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# Growth and Physiological Adaptation of *Salix matsudana* Koidz. to Periodic Submergence in the Hydro-Fluctuation Zone of the Three Gorges Dam Reservoir of China

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**Abstract:** Submergence-tolerant trees are essential for vegetation restoration of the hydro-fluctuation zone of the Three Gorges Dam Reservoir (TGDR) area. Thus, it is of great significance to select the submergence-tolerant plant species by conducting in situ studies. To restore degraded riparian vegetation under the circumstances of dynamic impoundment of the TGDR, *Salix matsudana* Koidz., a flooding-tolerant native tree species, was introduced to conduct an in situ practical study to test its performance in re-vegetating and restoring the hydro-fluctuation zone of the TGDR. Effects of periodic moderate submergence (MS) and deep submergence (DS) on photosynthesis and growth of *Salix matsudana* Koidz. were investigated after three water cycles compared to a control (i.e., shallow submergence, abbreviated as SS) in order to specifically assess its application prospects in vegetation restoration under such extreme environment. Results showed that net photosynthetic rate ($P_n$), intrinsic water use efficiency (WUEi) and limiting value of stomata (Ls) of *S. matsudana* were significantly reduced in DS. However, pigment content had no significant change in all submergence treatments. Diameter at breast height (DBH) and tree height of *S. matsudana* were significantly decreased in both MS and DS when compared to that of SS, respectively. In contrast, the primary branch number of *S. matsudana* was significantly increased as submergence increased. In addition, relative diameter and height growth rates of *S. matsudana* were also reduced under submergence. Considering the sustained growth of this species, *S. matsudana* saplings are tolerant to long-term periodic submergence and can be applied to the vegetative restoration of the hydro-fluctuation zone of the TGDR region.

**Keywords:** Three Gorges Dam Reservoir; hydro-fluctuation zone; *Salix matsudana*; growth; photosynthesis

## 1. Introduction

The Three Gorges Dam (TGD) is the largest dam ever built in the world [1], which is located in the upper reaches of the Yangtze River. After its formal impoundment in 2008, the water level fluctuates from 145 m a.s.l. in summer to 175 m a.s.l. in winter annually, which formed a huge hydro-fluctuation zone with an area of 350 km$^2$ and a water level fluctuation of 30 m [2,3]. The TGD had totally reversed the submergence season and increased the submergence depth and duration when compared to the original hydrological regime [4,5]. This artificial regime has totally changed the habitat of the natural vegetation. Many natural plants die gradually due to intolerance to this great change of their habitats [6]. Vegetation degradation of the hydro-fluctuation zone of the Three Gorges Dam Reservoir (TGDR) caused serious degradation of its ecosystem function, resulting in many serious environmental problems [7], such as soil erosion, water pollution, etc. These problems have posed a serious threat to the long-term security operation of the TGDR and need to be solved.

Spontaneous and artificial recovery are two main methods for vegetation restoration [8], which plays an important role in restoring the structure and function of the newly formed riparian ecosystem [9]. Plants, as the principal part of ecosystem function [10], can absorb the pollutions and prevent soil erosion in the TGDR [11–15]. Moreover, they can beautify the environment of the TGDR. Therefore, artificial vegetation restoration was recommended to be used in vegetation restoration of the hydro-fluctuation zone of the TGDR region [16].

In artificial vegetation restoration of the TGDR, many flooding-tolerant plants are needed. Therefore, evaluation of plants for flood tolerance is needed for vegetation restoration of the hydro-fluctuation zone of the TGDR region [17]. In former studies, many suitable plants were selected through experiments that simulated flooding [18–20]. However, the simulated growth condition of these studies differed from the actual situation of the TGDR [5], especially in submergence depth and duration. These great differences may cause the screened plants to die after planting in the hydro-fluctuation zone of the TGDR.

Plant survival in submergence condition is not only associated with the water tolerance of plants, but is also related to plant recovery after submergence. Former studies showed that plants will suffer oxidation from high oxygen and light condition after exposure from submergence with low oxygen and light condition [21–23]. This will cause plant growth decrease or even death [24]. Thus, it is important to consider the recovery stage when assessing flooding-tolerance in plants [25]. Therefore, the aim of this study was to assess plant submergence resistance based on de-submergence recovery under in situ conditions of the TGDR.

*Salix* spp. is a recommended species for riparian restoration in western countries for its easy propagation from cuttings and rapid growth and wide tolerance to soil flooding [26–28]. Many studies have addressed the tolerance of *Salix* spp. to flooding [29,30]. In general, *Salix* spp. have several physiological and morphological characteristics that allow them to endure a variety of water stresses [31]. These changes include controlling of photosynthesis and related gene expression under oxygen deprivation [32,33] and forming adventitious roots [34,35], lenticels and aerenchyma tissues [35] and elongate shoot parts to facilitate aeration of the inundated roots. These morphological adaptations increase the aeration to alleviate oxygen deficiency caused by flooding [26]. Despite having these morphological and physiological adaptations, the growths of *Salix* spp. were also decreased under flooding [31,35]. However, interspecific differences in flooding tolerance of *Salix* species were varied. *Salix subfragilis* L. was more tolerant to flooding than *Salix gracilistyla* Miq. due to higher root ratio under flooding [36]. *Salix viminalis* L., with a higher dry mass and greater resprouting capacity, had a higher tolerance to tidal flooding than *Salix alba* L. [37]. Moreover, Zhong et al. [38] also found that submergence restricted the growth of *Salix babylonica* L., but it recovered quickly after submergence. Unlike submergence, waterlogging had no significant inhibition on growth and re-growth of this species. Planting study in the Meishan reservoir has shown that *Salix matsudana* Koidz. can survive and grow well in the hydro-fluctuation zone of the Meishan reservoir [39].

These studies suggest that the interspecific difference in plant growth and metabolism of *Salix* are related to the intensity of flooding and different species in the same category may respond differently to water stress. However, whether *Salix* can withstand the long-term deep submergence of the TGDR is not yet clear. The aim of this study was to investigate the application of *S. matsudana*, a flooding-tolerant native tree species, in artificial vegetation restoration of the hydro-fluctuation zone of the TGDR region. For this purpose, an in situ experiment was conducted to test the recovery of photosynthesis and growth of *S. matsudana* after three-year periodic deep submergence in situ. Based on the performance presented in the literature on *Salix* species that we studied, we hypothesized that the growth and photosynthesis of *S. matsudana* saplings would recover to control level after such extreme submergence.

## 2. Materials and Methods

### 2.1. Research Site Description

The experiment was conducted in a *S. matsudana* plantation with an area of 600 $m^2$ in Ruxi River basin located 32 km northeast of Zhong County, Chongqing municipality of China (30°24′16″–30°24′56″ N, 108°08′03″–108°08′21″ E). Ruxi River is one of the largest tributaries of the TGDR [40] with subtropical southeast monsoonal climate and average annual temperature of 18.2 °C. Mean annual precipitation is 1200 mm and relative humidity is 80%. The soil type of the site is purple soil [Regosols in Food and Agriculture Organization (FAO) Taxonomy or Entisols in United States Department of Agriculture (USDA) Taxonomy) [19].

To rehabilitate the vegetation of the hydro-fluctuation zone of the TGDR, an artificial revegetation between 165 m a.s.l. and 175 m a.s.l. through reforestation with two-year-old *S. matsudana* saplings was conducted in this site in April 2012. The mean plant height and diameter at breast height (1.3 m above the ground) of saplings prior to planting were 1.53 m and 3.00 mm, respectively. After transport from Dajuyuan nursery of Chongqing, 600 saplings were immediately planted in the site with a spacing of 1 m × 1 m and well-watered once immediately after being planted, and then weeded in mid-June of 2012. After that, there is no watering or weeding any more in the following years. Until measurement, these saplings grew well and experienced three cycles of water level change imposed by the TGDR. The water level change of the TGDR in Zhong County during the experiment was shown in Figure 1. The water level of the reservoir began to gradually rise from 145 m a.s.l. to 175 m a.s.l. in late autumn (September–October) each year, and kept the highest water level about two months (November–December). After that period, the water level began to drop gradually from 175 m a.s.l. to 145 m a.s.l. over a long time (January–May), and kept the lowest water level to September.

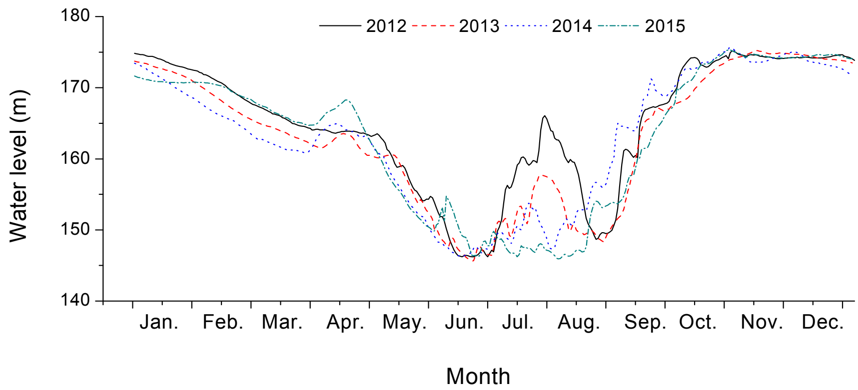


**Figure 1.** Water level changes of the hydro-fluctuation zone of the Three Gorges Dam Reservoir (TGDR) in Zhong County from January 2012 through December 2015.

### 2.2. Experimental Design

The three submergence treatments of the in situ experiment in the hydro-fluctuation zone of Ruxi River were shallow submergence (SS, serving as control, at the elevation of 175 m a.s.l.), moderate submergence (MS, at the elevation of 170 m a.s.l.) and deep submergence (DS, at the elevation of 165 m a.s.l.). In each treatment, nine representative trees at each elevation were randomly selected and tagged on 12 July 2015 in the middle of their 4th growing season for further testing. Trees located at the edge of the plantation zone were abandoned to avoid the edge effect. The submergence depth and duration of each treatment at different elevation during the three water cycles were measured (Table 1). The submergence depth and duration increased with elevation drop, on the contrary, the exposure duration decreased with elevation drop. The trees had leaves when submerged, and the leaves of the trees were lost during submergence. The trees regenerate the new leaves two weeks later after exposure from the submergence.

**Table 1.** Submergence depth and duration of each elevation during the three water cycles of the hydro-fluctuation zone of the TGDR in Zhong County.

| Treatment | Elevation (Submergence Depth ‡) (m) | Submergence Duration (Exposure Duration §) (day) | | |
|---|---|---|---|---|
| | | From July 2012 to June 2013 | From July 2013 to June 2014 | From July 2014 to June 2015 |
| DS | 165 (10) | 175 (190) | 158 (207) | 217 (148) |
| MS | 170 (5) | 125 (240) | 101 (264) | 141 (224) |
| SS | 175 (0) | 2 (363) | 5 (360) | 8 (357) |

‡ The submergence depth refers to the water depth above the soil surface in which saplings planted. The submergence depth above the top of the saplings varied due to operation of the TGDR, and can be calculated as the difference between the submergence depth given in this table and the tree height. § The exposure duration is calculated by the difference between the days of a full year and the days of submergence. DS: deep submergence; MS: moderate submergence; SS: shallow submergence.

### 2.3. Measurement of Physiological Responses

Gas exchange was measured on 12 July 2015 using a portable infrared gas analyzer (Li-6400) with a 6 cm$^2$ leaf chamber and a red/blue light source (Li-Cor, Lincoln, NE, USA). Leaves were induced under saturated light illumination of 1000 μmol·m$^{-2}$·s$^{-1}$. The test was conducted between 10:00–15:00 on a fine day [41] with a photosynthetic photon flux density of 1000 μmol·m$^{-2}$·s$^{-1}$ and a flow rate of 500 μmol·s$^{-1}$. The $CO_2$ levels during the measurements were not controlled and were 357.4 ± 0.75 μmol·m$^{-2}$·s$^{-1}$ in the cuvette. The fifth to seventh mature and intact leaf located on a branch in the upper canopy was utilized for the measurements of net photosynthetic rate ($P_n$), stomata conductance ($g_s$), intercellular $CO_2$ concentration ($C_i$) and ambient $CO_2$ concentration ($C_a$). The test leaf was labeled with a marker pen after data recorded, and then rapidly picked and put in cool condition to take to the laboratory. Leaf area in the chamber was measured by WinRHIZO, LC4800-II LA2400. The intrinsic water use efficiency (WUEi) and the limiting value of stomata (Ls) were calculated as $P_n/g_s$ and $(C_a–C_i)/C_a$, respectively [42,43]. Chlorophyll a, chlorophyll b and carotenoid (Car) content of the test leaf was extracted by 80% acetone in the dark for 72 h at 4 °C and measured the absorbance of extracts at 663, 646 and 470 nm with spectrophotometer UV/VIS 2550 (Shimadzu, Japan) [44]. The chlorophylls (Chls) content and chlorophyll a/b (Chl a/b) were the sum and ratio of chlorophyll a and chlorophyll b.

### 2.4. Measurement of Plant Growth

The measurements on 12 July 2015 included tree height, diameters at breast height (1.3 m from the ground) (DBH), crown diameter and primary branch number. A standard meter pole (with an accuracy of 1.0 cm) was used to measure the tree height. Vernier caliper was used to measure the DBH of the saplings at two perpendicular directions and the average value was calculated. Measuring tape was used to measure the east–west crown diameter and south–north crown diameter, and the average value was used to calculate the crown area using the formula of area of a circle. Numbers of primary branch with length equal to or greater than 10 cm on the trunk were recorded. The relative height growth rate (RHGR) and the relative diameter growth rate (RDGR) of saplings during the time period from 1 April 2012 to 12 July 2015 were calculated following the reference of Masaka et al. [45].

### 2.5. Data Analysis

SPSS 16.0 (Chicago, IL, USA) and Microsoft 2007 software were used to analyze the data. One-way ANOVA was used to assess the influence of submergence treatment on growth and photosynthesis of *S. matsudana* saplings, followed by a Tukey-HSD post hoc test. Correlations between growth and photosynthetic parameters were calculated by Pearson's correlations.

## 3. Results

### 3.1. Gas Exchange Response

After experiencing three annual cycles of periodic submergence in the hydro-fluctuation zone of the TGDR, the mean $P_n$ and WUEi of *S. matsudana* in DS were significantly lower than that in SS ($p = 0.034$, 0.001, respectively), with an 18% and 42% decrease, respectively, whereas there was no significant difference in $P_n$ and WUEi between MS and SS, respectively (both $p > 0.05$) (Figure 2a,c). The mean $g_s$ were not affected by the submergence treatment ($p > 0.05$) (Figure 2b). The mean Ls in DS was significantly lower than that in SS ($p < 0.001$), with a decrease of 35%, while there was no significant difference in Ls between MS and SS ($p > 0.05$) (Figure 2d).

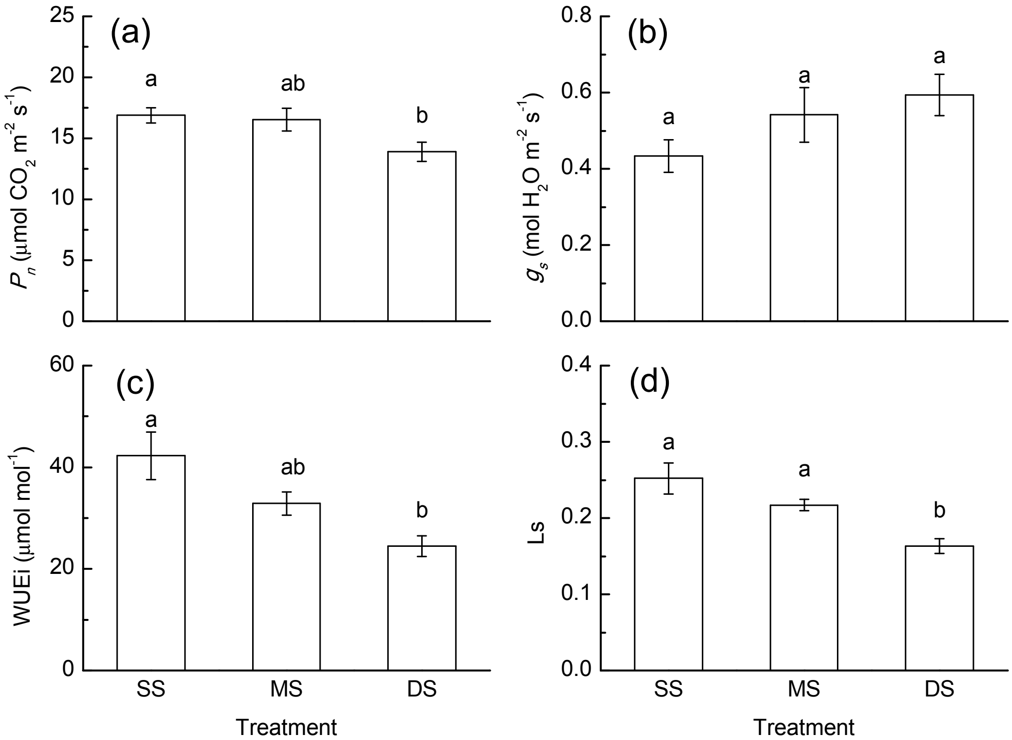


**Figure 2.** Net photosynthetic rate ($P_n$) (**a**), stomata conductance ($g_s$) (**b**), intrinsic water use efficiency (WUEi) (**c**) and limiting value of stomata (Ls) (**d**) of *S. matsudana* under shallow submergence (SS), moderate submergence (MS) and deep submergence (DS) treatment in the hydro-fluctuation zone of the TGDR. Different letters on each bar represent significant difference among treatments at the 0.05 level. Values are means ± standard error ($n = 9$).

### 3.2. Pigment Content

In all saplings, there was no significant difference in content of chlorophylls and carotenoids, ratio of Chl a/b and ratio of Chls/Car among the three treatments (all $p > 0.05$) (Figure 3).

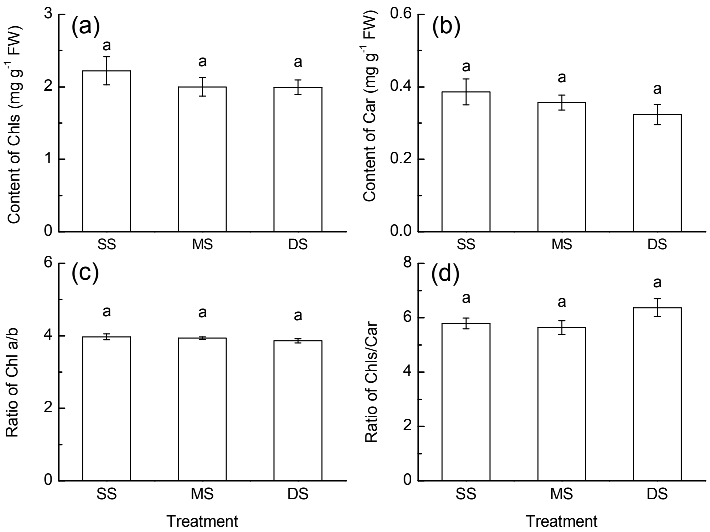


**Figure 3.** Chlorophylls (Chls) content (**a**), carotenoid (Car) content (**b**), ratio of chlorophyll a/b (Chl a/b) (**c**) and ratio of chlorophylls/carotenoid (Chls/Car) (**d**) of *S. matsudana* under shallow submergence (SS), moderate submergence (MS) and deep submergence (DS) treatment in the hydro-fluctuation zone of the TGDR. Different letters on each bar represent significant difference among treatments at the 0.05 level. Values are means ± standard error ($n$ = 9).

## 3.3. Growth Response

The mean DBH and tree height of *S. matsudana* were significantly decreased in MS ($p < 0.001$, $p = 0.04$, respectively) and DS (both $p < 0.001$) as compared to that in SS, with a 39% and 33% decrease, as well as 43% and 44% decrease, respectively (Figure 4a,b). There was no significant difference to be detected in crown area under all treatment ($p > 0.05$) (Figure 4c). However, primary branch number was significantly increased as submergence increased ($p < 0.001$) (Figure 4d). RDGR and RHGR of *S. matsudana* was significantly decreased in MS ($p = 0.001$, 0.032, respectively) and DS ($p < 0.001$, $p = 0.002$, respectively) as compared to that in SS, respectively, while there was no significant difference between MS and DS ($p > 0.05$) (Figure 5a,b).

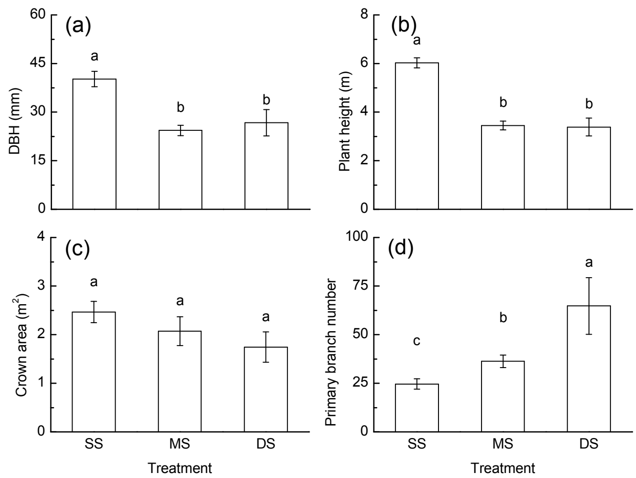


**Figure 4.** Diameter at breast height (DBH) (**a**), tree height (**b**), crown area (**c**) and primary branch number (**d**) of *S. matsudana* under shallow submergence (SS), moderate submergence (MS) and deep submergence (DS) treatment in the hydro-fluctuation zone of the TGDR. Different letters on each bar represent significant difference among treatments at the 0.05 level. Values are means ± standard error ($n$ = 9).

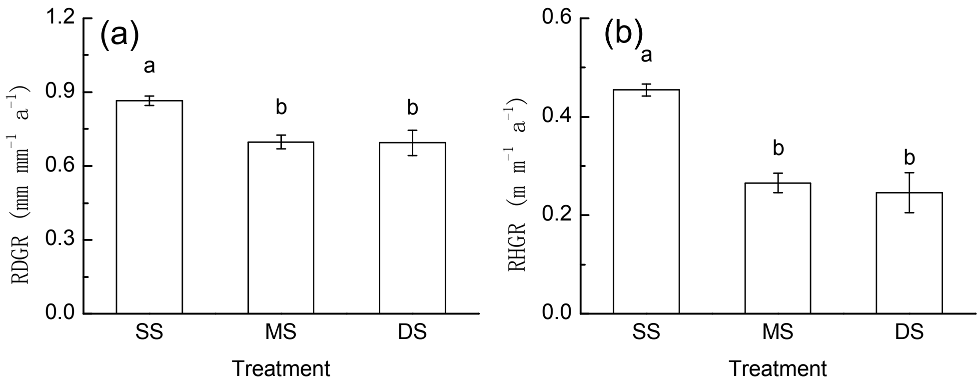


**Figure 5.** Relative diameter growth rate (RDGR) (**a**) and relative height growth rate (RHGR) (**b**) of *S. matsudana* under shallow submergence (SS), moderate submergence (MS) and deep submergence (DS) treatment in the hydro-fluctuation zone of the TGDR. Different letters on each bar represent significant difference among treatments at the 0.05 level. Values are means ± standard error ($n$ = 9).

### 3.4. Correlation

Based on Pearson correlations analysis, there were significant correlations between $P_n$ and growth indices, except for primary branch number in *S. matsudana*. WUEi and Ls also exhibited a significant correlation with tree height (Table 2).

**Table 2.** Correlations between gas exchange parameters and growth indexes for *S. matsudana* saplings ($n$ = 27).

| Indexes | DBH ‡ | TH | CA | PBN |
|---|---|---|---|---|
| $P_n$ | 0.72 *** | 0.588 ** | 0.49 ** | −0.291 |
| $g_s$ | 0.158 | −0.048 | 0.298 | 0.095 |
| WUEi | 0.312 | 0.418 * | 0.028 | −0.301 |
| Ls | 0.377 | 0.46 * | 0.095 | −0.352 |

‡ Diameter at breast height (DBH), tree height (TH), crown area (CA), primary branch number (PBN), net photosynthetic rate ($P_n$), stomata conductance ($g_s$), intrinsic water use efficiency (WUEi) and limiting value of stomata (Ls). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

## 4. Discussion

Selection of submergence-tolerant plant species is the foundation of artificial vegetation restoration of the hydro-fluctuation zone in the TGDR region. With the hydro-fluctuation zone submerged and exposed, plant habitat in this region will be greatly changed. Although plants could endure energy deficit caused by long-term submergence, physiological difficulties like membrane damage and cell death caused by free oxygen radical after rapid exposure to air may affect plant survival [46,47]. Therefore, when assessing plant adaptation, both water tolerance and regrowth after water draining should be considered [25]. Moreover, multiple cycles of water level change also need to be considered when assessing plant submergence tolerance.

### 4.1. Photosynthesis Response to Periodic Submergence

Photosynthetic recovery after submergence will help the plants store more carbohydrates [48]. This will provide more energy for plants to resist the next submergence [49]. Efficient photosynthetic acclimation is also important in post-submergence growth recovery due to growth inhibition caused by photo-oxidative damage that results from high irradiance [50]. Thus, the recovery of photosynthesis is a criterion in evaluating the flooding tolerance of plants. Submergence intensity and duration will affect photosynthetic recovery of plant after submergence [51]. Furthermore, plant resistance to submergence will also affect the recovery. In this study, photosynthetic parameters of *S. matsudana* under moderate submergence (MS) recovered to the control level. *Salix nigra* showed the same results under periodic flooding treatment [32]. Other plants, like *Styrax pohlii* [52], *Melaleuca alternifolia* [53] and *Populus deltoides* [54], also restored their photosynthesis to control level after the water was drained. The maintenances of photosynthetic parameters suggested that *S. matsudana* had strong resistance to periodic moderate submergence. In the field, *S. matsudana* could quickly regenerate new leaves at middle elevation after exposure.

Photosynthetic decline in response to deep submergence is common in many plants, even in some tolerant species, because deep submergence involves energy deficit due to low oxygen and light [55]. Zhao et al. [56] reported that after flooding 75 d, $P_n$ in *Salix integra* cv. Hongpi seedlings was only 54% of the control. *S. nigra* also showed a significant decrease in $P_n$ in flooding condition [32]. The photosynthetic reduction was mainly caused by stomatal closure and non-stomatal (metabolic) inhibition [57]. In the present study, the $P_n$ and Ls decreased, while $C_i$ increased (data not shown) in DS. Thus, non-stomata limitation was one of the factors that caused the reduction in $P_n$ of *S. matsudana* in response to long-term deep submergence [57]. The reason for the lack of correspondence between $g_s$ and $P_n$ in DS in our present study might be attributed to the damage of the structure and function of the photosystem, and the decrease of photosynthetic activity of the leaf mesophyll cells [57]. Previous study of Herrera et al. [58] on *Campsiandra laurifolia* also found a lack of correspondence between $g_s$ and $P_n$. This result suggested that high intensity and long duration of submergence had affected the physiology of *S. matsudana*. Fan et al. [5] summarized the studies on plant recovery after submergence of the hydro-fluctuation zone of the TGDR region, and found that plant recovery after submergence had significant relation to submergence time and depth. In our present study, the decreased net photosynthetic rate of *S. matsudana* was consistent with this result. This result may be caused by decreased expression of photosynthetic genes like oxygen-evolving complex, large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase and ferredoxin [33].

In photosynthesis, chlorophyll a and b are predominantly bound to the photosynthetic reaction center and the light-harvesting chlorophyll a/b protein complex, respectively [59]. Therefore, leaf chlorophyll content can affect the photosynthesis of plants, then affect the accumulation of plant dry matter. Carotenoid can be used as antioxidant to scavenge oxygen radical and protect chlorophyll [60,61]. Former research showed that submergence generally caused chlorophyll degradation and a change in Chl a/b [56]. A field study conducted in the TGDR on *Salix variegata* also found the same results [62,63]. In this study, pigment contents of *S. matsudana* had no significant difference among the three submergence treatments. These results suggested that *S. matsudana* could recover its pigment content after submergence. This is one of the reasons for photosynthesis recovery.

### *4.2. Growth Response to Periodic Submergence*

The survival and regrowth of plants after submergence is most important in assessing plant tolerance to submergence [64]. Frequent floods may increase tree mortality [65]. Reduced plant survival and growth in response to flooding is common among many species [30,36,66]. An investigation conducted in the TGDR found that *S. matsudana* and *S. variegate* were distributed in the water level fluctuation zone and they could endure 210 days of 5 m-deep submergence with a survival rate of 13% and 47%, respectively [62]. However, the survival rates of *S. matsudana* in high and moderate elevation and low elevation of the present study were 100% and 80%, respectively, after experiencing three years of water level changes, suggesting that this species adapted to the stressful condition of TGDR. It is stated that energy deficit, caused by respiration inhibition in oxygen deprivation, is one of the most severe problems for plants under flooding [67]. Under anoxia condition, synthesis of anaerobic protein will protect the membrane structure of mitochondria [68] to maintain energy supply. Besides, some woody plants slow down metabolism upon submergence to preserve starch reserves in the tap-root and to maintain the capacity of regrowth on de-submergence [69]. These strategies may be the reasons for the high survival rate of *S. matsudana*.

The survival and growth of a plant is a comprehensive response of habitat adaptation [63,70,71]. The sustainable growth of plants in the hydro-fluctuation zone of the TGDR is very important in this region. In the present study, the mean of DBH and tree height of *S. matsudana* in MS and DS were significantly lower than that in SS. In the TGDR, plants are in a quiescent state with no shoot elongation during winter submergence [55]. Their biomass production period is mainly in the exposure duration. Since the exposure duration of MS was shorter than SS, the growth of *S. matsudana* was significantly inhibited by submergence despite the recovered $P_n$ of MS. In contrast to the recovery of $P_n$ of *S. matsudana* in MS, $P_n$ of *S. matsudana* in DS was significantly lower. Moreover, the exposure duration of DS was shorter than MS. These caused a lower growth of *S. matsudana* in DS. Li et al. [72] found that the recovery growth of *D. chinense* seedlings decreased as submergence duration increased. A decreased growth of *Salix triandroides* was also shown in a submergence simulation study [73]. Thus, the slow recovery rate might be another reason for its lower growth. The primary branch number was significantly increased with submergence increase. In the former research, *Salix* species were dominated in the riparian zone due to tolerance to prolonged flooding through their high regenerative capacity [37]. In the present study, the high increased primary branch number confirmed its high regenerative capacity. After water recession, plants tend to grow more branches and leaves to gain more energy to meet the high energy expenditure under deep submergence [74]. However, the crown area was not affected by submergence. The reason for this phenomenon was that the most branches of last year died in submergence, and several new short branches grew on the trunk after exposure. With submergence increase, this phenomenon was more obvious. Former research found that *Taxodium distichum* as a high flooding-tolerant species also showed dieback in some apical shoots and no leaf expansion took place in submergence condition, moreover, dieback after water withdrawal became more serious [66]. In *S. matsudana*, shoot dieback also appeared under submergence. Higher re-sprouting capacity of *Salix* will cost much energy, leading to short branch elongation.

Relative growth rate is another factor reflecting the adaptation of a plant. In this study, the relative DBH and tree height growth rates were positive, suggesting that *S. matsudana* could maintain a constant growth under three years of periodic submergence. The relative DBH and tree height growth rates under MS and DS were significantly lower than SS, indicating that submergence had inhibited the growth of this plant. Despite the leaf abscission and part branch death of *S. matsudana* under submergence, the growth rate of this plant is sufficient to maintain its survival and growth in the hydro-fluctuation zone of the TGDR.

## 5. Conclusions

The photosynthesis and growth recovery of *S. matsudana* after submergence were various due to the difference of submergence depth and duration of each elevation. The pigment content of this plant after exposure recovered to control level, but the photosynthesis and growth were significantly affected by long-term deep submergence. Combined with the relative DBH and tree height growth, *S. matsudana* could adapt to the hydro-fluctuation zone of the TGDR and be applied to artificial vegetation restoration of this region.

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**Author Contributions:** C.W. analyzed the data and wrote the paper; C.W. and Y.X. performed the experiments; C.L. conceived and designed the experiments. The remaining authors contributed to refining the ideas, carrying out additional analyses and finalizing this paper.

**Conflicts of Interest:** The authors declare no conflict of interest.

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