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Effects of reverse seasonal submersion on the germination and persistence of soil seed banks in hydro-fluctuation belts

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Abstract

The construction of the Three Gorges Dam has resulted in the occurrence of reverse seasonal water-level fluctuations. The species composition and quantity of riparian soil seed banks collected from four hydro-fluctuation belts were assessed by simulating different submersion cycles to determine the effects of reverse seasonal water-level fluctuations on the germination and persistence of soil seed banks in the Three Gorges Reservoir Region. Results showed the number of species that germinated from the soil seed bank decreased with submersion. The number of germinated seeds in soil seed banks after submersion for 7 months in Xingshan, Zigui, Wanzhou, and Zhongxian decreased by 60%, 53%, 57%, and 57%, respectively, relative to the control. The species diversity index and seed density of germinated seeds in soil seed banks also significantly decreased with prolongation of submersion time. Seed density decreased by 93%, 83%, 76%, and 72%, respectively, after 7 months of submersion. Species composition and dominance within the soil seed bank changed over time due to submersion. In general, reverse seasonal submersion negatively impacts the germination and persistence of soil seed banks. The response of soil seed bank germination and persistence to reverse seasonal submersion became the key factor determining the heterogeneity in the spatial distribution of the soil seed bank in hydro-fluctuation belts due to the large differences in submersion time between areas at various elevations.

KEYWORDS

hydro-fluctuation belts, life form, seed density, species composition, Three Gorges Reservoir area

1 | INTRODUCTION

Soil seed banks are the main sources of material for the propagation of various plant communities. The germination and persistence of soil seed banks influence the regeneration and succession of plant communities (Collins, Conway, Mason, & Gunnels, 2013; Lu et al., 2010). The activity of soil seed banks, especially in response to various stress factors such as submersion and drought, often changes and affects seed germination and persistence (Goodman, Ganf, Maier, & Dandy, 2011). Waterlogging stress is an important factor affecting the germination and persistence of soil seed banks in riparian zones. Long-term submersion can cause the soil to form an anaerobic environment and affect the vitality of plant seeds in the soil seed bank (Robertson & James, 2007). There are considerable differences in the manner and ability of riparian plant seeds adapting to flooding. Some plant seeds with low flooding tolerance lose their activity under submersion stress (Chen & Xie, 2007); other plant seeds have adapted to submersion, which allows them to sustain high germination rates after long-term submersion (Kolb & Joly, 2010), and some plant seeds have dormancy characteristics, for which submersion is beneficial to the completion of the post-ripening of seeds and facilitates germination (Pierce & King, 2007). Therefore, submersion can not only lead to changes in the number of active seeds in soil seed banks but also affect the composition and diversity of plants within the soil seed banks and finally alter the germination and persistence of soil seed banks (Altenfelder, Schmitz, Poschlod, Kollmann, & Albrecht, 2016; Capon, 2007). Understanding the persistence of soil seed banks to submersion can provide scientific bases for evaluating the recovery potential of soil seed banks during ecological restoration of riparian zones (Wall & Stevens, 2015; Wang, Wang, Lu, Jiang, & Wang, 2016).

The Three Gorges Project is one of the world's largest water conservancy and hydropower projects. According to the operation plan of "reserving clean water and flushing dirty water," the water level of the Three Gorges Reservoir is running at about 145 m in the flood season from June to September of each year. At the end of flood season, the water level rises from 145 to 175 m until May of the following year, by which the water level gradually decreases from 175 to 145 m. A drop zone with a vertical difference of 30 m and an area of 350 km^2 is formed in the reservoir area. Water-level fluctuations occurred from the "summer exposed-winter submerged" before the impoundment to "summer submerged-winter exposed" (New & Xie, 2008). Significant reverse seasonal water-level fluctuation has resulted in the disappearance of shrubs and other plants that cannot adapt to the new water-level fluctuation pattern (Chen, Wang, & Jia, 2013). Furthermore, riparian plant communities have been drastically degraded, subsequently changing into grass slopes that are predominated by annual and perennial herbaceous plants (Lu, Li, Jiang, Huang, & Bao, 2010; Su et al., 2013). The riparian plant communities show significant spatial heterogeneity due to extensive variations in submersion cycles across altitudes (Ye, Zhang, Deng, & Zhang, 2013). Flood patterns also largely influence the species composition and spatial distribution of seed stocks in soil seed banks (Hölzel & Otte, 2004; James, Capon, White, Rayburg, & Thoms, 2007). Lu, Li, Huang, et al. (2010) investigated the effects of flood patterns on riparian soil seed banks and vegetation in the incipient Three Gorges Reservoir and found that reverse seasonal water-level fluctuations decrease species diversity and seed density of the riparian soil seed banks as most surviving woody plants and perennials were not observed in the seed bank. Significant spatial heterogeneity along the altitudinal gradient of the seed bank has also been observed (Yuan, Liu, Li, & Li, 2007; Zhang, Chen, Chen, Wang, & Wang, 2016). The degradation of soil seed banks and the increase in spatial distribution heterogeneity may be caused by heterogeneity and degradation of the standing plant communities and the seed rain induced by reverse seasonal water-level fluctuations (Wu et al., 2016). However, the stress of long-term submersion on the germination and persistence of soil seed banks may also contribute to this. Recent studies have shown that reverse seasonal submersion decreases the germination capacity of some riparian species (Shen, Zeng, Lei, Su, & Huang, 2011; Wang et al., 2008). However, the effect of submersion on the germination and persistence of riparian soil seed banks remains unclear. In this study, the natural seed banks of four different plots in the Three Gorges Reservoir area were collected, and control experiments of submersion were conducted by simulating the submersion cycles at different levels, with the purpose of (a) identifying the species of the germinated seeds from each soil seed bank after different submersion times to analyse the effects of submersion on species composition, biodiversity, and life form in the soil seed banks; (b) measuring the quantity of germinated seeds from each soil seed bank after different submersion times and analysing the effects of submersion on seed density of the soil seed banks; and (c) comparing the differences in species composition, diversity, and seed density of soil seed banks under different submersion times to reveal the effects of reverse seasonal submersion on the germination and persistence of soil seed banks in the riparian zones and elucidate the mechanism underlying its degradation and spatial distribution heterogeneity.

2 | MATERIALS AND METHODS

2.1 | Study sites

Experimental sites were set up in the riparian zone of four typical areas in the Three Gorges Reservoir area: Xingshan county and Zigui county of Hubei Province, and Wanzhou city and Zhongxian county of Chongqing Municipality (Figure 1). The riparian plant communities are predominated by *Cynodon dactylon*, *Digitaria sanguinalis*, and *Setaria viridis*.

2.2 | Seed bank sampling

Sample collection was conducted at the four sites. Sixteen quadrats of 1 × 1 m^2 were randomly established, and the surface plants were removed from each site. Soil samples were collected at a sampling depth of 15 cm with a 8-cm diameter soil sampler; three soil samples were collected from each quadrat. The collected soil samples were loaded into a self-sealing bag and labelled. A total of 48 soil samples were collected from each study site, and 192 soil seed bank samples were collected from the four sites. Debris was removed from the soil

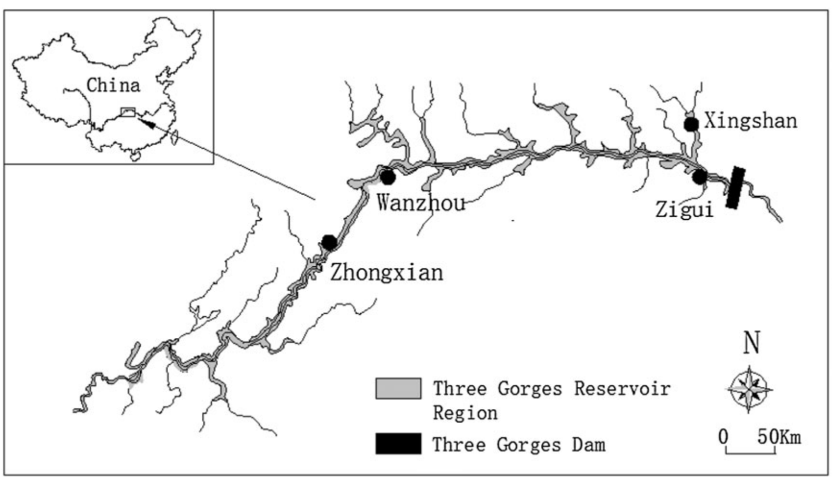

FIGURE 1 The location of field experimental plots

samples and then naturally dried. After crushing, stones and impurities were removed using a 4-mm sieve; the remaining soil was used in the subsequent experiments (Lu, Li, Huang, et al., 2010).

2.3 | Germination experiments

Submersion at different altitudes was simulated based on the water-level fluctuation patterns in the Three Gorges reservoir area, and the submersion levels were set for 0 (control), 5, 6, and 7 months, corresponding to periods of submersion at altitudes of 175, 170, 160, and 150 m, respectively. The submersion experiment was initiated in October and terminated in May of the following year. Each of the soil samples collected from the above four sites were wrapped in a high-density osmotic coat and placed in a water tank with a ventilation pump to simulate submersion. Each treatment level at each site was repeated 12 times.

The seedling emergence method was used to quantify seed bank species composition and density (Gnjter, Vermeij, Bekker, & Bakker, 1996). At the end of each submersion gradient, the soil samples of each treatment level were spread on a germination disc (20 cm × 15 cm × 5 cm) with a dry-sand thickness of about 3 cm, and soil thickness less than 2 cm. The dry sand used in the germination plate was baked in an oven at 120°C for 12 hr to ensure that all the seeds in the sand were inactivated. The germination dish was randomly placed in a climate-controlled box and cultured at 25°C with light intensity of 24,000 lux and relative humidity of 60%. Water was applied to the soil every day to keep the soil moist, and the emergence of seedlings was monitored and identified. Seedling species and quantity were recorded and then removed. The germination in each treatment ended only when no germination was observed for 2 weeks. Seedlings that could not be identified were transplanted to a single flower pot to allow it grow into a complete plant, which was then identified. The species and number of germinating seeds from each sampling quadrat were recorded.

2.4 | Data analysis

The species and life form spectra of the soil seed bank were analysed using each soil sample as the statistical analysis unit. The seed density of each plant species in the soil seed bank was calculated by converting the number of seeds in the sampling area into the number in 1 m^2. The importance value of each plant species of the soil seed bank was calculated as follows:

$$\textit{Species importance} = \textit{Relative density} + \textit{Relative frequency}.$$

The species diversity index of each soil seed bank was further calculated as follows:

Shannon-Wiener Diversity Index:

$$H = -\sum_{i=1}^{S} (P_i \ln P_i),$$

where N is the total number of individuals of all species; Ni is the number of individuals of species i; Pi is the ratio of the ith species to the total number of species; and S is the number of species.

Using submersion time as the independent variable, and the species diversity index and seed density of the soil seed bank with different treatment as dependent variables, one-way ANOVA was performed to analyse changes in species diversity and density in response to various submersion terms.

3 | RESULTS

3.1 | Effects of submersion on species composition and diversity

Species composition of the soil seed bank differed significantly between the control group (0 month submersion) and the 7-month submersion group (Table 1). Eight species, such as *D. sanguinalis*, *S. viridis*, *Paspalum paspaloides*, germinated both in the control and submersion groups. However, 20 species, including *Artemisia argyi*, *Imperata cylindrica*, and *Polygonum aviculare*, germinated in the control group but not after prolonged submersion. Five plant species did not germinate in the control group but emerged in the submersion group, which included *Trigonotis peduncularis*, *Cyperus microiria*, and *Mazus japonicus*. These findings indicate that submersion induced changes in the species composition of the soil seed banks.

Submersion decreased the number and species diversity of soil seed banks (Table 2). In the control group, 27 species in the soil seed banks of the four sites were observed, which belonged to 11 families and 25 genera. Among these, 15, 15, 14, and 14 species germinated in the soil seed bank of the four research plots, namely, Xingshan, Zigui, Wanzhou, and Zhongxian, respectively. After 5 months of submersion, 21 plant species in the soil seed banks of the four sites were observed, which belonged to nine families and 20 genera. Approximately 11, 9, 9, and 11 species were germinated in the soil seed bank of the four research plots. After 6 months of submersion, 16 plant species in the soil seed banks of the four sites were observed, which belonged to 10 families and 16 genera. Approximately 8, 8, 6, and 8 species germinated in the soil seed bank of the four research plots. After 7 months of submersion, only 13 plant species were observed, belonging to eight families and 13 genera. Only 6, 7, 6, and 6 plants were germinated in the soil seed banks of the four research plots, which decreased by 60.0%, 53.3%, 57.1%, and 57.1%, respectively, compared with the control.

The species diversity index of the soil seed bank decreased with less germinating species while submerged. The Shannon–Wiener species diversity indexes of the seed germplasm of the four seed bank plots in Qianxian Mountain, Zigui, Wanzhou, and Zhongxian counties were 1.76, 1.84, 1.70, and 2.06, respectively. After 7 months of submersion, species diversity index decreased by 96.6%, 87.0%, 72.9%, and 52.4%, respectively.

3.2 | Effects of submersion on life form spectra

The adaptability of different plant seeds to submersion is variable. Twelve annuals and nine perennial herbs germinated from the soil seed bank at the beginning of submersion but did not germinate after long submersion. Four annuals and one perennial herb showed higher germination rates at the beginning of submersion from the soil seed bank, which then gradually decreased. Five kinds of annual and one perennial herb rarely germinated at the beginning of submersion but then

TABLE 1 Effect of submersion on species germination in soil seed banks

	Seed density (seeds/m^2) Xingshan		Zigui		Wanzhou		Zhongxian	
Species	**0 month**	**7 months**	**0 month**	**7 months**	**0 month**	**7 months**	**0 month**	**7 months**
Artemisia argyi	33.17 ± 22.37		99.52 ± 30.01		33.17 ± 22.37			
Imperata cylindrica	33.17 ± 22.37							
Polygonum aviculare							66.35 ± 28.29	
Xanthium sibiricum	33.17 ± 22.37		132.70 ± 37.43		149.28 ± 25.99		99.52 ± 30.01	
Bidens frondosa	66.35 ± 28.29		414.68 ± 82.94		99.52 ± 38.74		215.63 ± 51.73	
Trigonotis peduncularis								132.70 ± 44.73
Setaria viridis	464.44 ± 70.73		563.96 ± 122.09		613.72 ± 57.24	16.59 ± 16.59	1044.98 ± 69.84	497.61 ± 67.10
Cynodon dactylon	580.55 ± 51.73				331.74 ± 44.73		381.50 ± 51.73	
Arthraxon hispidus			66.35 ± 28.29					
Cyperus microiria						66.35 ± 28.29		
Alternanthera philoxeroides					182.46 ± 51.73			
Pennisetum alopecuroides			16.59 ± 16.59					
Eclipta prostrata	82.94 ± 29.59			16.59 ± 16.59	82.94 ± 45.56		66.35 ± 28.29	33.17 ± 22.37
窗体顶端 *Humulus scandens*					49.76 ± 25.99		82.94 ± 29.59	
Digitaria sanguinalis	447.85 ± 43.31		2272.43 ± 489.68	663.48 ± 230.27	1592.36 ± 183.35	663.48 ± 120.86	348.33 ± 49.76	
Hemarthria altissima							447.85 ± 60.64	
Gonostegia hirta	33.17 ± 22.37		315.15 ± 38.41					
Artemisia carvifolia							199.04 ± 49.00	
Abutilon theophrasti	182.46 ± 57.24	16.59 ± 16.59						
Gnaphalium affine		16.59 ± 16.59	16.59 ± 16.59	33.17 ± 22.37		49.76 ± 25.99	248.81 ± 43.31	33.17 ± 22.37
Paspalum paspaloides	381.50 ± 51.73	33.17 ± 22.37	729.83 ± 125.73	116.11 ± 51.73	298.57 ± 45.84	49.76 ± 25.99	281.98 ± 38.41	199.04 ± 49.00
Polygonum hydropiper	16.59 ± 16.59		82.94 ± 38.41				132.70 ± 37.43	
Acalypha australis			16.59 ± 16.59					
Mazus japonicus		16.59 ± 16.59				49.76 ± 25.99		
Pouzolzia zeylanica		49.76 ± 25.99		16.59 ± 16.59				
Cyperus rotundus	16.59 ± 16.59							
Conyza Canadensis			331.74 ± 44.73		182.46 ± 57.24			116.11 ± 38.41
Amaranthus lividus	33.17 ± 22.37				33.17 ± 22.37		16.59 ± 16.59	
Phyllanthus urinaria	66.35 ± 28.29	33.17 ± 22.37	315.15 ± 45.56	16.59 ± 16.59				
Erigeron annuus				33.17 ± 22.37				
Galium aparine					66.35 ± 28.29			
Oxalis corniculata			16.59 ± 16.59		16.59 ± 16.59			

TABLE 2 Effects of submersion on the species diversity of germinated seeds in soil seed banks

Flooding duration (months)	Xinshan		Zigui		Wanzhou		Zhongxian	
	Number of species	Shannon–Wiener index	Number of species	Shannon–Wiener index	Number of species	Shannon–Wiener index	Number of species	Shannon–Wiener index
0	15	1.76 ± 0.05a	15	1.84 ± 0.06a	14	1.70 ± 0.07a	14	2.06 ± 0.03a
5	12	1.42 ± 0.10b	11	1.33 ± 0.08b	9	1.17 ± 0.07b	11	1.54 ± 0.05b
6	9	1.02 ± 0.12b	8	1.22 ± 0.08b	7	1.05 ± 0.05b	8	1.09 ± 0.10c
7	6	0.06 ± 0.06c	7	0.24 ± 0.12c	6	0.46 ± 0.13c	6	0.98 ± 0.11c
F value; Sig.		73.936; 0.000		59.232; 0.000		36.019; 0.000		35.171; 0.000

Note. Different letters in the columns indicate significant differences ($P < 0.05$).

gradually increased and emerged (Table 1). The decreased number of perennials in the soil seed bank during the whole submersion process was more extensive than that of the annual plants. The life form spectrum of the soil seed bank significantly varied after submersion cycles (Table 3). Approximately 17 annuals and 10 perennial herbs were observed, accounting for 62.3% and 37.0% of the soil seed bank, respectively, and the proportion of germinating annual seeds from the soil seed bank was significantly higher than that of perennials. The proportion of perennials in the soil seed bank in Xushan, Zigui, Wanzhou, and Zhongxian counties was 38.5%, 29.0%, 38.6%, and 31.7%, respectively. The proportion of annual plants was 61.5%, 71.0%, 61.5%, and 68.3%, respectively, before submersion. After 7 months of submersion, seeds of 11 annuals and two perennial herbs germinated in the four soil samples, accounting for 84.6% and 15.4% of soil seed bank, respectively. The proportion of annuals further increased, whereas that of perennial herbs decreased. Among these four sites, changes in life form spectra in Wanzhou and Zhongxian countries were significant ($P < 0.01$), whereas those in Xingshan and Zigui counties were not.

3.3 | Effects of submersion on seed density

The number of germinated seeds in the soil seed bank was significantly affected by submersion ($P < 0.05$). With the prolongation of submersion time, the density of germinated seeds in the soil seed bank decreased (Figure 2). The density of germinating seeds in the four soil samples from Xingshan, Zigui, Wanzhou, and Zhongxian was 2,471.47 seeds per m^2; 5,390.79 seeds per m^2; 3,732.09 seeds per m^2; and 3,632.56 seeds per m^2, respectively, before submersion. After 5 months of submersion, the germination seed density decreased to 1,575.80 seeds per m^2; 3,947.72 seeds per m^2; 2,421.71 seeds per m^2; and 2,637.34 seeds per m^2, respectively, representing a decrease of 36.2%, 26.8%, 35.1%, and 27.4%, respectively. After 6 months of submersion, the germination density of the soil seed bank was reduced to 646.90 seeds per m^2; 2,886.15 seeds per m^2; 1,476.25 seeds per m^2; and 1,841.16 seeds per m^2, respectively, indicating a decrease of 73.8%, 46.5%, 60.4%, and 49.3%, respectively. After 7 months of submersion, the seed germination density of the soil seed

TABLE 3 Effects of submersion on the life-form composition of germinated species from seed banks

Flooding duration (months)	Xingshan		Zigui		Wanzhou		Zhongxian	
	Annual (%)	Pernnial herb (%)	Annual (%)	Pernnial herb (%)	Annual (%)	Pernnial herb (%)	Annual (%)	Pernnial herb (%)
0	61.50 ± 2.90	38.50 ± 2.90	70.99 ± 1.54	29.01 ± 1.54	61.45 ± 2.40b	38.55 ± 2.40a	68.26 ± 1.51a	31.74 ± 1.51b
5	72.90 ± 2.45	27.10 ± 2.45	75.28 ± 3.51	24.72 ± 3.51	79.71 ± 3.41a	20.29 ± 3.41b	67.02 ± 2.67b	32.98 ± 2.67ab
6	71.25 ± 4.58	28.75 ± 4.58	61.94 ± 2.29	38.06 ± 2.29	66.94 ± 1.31b	33.06 ± 1.31a	60.00 ± 2.25BC	40.00 ± 2.25a
7	55.56 ± 17.57	44.44 ± 17.57	67.42 ± 11.70	32.58 ± 11.70	93.47 ± 3.51a	6.53 ± 3.51b	79.17 ± 4.87a	20.83 ± 4.87b
F value; Sig.	1.080; 0.368		0.927; 0.436		25.971; 0.000		6.584; 0.001	

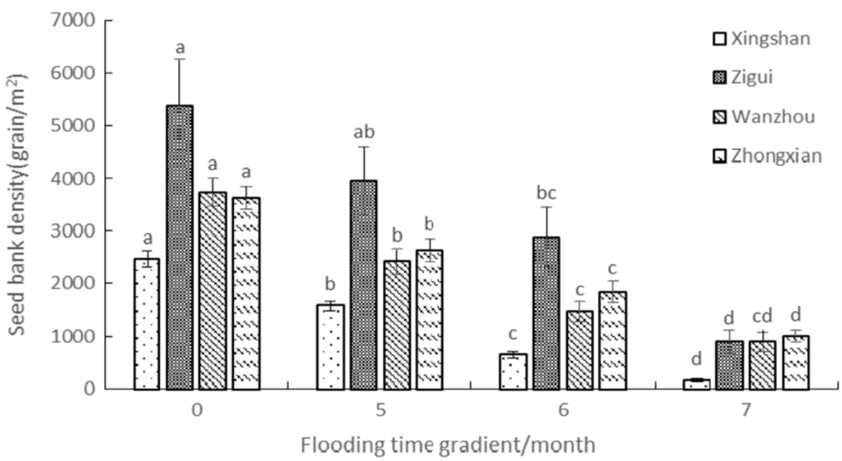

FIGURE 2 Variations in seed density of soil seed banks (mean ± SE) under different submersion duration. Different letters in the same column indicate significant differences

bank in the four plots was only 165.87 seeds per m^2; 895.70 seeds per m^2; 895.70 seeds per m^2; and 1,011.81 seeds per m^2, respectively, showing a decrease of 93.3%, 83.4%, 76.0%, and 72.2%.

3.4 | Effects of submersion on the predominant species

Submersion also caused significant changes in the germination of the predominant species of the soil seed bank and seed density ($P < 0.05$; Figure 3). The first four predominant species of the soil seed bank in the four plots are used as example. The predominant species of the Xinshan soil seed bank before submersion included *P. paspaloides*, *S. viridis*, *D. sanguinalis*, and *C. dactylon*, accounting for 75.8% of the germinated seeds. After 5 months of submersion, *Cynodon davidiana* no longer germinated. After 7 months of submersion, only one out of the four predominant species, namely, *P. paspaloides*, was germinating, whereas the predominant species of the seed bank had become *Pouzolzia zeylanica*. The predominant species of the Zigui soil seed bank before submersion included *D. sanguinalis*, *P. paspaloides*, *S. viridis*, and *C. dactylon*, accounting for 73.9% of the germinated seeds. After 5 months of submersion, *C. dactylon* longer germinated. After 7 months of submersion, only two of the four predominant species, namely, *D. sanguinalis* and *P. paspaloides*, were germinating, and the predominant species of the seed bank had become *D. sanguinalis*. The predominant species of the Wanzhou soil seed bank before submersion were the same as that of the Xinshan soil seed bank, accounting for 76% of the germinated seeds. After 5 months of submersion, *C. dactylon* could no longer germinate. After 7 months of submersion, only *D. sanguinalis* was still germinating, whereas the predominant species of the seed bank had become *D. sanguinalis*. The predominant species of the soil seed bank at Zhong county before submersion included *S. viridis*, *Niu bian cao*, *D. sanguinalis*, and *C. dactylon*, accounting for 61.19% of the germinated seeds. After 5 months of submersion, *C. dactylon* no longer germinated. After 7 months of submersion, only *S. viridis* still germinated, and predominant species of the seed bank had become *S. viridis*.

4 | DISCUSSION

4.1 | Effects of reversal seasonal submersion on the germination and persistence of the soil seed bank

For wetland soil seed banks, appropriate submersion favours seed germination and improvement of plant species diversity (Ge, Liu, & Wang, 2013; Goodman et al., 2011). However, long-term submersion can cause changes in soil oxygen content, water content, and temperature, which in turn affect seed germination in soil seed banks (Vidal, Andrade, Andrade, & Mielke, 2014; Wang, Jiang, Lu, & Wang, 2013). Plant seeds maintain their own physiological activities under submerged conditions through anaerobic respiration, often consuming a large amount of nutrients, which is relatively inefficient relative to aerobic respiration (Gomes & Garcia, 2013; Kestring, Klein, & Rossi, 2009). The vitality of plant seeds decrease and their germination capability is gradually lost after prolonged submersion (Dixon, 2003; Vidal, et al., 2014). Finally, the number of germinated plant species and their seeds in the seed bank is declining, thereby resulting in the degradation of the soil seed banks (Nicol, Ganf, & Pelton, 2003; Robertson & James, 2007). In this study, the total number of species from germinated seeds in the soil seed bank decreased with the prolongation of submersion time. After 7 months of submersion, the number of species decreased from 27 to 13, of which 19 species disappeared, which eventually led to a decrease in species diversity of the soil seed bank. The seed density of the soil seed bank in the four plots also significantly decreased with submersion time. After 7 months of submersion, the density of the soil seed bank in the four

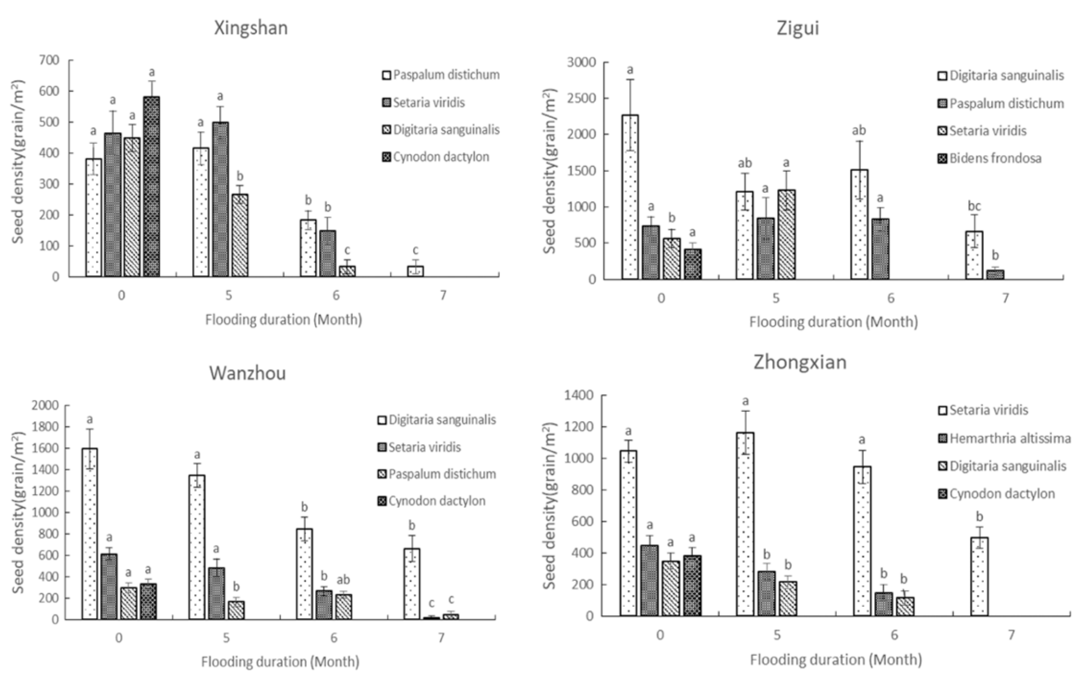

FIGURE 3 Changes in the predominant species that germinated from soil seed banks in response to submersion

plots decreased by 93.3%, 83.4%, 76.0%, and 72.2% relative to the control. Therefore, reversal season submersion reduces the germination performance and persistence of the soil seed bank.

The adaptability mechanism of different plant seeds to submersion is relatively variable (Cross et al., 2015; Lucas et al., 2012). Pierce and King (2007) argued that variations in seed germination performance of different species are largely dependent on the life history characteristics of the species. For some plant seeds with dormancy characteristics, autumn and winter submersion is beneficial for its post-ripening effect. Thus, submersion generally does not have a significant impact on seed vitality (Carta, Bedini, Müller, & Probert, 2013.). However, most riparian plant seeds usually have no dormant period after ripening and can germinate given the appropriate conditions. Submersion often has a significant effect on the vitality of seed bank (Forbis, 2010; Wall & Stevens, 2015). Plant species and their seed germination in the soil seed bank also change with submersion due to differences in the adaptability to submersion of seeds with different life history characteristics (Capon, 2007; Honda, 2008). Hölzel and Otte (2004) measured seedling regeneration in a wetland seed bank in response to submersion stress and found that the seed density of 21 germinated plant species significantly decreased under waterlogging stress, whereas that of two species increased. They believed that the reduction in seed density was related to germination conditions and seed dormancy characteristics. In wetlands that have increasing water levels in the summer, the germination rate of annual herbaceous plants and perennial herbaceous plants that needed high temperature to break the dormancy decreased with submersion, whereas that of winter annual and perennial plants that germinate during autumn and warm season was not affected (Hölzel & Otte, 2004; Honda, 2008). However, when the water-level fluctuation pattern alternates, species composition and the quantity of germinating seeds in the soil seed bank change accordingly (Howard & Wells, 2009; Nicol et al., 2003). Such a change may be due to occasional changes in water-level fluctuation pattern (Lucas et al., 2012; Osunkoya et al., 2014), but when the water-level fluctuation pattern had stabilized, alterations in germination rates of the soil seed bank were observed (Dixon, 2003; Nielsen, Podnar, Watts, & Wilson, 2012).

The pattern of the water-level fluctuation in the reservoir area of the Three Gorges Project is completely different from that before the construction of the project (New & Xie, 2008). The reverse seasonal water-level fluctuation of the reservoir area also affected the germination and life-form composition of the soil seed bank (Zhang et al., 2016). Lu, Li, Huang, et al. (2010) studied the soil seed bank and its germination during the early stages of the Three Gorges Reservoir, which showed that the germinated plants of the soil seed bank mainly comprised annual plants. Although there were still a small number of woody and perennial herbaceous plants in the soil seed bank, most of the woody plants and perennial herbaceous plants comprising the standing vegetation did not appear in the soil seed bank, and the composition of the soil seed bank significantly differed from the composition of the standing vegetation (Lu, Li, Huang, et al., 2010). The results of this study improve our understanding of this phenomenon; that is, reversal seasonal submersion inhibits the germination of majority of woody plant seeds and perennial herb seeds. In this study, five kinds of plants such as *Eupatorium odoratum* germinated during the entire submersion experiment, although the germination rate was reduced to some extent. A total of 22 species such as *C. dactylon* did not germinate after a long period of submersion. Six plant species did not germinate after a short period of submersion but started to germinate after long-term submersion. Seeds that germinated in autumn were inhibited and lost their activity (Chen et al., 2013; Chen & Xie, 2007). Those that were not affected by submersion are also dormant during autumn and winter (Chen, Chen, & Zhang, 2016). The life form composition of the germinated species in the soil seed bank changed with submersion, the proportion of annuals gradually increased, and the proportion of perennial herbs plants decreased.

4.2 | Effects of persistence of the soil seed bank on spatial distribution patterns

The composition and structure of the soil seed bank in the riparian zone showed significant spatial heterogeneity. The abundance and coverage of the plant community of soil seed bank in the low-altitude gradient were lower than that in the high-altitude gradient (Howard & Wells, 2009), and the soil seed bank subjected to moderate flooding exhibited the highest germination rate (James et al., 2007; Zhang et al., 2017). The spatial heterogeneity of the soil seed bank in the hydro-fluctuation belts of the Three Gorges Reservoir area was observed at the beginning of the reservoir. Although species diversity and seed density of the soil seed bank did not significantly differ among various altitudinal gradients, these increased with the elevation of riparian zones (Lu, Li, Jiang, et al., 2010). A recent study conducted by Zhang et al. (2016) showed that after 6 years of water-level fluctuations, the soil seed bank in that particular zone has adapted a spatial distribution pattern along the altitudinal gradient, and species diversity and seed density of the upper and middle soil seed banks are significantly higher than the lower part of the fluctuation belt.

The spatial distribution pattern of the soil seed bank was first related to the spatial distribution pattern of plant communities (Farrel et al., 2010; Shang et al., 2016). Under the influence of water-level fluctuations, due to increased submersion time in the riparian soil with lower altitudes, many riparian plants are unable to withstand long-term submersion, thereby making it difficult to establish and survive in the lower parts of the fluctuation belt. Thus, species diversity and vegetation coverage of the upper and middle plant communities are often higher than those of lower parts (Lu, Li, Huang, et al., 2010; Su et al., 2013). Because plant communities are direct sources of soil seeds and soil seed banks, their spatial variation may inevitably lead to spatial heterogeneity in seed rain (Warwick & Brock, 2003; Wu et al., 2016), and consequently in the initial soil seed bank (Calçada et al., 2015; Weiterová, 2008).

Changes in germination and persistence of soil seed banks caused by submersion have a more direct effect on the spatial distribution heterogeneity of soil seed banks in hydro-fluctuation belts (Nicol et al., 2003). The composition and quantity distribution of soil seed banks are related to the water-level fluctuation (James et al., 2007). The germination and persistence of soil seed banks decrease with prolongation of submersion, and the composition of the germinated plant species in the soil seed bank depends on the duration of the flood. As the duration of submersion increases, the abundance of species decreases, and the species' uniformity increases, and the species composition extensively varies (Altenfelder et al., 2016). We previously assessed the species composition, diversity, and seed density of the soil seed bank at different altitudes in the Three Gorges Reservoir area. Differences in water-level fluctuations, flood duration, and submersion frequency in different altitude gradient soils and water-level fluctuations indirectly affect the spatial distribution of soil seed banks (Zhang et al., 2016). The results of this study directly confirm the effect of submersion due to reverse seasonal water-level fluctuations on the spatial distribution pattern of the soil seed bank. The persistence characteristics of the soil seed bank decreased with submersion time, and the submersion time in the middle and lower part of the falling zone was longer than that in the middle and upper part. Therefore, the number of species and seed density of the soil seed bank in the lower part of the fluctuation belt is lower than those of the upper part of the fluctuation belt.

The pattern of water-level fluctuations is a crucial factor in various ecological processes involving riparian plant community regeneration (Dixon, 2003). Reverse seasonal water-level fluctuations have caused a series of changes in soil seed banks such as alterations in species number, a decrease in biodiversity, species composition simplification, a decrease in seed density, and spatial distribution heterogeneity in the Three Gorges Reservoir. These changes were observed during the primary reservoir impoundment and further progressed after six cycles of water-level fluctuation (Lu, Li, Huang, et al., 2010; Lu, Li, Jiang, et al., 2010). The degradation of soil seed banks induced the degradation of standing vegetation, which further affected soil seed banks (Zhang et al., 2017; Zhang, Chen, Wu, et al., 2017). It is thus possible that the plant community and soil seed bank will continue to change and reach an equilibrium that meets the changing hydrological conditions of the dam.

5 | CONCLUSIONS

Reverse seasonal submersion formed by the reservoir area after the construction of the Three Gorges Project significantly affects the germination and persistence of soil seed banks. Long-term and reverse seasonal submersion changes the soil environment of the fluctuation belt. The activity of plant seeds in the soil seed banks was affected, and the germination performance gradually deteriorated, thereby resulting in a decrease in plant species and abundance in the soil seed banks. The species diversity and seed density of the germinated seeds in the soil seed bank significantly decreased with submersion time. Due to variations in adaptability of different species to a submerged environment, the life-form spectra and predominant species of germinating seeds in soil seed banks also change. The proportion of annual plants increased significantly, whereas the proportion of perennials was significantly reduced. The submersion period caused by the reverse seasonal water-level fluctuations in the reservoir area gradually decreased with increasing altitude, which alters the submersion cycles experienced by different-altitude soil seed banks. Therefore, the germination and persistence of the soil seed bank vary with the altitude gradient of the fluctuation belt. This is also responsible for the observed degradation and spatial differences in the species and quantities of soil seed banks.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare. This study does not involve human participants or animals.

AUTHOR CONTRIBUTIONS

F. C. and Y. M. conceived the research idea and designed the experiments; Y. M., S. G., and C. C. performed the field investigations and germination experiments; and Y. M. and S. C. analysed the results and wrote the manuscript.

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