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Moderate inundation stimulates plant community assembly in the drawdown zone of China's Three Gorges Reservoir

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Abstract

Background: While a dam is constructed to adjust and store water resources, it has negative impacts on biodiversity of the corresponding ecosystems. In particular, the dam regulation induces water-level fluctuations (WLFs), resulting in remarkable effects on the riparian vegetation succession of the drawdown zone ecosystem. These riparian plant responses play important roles in the biodiversity conservation. However, in-depth investigative adequate studies are still lacking. The objective of this study was to assess the community assembly under the anti-seasonal WLFs of China's Three Gorges Reservoir (TGR). To analyze the WLFs' impacts on plant community, the drawdown zone of the TGR was divided into four sub-zones (zone I, II, III, and IV) according to the inundation periods. The community biomass, height, total coverage, and species diversity in each sub-zone were surveyed. To detect the response of individual plant to the WLFs, dominant plants of *Echinochloa crusgalli*, *Setaria viridis*, *Bidens pilosa*, and *Xanthium sibiricum* were selected as targeted species to compare the plant's morphological and physiological traits between non-flooded area and the moderately inundated area.

Results: The peaks of community biomass (1859.62 ± 663.77 g), total coverage ($103.93 \pm 11.81\%$), and diversity indexes were found in zone II that experienced 90 days of inundation. Community height and total coverage were both significantly negatively correlated to the inundated gradients. Generalized linear models and quadratic regression analyses revealed that community biomass, height, and total coverage were strongly related to the inundated gradients, implying that the inundation is the major factor contributing to the variation of the riparian vegetation patterns. The values of morphological traits (plant height and biomass) in the zone II were higher than those in the non-flooded zone, and were significantly positively correlated with physiological traits.

Conclusions: Community structure, diversity, and functional traits analysis indicated that the drawdown zone referencing to the 90-day inundation was suitable for the plant community establishment. Results on plant functional traits suggest the adaption of riparian plants to the TGR hydrological regime. However, further investigative studies with more plant species are necessary to elucidate their adaptation mechanisms.

Keywords: Water-level-fluctuating zone, Anti-seasonal inundation, Community assembly, Plant functional traits, The Three Gorges Reservoir (TGR)

Background

Riparian plants growing at the drawdown zone of rivers, lakes, and reservoirs, are the primary indicator of the riparian habitat [1]. They provide a corridor for biota, their above-ground biomass modifies flow and thus controls sediments and nutrients transport [2]. In addition, they moderate water temperature, stabilize

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riverbanks, and provide food for humans [3]. Vegetation is a critical portion of the riparian ecosystems, of which the succession is involved in the riverine evolution process [4]. The riparian plant community assembly is strongly influenced by the water-level fluctuations (WLFs) induced by natural and/or artificial flooding events. The WLFs with their extent, flow, duration of submergence and frequency, etc., usually form a unique pattern in lakes and rivers that affect riparian plant in a large scales including morphological changes, physiological variations as well as shifts in growth rate and/or growth form [5]. The inundation of the WLFs not only alters the soil physical–chemical characteristics and patterns of soil microorganism, but also the changes of plant uptake and accumulation of water and substrates as well as the light availability and temperature which are important factors for plant photosynthesis. Therefore, an understanding of plant community assembly in relation to the inundation changes is of great importance. Studies have reported the changes of diversity, patterns of plant community, soil seedbank and plant individual properties such as growth form and reproduction in response to natural flooding [5–9]. Although the knowledge governing the plant community assembly under disturbance is growing, gaps still exist on plant's adaption to the anti-seasonal WLFs, in particular with those infrastructural developments such as dam construction with inundation period ranging from weeks to months [10].

The Three Gorges Dam on the upper reaches of the Yangtze River, which is the dam (2309 m in length and 185 m in height) with the largest installed capacity of hydropower in the world, started to function in 2010. As a result, the capacities of flooding control, navigation as well as hydropower generation have remarkably increased. Simultaneously, the corresponding reservoir—the Three Gorges Reservoir (TGR) has been created with an area of 58,000 km² in total. The new hydrological regime of the TGR is seasonal reverse, with the water level fluctuating from 145 m above sea level during summer and up to 175 m during winter [11]. Field surveys have recently reported a decline of plant diversity and vegetation dominated by herbaceous in the drawdown zone of the TGR in contrast to its pre-dam patterns [12–15], which differ from the other vegetation patterns induced by dam regulation [16–20]. Understanding the newly created ecosystem process of the TGR is an urgent and crucial issue for environmental conservation and ecosystem sustainable management in the reservoir region. The regulation of TGR thereby provides us an opportunity to explore the mysterious realms regarding the effects of anti-seasonal hydrology on riparian vegetation.

Community assembly is mainly governed by abiotic gradients, propagule pressure, and species interactions [21]. The abiotic gradients, such as anti-seasonal WLFs, are considered as a disturbance to riparian plants, which vary in inundation frequency, period, and depth. The highest diversity and productivity are usually found in the intermediate disturbance zones with respect to time and/or space, following the intermediated disturbance hypothesis (IDH) [22, 23]. During plant growth, the complete life history is important than that of propagule pressure. Species interactions are the results of fitness during plant life history under anti-seasonal fluctuation, which are driven by water fluctuation disturbance, resources use efficiency, and inter- and intra-species competition. The individual properties during plant growth therefore could be assessed from the variations of plant functional traits [24, 25]. Plant changes, for instance shifts of growth rate and/or growth form, are often the results of changing physiological processes and are adaptive responses in basic phenomena such as photosynthesis, water and nutrient transport [5]. The contribution of factors for community assembly differs between each other, as well as their corresponding integrated effects. Identification of the main effect on community assembly may help to predict the community succession along with the TGR hydrological regime.

The aims of the current study are to demonstrate the response of riparian vegetation to the anti-seasonal fluctuation resulting from regulation of the TGR. We investigated community structure including biomass, height and total coverage, and diversity along inundation gradients (IGs). In addition, we tested the variations of plant functional traits of dominant plants between upland zone (UZ) that are non-inundated and zone II with submerged period corresponding to intermediate IG. To achieve this goal, we hypothesized that (1) the patterns of riparian plant community structure (biomass, height, and total coverage) and diversity of the TGR follow the IDH; (2) the community assembly is mainly driven by WLFs and (3) plant changes could be linked with functional traits. To our knowledge, this study is the first one linking plant community assembly and plant functional traits to anti-seasonal WLFs, which promotes understanding the vegetation succession on the drawdown zone ecosystem process.

Methods

Study area and the TGR inundation conditions

The TGR area is characterized by a subtropical monsoon climate with average annual temperature of 15 °C–18 °C and mean annual precipitation of 1000–1300 mm. The highest temperature in summer is up to 35 °C or even higher for several weeks, thereby vegetation in

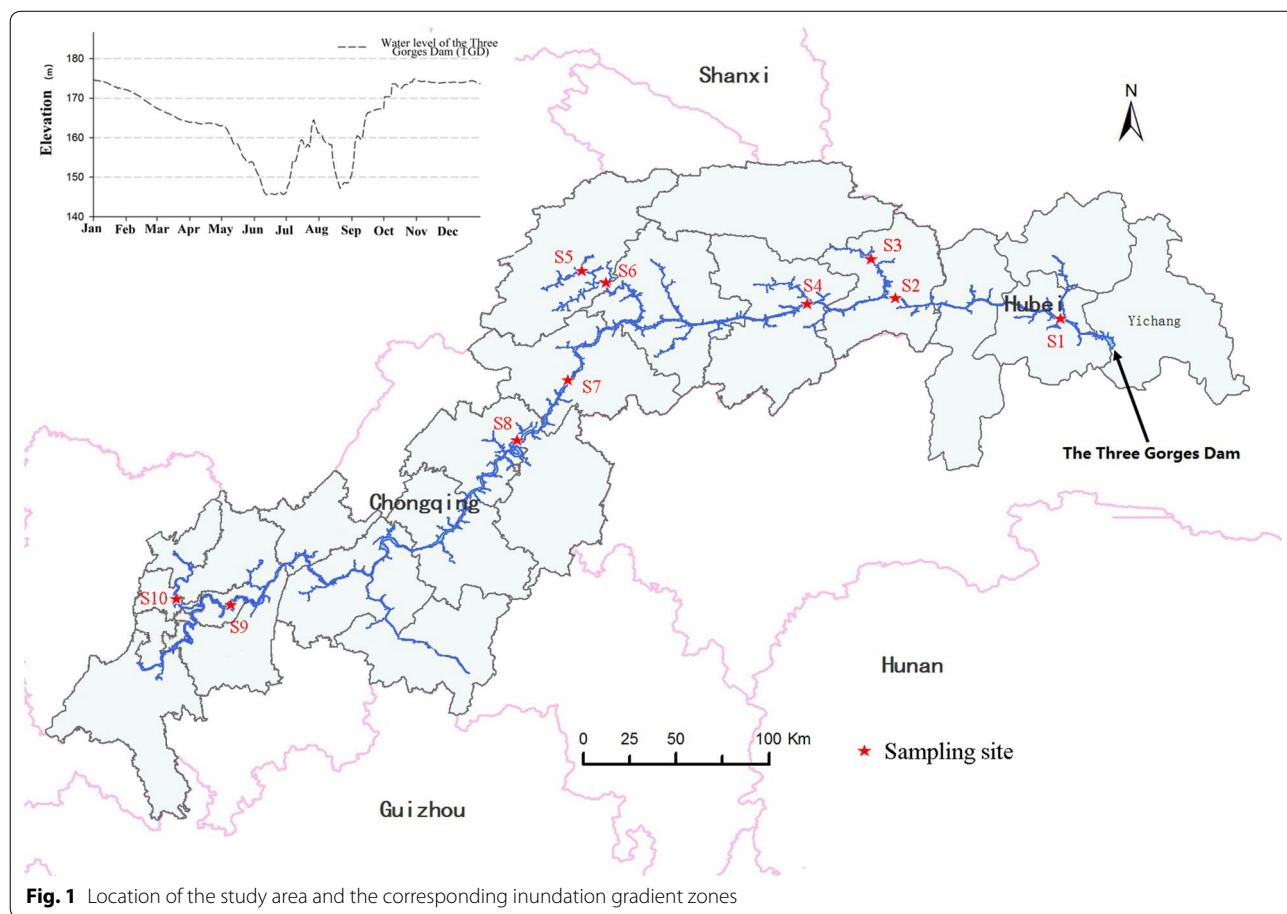
the drawdown zone of the TGR must endure summer drought and winter flooding. The soil types are red soil, purplish soil, yellow soil and paddy soil [26].

The dam construction was started in 1994 and the water level was raised to 139 m since 2003, which is 60 m higher than that of the natural water level of the Yangtze River. Experimental submergence of water up to 156 m in winters of 2006 and 2007 and 173 m in winters of 2008 and 2009 was implemented with the water level declining to 145 m in summers. Since 2010, the dam started full function with 30 m fluctuation ranging from 145 m to 175 m [26]. The annual anthropogenic water-level inundation lasts more than 8 months, the rise and fall of the water level cost time so the duration of winter submergence declines with elevation, i.e., the drawdown zone of lower elevations is inundated for a longer time. Under such inundation condition, plants at the drawdown zone of the TGR are highly affected, but could still germinate and grow when the inundation recedes (summer). Until the summer of 2012, the drawdown area below 156 m elevation has been inundated 7 times while that between 156 and 175 m is 4 times. In addition, during summer season, the drawdown area from 145 m to approximately

160 m is usually afflicted by natural floods from days to approximately 2 weeks.

Community properties survey

Field survey was conducted in the TGR region in August 2012. We selected sampling sites in the whole reservoir area distributing from the Xiangxi River estuary (Hubei province) to the city of Chongqing (Fig. 1), where most sites were correlated to our previous study [13]. By analyzing the inundation record from 2008 to 2011 (<http://www.ctg.com.cn/inc/sqsk.php>), we categorized the drawdown area into four sub-zones reflecting different immersion periods (zone I: 170–175 m of elevation, zone II: 165–170 m, zone III: 160–165 m, and zone IV: 145–160 m). Zone I, II and III are submerged during winter season, besides, zone III is inundated during in case of severe natural flooding in summer. Zone IV is affected by both winter submergence and summer natural flooding. Meanwhile, the upland zone (UZ) between 175 m and 180 m was included for comparison. In each site, sets of corresponding transects that are parallel to the water level with 50 m in length were defined in each sub-zone and the corresponding uplands. The representative



vegetation in each transect was selected and six 1×1 m quadrats were randomly chosen for investigating plant species, abundance, species average height, coverage (visually estimated), and plant aboveground biomass (obtained by harvesting). Plant species within the 50-m transects were recorded and the relative frequency of each species was calculated in order to select the species for further study. The slope gradients (SGs) of each quadrats were also recorded according to the technical regulations for land use status survey (1984) (five gradients: $\leq 2^\circ$, $2-6^\circ$, $6-15^\circ$, $15-25^\circ$ and $> 25^\circ$) [27]. Due to the fact that the height of the drawdown zone is less than 30 m in the tail area of the reservoir, a total of 10 sampling sites and 196 quadrats were finally established in the current study.

In order to examine the effect of IGs on riparian vegetation, we employed the indicators with community structure (biomass, height and total coverage) and diversity (species Richness, Shannon–Wiener index, Simpson index and Pielou index) in quadrats. For each indicator, data from the six quadrats in the same elevation zone of each sampling site were averaged. Generalized linear models (GLMs) were performed to analyze the abiotic effects on the riparian vegetation community properties, in which community biomass, total coverage, height and community diversity were used as dependent variations; simultaneously, the IGs, SGs and the sampling sites along the reservoir longitudinal gradients (LGs) were selected as fixed factors. Since we made an a priori assumption that community structure and diversity would follow the IDH; hence, quadratic regression analyses were used to determine if disturbance of IGs were significantly and unimodally related to community properties described above.

Plant functional traits investigation

After the vegetation survey described above, plants dominantly distributed both at the zone II where they were submerged for 90 days per year and the surrounding UZ (175–180 m) were chosen as the specimens for which the individual aboveground biomass and plant height (maximum height) were recorded. For each species, 10 healthy plants with fully extended leaves were selected randomly from the drawdown area and measured for photosynthetic characteristics with three replicates. Gas-exchange measurements of the net photosynthetic rate (P_n) were made from different healthy leaf tissues from 9:00 to 12:00 a.m. using a portable photosynthesis system (Yaxin-1102, Beijing Yaxinliyi Science and Technology, Beijing, China) under natural solar irradiance of $1500-1800 \mu\text{mol} (\text{m}^2 \text{s})^{-1}$. The changes in the transpiration rate (T_r), stomatal conductance (C_{leaf}) and intercellular CO_2 concentration ($\text{CO}_{2\text{int}}$) were recorded simultaneously.

Each selected leaf was examined for 15 s, followed by an interval of 25 s, and the cycle was repeated twice. Measurements in the surrounding upland area were conducted in parallel.

Data analysis

With significant difference test, in case of the assumption of homogeneity of variance was met, the differences of the community properties along the IGs were tested by one-way ANOVA, in other case, the Kruskal–Wallis H test was employed. The correlations among plant matrix and environmental variables were analyzed using Pearson correlation analysis at the 95% confidence level. The significant differences in the plant functional traits between zone II and the UZ were analyzed and the correlations within trait-parameter were performed with the same protocol as above. The GLMs, quadratic regression analyses and the other statistical analyses were performed using IBM SPSS 20.0 [28].

Results

Distribution patterns of community structure and α -diversity

We found that annual and perennial herbaceous plants were dominant species of the drawdown area. 190 plant species in 144 genera and 53 families were identified, among which Gramineae (15.26% of 190 species), Asteraceae (12.63%), Cyperaceae (6.32%) and Leguminosae (5.26%) were the most quantitatively abundant families, which is comparable to our previous study [13]. Four species, *Echinochloa crusgalli*, *Setaria viridis*, *Bidens pilosa* and *Xanthium sibiricum* with relative frequencies up to 27.55%, 29.1%, 27.55% and 20.1%, respectively, were selected for further study on functional traits. The α -diversity and community structure (biomass and total coverage) peaked at zone II, with the community height as an exception (Fig. 2). Regarding the diversity matrix (Fig. 2a), Shannon index fluctuated from 0.59 ± 0.40 (zone IV) to 0.88 ± 0.47 (zone II), Simpson index ranged from 0.35 ± 0.23 (zone IV) to 0.45 ± 0.24 (zone II), Pielou index amounted from 0.42 ± 0.27 (zone IV) to 0.51 ± 0.23 (zone II) and Richness index fluctuated from 2.83 ± 1.76 (zone IV) to 4.43 ± 2.48 (zone II). However, the differences did not vary significantly along IGs, which are different from a previous study [26]. With community structure, the variations along the IGs were very significant (biomass, $P < 0.001$; height and total coverage, $P < 0.001$ and $P < 0.001$, respectively), the average total coverage were between $103.93 \pm 11.81\%$ (zone II) and $44.39 \pm 35.46\%$ (zone IV) (Fig. 2b), the averaged biomass ranged from 674.18 ± 846.94 g in zone IV to 1859.62 ± 663.77 g in zone II (Fig. 2c) and the average

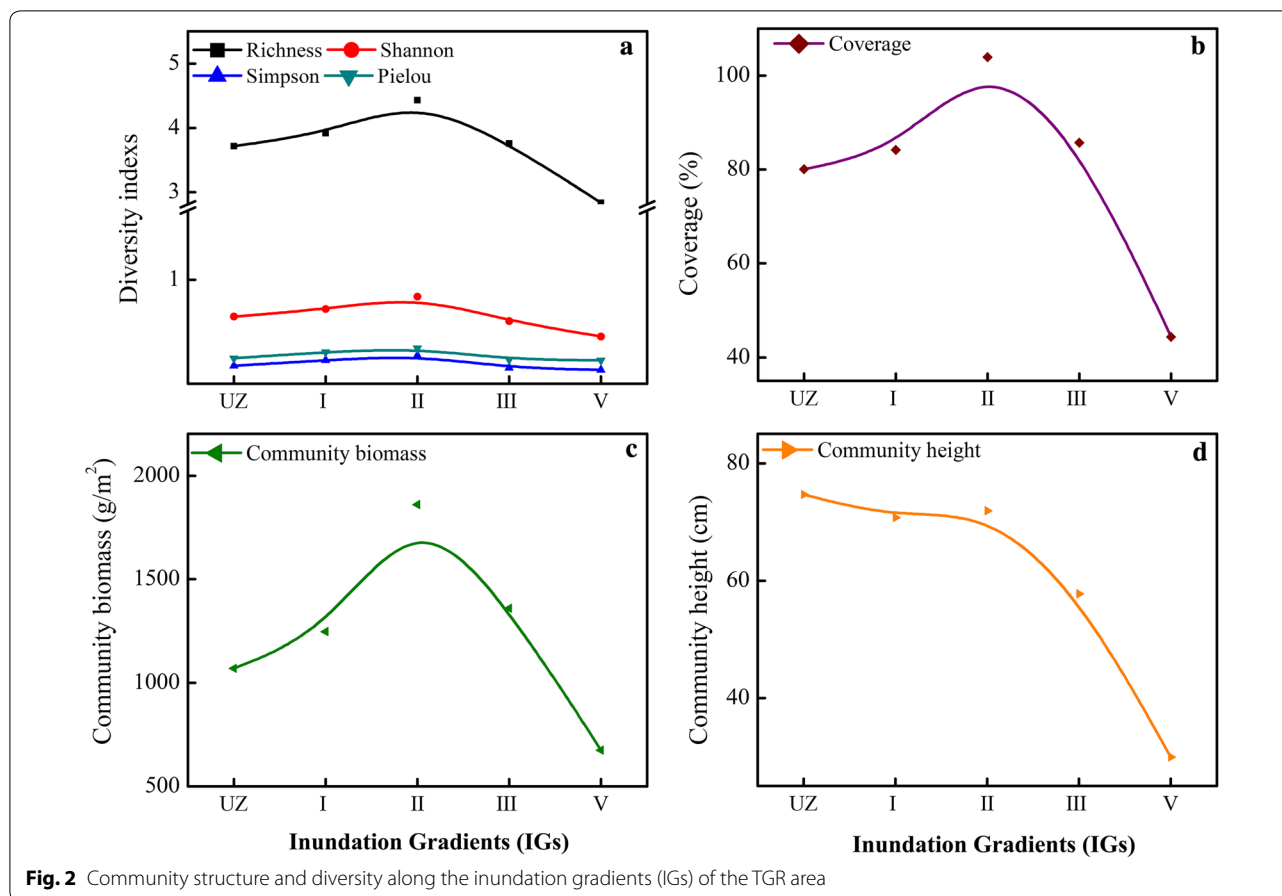


Table 1 Correlations of plant community structure, α -diversity along with inundation gradients

	IGs	Biomass	Height	Coverage	Shannon	Simpson	Pielou	Richness
IGs	1	-	-	-	-	-	-	-
Biomass	0.002	1	-	-	-	-	-	-
Height	-0.251**	0.409**	1	-	-	-	-	-
Coverage	-0.150*	0.428**	0.191**	1	-	-	-	-
Shannon	-0.070	-0.226*	-0.120	-0.048	1	-	-	-
Simpson	-0.045	-0.252*	-0.147*	-0.090	0.977**	1	-	-
Pielou	-0.035	-0.279*	-0.149	-0.130	0.945**	0.984**	1	-
Richness	-0.073	-0.176*	-0.042	0.106	0.804**	0.691**	0.613**	1

IGs, inundation gradients

* $P < 0.05$, ** $P < 0.01$

community height amounted from 74.66 ± 58.05 cm in UZ to 29.90 ± 7.98 cm in zone IV (Fig. 2d).

Relationships among community properties

The correlations of community properties along the IGs varied significantly (Table 1). Community height and total coverage were both significantly negatively correlated to the IGs ($r = -0.254$, $P < 0.001$ and $r = -0.145$,

$P < 0.05$, respectively). Community biomass was significantly positively correlated to the height and total coverage, while the negative correlations were found with diversities (Shannon, Simpson, Pielou and Richness indexes: $r = -0.226$, $P < 0.01$; $r = -0.252$, $P < 0.001$; $r = -0.279$, $P < 0.001$ and $r = -0.176$, $P < 0.05$, respectively). The results of GLMs (Table 2) revealed a highly significant effect of IGs on community biomass, height

Table 2 GLMs on the effects of environmental variables on riparian vegetation of the TGR

Source	IGs		LGs		SGs		IEs
	F	P	F	P	F	P	P
Biomass	7.744	<0.0001	1.730	0.088	0.922	0.453	>0.05
Height	10.026	<0.0001	10.667	<0.0001	0.519	0.722	HGs + LGs <0.0001
Coverage	13.303	<0.0001	1.721	0.090	0.590	0.670	>0.05
Richness	3.169	0.016	2.667	0.007	1.017	0.401	>0.05
Shannon	1.641	0.168	4.906	<0.0001	0.976	0.423	>0.05
Simpson	0.838	0.504	5.816	<0.0001	0.903	0.464	>0.05
Pielou	0.658	0.622	6.299	<0.0001	0.495	0.740	>0.05

IGs, inundation gradients; LGs, longitudinal gradients; SGs, slope gradients; IEs, interaction effects

Table 3 Quadratic analyses for community parameters regressed with the inundation gradients of the TGR

Dependent variables	Equation	Model summary					Parameter estimates		
		R square	F	df1	df2	P	Constant	b1	b2
Log ₁₀ (biomass)	Quadratic	0.224	27.881	2	193	<0.0001**	2.783	0.459	-0.135
Height	Quadratic	0.083	8.716	2	193	<0.0001**	72.277	6.236	-3.965
Coverage	Quadratic	0.177	20.727	2	193	<0.0001**	74.708	26.185	-7.965
Richness	Quadratic	0.033	3.285	2	193	0.040*	3.613	0.713	-0.222
Shannon	Quadratic	0.021	2.034	2	193	0.134	0.725	0.124	-0.041
Simpson	Quadratic	0.013	1.261	2	193	0.286	0.382	0.055	-0.017
Pielou	Quadratic	0.010	0.970	2	193	0.381	0.440	0.052	-0.016

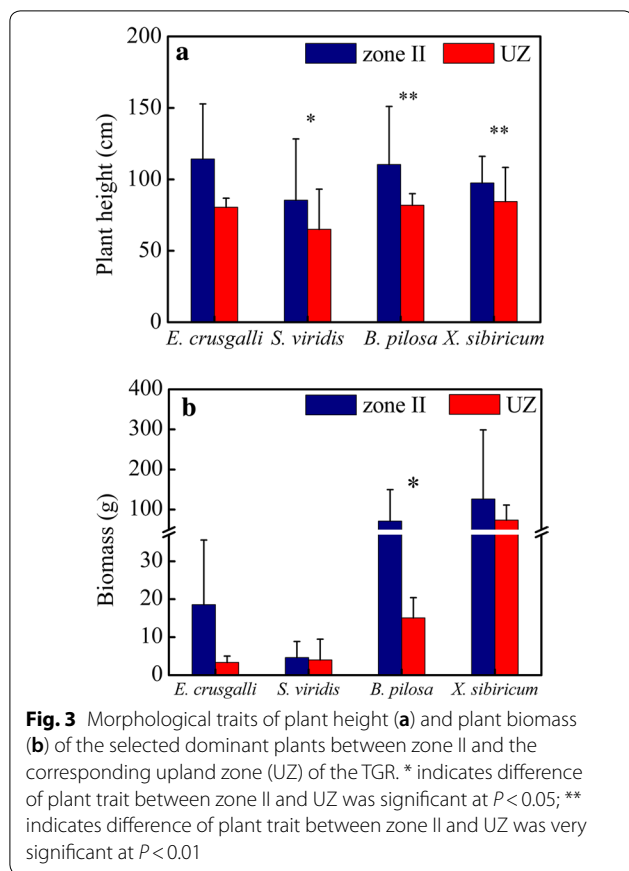
* indicates quadratic regressions that were significant at $P < 0.05$; ** indicate quadratic regressions that were significant at $P < 0.01$

and total coverage, whereas spatial heterogeneity of large scale (LGs in the current study) strongly affected the community diversity. The effects of SGs on community properties were not significant. Additionally, we only found a significant interaction effect between IG and LG on community height. While quadratic regression analyses (Table 3) showed that the community biomass, height and total coverage were strongly related to the IGs, the richness was significantly correlated with the community diversity. Overall, the IG was the major factor that led to the variation of the riparian vegetation patterns in the drawdown area of the TGR.

Plant morphological and physiological functional traits

The height and biomass of individual dominant plants in the zone II of the drawdown area were both higher than those in the UZs (Fig. 3). The differences in plant height were highly significant for *X. sibiricum* and *B. pilosa* ($P < 0.001$) and that for *S. viridis* was significant ($P < 0.05$). However, no significant differences were found for biomass ($P > 0.05$), except that of *B. pilosa*. Regarding the photosynthetic capacity of P_n , T_r , C_{leaf} and CO_{2int} (Fig. 4), P_n of *E. crusgalli* was $17.0 \pm 31.8 \mu\text{mol}/\text{m}^2 \text{ s}$ in the FZ, which was

significantly higher than that in the UZ ($4.7 \pm 7.7 \mu\text{mol}/\text{m}^2 \text{ s}$, $P = 0.029$). P_n of *X. sibiricum* in the zone II was $13.7 \pm 10.2 \mu\text{mol}/\text{m}^2 \text{ s}$ and slightly higher than that in the UZ ($13.6 \pm 9.3 \mu\text{mol}/\text{m}^2 \text{ s}$, $P = 0.975$). In contrast, results found in *S. viridis* and *B. pilosa*, ranged from $4.0 \pm 4.9 \mu\text{mol}/\text{m}^2 \text{ s}$ to $10.6 \pm 16.3 \mu\text{mol}/\text{m}^2 \text{ s}$ for *S. viridis* ($P = 0.028$) and from $3.4 \pm 2.6 \mu\text{mol}/\text{m}^2 \text{ s}$ to $6.1 \pm 10.9 \mu\text{mol}/\text{m}^2 \text{ s}$ for *B. pilosa* ($P = 0.365$) in the zone II and UZ, respectively (Fig. 4a). Regarding T_r (Fig. 4b), higher T_r in the zone II were found with *E. crusgalli* ($2.75 \pm 0.81 \text{ mmol}/\text{m}^2 \text{ s}$, $P = 0.685$) and *S. viridis* ($2.72 \pm 0.77 \text{ mmol}/\text{m}^2 \text{ s}$, $P = 0.153$) than that in the UZ. The T_r for *B. pilosa* in the UZ was found to be $3.01 \pm 2.0 \text{ mmol}/\text{m}^2 \text{ s}$, which is significantly higher than that in the zone II ($1.4 \pm 0.9 \text{ mmol}/\text{m}^2 \text{ s}$, $P = 0.0001$). The T_r for *X. sibiricum* in the UZ was determined as $6.2 \pm 6.3 \text{ mmol}/\text{m}^2 \text{ s}$ which is higher than that in the zone II ($4.3 \pm 4.4 \text{ mmol}/\text{m}^2 \text{ s}$, $P = 0.153$). With respect to $E. crusgalli$ and *S. viridis* in the zone II, the C_{leaf} (Fig. 4c) were significantly higher than those in the UZ, that is $90.5 \pm 32.0 \text{ mmol}/\text{m}^2 \text{ s}$ and $67.3 \pm 26.5 \text{ mmol}/\text{m}^2 \text{ s}$ for *E. crusgalli* ($P = 0.002$) and $84.6 \pm 34.8 \text{ mmol}/\text{m}^2 \text{ s}$ and $64.7 \pm 53.3 \text{ mmol}/\text{m}^2 \text{ s}$ for *S. viridis* ($P = 0.037$), respectively. Contrary results were obtained from *B. pilosa*



and *X. sibiricum*, amounting to 55.4 ± 32.4 $\text{mmol/m}^2 \text{ s}$ and 77.2 ± 39.5 $\text{mmol/m}^2 \text{ s}$ for *B. pilosa* ($P = 0.014$) and 193.7 ± 64.6 $\text{mmol/m}^2 \text{ s}$ and 211.1 ± 72.7 $\text{mmol/m}^2 \text{ s}$ for *X. sibiricum* ($P = 0.293$) in the zone II and UZ, respectively. Figure 4d shows higher concentrations of $\text{CO}_{2\text{int}}$ in *E. crusgalli* (239.5 ± 157.7 ppm, $P = 0.169$), *B. pilosa* (256.3 ± 125.1 ppm, $P = 0.790$) and *X. sibiricum* (256.6 ± 65.2 ppm, $P = 0.789$) in the UZ compared to those in the zone II, amounting to 177.7 ± 210.2 ppm, 248.7 ± 112.3 ppm, 252.3 ± 66.4 ppm for *E. crusgalli*, *B. pilosa*, *X. sibiricum*, respectively. $\text{CO}_{2\text{int}}$ of *S. viridis* was 204.1 ± 122.3 ppm in the zone II, which is significantly higher than that in the UZ (32.6 ± 48.2 ppm, $P = 0.0001$).

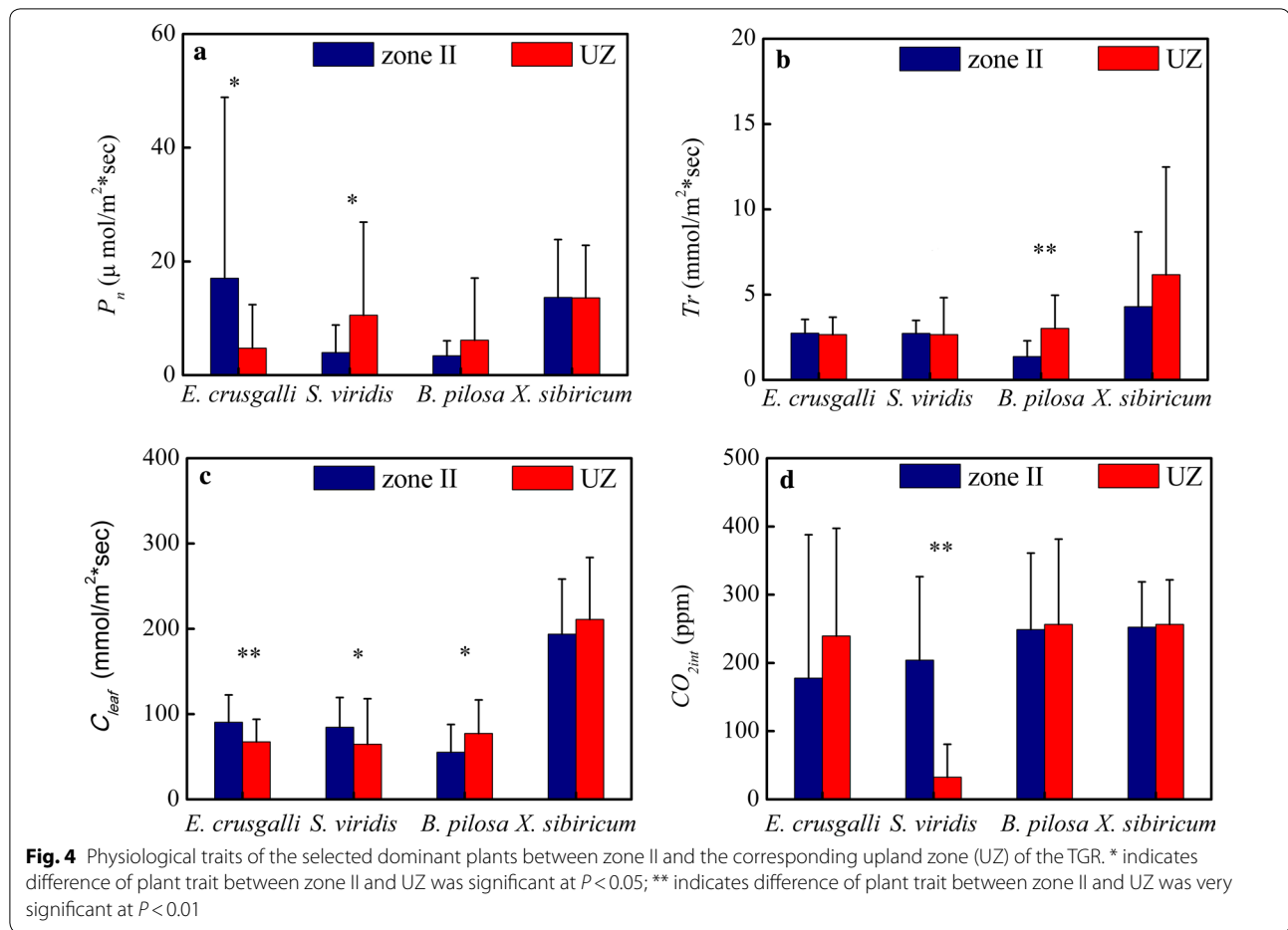
Plant biomass was positively correlated with T_r ($r = 0.544$, $P = 0.001$), C_{leaf} ($r = 0.784$, $P = 0.0001$) and height ($r = 0.619$, $P = 0.0001$) (Table 4). Significant correlation was also found between plant height and $\text{CO}_{2\text{int}}$ ($r = 0.438$, $P = 0.002$). Within the physiological traits matrix, P_n was found to be significantly correlated with T_r ($r = 0.485$, $P = 0.004$) and C_{leaf} ($r = 0.559$, $P = 0.001$), which is similar with a previous study [29]. The P_n and $\text{CO}_{2\text{int}}$ were negatively correlated, but not at a significant level in the current study ($r = -0.127$, $P = 0.437$).

Discussion

Community assembly in the drawdown area of the TGR

Totally, we identified 190 species, which is comparable to 170 species in a previous study in which the water level raised up to 173 m in elevation for the first time [13], both of which are lower than that of the pre-dam (377–550) [30, 31]. The results demonstrated that the inundation of the TGR disturb species that cannot tolerate submergence as recently proved by Arias et al. (2018) [23]. When comparing with the UZ (175–180 m) without inundation disturbance, we found that the anti-seasonal WLFs stimulated the plant growth, showing a highest diversity in zone II subjected to moderate inundation of about 90 days. The results are in consistency with those reported by Wittmann et al. (2008) in which tree species richness in the drawdown area (45 species/ha) is comparatively higher than that in non-inundated areas (24–36 species/ha) [32]. As mentioned above, inundation period of 90 days is intermediate disturbance in the current study. However, Arias et al. (2013) and Murray-Hudson et al. (2015) both observed plant diversity peaked at the submergence period of 6 months, corresponding to intermediate disturbance [33, 34]. Therefore, IGs vary with regions and time scales, and the diversity patterns are highly corresponding to those species with adaptation to the local hydrology. The lowest species diversities were found at the drawdown zone below 160 m in elevation (zone IV), indicating that a strong negative effect of inundation has occurred. The long-term submerged area is to some extent similar to perennial flooded area, in which lower diversity exhibit compare to the areas with alternation of wetting and drying [26].

Concerning community structure, both accretion and restriction on plant growth were observed. Community biomass and total coverage were the highest in zone II and lowest in zone IV (Fig. 2b, c). Therefore, there is an underlying direct connection between the anti-seasonal WLFs and the IDH. However, the community height and total coverage were negatively correlated to IGs (Table 1), which is in contradiction with a previous study [35], revealing the shifts in vegetation succession under the anti-seasonal WLFs. Results of GLMs (Table 2) and quadratic analyses (Table 3) both confirmed that IGs were strongly correlated to community structure of biomass, height and coverage. One possible reason is that the WLFs result in a homogenized flooding disturbance within each IG area, which is important for community assembly [36]. The establishment of plant community involves a certain biotic and abiotic factors, plant inter- and intra-competitions [37]; IGs are found to be important for community structure in the current study. In addition, soil moisture, porosity and nutrient availability, representing the heterogeneity conditions along the

**Table 4** The correlations of plant functional traits of the selected species in the TGR region

	P_n	T_r	C_{leaf}	CO_{2int}	Height	Biomass
P_n	1	–	–	–	–	–
T_r	0.485**	1	–	–	–	–
C_{leaf}	0.559**	0.757**	1	–	–	–
CO_{2int}	–0.127	0.261	0.308	1	–	–
Height	–0.035	0.049	0.253	0.438*	1	–
Biomass	0.349*	0.544**	0.784**	0.259	0.619**	1

P_n , net photosynthetic rate; T_r , transpiration rate; C_{leaf} , stomatal conductance and CO_{2int} , intercellular CO_2 concentration

* $P < 0.05$, ** $P < 0.01$

LGs, could be other important variables in explaining the observed diversity, community composition and plant morphological and physiological variables.

Plant's response to the TGR hydrological regime

The values of morphological traits in zone II were higher than the surrounding uplands (Fig. 3), this may be possibly due to the following reasons: (1) water inundation

that may have improved the soil nutrient conditions of the drawdown area, (2) the pattern of the soil seed bank homogenized within each IG area [38, 39], creating a uniform condition for germination and (3) variations in the plant physiological performances. *E. crusgalli* and *S. viridis* belonging to Gramineae showed similar tendency towards C_{leaf} and T_r , while the tendency of Asteraceae plants *B. pilosa* and *X. sibiricum* was all similar regarding

P_n , T_r , C_{leaf} and $\text{CO}_{2\text{int}}$. Therefore, plants belonging to the same family or genus show similar feedbacks under the same environmental changes. These were also found in plants of *Polygonum* (*P. cespitosum*, *P. hydropiper*, *P. lapathifolium*, and *P. persicaria*) [40]. In the current study, *E. crusgalli*, *S. viridis* and *B. pilosa* are C4 plants [41] which showed significant differences in traits between zone II and UZ, while *X. sibiricum* is a C3 plant and the trait-variations are without significant difference [41, 42]. Generally, C4 plants grow faster and thus higher physiological performances are expected, because individual phenotypic plasticity rather than ecotypic changes leads to the plants adaptation or tolerance to the entire habitat [43]. Plant growth mainly depends on its photosynthetic capacity [44], since P_n was positively correlated with C_{leaf} the increase in C_{leaf} may facilitate the P_n [45]. T_r was positively correlated with C_{leaf} in the current study ($r=0.757$, $P<0.001$), thus high temperature during summer in the study area may increase both T_r and C_{leaf} and finally promote plant photosynthesis. In addition, positive correlations among P_n , C_{leaf} and plant biomass revealed a relationship between physiological traits and morphological traits. Thereby, plant functional traits are sensitive to flooding disturbance and may illustrate plant's response to the TGR inundation regime. However, questions still exist on how the traits vary along the gradients of inundation and what are the patterns of functional traits among different species. Therefore, in-depth long-term investigations with more species in the drawdown area are suggested. For this purpose, a permanent site has been established in estuary of the Baijia Stream (site 6 in the current study) and the dynamics of vegetation succession were yearly investigated since 2008 [11]; our results are useful for understanding the responses of riparian vegetation to flooding [11, 46, 47].

Conclusions

Our results suggest that community assembly in the drawdown area of the TGR is highly correlated with the anti-seasonal WLFs. Shifts in plant diversity and community structure (biomass, height and total coverage) were observed as compared to the UZ (175–180 m). The anti-seasonal WLFs stimulated the plant growth and were found at both community and individual levels. Community biomass, total coverage and diversity are the highest in zone II that was submerged for 90 days, which followed the IDH. GLMs and quadratic analyses showed that IGs were the major factor that led to significant correlation with community structures while the LGs strongly affected diversity patterns. Plant morphological traits showed higher values in the zone II than those in the UZ. Species belonging to the same

family showed similar feedbacks on physiological traits. Thus, morphological and physiological traits are sensitive to the flooding, illustrating plant's response to the TGR inundation regime. However, vegetation succession is a time-scale process corresponding to the ecosystem evolution; hence, long-term investigation for studying the vegetation dynamics in response to environmental disturbances such as WLFs is necessary.

Abbreviations

TGD: Three Gorges Dam; TGR: Three Gorges Reservoir; IDH: Intermediate Disturbance Hypothesis; WLFs: Water-level fluctuations; UZ: Upland zone; IGs: Inundation gradients; LGs: Longitudinal gradients; SGs: Slope gradients; IEs: Interaction effects; GLMs: Generalized linear models; NAZC: National Agricultural Zoning Committee of China; P_n : Net photosynthetic rate; T_r : Transpiration rate; C_{leaf} : Stomatal conductance; $\text{CO}_{2\text{int}}$: Intercellular CO_2 concentration.

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Authors' contributions

ZC was responsible for the general design and drafted the manuscript; XY, MRN, HH and AS contributed to supported the writing of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors agreed to publish the paper.

Competing interest

The authors declare that they have no competing interests.

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