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RESEARCH ARTICLE

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Effect of soil water changes on photosynthetic characteristics of *Taxodium distichum* seedlings in the hydro-fluctuation belt of the Three Gorges Reservoir area

Abstract Four different kinds of water treatment were applied to examine the photosynthetic characteristics of baldcypress (*Taxodium distichum*) seedlings in the hydro-fluctuation belt of the Three Gorges Reservoir area. The aim was to shed light on the physio-ecological adaptation of this species to changing water levels for revegetation purposes. The water treatments were normal growth water condition (CK), light drought water stress (T1), growth under soil water saturation (T2) and growth with soil submersion (T3). T3 had the lowest content of photosynthetic pigment; T1 and T2 did not differ from CK in the content of chlorophyll and carotenoid. The ratio of chlorophyll *a* to *b* in the four groups ranged from 2.04 to 2.69 and the ratio of chlorophyll to carotenoid from 3.08 to 4.51. In group T1, the seedling of baldcypres had lower apparent light use efficiency, lower apparent CO_2 use efficiency and a lower net photosynthetic rate, with the net photosynthetic rate 24.9% lower than that of group CK. However, T2 and T3 did not differ from CK in apparent light use efficiency, apparent CO_2 use efficiency and net photosynthetic rate. Water use efficiency of the four treatments consistently increased as treatment was prolonged; the average water use efficiency of T3 was the lowest while that of CK was the highest. Correlation analysis showed that the net photosynthetic rate of baldcypress seedlings was positively related to transpiration rate, stomatal conductance, water use efficiency, apparent light use efficiency and apparent CO_2 use efficiency, but highly negatively related to the ratio of chlorophyll *a* to *b*. Net photosynthetic rate was not significantly related to the contents of chlorophyll and carotenoid, the ratio of chlorophyll to carotenoid, relative air humidity and intercellular CO_2 concentration. The transpiration rate was positively correlated with stomatal conductance and negatively related to water use efficiency. The results showed that different water treatments could effectively influence the baldcypress seedlings' content of photosynthetic pigment, leaf gas exchange and apparent resources use efficiency. The results verified that the species *T. distichum* takes on the features of a water-tolerant and hydrophilic plant, which can be considered as one of the species for the building of a forest protection system for the hydro-fluctuation belt in the Three Gorges Reservoir area. Baldcypress should not be planted in drought-stricken soils.

Keywords Three Gorges Reservoir area, hydro-fluctuation belt, soil water change, *Taxodium distichum* seedlings, photosynthetic characteristics

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1 Introduction

The Three Gorges Project in the Yangtze River has already created a hydro-fluctuation belt between water levels 145 and 175 m in the reservoir area, with an area of 298 km^2 stretching over a length of 2,000 km (Huang, 1994; Diao and Huang, 1999; Zhang et al., 2000). Due to annual periodic water level fluctuations, the soil water content in the hydro-fluctuation belt will be changed correspondingly.

The soils located at different elevations and/or slopes in the hydro-fluctuation belt will be subjected to a range of hydrological regimes, from drought to flooding, indicating several features of complexity, susceptibility and complication in soil water content changes. Such a cycle of soil water change will not only impact the photosynthetic characteristics in physio-ecological and growth development of the tree species currently growing at the hydro-fluctuation belt, but also bring about higher standards for screening suitable tree species for future reforestation projects in this area. If tree species well suited to such a dynamic hydrological environment can be selected through scientific experimentation with simultaneous understanding of the photosynthetic and physio-ecological characteristics of the species, it will assist considerably in both the hydro-fluctuation belt's vegetative restoration and the building of the forest protection system for the banks of the reservoir. Although many studies on the effects of soil water change on the photosynthetic characteristics of tree species (He and Ma, 2000; Chen et al., 2003; Liu et al., 2003; Ma et al., 2004) are currently available, related studies of the hydro-fluctuation belt of the Three Gorges Reservoir area have not yet been conducted. Applicable results of studies on suitable tree species for the hydro-fluctuation belt to be used for revegetative activities are still limited to the biological traits of the species (He et al., 1997; Xiao et al., 2000).

The aim of this study is to understand the photosynthetic characteristics and adaptive mechanisms of the plants under environmental conditions that mimic the hydro-fluctuation belt. Those species that perform well will be screened for their physio-ecological performance to provide both technical and theoretical support for their use in revegetation of the hydro-fluctuation belt of the Three Gorges Reservoir area.

2 Materials and methods

2.1 Tree species and location for the study

Seedlings of *Taxodium distichum* L. Rich (baldcypress), sown in the nursery in early March 2004, were collected as experimental material. In mid-June 2004, 120 homogeneous seedlings were transplanted into containers (13 cm wide, 12 cm deep, filled with purple soil; one plant per pot). The potted seedlings were moved to the Southwest China Normal University's Experimental Zone of Ecology (249 m elevation), to be acclimatized under the same conditions of soil substrate, illumination and watering. A transparent experimental booth, covered by plastic film to avoid natural rainwater, was built on July 25, 2004, the date water treatments began.

Baldcypress, originally grown in the southeastern part of North America, has now been widely spread over the entire world. Baldcypress has been grown successfully in China for 80 years. This species is characterized by fast growth, turgor at the basal stem, knee-like aerated roots and feathery, needle-like leaves. Baldcypress, water-tolerant species, is often grown in wetlands (Wang et al., 1995).

2.2 Experimental design

One hundred and twenty seedlings were randomly divided into four groups for different water treatments, including normal growth water condition (CK), growth under light drought water stress (T1), growth under soil water saturation (T2) and growth in soil submersion (T3). CK referred to normal growth conditions with soil water content between 60% and 63% of soil water field capacity (soil water content measured by weight), in which the seedlings had no wilting during sunny days. T1 seedlings were kept in soil water content between 47% and 50% of soil water field capacity, in which the fresh leaves of the seedlings wilted around 13:00 h and recovered around 17:00 h (Hu and Wang, 1998; Hu et al., 2000). T2 seedlings were kept in saturated soil water, while T3 seedlings remained flooded at 1 cm above the soil surface. Plastic basins with a width of 68 cm and a depth of 22 cm were used to hold the potted seedlings of group T3, with tap water being infused into the basins till flooding occurred at 1 cm above the soil surface (Bragina et al., 2001).

Tests were conducted at five-day intervals from the beginning of the experiment. There were five replicates for each time measurement in each treatment. The experiment ended on August 25, 2004.

2.3 Measurement of responses in leaf gas exchange

The third or fourth upper leaf from the canopy of each seedling was chosen to test responses of leaf gas exchanges using an American CI-310 Portable Operation System after being induced under saturated light illumination. All of the tests were conducted between 9:00 and 11:00 a.m. at a controlled indoor temperature of 25°C, with 400 μmol/L CO_2 and photosynthetically active radiation (PAR) 1,000 μmol photons/(m^2·s). The specific parameters included net photosynthetic rate (*Pn*), transpiration rate (*Tr*), stomatal conductance (g_s), air temperature (*Ta*), leaf temperature (*Tl*), relative air humidity (*RHi*) and intercellular CO_2 (*Ci*). The following three ratios were calculated: water use efficiency (*WUE*) = *Pn*/*Tr* (Nijs et al., 1997), apparent light use efficiency (*LUE*) = *Pn*/*PAR* (Long et al., 1993; Penuelas et al., 1998) and apparent CO_2 use efficiency (*CUE*) = *Pn/Ci* (He and Ma, 2000).

2.4 Photosynthetic pigment measurement

An endosmotic abstract method (Zou, 1995) was adopted for abstracting chlorophyll (*Chl*) and carotenoid (*Car*) from the leaves. Pigment content was tested by the Japanese made spectrophotometer 5220.

2.5 Statistical Analysis

In terms of indices measured, water treatment was regarded as an independent factor. One-way analysis of variance (One-way ANOVA) was employed to determine any significant differences between different treatment groups (GLM Procedures, SPSS 10.0 Version). Multiple pair-wise comparisons (Duncan's method) were used to determine significant differences at the 0.05 level between treatment groups in gas exchange responses and photosynthetic pigment content (Du, 2003).

3 Results

3.1 Change of photosynthetic pigments

The results of the analysis of variance (Table 1) showed that different water treatments had significant effect on the content of photosynthetic pigments of baldcypress seedlings. Along with soil water change, variation was observed in the contents of chlorophyll and carotenoid and in ratios of chlorophyll *a/b* and of *Chl/Car*. T3 had the lowest content of photosynthetic pigment (Fig. 1), compared to other three groups.

Table 1 The results of ANOVA of the effects of different water treatments on the physiological characteristics of baldcypress see- dlings

Character	*F* value	Probability	Significance
Content of *Chl (a+b)* (fw)	40.157	0.000	***
Content of *Chl (a+b)* (dw)	50.022	0.000	***
Content of *Car* (fw)	30.196	0.000	***
Content of *Car* (dw)	42.524	0.000	***
Ratio of *Chl a/b*	20.202	0.000	***
Ratio of *Chl/Car*	33.052	0.000	***
Pn	34.524	0.000	***
Tr	52.658	0.000	***
g_s	100.743	0.000	***
Ci	1.055	0.373	ns
WUE	18.223	0.000	***
LUE	35.109	0.000	***
CUE	26.627	0.000	***

Significance levels: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns $p > 0.05$. "fw" refers to fresh weight and "dw" means dry weight.

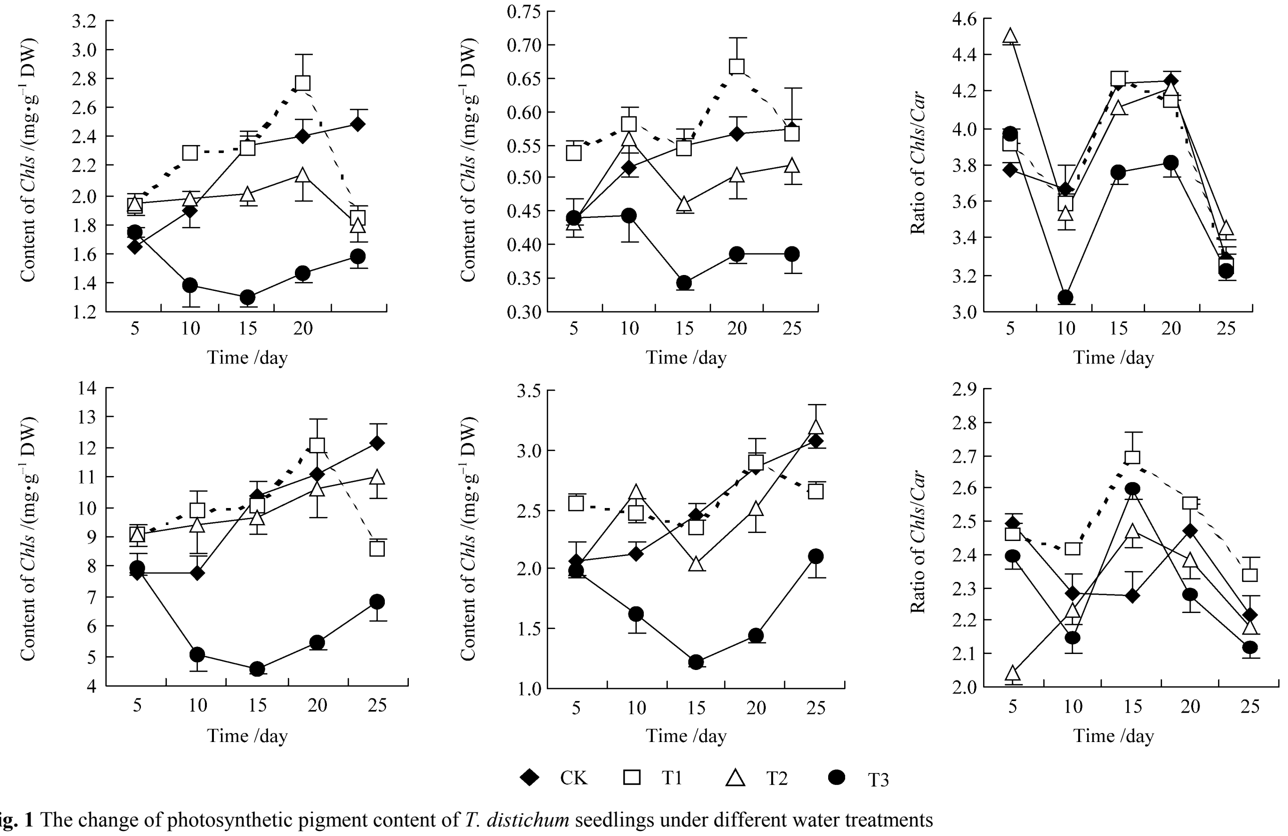

Fig. 1 The change of photosynthetic pigment content of *T. distichum* seedlings under different water treatments

Neither T1 nor T2 displayed significant differences from CK in the dry weight content of both chlorophyll and carotenoid. In contrast, the content in T3 was not only significantly lower than that of CK, but also significantly lower than that of either T1 or T2. During the entire experimental period, the change in the fresh weight content of both chlorophyll and carotenoid exhibited a similar trend as that in dry weight. In addition, the change in the ratio of Chl *a/b* was also similar compared to the change in the ratio of *Chl/Car*. The ratio of chlorophyll *a/b* was between 2.04 and 2.69 while the ratio of *Chl/Car* ranged from 3.08 to 4.51.

3.2 Responses of gas exchange

As shown in Table 1, photosynthetic gas exchange responses of *T. distichum* seedlings were significantly affected by the soil water gradient, where the effects on *Pn*, *Tr* and g_s were found to be highly significant.

Pn values varied differently in various groups as the treatment continued. In CK, *Pn* continuously increased; however, *Pn* continuously decreased both in T2 and T3. *Pn* in T1 alternated (Fig. 2). Mean *Pn* values over the experimental period revealed no significant differences between T2 and T3 and CK, although these three groups showed significant differences from that of T1. Under circumstances of drought water stress, baldcypress seedlings showed a lower average *Pn*, 24.9% lower than that of CK, whereas *Pn* values under conditions of saturated soil water and/or soil flooding were not significantly affected, but comparable to control plants, indicating that baldcypress is hydrophilic and a water-tolerant plant.

Baldcypress seedlings showed significant differences in *Tr* and g_s between treatments. Throughout the experimental period, mean values remained high in *Tr* and g_s as soil water increased, indicating a similarity of change between *Tr* and g_s under different treatments. As water treatments continued, mean values of *Tr* and g_s in T1, T2 and T3 showed a trend approaching that of CK, demonstrating the plasticity and adaptability of self-adjustment functions of baldcypress seedlings to adverse environments.

Pn changes did not synchronize with *Tr* and g_s, but g_s and *Tr* changed simultaneously.

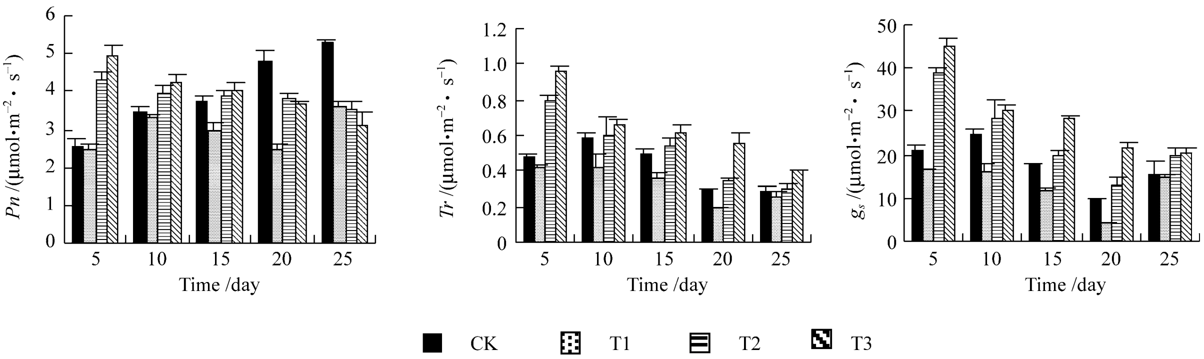

Fig. 2 The change of *Pn*, *Tr* and g_s of *T. distichum* seedlings under different water treatments (±SE)

3.3 Change of resources use efficiency

Different water treatments significantly affected resources use efficiency of baldcypress seedlings (Table 1). *WUE* increased sequentially in the four groups, among which CK showed an immediate increase, with the fifth mean *WUE* value being 2.9 times greater than of the first measurement, compared with an increase of only 0.51 in T3, as well as a 1.5 and 1.2-fold in T1 and T2, respectively. Mean *WUE* values during the experimental period were 11.0, 9.6, 8.8 and 6.6 μmol CO_2/mmol H_2O, respectively, in CK, T1, T2 and T3. CK showed the highest *WUE* in contrast to *WUE,* which decreased as soil water content increased in the other three groups.

A similar change in the trends between *LUE* and *CUE* in baldcypress seedlings was found, both of which were significantly impacted by water treatment (Fig. 3 and Table 1). Mean *LUE* values over the study period were 3.891, 2.911, 3.827 and 3.942 mmol CO_2/mol photons in CK, T1, T2 and T3, while mean *CUE* values were 9.722, 7.467, 9.564 and 9.807 mmol/mol CO_2 in CK, T1, T2 and T3. *LUE* and *CUE* in T1 were significantly different from the values in the other three groups. The latter three groups were comparable to each other, further indicating the adaptability of baldcypress seedlings to swamps and flooded environments.

3.4 Correlation analysis

Results of a correlation analysis demonstrated that *Pn* was positively correlated with *Tr*, g_s, *WUE*, *LUE* and *CUE* in baldcypress seedlings, exhibiting that *Pn* was affected by the latter factors. There was neither a significant correlation between *Pn* and the content of *Chl* and *Car*, nor with the ratios of *Chl/Car*, but a highly negative relationship with the ratio of *Chl a/b* was found.

No significant correlation was observed between *Pn* and *RHi* and *Ci*. While *Tr* was positively correlated to g_s, a highly negative relationship to *WUE* was found (see Table 2).

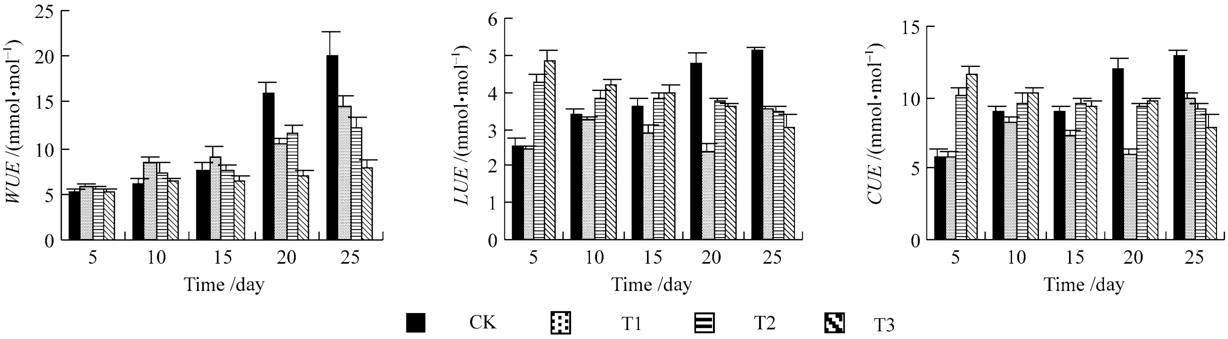

Fig. 3 The change of *WUE, LUE* and *CUE* of *T. distichum* seedlings under different water treatments (±SE)

Table 2 Correlations between *Pn* and other parameters in *T. distichum* seedlings

	Pn	*Tr*	g_s	*WUE*	*LUE*	*CUE*	*Chl* (dw)	*Car* (dw)	*Chl a/b*	*Chl/Car*
Tr	0.303**									
g_s	0.352**	0.891**								
WUE	0.364**	–0.683**	–0.539**							
LUE	0.999**	0.315**	0.364**	0.354**						
CUE	0.967**	0.254*	0.307**	0.393**	0.964**					
Chl (dw)	0.021	–0.421**	–0.488**	0.414**	–0.027	–0.036				
Car (dw)	–0.013	–0.474**	–0.499**	0.414**	–0.094	–0.060	0.820**			
Chl a/b	–0.273**	–0.180	–0.347**	–0.028	–0.274**	–0.311**	0.223*	0.142		
Chl/Car	–0.029	0.112	–0.072	–0.150	–0.024	–0.122	0.428**	0.121	0.397**	
RHi	0.053	–0.102	0.145	0.209*	0.051	0.140	–0.215*	–0.037	–0.551**	–0.748**
Ci	0.059	0.152	0.132	–0.143	0.067	–0.195	0.056	–0.076	0.184	0.357**

** Correlation is significant at the 0.01 level (2-tailed). * Correlation is significant at the 0.05 level (2-tailed).

4 Discussion

The content of chlorophyll in baldcypress seedlings when flooded was 36.5% lower than that in the control treatment, while the content of carotenoid under conditions of flooding remained 33.4% lower compared to the control. Interestingly, a significant reduction of content of photosynthetic pigments caused by flooding did not lead to a corresponding decline of *Pn*. This phenomenon was most likely induced by significantly higher g_s of baldcypress seedlings when flooded than that in CK. Although a significant decrease of photosynthetic pigment content impeded, to some degree, the photosynthesis of baldcypress seedlings, higher stomatal conductance could offset the decline of photosynthesis through gaining more CO_2 as well as improving gas exchange area, time and total volume. Furthermore, intercellular CO_2 concentration of baldcypress seedlings, when flooded, did not appear to be affected (Table 1), but was comparable to that in CK, implying that the capacity of mesophyllous cells for assimilating CO_2 was not depressed by maintaining a normal level in the control treatment, so that *Pn* was once again guaranteed to remain unchanged.

This study found that the ratio of *Chl/Car* was over 3:1, in contrast to the ratio of *Chl a/b* of less than 3:1, one of the important features of photosynthetic pigment content in baldcypress. In general, both ratios for common leaves are around 3:1 (Pan et al., 2004). The above proportions in photosynthetic pigment content, produced by illumination and many other factors, were closely correlated to the capacity of baldcypress seedlings for photosynthesis and photosynthetic physio-ecological adaptability to adverse environments. A ratio of *Chl/Car* exceeding 3:1 might enhance the proportion of chlorophyll in photosynthetic pigment and raise the capacity of photosynthesis, ensuring sufficient available reaction center pigment. A ratio of *Chl a/b* less than 3:1 might guarantee enough light-harvesting pigment to serve photosynthesis, so that the distributional proportion between chlorophylls *a* and *b* could be optimized (Lee et al., 1990; Scholes et al., 1997), further facilitating an optimal photosynthesis (Ronzhina et al., 2004). The *Pn* of baldcypress was negatively correlated with the ratio of *Chl a/b*, illustrating a reasonable distribution of photosynthetic pigment in baldcypress.

Pn of baldcypress seedlings was affected by a variety of factors, of which photosynthetic gas exchange parameters and resources use efficiency were of great importance (Anderson and Pezeshki, 1999; Eclan and Pezeshki, 2002; Wang and Cao, 2004). Mean *Pn* values during the experimental period were 3.96, 2.97, 3.904 and 4.00 $\mu molCO_2/(m^2 \cdot s)$ in CK, T1, T2 and T3. Whereas *Pn* was severely affected under drought water stress, baldcypress seedlings still maintained an ability to hold normal *Pn* even in wet and/or flooded environments. Such responses of *Pn* changes in baldcypress are closely related to g_s and *Tr*. In the hydro-fluctuation belt of the Three Gorges Reservoir area, where baldcypress seedlings were planted in an environment of overabundant soil water (T2 and T3, for instance), normal *Pn* was ultimately retained due to increments of g_s, *Tr* and *WUE*, enhancement or maintenance of *LUE* and *CUE*, improvement of physiological activity to synthesize more photosynthates for roots to overcome anaerobic conditions and the negative impact of surplus water. When baldcypress seedlings were planted in an environment with lack of soil water supply (T1, for example), *Pn* ultimately decreased due to a reduction in g_s and *Tr* and an increase in *WUE*, thus lessening *LUE* and *CUE*.

Since water treatment in T1 was completely different from that in T2 and T3, compared to CK, relationship analyses should further consider the correlations between photosynthetic gas exchange parameters within each single group. For example, *Pn* and *Tr* in each group followed a quadratic polynomial, of which $Pn = -0.001{,}4Tr^2 + 0.146{,}7Tr + 0.990{,}5$ ($R = 0.715$) for T3 appears to be superior to an integral *R* of the four groups as a whole (0.352**).

In conclusion, baldcypress can be considered one of the species for the building of forest protection systems in the hydro-fluctuation belt in the Three Gorges Reservoir area in terms of its adaptive characteristics of photosynthetic physio-ecology. For planting and cultivating in the area, the water-tolerant and hydrophilic features of baldcypress should be fully considered. This species should not be planted under drought-stricken soil conditions. Otherwise waste and damage will occur in the reforestation regions, endangering the safety of the reservoir banks and surrounding areas.

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