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Response and Environmental Adaptation of Plant Community to Periodic Flooding in the Riparian Zone of Three Gorges Reservoir, China

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ABSTRACT

The plant is an important component of the riparian ecosystem, which could reflect both the environmental and functional characteristics of the riparian zone. Studies on species composition, diversity, community structure, distribution pattern, and adaptation strategies of plant communities in the riparian zone of the Three Gorges Reservoir (TGR) will help to explore the maintaining mechanism of the plant communities' ecological function under severe water-level fluctuation. The paper reviewed the plant community characteristics, functional traits as well as their eco-physiological responses and environmental adaptations in this special ecological zone. Based on this, future research orientations in this field were also prospected, which may focus on the maintenance mechanism of the plant community, suitable plants selection and their adaptation mechanism, the relationship between plant functional traits and ecosystem functions, plant niche in the riparian zone, and the connectivity of riparian zone to the surrounding environment. The results can promote the correlational research on plant communities in the riparian zone and deepen the understanding of ecosystem services the riparian ecotone provides.

INTRODUCTION

Riparian zones are typical aquatic-terrestrial ecotones formed by the water-level periodic fluctuation of reservoir operation that could provide multiple ecological functions, such as stabilizing reservoir bank, purifying water quality, conserving biodiversity, beautifying the landscape, and ensuring reservoir system health (Zhu et al. 2020). The construction and operation of the Three Gorges Reservoir (TGR) of China, the largest hydropower dam in the world, has created a unique riparian zone with an area of 350 km^2 along the mainstream of the Yangtze River and its tributary due to anti-seasonal water-level fluctuation (i.e., water levels of 145 m in summer and 175 m in winter; Fig. 1) (Ye et al. 2017, Zhu et al. 2020). However, it also poses a significant impact on the ecosystem, land surface processes, and social economy in the reservoir area. In particular, the ecological degradation in the riparian zone has attracted widespread attention, and many studies have been conducted to explore the impacts of the TGR on landscape patterns (Wu et al. 2017, Chen et al. 2018), variations of vegetation distribution, and diversity (Hu et al. 2018, Zhu et al. 2019), as well as the spatial-temporal characteristics of the plant-soil system (Ye et al. 2020, Liu et al. 2021). Though these studies have elucidated the changes in the eco-hydrological environment since the reservoir impoundment, the dynamic characteristics and maintaining mechanism of the plant community function derived from the hydrological regime in the riparian zone of the reservoir are still unclear. Additionally, the response mechanism of plant communities in terms of functional traits or physiological ecology and their environmental adaptation to periodic flooding and drought stress (alternate wetting-drying conditions) at different altitudes have not been fully understood.

STATE OF THE ART

Plants are the important components of the riparian ecosystem, which could reflect both the environmental and functional characteristics of the riparian zone. Repeated submersion and exposure could greatly reduce the original vegetation and new plant communities gradually formed. Currently, research on plant communities in the riparian zone mainly concerns species composition and diversity (Zhang et al. 2016), community structure and its dynamics (Lei et al. 2015), physiological characteristics of dominant species (Ai 2013), plant ecological stoichiometry (Du et al. 2014), flooding-tolerant plants selection (Fan et al. 2015),

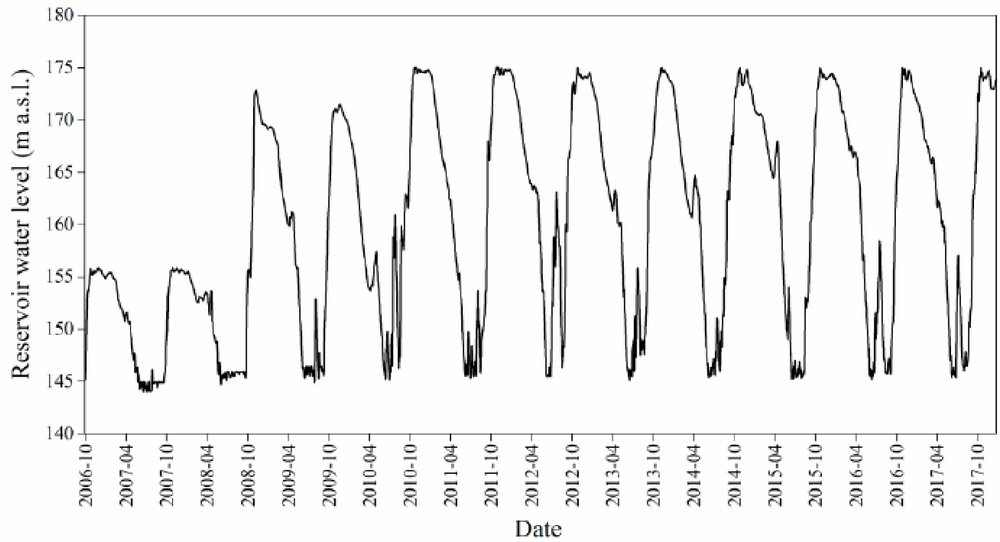

Fig. 1: Water-level fluctuation of the Three Gorges Reservoir during 2006-2017 (Data source: Zhang 2020).

the limiting factors and modes of vegetation restoration (Guo et al. 2012), and plant functional traits (Budelsky & Galatowitsch 2004).

Plant Community Composition and Species Diversity

Wang et al. (2011a) showed that plants in the riparian zone of the TGR were mainly distributed in the high-altitude localities with gentle slopes and fine texture. Species diversity and proportion of annual plants increased with elevation, and the plant composition was consistent with spatial variations of flooding disturbance intensity. Long-term winter submersion, dramatic water-level fluctuation, and high-temperature summer drought in the water-falling season are the driving factors of vegetation composition in this riparian zone. Zhang et al. (2016) found that since the experimental impoundment of the TGR in 2006, a large number of plant communities in the inundated area have disappeared, forming permanent waters and environmentally adaptable plant communities. Before impoundment, there were 769 species of vascular plants (belonging to 400 genera in 121 families) with annual herbs, perennial herbs, and shrubs being the dominant life forms; after impoundment, the vascular plants decreased to about 300 species, among which the proportion of annual herbs increased from 26.4% to 45.5%, perennial herbs decreased from 44.4% to 32.5%, and woody plants (arbors and shrubs) decreased from 23.7% to 15.2%, indicating that shrubs were no longer the dominant life form (Fig. 2). Actually, the existing vegetation types in the riparian zone of

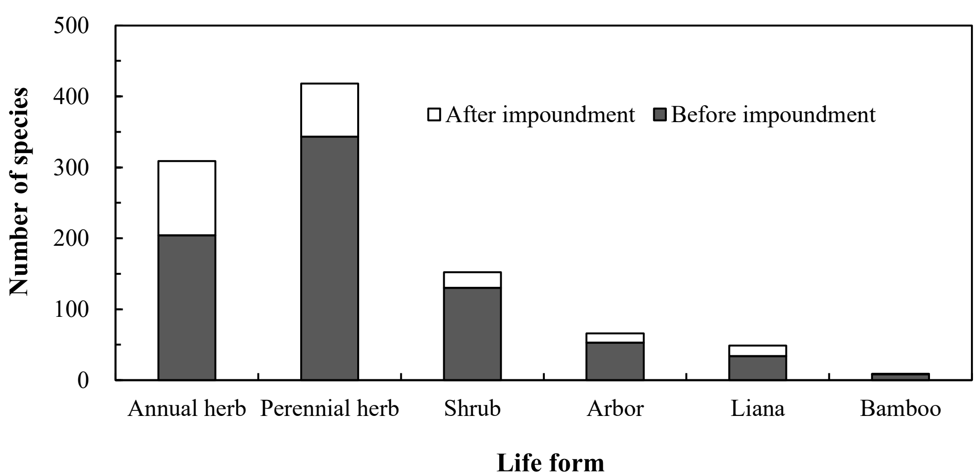

Fig. 2: Life form of vascular plants in the inundated area of the TGR before and after the reservoir impoundment (Data source: Zhang et al. 2016).

the TGR were predominantly annual and perennial herbs and the species diversity showed a "single peak" pattern along with the elevation, with the medium elevation (155-165 m) being the highest species diversity (Guo et al. 2019). Under the influence of repeated periodic water-level fluctuation, herbaceous plants (including annuals and perennials) would replace arbors, shrubs, lianas, and other life forms, which is an inevitable trend of the composition change in plant life forms in the riparian zone of the TGR.

Plant Ecological Stoichiometry

Ecological stoichiometric theory unifies ecology with elemental ratios and stoichiometric invariance that studies energy balance and multiple chemical elements (principally C, N, and P) balance in biological systems (Zhang et al. 2019). Plants generally adjust their element content and ratio for adapting to the ambient environmental changes. In the riparian zone of the TGR, the characteristics of plant communities and suitable plant selection are the most discussed topics. However, there are few studies regarding plant characteristics from the perspective of elements or ecological stoichiometry. Laboratory fertilization experiments revealed that plant growth in the riparian zone of the TGR was restricted by N, and N and P addition could relieve this restriction effect (Mi et al. 2016).

Suitable Propagules and Seed Selection

It is generally acknowledged that there are two ways for vegetation restoration, one is artificial construction like propagules planting or seed sowing; another is seed bank transplantation (Li et al. 2010a) The riparian zone of the TGR is characterized by high water-level drop, long duration, anti-seasonal and irregular flooding, with the flooding time of 150 m elevation (145-155 m) being about 8~10 months, 160 m (155-165 m) about 6~7 months, and 170 m (165-175 m) about 2~4 months (Fig. 3). According to these characteristics, Huang et al. (2013) divided the riparian zone into lower (146-156 m), middle (156-173 m) and upper (173-176 m) parts, and suggested that different measures should be taken for different parts to ensure both ecological benefits and landscape effects. The key to vegetation restoration in the riparian zone of the TGR is to select the species (propagules and seeds) that could tolerate the above-mentioned adverse stresses.

Artificial selection of adaptable plants could not only provide technical support for the construction of stable plant communities and ecological restoration but also enrich the species diversity. In recent years, many scholars have screened out a variety of adaptable species via actual or simulated flooding tests, the perennial herbaceous plants mainly included *Cynodon dactylon* (Liu & Liu 2005), *Paspalum paspaloides*, *Cyperus rotundus*, *Alternanthera philoxeroides* (Fan et al. 2015), *Iris pseudacorus* (Wang et al. 2008), and *Arundinella anomala* (Ye & Zeng 2013); the perennial woody plants mainly included *Chinese maple poplar*, *Vitex negundo* (Lu et al. 2010), *Ascendens mucronatum* (Yin et al. 2014), *Taxodium ascendens Brongn* (Li et al. 2011), etc. Liu et al. (2005) conducted plant adaptability tests in the field waters of the Yangtze River under limiting conditions, and the results displayed that *Cynodon dactylon* had strong adaptability and could survive such conditions as the flooding depth of 0-25 m. Ma et al. (2009) screened out two species (*Cynodon dactylon* and *Ficus tikoua*) with strong adaptability through in situ and simulated flooding experiments. Chen et al. (2008) found that short-term simulated flooding (10, 20, and 30 d) had no obvious negative effects on the survival rate and physiological activities of the annual herb *Polygonum hydropiper*. Wang et al. (2008) indicated that

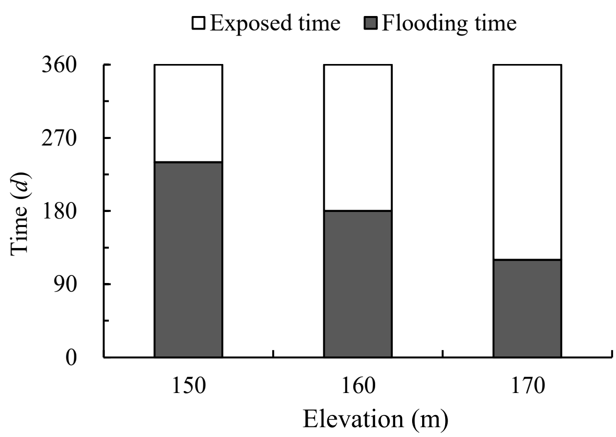

Fig. 3: The flooding time and exposure time of the water-level-fluctuation zone of the TGR (Data source: You et al. 2017).

Vetiveria zizanioides, *Acorus calamus*, and *Alternanthera philoxeroides* still had extremely high survival rates after long-term flooding. Some common annual herbs in the riparian zone of the TGR have a very low flooding tolerance and lost their germination ability after being flooded, for instance, *Humulus scandens*, *Bidens pilosa*, and *Cyperus nipponicus* (Wang et al. 2011b).

Vegetation Collocation Mode

It is commonly recognized that adaptable species were selected according to the flooding duration and depth at different elevations in the riparian zone (Du et al. 2012). Li et al. (2017) proposed that the collocation modes of "arbor-shrub-grass-lianas" for 177-170 m, "shrub-grass-lianas" for 170-160 m, and "grass-lianas" for 160-145 m should be adopted for different elevations in the riparian zone. Du et al. (2012) stated that in the ecological barrier area, plants with strong decontamination ability like *Cynodon dactylon*, *Acorus calamus*, and *Arundo donax* Linn. should also be collocated. Summarily, the adaptable species collocation in the riparian zone primarily focused on the following aspects: 1) Ecological benefits. Through the collocation of "arbor-shrub-grass-lianas", the vegetation coverage during the land-forming stage of the riparian zone could be guaranteed, and soil erosion could also be prevented; 2) Landscape effect. Species with landscape effect are used in the elevation of 170-177 m; 3) Economic benefits. In the upper part of the riparian zone with a longer land-forming period and the ecological barrier area, the combination of aquatic flowers and plants, forage grass, fruit trees, and mulberry could not only meet the pollution intercepting effect but also have certain economic benefits.

Plant Functional Traits and Their Environmental Adaptability in The Riparian Zone

Plant functional traits play an indicative role in the ecosystem's functional changes. Nowadays, it has become an important hotspot of ecological research, especially ecological function research under varying environments (Meng et al. 2007, Feng et al. 2008). Studies showed that the plant functional traits in the riparian zone of the TGR exhibited homogeneity at the watershed scale; the specific root length had a high variability and the main stem mass had a low variability (Hou 2019). Plants mostly suffer stress under the harsh environmental conditions of the riparian zone; the high variability of specific root length thus denotes the sensitivity of plants to different habitats (Hou 2019). Moreover, plants behave with different functional traits for different flooding gradients, with plant total length, main stem dry matter, and chlorophyll content increasing along with the elevation. While root length/plant total length and leaf water content decreased with elevation, both stem water content and leaf thickness firstly increased and then decreased (Hou 2019). With the progress of elevation, high-temperature summer drought became a new limiting factor, and plants adapted to the adverse stress by enhancing tissue construction investment at the elevation of 170-175 m.

Due to the differences in plant functional traits, different plant species will choose different environmental adaptive strategies to occupy the appropriate ecological niche. Gramineous plants generally have a strong tillering ability, and their greater specific root length could make water and nutrients absorption and cycle more effectively thereby improving the growth rate and occupying an ecological niche even in the lower part (with a short initial exposure time) of the riparian zone. This kind of environmental adaptive strategy can also be suitable for other ecological environments, which is the reason why most gramineous plants are widely distributed in the world. Hygrophyte plants generally live near the water with runty bodies and undeveloped mechanical tissue and maintain the plant erect through high water content. The species of slow-growing and distributed in resources-limited habitats usually have relatively small specific leaf areas (Brown et al. 1999), while plants with larger specific leaf areas have a stronger ability to maintain nutrients (Pan et al. 2009). The specific leaf area and main stem dry matter of herbaceous plants in Compositae and Malvaceae families are significantly higher than those of other species, as ascribed to the environmental and phylogenetic effects that need to not only complete the life history in a short time but to increase the investment in mechanical tissue construction to resist the high-temperature summer drought.

Eco-Physiological Responses and Adaptation Strategies of Plant Communities to Alternate Drying-Wetting Environments

Eco-physiological Responses

The anti-seasonal water-level fluctuation may induce changes in the eco-physiological adaptability of the original plants in the riparian zone, and meanwhile, the adaptable plants are required to have high water and drought tolerance. Changes in plant eco-physiological adaptability mainly behave as substance metabolism and photosynthetic physiology.

Metabolic Response

Alternate wetting-drying stress in the riparian zone would directly affect the physiological and biochemical characteristics of plant roots and indirectly affect the physiological and biochemical processes of aboveground parts (Vartapetian

& Jackson 1997). Under alternate wetting-drying stress in the riparian zone of the TGR, the accumulation of hydroxyl radicals, hydrogen peroxide, and oxygen radicals in roots resulted in membrane lipid peroxidation reaction, and DNA, macromolecular protein, and membrane structure were damaged. Plant roots could produce a large amount of malic acid and shikimic acid, which could prevent the accumulation of root biomass to adapt to the flooding environment (Ai 2013). Plants could adapt to the mild drought and saturated environment by maintaining their metabolism and growth at the same level as conventional growth. Besides, through the adaptive changes of metabolic pathways, plants could also reduce or eliminate the production of toxic substances and promote the production of metabolic substances that are resistant to adverse conditions (Zhong 1998). Malondialdehyde is one of the products of lipid peroxidation reaction, which can reflect the degree of oxidative damage. Malondialdehyde itself can also make the cell membrane function disorder, thus further damaging the biofilm function (Mccord & Fridovich 1969). To control reactive oxygen species (ROS) levels under adverse stress, plants activate some small molecular antioxidants and protective enzyme systems to remove or balance ROS production (Hegedus et al. 2001). Therefore, under the flooding conditions of the riparian zone of the TGR, elucidating changes in malondialdehyde, free proline, protective enzymes, and electrolyte characteristics in plants could provide insight into the physiological and biochemical adaptation mechanism of plants.

Photosynthetic Physio-Response

The effects of flooding stress on photosynthetic physiology and biochemistry of plants in the riparian zone can be reflected by the changes in photosynthetic gas exchange parameters such as chlorophyll, photosynthetic rate, transpiration rate, stomatal conductance, intercellular CO_2 concentration, light energy utilization rate, and internal water use efficiency. Luo et al. (2007, 2008) explored whether the physiological characteristics of several common terrestrial plants would be substantially affected by flooding from the aspects of plant photosynthesis, chlorophyll fluorescence, and underwater photosynthetic capacity. They found that the effect of flooding on the maximum photochemical efficiency of *Salix variegata* was less than that of *Arundinella anomala* with the underwater photosynthetic capacity of both species being significantly higher than that of typical terrestrial plants, and these two plants still had the underwater photosynthetic capacity even experiencing long-term flooding. In addition, Li et al. (2010b) simulated the water variation characteristics and designed four treatments (groups): normal growth water condition (NG), light drought stress (LD), soil water saturation (SW), and flooding stress (FS). The results revealed that the mean photosynthetic rate and stomatal conductance in the LD group were significantly lower than in NG, whereas the mean photosynthetic rate and stomatal conductance in SW and FS groups were significantly higher than in NG; photosynthetic pigment content in the FS group was always at the lowest level, which was affected obviously and showed lower light energy use efficiency, CO_2 use efficiency and net photosynthetic rate. On the contrary, the light energy use efficiency, CO_2 use efficiency, and net photosynthetic rate of the SW group were not significantly affected.

ADAPTATION STRATEGIES

Environmental variations considerably influenced seed germination, seedling construction as well as plant growth and development (Yamaguchi-Shinozaki & Shinozaki 2006). Plants can transfer extracellular signals to intracellular signals, and cope with environmental changes via a series of regulations from molecular to plant level. For example, plants can sense the light change through different types of photoreceptors, and then regulate different developmental stages, sense water stress, induce related gene expression, stimulate root growth downward, etc.; low-temperature stress induces the reorganization of the cytoskeleton to maintain the cell morphology and structure and meanwhile accumulates lots of compatible small molecule metabolites to enhance the water retention ability of cells (Zhang et al. 2009).

Plants adapt to flooding stress mainly through the following three strategies:

"Escape" by morphological anatomy structure as well as physiological and biochemical adjustment. Flooding creates a hypoxic environment, plants can better adapt to environmental changes through morphological structure, physiological and biochemical "escape", such as the formation of adventitious roots, aerenchyma, stem elongation, antioxidant enzyme activity, and energy metabolism regulation to enhance plant tolerance to flooding (Ahmed et al. 2013).

"Silence" by inhibiting adventitious roots, aerenchyma, and stem elongation to reduce the consumption of energy storage material. In contrast to the "escape" strategy with high energy investment, the energy metabolic rate of the "silence" strategy was significantly lower (Bailey-Serres & Voesenek 2010). Through the "silence" strategy, plants can not only reduce the energy storage consumption, such as inhibiting plant growth, elongation of internode or stem, adventitious root generation, etc., but also maintain the minimum oxygen consumption of plants, to tolerate long-term flooding stress (Bailey-Serres & Voesenek 2010).

Accumulating large amounts of non-structural carbohydrates enhances the tolerance to flooding stress and maintains the plants' survival (Palacio et al. 2014). Herbaceous plants can store photo contract products in their stems to resist long-term adverse environmental effects (Slewinski 2012). However, plants tended to transfer photo contact products from damaged and non-damaged tissues to roots and stems when facing periodic environmental stress. For this, some scholars have proposed that under periodic environmental stress, there may be a mixed tolerance strategy to deal with the relationship between photo contract product storage and plant survival and growth.

CONCLUSION AND FUTURE DIRECTIONS

In conclusion, since the impoundment of the TGR, many achievements have been made in the characteristics of plant communities in the riparian zone and their responses and adaptation to flooding stress, which have laid an important foundation for understanding the ecological function maintenance mechanism of plant communities in this particular riparian ecotone. However, there are still many unanswered questions to be further explored.

Over the past decade, many scholars have conducted a series of explorations on ecological restoration of the TGR from theory to practice, which not only enriched the species and seed banks suitable for artificial construction but also theoretically explored the flooding tolerance mechanism of suitable species. However, the effects of periodic flooding on the physiological and ecological characteristics of adaptable plants are still poorly understood, such as whether adaptive evolution of suitable plants occurs. After many years of natural restoration, there is also a lack of large-scale understanding of the ecological environment and the changes in seed banks in the reservoir area. Moreover, whether the water-level scheduling scheme has a positive effect on the seed dispersal in the riparian zone, and thus is conducive to the population dispersal of adaptable species.

The selection of suitable plants is the basis of vegetation restoration and construction in the riparian zone. However, the simulated flooding experiment is predominantly applied during the selection process, and more attention is paid to the measurement of flooding-tolerance ability, few were given to the drought-tolerance of plants in the summer. The simulation experiment is beneficial to the study of mechanisms, but it also has obvious shortcomings. First, the water environment, light conditions at different water depths, soil structure, and site climate cannot completely simulate the natural conditions in the riparian zone. Second, the experimental period is relatively short, and the research results may not apply to the field circumstance. Therefore, the simulation experiment only provides limited life information of suitable plants, and the selected flooding-tolerant plants can only be used for vegetation construction after being verified in the field under the alternate drying-wetting environment.

Plant functional traits define the ability of plants to grow, reproduce and survive in a specific environment, which may be related to the effects of plants on environmental changes and disturbances, as well as the responses of plants to biochemical cycles and disturbances. Future studies on the relationship between plant functional traits and ecosystem functions should focus on the relationship between above- and below-ground plant traits and their effects on ecosystem functions, ecosystem functional diversity, ecosystem functions at different temporal and spatial scales, and global changes.

Strengthen the research of plant niche in the riparian zone. Niche quantitatively reflects the interaction between species and habitats. The study of species' niches is beneficial to understand interspecific relationships, biodiversity, community structure and dynamic succession, population evolution, the relationship between organisms and the environment, etc. It is also an effective means for vegetation restoration and community construction in the riparian zone.

Strengthen the research on the connectivity between the riparian zone and the ambient environment, such as under the combined effects of biotic and abiotic factors of the aquatic-terrestrial ecosystem, water-level fluctuation characteristics, vegetation succession trend, community change characteristics, and ecological environment changes. The research on the interaction mechanism of each factor should also be strengthened.

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