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이학석사학위논문

**Direct and indirect impacts of tidal  
restriction on the responses of marsh plant  
*Bolboschoenus planiculmis***

조류 단절의 직·간접적인 영향에 의한  
습지식물 좀매자기의 반응

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양현영

**Direct and indirect impacts of tidal  
restriction on the responses of marsh plant  
*Bolboschoenus planiculmis***

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## Abstract

Tidal restriction caused by artificial constructions can give direct and indirect impacts on estuarial ecosystems. It affects not only tidal regimes and flooding regimes directly but also interspecies interactions among marsh plants indirectly. However, there was little understanding of the impacts of the tidal restriction on the responses of marsh plants. Therefore, this study focused on the responses of marsh plant, *Bolboschoenus planiculmis*, to the direct and indirect impacts of tidal restriction, such as changes of the tide, interspecies interaction, and seasonal flooding regimes.

First, a field study was conducted to compare the responses of *B. planiculmis* and environmental variables between tidal marsh and tidal-restricted marsh. The tidal-restricted marsh had deeper water depth and higher dominance of the other species compared to the tidal marsh. *B. planiculmis* in the tidal-restricted marsh showed lower density, higher asexual reproduction, and higher short-rhizome density. On the other hand, the tidal marsh population showed a higher density, higher sexual reproduction, and lower short-rhizome density. The result of RDA indicated *B. planiculmis* with the less density in the tidal-restricted marsh would allocate more energy to consolidate the original habitat. On the other hand, the tidal marsh population with the high density would invest energy to extend new area.

Secondly, a greenhouse experiment was performed to investigate the effects of tide on the interspecies interaction and the responses of *B. planiculmis*. The interspecies interaction of *B. planiculmis* against *Carex scabrifolia* was changed from competition to neutral with increased tidal regimes. Both the tide and the interspecies interaction reduced the growth of *B. planiculmis*. The tide resulted in

thinner stem of *B. planiculmis* which supported the avoidance strategy to tide; however, *C. scabrifolia* did not show any plastic responses. These results can explain the real distribution of the two species: *B. planiculmis* is disadvantaged from the competitive *C. scabrifolia* in high elevation; however, it can dominate low elevation with abilities to avoid tidal stress.

Thirdly, a greenhouse experiment was conducted to clarify the effects of seasonal flooding regimes on the responses of *B. planiculmis*. Flooding duration affected the survival and growth, while flooding depth influenced the reproduction. The natural seasonal flooding from summer to autumn did not seem to bring negative impacts on the survival, growth, and reproduction of *B. planiculmis*. On the other hand, the extended seasonal flooding from spring to autumn reduced the survival and seedling density. It increased the biomass after the shoot length reached the water surface. Shortened seasonal flooding after summer did not influence negatively on the survival and reproduction, but the biomass was less than in natural or extended seasonal flooding.

This study indicates the impacts of artificial construction should be minimized to conserve the *B. planiculmis* sustainably. I suggest managing competitive species low through tidal fluctuation and preventing early flooding.

**Keywords:** Tidal restriction, Estuary, Tide, Interspecies interaction, Seasonal flooding, Flooding duration, Flooding depth, *Bolboschoenus planiculmis*

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## **Chapter I. General introduction**

## **1.1. Tidal restriction**

Tidal restriction can bring significant impacts on estuarial ecosystems (Colonnello and Medina 1998, Syvitski et al. 2005). The tidal restriction is caused by artificial constructions such as dams, seawalls, and dikes to secure rice paddy, freshwater, and flood protection at the mouth of rivers (Roman et al. 1984, Le et al. 2007). Direct impacts of tidal restriction can reduce the intensity or frequency of tidal regimes (Falconer et al. 2009) and can alter the flooding regimes regarding flooding duration or flooding depth (Le et al. 2007). For example, the tidal restriction makes impounded marshes in short-term that remain permanently inundated depending on seasonal precipitation (Montague et al. 1987, Mora and Burdick 2013). In long-term, the tidal restriction can change the wetland to the drained land (Portnoy 1999). These changes can result in indirect impacts on interspecies interaction, sediment flux, salinity, or herbivory (Ibáñez et al. 1996, Tanner et al. 2002, Ritter et al. 2008). Marsh plants face these direct and indirect impacts of tidal restriction at first, so their responses to these impacts have been separately studied in such as physical, chemical, or biological impacts of tidal restriction (Portnoy and Giblin 1997, Sun et al. 2003, Silinski et al. 2018). However, these separated understandings have limitations to deal with the comprehensive changes caused by tidal restriction. Therefore, there is a need to understand both direct and indirect impacts of tidal restriction on the responses of marsh plants, which is essential to understand the changes in structures and functions of estuaries (Ritter et al. 2008, Bornette and Puijalon 2011).

## **1.2. Responses of marsh plant**

The marsh plants have flexible morphological plasticity to various environmental conditions (De Kroon et al. 2005, Gratani 2014). For example, first, marsh plants either try to avoid or tolerant mechanical conditions such as tide, wind, and touch. Avoidance strategy includes flexible stem, thin stem, short height, and more developed roots for preventing from uprooting caused by strong mechanical stress. On the other hand, tolerance strategy causes stiffer stem, elongated height, and higher breaking point to resist weak mechanical stress (Puijalon et al. 2011, Silinski et al. 2018). Secondly, marsh plants react differently to flooding condition. They can facilitate biomass allocation to aboveground and elongate stem to escape from inundation, called escape strategy. Some plants repress their growth and energy consumption to endure the inundation, called quiescent strategy (Manzur et al. 2009, Hattori et al. 2011). Lastly, foraging hypothesis explains the allocation to different functionalized rhizomes. When the belowground competition is high, the plants produce short-rhizome (phalanx form) to consolidate the original habitats and to tolerate stressful conditions. On the other hand, they generate long-rhizome (guerrilla form) to expand and occupy new areas in a less competition condition (Ye et al. 2006, Ikegami et al. 2007). The foraging hypothesis also includes sexual or asexual reproduction modes. Plants reproduce sexually to move short- or long-distance in higher intraspecies competition, while they prefer asexual reproduction in lower intraspecies competition and higher abiotic stress (Weiner 1988, Sun et al. 2001, Olejniczak 2003). Based on these hypotheses, it is possible to understand the direct and indirect impacts of tidal restriction on the marsh plants. These responses should be fully considered to predict vegetation dynamics (Bornette and Puijalon 2011) and to preserve marsh plants (Ritter et al. 2008).

### 1.3. Study species

*Bolboschoenus planiculmis* (F. Schmidt) T. V. Egorova is a representative estuarial marsh plant. It distributes in East Asia, Middle Asia, Central Europe, and Iran, and it forms monodominant populations or mixed communities in estuaries, reclaimed rice paddies, and lagoons (Amini Rad et al. 2010, Jung and Choi 2011, Hroudová et al. 2014, Liu et al. 2016b). It was previously called *Scirpus planiculmis* (F. Schmidt) T. V. Egorova. It plays significant roles to maintain the structures of estuaries by trapping sediments (Yang 1998) and to provide major food sources for migratory birds (Kim et al. 2013). Because *B. planiculmis* dwell in the low elevation which is the nearest to the water body, it can be affected mainly by tidal restriction caused by artificial constructions. *B. planiculmis* is a clonal plant that has flexible morphological plasticity to environmental changes, so previous studies focused on its responses to diverse environmental conditions such as water depth, burial depth, drought, flooding frequency, and salinity (Huang et al. 2013, Hroudová et al. 2014, Liu et al. 2016b, Xue et al. 2017). However, there is a lack of comprehensive understanding of direct and indirect impacts of tidal restriction on the responses of *B. planiculmis*, so a critical gap exists to predict and preserve the population.

## **1.4. Objectives of this study**

The objective is to understand the responses of *B. planiculmis* to the direct and indirect impacts of tidal restriction regarding tide, interspecies interaction, and seasonal flooding regimes. For the objective, each chapter has their own objectives.

In Chapter II, the responses of *B. planiculmis* and environmental factors between tidal marsh and tidal-restricted marsh were compared in the field survey. In addition, the relationships between allocation ratios and environmental variables were analyzed. In Chapter III, the effects of tide on the interspecies interaction and responses of *B. planiculmis* was investigated in a greenhouse experiment, based on the stress-gradient hypothesis. In Chapter IV, the effects of seasonal flooding patterns on the responses of *B. planiculmis* was examined regarding flooding duration and flooding depth. Lastly, Chapter V summarized the discussions and suggested the sustainable management for *B. planiculmis* conservation.

Through this study, it will be possible to understand the impacts of tidal restriction on the responses of *B. planiculmis*. It can help to infer the impacts of tidal restriction on the structures and functions of estuarial ecosystems and to suggest sustainable management plans for conserving the population.

**Chapter II. Responses of *B. planiculmis* between tidal  
marshes and tidal-restricted marshes on the west  
coast of Korea**

## 2.1. Introduction

Tidal marshes have been exposed to tidal restriction caused by artificial constructions. The artificial constructions can bring direct impacts on the hydrology such as flooding frequency, depth, and duration (Byun et al. 2004, Suh et al. 2014). For example, a dike can result in impounded marshes that are permanently flooded for short-term (Montague et al. 1987) or seasonally waterlogged site or drained upland for long-term (Portnoy 1999). These hydrological changes can affect sediment transportation (Delgado et al. 2013, Gao et al. 2018), nutrients (Portnoy 1999, Ritter et al. 2008), and salinity regimes (Mora and Burdick 2013). Besides, marsh plants face unexpected interspecific competition facilitated by the hydrological changes (Sun et al. 2003, Qi et al. 2016). The tidal restriction caused by artificial constructions is common in worldwide with a broad range of impacts, so efforts to understand the responses of the marsh plants to the tidal restriction have been raised (Haltiner et al. 1996, Tanner et al. 2002, Beauchard et al. 2011, Elliott et al. 2016). Previous studies focused on the responses of marsh plants to the direct impacts of the tidal restriction such as the changes of flooding regimes and mechanical conditions (Le et al. 2007, Falconer et al. 2009). Other studies dealt with indirect consequences of tidal restriction, for example, succession (Roman et al. 1984, Warren et al. 2002) and invasion (Bart and Hartman 2000). However, comprehensive understanding of direct and indirect impacts of tidal restriction is still lacked. It should be fully considered to predict vegetation dynamics (Bornette and Puijalón 2011) and to preserve marsh plants (Ritter et al. 2008).

One of the essential responses of marsh plants is morphological plasticity under various environmental changes (Richards et al. 2005). The marsh plants allocate limited energy to different organs or strategies for responding to diverse

environmental conditions such as flooding, mechanical condition, and competition (Weiner 1988, Manzur et al. 2009, Puijalon et al. 2011). These plastic responses may help them to endure in the novel environment, to colonize new habitats, and to adapt to environmental changes (Ghalambor et al. 2007, Silinski et al. 2018). For example, marsh plant can select whether it invests energy to sexual or asexual reproductions. Sexual reproduction enables them to occupy new habitats by short- and long-distance seed dispersal to avoid stresses that may lower germination success (Sun et al. 2001, Mony et al. 2010). On the other hand, asexual reproduction by vegetative organs helps the local population keep persisting against disturbances (Ott and Hartnett 2012). Another plastic response is a change in biomass allocation patterns. Increased aboveground biomass can result from the shortage of incident light or oxygen (Manzur et al. 2009, Poorter et al. 2012). Belowground biomass becomes higher to obtain insufficient moisture and nutrient (Edwards et al. 2003, Mccarthy and Enquist 2007) or to tolerate uprooting by waves (Puijalon et al. 2008b, Silinski et al. 2018). Additionally, clonal plants have been known to allocate energy into different functionalized rhizomes within one clone. A very short-rhizome (SRR or phalanx form, < mm) plays a role in consolidating the original patch and tolerating stressful conditions, while a long rhizome (LRR or guerrilla form, > mm) contributes to expand and occupy the new area (Ye et al. 2006, Ikegami et al. 2007). Understanding these plastic responses of marsh plant is essential to evaluate the fitness (Puijalon et al. 2005), to preserve the local population (Chevin et al. 2013), and to forecast the structures and functions of estuaries (Nicotra et al. 2010, Qi et al. 2016), in particular for species which is crucial to maintain the ecosystem.

This study was performed to answer a question about whether *B. planiculmis* shows different responses regarding the growth, reproduction, and allocation

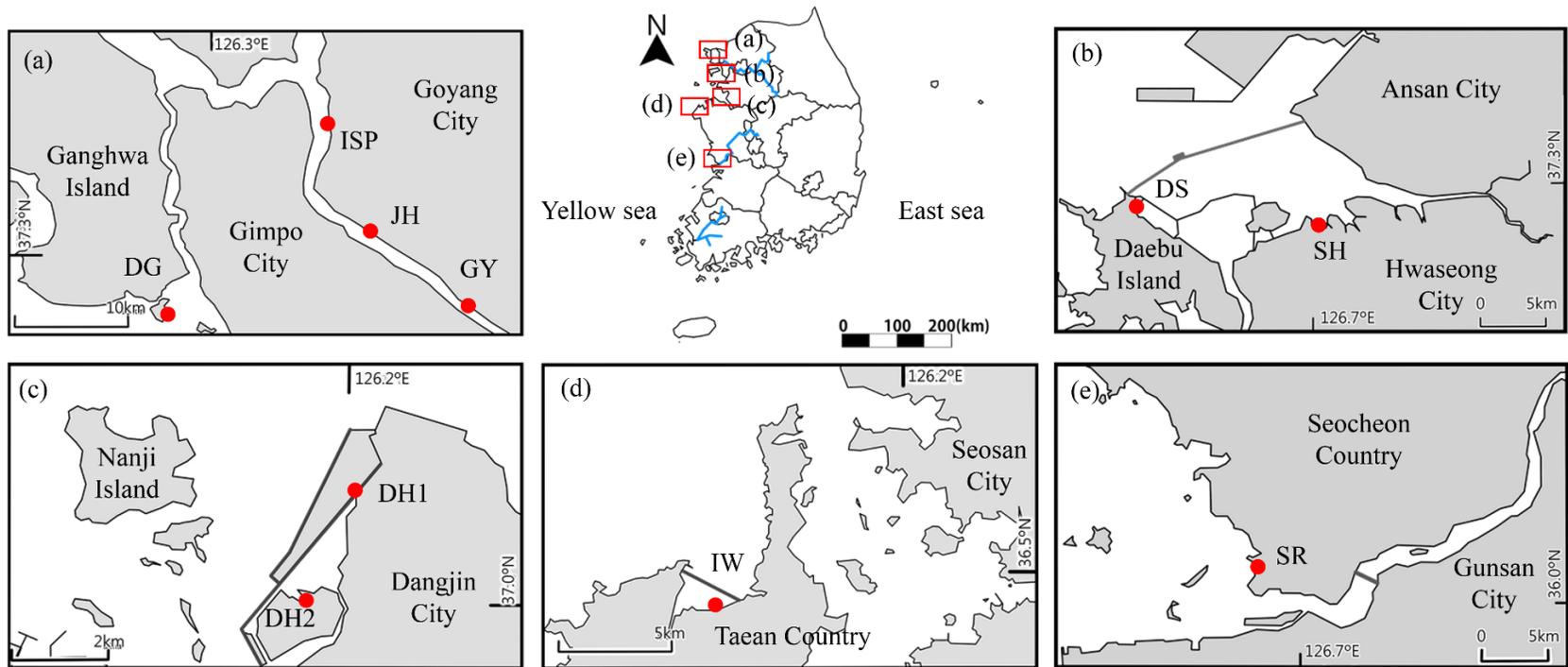
between tidal marsh and tidal-restricted marsh. This study conducted two objectives; (1) to compare the responses of *B. planiculmis* and environmental variables between tidal marsh and tidal-restricted marsh, (2) to analyze the relationships between allocation ratios and environmental variables. To conduct these objectives, two hypotheses were built up; (1) responses of *B. planiculmis* are different between tidal marsh and tidal-restricted marsh, (2) these differences are caused by specific environmental variables induced by tidal restriction.

## **2.2. Methods**

### **2.2.1. Study sites**

Study sites were located along the west coastline of South Korea. Five sites were located at tidal marshes, and the other five sites were placed at tidal-restricted marshes. Among the five tidal marsh sites, three tidal marshes, called Goyang, Janghang, and Isanpo, were located at the freshwater tidal marsh at Han River estuary (Fig. 1a) which is the only tidal-open estuary in South Korea. Each site was more than 8 km away and not connected to each other. The other two tidal marshes were marshes in high elevation at tidal-flat of Donggeom (Fig. 1a) and Songrim (Fig. 1e). On the other hand, the tidal-restricted marsh sites were blocked by artificial seawalls. Daesong and Sihwa marshes were surrounded by Sihwa seawall, but the Daesong marsh was separated from the Sihwa marsh by an additional levee (Fig. 1b). Daeho seawall (Fig. 1c) and Iwon seawall (Fig. 1d) included two and one tidal-restricted marshes, respectively. Two tidal-restricted marshes in Deaho seawall were apart 3 km and isolated to each other by an additional levee.

Table 1 summarized the locations and environmental variables of each sites: ISP (Isanpo tidal marsh), JH (Janghang tidal marsh), GY (Goyang tidal marsh), DG (Donggeom tidal marsh), SR (Songrim tidal marsh), DS (Daesong tidal-restricted marsh), SH (Sihwa tidal-restricted marsh), DH (Daeho tidal-restricted marsh), IW (Iwon tidal-restricted marsh). The tidal marshes were flooded at spring tides at least biweekly and after heavy rain season, while the tidal-restricted marshes were impounded in the seawalls and inundated permanently except for extreme dry spring. Around 60 % of the annual precipitation falls from June to August in all sites due to Asia Monsoon Climate zone (Administration 2011).



**Figure 1. Study sites in tidal marshes and tidal-restricted marshes along the west coastline of South Korea.** (a) Isanpo (ISP), Janghang (JH), and Goyang (GY) tidal marshes at Han River estuary and Donggeom (DG) tidal marsh at tidal flat; (b) Daesong (DS) and Sihwa (SH) tidal-restricted marshes; (c) Daeho1 (DH1) and Daeho 2 (DH2) tidal-restricted marshes; (d) Iwon (IW) tidal-restricted marsh; (e) Songrim (SR) tidal marsh at tidal flat.

**Table 1. Summary of the locations and environmental variables in tidal marsh sites and tidal-restricted marsh sites**

	Tidal marsh					Tidal-restricted marsh				
Sites	ISP	JH	GY	DG	SR	DS	SH	DH1	DH2	IW
Extent (m)	25 × 50	25 × 50	25 × 50	10 × 20	25 × 50	25 × 50	25 × 50	25 × 50	50 × 50	25 × 50
Location	37°43'33.76"N 126°41'16.61"E	37°38'21.92"N 126°44'46.37"E	37°35'46.55"N 126°49'12.50"E	37°35'10.18"N 126°30'24.78"E	36°1'32.32"N 126°39'47.23"E	37°17'12.71"N 126°35'14.88"E	37°15'30.28"N 126°42'52.71"E	37°2'13.56"N 126°29'8.48"E	37°1'31.89"N 126°28'48.89"E	36°53'50.45"N 126°16'15.94"E
<b>Abiotic</b>										
Topographic level	Freshwater tidal marsh			High elevation in tidal flat		Artificial seawalls intercepted				
Flooding (Origin of flooding)	Spring tides, Heavy rain (Tide & Rain)			Spring tides (Tide & Rain)		Permanent flooding except for extreme dry spring (Rain)				Sporadic (Rain)
Annual mean tidal range (m)	3.5 (1.1–6.0)			4.6 (1.4–7.9)	3.7 (1.3–6.1)	-	-	-	-	-
Annual total precipitation(mm)	1450.5			1346.7	1202.0	1312.3			1285.7	
Annual mean temperature (°C)	12.5 (–2.4–25.7)			11.1 (–3.8–24.5)	12.8 (–0.4–25.7)	12.0 (–2.9–25.6)			11.9 (–2.0–25.1)	
Seawall built year	-	-	-	-	-	1994	1994	1989	1989	1992
Soil texture	Clay			Sandy clay		Silty clay				
<b>Biotic</b>										
Coverage (%)	80–100	60–80	70–90	60–80	90–100	30–50	40–60	40–60	70–80	20–40
Shoot length (cm)	70–90	60–75	65–75	60–90	40–60	80–90	60–80	65–85	75–95	70–100
Companion species	<i>Scirpus triqueter</i> , <i>Echinochloa crusgalli</i> , <i>Phragmites australis</i>	<i>Echinochloa crusgalli</i> , <i>Phragmites australis</i>	<i>Scirpus triqueter</i> , <i>Phragmites australis</i>	<i>Triglochin maritimum</i> , <i>Phragmites australis</i> , <i>Carex scabrifolia</i>	<i>Carex scabrifolia</i>	<i>Phragmites australis</i> , <i>Diplachne fusca</i>	<i>Echinochloa crus-galli</i> , <i>Phragmites australis</i> , <i>Erigeron canadensis</i>	<i>Phragmites australis</i>	<i>Phragmites australis</i> , <i>Diplachne fusca</i>	<i>Phragmites australis</i> , <i>Erigeron Canadensis</i> , <i>Carex scabrifolia</i>

Annual mean tidal range was the average of a year data, available in KHOA Smart Tide Forecast, Korea Hydrographic and Oceanographic Agency. Annual total precipitation and Annual mean temperature was the average of 30 years data, available in Smart Weather Service, Korea Meteorological Administration.



**Figure 2. Study sites and study species.** (a) One of the tidal-restricted marsh (DH1) which was permanently flooded due to blocking by artificial constructions, (b) One of the tidal marsh (ISP) which was exposed to tidal flooding biweekly, (c) *B. planiculmis* with flower in August, (d) Tubers of *B. planiculmis* in September.

### 2.2.2. Sampling method

In each site, ten permanent quadrats (1 m × 1 m) were haphazardly established 3–5 m away from the other quadrats on April 2017, by reference to previous studies (Sun et al. 2001, Sun et al. 2002, Ning et al. 2014). Those quadrats were installed parallel to the water body and located at the edge of marshes. In each quadrat, density, coverage, and shoot length of all species individual were recorded monthly. The number of ramets was considered as a density of the species. Based on the monthly observation, vegetation sampling was conducted in early-September when the aboveground parts of *B. planiculmis* started to senesce, and the belowground parts developed most (Karagatzides and Hutchinson 1991, Sun et al. 2002). To estimate biomass allocation ratio, aboveground parts were clipped at the sediment surface on each quadrat. The belowground parts were extracted using a 20 cm diameter and 15 cm depth stainless steel core at the middle of each quadrat. After extracting the core, 15 cm depth of soil was dug further down, while the most belowground parts of *B. planiculmis* were moribund so not used for analyzing data (see Sun et al. 2002, Kim et al. 2013, Ning et al. 2014). To calculate relative short-rhizome density ratio, we collected 3–5 clonal fragments that were not directly connected to avoid sampling from the same individuals (see Sun et al. 2002, Ning et al. 2014). The length of rhizomes was measured from the bottom of a parent ramet to the bottom of the first daughter ramet.

Triplicates of undisturbed soil samples were mixed per quadrat for measuring soil salinity (SS), soil moisture (SM), soil organic matter (SOM), soil pH,  $\text{NO}_3^-$ -N,  $\text{NH}_4^+$ -N, and  $\text{PO}_4^{3-}$ -P. Water depth was recorded five times for calculating the average per quadrat. The recording water depths and collecting soil samples were conducted at least three days after raining or spring tides when the soil moisture

became stable (Kim et al. 2004). All of the vegetation and soil samples were sealed with plastic bags and transported to the laboratory within ice containers.

### **2.2.3. Sample processing**

The aboveground parts were washed and separated into flower and stem, counting the number of flowering ramets. The belowground parts were washed through a 1 mm sieve and divided into rhizome, tuber, and root. The harvested materials were weighted to 0.01 g after 72 hours drying at 80 °C. Relative belowground biomass was estimated as the ratio of the belowground biomass over the total biomass. The flowering rate was calculated as the number of flowering ramets over the number of total ramets. Relative short-rhizome density was the number of unmeasurable rhizomes (maximum of a few millimeters) divided by the total number of rhizomes (Ikegami et al. 2007).

Based on the field data, the importance value index (IV) was calculated which has been commonly used to measure the dominance of a target species over the other species. The index was the sum of relative density, relative coverage, and relative frequency and divided by 3. The higher IV of the target species means the species is a leading dominant, while the lower IV of the target species means the other species are leading dominant (McIntosh 1957). This study used the IV of the other species (neighbor IV) to reflect the dominance of the other species.

$$IV = (Relative\ Density(\%) + Relative\ Coverage(\%) + Relative\ Frequency(\%))/3$$

$$neighbor\ IV = 100 - B.\ planiculmis\ IV$$

Soil samples were penetrated through a 2 mm sieve to remove organic materials and gravels and then separated into two parts. One part was air-dried under a shaded condition for SS and soil pH measurements. PC-2000 (THERMO EUTECH, Singapore) was used to measure SS and soil pH after mixing the dried soil and deionized water at a ratio of 1:5. Another part remained as fresh soil for measuring SM, SOM, and nutrient contents. The SM was calculated as  $((W-D)/W) \times 100$  (%). W was the fresh soil weight, and D was the dry soil weight for 72 hours at 105 °C. The remaining soil was burned for 4 hours at 550 °C for measuring SOM, based on the loss on ignition method (Boyle 2004). To estimate the contents of  $\text{NO}_3^-$ -N (mg  $\text{kg}^{-1}$ ) and  $\text{NH}_4^+$ -N (mg  $\text{kg}^{-1}$ ), the soil was extracted by 2M KCl, and hydrazine method (Kamphake et al. 1967) and indophenol methods (SolÓrzano 1969) were conducted, respectively. The content of  $\text{PO}_4^{3-}$ -P (mg  $\text{kg}^{-1}$ ) was estimated by ascorbic acid reduction method (Murphy and Riley 1962), after extracting the soil with Bray No. 1 solution (Bray and Kurtz 1945).

#### **2.2.4. Statistical analyses**

Due to the great site variations of absolute values, relative proportion values were used for sexual allocation, biomass allocation, and rhizome allocation. These data were the final growth data in September, showing the highest ramet density and growth. First, linear mixed models (LMMs) were conducted to compare the overall responses of *B. planiculmis* and environmental variables between tidal marsh and tidal-restricted marsh. The responses included total biomass, individual biomass, shoot length, the number of rhizomes per ramet, rhizome length, rhizome diameter, and biomass allocation to each organ. Environmental variables included SS, SOM, soil pH,  $\text{NO}_3^-$ -N,  $\text{NH}_4^+$ -N,  $\text{PO}_4^{3-}$ -P, and neighbor IV. Generalized mixed models

(GLMMs) were used to test the significant difference of the relative flowering density and relative short-rhizome density with binomial distribution, and the ramet density with poisson distribution between tidal marsh and tidal-restricted marsh. These LMMs and GLMMs were used with the tidal regime as a fixed factor and the site as a random factor (McKone and Lively 1993) from the 'lme4' package (Bates et al. 2015). Because the water depth was zero-inflated data, it was analyzed by LMM from the 'glmmADMB' package (Ben Bolker et al. 2012). Normality assumption and homoscedasticity assumption for each variable were tested graphically. Tukey's honestly significant difference (HSD) test was conducted at the 0.05 significance level for multiple comparisons of each site. The belowground parts of a single quadrat located in Daesong site was lost, so it was not used for statistical analysis.

Secondly, multivariate analyses were performed to investigate the relationships between the three allocation ratios and environmental variables with redundancy analysis (RDA). The vegetation data matrix was composed of the three allocation ratios, and the environment data matrix consisted of soil variables (i.e., SS, SM, SOM, soil pH,  $\text{NO}_3^-$ -N,  $\text{NH}_4^+$ -N,  $\text{PO}_4^{3-}$ -P), water depth, the density of *B. planiculmis*, and neighbor IV. A final model was determined by forward selection method. The water depth was added to the final model after checking the collinearity because it was significantly different between tidal marsh and tidal-restriction marsh in the LMMs. All statistical analyses were performed with R version 3.4.3 (Development Core Team 2008). The values were considered as significantly different at  $p < 0.05$ .

## **2.3. Results**

### **2.3.1. Overall responses of *B. planiculmis* between tidal marsh and tidal-restricted marsh**

There was a significant difference between the tidal marsh and tidal-restricted marsh in the total ramet density but not in the other responses (Table 2). The total ramet density was higher in the tidal marsh than the tidal-restricted marsh ( $p < 0.001$ ). Even though the total biomass per unit area in the tidal marsh was higher than the tidal-restricted marsh, it was not significantly different due to high site variations (Appendix 1). On the other hand, the individual biomass was higher in tidal-restricted marsh without significant difference. Shoot length did not show significant differences between tidal marsh and tidal-restricted marsh. The number of rhizomes, rhizome length, and rhizome diameter were not significantly different as well. Compared to other responses, the ramet density showed a substantial difference between tidal marsh and tidal-restricted marsh.

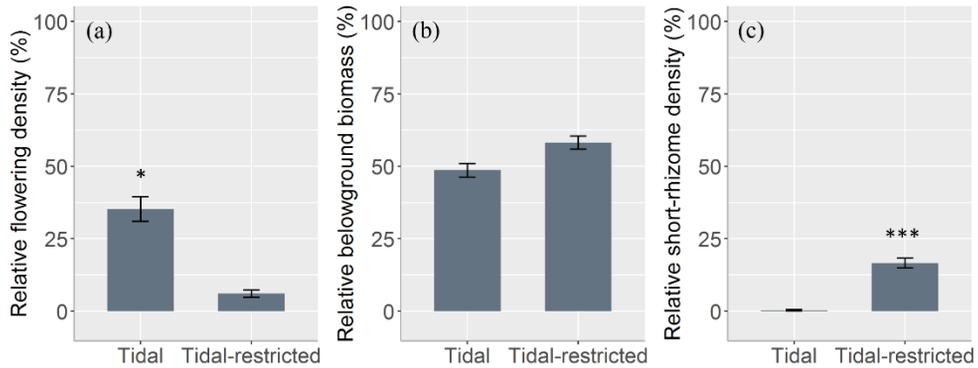
**Table 2. The overall responses between tidal marsh and tidal-restricted marsh**

	Tidal marsh (n=50)	Tidal-restricted marsh (n=49)	p
	Mean ( $\pm$ SD)	Mean ( $\pm$ SD)	
Total ramet density (ramet m <sup>-2</sup> )	<b>1046.08 (<math>\pm</math>487.70)</b>	<b>128.65 (<math>\pm</math>99.77)</b>	***
Total biomass (g m <sup>-2</sup> )	329.01 ( $\pm$ 116.07)	141.40 ( $\pm$ 100.43)	ns
Individual biomass (g)	0.43 ( $\pm$ 0.36)	1.18 ( $\pm$ 0.52)	ns
Shoot length (cm)	69.54 ( $\pm$ 12.58)	77.28 ( $\pm$ 9.66)	ns
Rhizome number per ramet	2.20 ( $\pm$ 0.34)	2.33 ( $\pm$ 0.62)	ns
Rhizome length (cm)	6.98 ( $\pm$ 1.92)	5.59 ( $\pm$ 2.07)	ns
Rhizome diameter (mm)	1.85 ( $\pm$ 0.42)	2.12 ( $\pm$ 0.49)	ns

The significance level: \*\*\* $p < 0.001$  and <sup>ns</sup> $p \geq 0.05$ . The tidal-restricted marsh had 49 replicates excluding a missing belowground datum in DS site. SD means a standard deviation.

### **2.3.2. Sexual, biomass, and rhizome allocation**

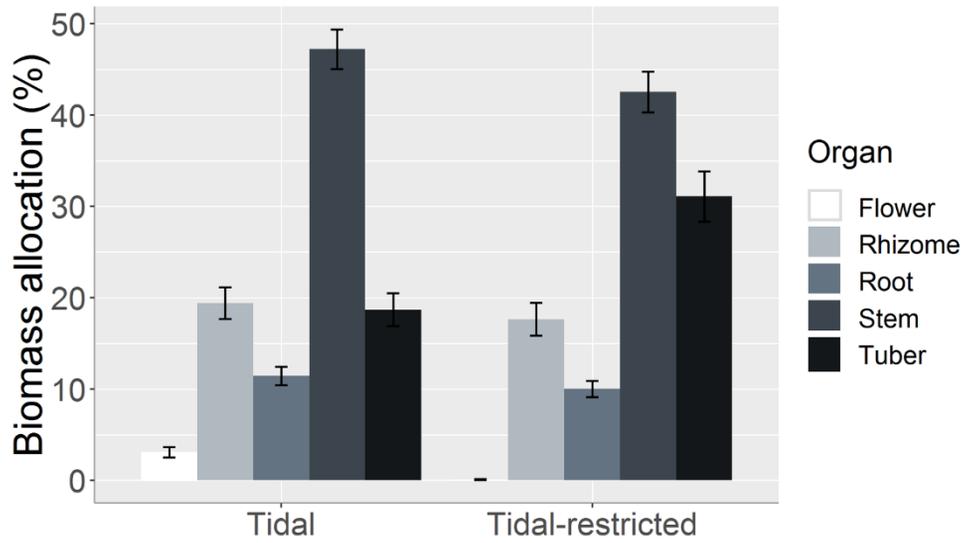
Among the three relative allocation ratios, two allocation ratios showed significant differences. The relative flowering density was higher in the tidal marsh than the tidal-restricted marsh (each  $35.27 \pm 29.68 \text{ \% m}^{-2}$  and  $6.15 \pm 8.99 \text{ \% m}^{-2}$ , mean  $\pm$  standard deviation,  $p < 0.05$ , Fig. 3a). The relative short-rhizome density was higher in the tidal-restricted marsh than the tidal marsh (each  $16.63 \pm 11.63 \text{ \% m}^{-2}$  and  $0.32 \pm 1.62 \text{ \% m}^{-2}$ ,  $p < 0.001$ , Fig. 3c). Otherwise, there was no significant difference of the relative belowground biomass between tidal marsh and tidal-restricted marsh (each  $48.66 \pm 16.53 \text{ \% m}^{-2}$  and  $56.69 \pm 15.82 \text{ \% m}^{-2}$ , Fig. 3b). Therefore, the counterpart of these allocation ratios showed the opposite results. Relative vegetative density was lower ( $p < 0.05$ ), and relative long-rhizome density was higher ( $p < 0.001$ ) in the tidal marsh than the tidal-restricted marsh. However, the relative aboveground biomass was not different between tidal marsh and tidal-restricted marsh (data were not shown).



**Figure 3. The allocation ratios of *B. planiculmis* between tidal marsh and tidal-restricted marsh.** (a) Relative flowering density (n=50 for tidal marsh, n=50 for tidal-restricted marsh), (b) Relative belowground biomass (n=50 for tidal marsh, n=49 for tidal-restricted marsh excluding a missing belowground datum in DS site), (c) Relative short-rhizome density (n=50 for tidal marsh, n=49 for tidal-restricted marsh excluding a missing belowground datum in DS site) with standard error bars. The significance level: \*\*\* $p < 0.001$  and \* $p < 0.05$ .

### 2.3.3. Biomass allocations to each organ

*B. planiculmis* in the tidal marsh and the tidal-restricted marsh showed similar biomass allocation patterns (Fig. 4). Both tidal marsh population and tidal-restricted marsh population showed the highest biomass allocation to stem ( $47.21 \pm 15.40 \% \text{ m}^{-2}$  and  $42.54 \pm 15.71 \% \text{ m}^{-2}$ , respectively), while there was no difference between tidal marsh and tidal-restricted marsh. Even though there was no significant difference, tuber biomass allocation tended to be higher in the tidal-restricted marsh ( $31.11 \pm 19.31 \% \text{ m}^{-2}$ ) than the tidal marsh ( $18.69 \pm 12.69 \% \text{ m}^{-2}$ ). On the other hand, flower biomass was almost negligible in the tidal-restricted marsh ( $0.12 \pm 0.27 \% \text{ m}^{-2}$ ), while it was slightly higher in the tidal marsh ( $3.11 \pm 4.00 \% \text{ m}^{-2}$ ) without significant difference. Allocations to rhizome were similar between tidal marsh and tidal-restricted marsh (each  $19.39 \pm 12.22 \% \text{ m}^{-2}$  and  $17.65 \pm 12.62 \% \text{ m}^{-2}$ ). Root biomass allocations also did not show any difference between tidal marsh and tidal-restricted marsh (each  $11.45 \pm 7.14 \% \text{ m}^{-2}$  and  $10.02 \pm 6.20 \% \text{ m}^{-2}$ ).



**Figure 4. Biomass allocations to each organ between tidal marsh and tidal-restricted marsh.** Mean relative dry biomass per  $m^{-2}$  for each organ: flower, rhizome, root, stem, and tuber with standard error bars (n=50 for tidal marsh, n=49 for tidal-restricted marsh excluding a missing belowground datum in DS site).

### 2.3.4. Environmental variables

The water depth and the neighbor IV were significantly higher in the tidal-restricted marsh than the tidal marsh (each  $p < 0.001$ ,  $p < 0.05$ , Table 3). The mean water depth in the tidal marsh was 0 cm because they were usually exposed to the air expect for spring tides biweekly. On the other hand, the water depth in the tidal-restricted marsh varied from 0 cm to above 25 cm (Appendix 2). The soil pH, SOM, SM, and  $\text{NO}_3^-$ -N showed little difference between tidal marsh and tidal-restricted marsh. SS was higher in the tidal-restricted marsh than in the tidal marsh; however, without significant difference.  $\text{PO}_4^{3-}$ -P and  $\text{NH}_4^+$ -N were higher in the tidal marsh than the tidal-restricted marsh without difference due to high site variations (Appendix 2).

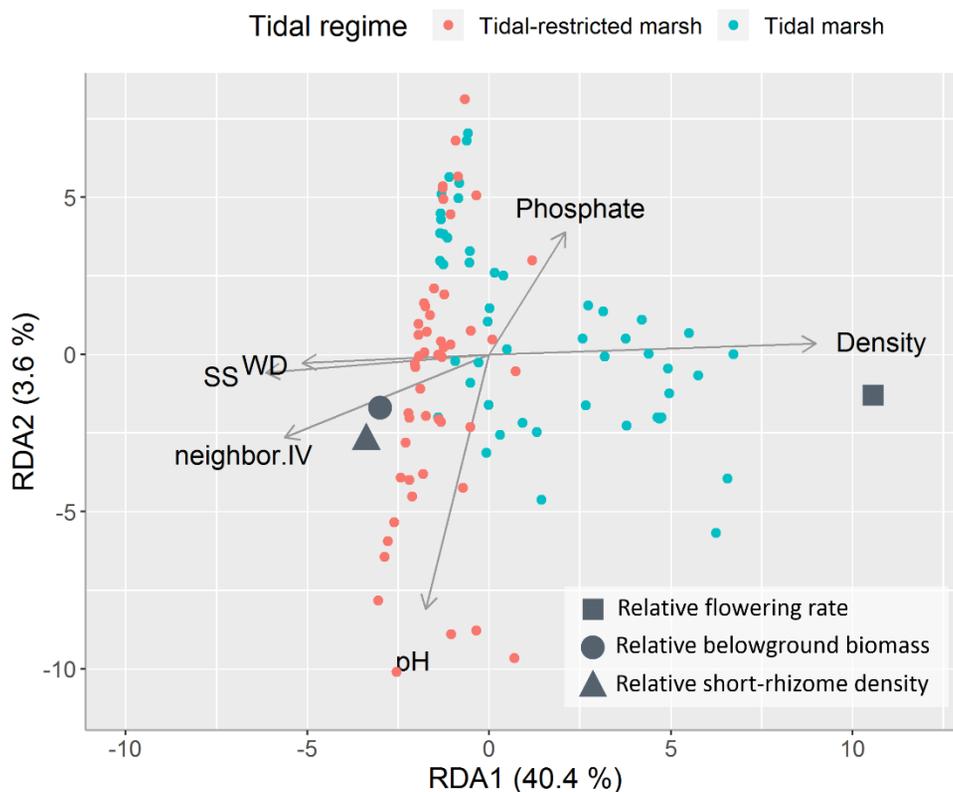
**Table 3. The environmental variables between tidal marsh and tidal-restricted marsh**

	Tidal marsh (n=50)	Tidal-restricted marsh (n=50)	p
	Mean ( $\pm$ SD)	Mean ( $\pm$ SD)	
Water Depth (cm)	<b>0.00 (<math>\pm</math>0.00)</b>	<b>9.29 (<math>\pm</math>8.44)</b>	***
Neighbor IV	<b>20.01 (<math>\pm</math>15.21)</b>	<b>51.82 (<math>\pm</math>18.42)</b>	*
Soil pH	6.80 ( $\pm$ 1.12)	7.90 ( $\pm$ 0.63)	ns
Soil Salinity (ppt)	0.31 ( $\pm$ 0.33)	0.69 ( $\pm$ 0.44)	ns
Soil Organic Matter (%)	3.11 ( $\pm$ 1.49)	2.28 ( $\pm$ 0.57)	ns
Soil Moisture (%)	28.69 ( $\pm$ 4.61)	25.82 ( $\pm$ 2.61)	ns
$\text{PO}_4^{3-}$ -P ( $\text{mg kg}^{-1}$ )	24.61 ( $\pm$ 20.28)	9.70 ( $\pm$ 6.22)	ns
$\text{NO}_3^-$ -N ( $\text{mg kg}^{-1}$ )	1.61 ( $\pm$ 1.36)	1.70 ( $\pm$ 1.04)	ns
$\text{NH}_4^+$ -N ( $\text{mg kg}^{-1}$ )	32.56 ( $\pm$ 26.14)	17.32 ( $\pm$ 16.32)	ns

The significance level: \*\*\*  $p < 0.001$ , \*  $p < 0.05$ , and <sup>ns</sup> $p \geq 0.05$ . SD means a standard deviation.

### 2.3.5. Relationships between allocation ratios and environmental variables

The RDA ordination was significant ( $p < 0.001$ ,  $F=12.52$ ,  $df=6$ ). The first axis was significant as well ( $p < 0.001$ ,  $F=69.64$ ,  $df=1$ ). The first axis of RDA was positively correlated with the density of *B. planiculmis* (0.939) and  $\text{PO}_4^{3-}\text{-P}$  (0.219), while negatively correlated with neighbor IV ( $-0.588$ ), water depth ( $-0.536$ ), soil salinity ( $-0.641$ ), and soil pH ( $-0.182$ ). The second axis was positively correlated with  $\text{PO}_4^{3-}\text{-P}$  (0.407), while negatively correlated with soil pH ( $-0.846$ ) and neighbor IV ( $-0.276$ ) (Fig. 5 and Table 4). The sum of canonical eigenvalues explained the 44.0 % of total variance, with the 40.4 % from the first axis, and 3.6 % from the second axis (Table 4). The adjusted  $R^2$  was 0.41. The relative flowering rate became higher when the density of *B. planiculmis* increased, while the relative short-rhizome density and the relative belowground biomass increased with higher neighbor IV, soil salinity, and water depth.



**Figure 5. An ordination conducted by RDA showing the relationships between allocation ratios and environmental variables.** Environmental variables were recorded as abbreviations. Density. The number of *B. planiculmis* ramets per quadrat; Neighbor IV. Importance value of the other species; WD. Water depth; SS. Soil salinity; pH. Soil pH; and Phosphate.  $\text{PO}_4^{3-}\text{-P}$ . The red points were quadrats in the tidal-restricted marsh, while the blue points were quadrats in the tidal marsh.

**Table 4. The summary of RDA**

	RDA1***	RDA2
Eigenvalues	453.17	40.54
Proportion of variance (%)	0.404	0.036
Cumulative variance (%)	0.404	0.440
Density***	0.939	0.036
neighbor IV	-0.588	-0.276
WD***	-0.536	-0.027
SS***	-0.641	-0.059
pH**	-0.182	-0.846
Phosphate*	0.219	0.407

Environmental variables were recorded as abbreviations. Density. The number of *B. planiculmis* ramets per quadrat; Neighbor IV. Importance value of the other species; WD. Water depth; SS. Soil salinity; pH. Soil pH; and Phosphate.  $\text{PO}_4^{3-}$ -P. The significance level: \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , and \* $p < 0.05$  (n=99 excluding a missing datum in the DS site).

## **2.4. Discussion**

In this study, *B. planiculmis* in the tidal marsh showed higher density and sexual reproduction, while *B. planiculmis* in the tidal-restricted marsh showed higher short-rhizome density. On the other hand, the biomass allocations to belowground and aboveground were not different between tidal marsh and tidal-restricted marsh. The water depth and the dominance of the other species were higher in the tidal-restricted marsh. These results supported the first hypothesis showing different responses of *B. planiculmis* and environmental variables between tidal marsh and tidal-restricted marsh. For the second hypothesis, the sexual reproduction seemed to become higher with the intense intraspecies competition. The relative short-rhizome density and the relative belowground biomass were likely to increase with deeper water depth, higher dominance of the other species, and higher soil salinity.

### **2.4.1. Environmental variables and the responses of *B. planiculmis* in tidal marshes**

In this study, the tidal marsh had relative shallower water depth and the lower dominance of the other species (Table 3). The water depth was 0 cm. It was because the tidal marsh was usually exposed to the air except for the spring tide biweekly, and the sampling was conducted at least three days after the spring tide or rains for stabilized soil moisture. The dominance of the other species was relatively low because the ability of each species to the environmental stress in the tidal marsh might be different. *Bolboschoenus spp.* had strong abilities to adapt the tidal and flooding stress (Carus et al. 2016, Silinski et al. 2018), which might enable them to locate in the lowest elevation (You 2008, Kim et al. 2016). However, the major

companion species, *Phragmites australis* and *Carex scabrifolia* preferred higher elevation (Bang et al. 2018), probably due to the less ability to tidal stress.

*B. planiculmis* grown in the tidal marsh produced higher density around 1046 ramet m<sup>-2</sup> than 128 ramet m<sup>-2</sup> in the tidal-restricted marsh (Table 2). The increased density in a tidal marsh than a sheltered marsh could also be observed in *Bolboschoenus maritimus* (Silinski et al. 2018). They explained this phenomenon as a self-adapting mechanism to attenuate wave strength with dense ramets. In this study, the higher ramet density of *B. planiculmis* in the tidal marsh seemed to affect the flowering rate. Generally, the flowering rate of clonal plants increases when the ramet density becomes higher (Sun et al. 2001, Sun et al. 2002, Olejniczak 2003). The number of flowering ramets was known to indicate the sexual reproductive response, while the number of vegetative ramets could indicate the asexual reproduction response (Sun et al. 2001, Chen et al. 2015). The sexual reproduction may help to escape the higher intraspecies competition and to occupy the new area. However, the vegetative reproduction seems to be a proper in lower density due to its low mortality than seeds (Ikegami et al. 2012). This study also showed the higher flowering rate in the tidal marsh where the ramet density was higher than the tidal-restricted marsh, which supported the sexual-aseexual strategies (Fig. 3a, Fig. 5).

#### **2.4.2. Environmental variables and the responses of *B. planiculmis* in tidal-restricted marshes**

In this study, the tidal-restricted marsh usually had a deeper water depth and higher dominance of the other species (Table 3). Tidal restrictions would cause the impounded marsh that was permanently inundated for short-term and drained marsh

for long-term (Montague et al. 1987). Among the five tidal-restricted marshes, four marshes were flooded permanently. One saturated marsh, Iwon tidal-restricted marsh, was inundated sporadically after rains. Under the permanent flooding without the tide, *B. planiculmis*, the early successional species, can be easily replaced by the other competitive species such as *Phragmites australis*, *Echinochloa crusgalli*, and *Echinochloa caudate* (Bornette and Puijalon 2011, Ning et al. 2014, Liu et al. 2016a). In this study, the dominant occupancy by the other species in the tidal-restricted marsh might be competitive to *B. planiculmis* reducing its density and coverage.

*B. planiculmis* in the tidal-restricted marsh tended to increase tuber biomass allocation and to decrease flower and stem biomass allocation compared to the tidal marsh population (Fig. 4). The tidal-restricted marsh had a deeper water depth. However, the increased water depth did not affect or rather decreased the tuber biomass allocation (Clevering and Hundscheid 1998, Blanch et al. 1999), which could not explain the result of this study. On the other hand, the dominant occupancy of the other species in the tidal-restricted marsh might be able to explain this result. The higher density of a neighbor species increased the allocation to the belowground biomass of a target species when the neighbor species was more competitive than the target species (Wu and Yu 2004). The increased belowground biomass would enhance the ability to capture belowground resources such as water and nutrients under harsh competition (Edwards et al. 2003, Mccarthy and Enquist 2007). Besides, the increased tuber biomass can facilitate the shoot elongation with the stored energy in tubers (Blanch et al. 1999). In short, *B. planiculmis* in the tidal-restricted marsh might allocate more energy to belowground, especially tuber, due to higher belowground competition under the dominance of the other species (Fig. 5). Further study should include belowground biomass of other species as covariate variables.

Relative short-rhizome or phalanx rhizome has been recognized to consolidate the original habitats, while the relative long-rhizome or guerrilla rhizome has been known to find a new area (Doust 1981, Humphrey and Pyke 1998, Ye et al. 2006). In this study, relative short-rhizome density was higher in the tidal-restricted marsh where the dominance of the other species was higher (Fig. 5). This result corresponded to previous studies that maintained severe competitive stress or too small patch could result in the high number of short-rhizomes or phalanx rhizome for *Scirpus olneyi*, *Amphibromus scabrivalvis*, and *Carex* spp. (Bernard 1990, Cheplick 1997, Ikegami et al. 2007). Based on these previous studies, the dominance of the neighbor species in the tidal-restricted marsh would play a role as competition to *B. planiculmis*. Besides, the relative short-rhizome rarely appeared in the tidal marsh where intraspecies competition was higher than the tidal-restricted marsh. A possible explanation is that interspecific competition might have more significant impacts on the short-rhizome density than competition within the same species (Cheplick 1997, Ikegami et al. 2007). It could be because that the short-rhizome was beneficial to persist under the stressful areas, making better use of the local resources among many neighbor species (Humphrey and Pyke 1998).

### **2.4.3. Limitations and righteousness of this study**

More direct factors caused by tidal restriction could affect the observed responses, such as flow speed, flooding frequency, and flooding durations (Mora and Burdick 2013, Silinski et al. 2018). These changes are one of the major factors to affect the responses of marsh plants (Kaelke and Dawson 2003). Besides, less-related or unrelated factors also could contribute to these results. Altered sediment dynamics by tidal restriction could affect the growth and allocation patterns of populations (Li

et al. 2014). Grazing by livestock or wildlife might be another potential factor to disturb the vegetation responses (Greet et al. 2013). Different land use among sites, such as cultivation field, military area, and non-use area, might affect the responses of marsh plant. Nevertheless, sites were haphazardly selected, and these factors were not systematically varied. Therefore, I maintain the tidal-restriction would be the most fundamental factor to contribute the responses of *B. planiculmis* by inducing direct and indirect impacts.

## 2.5. Conclusion

This study investigated the responses of *B. planiculmis* and environmental variables between tidal marsh and tidal-restricted marsh. The tidal marsh population increased the sexual reproduction and relative long-rhizome with higher density. On the other hand, the tidal-restricted marsh population preferred the asexual reproduction and relative short-rhizome with less density. These responses could result from deeper water and intense occupancy of the other species, which might be caused by tidal restriction. This study proposed *B. planiculmis* would favor the tidal marsh rather than the tidal-restricted marsh where the local population could not grow easily and might experience intense interspecies interaction. The interspecies interaction and hydrodynamics including flooding depth, flooding frequency, and flooding duration should be considered to preserve and restore the *B. planiculmis* marsh. Future study is needed to clarify the effects of these environmental variables on the responses of *B. planiculmis*.

**Chapter III. Effects of tide on the interspecies  
interaction and responses of *B. planiculmis***

### **3.1. Introduction**

Marsh plants are exposed to various impacts of abiotic and biotic factors that can determine their distribution. The abiotic stress can change the plant-plant interactions along the increased environmental stress gradients. According to the stress-gradient hypothesis (SGH), the plant-plant interaction is competition when the abiotic stress is low; however, it becomes facilitation when the abiotic stress increases (Maestre et al. 2009, Qi et al. 2018). The SGH has widely explained the interspecies interaction in various environmental gradients in estuaries such as salinity, water depth, and clipping (Wang and Li 2016, Zhou et al. 2018). Not only these factors but also tidal regime is one of the major abiotic factors of estuaries, which varies from at least biweekly to twice a day (Armstrong et al. 1985, Pennings et al. 2005). The tidal regime significantly affects the marsh plants in low elevation by increasing mechanical stress and flooding depth, while it less affects the plants in high elevation (Leonard and Luther 1995, Silinski et al. 2018). Nevertheless, there was little understanding of the effects of tidal regimes on the plant-plant interactions.

Each plant responds to the tidal exposure differently using avoidance strategy or tolerance strategy. The avoidance strategy is to minimize the mechanical stress by changing the plastic responses, for example, short shoot length, flexible shoot, higher density, and increased allocation to belowground for preventing from uprooting (Niklas 1998, Doyle 2001, Puijalon et al. 2008b, Silinski et al. 2018). On the other hand, the tolerance strategy means efforts to maximize the resistance to the mechanical tipping point just before breaking, which includes long shoot length, higher tissue rigidity, and higher allocation to aboveground biomass (Coops and Van der Velde 1996, Puijalon et al. 2008b, Puijalon et al. 2011). The difference ability of

each species may result in the shift of interspecies interaction under tidal condition and non-tidal condition.

*B. planiculmis* is an early successional species in estuaries and dwells in the nearest water body in low elevation (Kim et al. 2013, Wang and Li 2016). Also, it faces intense interspecies interactions with plants in middle elevation such as *Phragmites australis*, *Echinochloa* spp., and *Carex scabrifolia* (Kim et al. 2013, Wang and Li 2016). Effects of abiotic factors or biotic factors on the responses of *Bolboschoenus* spp. have been separately studied regarding flooding regimes, salinity, grazing, and interspecies interaction (Kim et al. 2013, Liu et al. 2016a, Xue et al. 2017). However, in the real world, the responses of *B. planiculmis* can be affected by interspecies interaction shift along the environmental stress gradients. Recently, Zhou et al. (2018) clarified the effects of the increased water depth and water fluctuation could change the interspecies interaction of *P. australis* against *B. planiculmis*. However, there is still a need to understand the tidal effects on the interspecies interaction shifts of *B. planiculmis*.

In this study, a greenhouse experiment was conducted to investigate the interspecies interaction and responses of *B. planiculmis* under the tidal regimes with *C. scabrifolia* as a neighbor species. The growth, morphological plasticity, and reproduction of two species *B. planiculmis* and *C. scabrifolia* were measured with two regimes (tide and interspecies interaction). The objective of this study was to clarify the impacts of the tide on the interspecies interaction and responses of *B. planiculmis*. Two hypotheses were built up; (1) tidal regimes change the responses such as growth, morphological plasticity, and reproduction of *B. planiculmis*, (2) the tidal regimes change the interspecies interaction of *B. planiculmis* against *C. scabrifolia* along with the tidal stress gradient.

## 3.2. Methods

### 3.2.1. Collection of *B. planiculmis* and *C. scabrifolia* seedlings

*B. planiculmis* is a perennial clonal plant with 20–100 cm height and dominates in lower elevation in estuaries (Kim et al. 2013). *C. scabrifolia* was selected as a neighbor species since it has similar life cycle and size with *B. planiculmis* among the other companion species. *C. scabrifolia* is also a perennial clonal plant with 30–100 cm height and overwhelms in low to the middle elevation in estuaries. Both species usually were co-observed and reproduced with both sexual and asexual organs (Wang and Li 2016).

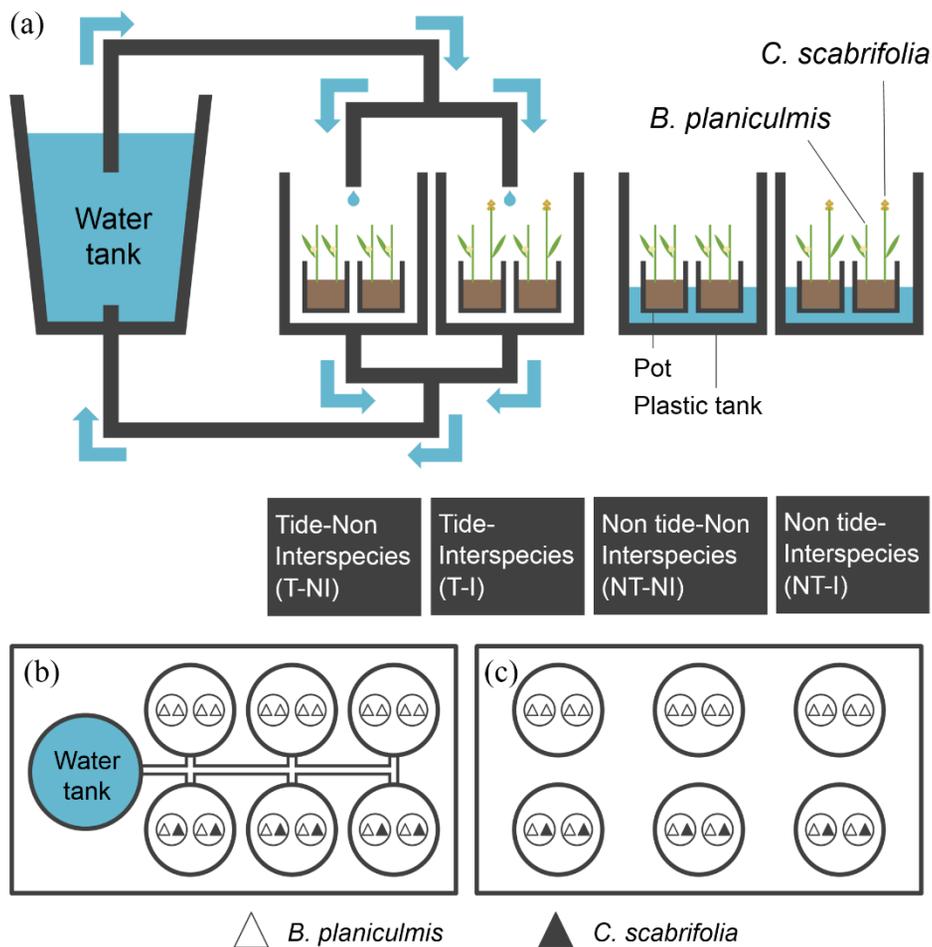
In May 15<sup>th</sup>, seedlings of *B. planiculmis* and *C. scabrifolia* were collected at Gongreong-river, Paju, South Korea (lat 37°45'31.00"N, long 126°41'43.75"E) where the mean temperature was from –12.4°C to 28.3°C, the mean precipitation was 947.8 mm, and the salinity was from 0 ppt to 5 ppt (Administration 2011, Ha et al. 2018). In the field, the shoot length of *B. planiculmis* was around 10.0±3.24 cm, and the shoot length of *C. scabrifolia* was 42.25±5.36 cm. Different shoot length for two species were used because *C. scabrifolia* usually grew faster than *B. planiculmis*, and these differences seemed more realistic in field. Seedlings of two species were transported to a laboratory within a moist and cool plastic container. After wrapping their roots with the field soil, each seedling was transplanted in a 200 L pot respectively with a 10 cm depth of 1 mm sandy soil. At the age of 7 days, pairs of seedlings were chosen to be used for the experiment.

### 3.2.2. Experimental design and sample processing

Growth and responses of each species were examined under the presence and absence of tides and interspecies interaction. The tidal regimes reflected the maximum tidal exposure, twice a day, (1) tidal treatment: an hour flooding up to 40 cm and 11 hour drainage at  $-5$  cm from the soil surface, a total 12 hour cycle was repeated two times a day; (2) non-tidal treatment: keeping the water at  $-5$  cm from the soil surface. Rising and falling tides were imitated by pumping motors (Synkra 1.5, SICCE) with 15 L/min velocity from a 300 L water tank, and the flow direction was unidirectional. The interspecies interaction regimes imitated the common plant-plant interaction in the field, (1) interspecies interaction treatment: one *B. planiculmis* seedling and one *C. scabrifolia* seedling per pot; (2) non-interspecies interaction treatment: two *B. planiculmis* seedlings per pot. This ratio between species reflected the relative dominance of neighbor species in the field (Table 3). Therefore, two ramets were transplanted to a pot (15 cm diameter and 15 cm height) which contained a 15 cm depth of 1 mm sandy soil. Two pots were contained in a plastic tank (44 cm diameter and 53 cm height) to control tidal regimes (Fig. 6).

The effects of tide and interspecies interaction were examined from early-May to early-October 2018, in a greenhouse located at Seoul National University, Seoul, South Korea (lat  $37^{\circ}27'34.12''\text{N}$ , long  $126^{\circ}56'52.24''\text{E}$ ). There were total 24 pots with four treatments and six replicates. Salinity was not considered for this experiment because *B. planiculmis* could dominate in the freshwater tidal wetlands where the salinity was around 0.5 ppt (Table 3), and it could survive at both freshwater (0 ppt) and estuarine condition (up to 10 ppt) with no biomass difference (Xue et al. 2017). For the clear water quality, pots were entirely drained off and filled with tap water every other week. Final biomass was harvested on October 8<sup>th</sup> and

washed through a 1 mm sieve. *B. planiculmis* were separated into flower, stem, rhizome, tuber, and root, while *C. scabrifolia* was divided into flower, stem, rhizome, and root since it did not produce tuber. Plant materials were dried at 80 °C for 72 hours. The rhizome and root of two species were carefully separated based on the rhizome morphology keeping the rhizome and root unbroken.



**Figure 6. Experimental design.** (a) Tide and interspecies interaction experiment flowchart, (b) Aeroview of the T-NI and T-I treatment, (c) Aeroview of the NT-NI and NT-I treatment.

### 3.2.3. Statistical analyses

First, the relative interaction index (RII) of *B. planiculmis* was compared between tidal treatment and non-tidal treatment. The RII is a proper index to measure the plant-plant interactions from competition to facilitation symmetrically (Armas et al. 2004). The RII was calculated by this equation.

$$\text{RII} = \frac{B_W - B_O}{B_W + B_O}$$

$B_W$  is the total biomass of a target species grown in mixed culture, while  $B_O$  is the total biomass of the target species grown in monoculture. When the RII is 0, it indicated there is no significant interaction between two species (neutral). The positive RII means the interaction is facilitative to the target species, while the negative RII indicates the interaction is competitive to the target species. Whether the mean RII values were different from 0 was checked by one-sample t-test. Normality assumption was confirmed by Shapiro test.

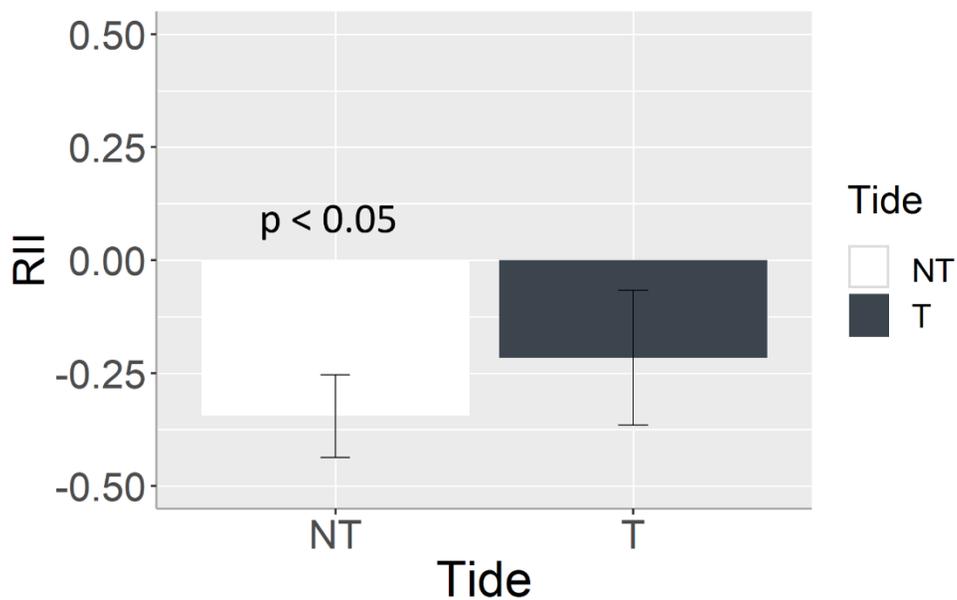
Secondly, two-way ANOVA was conducted to explain the variance of total biomass per pot, individual biomass, biomass allocations, density, shoot length, stem width, sum of the rhizome length, flowering rate, and the number of tubers of *B. planiculmis* with two categories (tide and interspecies interaction). These data were log or square transformed to meet the assumptions. Normality assumption was checked by Shapiro test, and homoscedasticity assumption was identified with Levene's test in 'car package' in R. Post-hoc analyses were done by Tukey's honestly test in 'agricolae package'.

Lastly, the total biomass, individual biomass, biomass allocations, density, shoot length, stem width, sum of the rhizome length, and flowering rate of *C. scabrifolia* were also compared with Student's t-test between tidal treatment and non-tidal treatment. Normality assumption was verified by the Shapiro test. All statistical analyses were performed with R version 3.4.3 (Development Core Team 2008). The values were considered as significantly different at  $p < 0.05$ .

### 3.3. Results

#### 3.3.1. RII shift of *B. planiculmis* depending on the tidal regimes

The mean RII value of *B. planiculmis* was significantly negative when *B. planiculmis* grew in non-tidal treatment (competitive) ( $p < 0.05$ , Fig. 7). However, the mean RII value of tidal treatment was not different from 0 (neutral). Even though both RII values were negative, the RII value was increased according to tidal regimes.



**Figure 7. The mean RII value of *B. planiculmis* between non-tidal treatment and tidal treatment. NT indicates non-tidal treatment; T indicates tidal treatment.**

### 3.3.2. The growth of *B. planiculmis*

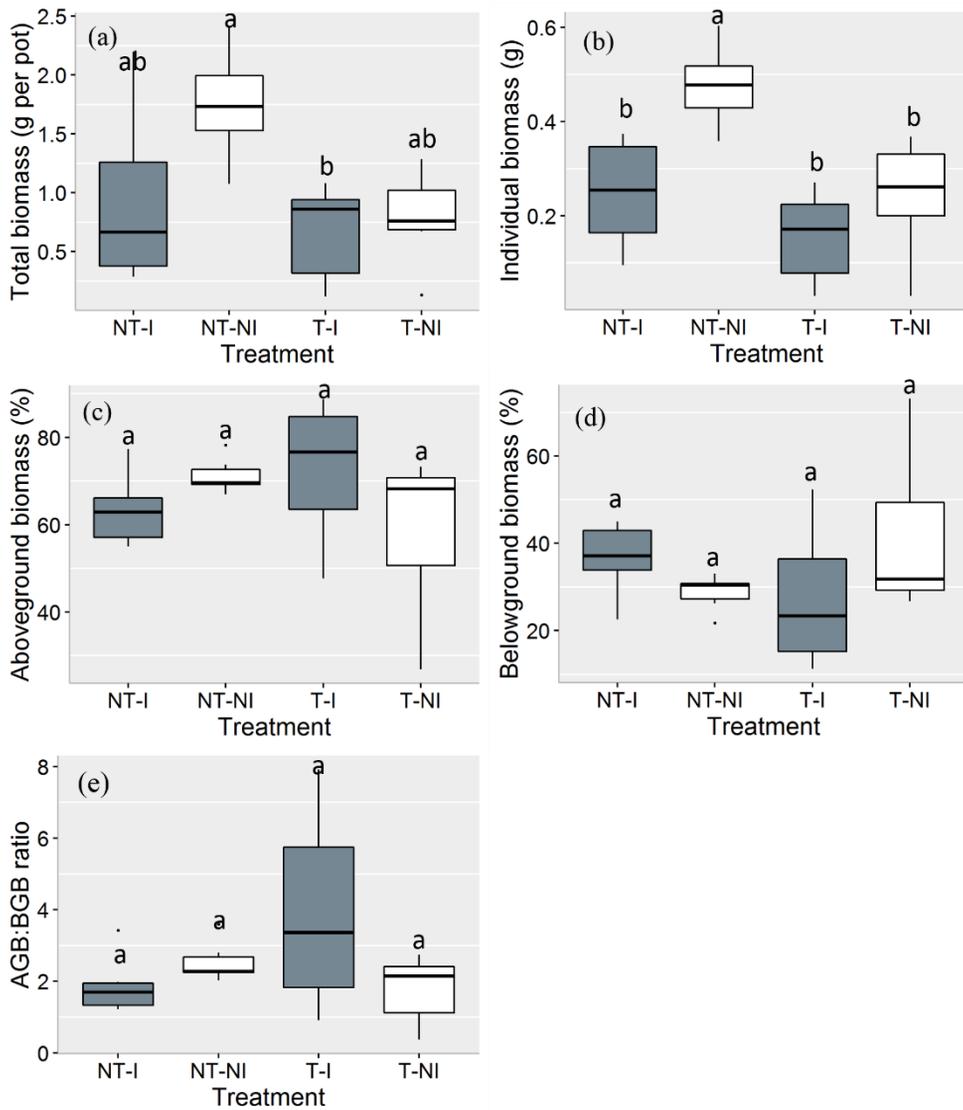
The total biomass per pot was affected by tidal regimes ( $p < 0.05$ ,  $F=7.985$ ,  $df=1$ ) and interspecies interaction regimes ( $p < 0.05$ ,  $F=4.724$ ,  $df=1$ ), with no interaction (Table 5). The total biomass of control treatment (NT-NI) was higher than the tide and interspecies interaction treatment (T-I) ( $p < 0.05$ , Fig. 8a). Similarly, the individual biomass was changed by both the tidal regimes ( $p < 0.01$ ,  $F=13.975$ ,  $df=1$ ) and the interspecies interaction regimes ( $p < 0.01$ ,  $F=12.970$ ,  $df=1$ ) with no interaction (Table 5). The control treatment (NT-NI) was higher than the other treatments significantly ( $p < 0.05$ , Fig. 8b). The total biomass and the individual biomass were lower in the tidal treatment than the non-tidal treatment, and lower in the interspecies interaction treatment than the non-interspecies interaction treatment.

The relative aboveground biomass was not affected by the tidal regimes and interspecies interaction regimes (Table 5). There was no interaction as well. Even though the mean relative aboveground biomass was highest in the tide and interspecies interaction treatment (T-I), all treatments were not different among them (Fig. 8c). The relative belowground biomass was not affected by the tidal regimes and interspecies interaction regimes but their interaction ( $p < 0.05$ ,  $F=4.575$ ,  $df=1$ , Table 5). The tide and interspecies interaction treatment (T-I) had the lowest relative belowground biomass; however, without differences among treatments (Fig. 8d). Similarly, the interaction between tidal regimes and interspecies interaction regimes influenced on the AGB:BGB ratio ( $p < 0.05$ ,  $F=5.005$ ,  $df=1$ , Table 5). The tide and interspecies interaction treatment (T-I) showed the highest AGB:BGB ratio; however, without Tukey's significance (Fig. 8e).

**Table 5. Two-way ANOVA tables for the growth of *B. planiculmis* with two regimes (tide and interspecies interaction, n=24)**

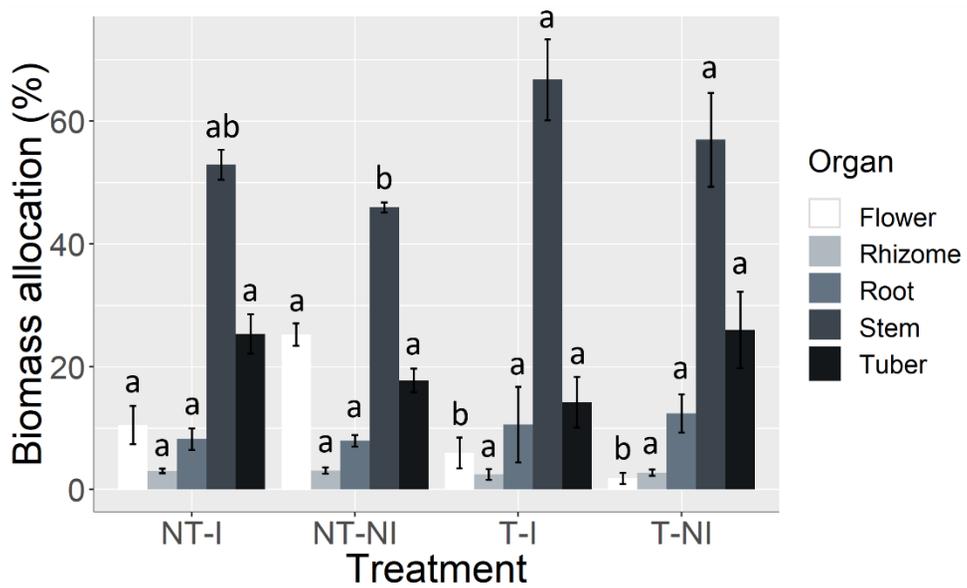
	Tidal regimes (T)		Interspecies interaction regimes (I)		T × I	
	F <sub>(1,20)</sub>	p	F <sub>(1,20)</sub>	p	F <sub>(1,20)</sub>	p
Total biomass (g per pot)	<b>7.985</b>	*	<b>4.724</b>	*	2.695	ns
Individual biomass (g)	<b>13.975</b>	**	<b>12.970</b>	**	2.619	ns
Aboveground biomass (%)	0.081	ns	0.329	ns	4.094	0.05
Belowground biomass (%)	0.002	ns	0.452	ns	<b>4.575</b>	*
AGB:BGB ratio	0.316	ns	0.900	ns	<b>5.005</b>	*
Flower biomass (%)	<b>22.028</b>	***	1.359	ns	<b>8.417</b>	**
Stem biomass (%)	<b>4.638</b>	*	2.676	ns	0.070	ns
Rhizome biomass (%)	1.282	ns	0.385	ns	0.348	ns
Tuber biomass (%)	0.533	ns	0.376	ns	<b>5.715</b>	*
Root biomass (%)	0.233	ns	0.608	ns	0.590	ns

The significance level: \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , and <sup>ns</sup> $p \geq 0.05$ .



**Figure 8. The growth of *B. planiculmis* among the treatments.** (a) Total biomass of each treatment, (b) Individual biomass of each treatment, (c) Relative aboveground biomass of each treatment, (d) Relative belowground biomass of each treatment, (e) AGB:BGB ratio of each treatment. Different letters indicate significant difference among treatment. NT indicates non-tidal treatment; T indicates tidal treatment; NI indicates non-interspecies interaction treatment; I indicates interspecies interaction treatment.

Biomass allocations to different organs were varied depending on the treatments (Fig. 9). Relative flower biomass was affected by the tidal regimes ( $p < 0.001$ ,  $F=22.028$ ,  $df=1$ ) and the interaction between tidal and interspecies interaction regimes ( $p < 0.01$ ,  $F=8.417$ ,  $df=1$ , Table 5). Among the treatments, the relative flower biomass of tidal treatments (T-I and T-NI) were significantly lower than the non-tidal treatment (NT-I and NT-NI) (both  $p < 0.05$ , Fig. 9). Relative stem biomass was influenced by the tidal regimes ( $p < 0.05$ ,  $F=4.638$ ,  $df=1$ , Table 5) showing higher allocation to stem in the tidal treatments (T-I and T-NI) than the control treatment, NT-NI (both  $p < 0.05$ , Fig. 9). Allocation to tuber seemed to be affected by the interaction between tidal regimes and interspecies interaction regimes ( $p < 0.05$ ,  $F=5.715$ ,  $df=1$ , Table 5); however, without Tukey's significant (Fig. 9). Allocations to rhizome and root were not changed by the tidal regimes, interspecies interaction regimes, and their interaction among the treatments (Table 5 and Fig. 9).



**Figure 9. Biomass allocations to each organ of *B. planiculmis* among the treatments.** Different letters indicate a significant difference in the same organ among the treatments. NT indicates non-tidal treatment; T indicates tidal treatment; NI indicates non-interspecies interaction treatment; I indicates interspecies interaction treatment.

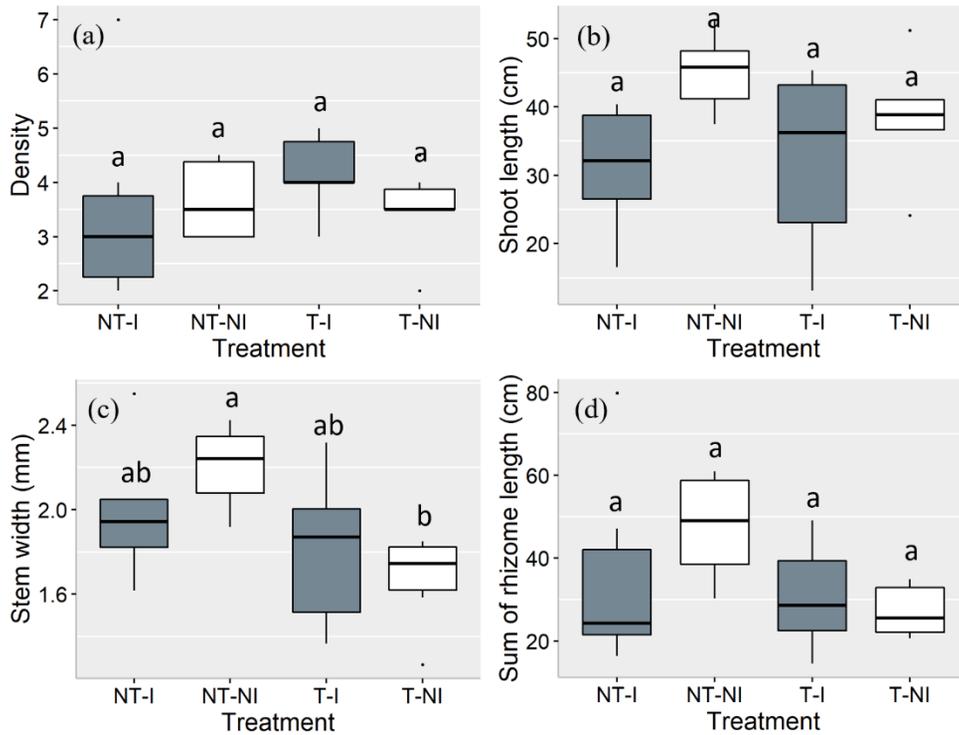
### **3.3.3. The morphological plasticity of *B. planiculmis***

The density was not affected by the tidal regimes, interspecies interaction regimes, and their interaction (Table 6). The control treatment (NT-NI) was not different from the other treatments (Fig. 10a). The shoot length was altered by interspecies interaction regimes ( $p < 0.05$ ,  $F=5.949$ ,  $df=1$ , Table 6). The interspecies interaction treatment reduced the shoot length than non-interspecies interaction treatment did; however, without Tukey's difference (Fig. 10b). The tidal regimes influence on the stem width ( $p < 0.01$ ,  $F=9.237$ ,  $df=1$ , Table 6), while the interspecies interaction regimes did not. The stem width was thinner in the tidal treatment (T-I and T-NI) than in the non-tidal treatment (NT-I and NT-NI). The tide and non-interspecies interaction treatment (T-NI) showed a thinner stem width compared to the control treatment (Fig. 10c). The sum of rhizome length showed no difference according to the tidal regimes, interspecies interaction regimes, and their interaction. It was slightly longer in the control treatment (NT-NI) than the other treatments but without any significant difference (Fig. 10d).

**Table 6. Two-way ANOVA tables for the morphological plasticity of *B. planiculmis* with two regimes (tide and interspecies interaction, n=24)**

	Tidal regimes (T)		Interspecies interaction regimes (I)		T × I	
	F <sub>(1,20)</sub>	p	F <sub>(1,20)</sub>	p	F <sub>(1,20)</sub>	p
Density (shoot per pot)	0.462	ns	0.150	ns	1.178	ns
Shoot length (cm)	0.427	ns	<b>5.949</b>	*	0.685	ns
Stem width (mm)	<b>9.237</b>	**	0.112	ns	2.231	ns
Sum of rhizome length (cm)	3.753	ns	0.757	ns	1.866	ns

The significance level: \*\* $p < 0.01$ , \* $p < 0.05$ , and <sup>ns</sup> $p \geq 0.05$ .



**Figure 10. The morphological plasticity of *B. planiculmis* among the treatments.** (a) The density of each treatment, (b) The shoot length of each treatment, (c) The stem width of each treatment, (d) The sum of the rhizome length of each treatment. Different letters indicate significant difference among the treatment. NT indicates non-tidal treatment; T indicates tidal treatment; NI indicates non-interspecies interaction treatment; I indicates interspecies interaction treatment.

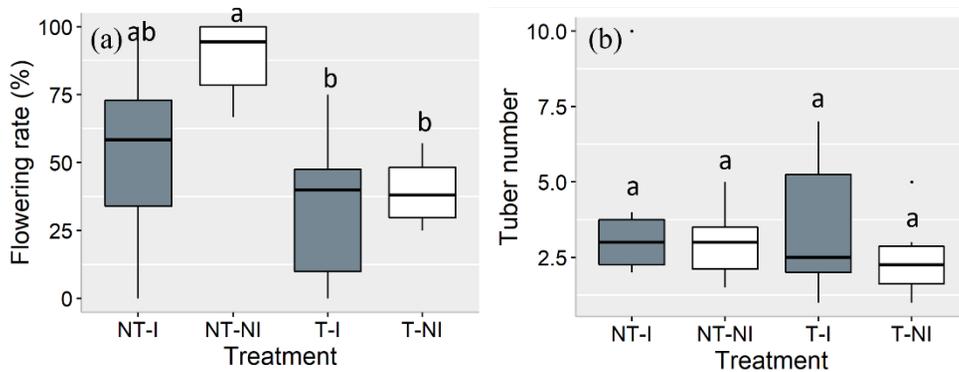
### **3.3.4. Reproduction of *B. planiculmis***

The flowering rate was influenced by the only tidal regimes ( $p < 0.01$ ,  $F=11.172$ ,  $df=1$ ), regardless of the interspecies interaction regimes and their interaction (Table 7). It was lower in the tidal treatment than the non-tidal treatment. The control treatment (NT-NI) showed the higher flowering rate than the tide and interspecies interaction treatment (T-I) and the tide and non- interspecies interaction treatment (T-NI) (both  $p < 0.05$ , Fig. 11a). The number of tubers was not affected by the tidal regimes, interspecies interaction regimes, and their interaction (Table 7). The number of tubers was almost same among the treatments (Fig. 11b).

**Table 7. Two-way ANOVA tables for reproduction of *B. planiculmis* with two categories (tide and interspecies interaction, n=24)**

	Tidal regime (T)		Interspecies interaction regime (I)		T × I	
	F <sub>(1,20)</sub>	p	F <sub>(1,20)</sub>	p	F <sub>(1,20)</sub>	p
Flowering rate (%)	<b>11.172</b>	<b>**</b>	3.921	ns	2.127	ns
Tuber number (per pot)	0.470	ns	1.066	ns	0.006	ns

The significance level: **\*\*** $p < 0.01$  and *ns* $p \geq 0.05$ .



**Figure 11. Reproduction of *B. planiculmis* among the treatments.** (a) The flowering rate of each treatment, (b) The number of tubers per pot of each treatment. Different letters indicate significant difference among the treatments. NT indicates non-tidal treatment; T indicates tidal treatment; NI indicates non-interspecies interaction treatment; I indicates interspecies interaction treatment.

### 3.4. Discussion

In this study, the interspecies interaction was negative to *B. planiculmis* in the non-tidal treatment; however, it was changed to neutral in the tidal treatment. The tide and interspecies interaction brought negative impacts on the growth of *B. planiculmis*. Tide induced the thinner stem width, but it did not result in the other plastic responses. Interspecies interaction reduced the shoot length regardless of the tidal regimes.

#### 3.4.1. Interspecies interaction shift depending on the tidal regimes

The mean RII value of *B. planiculmis* was negative in stable condition; however, it became neutral in the tidal condition (Fig. 7). This result corresponded with the SGH in that the interaction was changed from competition to neutral according to the environmental stress gradients (He et al. 2013, Qi et al. 2018), even though the facilitation was not observed in this study. The lack of facilitation in harsh environment commonly appeared depending on the stress type, species, and the degree of stress (Choler et al. 2001, Maestre et al. 2009, Qi et al. 2018). A possible explanation of the RII shift is that each species has different ability to avoid or tolerant of the tidal flooding stress. Similar species, *B. maritimus* which located in the water frontier zone, showed higher ability to avoid the currents with flexible plasticity (Carus et al. 2016, Silinski et al. 2018). This study also showed significant flexible responses (thinner stem width) of *B. planiculmis* compared to *C. scabrifolia* (Fig. 10 and Appendix 3, see discussion 2).

### 3.4.2. Effects of the tidal regimes on *B. planiculmis*

Tidal stress can reduce the biomass of diverse species (Szmeja 1994, Doyle 2001, Sun et al. 2002, Puijalon et al. 2008b), which was supported by this study. The individual biomass and the total biomass per pot of the tidal treatment was only 50 % of the non-tidal treatment, showing the tidal flooding was the major stress to *B. planiculmis* (Fig. 8).

Tides also can give important impacts on the plasticity of marsh plants. For example, plant exposed to tides showed denser, shorter, thinner, flexible shoots, longer root, and decreased AGB:BGB ratio to prevent from uprooting. Otherwise, plants made stiffer and longer shoots, shorter root, and increased AGB:BGB ratio to tolerate the relatively weak tidal stress in sheltered marshes (Blanchette 1997, Peralta et al. 2008, Silinski et al. 2018). This study showed the thinner stem width in the tidal treatment (Fig. 10c), which supported the avoidance strategy. The thinner, smaller, and more flexible stems can avoid the wave stress than the counterparts by reducing exposed surface (Puijalon et al. 2008a, Silinski et al. 2015, Silinski et al. 2018). However, the other plastic responses were not observed regarding the density, shoot length, rhizome length, and AGB:BGB ratio in this study (Fig. 8 and 10). Some studies revealed these responses could be plastic or non-plastic depending on the species (see Puijalon et al. (2008b) for the density and height, Szmeja (1994) for the root length). Rather, *B. planiculmis* increased the allocation to stem biomass in the tidal treatment, which contrasted to the avoidance strategy (Fig. 9). A possible explanation was that the tidal treatment induced not only mechanical stress but also short-period flooding stress compared to the non-tidal treatment, so it facilitated the stem elongation (Chen et al. 2011, Hattori et al. 2011).

Reproduction of marsh plants can be affected by mechanical stress, including water flow and wind (Niklas 1998, Puijalon et al. 2008b). Under tidal exposure, sexual reproduction decreases but asexual reproduction increases with a trade-off relationship (Sun et al. 2002, Puijalon et al. 2008b), since the asexual reproduction is better to endure the environmental stress (Ott and Hartnett 2012). In this study, it was possible to observe the sexual reproduction of *B. planiculmis* was inhibited by the tidal treatment, while the asexual reproduction, the number of tubers and biomass allocation to the tuber, did not increase (Fig. 9 and 11).

### **3.4.3. Effects of the interspecies interaction on *B. planiculmis***

Interspecies interaction usually changed the biomass and morphological plasticity of marsh plants (Curt et al. 2005, Gratani 2014), and the interspecies interaction could be affected by environmental stress gradients (Zhou et al. 2018). In this study, the interspecies interaction was also changed by the tidal regimes (Fig. 7). The competition that did not occur in the tidal treatment appeared in the non-tidal treatment, and it reduced the individual biomass of *B. planiculmis* (Fig. 8b). On the other hand, the interaction caused by *C. scabrifolia* decreased the shoot length of *B. planiculmis* regardless of the tidal regimes (Fig. 8b). This result was supported by Costa et al. (2003) that interspecies interactions caused by a neighbor species reduced the maximum height of a target species. The effects of interspecies interaction shift caused by the tidal regimes were not different in the density, the stem width, the sum of rhizome, the number of tubers, the flowering rate, and biomass allocations of *B. planiculmis* (Fig. 9, 10, and 11).

#### 3.4.4. Distributions in the field

Both tide and interspecies interaction brought negative impacts on the growth of *B. planiculmis*. The interspecies interaction of *B. planiculmis* was negative caused by *C. scabrifolia* in the stable condition. However, it became neutral when the tidal stress increased to twice per day. This result could explain the real distributions of these two species in estuaries. *B. planiculmis* was closer to the water body and exposed to tides more frequently, while *C. scabrifolia* dominated higher elevation with rigid and dense rhizomes (Bang et al. 2018). Therefore, this study reflected well their distributions in that the stress tolerant species, *B. planiculmis*, is disadvantaged by the competitive species, *C. scabrifolia* in the more stable environment (high elevation), while *B. planiculmis* adapts well in the tide exposure environment (low elevation) than *C. scabrifolia* does. Therefore, even though the tide is also stress to *B. planiculmis*, this species can dominate with effective ability to avoid the tide in the low elevation; however, it may be overwhelmed by the other competitive species such as *C. scabrifolia* in the high elevation.

### 3.5. Conclusion

In this study, the tide changed the interspecies interaction of *B. planiculmis* against *C. scabrifolia*. *B. planiculmis* was disadvantaged by *C. scabrifolia* in the non-tidal treatment; however, the relationship became neutral in the tidal treatment. Both tide and interspecies interaction brought negative impacts on the growth of *B. planiculmis*. Tide induced the thinner stem of *B. planiculmis*, which supported the avoidance strategy; however, the other plastic responses were not observed. Interspecies interaction decreased the shoot length of *B. planiculmis* regardless of the tidal regimes. These results explained well the real distribution of these two species in the field condition. *B. planiculmis* with less competitive but effective ability to avoid the tidal stress would dominate in the low elevation; however, it may be overwhelmed by the competitive species, *C. scabrifolia* in the high elevation.

**Chapter IV. Effects of seasonal flooding regimes on  
the responses of *B. planiculmis* in the East Asian  
Monsoon**

## 4.1. Introduction

Seasonal flooding regime is an important factor in determining the hydrodynamics of the estuarine ecosystem along with the tidal regime. Hydrodynamics, sediment, and turbidity of estuaries depend on time, mostly in relation to seasons (Syvitski et al. 2005). For example, macro-scale estuaries can be mostly overwhelmed by river flow for several months depending on monsoon season (Tamura et al. 2010, Sridhar et al. 2015). Seasonality of flooding can affect the survival, growth, and reproduction of marsh plants and even zonation patterns (Kaelke and Dawson 2003, Van Eck et al. 2006, Chen and Xie 2009). These seasonal flooding regimes determine the flooding duration or flooding depth, which can induce diverse responses of marsh plants against the flooding stress (Kaelke and Dawson 2003, Greet et al. 2013). For example, escape strategy makes plants to elongate their leaves and stems to keep above the water surface; however, quiescent strategy makes plants to repress their growth until the flooding finishes (Manzur et al. 2009, Hattori et al. 2011).

East Asian monsoon climate is composed of distinct rainy seasons. In Korea, spring season brings about relatively weak precipitation from April to mid-June. Summer moon season, called *Changma*, results in intense rainfall from late-June to mid-July. Autumn rainy season is usually a result of storms, and it lasts from late-August to September, called *Kaul Changma* (Qian et al. 2002, Han and Byun 2006). These seasonal monsoons affect the hydrological changes of major estuaries in Korea, showing the highest flow and deeper water depth in summer (Park et al. 2002, Kim and Kim 2016).

However, the duration and depth of seasonal flooding patterns can be easily changed by anthropogenic disturbances. It can be deeper due to sea-level change (Kim and Lee 2010) or longer by artificial constructions that make impounded marsh

to be permanently flooded (Montague et al. 1987, Portnoy 1999). These altered seasonal flooding regimes can change not only the responses of marsh plants (Stromberg et al. 2007) but also the structures and functions of ecosystems (Colonnello and Medina 1998, Syvitski et al. 2005, Kim et al. 2015). Nevertheless, there have been few studies about the responses of marsh plants to the seasonal flooding regimes in the East Asian Monsoon climate.

*B. planiculmis* is one of the important species in estuaries of East Asia. *Bolboschoenus* spp. maintain the structure of estuaries by trapping sediment (Yang 1998). They are also the major food for migratory birds (Ma et al. 1999, Kim et al. 2013). Because *B. planiculmis* dwells in the lower elevation, it is facing the closest to the seasonal flooding regimes. Further, the seasonal flooding regimes that *B. planiculmis* adapts can be changed by sea-level change or artificial constructions (Montague et al. 1987, Kim and Lee 2010), which may reduce the habitat of this species (Sun et al. 2003, Xue et al. 2017). Therefore, the seasonal flooding regimes would bring critical impacts on not only *B. planiculmis* population but also the structure and functions of the estuarial ecosystem.

In this study, a greenhouse experiment was conducted to compare the responses of *B. planiculmis* under different seasonal flooding regimes. The survival, growth, and reproduction were measured as responses, and the flooding duration and flooding depth were controlled to imitate the seasonal flooding regimes in the East Asian Monsoon climate. The objective of this study was to clarify the effects of seasonal flooding regimes on the responses of *B. planiculmis* for inferring the impacts of altered seasonal flooding regimes caused by sea-level rising or artificial constructions. A hypothesis was built up; the flooding duration and flooding depth change the survival, growth, and reproduction of *B. planiculmis*.

## **4.2. Methods**

### **4.2.1. Collection of *B. planiculmis* seedlings**

On April 8<sup>th</sup>, unsprouted tubers of *B. planiculmis* with similar mass ( $1.19 \pm 0.38$  g) were randomly collected at Haengju-naru wetland, Goyang, South Korea (lat  $37^{\circ}35'46.26''$ N, long  $126^{\circ}49'12.42''$ E), where exposed to tidal fluctuation during spring tides. Seedlings grown from rhizomes were obtained with similar shoot length ( $4.73 \pm 1.12$  cm) at Gongreong-river, Paju, South Korea (lat  $37^{\circ}45'31.00''$ N, long  $126^{\circ}41'43.75''$ E), that shared the same waterbody with the previous location. The tubers and seedlings of *B. planiculmis* were transported to a laboratory within moist and cool plastic containers. After washing them through 1 mm sieve, tubers and seedlings were transplanted in a 200 L pot respectively with a 10 cm depth of 1 mm sandy soil. At the age of 7 days, pairs of seedlings, one sprouted from tubers and the other grown from rhizomes, with similar shoot lengths ( $6.09 \pm 3.20$  cm and  $5.89 \pm 1.23$  cm, respectively) were chosen to be used for the experiment.

### **4.2.2. Experimental design and sample processing**

Responses of *B. planiculmis* were examined under four flooding duration regimes and three flooding depth regimes. The flooding duration regimes reflected the East Asia Monsoon climate zone; (1) 0-month flooding representing a non-flooding regime as a control, (2) 6-month flooding (Apr–Oct) for an extended flooding regime, (3) 4-month flooding (Jun–Oct) to imitate a natural flooding regime with dry spring and heavy rain in summer and autumn, and (4) 2-month flooding (Aug–Oct) for a shortened flooding regime. The flooding depth regimes were chosen considering the effects of the sea-level rise in South Korea (Kim and Lee 2010); (1) 0-cm depth

representing a non-flooding regime as a control, (2) 20-cm depth for an intermediate flooding, and (3) 40-cm depth for the expected maximum sea-level rise in South Korea. The 0-month and 0-cm combination was a control treatment. The effects of flooding duration, flooding depth, and their interactions were examined from the middle of April to early-October 2018, in a greenhouse located at Seoul National University, Seoul, South Korea (lat 37°27'34.12"N, long 126°56'52.24"E). Total 35 pots with seven treatments and five replicates were arranged randomly. Every pair of seedlings were transported to a pot (53 cm height and 33 diameter) with a 10 cm depth of 1 mm sandy soil, considering the mean rhizome length (Table 2). Holes were drilled every 0 cm, 20 cm, and 40 cm above the soil surface for each pot to maintain the flooding depth. Water depth and water quality were managed daily with tap water. Salinity was not considered for this experiment because *B. planiculmis* could dominate in freshwater tidal wetlands where the salinity was around 0.5 ppt (Table 3), and it could survive at both freshwater (0 ppt) and estuarine condition (up to 10 ppt) with no biomass difference (Xue et al. 2017). For the clear water quality, pots were entirely drained off and filled with tap water every other week.

The growth of *B. planiculmis* was recorded weekly during the experiment such as shoot length, shoot density, and survival rate (counting death when every shoot died in a pot). If none of the shoots was survived in a pot, the dead plant material was not included for the final biomass calculation. Final biomass was harvested on October 8<sup>th</sup> and washed through a 1 mm sieve. Those materials were separated into flower, stem, rhizome, tuber, and root and dried at 80 °C for 72 hours. The stem width was measured at the surface level.

### 4.2.3. Statistical analyses

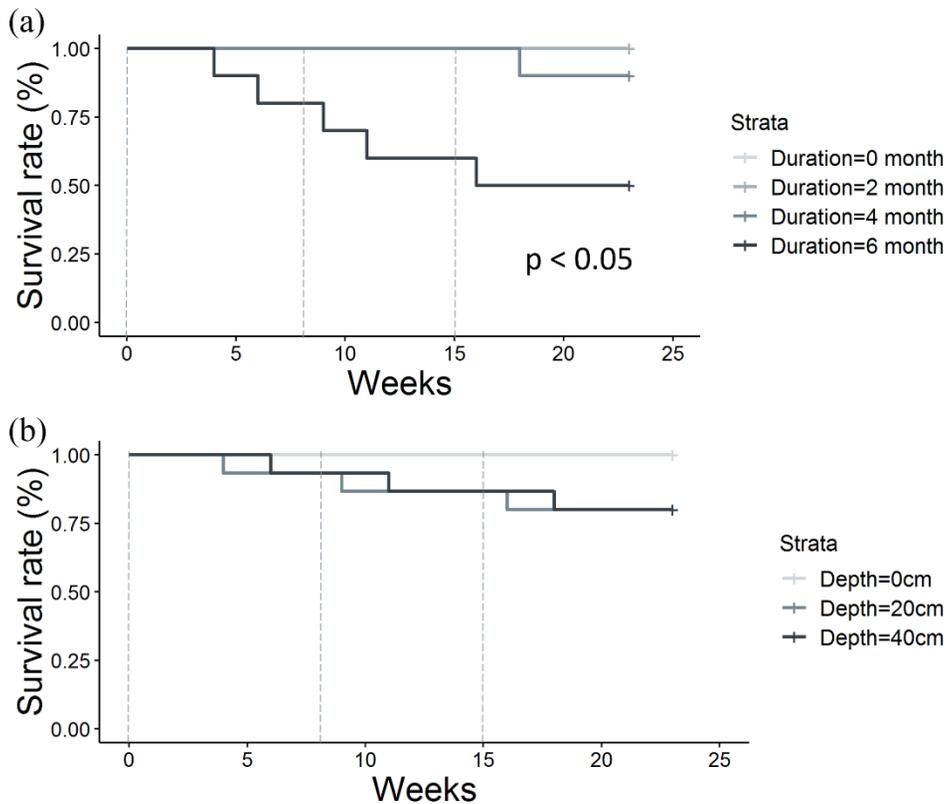
First, linear models (LMs) were conducted to compare the weekly shoot length, weekly density, total biomass, biomass allocation, stem width, leaf length, and the sum of the rhizome length with the flooding duration, flooding depth, and their interaction as explanatory variables. These data were log or square transformed to meet the normality and homoscedasticity assumptions. Generalized Linear Models (GLMs) were used to explain the flowering rate with a quasibinomial distribution and the number of tubers with a quasipoisson distribution for the same explanatory variables. The LMs were fitted based on the stepwise method, and GLMs were fitted with the lowest AIC value of poisson distribution. Assumptions for each variable were checked by graphically.

Secondly, Cox Proportional-Hazards Models (CPHMs) were used for the weekly survival rate and flowering rate of *B. planiculmis* with the flooding duration, flooding depth, and their interactions as explanatory variables. A likelihood ratio test was used for the global statistical significance of the model, and a log-rank test was used for the differences between groups (Bradburn et al. 2003). CPHMs and assumption checking were conducted from ‘Survival’ and ‘Survminer’ packages in R (Kassambara et al. 2018, Terneau 2018). All statistical analyses were performed with R version 3.4.3 (Development Core Team 2008). The values were considered as significantly different at  $p < 0.05$ .

## **4.3. Results**

### **4.3.1. Weekly survival rate**

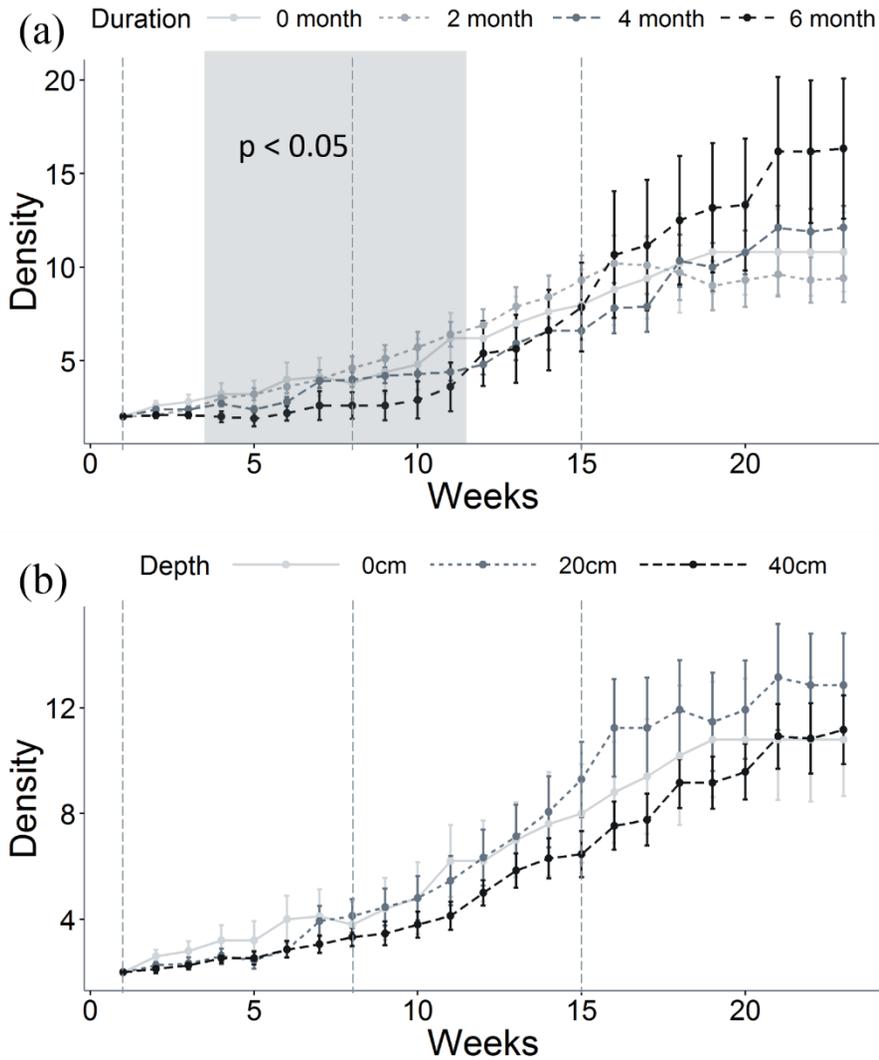
Among 35 pots, all individuals of 6 pots were died before the end of the experiment, turning to black with abscission. 5 of 6 dead pots were from the 6-month flooding, and the one dead pot was observed in the 4-month flooding. The survival of *B. planiculmis* in the extended flooding duration (6-month flooding) was just 50 % of the survival in the other flooding durations (Fig. 12a). The death happened from the seedling stage (4<sup>th</sup> week) to the adult stage (18<sup>th</sup> week). On the other hand, the flooding depth did not affect the survival rate (Fig. 12b). There was no interaction of the flooding duration and flooding depth on the survival rate of *B. planiculmis* during the whole growing season.



**Figure 12. The survival rate of *B. planiculmis* during the growing season.** (a) Effects of the flooding duration on the weekly survival rate. Likelihood ratio test ( $p < 0.01$ ,  $F=11.82$ ,  $df=3$ ), Wald test ( $p > 0.05$ ,  $F=3.12$ ,  $df=3$ ), and Score (log-rank) test ( $p < 0.01$ ,  $F=12.88$ ,  $df=3$ ), (b) Effects of the flooding depth on the weekly survival rate. Likelihood ratio test ( $p > 0.05$ ,  $F=2.01$ ,  $df=2$ ), Wald test ( $p > 0.05$ ,  $F=0$ ,  $df=2$ ), and Score (log-rank) test ( $p > 0.05$ ,  $F=1.1$ ,  $df=2$ ). The vertical dashed lines indicate the beginning of each flooding duration. The 6-month, 4-month, and 2-month flooding were started from the 1<sup>st</sup> week (May, 15<sup>th</sup>), 8<sup>th</sup> week (June, 20<sup>th</sup>), and 15<sup>th</sup> week (Aug, 8<sup>th</sup>) respectively.

### 4.3.2. Weekly density growth

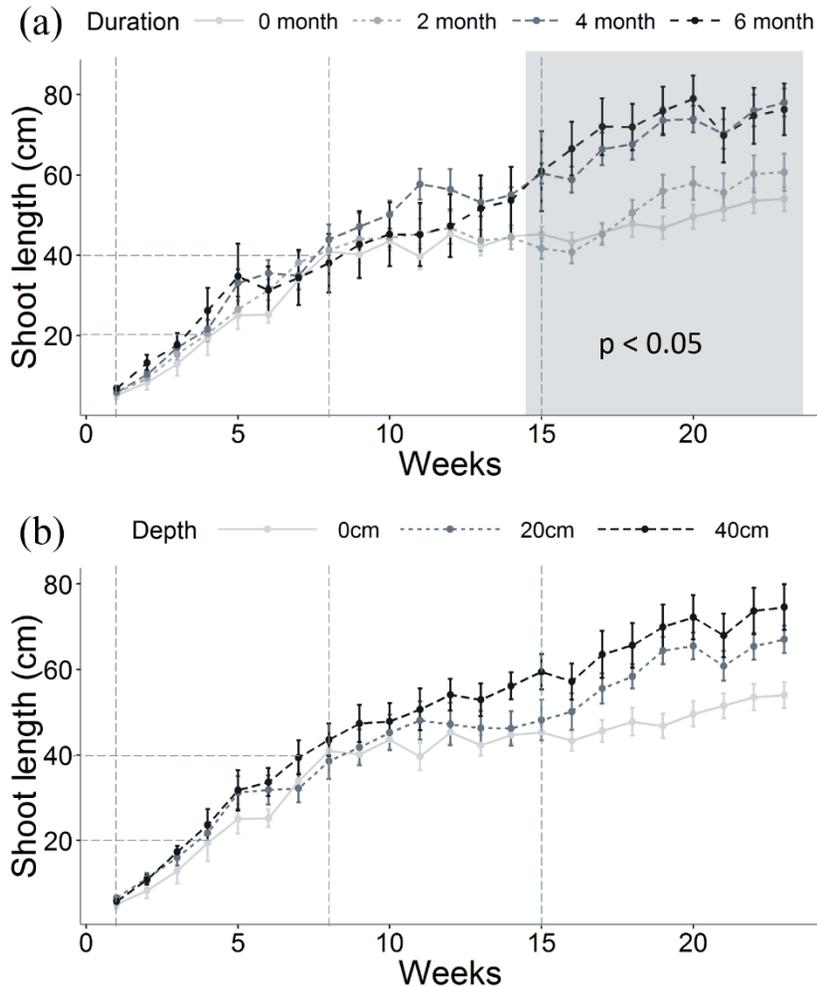
The ramet density per pot was significantly lower in the extended flooding duration ( $p < 0.05$ ) than the other flooding durations, but only from mid-May (4<sup>th</sup> week) to mid-July (11<sup>th</sup> week) (Fig. 13a). During the period, the density was lower in the 6-month flooding duration. The order was overturned after early-August (15<sup>th</sup> week) but without significant difference. On the other hand, the density was not affected by the flooding depth during the whole growing season (Fig. 13b). There was no interaction of the flooding duration and flooding depth on the weekly density of *B. planiculmis*.



**Figure 13.** The weekly density of *B. planiculmis* during the growing season. (a) Effects of the flooding duration on the weekly density, (b) Effects of the flooding depth on the weekly density. The vertical dashed lines indicate the beginning of each flooding duration. The 6-month, 4-month, and 2-month flooding were started from the 1<sup>st</sup> week (May, 15<sup>th</sup>), 8<sup>th</sup> week (June, 20<sup>th</sup>), and 15<sup>th</sup> week (Aug, 8<sup>th</sup>) respectively.

### 4.3.3. Weekly shoot length growth

Before early-Aug (15<sup>th</sup> week), the shoot lengths of *B. planiculmis* were almost same among the flooding durations. However, the shoot length became higher in the 6-month and 4-month flooding (both  $p < 0.05$ ) than the 0-month flooding from early-Aug (15<sup>th</sup> week) to the end of the experiment (Fig. 14a). On the other hand, the flooding depth did not seem to influence the shoot length during the whole growing season; however, showing a positive trend with the flooding depth (Fig. 14b). The flooding duration and flooding depth did not cause interaction effects on the shoot length.

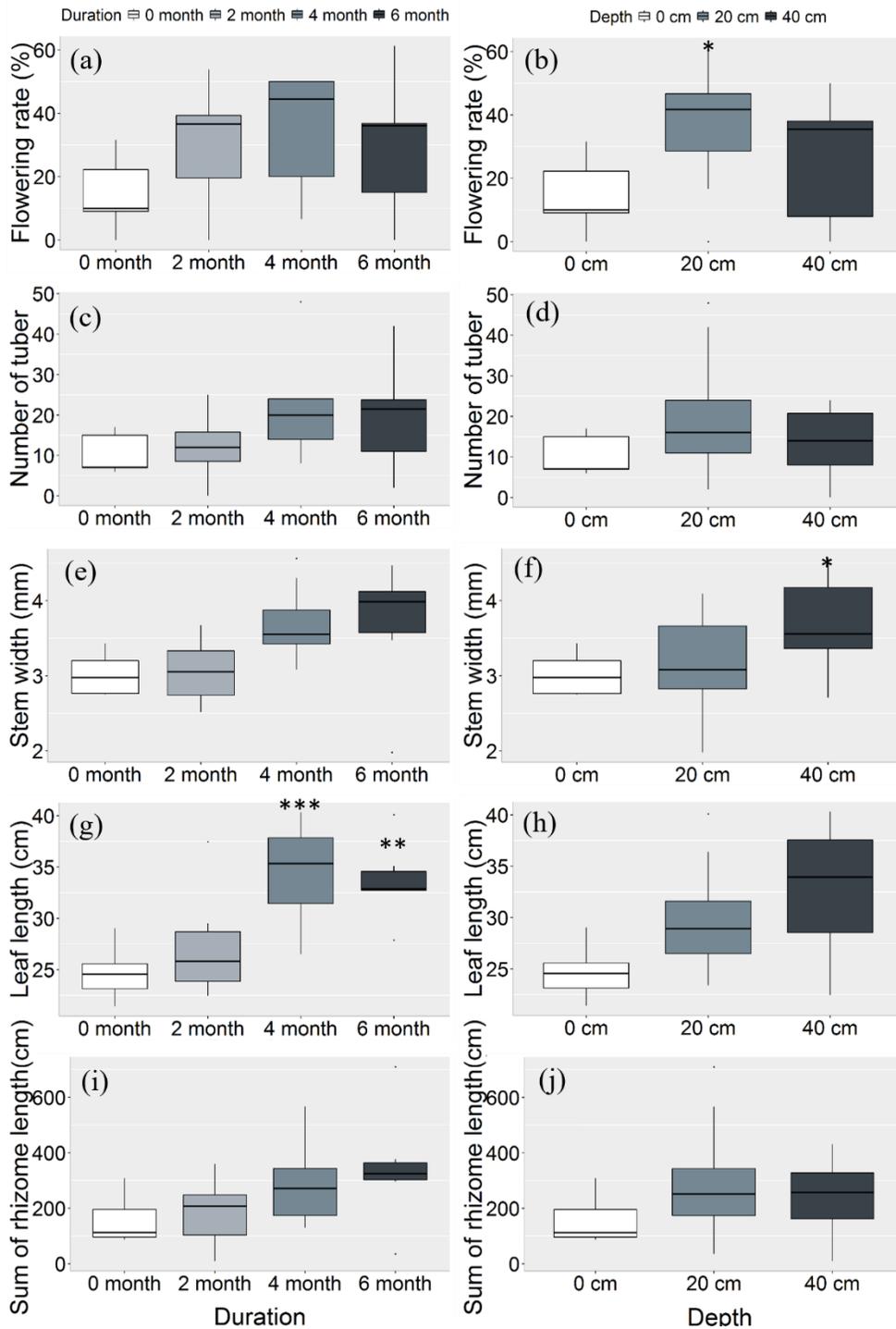


**Figure 14. Weekly shoot length of *B. planiculmis* during the growing season.**

(a) Effects of the flooding duration on the weekly shoot length, (b) Effects of the flooding depth on the weekly shoot length. The vertical dashed lines indicate the beginning of each flooding duration. The 6-month, 4-month, and 2-month flooding were started from the 1<sup>st</sup> week (May, 15<sup>th</sup>), 8<sup>th</sup> week (June, 20<sup>th</sup>), and 15<sup>th</sup> week (Aug, 8<sup>th</sup>) respectively. The horizontal dashed line indicated the 20 cm depth (intermediate depth) and 40 cm depth (deepest depth). The mean shoot lengths for every treatment were higher than the intermediate depth at 4<sup>th</sup> week and higher than the deepest depth at 9<sup>th</sup> week.

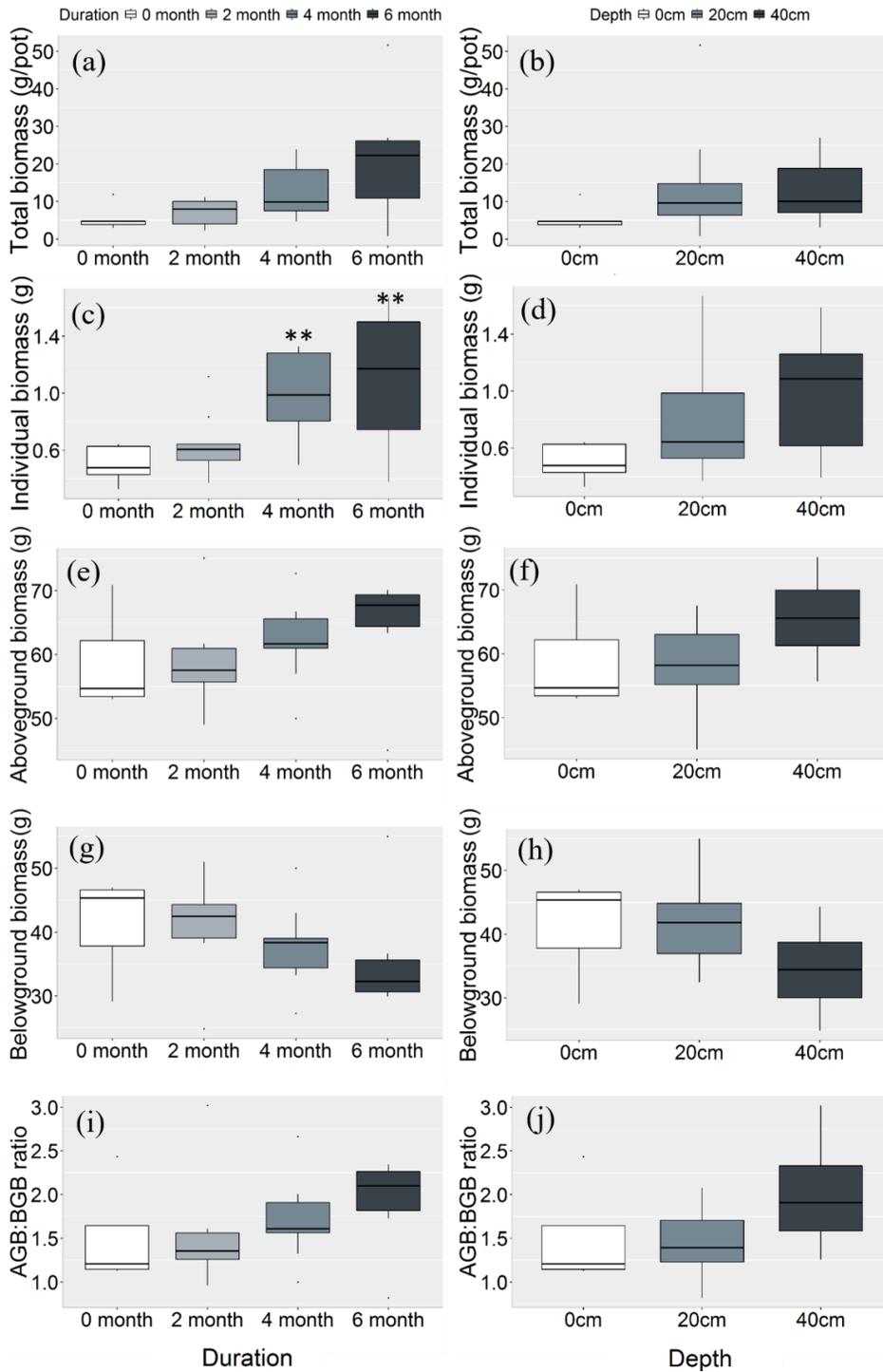
#### **4.3.4. Reproductive, morphological plastic, and growth responses**

The flooding duration did not affect the flowering rate (Fig. 15a). On the other hand, the flowering rate was significantly higher in the 20-cm flooding ( $p < 0.05$ ) than the 0-cm and 40-cm flooding (Fig. 15b). The number of tubers per pot was not different according to the flooding duration and flooding depth (Fig. 15c and d). Stem width was wider at the 40-cm flooding than the 0-cm and 20-cm flooding ( $p < 0.05$ ) (Fig. 15f). Even though the flooding duration made a similar trend, there was no significant difference in the stem width among the flooding durations (Fig. 15e). The leaf length was longer in the 4-month and 6-month flooding than the shorter durations (each  $p < 0.001$  and  $p < 0.01$ , Fig. 15g). Flooding depth did not influence the leaf length; however, showing a positive trend with the flooding depth (Fig. 15h). The sum of the rhizome length per pot showed similar results with the leaf length. Longer flooding duration and deeper flooding depth tended to make longer rhizome length compared to the shorter and shallower duration, but without significance (Fig. 15 i and j). All the responses did not show an interaction between the flooding duration and flooding depth.



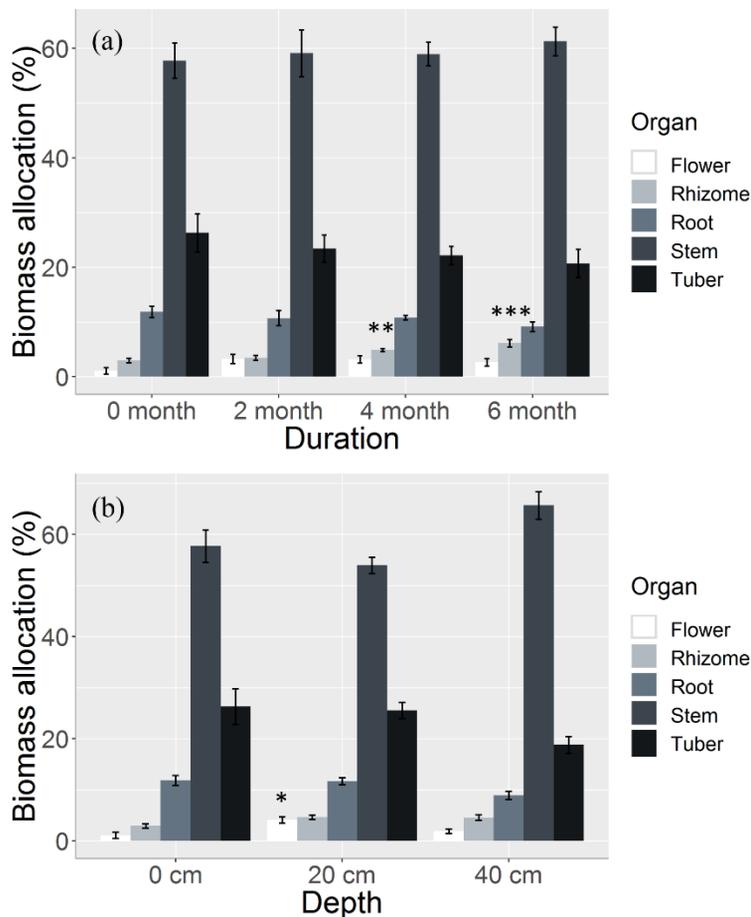
**Figure 15. The reproductive and morphological plastic responses of *B. planiculmis* at the harvest season.** The significance level: \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , and \* $p < 0.05$ .

The total biomass per pot was not different under the flooding durations and flooding depths (Fig. 16 a and b). However, they tended to increase the total biomass with longer and deeper flooding. The individual biomass became bigger when the flooding duration was longer. The 6-month and 4-month flooding resulted in significant bigger biomass than the 0-month flooding (both  $p < 0.01$ , Fig. 16c). Otherwise, the flooding depth did not bring a significant impact on the individual biomass (Fig. 16d). The relative aboveground biomass was not different among the treatments, but it showed positive trends with the increased flooding duration and flooding depth (Fig. 16 e and f). The relative belowground biomass was also not significantly different but with negative trends with the flooding duration and flooding depth (Fig. 16 g and h). Therefore, the AGB:BGB ratio was not significantly different among the treatments, but with a positive trend with the increased flooding duration and flooding depth (Fig. 16 i and j).



**Figure 16. The growth of *B. planiculmis* at the harvest season. The significance level: \*\* $p < 0.01$ .**

Most of the biomass were allocated to the stem (Fig. 17). The 4-month and 6-month flooding duration increased the biomass allocation to rhizome than the 0-month and 2-month flooding did (each  $p < 0.01$  and  $p < 0.001$ , Fig. 17a). On the other hand, the 20-cm flooding depth showed higher biomass allocation to the flower ( $p < 0.05$ , Fig. 17b). Allocations to the stem, tuber, and root were not different according to the flooding duration and flooding depth. All the variables did not show the interactions between flooding duration and flooding depth.



**Figure 17. Biomass allocations to each organ of *B. planiculmis* at the harvest season.** (a) Effects of the flooding duration on the biomass allocation to each organ, (b) Effects of the flooding depth on the biomass allocation to each organ.

The significance level: \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , and \* $p < 0.05$ .

## **4.4. Discussion**

In this study, *B. planiculmis* changed the survival and growth depending on the flooding duration. The reproduction of *B. planiculmis* was affected by the flooding depth, which supported the hypothesis. However, most of the changes were attributed to the flooding duration than the flooding depth.

### **4.4.1. Effects of the flooding duration on the responses**

Flooding duration influenced mostly on the survival of *B. planiculmis*. The species showed half of the survival rate under the extended flooding (from spring to autumn), regardless of the flooding depth (Fig. 12 a and b). This study showed a similar result with previous studies that revealed the survival rate reacted sensitively to flooding duration during seedling stages (Kaelke and Dawson 2003, Garssen et al. 2015). Another study pointed out the survival of adult floodplain species could also be decreased under the extended flooding (Gattringer et al. 2018). In this study, *B. planiculmis* also showed lower adult survival rate at 6-month flooding, which indicated that the extended flooding duration would reduce the survival rate during the whole life stage.

The growth responses to flooding duration were varied in this study. The weekly density and weekly shoot length were contrasted each other depending on life stages. Density was inhibited by the extended flooding until the seedling stage; however, it was recovered after the 11<sup>th</sup> week (Fig. 13a). Mauchamp et al. (2001) also revealed the seedlings density of *Phragmites australis*, macro-emergent plant, was limited in total submergence than in partial or non-submergence due to the lack of photosynthesis under the water. This study supported this phenomenon in that the

reduced density in early flooding was recovered after the mean shoot length reached the water surface at 9<sup>th</sup> week (Fig. 14a). Oppositely, the shoot length was not different until the seedling stage; however, the shoot length of 6-month and 4-month flooding became higher than that of 0-cm flooding after growing above the water surface (Fig. 14a). The partial flooding can induce the wetland plants to elongate their shoot length for better gas exchange (avoidance strategy) (Hattori et al. 2011, Striker et al. 2012), which was supported by this study. Besides, plants exposed to long flooding duration can result in wider stem in order to acclimate the flooding stress (De Oliveira and July 2010, Silinski et al. 2018). Even though this study did not show a significant difference according to the flooding duration, it had a similar trend with the wider stem under longer duration (Fig. 15e). The sum of the rhizome length also showed a similar trend but without significance (Fig. 15i). One of the primary function of rhizomes is to transport oxygen, water, and nutrients (Weisner and Strand 1996, Pennings and Callaway 2000). The result of this study coincided with Garssen et al. (2015) maintaining that plants might generate more root porosity to move oxygen under extended flooding.

The total biomass per pot was not changed by the flooding duration (Fig. 16a), while the individual biomass was higher in the 4-month and 6-month flooding than the shorter duration (Fig. 16c). The increased individual biomass could be explained by the longer shoot length and wider stem in this study. However, many studies observed the decreased plant biomass under extended flooding (Casanova and Brock 2000, Van Eck et al. 2004, Chen et al. 2010, Gattringer et al. 2018). Our result corresponded to the result of Voesenek et al. (2004) and Mauchamp et al. (2001) that if the species can elongate their shoot length above the water surface, they can stimulate the biomass growth. A possible explanation may be that *B. planiculmis*

could endure the flooding stress initially due to stored energy in the tuber. Once it reaches the water surface, it can photosynthesize better with the wider stem and longer leaf than plants grown in the shorter flooding duration. In this study, *B. planiculmis* tended to allocate more energy to the aboveground biomass than the belowground biomass in the extended flooding duration (Fig. 16 e and g). This result indicates the escape strategy through shoot elongation like *Rumex palustris* and *Carex brevicuspis* (Chen et al. 2011, Chen et al. 2015).

Flooding duration did not affect the reproduction of *B. planiculmis*. The flowering rate, the sexual organ biomass, the number of tubers and asexual organ biomass were not different according to the flooding duration (Fig. 15 and 17). Generally, clonal species can select sexual or asexual reproduction under various environmental conditions; however, these responses to flooding duration seem to be species-specific. For example, *Carex brevicuspis* preferred sexual reproduction in a longer flooding condition, while it more allocated asexual reproduction in a stable condition (Chen et al. 2015). Lenssen et al. (2004) revealed *Ranunculus reptans* produced the highest number of flowers in the non-flooding, the lowest number in the short flooding, and intermediate number in the long flooding. This study conformed to the *Zizania latifolia* which did not show the different number of flowers according to flooding duration (Wang et al. 2014).

#### **4.4.2. Effects of the flooding depth on the responses**

Survival and growth of *B. planiculmis* were not affected by the flooding depth. There were no significant effects on the survival rate, the shoot length, the shoot density, the number of tubers, the leaf length, the sum of rhizome length, the total biomass,

the relative aboveground biomass, and the relative belowground biomass during the whole life stages (Fig. 12–17). However, significant effects of the flooding depth have been prevailing in previous studies. Most of the emergent plants increased their shoot length under the deeper flooding depth to avoid the flooding stress as the escape strategy (Hellings and Gallagher 1992, Blanch et al. 1999, Wang et al. 2014). Some species maintained lower density, shorter shoot length, or reduced total biomass to endure the flooding stress as the quiescent strategy (Manzur et al. 2009, Wang et al. 2014) or fail to adaptation (Gattringer et al. 2018). In this study, it was interesting the 5 cm seedling could survive and grow under the 20-cm and 40-cm flooding depth without any harm (Fig. 12b, 13b, and 14b). It indicates the seedlings of *B. planiculmis* could survive in the complete submergence for at least eight weeks until the mean shoot length reached to the water surface. A possible explanation may be that saved energy in tuber would support the survival and growth of the seedlings under the water surface. Liu et al. (2016a) found a similar result that the seedlings of *B. planiculmis* from tuber were not affected by the maximum 20-cm flooding depth regarding shoot density, shoot length, and total biomass. Another possibility is because there was no interspecies interaction and turbidity, they could receive enough incident light without intervening.

Flooding depth influenced on the sexual reproduction. In the intermediate flooding depth, the flowering rate and the biomass allocation to the sexual organ (flower) were higher than in the non-flooding and deep flooding (Fig. 15b and 17b). These results agreed with previous studies observing that amphibious responders, plants with high morphological plasticity responding to flooding, can reproduce in various flooding regimes with species-specific preference (Crosslé and Brock 2002, Warwick and Brock 2003). In this study, *B. planiculmis* could produce the sexual

organs (flower) at every flooding depth, but it seemed to prefer at the 20-cm flooding. On the other hand, the number of tubers and the biomass allocation to the asexual organs (tuber) were not affected by the flooding depth (Fig. 15b and 17b). According to previous studies, deeper flooding depth could give adverse effects on the number of tubers but no effects on the tuber biomass allocation of *Bolboschoenus* spp. (Clevering and Hundscheid 1998, Liu et al. 2016b, An et al. 2018). However, this study interestingly did not show the reduced number of tubers and unchanged tuber biomass allocation. Instead, it showed the unchanged number of tubers and reduced tuber biomass allocation with deeper flooding, which might indicate the possibility of trade-off relationships between the number and size of tubers (Hangelbroek and Santamaría 2004).

#### **4.4.3. Seasonal flooding regimes**

Generally, the flooding duration affected strongly on the survival and growth, while the flooding depth influenced on sexual reproduction of *B. planiculmis*. Overall, the impacts of flooding duration were more significant than the impacts of flooding depth. Flooding duration may be a major factor of the seasonal flooding patterns. Natural seasonal flooding in the East Asian Monsoon climate, from summer to autumn, did not seem to bring negative impacts on the survival and reproduction, rather it increased the growth of *B. planiculmis* compared to the non-flooding regime. This result indicated the possibility that this species may adapt well to the seasonal flooding patterns caused by the East Asia Monsoon climate. However, the altered seasonal flooding patterns affected the survival and growth of *B. planiculmis* negatively depending on the life stages. The extended flooding, from spring to autumn, reduced the survival rate and density of seedlings. After reaching the water

surface, the seedling density could be recovered, and *B. planiculmis* could increase the biomass than the non-flooding. The shortened flooding did not influence negatively on the survival and reproduction, but the individual biomass was decreased compared to the natural and extended flooding.

## 4.5. Conclusion

In this study, *B. planiculmis* altered the survival, growth, and reproduction according to the flooding duration and the flooding depth. Generally, the flooding duration affected the survival and growth, while the flooding depth influenced on the sexual reproduction. It seems to be important to know which life stage will be exposed to seasonal flooding regimes. In this study, the natural seasonal flooding regime in the East Asian Monsoon climate did not negatively influence the survival, growth, and reproduction. Even it increased the shoot length and individual biomass compared to the non-flooding. When the seasonal flooding regime was extended from spring to autumn due to sea-level change or artificial constructions, *B. planiculmis* responded negatively in the survival and growth during the seedling stage. The shortened flooding after summer did not reduce the survival, but it repressed the shoot length and biomass compared to natural and extended seasonal flooding.

## **Chapter V. General discussion**

## **5.1. Impacts of tidal restriction**

Tidal restriction caused by artificial constriction causes significant direct and indirect impacts on the estuaries. For example, tidal regimes usually occur from twice a day to biweekly; however, the tidal restriction reduces the intensity and frequency of tide (Coops and Van der Velde 1996, Ritter et al. 2008). If the tidal restriction makes impounded marsh, the flooding duration and flooding depth can be longer and deeper depending on seasons (Montague et al. 1987, Portnoy 1999, Mora and Burdick 2013). Interspecies interaction among marsh plants can be indirectly changed by the tidal restriction as well (Sun et al. 2003, Ritter et al. 2008). These changes can affect the responses of marsh plants regarding survival, growth, and reproduction (Kaelke and Dawson 2003, Silinski et al. 2018). Nevertheless, there have been few studies to clarify the comprehensive impacts caused by the tidal restriction on the responses of the marsh plants. This study was conducted to investigate the direct and indirect impacts of tidal restriction regarding tide, interspecific competition, and seasonal flooding on the responses of marsh plant, *B. planiculmis*.

## **5.2. Responses of *B. planiculmis* and environmental variables between tidal marsh and tidal-restricted marsh**

In Chapter II, the responses of *B. planiculmis* and the environmental variables were compared between tidal marsh and tidal-restricted marsh in the field. The water depth was deeper in the tidal-restricted marsh (Table 3). It was because the tidal restriction made impounded marsh with little drainage capacity where it remained inundated with freshwater (Ritter et al. 2008). The dominance of the other species was higher in the tidal-restricted marsh than the tidal marsh (Table 3). A possible explanation is that each species has different ability to competition and

environmental stress such as tide (Bang et al. 2018, Silinski et al. 2018), which makes the *B. planiculmis* dominated in the tidal marsh but was overwhelmed by the other species in the tidal-restricted marsh. In the tidal-restricted marsh, *B. planiculmis* showed lower ramet density, lower sexual reproduction, and higher relative short-rhizome density. On the other hand, *B. planiculmis* in the tidal marsh generated higher density, higher sexual reproduction, and lower relative short-rhizome density. However, there was no difference of total biomass, individual biomass, biomass allocation, shoot length, rhizome number, rhizome length, and rhizome diameter (Table 2). In RDA, the sexual reproductive ramet became higher with the increased the density, while the relative short-rhizome density and the relative belowground biomass had positive relationships with water depth, the dominance of the other species, and soil salinity (Fig. 5). Higher sexual reproduction in the tidal marsh supported previous studies that observed higher sexual reproduction in increased density to avoid the intraspecific competition and find new habitat (Sun et al. 2001, Olejniczak 2003). The relative short-rhizome allocation supported the foraging hypothesis that short-rhizome increased to consolidate the original patch under intense belowground interspecific competition (Cheplick 1997, Ikegami et al. 2007). In the tidal marsh, *B. planiculmis* can expand their habitats through the sexual reproduction and the long-rhizome, while the plants in the tidal-restricted marsh allocate more energy to the asexual reproduction and the short-rhizome to consolidate the original patch against the increased interspecific competition.

### 5.3. Effects of tide on the interspecies interaction and responses of *B. planiculmis*

In Chapter III, the effects of tide on the interspecies interaction and the responses of *B. planiculmis* were examined. The interspecies interaction of *B. planiculmis* against *C. scabrifolia* was competitive in the non-tidal treatment; however, it was shifted to neutral in the tidal treatment (Fig. 7). Both tide and interspecies interaction reduced the total biomass and the individual biomass, which agreed with previous studies maintained that both factors could be major stress to marsh plants (Costa et al. 2003, Pennings et al. 2005, Engels et al. 2011, Nunes and Camargo 2018). Tidal exposure can result in avoidance strategy or tolerance strategy of marsh plants (Puijalón et al. 2008b, Silinski et al. 2018). In this study, *B. planiculmis* showed thinner stem width in the tidal treatment (Fig. 10c), which supported the avoidance strategy in that thinner stem could reduce the surface exposure to tide (Silinski et al. 2015). However, the other plastic responses were not observed (Fig. 8 and 10). Under tidal exposure, the sexual reproduction decreases but the asexual reproduction increases as a trade-off relationship (Sun et al. 2002, Puijalón et al. 2008b). *B. planiculmis* in this study reduced the flower biomass allocation in the tidal treatment; however, it did not increase the tuber biomass allocation, which indicated there was no a trade-off relationship. The interspecies interaction reduced the shoot length of *B. planiculmis* regardless of the tidal regimes (Fig. 10b). Costa et al. (2003) also found that interspecies interaction caused by a neighbor species decreased a height of the target species as a competitive impact. These results can explain the real distribution of *B. planiculmis* and *C. scabrifolia*. *B. planiculmis* is pushed out from the high elevation where *C. scabrifolia* plays a role as a competitor to the low elevation where *B. planiculmis* can avoid tidal stress well.

#### **5.4. Effects of seasonal flooding regimes on responses of *B. planiculmis***

In Chapter IV, the effects of simulated seasonal flooding regimes on the responses of *B. planiculmis* were studied. Flooding duration and flooding depth were controlled to imitate the seasonal flooding regimes. In this study, the flooding duration affected the survival and growth of *B. planiculmis* (Fig. 12–16). The longer flooding duration reduced the survival and density of seedlings but increased the shoot height and aboveground biomass (Fig. 12a, 13a, 14a, and 16e), which supported the escape strategy (Hattori et al. 2011). On the other hand, the flooding depth did not influence the survival and growth; however, it influenced the sexual reproduction. *B. planiculmis* in the intermediate depth (20 cm) had the highest flowering rate and sexual organ (flower) biomass (Fig. 15b and 17b), which seemed to be species-specific responses (Crosslé and Brock 2002, Warwick and Brock 2003). Overall, the flooding duration brought more critical impacts on the responses of *B. planiculmis* than the flooding depth did. In this study, the natural seasonal flooding from summer to autumn did not seem to bring negative impacts on the survival, growth, and reproduction of *B. planiculmis*. Rather, the natural seasonal flooding increased the shoot length and biomass compared to the non-flooding (Fig. 14a and 16c). However, if a tidal restriction or sea-level rise make a permanently inundated marsh, the seasonal flooding regime can be extended from spring to autumn. The extended seasonal flooding decreased the survival and growth of *B. planiculmis* seedlings in this study (Fig. 12a and 13a). The shorted flooding after summer did not reduce the survive (Fig. 12a), but it repressed the shoot length and biomass compared to the natural and the extended seasonal flooding (Fig. 14a and 16c).

## 5.5. Applications for sustainable conservation

Tidal restriction caused by artificial constructions, such as a dam, seawall, and dike, can decrease tidal intensity or frequency directly (Coops and Van der Velde 1996, Ritter et al. 2008). The constructions can also make impounded marsh that remains permanently inundated with freshwater (Montague et al. 1987, Portnoy 1999, Mora and Burdick 2013). These changes can result in the dominance of the other species indirectly that prefers high elevation or standing water (Sun et al. 2003, Ritter et al. 2008). These direct and indirect impacts of tidal restriction would bring negative influences on the responses of *B. planiculmis*. To manage and conserve the *B. planiculmis* sustainably, the tidal restriction caused by artificial constructions should be minimized in estuaries. For example, the tidal fluctuation should be maintained, competitive neighbor species should be managed low, and early flooding should be prevented. These efforts could help to maintain the structures and functions of the estuarial ecosystem.

In addition, to maintain sustainable *B. planiculmis* community, it should be well balanced between the disturbance caused by the tidal flooding and the succession to dry land, in the low elevation of the estuaries. Therefore, it would be helpful to approach with an ascendent perspective which deals with both the organizing ability (ascendency) and the disorganizing ability (redundancy) of the ecosystem (Ulanowicz 1997).

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## **Appendix**

## Appendix 1. The responses of *B. planiculmis* at each site

Tidal regime	Site	Density***	Total biomass	Individual biomass	Shoot length	Rhizome number	Rhizome length	Rhizome diameter	Relative flowering density*	Relative belowground biomass	Relative short-rhizome density***
Tidal marsh (n=50)	ISP	1686.30 <sup>a</sup> (±295.34)	450.03 <sup>a</sup> (± 90.57)	0.27 <sup>d</sup> (± 0.05)	82.32 <sup>abc</sup> (± 5.91)	2.08 <sup>bc</sup> (± 0.35)	7.95 <sup>ab</sup> (± 1.57)	1.68 <sup>de</sup> (± 0.31)	57.63 <sup>b</sup> (± 13.80)	37.74 <sup>cd</sup> (± 8.38)	0.00 <sup>e</sup> (± 0.00)
	JH	1076.90 <sup>bc</sup> (± 148.40)	416.75 <sup>a</sup> (± 98.47)	0.40 <sup>cd</sup> (± 0.11)	69.60 <sup>d</sup> (± 6.99)	2.12 <sup>bc</sup> (± 0.19)	5.33 <sup>cd</sup> (± 0.83)	1.76 <sup>cde</sup> (± 0.21)	76.83 <sup>a</sup> (± 15.06)	31.24 <sup>d</sup> (± 9.47)	0.91 <sup>cde</sup> (± 2.874)
	GY	911.90 <sup>c</sup> (± 199.46)	244.46 <sup>bc</sup> (± 62.63)	0.28 <sup>d</sup> (± 0.08)	71.22 <sup>d</sup> (± 3.72)	2.16 <sup>bc</sup> (± 0.51)	8.79 <sup>a</sup> (± 1.04)	2.16 <sup>abcd</sup> (± 0.36)	11.71 <sup>d</sup> (± 8.97)	55.59 <sup>abc</sup> (± 10.23)	0.00 <sup>e</sup> (± 0.00)
	DG	317.20 <sup>d</sup> (± 111.84)	289.96 <sup>b</sup> (± 71.38)	1.01 <sup>bcd</sup> (± 0.46)	74.04 <sup>bcd</sup> (± 6.84)	2.30 <sup>abc</sup> (± 0.30)	7.98 <sup>ab</sup> (± 1.28)	2.28 <sup>abc</sup> (± 0.30)	3.80 <sup>d</sup> (± 3.00)	47.47 <sup>bcd</sup> (± 9.67)	0.00 <sup>e</sup> (± 0.00)
	SL	1238.10 <sup>b</sup> (± 228.24)	243.84 <sup>bcd</sup> (± 73.52)	0.20 <sup>d</sup> (± 0.05)	50.52 <sup>e</sup> (± 11.24)	2.34 <sup>abc</sup> (± 0.27)	4.84 <sup>cd</sup> (± 0.82)	1.43 <sup>e</sup> (± 0.23)	26.40 <sup>c</sup> (± 10.40)	71.28 <sup>a</sup> (± 8.15)	0.71 <sup>de</sup> (± 2.26)
Tidal-restricted marsh (n=49)	DS	54.00 <sup>e</sup> (± 20.84)	69.44 <sup>e</sup> (± 28.60)	1.37 <sup>b</sup> (± 0.57)	84.20 <sup>ab</sup> (± 7.50)	1.92 <sup>c</sup> (± 0.82)	8.20 <sup>ab</sup> (± 2.41)	2.35 <sup>ab</sup> (± 0.41)	0.29 <sup>d</sup> (± 0.65)	62.97 <sup>ab</sup> (± 20.39)	11.89 <sup>bc</sup> (± 9.870)
	SH	121.60 <sup>de</sup> (± 62.85)	137.85 <sup>de</sup> (± 65.28)	1.24 <sup>b</sup> (± 0.56)	70.34 <sup>d</sup> (± 6.51)	2.14 <sup>bc</sup> (± 0.34)	4.07 <sup>d</sup> (± 1.50)	1.88 <sup>bcd</sup> (± 0.32)	11.72 <sup>d</sup> (± 8.90)	56.64 <sup>ab</sup> (± 17.88)	26.88 <sup>a</sup> (± 13.40)
	DH1	79.20 <sup>e</sup> (± 25.36)	69.91 <sup>e</sup> (± 37.17)	0.95 <sup>bcd</sup> (± 0.55)	72.34 <sup>cd</sup> (± 4.94)	2.04 <sup>bc</sup> (± 0.61)	5.14 <sup>cd</sup> (± 1.06)	1.79 <sup>cde</sup> (± 0.38)	4.19 <sup>d</sup> (± 5.50)	53.75 <sup>abc</sup> (± 16.20)	11.49 <sup>bcd</sup> (± 8.076)
	DH2	259.80 <sup>de</sup> (± 105.51)	281.21 <sup>b</sup> (± 68.93)	1.17 <sup>bc</sup> (± 0.41)	86.34 <sup>a</sup> (± 6.30)	2.66 <sup>ab</sup> (± 0.61)	4.58 <sup>cd</sup> (± 0.96)	2.49 <sup>a</sup> (± 0.59)	9.39 <sup>d</sup> (± 8.55)	54.01 <sup>abc</sup> (± 8.69)	12.32 <sup>b</sup> (± 8.08)
	IW	57.60 <sup>e</sup> (± 26.37)	150.01 <sup>cde</sup> (± 98.53)	2.76 <sup>a</sup> (± 1.37)	73.18 <sup>cd</sup> (± 10.57)	2.90 <sup>a</sup> (± 0.37)	6.23 <sup>bc</sup> (± 1.65)	2.09 <sup>abcd</sup> (± 0.41)	5.15 <sup>d</sup> (± 12.95)	64.07 <sup>ab</sup> (± 14.21)	20.11 <sup>ab</sup> (± 10.81)

The units of each response were recorded: Density (ramet m<sup>-2</sup>), Total biomass (g m<sup>-2</sup>), Individual biomass (g), Shoot length (cm), Rhizome number per ramet (count), Rhizome length (cm), Rhizome diameter (mm), Relative flowering density (%), Relative belowground biomass (%), and Relative short-rhizome density (%). Data consisted of the mean and standard deviation within parentheses. Different letters indicated a significant difference between sites ( $p < 0.05$ , Tukey's HSD test). The significance level: \*\*\* $p < 0.001$  and \* $p < 0.05$ .

## Appendix 2. The environmental variables of each site

Tidal regime	Site	pH	SS	SOM	SM	Phosphate	Nitrate	Ammonium	WD***	Neighbor IV*
Tidal marsh (n=50)	ISP	7.24 <sup>cd</sup> (± 0.14)	0.09 <sup>e</sup> (± 0.03)	3.15 <sup>a</sup> (± 0.17)	28.57 <sup>b</sup> (± 1.15)	18.76 <sup>bc</sup> (± 8.56)	1.35 <sup>bcd</sup> (± 1.00)	17.48 <sup>bc</sup> (± 10.23)	0.00 <sup>d</sup> (± 0.00)	13.53 <sup>ef</sup> (± 12.16)
	JH	7.18 <sup>d</sup> (± 0.24)	0.16 <sup>de</sup> (± 0.03)	2.83 <sup>bcd</sup> (± 0.21)	28.70 <sup>b</sup> (± 1.02)	23.528 <sup>b</sup> (± 0.46)	2.07 <sup>abc</sup> (± 1.00)	39.94 <sup>ab</sup> (± 25.92)	0.00 <sup>d</sup> (± 0.00)	27.65 <sup>de</sup> (± 4.41)
	GY	7.58 <sup>bcd</sup> (± 0.46)	0.08 <sup>e</sup> (± 0.02)	2.80 <sup>bcd</sup> (± 0.25)	29.25 <sup>b</sup> (± 1.71)	51.869 <sup>a</sup> (± 30.23)	2.97 <sup>a</sup> (± 1.74)	38.88 <sup>ab</sup> (± 24.07)	0.00 <sup>d</sup> (± 0.00)	25.84 <sup>de</sup> (± 4.69)
	DG	4.73 <sup>e</sup> (± 0.72)	0.85 <sup>b</sup> (± 0.36)	5.34 <sup>a</sup> (± 1.84)	34.61 <sup>a</sup> (± 5.26)	13.97 <sup>bc</sup> (± 5.42)	1.31 <sup>bcd</sup> (± 0.60)	58.13 <sup>a</sup> (± 26.10)	0.00 <sup>d</sup> (± 0.00)	33.04 <sup>cd</sup> (± 17.70)
	SR	7.27 <sup>bcd</sup> (± 0.32)	0.35 <sup>cde</sup> (± 0.08)	1.44 <sup>e</sup> (± 0.09)	22.33 <sup>de</sup> (± 0.82)	14.84 <sup>bc</sup> (± 9.10)	0.38 <sup>d</sup> (± 0.84)	8.37 <sup>c</sup> (± 5.04)	0.00 <sup>d</sup> (± 0.00)	0.00 <sup>f</sup> (± 0.00)
Tidal-restricted marsh (n=50)	DS	7.84 <sup>bc</sup> (± 0.60)	0.44 <sup>cde</sup> (± 0.36)	2.92 <sup>bc</sup> (± 0.43)	25.31 <sup>cd</sup> (± 1.54)	5.57 <sup>c</sup> (± 2.82)	1.76 <sup>abc</sup> (± 0.64)	4.74 <sup>c</sup> (± 7.50)	20.24 <sup>a</sup> (± 1.73)	59.54 <sup>ab</sup> (± 11.37)
	SH	7.87 <sup>bc</sup> (± 0.46)	0.49 <sup>cd</sup> (± 0.49)	1.59 <sup>e</sup> (± 0.15)	27.44 <sup>bc</sup> (± 2.17)	14.74 <sup>bc</sup> (± 6.28)	2.21 <sup>ab</sup> (± 0.88)	36.54 <sup>ab</sup> (± 19.10)	3.48 <sup>c</sup> (± 2.54)	56.62 <sup>ab</sup> (± 15.57)
	DH1	7.90 <sup>b</sup> (± 0.35)	0.68 <sup>bc</sup> (± 0.14)	1.97 <sup>de</sup> (± 0.31)	27.33 <sup>bc</sup> (± 1.32)	12.78 <sup>bc</sup> (± 4.72)	1.87 <sup>abc</sup> (± 1.22)	10.94 <sup>c</sup> (± 6.36)	8.60 <sup>b</sup> (± 1.14)	47.93 <sup>bc</sup> (± 10.14)
	DH2	7.24 <sup>cd</sup> (± 0.51)	0.52 <sup>bcd</sup> (± 0.43)	2.72 <sup>bcd</sup> (± 0.19)	27.05 <sup>bc</sup> (± 1.79)	8.08 <sup>bc</sup> (± 6.10)	2.04 <sup>abc</sup> (± 1.20)	16.72 <sup>bc</sup> (± 10.54)	10.14 <sup>b</sup> (± 1.45)	25.21 <sup>de</sup> (± 10.25)
	IW	8.66 <sup>a</sup> (± 0.30)	1.31 <sup>a</sup> (± 0.43)	2.20 <sup>cde</sup> (± 0.36)	21.96 <sup>e</sup> (± 1.39)	7.34 <sup>bc</sup> (± 6.41)	0.65 <sup>cd</sup> (± 0.48)	17.68 <sup>bc</sup> (± 16.56)	0.00 <sup>d</sup> (± 0.00)	69.81 <sup>a</sup> (± 7.09)

Environmental variables were abbreviated. SS. Soil salinity (ppt); SOM. Soil organic matter (%); SM. Soil moisture (%); Phosphate.  $\text{PO}_4^{3-}\text{-P}$  (mg  $\text{kg}^{-1}$ ); Nitrate.  $\text{NO}_3^-\text{-N}$  (mg  $\text{kg}^{-1}$ ), Ammonium.  $\text{NH}_4^+\text{-N}$  (mg  $\text{kg}^{-1}$ ); WD. Water depth (cm); Neighbor IV. Importance value of the other species (%). Data consisted of the mean and standard deviation within parentheses. Different letters indicated a significant difference between sites ( $P < 0.05$ , Tukey's HSD test). The significance level: \*\*\* $p < 0.001$  and \* $p < 0.05$ .

**Appendix 3. Responses of *C. scabrifolia* between tidal treatment and non-tidal treatment (n=6, each)**

	Tidal treatment (n=6)	Non-tidal treatment (n=6)	p
	Mean ( $\pm$ SD)	Mean ( $\pm$ SD)	
<b>Total biomass (g per pot)</b>	1.13 ( $\pm$ 0.79)	1.97 ( $\pm$ 1.08)	ns
<b>Individual biomass (g)</b>	0.31 ( $\pm$ 0.09)	0.47 ( $\pm$ 0.20)	ns
<b>Aboveground biomass (%)</b>	72.85 ( $\pm$ 7.26)	73.65 ( $\pm$ 4.38)	ns
<b>Belowground biomass (%)</b>	27.15 ( $\pm$ 7.26)	26.35 ( $\pm$ 4.38)	ns
<b>AGB:BGB ratio</b>	3.04 ( $\pm$ 1.63)	2.87 ( $\pm$ 0.56)	ns
<b>Flower biomass (%)</b>	0.00 ( $\pm$ 0.00)	0.00 ( $\pm$ 0.00)	ns
<b>Stem biomass (%)</b>	57.75 ( $\pm$ 9.58)	58.44 ( $\pm$ 5.32)	ns
<b>Rhizome biomass (%)</b>	20.84 ( $\pm$ 7.83)	22.16 ( $\pm$ 3.97)	ns
<b>Root biomass (%)</b>	21.41 ( $\pm$ 7.11)	19.40 ( $\pm$ 2.29)	ns
<b>Density (shoot per pot)</b>	3.67 ( $\pm$ 2.42)	4.33 ( $\pm$ 2.94)	ns
<b>Shoot length (cm)</b>	30.06 ( $\pm$ 2.93)	36.03 ( $\pm$ 7.33)	ns
<b>Stem width (mm)</b>	1.69 ( $\pm$ 0.43)	2.10 ( $\pm$ 0.38)	ns
<b>Sum of the rhizome (cm)</b>	34.10 ( $\pm$ 6.79)	43.63 ( $\pm$ 24.37)	ns
<b>Flowering rate (%)</b>	0.00 ( $\pm$ 0.00)	0.00 ( $\pm$ 0.00)	ns

The significance level: ns =  $p \geq 0.05$ . SD means a standard deviation.

## 국문 초록

인공적인 구조물 건설로 인해 야기되는 조류 단절은 하구 생태계에 직·간접적인 영향을 줄 수 있다. 직접적으로는 조류 흐름이나 침수 유형을 변화시키며, 간접적으로는 습지식물의 종간 상호작용에 영향을 미친다. 하지만 방조제로 인한 조류 단절이 습지식물의 반응에 어떤 영향을 주는지에 대한 이해가 부족한 실정이다. 따라서, 이 연구는 조류 단절의 직·간접적인 영향 (조류, 종간 상호작용, 계절적 침수유형의 변화)에 습지식물인 쯤매자기가 어떻게 반응하는지를 이해하는데 초점을 맞췄다.

첫번째로, 조류 습지와 방조제 습지에서 쯤매자기의 반응과 환경 요인을 비교하기 위해 현장 조사가 실시되었다. 방조제 습지에서는 조류 습지에 비해 침수 깊이가 깊고, 다른 종의 우점도가 높았다. 쯤매자기는 낮은 밀도, 높은 무성생식 비율, 그리고 높은 짧은 근경 밀도를 보였다. 반면에 조류 습지에서는 높은 밀도, 높은 유성생식 비율, 그리고 낮은 짧은 근경 밀도를 보였다. RDA 결과는 수심이 깊고, 다른 종들이 우점도가 높은 방조제 습지에서는 쯤매자기의 밀도가 낮고, 기존의 서식지를 유지하는데 더 많은 에너지를 투자하는 것을 시사했다. 반면에, 수심이 거의 없고, 다른 종들의 우점도가 낮은 조류 습지에서는 쯤매자기의 밀도가 높고, 새로운 서식지로 확장하는데 더 많은 에너지를 투자하는 것을 시사했다.

두번째로, 조류 유무가 쯤매자기의 종간 상호작용과 반응에 어떤 영향을 미치는지 알아보기 위해 온실 실험을 수행했다. 쯤매자기와 천일사초의 종간 상호작용은 조류 흐름이 없을 때는 경쟁적인 관계이다가, 조류 흐름이 있을 때는 중성적인 관계로 변화했다. 조류와 종간 상호작용은

모두 좀매자기의 성장을 저해시켰다. 조류가 있을 때, 좀매자기는 얇은 줄기를 만드는 형태적 가소성을 보였고, 이는 조류 스트레스를 피하기 위한 도피 전략으로 보인다. 천일사초는 뚜렷한 형태적 가소성이 관찰되지 않았다. 이 결과는 좀매자기와 천일사초, 두 종의 실제 분포를 설명할 수 있다: 높은 고도에서는 조류 스트레스가 낮고, 좀매자기가 천일사초와의 경쟁에 의해 불리하다. 하지만 조류 스트레스를 효과적으로 피할 수 있는 좀매자기는 낮은 고도에서 우점할 수 있다.

세번째로, 계절적 침수 유형이 좀매자기의 반응에 미치는 영향을 명확히 하기 위해 온실 실험을 수행했다. 침수 기간은 좀매자기의 생존과 생장에 영향을 미치는 반면, 침수 깊이는 번식에 영향을 미쳤다. 여름부터 가을까지 침수되는 자연적인 계절 침수유형에서는 생존, 성장, 그리고 번식이 부정적인 영향을 받지 않았다. 반면에, 봄부터 가을까지 침수 기간이 연장된 유형에서는 유묘의 생존과 밀도가 줄어들었다. 좀매자기의 지상부가 수면 위로 올라온 후부터는 생체량이 증가되었다. 한편, 여름 이후만 짧게 침수된 유형에서는 생존이나 번식이 영향 받지 않았으나 생체량이 감소했다.

이 결과는 좀매자기의 지속가능한 보존을 위해서 방조제의 영향을 최소화해야 함을 시사한다. 조류 흐름을 유지함을 통해 경쟁종을 저감해주고, 이른 침수를 예방해주는 것을 제안한다.

**주요어:** 조류 단절, 하구, 조류, 종간 상호작용, 계절적 침수, 침수 기간, 침수 깊이, 좀매자기

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