Flora 285 (2021) 151960

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Seasonal flooding regime effects on the survival, growth, and reproduction of *Bolboschoenus planiculmis* under East Asian monsoon

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ARTICLE INFO

Edited by Hermann Heilmeier

Keywords:
Estuarine ecosystems
Flooding duration
Flooding depth
Marsh plant
Shoot growth

ABSTRACT

Seasonal flooding regimes are key hydrodynamic features in estuarine ecosystems, and are mainly influenced by climatic conditions. Today, the original seasonal flooding regimes can be altered due to artificial infrastructure or following sea-level rise. Although the altered flooding regimes determine flooding duration and depth, which further influence growth and development of marsh plants, little is known about the effects of seasonal flooding regimes on marsh plants under the East Asian monsoon climate zone. Therefore, we investigated the effects of different seasonal flooding regimes on survival, growth, and reproduction of the marsh plant *Bolboschoenus planiculmis.* A greenhouse experiment was conducted to compare the responses of *B. planiculmis* under combinations of four flooding durations (0-month, 2-month, 3.5-month, and 5-month) and flooding depths (0-cm, 20-cm, and 40-cm). Flooding duration affected the survival and growth of *B. planiculmis*: Extended flooding (5-month) decreased the survival rate and initial shoot density, while shoot length and biomass increased under extended (5-month) and natural (3.5-month) seasonal flooding after shoots reached the water surface. The flooding depth affected sexual reproduction: Medium flooding depth (20-cm) resulted in the highest flowering rate. According to the results, the natural seasonal flooding duration in the East Asian monsoon climate did not negatively influence survival, growth, and reproduction of *B. planiculmis*. However, if the seasonal flooding duration was extended, *B. planiculmis* responded negatively to survival and growth during the young stage. The shortened seasonal flooding duration resulted in the repressed shoot length and biomass of *B. planiculmis.* For the sustainable conservation of *B. planiculmis* under East Asian monsoon, it is important to maintain the original seasonal flooding regimes and minimize the effects of embankment on the seasonal flooding regimes.

1. Introduction

Seasonal flooding regimes are key features of hydrodynamics in estuarine ecosystems. The hydrodynamics, sediment dynamics, and turbidity of estuaries vary over time, mostly in relation to the prevailing seasons in estuaries (Syvitski et al., 2005). For example, increased river flow during the monsoon season could overwhelm macro-scale estuaries, based on changes in flooding duration and depth (Sridhar et al., 2015; Tamura et al., 2010). Dynamics in flooding duration and depth due to seasonal flooding regimes could induce diverse responses in marsh plants. For example, carbon and nitrogen allocation in marsh plants were altered (Kaelke and Dawson, 2003), the dominance of marsh plants shifted from natural to exotic species due to different life history strategies (Greet et al., 2013), and the survival rates and biomass were changed (Chen and Xie, 2009). Therefore, flooding seasonality is one of the essential factors influencing survival, growth, and reproduction of marsh plants, in addition to their zonation (Chen and Xie, 2009; Kaelke and Dawson, 2003; van Eck et al., 2006).

Today, anthropogenic disturbances change the original patterns of seasonal flooding (Kaelke and Dawson, 2003). For example, man-made embankments that impound the water and lead to permanent flooding of marshes can extend the seasonal flooding duration (Montague et al., 1987; Portnoy, 1999). If these constructions accelerate the rate of sediment accumulation, the wetlands become land resulting in shortened flooding duration or more shallow flooding depth (Montague et al., 1987; Portnoy, 1999). The sea-level change due to climate change can also make seasonal flooding depths greater and flooding duration longer (Kim and Lee, 2010). Such altered seasonal flooding regimes could not only influence the responses of marsh plants (Stromberg et al., 2007) but also entire ecosystem structure and function (Colonnello and Medina, 1998; Kim et al., 2015; Syvitski et al., 2005). However, only a few studies have explored the responses of marsh plants to different seasonal

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https://doi.org/10.1016/j.flora.2021.151960
Received 24 May 2021; Received in revised form 22 September 2021; Accepted 26 October 2021

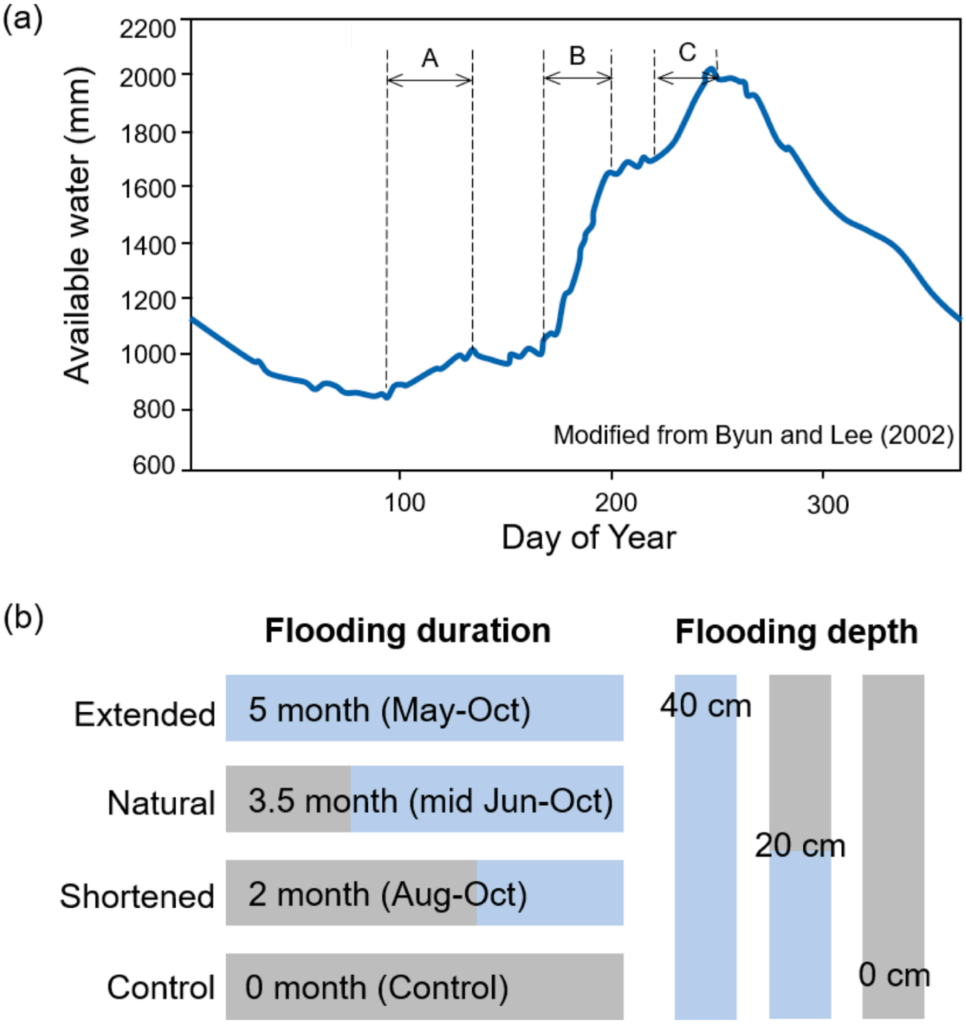

Fig. 1. Available water resources (accumulated precipitation) in the East Asia monsoon and in the experimental design. (a) Mean available water resources for 24 years (1974–1997) in 64 stations in Korea modified from Byun and Lee (2002). A is *Bom Changma*, B is *Changma*, C is *Kaul Changma*, (b) Experimental design with four flooding duration treatments, and three flooding depth treatments ($n = 5$). The flooding duration mimicked the East Asian monsoon precipitation in Korea.

flooding regimes under the East Asian monsoon.

The precipitation in East Asian monsoon has a strong seasonality that affects the hydrological regimes in wetlands. In Korea, the spring season experiences relatively weak precipitation from April to mid-June (*Bom Changma*). The summer monsoon season, called *Changma*, experiences intense rainfall from late June to mid-July. The autumn rainy season is usually a result of storms, lasts from mid-August to September, and is called *Kaul Changma* (Byun and Lee, 2002; Han and Byun, 2006; Qian et al., 2002) (see Fig. 1a). These seasonal precipitation patterns are major factors determining hydrological regimes in wetlands in Korea, with the highest flow and greatest depths during the summer monsoon season (Kim and Kim, 2016; Park et al., 2002). However, Korea has recently experienced considerable changes in seasonal flooding regimes in estuarial wetlands due to the construction of embankments and reclamation activities (Melville et al., 2016; Moores et al., 2016; Murray et al., 2014). Yang et al. (2021) reported that these constructions brought two opposite results in estuarian wetlands in Korea. On the one hand, the embankments caused impounded and permanent flooding so the seasonal flooding duration was extended and flooding depth was deeper. On the other hand, in case the constructions accelerated drainage, the seasonal flooding duration was shortened (flooded only after heavy rain in summer) and flooding depth was more shallower.

The estuarine plant *Bolboschoenus planiculmis* (F. Schmidt) T. V. Egorova is a proper species to examine the effects of altered seasonal flooding regimes on survival, growth, and reproduction. It is distributed in East Asia, Middle Asia, and Central Europe, and forms monodominant populations or mixed communities in estuaries, reclaimed rice paddies, and lagoons (Jung and Choi, 2011; Hroudová et al., 2014; Liu et al., 2016a). The species is one of the important marsh plants in the estuaries of East Asia, because it facilitates the maintenance of ecological structure and function by trapping sediment (Yang, 1998) and is a major food source for endangered migratory birds such as Swan gees (*Anser cygnoides*) and cranes (*Grus* spp.) (Kim et al., 2013; Liu et al., 2016a; Ma et al., 1999). Since *B. planiculmis* dwells at lower elevations, it is one of the species most vulnerable to altered seasonal flooding regimes following the construction of artificial features or sea-level rise (Kim and Lee, 2010; Montague et al., 1987; Yang et al., 2020). *Bolboschoenus planiculmis* in tidal marshes is usually flooded twice a month during spring tides before the summer monsoon. When the summer monsoon starts at the end of June, the heavy rain usually increases the water level in estuaries and makes *B. planiculmis* continuously flooded until the passing of typhoon in September (Yang et al., 2021).

In this study, a greenhouse experiment was conducted to compare the survival, growth, and reproduction of *B. planiculmis* under different seasonal flooding regimes. The flooding durations (0-month, 2-month, 3.5-month, and 5-month) and the flooding depths (0-cm, 20-cm, and 40-cm) imitated the seasonal flooding regimes in the East Asian monsoon climate. The 3.5-month duration represented the natural seasonal flooding duration of *B. planiculmis* in major estuaries in Korea. Other durations indicated shortened and extended flooding duration respectively due to the embankment constructions. The different flooding depths reflected the possibility of sea-level rise. The objective is to investigate the effects of seasonal flooding regimes on the development of *B. planiculmis* population for deciding its favorable range under changing conditions in Korean estuaries. We evaluated the following null hypothesis: Changes in seasonal flooding regimes does not affect the survival, growth, and reproduction of *B. planiculmis*.

2. Methods

2.1. Collection and preparation of B. planiculmis tubers

On April 8th, 2018, 120 unsprouted tubers of *B. planiculmis* with similar mass (1.19 ± 0.38 g) were collected randomly at Haengju-naru wetland, Goyang, South Korea (37° 35′ 46.26″ N, 126° 49′ 12.42″ E). The mean monthly temperature ranges from −2.4 °C (January) to 25.7 °C (August), the mean annual precipitation is 1451 mm (Korea Meteorological Administration, 2018), and the soil salinity is 0–5‰ (Yang et al., unpublished data). The annual mean tide level is 3.5 m, mean low water is 1.1 m, and mean high water is 6.0 m at the nearest Kanghwa observatory (Korea Hydrographic and Oceanographic Agency, 2018). *Bolboschoenus planiculmis* was the dominant plant species at lower elevations (≈ 6 m) and was exposed to the tide for more than two days weekly. The tubers of *B. planiculmis* were transported to the laboratory in moist and cool plastic containers. After washing through a 1 mm sieve, each tuber was transplanted temporarily in a 200 L pot filled with sandy soil with a mean grain size of 1 mm. Freshwater was given once a week (2 L per time) and the temperature was maintained with an average and standard deviation of 21.2 ± 2.5 °C under solar radiation. On May 2nd, pairs of sprouted tubers with similar shoot length (6.09 ± 3.20 cm) were selected for the experiments.

2.2. Experimental design and sample processing

Survival, growth, and reproduction of *B. planiculmis* were examined under four flooding duration and three flooding depth regimes (Fig. 1b). The flooding duration regimes reflected the East Asia monsoon climate zone: (1) 0-month treatment for non-flooding as a control, (2) 5-month treatment (May 2nd–October 8th) for extended flooding due to impounded water in embankments, (3) 3.5-month treatment (June 20th– October 8th) for the natural flooding with relatively dry spring and heavy rain in summer and autumn, and (4) 2-month treatment (August 8th–October 8th) for shortened flooding. The flooding depth regimes were selected based on the expected sea-level rise in South Korea (Kim and Lee, 2010): (1) 0-cm treatment for non-flooding as the control, (2) 20-cm treatment for intermediate flooding, and (3) 40-cm treatment for the expected maximum sea-level rise. The 0-month and 0-cm combination was the control treatment. The effects of flooding duration, flooding depth, and their interactions were examined from May 2nd to October 8th, 2018, in a greenhouse at Seoul National University, Seoul, South Korea (37° 27′ 34.12″ N, 126° 56′ 52.24″ E). The temperature and air humidity in the greenhouse were systemically controlled with an average and standard deviation of temperature of 23.0 ± 3.6 °C with a range of 10.5–34.0 °C, and an air humidity of 66.1 ± 18.9% with range 18.3–99.9%. A total of 35 pots with seven treatments (3 durations × 2 depths = 6 treatments and one control treatment) and five replicates were arranged randomly. A pair of sprouted tubers was transplanted into a pot (53 cm height and 33 cm diameter) with a mean grain size of 1 mm up to 10 cm depth, considering mean rhizome length (Yang et al., 2021). Holes were drilled every 0 cm, 20 cm, and 40 cm above the soil surface in each pot to maintain flooding depth. Water depth and water quality were managed daily with tap water. Salinity was not considered in the experiment because *B. planiculmis* can survive in both freshwater (0‰) and estuarine conditions (up to 10‰) with no variation in biomass (Xue et al., 2017). Five grams of solid fertilizer (11–8–7 NPK, HYPONeX, Korea) was applied per pot at the beginning of the experiment.

Growth of *B. planiculmis* was recorded weekly during the experiment, including shoot length, shoot density, and survival rate (counted as death when all shoots in a pot died). If none of the shoots survived in a pot, the dead plant material was not included in the final biomass calculation. Final biomass was harvested on October 8th and washed through a 1 mm sieve. These materials were separated into flowers, stems, rhizomes, tubers, and roots, and dried at 80 °C for 72 h. The ratio of aboveground biomass (AGB,%) was calculated as the sum of flowers and stems biomass over total biomass, whereas the ratio of belowground biomass (BGB,%) was calculated as the sum of rhizomes, tubers, and roots biomass over total biomass. The ratio of aboveground biomass to belowground biomass (AGB:BGB ratio) was based on dry aboveground biomass to dry belowground biomass. Density was the number of shoots per pot. Shoot length was measured from the soil surface to the end of the shoot and averaged per pot. Leaf length was measured from the leaf tip to the stem and averaged per pot. The stem diameter of each shoot was measured at the soil surface level using a Vernier caliper and averaged per pot. The sum of rhizome length was the total length of rhizomes per pot. The flowering rate was the ratio of the flowering shoots to the total number of shoots per pot. In addition, the number of tubers per pot was also counted.

2.3. Statistical analyses

Linear models (LMs) were used to compare the weekly shoot length, weekly shoot density, total biomass, biomass allocation, stem diameter, leaf length, and the sum of the rhizome length, with flooding duration, flooding depth, and their interaction as independent variables. The data were log or square transformed to meet the normality and homoscedasticity assumptions. Generalized linear models (GLMs) were used to explain the flowering rate using a quasibinomial distribution and the number of tubers using a quasi-Poisson distribution for the same independent variables. The LMs were fitted based on the stepwise method, and GLMs were fitted with the lowest Akaike Information Criterion (AIC) value of the Poisson distribution. Normality was checked using the Shapiro test, and homoscedasticity was evaluated using Levene's test using the 'car' package in R.

Cox Proportional-Hazards Models (CPHMs) were used for the comparison of weekly survival rates of *B. planiculmis* based on flooding duration, flooding depth, and their interactions as independent variables. A likelihood ratio test was used to evaluate the global statistical significance of the model, and a log-rank test was used to determine differences between groups (Bradburn et al., 2003). CPHMs and assumption checking were conducted using the 'Survival' and 'Survminer' packages in R (Kassambara et al., 2018; Terneau, 2018). All statistical analyses were performed using R v3.4.3 (R Development Core Team, 2008). The values were considered significantly different at $p <$ 0.05.

3. Results

3.1. Weekly survival rate

Among the 35 pots, shoots of 5 pots died before the end of the experiment, turning black with abscission. Four out of the 5 pots with dead shoots were from the 5-month treatment (2 pots for 20-cm treatment, 2 pots for 40-cm treatment), and the remaining one dead pot was the combination of 3.5-month and 40-cm treatment. The survival rate of *B. planiculmis* under the extended flooding treatment (i.e., 5-month treatment) decreased significantly ($p = 0.008$, $F = 11.82$, df = 3 in the likelihood ratio test) to 50% compared to the survival rates under the shorter durations (Fig. 2a). Death occurred from the young state (4th week) to the mature state (18th week). Conversely, flooding depth did

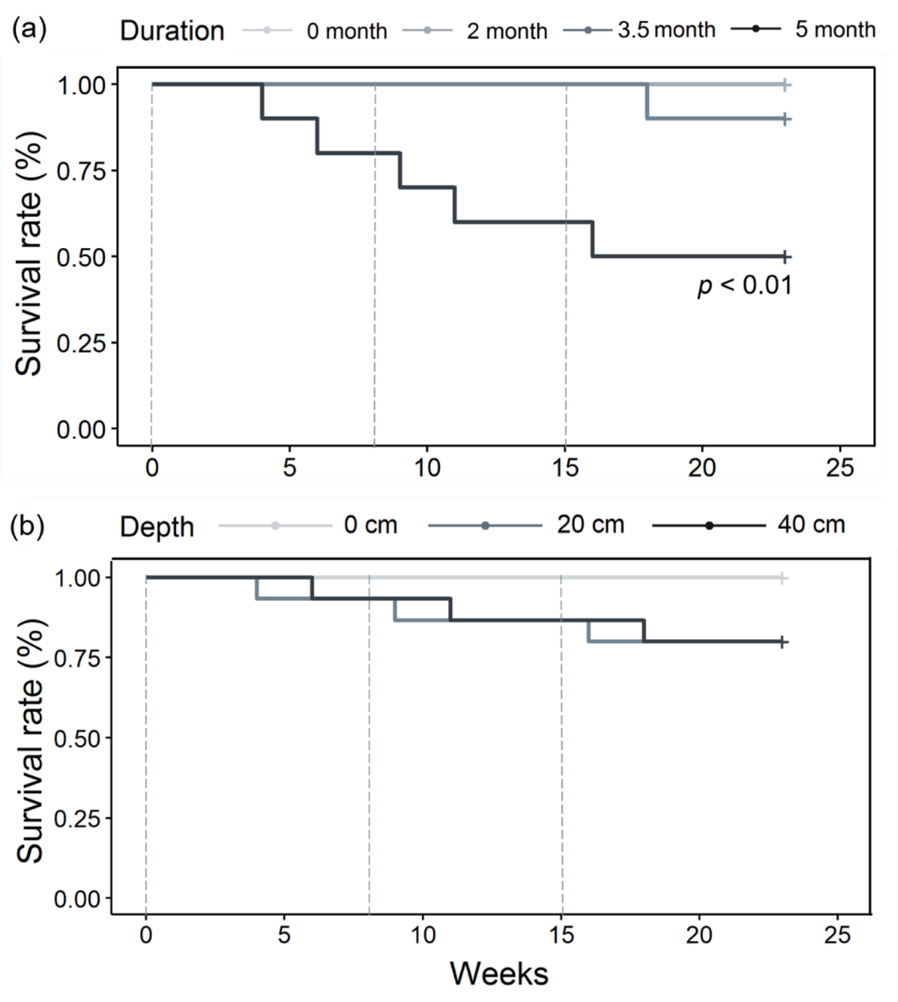

Fig. 3. Weekly shoot density and shoot length of *Bolboschoenus planiculmis* individuals during the growing season (a) Effects of flooding duration on weekly shoot density, (b) Effects of flooding depth on weekly shoot density, (c) Effects of flooding duration on the weekly shoot length, and (d) Effects of flooding depth on weekly shoot length. Vertical dashed lines indicate the beginning of each flooding duration. The 5-month, 3.5-month, and 2-month flooding treatments began from the 1st week (May, 15th), 8th week (June, 20th), and 15th week (August 8th), respectively. The horizontal dashed line indicates the 20-cm and 40-cm depths. Mean shoot length for every treatment were higher than the mean shoot length in the 20-cm depth at 4th week and higher than under the 40-cm depth at 9th week. Shaded area is for $p < 0.05$.

not significantly affect the survival rate (Fig. 2b). In addition, there was no interaction effect of flooding duration and flooding depth on the survival rate of *B. planiculmis* during the growing season.

3.2. *Weekly shoot density and shoot length growth*

The initial shoot density per pot under the 5-month treatment was significantly lower ($p = 0.01–0.04$, $F = 0.01–0.03$) than under the other flooding durations from mid-May (4th week) to mid-July (11th week) (Fig. 3a). The order was reversed after early August (15th week), but with no significant difference. Conversely, flooding depth did not influence shoot density during the entire growing season (Fig. 3b). At harvest, the final shoot density per pot ranged from 2 to 30, with a mean density and standard error of 12 ± 1. There was no interactive effect of flooding duration and flooding depth on the weekly shoot density of *B. planiculmis*.

Before early-August (15th week), the shoot lengths of *B. planiculmis* were almost similar among the flooding duration treatments. However, shoot length increased under the 5-month and 3.5-month treatments (both $p = 0.01–0.04$, $F = 0.01–0.05$) compared to the 0-month treatment from early-August (15th week) to the end of the experiment (Fig. 3c). At harvest, shoot length was on average 76 ± 6 cm (5-month treatment) and 78 ± 4 cm (3.5-month treatments), which was about 20 cm more than in the control treatment. Conversely, flooding depth did not influence shoot length during the entire growing season (Fig. 3d). In addition, flooding duration and flooding depth did not cause interaction effects on the shoot length.

3.3. *Growth and reproductive responses at harvest*

Table 1 and Fig. 4 summarize the LM and GLM results for the growth and reproduction responses of *B. planiculmis* under different flooding durations and flooding depths. Total biomass per pot was increased significantly under the 5-month treatment, at 22 ± 7 g per pot ($p = 0.02$, $t = 2.57$) compared to the shorter treatments, while there were no differences among the flooding depth treatments (Fig. 4a,b). Individual biomass was almost twice greater under the 3.5-month and 5-month treatments than under the 2-month treatment ($p = 0.02$, $t = 2.48$; $p = 0.02$, $t = 2.46$; Fig. 4c). However, flooding depth did not influence individual biomass significantly (Fig. 4d). AGB (i.e., aboveground biomass ratio) was on average 62 ± 2% and did not significantly vary among flooding duration treatments, while it increased under the deeper flooding depth treatment (Fig. 4e,f). Similarly, there were no significant differences in BGB (i.e., belowground biomass ratio) under flooding duration treatments but flooding depth treatments (Fig. 4g,h). As a result, the AGB:BGB ratio did not vary significantly among flooding duration and depth treatments with a mean of 2.1 ± 0.4 (Fig. 4i,j).

Flooding duration did not influence flowering rate (Fig. 4k). However, flowering rate was 6% higher under the 20-cm treatment (40%, $p = 0.03$, $t = 2.28$; Fig. 4l) than under 0-cm and 40-cm flooding depth treatments. The number of tubers per pot was 16 ± 2, which did not significantly vary among flooding duration and flooding depth treatments (Fig. 4m,n). Stem diameter was 15–20% greater under the 40-cm treatment than under other flooding depth treatments ($p = 0.02$, $t = 2.50$; Fig. 4p). Similarly, the stem diameter was greater under longer

Table 1
Linear model and generalized linear model results for the growth and reproduction responses of *Bolboschoenus planiculmis* based on flooding duration and flooding depth ($n = 5$).

	Duration		Depth		Duration × Depth	
	$F_{(3,\ 33)}$	p	$F_{(2,\ 33)}$	P	$F_{(2,33)}$	p
Total biomass (g per pot)	3.75	**0.02***	†	†	†	†
Individual biomass (g)	**4.38**	**0.01***	†	†	†	†
Aboveground biomass ratio AGB (%)	†	†	**4.47**	**0.02***	†	†
Belowground biomass ratio BGB (%)	†	†	**3.85**	**0.04***	†	†
AGB:BGB ratio	†	†	2.41	0.11	†	†
Flower biomass (%)	†	†	**4.50**	**0.02***	†	†
Stem biomass (%)	†	†	**5.91**	**0.01****	†	†
Rhizome biomass (%)	**3.91**	**0.02***	†	†	†	†
Tuber biomass (%)	†	†	†	†	†	†
Root biomass (%)	†	†	3.12	0.06	†	†
Density (shoots per pot)	†	†	†	†	†	†
Leaf length (cm)	**9.67**	**0.001*****	†	†	†	†
Stem diameter (mm)	**4.20**	**0.01****	**4.20**	**0.01****	†	†
Sum of rhizome length (cm)	†	†	†	†	†	†
Flowering rate (%)	†	†	**6.49** (X^2)	**0.04***	†	†
Tuber number (per pot)	†	†	†	†	†	†

Significance level: ***, $p < 0.001$.
**, $p < 0.01$.
*, $p < 0.05$. † Removed after model fitting.

flooding duration treatments (Fig. 4o). Leaf length was ≈30% higher under the 3.5-month and 5-month treatments than under the 0-month duration treatment (each $p = 0.0003$, $t = 4.15$; $p = 0.001$, $F = 3.68$; Fig. 4q), regardless of flooding depth (Fig. 4r). The sums of rhizome length per pot were 253 ± 5 cm and not significantly different among flooding duration and depth treatments (Fig. 4s,t). None of the responses revealed an interaction between flooding duration and flooding depth.

Biomass allocation to each organ varied depending on the flooding duration and flooding depth. Biomass allocation to the rhizome was significantly higher under the 5-month treatment than under the control treatment ($p = 0.01$, $t = 2.61$; Fig. 5a). Allocation to flowers was higher under 20-cm treatment compared to control treatment ($p = 0.02$, $t = 2.54$; Fig. 5b). The LM result of allocation to the stems under flooding depth treatments was significant (Table 1), showing the increasing trend for deeper treatment (Fig. 5b). Allocations to the tubers and roots did not differ as dependent on flooding duration and flooding depth. In addition, none of the variables revealed an interaction between flooding duration and flooding depth.

4. Discussion

In this study, the survival rates and growth in *B. planiculmis* changed mostly depending on the flooding duration, while flooding depth influenced *B. planiculmis* reproduction, which dismissed the null hypothesis. Furthermore, natural flooding duration (i.e., 3.5-month treatment) did not bring negative effects on survival, growth, and reproduction of *B. planiculmis* compared to extended and shortened flooding duration.

4.1. Effects of flooding duration on responses

Survival of *B. planiculmis* was notably influenced by flooding duration not by flooding depth. The species exhibited significantly lower survival rate under extended flooding (from spring to autumn) than shorter flooding (from summer to autumn; from late-summer to autumn)

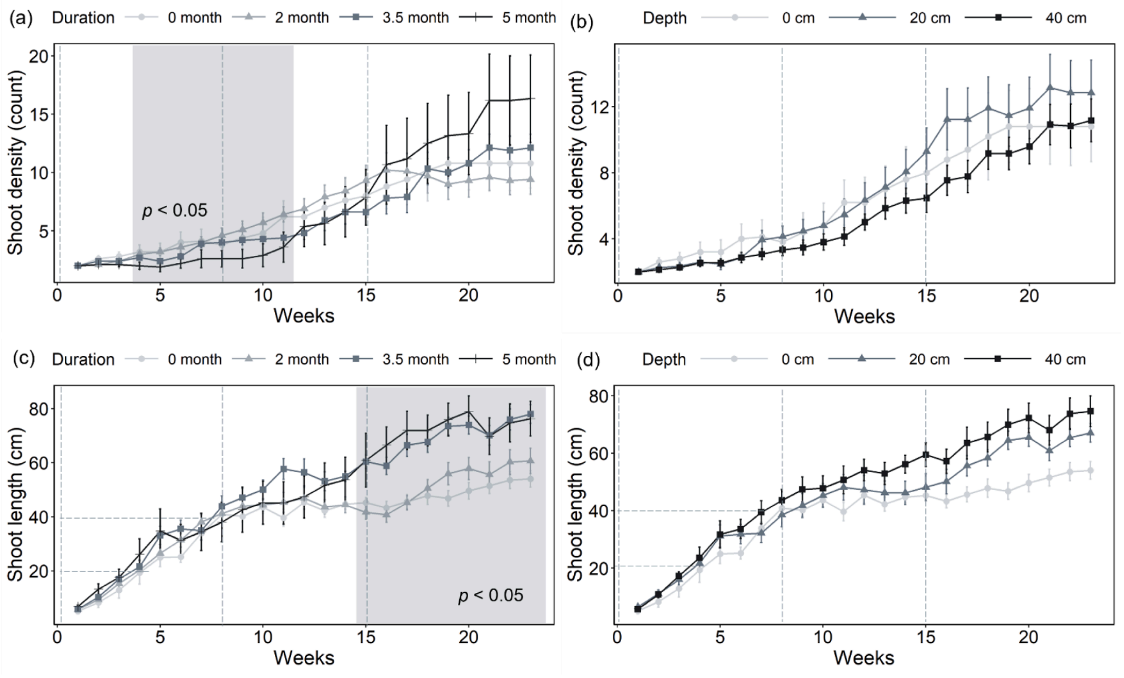

Fig. 2. The survival rate of *Bolboschoenus planiculmis* during the growing season (a) Effects of flooding duration on weekly survival rate of *B. planiculmis* ($n = 5$). Likelihood ratio test ($p = 0.008$, $F = 11.82$, df = 3), (b) Effects of flooding depth on the weekly survival rate of *B. planiculmis* ($n = 5$). Likelihood ratio test ($p = 0.40$, $F = 2.01$, df = 2). The vertical dashed lines indicate the beginning of each flooding duration. The 5-month, 3.5-month, and 2-month treatments were started from the 1st week (May, 15th), 8th week (June, 20th), and 15th week (August 8th), respectively.

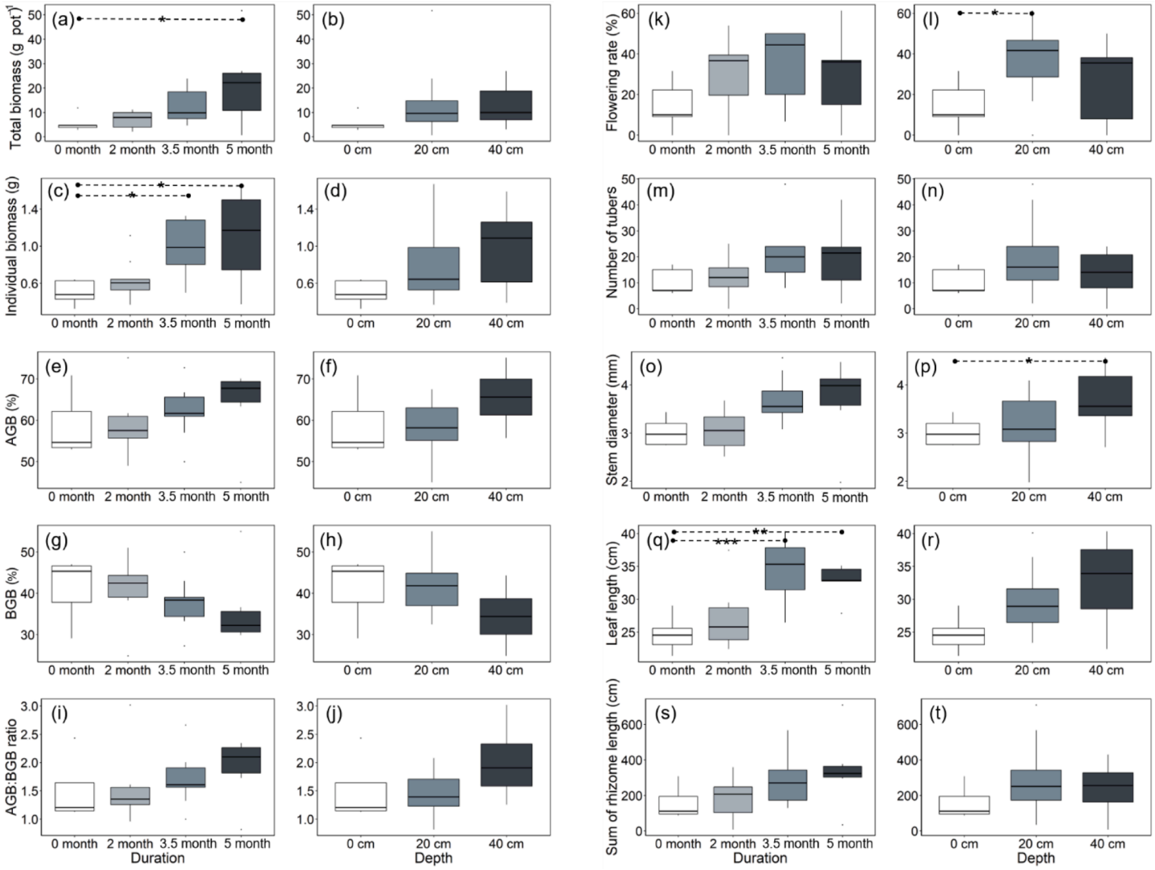

Fig. 4. Growth and reproduction responses of *Bolboschoenus planiculmis* at harvest. Each response to flooding duration and flooding depth is presented. Significance level: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$. AGB: Above-ground biomass ratio, BGB: below-ground biomass ratio.

(Fig. 2a,b). These results revealed the presence of flooding during young stage was critical to emergence and development of *B. planiculmis* growing from tubers. This is similar with the findings of previous studies dealing with seedlings (Garssen et al., 2015; Kaelke and Dawson, 2003) and plants from tubers (An et al., 2018). For example, An et al. (2018) revealed that initial emergence of *B. planiculmis* from tuber was negatively affected by water level, especially greater than 20 cm. Another interesting point was that natural flooding duration (from summer to autumn) did not significantly reduce survival of *B. planiculmis*, regardless of flooding depth (Fig. 2a,b). These results provide a possibility that this species is robust to flooding caused by East Asia monsoon during summer; however, it is vulnerable to initial flooding possibly caused by embankment (Yang et al., 2021).

The growth responses to flooding duration were varied in the present study. Weekly shoot density and shoot length exhibited opposite trends at different life stages. For example, shoot density was inhibited under extended flooding during the young stage; however, it recovered after the mean shoot length reached the water surface at the 9th week (Fig. 3a). These results are consistent with the findings of Blanch et al. (1999) showing that the plant density of *Bolboschoenus medianus* grown from tuber was inhibited under total submergence due to lower rates of photosynthesis underwater but not under partial or non-submergence. In contrast, shoot length did not vary during the young stage, while shoot length under the 5-month and 3.5-month treatments became higher than under the 0-month treatment after growth above the water surface (Fig. 3c). Partial flooding can induce the elongation of shoots of some wetland plants including seedlings (Hattori et al., 2011; Striker et al., 2012) and plants from tubers (Blanch et al., 1999) for enhanced gaseous exchange as an adaptation strategy. This study supported *B. planiculmis* revealed the adaptation strategy.

Unexpectedly, total biomass per pot and individual biomass increased with extended flooding duration in case the plants survived (Fig. 4a and c). However, many studies have reported a decreased plant biomass under extended flooding (Casanova and Brock, 2000; Chen et al., 2010; Gattringer et al., 2018; van Eck et al., 2004). Our results are consistent with the findings of Voesenek et al. (2004) and Mauchamp et al. (2001), who observed that once the species can extend their shoots above the water surface, they have a greater capacity to enhance biomass growth. Due to the greater leaf length and shoot length under the 3.5-month and 5-month treatments, *B. planiculmis* might be able to enhance its photosynthesis capacity and increase the biomass. However, the increased biomass under long exposure has been observed in seedling plants and little has been known for plants from tubers. A better understanding is needed for the relationships between flooding durations and biomass in *B. planiculmis*.

4.2. Effects of flooding depth on responses

In this study, survival and growth rates of *B. planiculmis* were largely unaffected by flooding depth throughout the entire life history. However, significant effects of flooding depth have been observed in other studies. Numerous emergent plants have been reported to increase their shoot length under great flooding depths to evade flooding stress (Blanch et al., 1999; Hellings and Gallagher, 1992; Wang et al., 2014). Conversely, some species exhibit decreased shoot density, decreased shoot length, and reduced total biomass to endure flooding stress via a quiescent strategy (Manzur et al., 2009; Wang et al., 2014) or fail to adapt (An et al., 2018; Gattringer et al., 2018). This study does not claim that the flooding depth was not important at all, but rather that the impact of flooding depth could be relative depending on plant growth

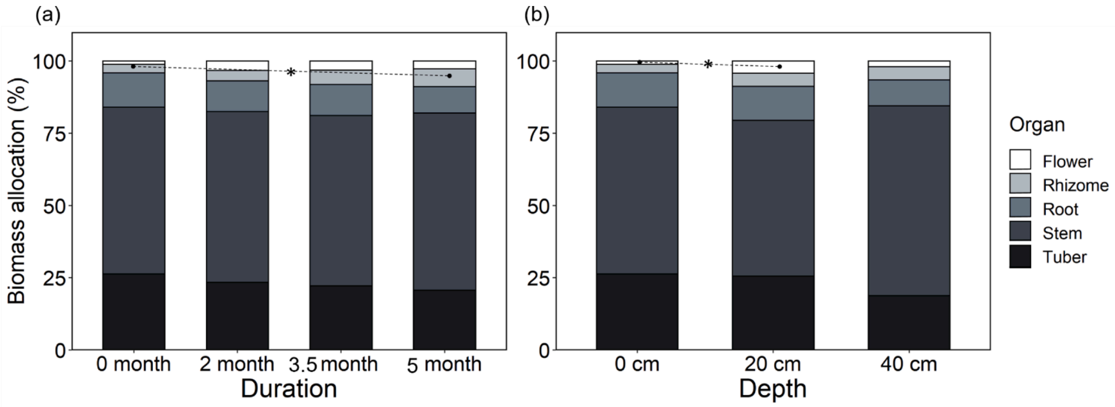

Fig. 5. Biomass allocation to each *Bolboschoenus planiculmis* organ at harvest. (a) Effects of flooding duration on biomass allocation to each organ, (b) Effects of flooding depth on biomass allocation to each organ. Significance level: *, $p < 0.05$.

and timing of flooding (see Mauchamp et al., 2001).

Notably, 5 cm young plants originated from tubers could survive and grow under 20-cm and 40-cm flooding depths (Fig. 2b, 3b, 3d), which indicates that *B. planiculmis* could survive complete submergence for at least eight weeks until the shoots reached the water surface. A potential explanation is that energy saved in tubers would support survival and growth of the young vegetation under the water surface. Liu et al. (2016a) found a similar result that showed 20-cm flooding depth did not affect *B. planiculmis* growing from tubers in terms of shoot density, shoot length, and total biomass.

Our results showed that flooding depth influenced sexual reproduction. *Bolboschoenus planiculmis* could produce sexual organs (flowers) at every flooding depth, although the highest amounts of biomass allocation of sexual organs were observed at the depth of 20-cm than at non-flooding and high flooding conditions (Fig. 4i and 5). This result is consistent with the findings of previous studies, which observed that amphibious responders, plants exhibiting high morphological plasticity in response to flooding, could reproduce in various flooding regimes with species-specific patterns (Crosslé and Brock, 2002; Warwick and Brock, 2003). In contrast, flooding depth did not influence the number and biomass allocation to the asexual organs (tubers) (Figs. 4n and 5b). According to previous studies, greater flooding depths could adversely affect the number of tubers, although it had no effect on biomass allocation to *Bolboschoenus* spp. tubers (An et al., 2018; Clevering and Hundscheid, 1998; Liu et al., 2016b). However, we did not observe a decrease in the number of tubers but unaltered tuber biomass allocation.

4.3. Seasonal flooding regimes

Generally, in this study, flooding duration influenced survival and growth, while flooding depth influenced sexual reproduction, and the impacts of flooding duration were more considerable than the impacts of flooding depth on *B. planiculmis*. According to the results, the natural seasonal flooding duration (from summer to autumn) in the East Asian monsoon climate might not negatively influence survival, growth, and reproduction of *B. planiculmis*, and could even increase shoot length and biomass, when compared to non-flooding. When the seasonal flooding regime extended from spring to autumn due to sea-level change or artificial embankment, *B. planiculmis* exhibited relatively poor survival and growth rates during the young stage. In addition, relatively short flooding regimes after summer did not decrease survival rates; however, it repressed shoot length and biomass compared to the natural seasonal flooding duration. Thus, it is critical to know which life stages of *B. planiculmis* would be exposed to seasonal flooding. For the sustainable conservation of *B. planiculmis* under East Asian monsoon, it is important to maintain the original seasonal flooding regimes and minimize the effects of embankment on the seasonal flooding regimes.

CRediT authorship contribution statement

Hyunyoung Yang: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Jae Hyun Kim:** Methodology, Investigation, Validation, Writing – review & editing. **Eun Ju Lee:** Supervision, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

The authors thank the editor and two reviewers who helped to improve the quality of the paper. We would also like to thank the Seoul National University for providing a greenhouse, the members of the Laboratory of Plant Ecology, such as Shinyeong Park, Bokyung Kim, Dokyung Ryu, Suwan Park, Yoonjeong Heo, Youngeun kim, Minwoo Oh, Seungkyung Lee, and Saeromi Mun, for helping with the experimental management activities and harvest. The first author was financially supported from Kwanjeong Educational Foundation.

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