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RESEARCH ARTICLE

LI Changxiao, ZHONG Zhangcheng

Photosynthetic physio-response of *Taxodium ascendens* seedlings to different soil water gradients

Abstract Four different kinds of water treatments were applied to study the photosynthetic eco-physiological characteristics of *Taxodium ascendens* seedlings in the environment of the Three Gorges hydro-fluctuation belt. The four kinds of water treatments were: normal growth water condition (CK), light drought stress (T1), soil water saturation (T2), and soil submersion (T3). The results showed that different water treatments could effectively influence the content of the photosynthetic pigment, leaf gas exchange and apparent resources use efficiency of *T. ascendens* seedlings. It was also demonstrated that the *T. ascendens* seedlings could not only tolerate water submersion and wet conditions but also endure a certain degree of drought. To establish a protection forest system in the hydro-fluctuation belt in the Three Gorges Reservoir Area, the species *T. ascendens* is suitable for planting in conditions of root submersion or water-saturated soil. In case it is planted in drought conditions, this tree species should be watered appropriately in order to keep its normal net photosynthetic rate.

Keywords Three Gorges Reservoir Area, hydro-fluctuation belt, *Taxodium ascendens* seedlings, soil water gradients, photosynthetic physio-response

1 Introduction

The Three Gorges Reservoir Area of the Yangtze River is characterized by annual periodic water level fluctuations (between 145 m and 175 m) (Huang, 1994; Diao and Huang, 1999; Xiao et al., 2000; Zhang et al., 2000), thus leading to the occurrence of the hydro-fluctuation belt along the riparian banks. Soil water content in the hydro-fluctuation belt is subjected to a range of hydrological regimes from drought to submergence, which brings more difficulty in building and protecting the vegetation systems in the hydro-fluctuation belt. Such a gradient change in soil water content will easily influence the tree species pondcypress (*Taxodium ascendens* Brongn.). This species is suitable for planting in the hydro-fluctuation belt because of its growth, development and physio-ecological characteristics, in particular, its photosynthetic traits. Compared to more in-depth and detailed studies on the baldcypress (*T. distichum* L. Rich) (Cao et al., 1995; Wang et al., 1995, 1998; Conner et al., 1997; Pezeshki and Santos, 1998; Huang et al., 2000; Middleton, 2000; Eclan and Pezeshki, 2002; Wang and Cao, 2002, 2003, 2004; Zheng et al., 2004), the foci of previous research related to the pondcypress were primarily on its biological traits, growth and development (Li, 1993; Cao et al., 1995; Gu et al., 1995; Wu et al., 1995, 1996; Wang et al., 1995, 1998; Fan and Lin, 1997; Huang and Huang, 1997; Yin and Chen, 1997; Tao et al., 1998; Li et al., 1999; Zeng and Xue, 1999; Zhou et al., 1999; Huang et al., 2000) while relatively little is known about its photosynthetic eco-physiological responses to diverse soil water stresses.

The purpose of this research is to explore the mechanisms of responses of pondcypress in photosynthetic physio-ecology as well as its adaptive strategies under different soil water conditions, in order to provide the technical and theoretical support for vegetation restoration of the hydro-fluctuation belt of the Three Gorges Reservoir Area.

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LI Changxiao, ZHONG Zhangcheng (✉)
College of Life Sciences, Southwest China Normal University, Chongqing 400715, China
The State Education Ministry's Key Laboratory for the Eco-environment of Three Gorges Reservoir Area, Southwest China Normal University, Chongqing 400715, China
E-mail: zzhong@swnu.edu.cn

2 Materials and methods

2.1 Tree species and location for the study

Seedlings of pondcypress, from seeds sown in a local nursery in early March 2004, were selected for the experiment. In mid June 2004, 120 seedlings of similar size were transplanted in pots 13 cm in diameter and filled with 12 cm deep purple soil.

Each seedling was placed in one pot. Then, seedlings were placed in the Ecological Experimental Zone of Southwest China Normal University (with an altitude of 249 m) and allowed to acclimate to illumination and water management prior to treatments. A water-proof shed, covered by transparent plastic film preventing natural rain was built on July 25, 2004, which was also the date that water treatments began.

2.2 Experimental design

The 120 seedlings were randomly divided into four groups for different water treatments during plant growth, including normal water regime (CK), light drought stress (T1), soil water saturation (T2), and submersion (T3). CK had soil water contents between 60%–63% of soil water field capacity (soil water content measured by weighing), under which regime the pondcypress seedlings showed no wilting during sunny days. T1 was kept at soil water contents between 47%–50% of soil water field capacity, under which regime the fresh leaves of the seedlings wilted around 13:00 and recovered around 17:00 (Guo and Tian, 1994; Hu and Wang, 1998; Hu et al., 2000). In T2, soil was saturated, while in T3 the soil remained flooded 1 cm above the surface. Plastic basins with a diameter 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 1 cm above the soil surface (Bragina et al., 2001). Soil water contents in T2 were checked at 2 h intervals from 6:00 to 24:00, with soils being moistened if necessary. When submersion in T3 was lower than 0.8 cm, infusing tap water was adopted until submersion reached 1 cm above the soil surface.

Five samplings were conducted at 5 d intervals from the beginning of the experiment. There were five replicates of each sampling in each treatment. The experimentation ended on August 25, 2004.

2.3 Measurement of leaf gas exchange responses

The third or fourth upper leaf from each seedling crown was chosen to test responses of leaf gas exchange, using the CI-310 Portable Operation System (made in USA), after being induced under saturated light illumination. All of the tests were conducted between 9:00–11:00 at a controlled indoor temperature of 25°C, with 400 μmol/L CO_2 and photosynthetically active radiation (*PAR*) 1,000 μmol photons/($m^2 \cdot s$). 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 water use efficiency (*WUE*) = *Pn/Tr* (Nijs et al., 1997), apparent light use efficiency (*LUE*) = *Pn/PAR* (Long et al., 1993), apparent CO_2 use efficiency (*CUE*) = *Pn/Ci*.

2.4 Photosynthetic pigment measurement

The endosmotic extraction method (Zhou, 1995) was adopted for extracting chlorophyll (*Chl*) and carotenoid (*Car*) from the leaves. Content of pigments was tested by the Spectrophotometer 5220 (made in Japan).

2.5 Statistical analysis

Water treatment was regarded as an independent factor and respective measured indices as dependent factors. One-way analysis of variance (One-way ANOVA) was employed to determine any significant overall 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 individual 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 effects on the contents of photosynthetic pigments of pondcypress seedlings. T3 seedlings (flooding treatment) had the lowest contents of photosynthetic pigment (highly significant, Fig. 1) compared to the other three groups. However, T2 displayed significantly higher contents compared to CK either in chlorophyll or carotenoid content (dry weight basis), while T1 exhibited lower contents of photosynthetic pigments than that in CK but higher contents than that in T3 on a dry weight basis. During the entire experimental period, the ratio of chlorophyll a/b was between 2.124–2.644 while the ratio of *Chl/Car* was 3.331–4.387.

Table 1 The results of ANOVA indicating the effects of different water treatments on the physiological characteristics of pondcypress seedlings

Character	*F* value	Probability	Significance
Chl (*a* + *b*) (fw[a])	12.403	0.000	***
Chl (*a* + *b*) (dw[b])	32.078	0.000	***
Car (fw)	11.790	0.000	***
Car (dw)	44.492	0.000	***
Chl a/b	4.057	0.010	*
Chl (*a* + *b*)/*Car*	8.382	0.000	***
Pn	39.115	0.000	***
Tr	61.621	0.000	***
g_s	71.170	0.000	***
WUE	18.425	0.000	***
LUE	38.309	0.000	***
CUE	38.565	0.000	***

Significance levels: *** $P < 0.001$; ** $P < 0.01$; *$P < 0.05$; ns $P > 0.05$. [a]fw = fresh weight, [b]dw = dry weight. Same for below.

3.2 Responses of gas exchange

As shown in Table 1, *Pn*, *Tr*, and g_s of *T. ascendens* seedlings were significantly affected by the soil water regimes. Physiological responses of photosynthetic gas exchange

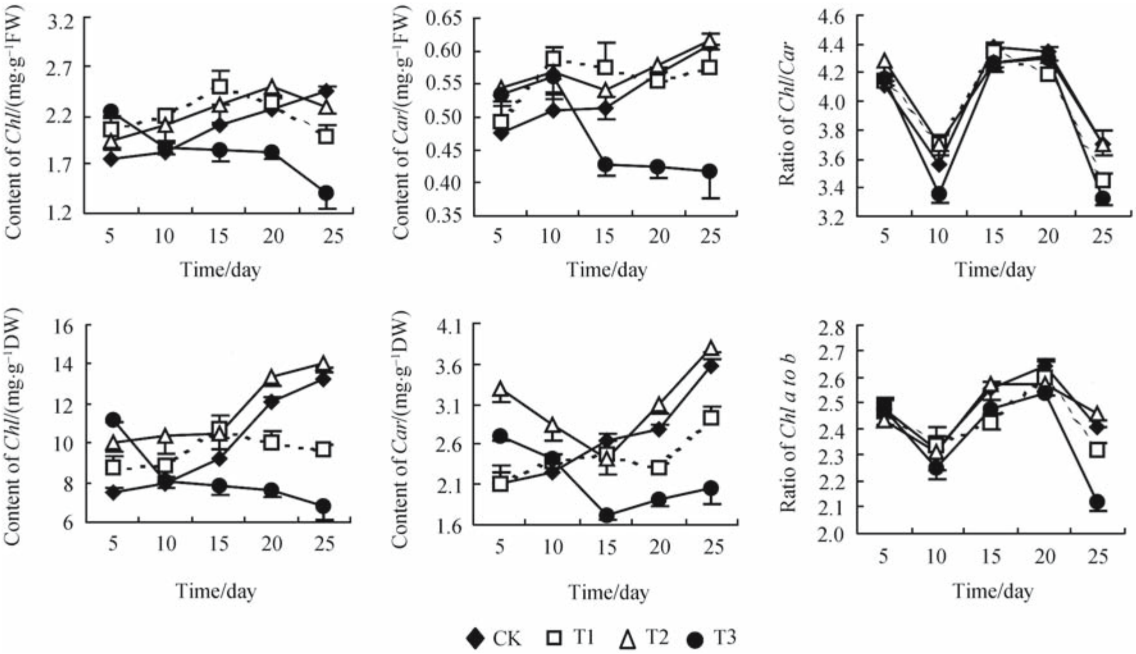

Fig. 1 Changes of photosynthetic pigment content of *T. ascendens* seedlings under different water treatments Standard errors are shown one-sided.

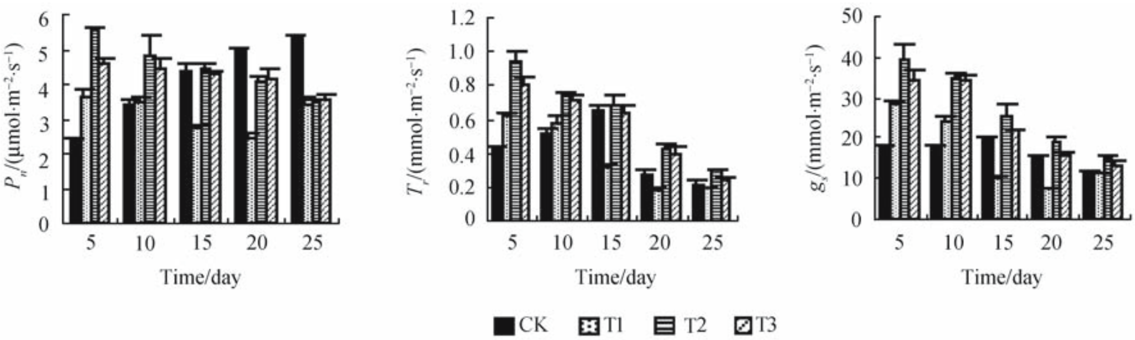

Fig. 2 The change of *Pn*, *Tr* and g_s of *T. ascendens* seedlings under different water treatments (+SE)

varied differently in various groups as the treatment was prolonged.

In CK, *Pn* was continuously increased; however, *Pn* was continuously decreased both in T2 and T3. In contrast, *Pn* in T1 was increased after its initial decrease. Mean *Pn* values over the experimental period revealed no significant differences between T2 and T3, but were higher than that in CK. Mean *Pn* value in T2 showed highest among the four groups, with 9.421% significantly higher than that in CK, while T1 demonstrated a highly significant lower value than the other three groups, with 23.062% lower compared to CK. That is to say pondcypress seedlings have relatively higher *Pn* in the environments of saturated soil water and/or soil flooding when compared to control plants.

Pondcypress seedlings indicated a similarity of change between *Tr* and g_s in different treatments. Mean values of T2 and T3 were significantly higher than that of CK in *Tr* and g_s respectively. Whereas, T1 showed no significant difference with CK in mean values in *Tr* and g_s, respectively, although lower values were found in T1. In the four treatments T2 revealed the highest mean values both in *Tr* and g_s. Throughout the experimental period, mean values of *Tr* and g_s in T2 and T3 decreased as water treatment was continued. This was different from those in T1 where mean values increased after first being decreased, and also different from those in CK where values decreased after initially being increased.

3.3 Change of resources use efficiency

The different water treatments significantly influenced the resources use efficiency of pondcypress seedlings (Table 1). The water use efficiency (*WUE*) was increased in all four groups, among which CK showed a 3.439-fold overall increase, compared to 0.946-fold in T2, as well as 1.946- and 1.667-fold in T1 and T3, respectively. Mean *WUE* values during the experimental period showed no significant difference between T2 and T3, both of which were, however, significantly lower in value than that of T1 and CK (Fig. 3).

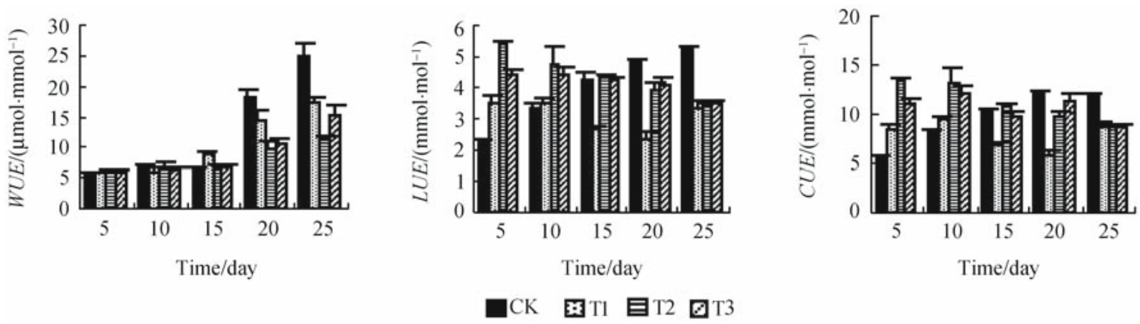

Fig. 3 The change of *WUE*, *LUE* and *CUE* of *T. ascendens* seedlings under different water treatments (+SE)

Mean *LUE* and *CUE* values over the study period showed no significant differences between T2 and T3, respectively, but both were significantly higher than that of T1 and CK. Pondcypress seedlings displayed higher *LUE* and *CUE* values in the environments of saturated soil and/or soil flooding when compared to control plants. On the other hand, lower *LUE* and *CUE* values were found under the circumstances of soil water drought stress.

3.4 Correlative analysis

Results of Pearson's correlation analysis demonstrated that *Pn* was (highly) positively correlated with *Tr*, g_s, *LUE*, *CUE*, content of *Chl* (dw), and content of *Car* (dw) in pondcypress seedlings. In contrast, there was no significant correlation between *Pn* and *WUE*, content of *Chl* (fw), content of *Car* (fw), ratio of *Chl/Car, Chl a/b*, *RHi* and *Ci*. While *Tr* was significantly positively correlated with g_s; a highly negative relationship with *WUE* was found.

4 Discussion

The periodic water-table fluctuation will have some unique impact on the physio-ecological characteristics of suitable plants grown in the hydro-fluctuation belt in the Three Gorges Reservoir Area, of which the photosynthetic responses of suitable plants should be an important field for research. Pondcypress (*T. ascendens*), native to the southeastern swampy part of North America, belongs to the *Taxodium*, *Taxodiaceae*, gymnosperm (Wang et al., 1995, 1998). This species is characterized by turgor at the basal stem, knee-like aerial roots (Gu et al., 1995; Tao et al., 1998) and water-tolerance. In China, pondcypress often grows in the Yangtze River valleys (Zeng and Xue, 1999).

Content of chlorophyll in pondcypress seedlings in flooding conditions over the entire experimental period (being calculated in average in dw, same for below) was 16.951% lower than that in the control. In contrast, it was 16.233% higher in soil water saturation condition than that in the control. Whilst the content of carotenoid in flooding remained 19.393% lower compared to the control, the content of carotenoid in soil water saturation condition was 15.387% higher than that in the control. The above results showed that the synthetic quantity of photosynthetic pigments in pondcypress seedlings had been relatively reduced in the environment of submersion, which was different from an increase in synthetic quantity in soil water saturation. Interestingly, the apparent reduction of content of photosynthetic pigments caused by flooding did not lead to a corresponding decline of *Pn*. This phenomenon infers that the content of photosynthetic pigments in pondcypress seedlings in flooding and/or soil water saturation was at least sufficient for photosynthesis, that is, the necessary quantity of molecules of photosynthetic pigments was, to some extent, guaranteed for photosynthesis. One of the important factors for such a result will be related to the distributional proportion of photosynthetic pigments in pondcypress seedlings. The ratio of *Chl/Car* was over 3:1, in contrast to the ratio of *Chl a/b* which was less than 3:1, of which both ratios in leaves are commonly around 3:1 (Pan

Table 2 Correlations between P_n and other photosynthetic parameters of *T. ascendens* seedlings

	Pn	*Tr*	g_s	*WUE*	*LUE*	*CUE*	*Chl* (dw)	*Car* (dw)	*Chl a/b*	*Chl/Car*
Tr	0.433**									
g_s	0.515**	0.905**								
WUE	0.160	–0.752**	–0.589**							
LUE	1.000**	0.434**	0.516**	0.159						
CUE	0.964**	0.463**	0.564**	0.081	0.964**					
Chl (dw)	0.230*	–0.198*	–0.116	0.334**	0.226*	0.175				
Car (dw)	0.280**	–0.078	0.048	0.310**	0.278**	0.233*	0.754**			
Chl a/b	–0.006	–0.059	–0.147	0.016	–0.015	–0.054	0.284**	0.072		
Chl/Car	0.031	0.188	0.010	–0.226*	0.021	–0.036	0.184	–0.102	0.710**	
RHi	0.063	–0.220*	–0.033	0.386**	0.070	0.059	0.081	0.369**	–0.512**	–0.781**
Ci	0.050	–0.130	–0.195	0.239*	0.047	–0.211*	0.133	0.085	0.150	0.234*

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

et al., 2004). The photosynthetic unit was composed of a light-harvesting pigment system and reaction center. The reaction center pigment included only a few quantity of *Chl a*, and all other pigments were for light-harvesting including a large quantity of *Chl a*, entire *Chl b*, carotene and carotenol. The high proportion of chlorophyll in photosynthetic pigment (compared to carotenoids) probably promoted the capacity of photosynthesis without compromising the available reaction center pigment. Likewise, the ratio of *Chl a/b* below 3:1 might guarantee enough light-harvesting pigment due to an optimized distribution between chlorophyll a and b, further promoting photosynthesis (Scholes et al., 1997). The proportions in photosynthetic pigment content were conducive to ensuring supply of sufficient photosynthetic pigments and provided optimal photosynthesis for pondcypress seedlings (Ronzhina et al., 2004).

Under different hydrological regimes, *Pn* in pondcypress seedlings is one of the key indicators to verify the capacity of responses in photosynthetic physio-ecology to adverse environments. Mean *Pn* values during the experimental period were 4.076, 3.136, 4.460, and 4.208 μmol CO_2 /($m^2 \cdot s$) in CK, T1, T2 and T3, respectively. There was no significant difference in average *Pn* between T3 and CK, which illustrated that pondcypress seedlings had positive responses in net photosynthetic rate in the environment of soil flooding, compared to negative responses in net photosynthetic rate under conditions of light drought water stress. The highest *Pn* being in T2, with the value being significantly higher than that in CK, indicated that net photosynthetic rate was optimal under the treatment of soil water saturation. However, *Pn* in different hydrological regimes was not equivalent to photosynthetic assimilation, probably due to more consumption of the photosynthesized products for resistance against stresses such as drought and flooding.

Such responses of *Pn* in pondcypress should be closely linked with gas exchange parameters and resources use efficiency. Mean *Tr* values of pondcypress seedlings over the study period were 0.42, 0.38, 0.616, 0.56 mmol/($m^2 \cdot s$) in CK, T1, T2 and T3, respectively. Similar changes were found in g_s values which were 16.612, 16.296, 26.916, 23.924 mmol/($m^2 \cdot s$) in CK, T1, T2 and T3, respectively. Furthermore, the above changes of *Tr* and g_s in various treatment groups had a similarity with that of *Pn*. Although mean values of *Tr* and g_s in T1 throughout the entire experimental period were not significantly different from that in CK, a significant difference in *Pn* was found between T1 and CK, indicating that mild drought stress could significantly reduce *Pn* of pondcypress seedlings, but not apparently impact *Tr* and g_s. This means that under mild drought stress conditions, pondcypress seedlings still remained at normal levels of *Tr* and g_s compared to CK, and probably had a relatively higher photosynthesized response. Thus, this study verified that pondcypress seedlings were not only water-tolerant but could also endure drought.

In the hydro-fluctuation belt of the Three Gorges Reservoir Area, when pondcypress seedlings were planted in such an environment of superfluous soil water (T2 and T3, for instance), normal *Pn* was ultimately maintained due to the increment of g_s, *Tr* and *WUE*, enhancement or maintenance of *LUE* and *CUE*, and possibly also due to the improvement of physiological activity to synthesize more photosynthates for roots to overcome the negative impact of anaerobic conditions. On the other hand, when pondcypress seedlings were planted in a drought soil environment (T1, for example), *Pn* was ultimately decreased due to the slight decline of g_s and *Tr*, and increase of *WUE*, further leading to reductions of *LUE* and *CUE*.

Different soil water gradients will influence the characteristics of photosynthetic physio-ecological response of tree species (Anderson and Pezeshki, 1999; He and Ma, 2000; Chen et al., 2003; Liu et al., 2003; Simone et al., 2003; Zhao et al., 2003; Ma et al., 2004; Shi et al., 2004). A range of physiological traits in the photosynthesis of pondcypress seedlings will be subjected to water level fluctuations in the hydro-fluctuation belt of the Three Gorges Reservoir Area. Our experimental results showed that pondcypress can adapt well to different water regimes, with higher photosynthetic responses and plasticity to adverse water stresses as indicated in the tree's water-tolerance and drought-enduring characteristics. When establishing a protective forest system in the hydro-fluctuation belt in the Three Gorges Reservoir Area, pondcypress seedlings could be planted in the environments of soil water saturation and/or of soil flooding. Under mild drought conditions, pondcypress seedlings should be watered appropriately for them to survive under normal net photosynthetic rates.

As pondcypress seedlings during this experimentation were in a period of growth, the overall time period for treatment and observation in further research should be set longer. Indicators such as height and diameter growth, biomass, and survival rate should also be considered to measure for integrated analysis. On the other hand, pots were too small and the filled soils were too little, as such, spaces could not meet the growth need of pondcypress seedlings. All of these shortcomings should be solved in future studies.

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References

Anderson P H, Pezeshki S R (1999). The effects of intermittent flooding on seedlings of three forest species. Photosynthetica, 37(4): 543–552

Bragina T V, Martinovich L I, Rodionova N A (2001). Ethylene-induced activation of xylanase in adventitious roots of maize as a response to the stress effect of root submersion. Appl Biochem Microbiol, 37(6): 618–621

Cao F L, Fang S Z, Tang L Z, Xu L A, Liu C L, Huang J H, Sun Y L (1995). A study on provenance test of *Taxodium distichum* seeds. J Nanjing For Univ, 19(1): 65–70 (in Chinese)

Chen D X, Li Y D, Luo T S, Chen B F, Lin M X (2003). Study on photosynthetic physiological ecology of *Cryptocarya chinensis* in tropical mountain rain forest in Jianfengling, Hainan Island. For Res, 16(5): 540–547 (in Chinese)

Conner W H, Mcleod K W, McCarron J K (1997). Flooding and salinity effects on growth and survival of four common forested wetland species. Wetlands Ecol Manag, 5: 99–109

Diao C T, Huang J H (1999). A preliminary study on land resources of the water-level-fluctuating zone in the Three Gorges Reservoir. Resour Environ Yangtze Basin, 8(1): 75–80 (in Chinese)

Du R Q (2003). Biostatistics. 2nd ed. Beijing: Higher Education Press, 104–116 (in Chinese)

Eclan J M, Pezeshki S R (2002). Effects of flooding on susceptibility of *Taxodium distichum* L. seedlings to drought. Photosynthetica, 40(2): 177–182

Fan X J, Lin Z H (1997). Increasing afforested survival ratio of bare-rooted seedlings of *Taxodium ascendens* Brongn. J Jiangsu For Technol, 24(1): 49–50 (in Chinese)

Gu Y Q, She W, Huang H Q (1995). Regular investigation of plantation increment in *Taxodium ascendens*. J Jiangsu For Sci Technol, 22(1): 12–16 (in Chinese)

Guo L S, Tian Y L (1994). Study on the relationship between the photosynthetic features of four coniferous species saplings and air humidity. Acta Ecol Sin, 14(2): 136–141 (in Chinese)

He W M, Ma F Y (2000). Effects of water gradient on fluorescence characteristics and gas exchange in *Sabina vulgaris* seedlings. Acta Phytoecol Sin, 24(5): 630–634 (in Chinese)

Hu X S, Wang S J (1998). A review of studies on water stress and drought tolerance in tree species. Sci Silv Sin, 34(2): 77–88 (in Chinese)

Hu Z S, Xu C Q, Fu R S (2000). Physiological response for *Castanea henryi* seedling under water stress and the action of 6-BA. J Fujian For Coll, 20(3): 1–4 (in Chinese)

Huang J H (1994). Development and utilization of land resources of water-level-fluctuating zone in the Three Gorges Reservoir. J Southwest China Norm Univ (Nat Sci), 19(5): 528–533 (in Chinese)

Huang L B, Wang Q M, Li X C, Wang W, Chen Z Y, Jiang Z X, Zhang J F, Sun Y Z, Wang Y C, LI W, Zhong W Q, Lu X A (2000). Studies on the variation of provenances and families in Genus *Taxodium*: Variation on shoot cutting rooting ability. J Jiangsu For Sci Technol, 27(1): 1–6 (in Chinese)

Huang W D, Huang B L (1997). Coexistence gain of populations and tree stand control in agroforestry system. J Nanjing For Univ (Nat Sci Ed), 21(2): 22–26 (in Chinese)

Li P S, Ni H G, Wang C F, Fan J S, Yin Y L, Chen Y H (1999). Comparative study on afforestation of *Taxodium "Zhongshansa* 302*"* and pondcypress (*Distichum ascendens*) seedlings on the bottomlands. J Jiangsu For Technol, 26(2): 33–35 (in Chinese)

Li Z Y (1993). Studies on water tolerance of different tree species in Lixiahe region. J Jiangsu For Sci Technol, 20(1): 28–29 (in Chinese)

Liu W L, Xie S X, Yu L F (2003). Physiological response of several karst common tree species seedlings to water stress. Guizhou Sci, 21(3): 51–55 (in Chinese)

Long S P, Baker N R, Raines C A (1993). Analyzing the responses of photosynthetic CO_2 assimilation to long-term elevation of atmospheric CO_2 concentration. Vegetation, 104/105: 33–45

Ma C C, Gao Y B, Wang J L, Guo H Y (2004). Ecological adaptation of *Caragana opulens* on the Inner Mongolia plateau: Photosynthesis and water metabolism. Acta Phytoecol Sin, 28(3): 305–311 (in Chinese)

Middleton B (2000). Hydrochory, seed banks, and regeneration dynamics along the landscape boundaries of a forested wetland. Plant Ecology, 146: 169–184

Nijs I, Ferris R, Blum H (1997). Stomatal regulation in a changing climate: A field study using free air temperature increase (FATI) and free air CO_2 enrichment. Plant, Cell Environ, 20: 1,041–1,050

Pan R C, Wang X J, Li N H (2004). Plant Physiology. 5th ed. Beijing: Higher Education Press, 64–68 (in Chinese)

Pezeshki S R, Santos M I (1998). Relationships among rhizosphere oxygen deficiency, root restriction, photosynthesis, and growth in baldcypress (*Taxodium distichum* L.) seedlings. Photosynthetica, 35(3): 381–390

Ronzhina D A, Nekrasova G F, P'yankov V I (2004). Comparative characterization of the pigment complex in emergent, floating, and submerged leaves of hydrophytes. Russ J Plant Physiol, 51(1): 21–27

Scholes J D, Press M C, Zipperlen S W (1997). Differences in light energy utilization and dissipation between dipterocarp rainforest tree seedlings. Oecologia, 109: 41–48

Shi S Q, Yuan Y X, Yang M S (2004). Effects of water stress on photochemical quenching and non-photochemical quenching of chlorophyll a fluorescence in four tree seedlings. Sci Silv Sin, 40(1): 168–173 (in Chinese)

Simone O D, Junk W J, Schmidt W (2003). Central Amazon floodplain forests: Root adaptations to prolonged flooding. Russ J Plant Physiol, 50(6): 848–855

Tao R Z, Jiang Z H, Fei B H, Wang C G, Ke S H (1998). A study on effects of intermittent flood upon the physical and mechanical properties of the wood of *Taxodium ascendens*. Sci Silv Sin, 34(3): 110–114 (in Chinese)

Wang G B, Cao F L (2002). Reviews on resistance of baldcypress. J Nanjing For Univ (Nat Sci Ed), 26(6): 78–82 (in Chinese)

Wang G B, Cao F L (2003). Effects of salinity on growth and physiology of baldcypress seedlings. J Nanjing For Univ (Nat Sci Ed). 27(3): 11–14 (in Chinese)

Wang G B, Cao F L (2004). Effects of soil water and salt contents on photosynthetic characteristics. J Nanjing For Univ (Nat Sci Ed), 28(3): 14–18 (in Chinese)

Wang Q M, Jiang Z P, Lv X S, Zhang J F, Lu K J, Sun Y Z, Guo S X, Wu M J, Lu X A (1995). Studies on the variation of provenances and families in Genus *Taxodium*: Introduction to the genus. J Jiangsu For Sci Technol, 22(2): 14–18 (in Chinese)

Wang Q M, Wang W, Jiang Z X, Zhang J F, Sun Y Z, Qin B Y, Yan Z Q, Sun Z W, Fang X R, Lu X A, Zhou B Y, Song W P (1998). Studies on the variation of provenances and families in Genus *Taxodium*: Growth and biomass variation. J Jiangsu For Sci Technol, 25(1): 1–6 (in Chinese)

Wu Z Y, Chu J M, Tang M R, Chai S M, Dong Z P (1995). Effects of different sites on the growth of *Taxodium ascendens*. J Zhejiang For Coll, 12(2): 144–48 (in Chinese)

Wu Z Y, Chu J M, Tang M R, Chai S M, Tong Z P (1996). Effects of soil drainage on morphological structure and growth of *Taxodium ascendens*. J Zhejiang For Coll, 13(3): 364–366 (in Chinese)

Xiao W F, Li J W, Yu C Q, Ma J, Cheng R M, Liu S Y, Wang J X, Guo J W (2000). Terrestrial Animal and Plant Ecology of the Three Gorges of Yangtze River. Chongqing: Southwest China Normal University Press, 1–20 (in Chinese)

Yin Y L, Chen Y H (1997). The survey and evaluation of comparative plantation of *Taxodium* 'Zhongshansa' and *T. ascendens*, *T. distichum* and *Metasequoia glyptostroboides*. J Plant Resour Environ, 6(3): 23–28 (in Chinese)

Zeng H Q, Xue J H (1999). The summary of study on *Taxodium ascendens* forest in Jiangsu Province. J Jiangsu For Technol, 26(3): 52–55 (in Chinese)

Zhang H J, Gao Z Q, Xie M S, Wang Y J, Li J (2000). Overall arrangement of multi-functional protection forest system in the Three-Gorges Reservoir Area of the Yangtze River. Resour Environ Yangtze Basin, 9(4): 479–486 (in Chinese)

Zhao P, Zeng X P, Peng S L (2003). Ecological adaptation of leaf gas exchange of trees used for re-vegetation under different experimental light regimes. Chin J Ecol, 22(3): 1–8 (in Chinese)

Zheng S F, Chen Y J, Chen W P, Liao B W, Song X Y, Li W (2004). Adaptability of several mangrove species and *Taxodium distichum* on deep water mudflat. For Res, 17(5): 654–659 (in Chinese)

Zhou L, Fu X Y, Zhang Z Y, Ma Y X, Zhu G S (1999). On plantation density models of *Taxodium ascendens* in Lixiahe region of Jiangsu province. J Zhejiang For Coll, 16(2): 145–150 (in Chinese)

Zou Q (1995). Experimental Introduction to Plant Physiology and Biochemistry. Beijing: Chinese Agricultural Press, 36–39 (in Chinese)