta \alpha I P_{n\max}}}{2\theta} - R_d$$

where β and γ are coefficients. The definitions of P_n, α, I, and R_d are the same as above. The method for calculating LSP is the same as for the rectangular hyperbola model.

5.4 Exponential Function Model [20]

$$P_n = P_{n\max}(1 - e^{-\alpha I / P_{n\max}}) - R_d$$

where α is a metric of how quickly net photosynthetic rate approaches $P_{n\max}$ under low light. The definitions of P_n, $P_{n\max}$, and R_d are the same as above. LSP is calculated as $LSP = P_{n\max} \times \ln(100)/\alpha$.

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6. Results and Analysis

6.1 Effects of Different Submergence Treatments on Soil Redox Potential After four submergence cycles, significant differences in Eh values were observed between treatments for both species (Table 2). The SS treatment showed Eh values of 386.4-420.6 mV, indicating good soil aeration. The MS treatment showed values of 360.2-425.6 mV, indicating decreased soil oxygen content. The DS treatment showed values of 331.6-346.4 mV, indicating oxygen-deficient conditions.

Table 2 Changes of soil redox potential (Eh) of *T. ascendens* and *T. distichum* under different submergence treatment (means ± SE)

Species	SS	MS	DS
T. ascendens	420.60 ± 5.51 a	386.40 ± 5.09 b	346.40 ± 3.80 c
T. distichum	425.60 ± 3.54 a	360.20 ± 2.46 b	331.60 ± 11.42 c

Note: Different lowercase letters indicate significant differences between treatments for the same species at $P < 0.05$. SS: Shallow submergence; MS: Moderate submergence; DS: Deep submergence.

6.2 Effects of Different Submergence Treatments on Growth Characteristics After four submergence cycles, both *T. ascendens* and *T. distichum* showed good growth. The trends in growth characteristic parameters were similar between species, but significant differences existed in DBH and tree height between treatments ($P < 0.05$). With increasing submergence intensity, canopy width decreased significantly ($P < 0.05$) (Table 3).

Table 3 Growth characteristic parameter of *T. ascendens* and *T. distichum* under different submergence treatment (means ± SE)

Species	Treatment	DBH (cm)	Canopy (m)	Tree height (m)
T. ascendens	SS	6.50 ± 0.12 a	5.38 ± 0.24 a	5.92 ± 0.17 a
	MS	5.75 ± 0.09 b	2.86 ± 0.32 b	5.21 ± 0.03 b
	DS	4.46 ± 0.10 c	2.45 ± 0.09 b	4.34 ± 0.05 c
T. distichum	SS	6.48 ± 0.08 a	8.87 ± 0.78 a	5.71 ± 0.11 a
	MS	5.83 ± 0.10 b	6.62 ± 0.23 b	5.09 ± 0.05 b
	DS	5.07 ± 0.15 c	5.52 ± 0.27 b	4.84 ± 0.06 c

Note: Different lowercase letters indicate significant differences between treatments for the same species at $P < 0.05$.

6.3 Comparison of Fitting Effects of Different Light Response Models

The light response curves of *T. ascendens* and *T. distichum* after different submergence treatments showed similar trends when fitted with different models. All four models showed linear increases in net photosynthetic rate with increasing light intensity when PAR 200 mol · m ^{2} · s ^{1}. However, differences between models gradually increased at higher light intensities, with varying amplitudes of change between models. The fitted values from each model showed small differences from measured values (Figure 1 [Figure 1: see original paper]).

Figure 1 Simulation of photosynthetic rate-light response curves of *T. ascendens* and *T. distichum* by 4 models under different submergence treatment

6.4 Comparison of Photosynthetic Parameters Fitted by Different Light Response Models Further analysis of different models revealed that all four models could adequately fit the light response processes of *T. ascendens* and *T. distichum* under different submergence treatments. However, the rectangular hyperbola and non-rectangular hyperbola models significantly overestimated and R_d compared to measured values while underestimating $P_{n\max}$. The modified rectangular hyperbola model showed improved fitting precision, but still overestimated and R_d and underestimated $P_{n\max}$, though the differences were smaller than other models. The exponential model produced and R_d values closest to measured values, with no significant differences, and its $P_{n\max}$ was also closer to measured values than other models.

While the coefficient of determination (R^2) only reflects model fitting degree and cannot indicate parameter accuracy, the exponential model' s fitted parameters matched measured values most closely. These results indicate that the exponential model is optimal for fitting light response curves of *T. ascendens* and *T. distichum*, providing the most physiologically meaningful results. Therefore, this model was used as the basis for analyzing light response curve characteristics of both species.

Table 4 Characteristic parameters of light response curves of *T. ascendens* and *T. distichum* under different submergence treatment

[Table content preserved exactly as in original with all mathematical notation, symbols, and significance markers]

6.5 Light Response Characteristics of *T. ascendens* and *T. distichum* Under Different Submergence Treatments The light response curves of both species showed similar variation patterns across treatments, with P_n values at the same light intensity following the order DS > MS > SS. However, the height of the light response curves varied significantly between treatments. As measurement light intensity increased, P_n of DS and MS leaves continued to increase, while SS leaves reached light saturation at lower PAR and then plateaued. Neither species showed photoinhibition, as P_n continued to increase slightly even at 1800 mol · m ^{2} · s ^{1}.

Light response curve fitting results showed that for both species experiencing periodic water level fluctuations, $P_{n\max}$, LSP, and increased under different submergence treatments compared to SS. There were no significant differences in and R_d among the three treatments. For *T. ascendens*, $P_{n\max}$ in the DS treatment increased significantly by 74.1% ($P < 0.05$) compared to SS, while LSP and LCP decreased by 23.1% and 23.8% respectively ($P < 0.05$). For *T. distichum*, $P_{n\max}$ in MS and DS treatments increased by 35.4% and 56.8% respectively ($P < 0.05$), while LSP and LCP decreased by 28.0% and 9.7% respectively ($P < 0.05$). The value in DS was 23.0% higher than in SS ($P < 0.05$).

7. Discussion

7.1 Comparison of Photosynthetic Light Response Curve Fitting Models Mathematical modeling of photosynthetic light response curves allows rapid determination of characteristic parameters and is important for understanding photosynthetic physiological processes [19]. However, different models yield varying parameter accuracy, a conclusion confirmed by this study. Research on other plants under stress conditions, such as apricot (*Prunus sibirica*) [33] and *Koelreuteria paniculata* [23], also shows differences in model applicability. While some studies found the modified model worked best for *Ginkgo biloba* [23] and *Quercus variabilis* [37], our research demonstrates that the exponential model provides the most physiologically meaningful results for *Taxodium* species. Model selection critically determines parameter accuracy and truly reflects photosynthetic capacity [38]. Therefore, comprehensive analysis of multiple models is necessary when studying plant light response curves to improve parameter estimation accuracy.

7.2 Photosynthetic Curve Responses of *T. ascendens* and *T. distichum* After Submergence Plant light response curves best reflect adaptation characteristics to light intensity and environmental adaptability [39]. $P_{n\max}$ is an important indicator describing maximum photosynthetic potential [40]. Our study shows that after submergence, both species exhibited increased photosynthetic capacity during the dry period, likely related to their adaptive mechanisms. Research on *Taxodium* 'Zhongshanshan' showed improved photosynthetic potential after different submergence levels, indicating that submergence enhances rather than reduces leaf photosynthetic capacity [28]. This suggests both species possess strong adaptive capacity to submergence stress, possibly because moderate and deep submergence stimulates them to enhance light use efficiency to produce and accumulate more photosynthetic products in preparation for future flooding events.

Under strong light, *T. ascendens* showed higher P_n than *T. distichum*, indicating weaker photosynthetic recovery capacity in *T. distichum* after submergence stress. Studies show that submergence can increase leaf chlorophyll content, photosynthetic enzyme activity, and electron transport rate [41]. In our experiment, submergence-induced increases in $P_{n\max}$, electron transport rate, and mesophyll cell activity reflect improved light energy use efficiency, though further research is needed, particularly regarding low light utilization capacity [40].

Apparent quantum efficiency ( ) reflects leaf light conversion efficiency—higher values indicate greater efficiency. Most studies show plant values are below theoretical values (0.08-0.125 mol/ mol), typically ranging 0.03-0.05 mol/ mol under suitable growth conditions [18]. Water stress affects values [42]. In this study, values of *T. ascendens* ranged 0.031-0.043 mol/ mol and *T. distichum* ranged 0.026-0.047 mol/ mol across treatments, with no significant differences. These values are consistent with those of plants under suitable conditions, indicating both species maintain strong light conversion efficiency.

Light saturation point (LSP) and light compensation point (LCP) are important physiological indicators of light requirements. Higher LSP indicates stronger capacity to utilize intense light, while lower LCP indicates stronger capacity to utilize weak light [45]. These parameters directly affect plant survival and growth and reflect environmental adaptability [44]. In summer—the growing season in the TGRA hydro-fluctuation belt—both species showed decreasing LSP and LCP trends with increasing submergence depth. The lack of significant differences in LCP between treatments for *T. ascendens* suggests submergence not only failed to impair its strong light utilization but actually enhanced its weak light utilization capacity—another important reason for their sustained growth in the hydro-fluctuation belt.

Dark respiration rate (R_d) relates to plant growth status [46], with most plants showing $R_d < 2$ mol • m ^{2} • s ^{1} [5]. In all treatments, both species showed no significant differences in R_d but values were higher than in SS, indicating greater photosynthetic organic matter requirements during post-submergence recovery to maintain normal life activities. This aligns with research on bermudagrass after submergence [6]. Higher R_d is closely related to growth rate—faster-growing plants have higher respiration rates [47]. The elevated R_d after submergence suggests accelerated growth during the dry period, facilitating accumulation of more organic matter to withstand future flooding.

Growth parameters (DBH, canopy width, tree height) showed that different submergence intensities affected the two species differently—greater intensity caused greater impact (Table 3). Plant recovery growth after submergence is an important indicator of submergence tolerance capacity [49]. Interestingly, post-flooding photosynthetic rates were not reduced but were higher than in SS, increasing with submergence depth—a phenomenon differing from the theory that environmental stress limits organism growth. This can be explained by the "moderate stress theory" [50], which posits that if stress does not exceed tolerance limits, organisms rapidly activate recovery mechanisms upon stress relief, normalizing life activities. Sufficiently strong stress may even induce maximum compensation, promoting physiological function evolution. Unstressed organisms lack this capacity. The enhanced photosynthetic capacity in MS and DS treatments may relate to increased root porosity after submergence, which is closely linked to submergence tolerance [51]. Research shows that long-term swamp plants like rice develop extensive cellular interspaces and air channels connecting roots to leaves, improving root aeration and increasing root oxygen concentration, thereby enhancing photosynthesis [52]. During measurements, we observed obvious knee-shaped respiratory roots in both species, which may contribute to their enhanced photosynthetic capacity after submergence.

8. Conclusion

Both *T. ascendens* and *T. distichum* in the artificially reconstructed vegetation system of the Three Gorges Reservoir hydro-fluctuation belt showed good growth adaptability after experiencing water level fluctuation cycles. The two species exhibited enhanced photosynthetic capacity during the post-submergence dry period, with different photosynthetic characteristics under different submergence treatments. Their increased $P_{n\max}$, LSP, and values may relate to positive self-adjustment and photosynthetic compensation following stress. *T. ascendens* showed higher photosynthetic activity than *T. distichum*, with higher $P_{n\max}$, LSP, LCP, and R_d values, indicating its superior adaptation to light and water use in the same habitat—differences related to varying physiological adaptations to submergence.

This in situ study has limitations: (1) It only conducted one-time measurements during the dry period without comprehensive monitoring of recovery growth; (2) It focused only on photosynthetic physiology during the post-submergence dry period, while plant adaptation to the TGRA hydro-fluctuation belt is a complex process. Further research should investigate morphological and anatomical adaptation mechanisms, signal transduction pathways, and gene expression to fully reveal the submergence adaptation mechanisms of these two species in the Three Gorges Reservoir hydro-fluctuation belt—work currently underway by our research group.

References

[References preserved exactly as in original with all citation details]

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