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Impacts of tidal restriction caused by embankments on the plastic growth responses of *Bolboschoenus planiculmis* in Korea

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ABSTRACT

Tidal restriction caused by embankments can have large impacts on estuarial ecosystems. It changes the tidal regimes, which influence the growth and development of marsh plants. Although large-scale tidal freshwater marshes are negatively or positively affected by the embankments especially around the Yellow Sea in Korea, little is known regarding how the tidal restriction changes the plastic growth responses of marsh plants, which may cause a population decline in the field. Therefore, we evaluated the impacts of tidal restriction on the growth, plasticity in morphology, reproduction, and biomass allocation of the important but vulnerable marsh plant *Bolboschoenus planiculmis* in Korea. These responses of *B. planiculmis* in tidal marshes and tide-restricted marshes were compared. The tide-restricted marshes experienced deeper water (9 cm) and greater dominance of other species (51%) than the tidal marshes (respectively 0 cm, 20%). Populations in the tide-restricted marshes revealed a lower density (128 ramets m^{-2}), decreased sexual reproduction ratio (6%), and higher short rhizome density ratio (17%) with a rapid increase in allocation to below ground biomass compared to the tidal marsh populations (respectively 1046 m^{-2}, 35%, and 0.3%). A redundancy analysis indicated that *B. planiculmis* with a low density in the tide-restricted marshes developed more short rhizomes and allocated more energy to below ground biomass in order to persist in the original habitats where neighbor species dominated. On the other hand, the tidal marsh populations with higher densities invested more energy to sexual reproduction and developed more long rhizomes to expand into new areas. In this paper, tidal restriction caused the dominance of neighbor species such as *Phragmites australis* in standing water and negative impacts on *B. planiculmis*. These results indicate that the impacts of tidal restriction caused by artificial structures should be minimized by maintaining natural tides for sustainable management of *B. planiculmis*.

1. Introduction

Coastal ecosystems including estuaries are essential due to their ecological functions such as providing primary production, shore protection, and core habitats for waterfowl (Heip et al., 1995; Shepard et al., 2011; Melville et al., 2016; Moores et al., 2016). However, the natural coastal areas around the Yellow Sea have been disappearing due to development in Korea and China (Ma et al., 2014; Murray et al., 2014; Melville et al., 2016; Moores et al., 2016). Dense artificial structures such as embankments in Korea have resulted in critical impacts on the coastal ecosystems, resulting in rapid and irreparable changes in the nature structures and functions of the ecosystem (Lie et al., 2008; Lee et al., 2014).

Among the coastal ecosystems, tidal freshwater marshes are one of the most vulnerable ecosystems undergoing artificial environmental changes. The tidal freshwater marshes are those marshes experiencing regular tides with salinity of less than 5 ppt (Van de Broek et al., 2018) and they are located at the mouths of estuaries where embankments are mainly built for flood protection or land reclamation. The artificial embankments largely affect hydrology, soil physiochemistry, and vegetation changes of the natural conditions by blocking tidal flow (Roman et al., 1984; Montague et al., 1987; Portnoy and Giblin, 1997; Mora and Burdick, 2013b). Tidal restriction can either drain the marshes in the long-term or can make permanently flooded marshes in the short-term where the drainage ability is low (Montague et al., 1987; Portnoy, 1999). In the latter case, the tide-restricted flooded marsh is submerged for a longer duration without tidal flows, which differs from the natural tidal cycles from daily to biweekly (spring tide). Due to these hydrological changes, the soil physiochemistry can also be altered, such as decreased amounts of nutrients (Portnoy and Giblin, 1997) and increased alkalinity (Portnoy, 1999), in tide-restricted marshes.

In the tide-restricted flooded marshes, plants need to adapt to the altered conditions such as permanent inundation and stable

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water without tidal cycles. This can result in decreased biomass of the original estuarial marsh plants (Konisky and Burdick, 2004) and can even result in changes in dominant species (Roman et al., 1984; Sun et al., 2003; Mora and Burdick, 2013a). Not only the abiotic factors but also the biotic factors induced by the abiotic changes can affect the plastic growth responses and distribution of the original marsh plants. For example, interspecific interactions under tide-restricted conditions resulted in reduced biomass (Yang et al., 2020), changes in morphology (Curt et al., 2005), shifts in rhizome strategy between phalanx (short) rhizome and guerilla (long) rhizome (Humphrey and Pyke, 1998; Ikegami et al., 2007), and restricted the distribution of the original marsh plants. The majority of studies have focused on the responses of the well-known species such as *Spartina* spp. and *Phragmites* spp. in salt marshes (Roman et al., 1984; Burdick et al., 1996; Konisky and Burdick, 2004). However, one of the most vulnerable plants under tidal restriction caused by embankment are early successional species in tidal freshwater marshes (Hammersmark et al., 2005) such as *Bolboschoenus planiculmis.*

B. planiculmis (F. Schmidt) T.V. Egorova is distributed in estuaries in East Asia, Middle Asia, and Central Europe, and forms monodominant populations or mixed communities in estuaries, reclaimed rice paddies, and lagoons (Jung and Choi, 2011; Hroudová et al., 2014; Liu et al., 2016). *B. planiculmis* provides a major food source for migratory endangered birds such as swan geese (*Anser cygnoides*) and cranes (*Grus* spp.) (Kim et al., 2013). Therefore, *B. planiculmis* is an essential plant for estuarine ecosystems, serving as a link between producers and important consumers of wetlands. However, this species is known to be declining in numbers in East Asia due to the degradation of estuarine marshes resulting from embankments and reclamation (You, 2008; Liu et al., 2016). Because *B. planiculmis* grows in low elevation nearest to the water body, it is expected to be significantly affected by tidal restriction caused by embankments. In East Asia, for example, heavy rain during summer monsoon can result in water accumulation in the tide-restricted marshes where the drainage is poor, causing increased flooding duration and depth. However, there have been few studies focused on gaining a comprehensive understanding of the impacts of tidal restriction on the plastic growth responses of *B. planiculmis* in the field. Understanding these responses of marsh plants is essential to evaluate fitness (Puijalon et al., 2005), preserve local populations (Chevin et al., 2013), and forecast the structures and functions of estuaries (Qi et al., 2016).

Monitoring the exact impacts of tidal restriction on marsh plants is necessary to provide insight for sustainable management and conservation of estuarine ecosystems. Therefore, our overarching goal was to understand why *B. planiculmis* has been declining under tide restriction. Our objective was to compare its plastic growth responses such as growth, plasticity in morphology, reproduction, and biomass allocation under tidal marshes and tide-restricted marshes in Korea. Tidal restriction can change many environmental conditions such as water fluctuation, soil conditions, and competition among other plants in the Yellow Sea. We hypothesized that these environmental differences in tide-restricted marshes reduce the growth, and alter other plastic growth responses of *B. planiculmis* in order to survive under the changed conditions. These results will be used as fundamental data to restore the ecosystem functions such as providing a primary food source for wildlife in estuaries.

2. Methods

2.1. Target species and study sites

B. planiculmis (F. Schmidt) T.V. Egorova is a perennial clonal plant with a height of 20–100 cm and it dominates at low elevations in estuaries in East Asia (Kim et al., 2013). It sprouts from tubers or seeds from April to May and flowers from May to July, and its above ground biomass dies back in October (Yang et al., 2020). It reproduces with both sexual and vegetative organs (Wang and Li, 2016). In Korea, *B. planiculmis* dwell on both tidal marshes exposed to natural tidal cycles and tide-restricted marshes blocked by embankments. Fig. 1 presents the morphology and two types of habitats of *B. planiculmis.*

Study sites were located along the western coastline (the Yellow Sea) of South Korea. Five sites were located at tidal marshes, and the other five sites were located at tide-restricted marshes. Among the five tidal marsh sites, three tidal marshes, Goyang, Janghang, and Isanpo, are located in the tidal marsh at the Han River estuary (Fig. 2a), which is one of the open estuaries in South Korea. Sites were separated by at least 8 km and were not connected to each other. The other two tidal marshes were located at high elevations in tidal flats of Donggeom (Fig. 2a) and Songrim (Fig. 2e). The tide-restricted marsh sites were blocked by embankments. Daesong and Sihwa marshes were surrounded by the Sihwa embankment, and the Daesong marsh was separated from the Sihwa marsh by an additional levee (Fig. 2b). The Daeho embankment (Fig. 2c) and Iwon embankment (Fig. 2d) included two and one tide-restricted marshes, respectively. Two tide-restricted marshes near the Deaho embankments were separated by 3 km and were isolated from each other by an additional levee.

Table 1 summarizes the locations and environmental factors for each site: ISP (Isanpo tidal marsh), JH (Janghang tidal marsh), GY (Goyang tidal marsh), DG (Donggeom tidal marsh), SR (Songrim tidal marsh), DS (Daesong tide-restricted marsh), SH (Sihwa tide-restricted marsh), DH (Daeho tide-restricted marsh), and IW (Iwon tide-restricted marsh). The tidal marshes were usually exposed to the air and flooded biweekly due to spring tides, while the tide-restricted marshes were impounded in embankments resulting in a permanent inundated or saturated condition.

2.2. Sampling method

At each site, ten permanent quadrats (1 × 1 m) with a total of 100 quadrats were randomly established 3–5 m apart on April 2017, following previous studies (Sun et al., 2002; Ning et al., 2014). These quadrats were installed parallel to the water body. In each quadrat, shoot density, coverage, frequency, and shoot length of each species were recorded in August when the above ground parts were most highly developed. Density was defined as the number of ramets of each species. Coverage of each species was the percentage area of the species in the quadrat. Frequency was 1 when the species existed or 0 if not. Mean shoot length of each species was measured after selecting five ramets per species and calculating the average. Based on monthly observations, *B. planiculmis* in a quadrat was sampled in early September, when the above ground parts of *B. planiculmis* started to senesce and the below ground parts were most highly developed (Karagatzides and Hutchinson, 1991; Sun et al., 2002).

Above ground parts of *B. planiculmis* were clipped at the sediment surface within a quadrat, and the remaining neighbor species were not clipped so as to easily distinguish their roots later. Below ground parts were extracted using a metal core (20 cm diameter and 15 cm depth) at the middle of each quadrat. We dug down a further 20 cm to check whether there were tubers of *B. planiculmis*, and most of them were moribund and not collected for analyses. Since the rhizome length of *B. planiculmis* was often longer than the diameter of the core, it was measured in the field. The rhizome length was defined from the bottom of a parent ramet to the bottom of the first daughter ramet. We selected five *B. planiculmis* ramets per quadrat, measured all linked rhizome lengths per ramet, and averaged them per quadrat. The rhizome

Fig. 1. Morphology and habitat types of *B. planiculmis*. (a) Flower and stem in above ground part; (b) Tuber in below ground part; (c) Tidal marshes where the marshes are exposed to natural tidal cycles; (d) Tide-restricted marshes where the water is impounded due to the artificial embankments.

diameters were measured at the same time by Vernier calipers at the middle point of the rhizome. Triplicates of undisturbed soil samples per quadrat were collected at 5 cm depth in early September. They were mixed to measure soil salinity (SS), soil moisture (SM), soil organic matter (SOM), soil pH, NO_3^-–N, NH_4^+–N, and PO_4^{3-}–P. Water depth was recorded five times to calculate the average per quadrat. All samples were sealed in plastic bags and transported to the laboratory within iced containers.

2.3. Sample processing

The above ground parts of *B. planiculmis* were washed and separated into flowers and stems, counting the number of flowering ramets. The below ground parts of *B. planiculmis* were carefully separated from the neighbor species based on the remaining above ground parts of neighbor species, keeping the above and below ground parts unbroken. They were washed through a 1 mm sieve and divided into rhizome, tuber, and fine root. To count the densities of rhizomes of *B. planiculmis*, the rhizomes in the core per quadrat (total of 1133) were separated into unmeasurable rhizomes (maximum of a few millimeter) and measurable rhizomes. The former were called phalanx (short) rhizomes, which are beneficial for the plant to be able to adapt to more stressful conditions due to severe competition, while the latter were called guerilla (long) rhizomes, which have an advantage in exploiting new open space (Humphrey and Pyke, 1998; Ikegami et al., 2007). The unmeasurable rhizomes were easily distinguished because they connected two tubers as if the tubers were stuck together.

The harvested materials were weighed to 0.01 g after 72 h of drying at 80 °C. The below ground dry biomass within the core was extrapolated into a quadrat by multiplying by a constant, $100/\pi$. Individual biomass was calculated by dividing the total biomass by the total ramet density. Allocation to the below ground biomass ratio was estimated as the ratio of below ground dry mass over the total dry mass. Flowering ramet density ratio was calculated as the number of flowering ramets divided by the total number of ramets. Phalanx rhizome density ratio was defined as the number of phalanx rhizomes divided by the total number of rhizomes (i.e., phalanx rhizomes + guerilla rhizomes).

Based on the field observations, the importance value (IV) was calculated per quadrat; this index is commonly used to measure the dominance of a target species over other species (Eq. (1)). A higher IV indicates that the target species is dominant, while a lower IV indicates that other species are dominant (Mcintosh, 1957). The IV of neighbor species was calculated to determine the dominance of neighbor species (Eq. (2)).

$$IV = (Relative\ Density\,(\%) + Relative\ Coverage\,(\%) + Relative\ Frequency\,(\%))/3 \qquad (1)$$

$$neighbor\ IV = 100 - B.\ planiculmis\ IV \qquad (2)$$

Soil samples were filtered through a 2 mm sieve to remove organic materials and gravel and then separated into two parts. One part was air-dried under shaded conditions for SS and soil pH measurements. A 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. The other part was maintained as fresh soil to measure SM, SOM, and nutrient contents. Soil moisture was calculated as ((W-D)/W) × 100 (%), where W is the fresh soil weight and D represents the dry soil weight after 72 h at 105 °C. The remaining soil was burned for four hours at 550 °C to measure SOM, based on the loss on ignition method (Boyle, 2004). To estimate the contents of NO_3^-–N (mg kg^{-1}) and NH_4^+–N (mg kg^{-1}), the soil was extracted using 2 M KCl and the hydrazine method (Kamphake et al., 1967) and indophenol methods (SolÓRzano, 1969), respectively. The content of PO_4^{3-}–P (mg kg^{-1}) was estimated by the ascorbic acid reduction method (Murphy and Riley, 1962) after extracting the soil with Bray No. 1 solution (Bray and Kurtz, 1945).

Table 1
Summary of the locations and environmental factors of tidal marsh sites and tide-restricted marsh sites.

	Tidal marsh					Tide-restricted marsh				
Sites	ISP (n = 10)	JH (n = 10)	GY (n = 10)	DG (n = 10)	SR (n = 10)	DS (n = 10)	SH (n = 10)	DH1 (n = 10)	DH2 (n = 10)	IW (n = 10)
Extent of marsh (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
Abiotic										
Topographic level	Tidal freshwater marsh	High elevation in tidal flat	Artificial embankments intercepted at tidal freshwater marsh							
Elevation (m)	~7	~2	~7	~6	~7	~0.5	~0.5	~0	~0	~0
Flooding (Water resource)	Flooded at only spring tides (Tide & Rain)					Permanent flooded (Impounded seawater & Rain)				Permanent saturated (Impounded seawater & 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)				
Embankment built year	–	–	–	–	–	1994	1994	1989	1989	1992
Soil texture	Clay			Sandy clay		Silty clay				
Biotic										
Coverage of *B. planiculmis* (%)	80–100	60–80	70–90	60–80	90–100	30–50	40–60	40–60	70–80	20–40
Shoot length of *B. planiculmis* (cm)	70–90	60–75	65–75	60–90	40–60	80–90	60–80	65–85	75–95	70–100
Neighbor species within quadrats	*Scirpus triqueter, Echinochloa crusgalli, Phragmites australis*	*Echinochloa crusgalli, Phragmites australis*	*Scirpus triqueter, Phragmites australis*	*Triglochin maritimum, Phragmites australis, Carex scabrifolia*	*Carex scabrifolia*	*Phragmites australis, Diplachne fusca*	*Echinochloa crusgalli, Phragmites australis, Erigeron canadensis*	*Phragmites australis*	*Phragmites australis, Diplachne fusca*	*Phragmites australis, Erigeron canadensis, Carex scabrifolia*

Annual mean tidal range is reported as the average (mean low water and mean high water in the parentheses) for a year, obtained at the nearest observatory from the KHOA Smart Tide Forecast, Korea Hydrographic and Oceanographic Agency. Annual total precipitation and annual mean temperature (mean monthly temperate range in the parentheses) are averages over 30 years, obtained from the Smart Weather Service, Korea Meteorological Administration.

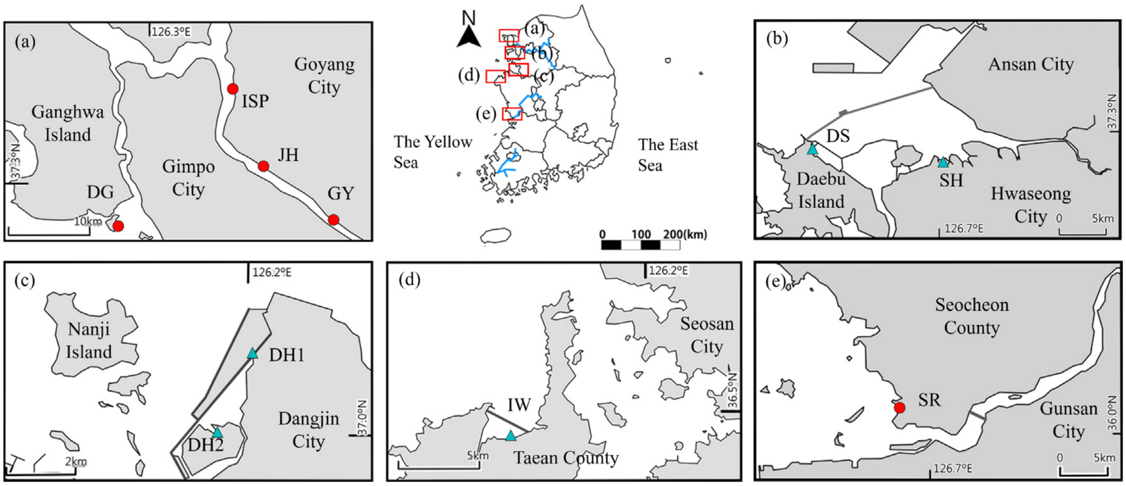

Fig. 2. Study sites in tidal marshes and tide-restricted marshes along the western coastline of South Korea. Red circles indicate tidal marshes and blue triangles indicate tide-restricted marshes. (a) Isanpo (ISP), Janghang (JH), and Goyang (GY) tidal marshes at the Han River estuary and the Donggeom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

2.4. Statistical analyses

Due to the high variations in absolute values among the sites, proportions of flowering ramet density, biomass allocation, and rhizome density were used for analyses. First, linear mixed models (LMMs) were used to compare total biomass, individual biomass, shoot length, number of rhizomes per ramet, rhizome length, rhizome diameter, and biomass allocation to each organ (flower, stem, rhizome, tuber, and fine root) of *B. planiculmis* between tidal marshes and tide-restricted marshes. Linear mixed models were also used to compare environmental variables between the two types of sites. The environmental variables of each quadrat included SS, SOM, soil pH, NO_3^-–N, NH_4^+–N, PO_4^{3-}–P, and neighbor IV. Second, generalized linear mixed models (GLMMs) were used to evaluate differences in the flowering ramet density ratio and phalanx rhizome density ratio of each quadrat with binomial distributions, and the total ramet density of each quadrat with a Poisson distribution, between tidal marshes and tide-restricted marshes. In these LMMs and GLMMs, the tidal regime was included as a fixed factor and the site was included as a random factor (McKone and Lively, 1993) using the 'lme4' package for R (Bates et al., 2015). Because the water depths were zero-inflated, it was analyzed by LMM using the 'glmmTMB' package (Bolker, 2019). The assumptions of normality and homoscedasticity for each variable were checked using the DHARMa package, which tested normality with KS test and homoscedasticity with graphics (Hartig, 2019). Third, standardized major axis (SMA) regression was used to compare the relationships between above- and below-ground biomass as well as each organ and total biomass.

The relationships between the responses and environmental variables were evaluated by a redundancy analysis (RDA). The vegetation data matrix was composed of the three responses (flowering ramet density ratio, below ground biomass allocation ratio, and phalanx rhizome density ratio), and the environment data matrix consisted of soil variables (i.e., SS, SM, SOM, soil pH, NO_3^-–N, NH_4^+–N, and PO_4^{3-}–P), water depth, the density of *B. planiculmis*, and neighbor IV. All statistical analyses were performed using R version 3.4.3 (R Development Core Team, 2008). The values were considered significant at $p < 0.05$.

3. Results

3.1. Plastic growth responses

We detected a significant difference of total ramet density between the tidal marshes and tide-restricted marshes but not in other response variables (Table 2). The total ramet density was 1047 ramets m^{-2} in the tidal marshes, which was significantly higher than 129 ramets m^{-2} in the tide-restricted marshes ($p < 0.001$, $F_{1,8} = 38.994$). Even though the total biomass per quadrat in the tidal marshes was slightly higher (329 g DM m^{-2}) than that in the tide-restricted marshes (141 g DM m^{-2}), the difference was not significant due to high among-site variations (Table A1). Individual biomass, shoot length, the number of rhizomes, rhizome length, and rhizome diameter were not significantly different between marsh types.

3.2. Sexual reproduction, rhizome, and above- and below-ground biomass ratio

The flowering ramet density ratio was 35% in the tidal marshes, which was significantly higher than the ratio (6%) in the tide-restricted marshes ($p<0.05$, $F_{1,8} = 6.225$, Fig. 3a). The phalanx rhizome density was much higher (mean±standardized deviation, 18±7 count m^{-2}) in tide-restricted marshes than in tidal marshes (0.3±0.4 count m^{-2}), while the number of guerilla rhizomes was 92±15 count m^{-2} in tide-restricted marshes and 108±4 count m^{-2} in tidal marshes. Thus, the phalanx rhizome density ratio was significantly higher in the tide-restricted marshes (16.54%) than in the tidal marshes (0.32%) ($p < 0.001$, $F_{1,8} = 28.674$, Fig. 3c). There was no significant difference in the below ground biomass ratio between tidal marshes and tide-restricted marshes ($p>0.05$, $F_{1,8} = 1.706$, Fig. 3b). However, based on the result of SMA regression, the slopes of below ground biomass over above ground biomass (i.e., above ground biomass as *x*-axis and below ground biomass as *y*-axis) were positive and significantly steeper in tide-restricted marshes than in tidal marshes ($p < 0.001$) (Fig. 4, Table 3). This result indicated that population in tide-restricted marshes allocated more biomass to the below ground biomass as the above ground biomass increased, while the population in the tidal marshes did not. In tidal marshes, the above ground biomass and below ground biomass were not

Table 2
Comparison of *B. planiculmis* plastic growth responses between tidal marshes and tide-restricted marshes.

	Tidal marshes (n = 50)	Tide-restricted marshes (n = 49)	df	*F* value	*p* value
	Mean (±SD)	Mean (±SD)			
Total ramet density (ramets m $^{-2}$)	1047 (±488)	129 (±100)	1, 8	38.99	***
Total biomass (g DM m $^{-2}$)	329 (±116)	141 (±100)	1, 8	10.28	ns
Individual biomass (g DM)	0.4 (±0.4)	1.2 (±0.5)	1, 8	15.50	ns
Shoot length (cm)	69.5 (±12.6)	77.3 (±9.7)	1, 8	1.56	ns
Rhizome number per ramet	2.2 (±0.3)	2.3 (±0.6)	1, 8	0.45	ns
Rhizome length between ramets (cm)	7.0 (±1.9)	6.0 (±2.1)	1, 8	1.54	ns
Rhizome diameter (mm)	1.9 (±0.4)	2.1 (±0.5)	1, 8	1.62	ns

F tests were done in linear mixed models (LMMs) and generalized linear mixed models (GLMMs). Significance level: *** $p < 0.001$ and ^{ns} $p \geq 0.05$. The tidal marshes had 50 replicates, while tide-restricted marshes had 49 replicates excluding missing below ground data for the Daesong (DS) site. SD: standard deviation.

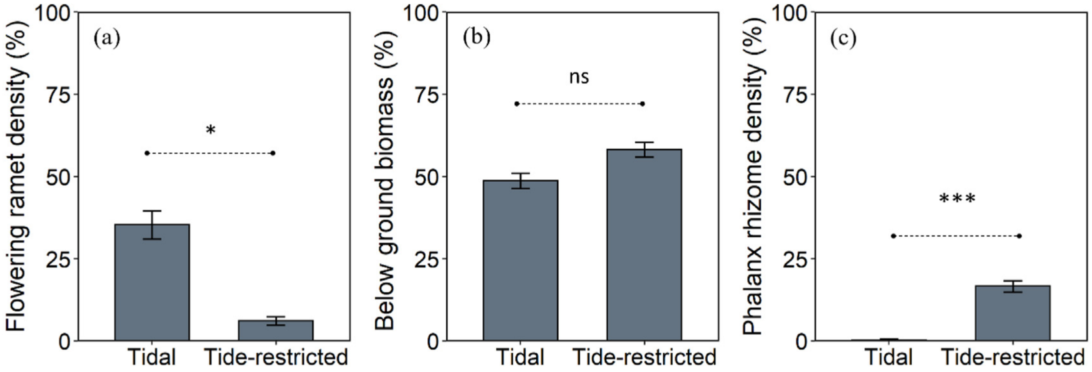

Fig. 3. Observed *B. planiculmis* reproduction, biomass, and rhizome ratios in tidal marshes and tide-restricted marshes. (a) flowering ramet density ratio (n = 50 for tidal marshes, n = 50 for tide-restricted marshes), (b) below ground biomass ratio (n = 50 for tidal marshes, n = 49 for tide-restricted marshes, excluding missing below ground data for the Daesong (DS) site), and (c) phalanx rhizome density ratio (n = 50 for tidal marshes, n = 49 for tide-restricted marshes, excluding missing below ground data for the DS site), with standard error bars. Significance level: $^{***}p < 0.001$ and * $p < 0.05$.

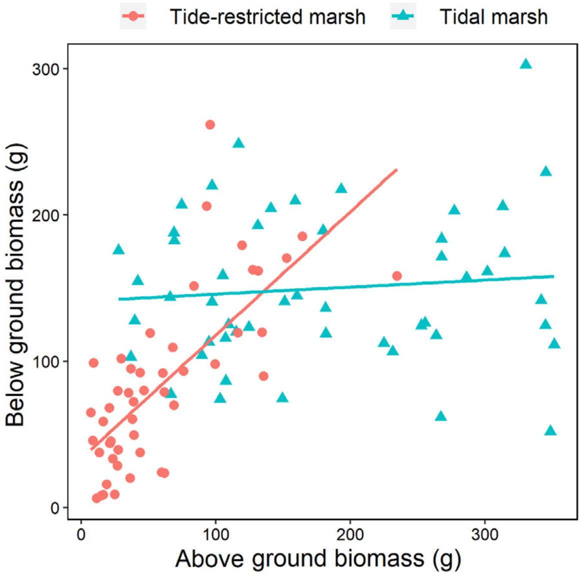

Fig. 4. Standardized major axis (SMA) regression for below- and above-ground biomass between tidal marshes and tide-restricted marshes. The tidal marshes had 50 replicates, while tide-restricted marshes had 49 replicates excluding missing below ground data for the Daesong (DS) site.

significantly correlated, showing a small amount of change of below ground biomass even under the increased above ground biomass.

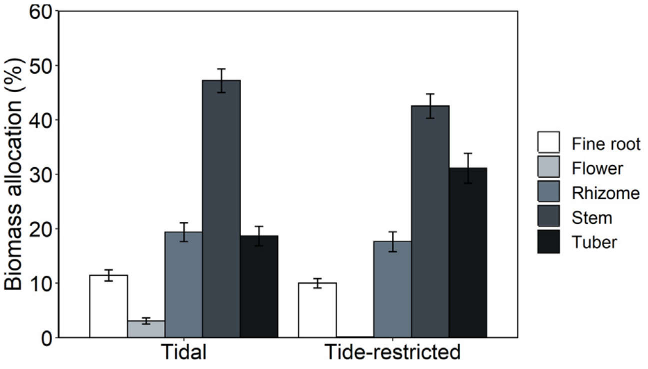

Fig. 5. Biomass allocation to each organ in the tidal marsh and tide-restricted marsh sites. Mean relative dry biomass per m^{-2} for each organ (fine root, flower, rhizome, stem, and tuber), with standard error bars (n = 50 for tidal marshes, n = 49 for tide-restricted marshes, excluding missing below ground data for the Daesong (DS) site).

3.3. Biomass allocation to each organ

B. planiculmis in both marsh types showed similar biomass allocation patterns for each organ (Fig. 5). Regardless of the marsh types, we observed the highest biomass allocation to stems without a significant difference ($p > 0.05$, $F_{1,8}$ = 1.012). Flower, rhizome, fine root, and tuber allocation were not significantly different between marsh types as well ($p > 0.05$, $F_{1,8}$ = 9.867; 0.206; 0.085; and 6.195). On the other hand, the slopes of each organ's biomass over total biomass (i.e., total biomass as x-axis

Table 3
Standardized major axis (SMA) regression for biomass of each organ between tidal marshes and tide-restricted marshes.

Dependent variable (g DM m $^{-2}$)	Independent variable (g DM m $^{-2}$)	Marsh type	Slope (Confidential interval)	df	Likelihood ratio	*p*-value for different slops	R^2	*p*-value for correlation
Below ground biomass	Above ground biomass	Tidal	0.51 (0.39–0.68)	1, 98	20.69	***	0.52	***
		Tide-restricted	1.17 (0.95–1.43)				0.01	ns
Flower biomass	Total biomass	Tidal	0.16 (0.13–0.19)	1, 98	207.60	***	0.45	***
		Tide-restricted	0.01 (0.00–0.01)				0.14	**
Stem biomass	Total biomass	Tidal	0.77 (0.67–0.89)	1, 98	20.47	***	0.75	***
		Tide-restricted	0.49 (0.44–0.56)				0.84	***
Rhizome biomass	Total biomass	Tidal	−0.23 (−0.31—0.17)	1, 98	0.18	ns	0.00	ns
		Tide-restricted	0.21 (0.17–0.26)				0.44	***
Root biomass	Total biomass	Tidal	0.18 (0.14–0.23)	1, 98	1.49		0.25	ns
		Tide-restricted	0.13 (0.10–0.16)				0.53	***
Tuber biomass	Total biomass	Tidal	0.32 (0.25–0.41)	1, 98	1.37	ns	0.20	**
		Tide-restricted	0.38 (0.33–0.46)				0.65	***

Likelihood ratio tests were done by standardized major axis (SMA) regression. Significance level: *** $p < 0.001$; ** $p < 0.01$; *$p < 0.05$; and ^{ns} $p \geq 0.05$. The tidal marshes had 50 replicates, while tide-restricted marshes had 49 replicates excluding missing below ground data for the Daesong (DS) site.

Table 4
Environmental variables in tidal and tide-restricted marshes.

	Tidal marshes (n = 50)	Tide-restricted marshes (n = 50)	df	*F* value	*p* value
	Mean (±SD)	Mean (±SD)			
Water depth (cm)	0.0 (±0.0)	9.3 (±8.4)	1, 8	106.57 (Chi)	***
Neighbor Importance value (IV)	20.0 (±15.2)	51.8 (±18.4)	1, 8	11.04	*
Soil pH	6.80 (±1.12)	7.90 (±0.63)	1, 8	3.75	ns
Soil salinity (ppt)	0.31 (±0.33)	0.69 (±0.44)	1, 8	3.09	ns
Soil organic matter (%)	3.11 (±1.49)	2.28 (±0.57)	1, 8	1.15	ns
Soil moisture (%)	28.7 (±4.6)	25.8 (±2.6)	1, 8	1.50	ns
PO_4^{3-}–P (mg kg $^{-1}$)	24.6 (±20.3)	9.7 (±6.2)	1, 8	9.07	ns
NO_3^-–N (mg kg $^{-1}$)	1.61 (±1.36)	1.70 (±1.04)	1, 8	0.03	ns
NH_4^+–N (mg kg $^{-1}$)	32.6 (±26.1)	17.3 (±16.3)	1, 8	1.92	ns

A Chi-squared test and *F* tests were done in linear mixed models (LMMs) and generalized linear mixed models (GLMMs). Significance level: ***$p < 0.001$, *$p < 0.05$, and $^{ns}p \geq 0.05$. SD: standard deviation. The statistical test of water depth is Chi-squared test because the glmmTMB package in R does not provide *F* test currently.

and each organ biomass as *y*-axis) showed more detailed relationships of biomass allocation to each organ (Table 3). The slopes of flower biomass over total biomass were positive and significantly steeper in tidal marshes than tide-restricted marshes ($p<0.001$). This result indicated that *B. planiculmis* in tidal marshes tended to allocate more biomass to flower biomass as total biomass increased than in tide-restricted marshes. Tidal marshes also had a positive and steeper slope of stem biomass over total biomass compared to tide-restricted marshes ($p < 0.001$). The slopes of rhizome biomass over total biomass were not significantly different in both types of marshes. The slopes of fine root biomass over total biomass were positive and significantly steeper in tide-restricted marshes ($p<0.05$), indicating *B. planiculmis* in tide-restricted marshes allocated more biomass to fine root biomass as total biomass increased than in tidal marshes. The slopes of tuber biomass over total biomass were not significantly different.

3.4. Environmental variables

The water depth and neighbor IV were higher in the tide-restricted marshes than in the tidal marshes ($p < 0.001$, *Chi* = 106.57; $p<0.05$, $F_{1,8} = 11.037$, Table 4). The mean water depth in the tidal marshes was 0 cm because these areas were usually exposed to the air, except for spring tides. The water depth in the tide-restricted marshes varied from 0 cm to above 25 cm (Table A2). The soil pH, SS, SOM, SM, PO_4^{3-}–P, NO_3^-–N, and NH_4^+–N did not show significant differences between the tidal marsh and tide-restricted marsh sites.

Table 5
Summary of redundancy analysis (RDA) results.

	RDA1***	RDA2
Eigenvalues	460.8	45.7
Proportion of variance (%)	41	4
Cumulative variance (%)	41	45
Density***	0.93	0.06
Neighbor Importance value (IV)	−0.58	−0.31
WD***	−0.53	−0.01
SS***	−0.65	−0.06
pH**	−0.18	−0.78
Phosphate*	0.22	0.39
SOM	0.09	0.74
SM	0.18	0.65
Ammonium	0.15	0.18
Nitrate	−0.04	0.04

Density, number of *B. planiculmis* ramets per quadrat; neighbor IV, importance value of other species; WD, water depth; SS, soil salinity; pH, soil pH; phosphate, PO_4^{3}–P; SOM, soil organic matter; SM, soil moisture; ammonium, NH_4^+–N; nitrate, NO_3^-–N. Correlations indicate correlations of environmental factors with the first two ordination axes. Significance level: ***$p<0.001$, ** $p<0.01$, *$p<0.05$, and $^{ns}p \geq 0.05$ ($n = 99$ excluding missing data for the Daesong (DS) site).

3.5. Relationships between B. planiculmis responses and environmental variables

The RDA ordination was significant ($p<0.001$, $F_{10,88} = 8.02$, Fig. 6 and Table 5). The first axis was also significant ($p<0.001$, $F_{1,95} = 74.52$). The first axis of RDA was positively correlated with the density of *B. planiculmis* (0.93) and PO_4^{3-}–P (0.22), while it was negatively correlated with SS (−0.65), neighbor IV (−0.58), water depth (−0.53), and soil pH (−0.18). The second axis was

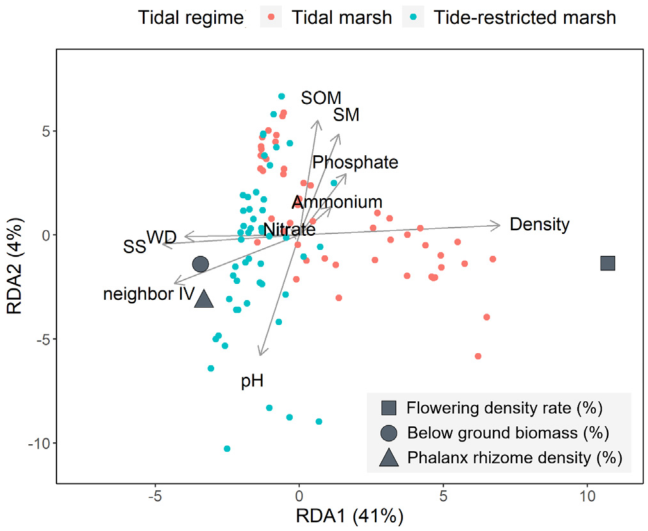

Fig. 6. Ordination by redundancy analysis (RDA) showing the relationships between reproduction, biomass, rhizome ratios and environmental variables. Density, number of *B. planiculmis* ramets per quadrat; neighbor IV, importance value of other species; WD, water depth; SS, soil salinity; pH, soil pH; phosphate, PO_4^{3}–P; SOM, soil organic matter; SM, soil moisture; ammonium, NH_4^{+}–N; nitrate, NO_3^{-}–N. Red points indicate quadrats in the tide-restricted marsh, and blue points indicate quadrats in the tidal marsh ($n = 50$ for tidal marshes, $n = 49$ for tide-restricted marshes, excluding missing below ground data for the Daesong (DS) site). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

positively correlated with PO_4^{3-}–P (0.39) and density (0.06) but negatively correlated with soil pH (−0.78), neighbor IV (−0.31), SS (−0.06), and water depth (−0.01). The sum of canonical eigenvalues explained 45% of total variance, with 41% explained by the first axis and 4% explained by the second axis (Table 4). The adjusted R^2 was 0.42. The flowering ramet density ratio increased as the density of *B. planiculmis* increased in tidal marshes, while the phalanx rhizome density ratio and the below ground biomass ratio increased with increasing neighbor IV, SS, and water depth in tide-restricted marshes.

4. Discussion

The tidal marshes showed 0 cm water depth because they were often exposed to the air, except for during the biweekly spring tides. On the other hand, tide-restricted marshes were flooded or saturated due to the embankments (Table 4). The dominance of other species depended on the tidal regimes, and was higher in the tide-restricted marshes than in the tidal marshes. Under the stable conditions without tides, *B. planiculmis* can be easily replaced by competitors such as *Phragmites australis*, *Echinochloa crusgalli*, and *Echinochloa caudate* (Bornette and Puijalon, 2011; Ning et al., 2014; Liu et al., 2016). On the other hand, the low dominance of other species in tidal marshes might be explained by the different abilities of species to respond to environmental stress. *Bolboschoenus* spp. have abilities to adapt to tidal and flooding stress (Carus et al., 2016; Silinski et al., 2018), which might enable them to inhabit lower elevations (You, 2008; Kim et al., 2016). However, the major neighbor species *Phragmites australis* and *Carex scabrifolia* prefer higher elevations (Sun et al., 2002; Bang et al., 2018), likely due to the reduced ability to respond to tidal flooding stress (Zhou et al., 2017). Recently, Yang et al. (2020) revealed that *B. planiculmis* effectively avoids the tidal stress and is not negatively affected by neighbor species *C. scabrifolira* under tidal influence; however, it is outcompeted by the neighbor species in the absence of tidal stress. This result supports the reduction of *B. planiculmis* in tide-restricted marshes, which was observed in this study.

B. planiculmis growing in the tidal marshes exhibited a higher density of around 1046 ramets m^{-2} compared to 128 ramets m^{-2} in the tide-restricted marshes (Table 2). Higher density in a tidal marsh than in a sheltered marsh has also been observed for a similar species, *Bolboschoenus maritimus* (Silinski et al., 2018). Silinski et al. (2018) described this phenomenon as a self-adapting mechanism to attenuate the effects of tidal strength with dense ramets, which might partly explain the results of this study.

Tidal regimes can change biomass allocation of marsh plants. In reduced tides, marsh plants develop above ground biomass to tolerate the weak waves, while they allocated highly to below ground biomass under increased tides to prevent uprooting (Blanchette, 1997; Peralta et al., 2008; Silinski et al., 2018). However, the present study did not agree with the results of previous studies but rather showed slightly more allocation to below ground biomass in tide-restricted marshes (Fig. 3b, Fig. 4, and Fig. 6). In the field, tide was not the only factor affected by tidal restriction. The tidal restriction also resulted in increased dominance of neighbor species (Table 4). The biomass allocation of *B. planiculmis* would be affected by both complicated impacts of reduced tide and increased dominance of neighbor species in the tide-restricted marshes (Szmeja, 1994). A possible clue for supporting this idea is the steeper slope of below ground biomass over above ground biomass in tide-restricted marshes (Table 3 and Fig. 4). In tide-restricted marshes, the higher occupancy of neighboring species appeared, and this can result in greater allocation to below ground biomass of *B. planiculmis* to withstand the below ground competition (Berendse and Möller, 2009; Poorter et al., 2012).

Marsh plants exposed to tides decrease sexual reproduction, while they increased vegetative reproduction to endure the environmental stress (Sun et al., 2002; Puijalon et al., 2008). However, *B. planiculmis* showed the opposite results with increased flowering ramet density in tidal marshes (Fig. 3a and Table 3). Our study is consistent with Chen et al. (2015), who noted that the higher sexual reproduction ratio in lower elevation plants could be a survival mechanism using tidal flow for seed dispersal. In addition, the higher ramet density of *B. planiculmis* in the tidal marshes might be another possible explanation for the increased flowering ramet density. Generally, the flowering ramet density of clonal plants increases as the total ramet density becomes increased (Sun et al., 2001, 2002; Olejniczak, 2003). The sexual reproduction through flowering can disperse seeds, which could help plants escape the local area where additional individuals have a low probability of survival in plant dense areas (Eriksson, 1989; Chen et al., 2015). Even though the seed germination in the field is very low in *B. planiculmis* (Nishihiro et al., 2004), it appeared to respond in a similar manner to other clonal plants.

To the best of the author's knowledge, impacts of tidal regimes on the phalanx rhizome density has not previously been studied. Instead, earlier studies revealed that severe competitive stress or small patch sizes could result in a high number of phalanx rhizomes in *Scirpus olneyi*, *Amphibromus scabrivalvis*, and *Carex* spp. (Bernard, 1990; Cheplick, 1997; Ikegami et al., 2007). Phalanx rhizomes can be beneficial for persistence in stressful restricted use of original habitats, while guerrilla rhizomes promote the occupation of new areas (Doust, 1981; Humphrey and Pyke, 1998; Ye et al., 2006). In this study, higher water depth, neighbor IV, and soil salinity in the tide-restricted marsh are likely to affect the higher phalanx rhizome density (Fig. 6), In particular, the neighbor IV was significantly higher in the tide-restricted marshes as a possible major factor to cause the development of phalanx rhizomes (Table 4); however, careful interpretations and further studies are needed to clarify the impacts of tidal regime and neighbor species on the increased phalanx rhizome density.

In this study, *B. planiculmis* responded in order to persist in the original habitats in tide-restricted marshes by more allocation to below ground biomass and higher phalanx rhizome density, while it attempted to expand its area in tidal marshes through seed dispersal and guerilla rhizome density. Considering the dramatically reduced ramet density, the tide-restricted condition limited *B. planiculmis* population by causing significant changes in hydrology (i.e., blocking tide and maintaining high water depth) and vegetation composition (e.g., dominating of neighbor species such as *Phragmites australis*). These changes can threaten not only the maintenance of the *B. planiculmis* population but also endangered migratory birds that feed on its tubers (You, 2008; Liu et al., 2016). To support this food web connectivity sustainably, as expected, this study showed that the impacts of tide-restriction on *B. planicumlis* should be minimized and that tidal fluctuation is essential. There recently have been many efforts to restore the structures and functions of original marshes through tidal restoration (Burdick et al., 1996; Warren et al., 2002). The basic understanding of how the estuarial plant *B. planiculmis* responds to tidal restriction gained through this study can help for better management for sustainable conservation.

5. Conclusion

In this study, differences in plastic growth responses of *B. planiculmis* and environmental variables between tidal marshes and tide-restricted marshes were evaluated. *Bolboscheonus planiculmis* in tidal marshes exhibited increased flowering ramet density, guerilla rhizomes density, and total ramet densities, while the tide-restricted marsh populations showed lower flowering ramet density, higher phalanx rhizomes density, and decreased total ramet densities. These differences could be explained by differences in increased water depth and dominance of neighbor species caused by tidal restriction. This study suggests that *B. planiculmis* favors tidal marshes by allocating resources to the seeds and guerrilla rhizomes to expand into adjacent areas. On the other hand, in the tide-restricted marshes, more resources are allocated to below ground biomass and more phalanx rhizomes are developed in order to persist in these habitats. To sustainably manage and conserve *B. planiculmis*, tidal restriction caused by embankments should be minimized (i.e., maintaining tidal fluctuation, managing competing species with the tides). Neighbor species and hydrodynamics, including flooding depth, flooding frequency, and flooding duration, should be considered in order to preserve and restore *B. planiculmis* marshes.

CRediT authorship contribution statement

Hyunyoung Yang: Conceptualization, Methodology, Software, Visualization, Investigation, Data curation, Validation, Writing - original draft. **Jae Hyun Kim:** Methodology, Investigation, Validation, Writing - reviewing and editing. **Eun Ju Lee:** Resources, Supervision, Writing - reviewing and editing.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2021.101616.

References

Bang, J.H., Bae, M.J., Lee, E.J., 2018. Plant distribution along an elevational gradient in a macrotidal salt marsh on the west coast of Korea. Aquat. Bot. 147, 52–60. http://dx.doi.org/10.1016/j.aquabot.2018.03.005.

Bates, D., Machler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. http://dx.doi.org/10.18637/jss.v067.i01.

Berendse, F., Möller, F., 2009. Effects of competition on root–shoot allocation in *Plantago lanceolata* L.: adaptive plasticity or ontogenetic drift? In: Van der Valk, A.G. (Ed.), Herbaceous Plant Ecology: Recent Advances in Plant Ecology. Springer Netherlands, Dordrecht, pp. 203–209.

Bernard, J.M., 1990. Life-history and vegetative reproduction in *Carex*. Can. J. Bot. 68, 1441–1448. http://dx.doi.org/10.1139/b90-182.

Blanchette, C.A., 1997. Size and survival of intertidal plants in response to wave action: A case study with *Fucus gardneri*. Ecology 78, 1563–1578. http://dx.doi.org/10.1890/0012-9658(1997)078[1563:SASOIP]2.0.CO;2.

Bolker, B., 2019. Getting started with the glmmTMB package.

Bornette, G., Puijalon, S., 2011. Response of aquatic plants to abiotic factors: a review. Aquat. Sci. 73, 1–14. http://dx.doi.org/10.1007/s00027-010-0162-7.

Bray, R.H., Kurtz, L.T., 1945. Determination of total, organic, and available forms of phosphorus in soils. Soil Sci. 59, 39–45. http://dx.doi.org/10.1097/00010694-194501000-00006.

Burdick, D.M., Dionne, M., Boumans, R.M., Short, F.T., 1996. Ecological responses to tidal restorations of two northern New England salt marshes. Wetlands Ecol. Manage 4, 129–144. http://dx.doi.org/10.1007/bf01876233.

Carus, J., Paul, M., Schroder, B., 2016. Vegetation as self-adaptive coastal protection: Reduction of current velocity and morphologic plasticity of a brackish marsh pioneer. Ecol. Evol. 6, 1579–1589. http://dx.doi.org/10.1002/ece3.1904.

Chen, X.S., Li, Y.F., Xie, Y.H., Deng, Z.M., Li, X., Li, F., Hou, Z.Y., 2015. Trade-off between allocation to reproductive ramets and rhizome buds in *Carex brevicuspis* populations along a small-scale elevational gradient. Sci. Rep. 5, 12688. http://dx.doi.org/10.1038/srep12688.

Cheplick, G.P., 1997. Responses to severe competitive stress in a clonal plant: Differences between genotypes. Oikos 79, 581–591. http://dx.doi.org/10.2307/3546902.

Chevin, L.M., Collins, S., Lefevre, F., 2013. Phenotypic plasticity and evolutionary demographic responses to climate change: taking theory out to the field. Funct. Ecol. 27, 966–979. http://dx.doi.org/10.1111/j.1365-2435.2012.02043.x.

Curt, T., Coll, L., Prevosto, B., Balandier, P., Kunstler, G., 2005. Plasticity in growth, biomass allocation and root morphology in beech seedlings as induced by irradiance and herbaceous competition. Ann. For. Sci. 62, 51–60. http://dx.doi.org/10.1051/forest:2004092.

Doust, L.L., 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus Repens*): I. The dynamics of ramets in contrasting habitats. J. Ecol. 69, 743–755. http://dx.doi.org/10.2307/2259633.

Eriksson, O., 1989. Seedling dynamics and life histories in clonal plants. Oikos 55, 231–238. http://dx.doi.org/10.2307/3565427.

Hammersmark, C.T., Fleenor, W.E., Schladow, S.G., 2005. Simulation of flood impact and habitat extent for a tidal freshwater marsh restoration. Ecol. Eng. 25, 137–152. http://dx.doi.org/10.1016/j.ecoleng.2005.02.008.

Hartig, F., 2019. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Heip, C.H.R., Goosen, N.K., Herman, P.M.J., Kromkamp, J., Middelburg, J.J., Soetaert, K., 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanogr. Mar. Biol. Annu. Rev. 33, 1–149.

Hroudová, Z., Zákravský, P., Flegrová, M., 2014. The tolerance to salinity and nutrient supply in four European *Bolboschoenus* species (*B. maritimus, B. laticarpus, B. planiculmis* and *B. yagara*) affects their vulnerability or expansiveness. Aquat. Bot. 112, 66–75. http://dx.doi.org/10.1016/j.aquabot.2013.07.012.

Humphrey, L.D., Pyke, D.A., 1998. Demographic and growth responses of a guerrilla and a phalanx perennial grass in competitive mixtures. J. Ecol. 86, 854–865. http://dx.doi.org/10.1046/j.1365-2745.1998.8650854.x.

Ikegami, M., Whigham, D.F., Werger, M.J.A., 2007. Responses of rhizome length and ramet production to resource availability in the clonal sedge *Scirpus olneyi* A. Gray. Plant Ecol. 189, 247–259. http://dx.doi.org/10.1007/s11258-006-9181-9.

Jung, J.D., Choi, H.K., 2011. Taxonomic study of Korean *Scirpus* L. s.l. (Cyperaceae) I. Morphology of *Bolboschoenus* (Asch.) Palla, Schoenoplectus (Rchb.) Palla, Schoenoplectiella Lye, Scirpus L. and *Trichophorum* Pers. Korean J. Pl. Taxon. 41, 16–34.

Kamphake, L.J., Hannah, S.A., Cohen, J.M., 1967. Automated analysis for nitrate by hydrazine reduction. Water Res. 1, 205. http://dx.doi.org/10.1016/0043-1354(67)90011-5.

Karagatzides, J.D., Hutchinson, I., 1991. Intraspecific comparisons of biomass dynamics in *Scirpus americanus* and *Scirpus maritimus* on the Fraser-River Delta. J. Ecol. 79, 459–476. http://dx.doi.org/10.2307/2260726.

Kim, J.Y., Im, R.Y., Do, Y., Kim, G.Y., Joo, G.J., 2016. Above-ground biomass estimation of tuberous bulrush (*Bolboschoenus planiculmis*) in mudflats using remotely sensed multispectral image. Ocean Sci. J. 51, 151–158. http://dx.doi.org/10.1007/s12601-016-0013-0.

Kim, G.Y., Kim, J.Y., Ganf, G.G., Lee, C.W., Joo, G.J., 2013. Impact of over-wintering waterfowl on tuberous bulrush (*Bolboschoenus planiculmis*) in tidal flats. Aquat. Bot. 107, 17–22. http://dx.doi.org/10.1016/j.aquabot.2013.01.004.

Konisky, R.A., Burdick, D.M., 2004. Effects of stressors on invasive and halophytic plants of New England salt marshes: A framework for predicting response to tidal restoration. Wetlands 24, 434–447. http://dx.doi.org/10.1672/0277-5212(2004)024[0434:Eosoia]2.0.Co;2.

Lee, C.H., Lee, B.Y., Chang, W.K., Hong, S., Song, S.J., Park, J., Kwon, B.O., Khim, J.S., 2014. Environmental and ecological effects of Lake Shihwa reclamation project in South Korea: A review. Ocean Coast. Manage. 102, 545–558. http://dx.doi.org/10.1016/j.ocecoaman.2013.12.018.

Lie, H.-J., Cho, C.-H., Lee, S., Kim, E.-S., Koo, B.-J., Noh, J.-H., 2008. Changes in marine environment by a large coastal development of the saemangeum reclamation project in Korea. Ocean Polar Res. 30, 475–484. http://dx.doi.org/10.4217/opr.2008.30.4.475.

Liu, B., Jiang, M., Tong, S.Z., Zhang, W.G., Wu, H.T., Liu, Y., Lu, X.G., 2016. Differential flooding impacts on *Echinochloa caudata* and *Scirpus planiculmis*: Implications for weed control in Wetlands. Wetlands 36, 979–984. http://dx.doi.org/10.1007/s13157-016-0805-0.

Ma, Z., Melville, D.S., Liu, J., Chen, Y., Yang, H., Ren, W., Zhang, Z., Piersma, T., Li, B., 2014. Rethinking China's new great wall. Science 346, 912–914. http://dx.doi.org/10.1126/science.1257258.

Mcintosh, R.P., 1957. The york woods, a case-history of forest succession in southern wisconsin. Ecology 38, 29–37. http://dx.doi.org/10.2307/1932123.

McKone, M.J., Lively, C.M., 1993. Statistical analysis of experiments conducted at multiple sites. Oikos 67, 184–186. http://dx.doi.org/10.2307/3545109.

Melville, D.S., Chen, Y., Ma, Z.J., 2016. Shorebirds along the Yellow Sea coast of China face an uncertain future - a review of threats. Emu 116, 100–110. http://dx.doi.org/10.1071/Mu15045.

Montague, C.L., Zale, A.V., Percival, H.F., 1987. Ecological effects of coastal marsh impoundments - a review. Environ. Manage. 11, 743–756. http://dx.doi.org/10.1007/Bf01867242.

Moores, N., Rogers, D.I., Rogers, K., Hansbro, P.M., 2016. Reclamation of tidal flats and shorebird declines in saemangeum and elsewhere in the Republic of Korea. Emu 116, 136–146. http://dx.doi.org/10.1071/Mu16006.

Mora, J.W., Burdick, D.M., 2013a. Effects of man-made berms upon plant communities in New England salt marshes. Wetlands Ecol. Manage. 21, 131–145. http://dx.doi.org/10.1007/s11273-013-9285-7.

Mora, J.W., Burdick, D.M., 2013b. The impact of man-made earthen barriers on the physical structure of New England tidal marshes (USA). Wetlands Ecol. Manage. 21, 387–398. http://dx.doi.org/10.1007/s11273-013-9309-3.

Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27, 31–36. http://dx.doi.org/10.1016/s0003-2670(00)88444-5.

Murray, N.J., Clemens, R.S., Phinn, S.R., Possingham, H.P., Fuller, R.A., 2014. Tracking the rapid loss of tidal wetlands in the Yellow Sea. Front. Ecol. Environ. 12, 267–272. http://dx.doi.org/10.1890/130260.

Ning, Y., Zhang, Z.X., Cui, L.J., Zou, C.L., 2014. Adaptive significance of and factors affecting plasticity of biomass allocation and rhizome morphology: A case study of the clonal plant *Scirpus Planiculmis* (Cyperaceae). Pol. J. Ecol. 62, 77–88. http://dx.doi.org/10.3161/104.062.0108.

Nishihiro, J., Araki, S., Fujiwara, N., Washitani, I., 2004. Germination characteristics of lakeshore plants under an artificially stabilized water regime. Aquat. Bot. 79, 333–343. http://dx.doi.org/10.1016/j.aquabot.2004.05.005.

Olejniczak, P., 2003. Optimal allocation to vegetative and sexual reproduction in plants: the effect of ramet density. Evol. Ecol. 17, 265–275. http://dx.doi.org/10.1023/a:1025572713483.

Peralta, G., van Duren, L.A., Morris, E.P., Bouma, T.J., 2008. Consequences of shoot density and stiffness for ecosystem engineering by benthic macrophytes in flow dominated areas: a hydrodynamic flume study. Mar. Ecol. Prog. Ser. 368, 103–115. http://dx.doi.org/10.3354/meps07574.

Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol. 193, 30–50. http://dx.doi.org/10.1111/j.1469-8137.2011.03952.x.

Portnoy, J.W., 1999. Salt marsh diking and restoration: Biogeochemical implications of altered wetland hydrology. Environ. Manage. 24, 111–120. http://dx.doi.org/10.1007/s002679900219.

Portnoy, J.W., Giblin, A.E., 1997. Effects of historic tidal restrictions on salt marsh sediment chemistry. Biogeochemistry 36, 275–303. http://dx.doi.org/10.1023/A:1005715520988.

Puijalon, S., Bornette, G., Sagnes, P., 2005. Adaptations to increasing hydraulic stress: morphology, hydrodynamics and fitness of two higher aquatic plant species. J. Exp. Bot. 56, 777–786. http://dx.doi.org/10.1093/jxb/eri063.

Puijalon, S., Lena, J.P., Riviere, N., Champagne, J.Y., Rostan, J.C., Bornette, G., 2008. Phenotypic plasticity in response to mechanical stress: hydrodynamic performance and fitness of four aquatic plant species. New Phytol. 177, 907–917. http://dx.doi.org/10.1111/j.1469-8137.2007.02314.x.

Qi, M., Sun, T., Zhan, M., Xue, S.F., 2016. Simulating dynamic vegetation changes in a tidal restriction area with relative stress tolerance curves. Wetlands 36, S31–S43. http://dx.doi.org/10.1007/s13157-015-0639-1.

R Development Core Team, 2008. R Core Team. R A Language and Environment for Statistical Computing 2014.

Roman, C.T., Niering, W.A., Warren, R.S., 1984. Salt-marsh vegetation change in response to tidal restriction. Environ. Manage. 8, 141–149. http://dx.doi.org/10.1007/Bf01866935.

Shepard, C.C., Crain, C.M., Beck, M.W., 2011. The protective role of coastal marshes: a systematic review and meta-analysis. PLoS One 6, e27374. http://dx.doi.org/10.1371/journal.pone.0027374.

Silinski, A., Schoutens, K., Puijalon, S., Schoelynck, J., Luyckx, D., Troch, P., Meire, P., Temmerman, S., 2018. Coping with waves: Plasticity in tidal marsh plants as self-adapting coastal ecosystem engineers. Limnol. Oceanogr. 63, 799–815. http://dx.doi.org/10.1002/lno.10671.

SolÓRzano, L., 1969. Determination of ammonia in natural waters by the phenolhypochlorite method 1 1 This research was fully supported by U.S. Atomic Energy Commission Contract No. ATS (11-1) GEN 10, P.A. 20. Limnol. Oceanogr. 14, 799–801. http://dx.doi.org/10.4319/lo.1969.14.5.0799.

Sun, S.C., Cai, Y.L., An, S.Q., 2002. Differences in morphology and biomass allocation of *Scirpus mariqueter* between creekside and inland communities in the Changjiang estuary, China. Wetlands 22, 786–793. http://dx.doi.org/10.1672/0277-5212(2002)022[0786:Dimaba]2.0.Co;2.

Sun, S.C., Cai, Y.L., Tian, X.J., 2003. Salt marsh vegetation change after a short-term tidal restriction in the Changjiang estuary. Wetlands 23, 257–266. http://dx.doi.org/10.1672/5-20.

Sun, S.C., Gao, X.M., Cai, Y.L., 2001. Variations in sexual and asexual reproduction of *Scirpus mariqueter* along an elevational gradient. Ecol. Res 16, 263–274. http://dx.doi.org/10.1046/j.1440-1703.2001.00395.x.

Szmeja, J., 1994. Effect of disturbances and interspecific competition in isoetid populations. Aquat. Bot. 48, 225–238. http://dx.doi.org/10.1016/0304-3770(94)90017-5.

Van de Broek, M., Vandendriessche, C., Poppelmonde, D., Merckx, R., Temmerman, S., Govers, G., 2018. Long-term organic carbon sequestration in tidal marsh sediments is dominated by old-aged allochthonous inputs in a macrotidal estuary. Glob. Change Biol. 24, 2498–2512. http://dx.doi.org/10.1111/gcb.14089.

Wang, C.H., Li, B., 2016. Salinity and disturbance mediate direct and indirect plant-plant interactions in an assembled marsh community. Oecologia 182, 139–152. http://dx.doi.org/10.1007/s00442-016-3650-1.

Warren, R.S., Fell, P.E., Rozsa, R., Brawley, A.H., Orsted, A.C., Olson, E.T., Swamy, V., Niering, W.A., 2002. Salt marsh restoration in Connecticut: 20 years of science and management. Restoration Ecol. 10, 497–513. http://dx.doi.org/10.1046/j.1526-100X.2002.01031.x.

Yang, H., Kim, J.H., Lee, E.J., 2020. Effects of tides on interspecific interactions and plastic growth responses of *Bolboschoenus planiculmis*. Flora 264, 151568. http://dx.doi.org/10.1016/j.flora.2020.151568.

Ye, X.H., Yu, F.H., Dong, M., 2006. A trade-off between guerrilla and phalanx growth forms in *Leymus secalinus* under different nutrient supplies. Ann. Bot. 98, 187–191. http://dx.doi.org/10.1093/aob/mcl086.

You, Y.H., 2008. Population decline cause of *Scirpus planiculmis* and its restoration plan in Han River Wetland Conservation Area. South Korea. J. Wet. Res. 10, 165–172.

Zhou, J., Zheng, L.D., Pan, X., Li, W., Kang, X.M., Li, J., Ning, Y., Zhang, M.X., Cui, L.J., 2017. Hydrological conditions affect the interspecific interaction between two emergent wetland species. Front. Plant Sci. 8 (2253), http://dx.doi.org/10.3389/fpls.2017.02253.