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Effects of flooding on seed viability and nutrient composition in three riparian shrubs and implications for restoration

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ABSTRACT

Constructions of large reservoirs (all over the world) have resulted in the degradation of riparian vegetation. The coverage and species biodiversity of riparian communities in the Three Gorges Reservoir area have dramatically decreased since the completion of the Three Gorges Project. The responses of three shrub seeds to flooding time were examined to investigate the potential use of soil seed banks for the ecological restoration of the drawdown zone in the Three Gorges Reservoir Area. The effects of flooding time on seed viability and seed nutrient composition for the riparian shrubs *Buxus ichangensis*, *Cornus paucinervis* and *Distylium chinense* were tested by simulating 0, 5, 6, 7, 8 and 9 month flooding periods under a controlled experiment. Results showed that seed viability decreased with the length of flooding treatment. Seeds of all three shrubs displayed relatively high viability and remained viable after six months of flooding. However, seed viability significantly decreased after seven months of flooding. After nine months of flooding, the seed viability of *B. ichangensis*, *C. paucinervis* and *D. chinense* decreased by 86.14%, 24.03% and 43.43%, respectively, compared with a non-flooded control. The protein, starch and soluble sugar content of seeds from the three shrubs decreased with flooding time. The seed bank samples of *D. chinense* and *B. ichangensis* showed the highest tolerance against short-term flooding, while the seeds of *C. paucinervis* exhibited the strongest tolerance against long-term flooding.

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Seed bank; tolerance; ecological restoration; drawdown zone; Three Gorges Reservoir area

Introduction

The construction of large dams significantly impacts river processes and their associated ecosystems and environments (Nilsson et al. 2005; New and Xie 2008). It has been

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estimated that more than 45,000 large dams have been constructed worldwide to mitigate floods, increase navigation capabilities, support irrigation, provide reliable water supplies and generate hydroelectricity (New and Xie 2008; Sun et al. 2012). The hydrological regimes of large rivers have undergone marked alterations in duration, timing, magnitude, and frequency of high and low water level fluctuations. These changes have caused the riparian vegetation and the ecosystem functions, including biodiversity conservation, pollutant decomposition, soil and water conservation and riverbank protection, to degrade seriously (Nilsson and Svedmark 2002; Merritt and Cooper 2015). The construction of the Three Gorges Project dramatically changes the flooding regime by raising the water level and altering flooding pattern of the riverbank from summer flooding-winter drought to summer drought-winter flooding. This fluctuation pattern leads to the dying out of many plant species that are not adapted to the long-term reverse seasonal flooding in winter (Chen and Xie 2007; Chen et al. 2013). This results in the severe degradation of riparian plant communities (Chen et al. 2016; Lu et al. 2010a).

The restoration of degraded riparian vegetation and functions have become a popular policy prescription over the previous two decades (New and Xie 2008). A series of researches on plant adaptation to the regulated flow regime, and experimental plantation projects on riparian vegetation restoration were applied after the completion of the Three Gorges Dam to improve the ecological environment of the Three Gorges Reservoir area. Field investigation indicated that these projects promoted the restoration of the riparian plant community (Su et al. 2013; Chen et al. 2016). However, few studies have investigated the adaptation and the adaptive ecophysiological mechanism of seeds to flooding and the potential use of soil seed banks in the ecological restoration of drawdown zones in the Three Gorges Reservoir area (Chen et al. 2013; Yang et al. 2014). The application of samples from the soil seed bank for vegetation restoration and reconstruction has been reported to be an effective method for ecological restoration of a degraded riparian ecosystem (Hong et al. 2012; O'Donnell et al. 2016). However, the development of the soil seed bank and seedling regeneration within the drawdown zone are limited by the altered flow regime (Hölzel and Otte 2010; Lu et al. 2010b). Changes to inundation regimes influence the viability and germination of seeds within the soil seed bank (Johnson 2004; Peterson and Baldwin 2004). The endurance of soil seed banks to altered flow regimes is critical for their successful application in riverbank restoration (Walls et al. 2005; Riis et al. 2014). The adaptive ability and mechanism of different plant seeds to submersion is relatively variable (Pierce and King 2007). It is thought that the viability of plant seeds with dormancy characteristics will not be significantly affected by flooding (Baskin et al. 2002; Kestring et al. 2009). The nutrient contents in seeds are related with the endurance and viability of seeds. Changes in seed nutrient content induced by flooding duration are usually accompanied by changes in seed viability (Perl 1988; Kolb and Joly 2010). The mechanism by which nutrients affect seed viability varies among different plant species (Perl 1988; Wang et al. 2009).

Buxus ichangensis, *Cornus paucinervis* and *Distylium chinense* are evergreen shrubs historically occurred on the riverbanks of the Three Gorges Reservoir area. The fruits of these three shrub are ripe in autumn. Usually, seeds experience short-term dormancy and will germinate once suitable conditions occur. Since the reverse seasonal water-level flooding in Three Gorges Reservoir area precludes seed germination, seed banks of these shrubs are formed after sufficient soil formation. All three species exhibit a well-developed root system and high resistance to water erosion, flooding and sand burial (Xue et al. 2007; Li et al. 2011). These shrubs are therefore considered prime candidates for the ecological recovery of the hydro-fluctuation belt, and have been planted within the drawdown zones in a series of experimental plantation projects in the Three Gorges reservoir area (Yang et al. 2014; Zhang et al. 2017). Investigation of the extent community indicated the plantation of these species promoted the reestablishment of riparian plant community (Su et al. 2013; Chen et al. 2016). However, seed responses to the altered flow regime have not been investigated. We hypothesize that seed banks of these shrubs retain their viability to a certain extent and can contribute to the restoration of drawdown zone in the Three Gorges Project and other large hydrological projects of southwest China. We performed a flooding experiment, the objectives of which were to: (1) assess changes in seed viability after 5–9 months of flooding to explore the endurance of seeds to flooding and the potential application of seed banks of the three shrubs in the ecological recovery of the drawdown zone; (2) examine the changes of starch, proteins and sugar contents of the resources in the three seed banks to investigate the ecophysiological response of the shrub seeds to long-term flooding.

Materials and methods

Study area

The Three Gorges Reservoir area is dominated by subtropical monsoon climate. Annual mean temperature is 17.7 °C, mean annual rainfall is about 1067 mm, and relative humidity ranges from 79% to 92%. The construction of the Three Gorges Project has greatly increased the water level in the reservoir area and transformed a large number of terrestrial ecosystems into riparian ecosystems, forming a drawdown zone of over 450 km^2. In the reservoir area, the flow regime varies considerably in response to the demands of flood control and power generation. The water level remains at approximately 145 m during June–September (flood season) and increases to 175 m at the end of October. The water level is then maintained at high levels until the following April (dry season), and the water level will then gradually decrease in May to 145 m. The reservoir water level amplitude is typically ∼30 m, and the riverbank is exposed in summer and submerged in winter. The riverbank flooding pattern is the reverse of the natural flood regimes of the Yangtze River (Chen and Xie 2007; Sun et al. 2012). After several cycles of water-level fluctuation, few trees and shrubs establish and survive on the drawdown zone. The riparian communities are dominated by annual herbs and perennial herbs including *Setaria viridis, Cynodon dactylon, Rumex dentatus* and *Psapalum distichum* (Chen et al. 2016; Zhang et al. 2017).

Study species and materials

B. ichangensis, *C. paucinervis* and *D. chinense* are shrubs of the Buxaceae, Cornaceae and Hamamelidaceae families, respectively. *B. ichangensis* only grows in Hubei province, *D. chinense* is found in Hubei and Sichuan province, and *C. paucinervis* is distributed in the southwest and eastern regions of China (Fu 2002). *B. ichangensis* grows to 15–100 cm in height and is usually distributed on sides of both beaches and cliffs at elevations below 1200 m. *C. paucinervis* plants are 50–200 cm in height, and they grow within rivers or on the riverbank at elevations below 2500 m. *D. chinense* is 50–100 cm in height and is mainly distributed within the riverbank at elevations below 200 m (Fu 2002). Mature fruits of each species were collected during October from the riverbank in Zigui County of the Three Gorges Reservoir area. All seeds were manually stripped off the fruits. Full and healthy seeds were selected for the following flooding experiment. The selected seeds were allowed to dry at room temperature for a week prior to the submersion experiment. The thousand-grain-weight and water content of seeds were tested by randomly selecting a subsample of seeds for each species. The thousand-grain-weight of *B. ichangensis, C. paucinervis* and *D. chinense* seeds was 2.02 g, 21.02 g and 2.30 g, respectively.

Flooding experiment setting

The flooding duration varies along altitude gradient: 145–150 m, 150–155 m, 155–160 m, 160–165 m, 165–170 m and 170–175 m of the draw-down zones are subject to approximately 270, 240, 210, 180 and 150 days of flooding, respectively (Lu et al., 2010a). The water-level fluctuation cycle in the Three Gorges Reservoir area was simulated to represent flooded treatments lasting for 9, 8, 7, 6 and 5 months with a control group (flooded for 0 month). First, 100 g of seeds of each species were weighed and mixed with 500 g of sterilized sand. The mixture was wrapped with high density permeable cloth, and this setup was considered one experimental unit. Thirty units of each species were placed in a water tank (100 cm (length) × 80 cm (width) × 70 cm (height)). Each tank was equipped with an air pump to aerate the water during the experiment, and the water depth remained at 65 cm to perform the flooding experiment. Six replicates were conducted for each treatment. Upon completion of each treatment, seeds were rinsed with double distilled water, dried with water absorbent paper, and subsequently tested for seed viability and nutritional components. The flooding experiment was carried out from October to June next year to simulate the inundation of a winter flooding cycle in the reservoir area.

Measurement of seed viability

To measure seed variability, 50 seeds were randomly selected from each flooding treatment as a replicate sample. Each seed was sliced open with a scalpel and subjected to a viability test experiment using 0.5% TTC (2,3,5-triphenyl tetrazol chloride) solution. Viability was determined based on the chromogenic reaction result according to the method described by Fang et al. (1998), and a viability percentage was calculated for the seeds of each shrub species and treatment. Six replicates were conducted for each treatment. A total of 300 seeds per treatment and 1800 seeds per species were analyzed in the experiments.

Determination of nutritional components in seeds

The protein, starch and soluble sugar contents of the seeds from each of the three shrub species were determined with six replicates for each experimental treatment. A total of 5 g seeds was sampled from each treatment for the determination of nutritional components. The content of protein was measured according to the method described by Vinayachandra and Chandrashekar (2008), and the content of starch and soluble sugar was determined using polarimetric analysis and the anthrone colorimetric method described by Sadasivam and Manickam (2008).

Data analysis

Multiple analysis of variance (MANOVA) with 'seed viability' as the dependent variable as well as 'species' and 'flooding duration' as fixed factors was used to investigate the effects of species, flooding duration and their interaction on viability. Then, the effects of

Table 1. The effect of species and flooding duration on seed viability.

Treatments	Type III of squares	df	Mean square	F	Mean ± SD	p
Species	6133.24	2	3066.62	2366.54	65.05 ± 0.16	<0.001
Flooding duration	22,273.64	5	4454.73	3437.76	65.05 ± 0.16	<0.001
Species × Flooding duration	8174.89	10	817.49	630.87		<0.001
Error	46.65	36	1.30			
Total	265,141.26	54				

variables were analyzed using one-way analysis of variance after In-transformation of data. Means were compared with least significant difference tests to explore the adaptive ability of plant seeds to flooding. Correlation analysis was applied to test the relationship among flooding duration, seed viability and seed nutrient content. All analyses were performed using the SPSS v.19.0 software.

Results

Effects of species and flooding duration on seed viability

MANOVA tests showed that species, flooding duration and their interaction had significant effects on seed viability (Table 1). Seed viability decreased continuously with the increase of flooding duration in the continuous flooding treatment. The response of seed viability varied among species (Figure 1). After 5 months of flooding, no significant difference in viability was detected for seeds of *B. ichangensis* and *D. chinense* compared with baseline ($n = 29$, $p < 0.05$). However, there was a significant decline of seed viability of *C. paucinervis* (df = 29, $p < 0.01$). After 6 months of flooding, a seed viability decrease was observed for *B. ichangensis* and *C. paucinervis*. However, seed viability of *D. chinense* was still comparable with baseline after 6 months. After 7 months of flooding, a significant decline in seed viability was detected for all three species. Compared with the control, the seed viability of *B. ichangensis*, *C. paucinervis* and *D. chinense* decreased by 82.40%, 19.13% and 36.13%, respectively. Seed viability continued to decrease with further flooding, but the rate of decrease was relatively lower. After 9 months of flooding, seed viability of *B. ichangensis*, *C. paucinervis* and *D. chinense* decreased by 86.14%, 24.03% and 43.43% compared with the control group. The maximum decrease was observed in *B. ichangensis*, *D. chinense* exhibited an intermediate decline of seed viability. *C. paucinervis* outperformed the other two species and remained at a relatively high viability.

Change in seed nutrient contents with flood duration

B. ichangensis and *C. paucinervis* contained the highest and lowest protein, starch and soluble sugar contents, respectively. Flooding duration had a significant effect on each of the protein, starch and soluble sugar content (df = 29, $p < 0.01$; $p < 0.05$; $p < 0.01$), and the total content of the three nutrients within seeds of each species (df = 5, $p < 0.01$), respectively. The seed nutrient contents of each species showed a significant decreasing trend with increased flooding duration. A significant decrease of nutrient contents was observed among the three species when seeds were inundated 7 months (Figure 2). After 9 months of flooding, the protein content of *B. ichangensis*, *C. paucinervis* and *D. chinense* seeds decreased by 94.60%, 76.41% 94.31%, respectively, compared with the control group. *B. ichangensis* and *D. chinense* exhibited a more significant decrease than *C. paucinervis*. The starch content of the shrub seeds also decreased by 78.47%, 52.63% and 72.78% for *B. ichangensis*, *C. paucinervis* and *D. chinense*, respectively. The maximum and minimum

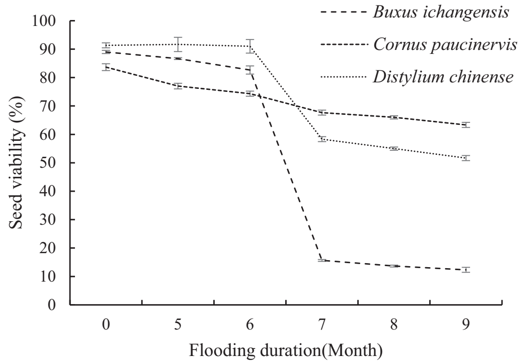

Figure 1. Seed viability of the three shrub species under different flooding duration. Values are means of all seeds ($n = 300$) exposed to each flooding duration (Mean ± SE).

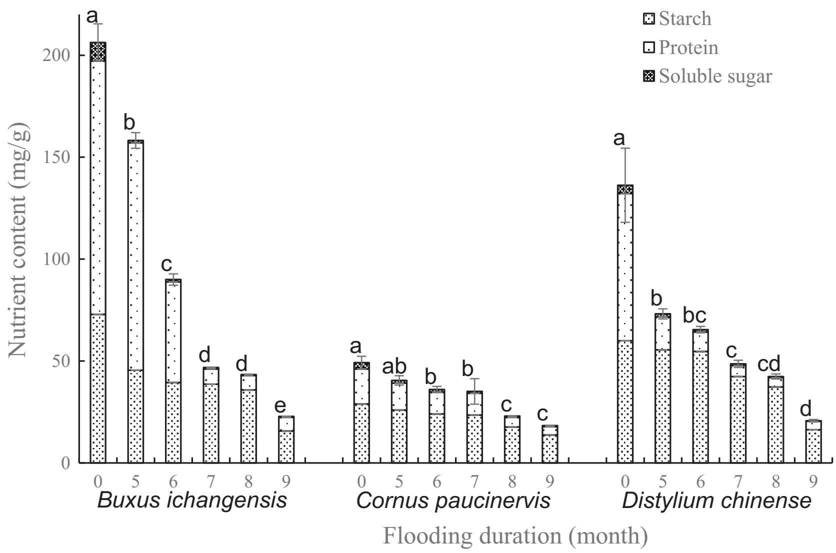

Figure 2. Response of nutrient contents in seeds of the three shrub species to flooding duration. The letters above the bars indicate the significant level ($p < 0.05$).

decreases in starch content were observed in *B. ichangensis* and *C. paucinervis,* respectively. The soluble sugar content of *B. ichangensis*, *C. paucinervis* and *D. chinense* seeds decreased by 97.84%, 82.87% and 93.62%, respectively. The maximum and minimum decrease was observed in *B. ichangensis* and *C. paucinervis,* respectively.

Correlations between seed viability and nutrient content changes

Protein and soluble sugar content of all three shrub seeds as well as the starch content of *B. ichangensis* and *C. paucinervis* seeds were negatively correlated with the flooding duration (df = 29, $p < 0.05$) (Table 2). In all cases, their content decreased with the increase in flooding duration. Although flood duration had a remarkable effect on the seed viability of the three shrub plants (Figure 1), the linear correlations between flood duration and seed viability were not significant.

Table 2. Correlation coefficients between the seed viability, seed nutrient content, and flooding duration.

Species	Factors	Flooding duration	Protein	Starch	Soluble sugar	Seed viability
Buxus ichangensis	Flooding duration	1	−0.880*	−0.963**	−0.932**	−0.777
	Protein		1	0.806	0.715	0.908*
	Starch			1	0.872*	0.703
	Soluble sugar				1	0.558
	Seed viability					1
Cornus paucinervis	Flooding duration	1	−0.922**	−0.862*	−0.992**	−0.956**
	Protein		1	0.833*	0.895*	0.984**
	Starch			1	0.810	0.912*
	Soluble sugar				1	0.924**
	Seed viability					1
Distylium chinense	Flooding duration	1	−0.952**	−0.794	−0.988**	−0.762
	Protein		1	0.579	0.986**	0.575
	Starch			1	0.703	0.886*
	Soluble sugar				1	0.675
	Seed viability					1

Note: *Significant difference at the 0.05 level, **Significant difference at the 0.01 level.

There was a positive correlation between seed viability trends and nutrients changes. Seed viability of *B. ichangensis* was positively correlated with its protein content (Correlation coefficient = 0.908, $p < 0.05$). However, correlations of seed viability with starch and soluble sugar content were not observed. The change in protein content was the major contributor to the decrease in seed bank viability of *B. ichangensis*. For *D. chinense*, a positive correlation was observed between seed viability and starch content change (Correlation coefficient = 0.886, $p < 0.05$). The correlations of seed viability with protein and soluble sugar content were not significant. Seed viability of *C. paucinervis* was positively correlated with protein, starch and soluble sugar content (Correlation coefficient = 0.984, 0.912, 0.924, $p < 0.05$), respectively.

Discussion

Flooding is an important factor affecting the germination and persistence of soil seed banks in the riparian zone (Capon 2007; Kettenring 2016). Short-term flooding stimulates seed germination of most species in soil seed banks, while prolonged flooding can cause the soil to form an anaerobic environment, as well as affect the vitality of plant seeds in the soil seed bank (Dixon 2003; Hölzel and Otte 2004).There are considerable differences in the manner and ability of riparian plant seeds adapting to flooding (Wang et al. 2009; Wagner and Oplinger 2017). Previous researches suggested that seeds with dormancy characteristics benefited from after-ripening caused by flooding during autumn and winter, during which the viability did not be significantly affected (Baskin et al. 2013; Kestring et al. 2009). Moderate flooding would not influence seed viability as it speeds up the seed dormancy (Baskin et al. 2002). However, seed viability declined dramatically when seeds were exposed to long-term flooding (Shen et al. 2011; Riis et al. 2014). In the present study, seeds of all the three shrubs could endure 5–6 months of flooding with higher seed viability as all of the three shrubs are hard-seeded species. The hard seed coat prevents immediate germination, and the seeds remain in a dormant state which increases the ability of seeds to adapt to flooding (Li et al. 2016). However, the response of seed viability to long-term flooding significantly varied among the three shrubs. The seed viability of the three shrubs significantly decreased with increasing flood duration. This pattern was particularly pronounced after 7 months of flooding when the viability of the seeds decreased most significantly. The seed viability of *C. paucinervis* and *D. chinense* still remained relatively high after being exposed 8–9 months of flooding, while of the seed viability of *B. ichangensis* declined dramatically in the 8 and 9 month treatments. The variation in tolerance to long-term flooding may result from species adaption to different habitat conditions. *D. chinense* and *B. ichangensis* are distributed on river bottomland, and *C. paucinervis* grows on riverbanks. The habitats of *D. chinense* and *B. ichangensis* are subjected to longer flooding duration than that of *C. paucinervis* (Xue et al. 2007; Liu et al. 2014).

Short-term flooding can cause a decrease in starch content and an increase of soluble sugar content (Fenner and Thompson 2005). This is because during flooding, the starch stored in seeds can be decomposed into a direct supply of soluble sugar to provide. However, the hypoxia associated with long-term flooding results in the respiratory metabolism pathway changing from aerobic respiration with low energy consumption to anaerobic respiration with high energy consumption, and the long-term consumption reduces the protein, starch and soluble sugar contents of the seeds (Gibbs and Greenway 2003; Fenner and Thompson 2005). These changes in the nutrient contents of seeds will further affect the seed viability (Perata and Alpi 1993). The simulated flooding period in this study is the same as the cycle of water-level fluctuation in the Three Gorges Reservoir area, with the shortest pre-specified flooding cycle of 5 months. This is much longer than the flooding period applied in other studies that have recently been reported (Shen et al. 2011; Tao et al. 2011). Our results show that the protein, starch and soluble sugar content of the seeds from the three shrub species decreased continuously with flooding duration. The trend in plant seed nutrients was consistent with the trend in seed viability, and different degrees of negative correlation were observed between the nutrient contents and the flooding duration.

The nutrient contents in seeds have a direct effect on the seed viability, but the mechanism by which nutrients affect seed viability varies among different plant species (Perl 1988; Wang et al. 2009). Fang et al. (1998) reported that seed viability index was most significantly affected by protein, followed by starch and crude fat, and that the viability index was least affected by soluble sugar. In the present study, correlations of protein, starch and soluble sugar contents with seed viability were observed in seeds of all shrub species. However, these correlations exhibited different significance levels. It suggested the physiological response of seed viability to long-term flooding differed among the three shrubs. The viability of *B. ichangensis* and *D. chinense* seeds was sensitive to the change in protein content and starch content, respectively. In contrast, the viability of *C. paucinervis* seeds was sensitive to all the changes in protein, starch and soluble sugar content.

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 and Xie 2008). The reverse seasonal water level fluctuation of the reservoir area significantly affected the germination and life-form composition of the soil seed bank (Zhang et al. 2016). The application of soil seed banks in riverbank restoration depends on the endurance of seeds in seed bank to altered flow regimes (Walls et al. 2005; Riis et al. 2014). The results of the current experiment showed that the soil seed bank of *B. ichangensis*, *D. chinense* and *C. paucinervis* would still be able to germinate during the next spring after one flooding cycle in the drawdown zone. However, seed viability and germination ability differ after flooding because different plant species have different flood-resistance abilities (Walls et al. 2005; Vidal et al. 2014). The seeds of *B. ichangensis* and *D. chinense* were best adapted to short-term flooding, and the seeds of *C. paucinervis* are even adapted to long-term flooding. The upper and lower areas of the drawdown zone were subject to 5 and 9 months of flooding annually, respectively, as a result of the difference in elevation. Therefore, there is also a significant difference in germination ability for the same species at different elevations of the drawdown zone. Previous researches indicated that seeds of the three shrubs germinated when flooding retreated, and that seedlings of the three shrubs could establish and survive on the drawdown zone (Xue et al. 2007; Li et al. 2016). Plants of the three shrubs have been successfully used in a serious of experimental restoration projects (Zhang et al. 2016). In general, examination of the seed response of three shrub species to flooding indicated that the seed bank of *C. paucinervis* can survive and be applied to ecological recovery within the entire hydro-fluctuation belt. However, the seed banks of *B. ichangensis* and *D. chinense* can survive and be used for the ecological restoration of medium and upper parts of the hydro-fluctuation belt. These research results can also be applied to other large water conservation and hydropower projects in southwest China which have the same flooding pattern as the Three Gorges Project.

Conclusion

Reverse seasonal flooding had a significant impact on the seed viability of three shrubs (*B. ichangensis*, *C. paucinervis*, *D. chinense*) by decreasing seed viability with flooding duration. The adaptability of seeds to flooding was significantly different among the three kinds of plants; the seeds of *B. ichangensis* and *D. chinense* were tolerant of short-term of flooding, whereas the seeds of *C. paucinervis* tolerated longer floods. Flooding also caused corresponding changes of nutrient contents in seeds. The contents of protein, starch and soluble sugar all decreased with increasing duration of flooding. The changes of nutrient contents in the seeds have a direct effect on the seed viability. The seed viability of *B. ichangensis* and *C. paucinervis* was mostly affected by the change of protein whereas the change of starch was the most important nutrient for viability in *D. chinense* seed. Examination of the seed adaptability of three shrub species to flooding indicated that the seed bank of *C. paucinervis* can survive and be applied to ecological recovery of the entire drawdown zone, while the seed banks of *B. ichangensis* and *D. chinense* can survive and be used for the ecological restoration of medium and upper parts of the drawdown zone in the Three Gorges Reservoir area.

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Disclosure statement

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