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Effects of tides on interspecific interactions and plastic growth responses of *Bolboschoenus planiculmis*

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ABSTRACT

Interspecific interactions between marsh plants can be shifted by abiotic factors. In estuaries, diverse factors such as salinity, soil, and tide can affect these relationships; however, the effects of tides are still poorly understood. In this study, we evaluated the effects of tidal stress on interspecific interactions and the plastic growth responses of *Bolboschoenus planiculmis* in a greenhouse experiment. Simulated tide changed the nature of interspecific interactions between *B. planiculmis* and *Carex scabrifolia*; the interaction was negative (competitive) in the non-tidal treatment but became neutral in the tidal treatment for *B. planiculmis*. Both tide and interspecific interactions decreased the biomass of *B. planiculmis*. The tide caused thinner stems which is in agreement with an avoidance strategy and decreased sexual reproduction in *B. planiculmis*; however, other plastic growth responses were not observed. *Carex scabrifolia* decreased biomass under tidal stress without any plastic ability under tidal stress. These results can help to explain the real distribution of these two species in the field. *Bolboschoenus planiculmis* with effective ability to avoid tidal stress would dominate at a low elevation; however, it may be outcompeted by its competitor *C. scabrifolia* at a high elevation. These findings indicate that tidal stress can alter interactions between stress-tolerant species and competitors in estuaries.

1. Introduction

Various abiotic and biotic factors can determine the distribution of marsh plants. Abiotic stress can change plant–plant interactions along environmental stress gradients. According to the stress gradient hypothesis (SGH), plant–plant interactions are negative (competition) when an abiotic stress is low and become positive (facilitation) when the abiotic stress increases (Maestre et al., 2009; Qi et al., 2018). As a result, stress-tolerant species that can endure the stress effectively dominate under stress conditions, while more competitive species dominate under non-stress conditions (Crain et al., 2004; Qi et al., 2018). The SGH can explain interspecific interactions along various environmental gradients in estuaries, such as gradients of salinity, water depth, and clipping (Wang and Li, 2016; Zhou et al., 2018). Tidal regime is another major abiotic factor in estuaries, varying from at least biweekly to twice a day (Armstrong et al., 1985; Pennings et al., 2005). The tidal regime significantly affects marsh plants at low elevations by increasing not only mechanical stress, but also flooding stress, while it has a weaker effect on plants at high elevations (Leonard and Luther, 1995; Silinski et al., 2018). Thus, understanding the effects of tide on plant–plant interactions (e.g., interspecific interaction, intraspecific interaction) has been examined recently in field and

greenhouse (Wang and Li, 2016; Carus, 2017).

Stress-tolerant plants can respond to tidal exposure effectively using an avoidance strategy or a tolerance strategy (Puijalon et al., 2011). In the avoidance strategy, mechanical stress is minimized by plastic growth responses, including reduced shoot length, flexible shoots, increased density to reduce the exposed surface, and increased allocation to belowground biomass to prevent uprooting (Niklas, 1998; Doyle, 2001; Puijalon et al., 2008b; Silinski et al., 2018). The tolerance strategy describes efforts to maximize resistance to the mechanical tipping point just before breaking, including increased shoot length, higher tissue rigidity, and greater allocation to aboveground biomass (Coops and Van der Velde, 1996; Puijalon et al., 2008b, 2011). Different plant species can have different levels of environmental tolerance ability, which can cause changes in interspecific interactions along the stress gradient (Zhou et al., 2018).

Bolboschoenus planiculmis (F. Schmidt) T. V. Egorova is an estuarine plant distributed in East Asia, Middle Asia, and Central Europe, and forms monodominant populations or mixed communities in estuaries, reclaimed rice paddies, and lagoons (Jung and Choi, 2011; Hroudová et al., 2014; Liu et al., 2016a). It is an early successional species and dwells nearest to water body at low elevations (Kim et al., 2013; Wang and Li, 2016), and is an important marsh plant that can provide food

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source for endangered migratory birds (Liu et al., 2016a; Kim et al., 2013). However, it is exposed to intense interspecific interactions with plants at middle elevations, such as *Phragmites australis*, *Echinochloa* spp., and *Carex scabrifolia* due to succession or changes in environment such as developing embankment (Liu et al., 2016a; Kim et al., 2013; Wang and Li, 2016). Although effects of individual abiotic or biotic factors on the responses of *Bolboschoenus* spp. have been studied including flooding regimes, salinity, grazing, and interspecific interactions (Kim et al., 2013; Liu et al., 2016b; Xue et al., 2017), the responses of *B. planiculmis* can be affected by more complicated condition such as shifts in interspecific interactions along environmental stress gradients. Recently, Zhou et al. (2018) clarified that increased water depth and its fluctuation altered the interspecific interactions between *B. planiculmis* and *P. australis*. However, in Korea, *B. planiculmis* is mainly exposed to frequent tidal cycles and high flow velocity, which results in both flooding stress and mechanical stress (Goesslink and Turner, 1978; Simpson et al., 1983). Considering these aspects is worthy for understanding interspecific interaction shifts in *B. planiculmis* with neighboring species.

In this study, we performed a greenhouse experiment to investigate the plastic growth responses of *B. planiculmis* under simulated tide and interspecific interaction treatments with *C. scabrifolia* as a neighboring species. We evaluated the following two hypotheses: (1) the interspecific interaction between *B. planiculmis* and *C. scabrifolia* changes along a tidal stress gradient, and (2) *B. planiculmis* alters its growth responses toward effective responses to tidal stress, while *C. scabrifolia* fails.

2. Methods

2.1. Collection of *B. planiculmis* and *C. scabrifolia* ramets

Bolboschoenus planiculmis (F. Schmidt) T. V. Egorova is a perennial clonal plant with a height of 20–100 cm; it dominates at low elevations in estuaries in East Asia (Kim et al., 2013). *Carex scabrifolia* Steud. was selected as a neighboring species since it has a more similar life cycle and size to *B. planiculmis* compared with other companion species. *Carex scabrifolia* is also a perennial clonal plant with a height of 30–100 cm; it dominates in areas of low to middle elevations in estuaries in East Asia. The species usually co-exists with *B. planiculmis* and reproduces with both sexual and vegetative organs in the field (Wang and Li, 2016).

On May 15th, 2018, 100 young ramets of each *B. planiculmis* and *C. scabrifolia* were randomly collected at Gongreong river, Paju, South Korea (37° 45' 31.00" N, 126° 41' 43.75" E), where the mean monthly temperature ranges from -5.1 °C (January) to 24.9 °C (August), the mean annual precipitation is 1458.7 mm (Korea Hydrographic and Oceanographic Agency, 2018), and soil salinity is 0–5‰ (Yang et al., unpublished data). Annual mean tide level is 3.5 m, mean low water is 1.1 m, and mean high water is 6.0 m at the nearest Kanghwa observatory (Korea Meteorological Administration, 2019). *Bolboschoenus planiculmis* dominated at the lower elevation (≈ 6 m), exposed to the tide more than two days per week, while *C. scabrifolia* occupied the higher elevation (> 7 m), inundated only less than one day per week. In the field, the mean and standard deviation of shoot length of the collected *B. planiculmis* ramets was 10.0 ± 3.2 cm, and the shoot length of the collected *C. scabrifolia* ramets was 42.2 ± 5.4 cm (mean $\pm$ standard deviation). Different shoot lengths for the two species reflected the different phenology (i.e., *C. scabrifolia* started to grow from middle of April; however, *B. planiculmis* grew from early May) in the field. All ramets of the two species were transported to a laboratory in a moist and cool plastic container. After wrapping their roots with field soil, each ramet was temporarily transplanted in a 200 L pot which was filled with sandy soil with a mean grain size of 1 mm. At the age of 7 days, pairs of survived ramets were chosen for the experiment.

2.2. Experimental design and sample processing

Plastic growth responses of *B. planiculmis* were examined under the presence and absence of tides and interspecific interactions. The two tidal treatments reflected each the maximum tidal exposure (i.e., twice a day) and the minimum tidal exposure as follows: (1) an hour of flooding up to 40 cm and 11-h of drainage at -5 cm from the soil surface for a 12-h cycle repeated two times a day (tidal treatment); and (2) maintenance of the water at -5 cm from the soil surface (non-tidal treatment). Rising and falling tides were imitated by pumping motors (Syncra 1.5; SICCE, Fort Lauderdale, FL, USA) with a velocity of 15 L/min from a 300 L water tank and a unidirectional flow direction. The two interaction treatments imitated common plant–plant interactions in the field as follows: (1) one *B. planiculmis* ramet and one *C. scabrifolia* ramet per pot (interspecific interaction treatment); and (2) two *B. planiculmis* ramets per pot (intraspecific interaction treatment). The 1:1 density reflected the relative dominance of *B. planiculmis* and neighboring species in the field (Yang et al., in progress). This experimental design is a replacement design rather than additive design (Snaydon, 1991), which made the results to indicate the relative importance of interspecific competition rather than intraspecific competition. A pair of ramets were transplanted to a pot (15 cm diameter and 15 cm height) which was filled with a mean grain size of 1 mm (15 cm depth). The size of the pot was decided based on the mean rhizome length and depth that the majority of belowground parts of *B. planiculmis* developed in the field (Yang et al., unpublished data). Two pots were contained in a tank (44 cm diameter, 53 cm height) to control tidal treatments as one replication (Fig. 1).

The effects of tide and interspecific interactions were examined from 17th May to 4th October 2018 in a greenhouse located at Seoul National University, Seoul, South Korea (37° 27' 34.12" N, 126° 56' 52.24" E). The temperature and air humidity in the greenhouse were systematically controlled with an average and standard deviation temperature of 23.0 ± 3.6 °C (range 10.5–34.0 °C), and air humidity of 66.1 ± 18.9 % (range 18.3–99.9 %). There were in total 24 pots with four treatments and six replicates; (1) T-I (Tidal and Interspecific interaction treatment), (2) NT-I (Non-tidal and Interspecific interaction treatment), (3) T-NI (Tidal and Intraspecific interaction treatment), and (4) NT-NI (Non-tidal and Intraspecific interaction treatment). Thus, in total 36 ramets of *B. planiculmis* were used, while in total 12 ramets of *C. scabrifolia* were used. In this study, salinity was not considered because *B. planiculmis* could survive in both freshwater (0‰) and brackish conditions (up to 10‰) with no biomass difference (Xue et al., 2017). To maintain water quality, pots were entirely drained and filled with tap water every other week. 5 g of solid fertilizer (11-8-7 NPK HY-PONeX KOREA) was applied per pot at the beginning of the experiment.

Final biomass per pot was harvested on October 8th and washed through a 1 mm sieve. *Bolboschoenus planiculmis* plants were separated into flower, stem, rhizome, tuber, and root parts, and *C. scabrifolia* plants were divided into flower, stem, rhizome, and root parts, since it did not produce tubers. The rhizomes and roots of the two species were carefully separated based on rhizome morphology, keeping each part unbroken. Plant materials were dried at 80 °C for 72-h. The ratio of aboveground biomass to belowground biomass (AGB:BGB ratio) was the ratio of dry aboveground biomass to dry belowground biomass. Density was the number of each species' shoots per pot. All shoot length was measured from the soil surface to the end of the shoot and averaged for each pot. Stem diameter of every shoot was measured at the soil surface level with a Vernier calipers and averaged for each pot. Sum of rhizome length was the total length of each species' rhizome per pot. Flowering rate was the ratio of the number of flowering ramets to the total number of ramets per pot. The number of tubers was also counted per pot.

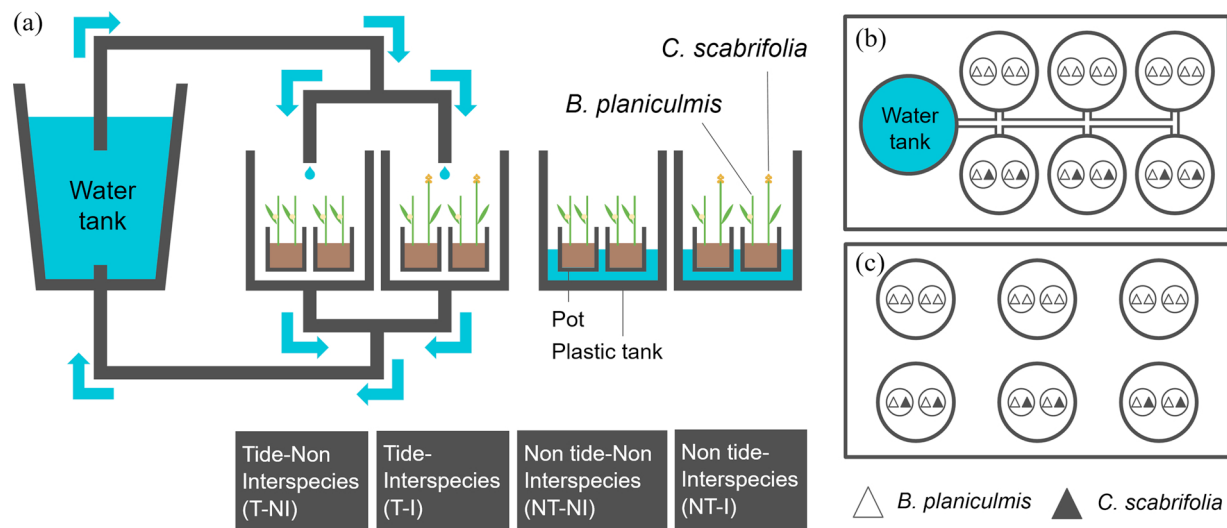


Fig. 1. Experimental design for *Bolboschoenus planiculmis* and *Carex scabrifolia*. (a) Tide and interspecific interaction experiment flowchart, (b) aerial view of the T-NI and T-I treatments, (c) aerial view of the NT-NI and NT-I treatments ($n = 3$).

2.3. Data analyses

The relative interaction index (RII) of *B. planiculmis* was compared between tidal and non-tidal treatments. This index measures plant–plant interactions according to the sign of the value from competition to facilitation (Armas et al., 2004). RII was calculated by the following equation:

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

B_W is the total biomass of a target species grown in a mixed culture with neighboring species and B_O is the total biomass of the target species grown in a monoculture. In this study, the target species is *B. planiculmis* and the neighboring species is *C. scabrifolia*. When RII is 0, there is no significant interaction between two species (neutral). Positive RII values indicate that the interaction is beneficial to the target species, and negative RII values indicate that the interaction is competitive to the target species. Differences in mean RII values per pot from 0 were checked by the one-sample *t*-test. Normality was confirmed by the Shapiro-Wilk test.

For analyzing the plastic growth responses of *B. planiculmis*, two-way ANOVA was conducted to explain the variance in total biomass per pot, individual biomass (total biomass per pot divided by the number of ramets per pot), biomass allocation, density, shoot length, stem diameter, sum of the rhizome length, flowering rate, and the number of tubers of *B. planiculmis* for two categories (tide and interspecific interaction). These data were log or square root transformed to meet normality and homoscedasticity assumptions. Normality was checked by the Shapiro test, and homoscedasticity was evaluated by Levene's test using the 'car' package in R. Post-hoc Tukey's honestly significant difference tests were performed using the 'agricolae' package.

To compare the plastic growth response of neighboring species *C. scabrifolia* under tidal treatment and non-tidal treatment, the total biomass, individual biomass, biomass allocation, density, shoot length, stem diameter, sum of the rhizome length, and flowering rate of *C. scabrifolia* were analyzed using Student's *t*-tests. Normality was verified by the Shapiro test. The comparison between interspecific and intraspecific interaction treatments for *C. scabrifolia* was not conducted due to limited space and labor and technical problem. All statistical analyses were performed using R version 3.4.3 (R Development Core Team, 2008). Values were considered significantly different at $p < 0.05$.

3. Results

3.1. RII shift for *B. Planiculmis* depending on tidal treatments

The mean and standard error RII value for *B. planiculmis* was -0.32 ± 0.07 with a range -0.63 to -0.02 for the non-tidal treatment. It was significantly negative (i.e., a competitive interaction) ($p = 0.04$, $t = -4.54$, One-sample *t* test; Fig. 2). However, the RII value for the tidal treatment was not significantly different from 0 (i.e., neutral) as -0.29 ± 0.24 ($p = 0.34$, $t = -1.23$). The RII value was shifted from negative to neutral in *B. planiculmis* depending on the tidal treatments.

3.2. Plastic growth responses of *B. Planiculmis*

Table 1 summarizes the two-way ANOVA results for the plastic growth response of *B. planiculmis* under tidal treatments (NT and T) and interaction treatments (NI and I). A significant difference in total biomass of *B. planiculmis* per pot was found between non-tidal treatment (1.34 ± 0.29 g) and tidal treatment (0.73 ± 0.20 g) ($p = 0.03$, $F = 7.48$). Interspecific interaction treatment also resulted in a decrease of total biomass of *B. planiculmis* compared to intraspecific interaction

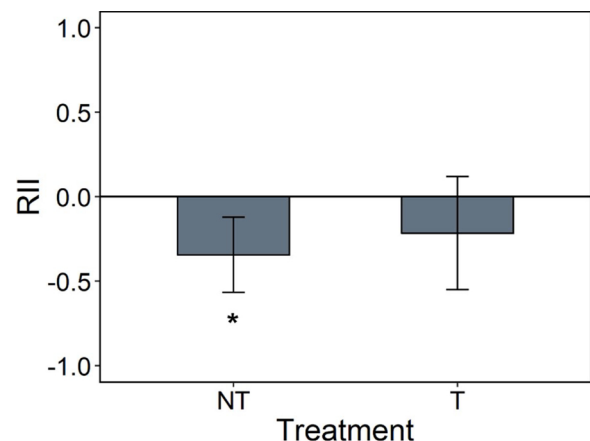
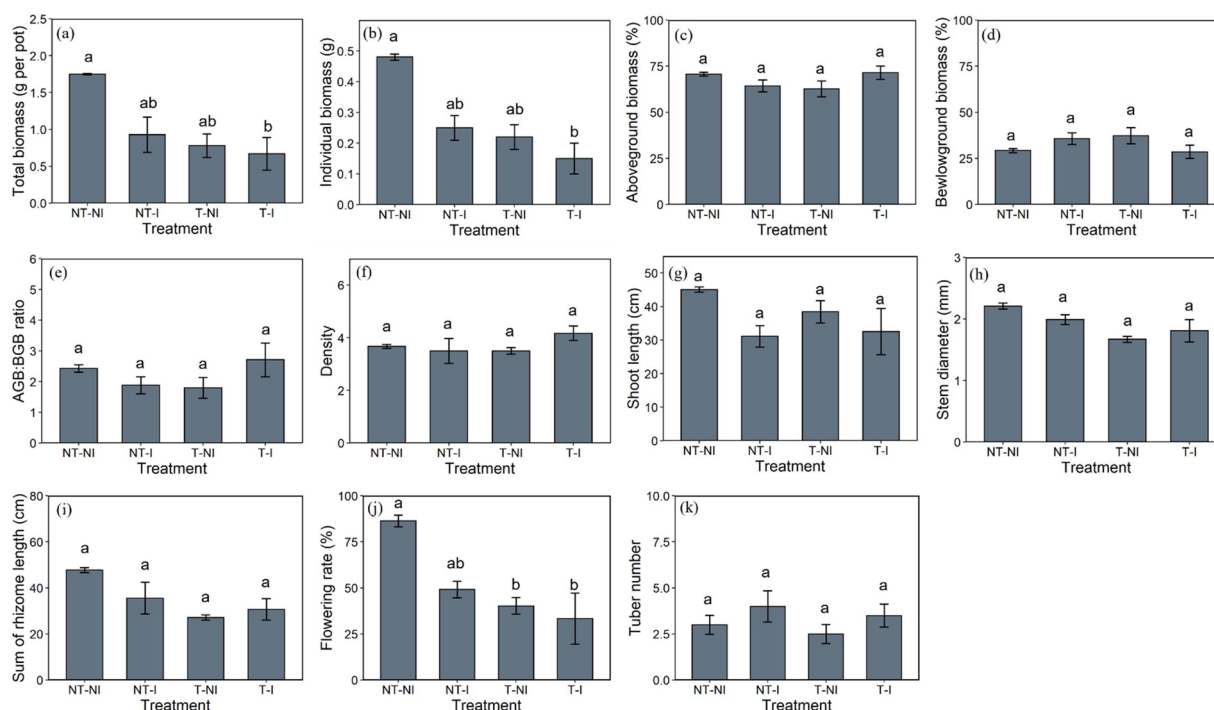


Fig. 2. Mean RII values for *Bolboschoenus planiculmis* in non-tidal and tidal treatments. NT indicates non-tidal treatment; T indicates tidal treatment. Significance level: *, $p < 0.05$. Bars mean standard errors ($n = 3$).

Table 1Two-way ANOVA tables for the plastic growth responses of *Bolboschoenus planiculmis* with two treatments (tide and interspecific interaction, n = 3).

	Tidal treatments (T)		Interspecific interaction treatments (I)		T × I	
	F(1, 8)	p	F(1, 8)	p	F(1, 8)	p
Total biomass (g per pot)	7.476	0.026*	4.423	0.069 ^{ns}	2.523	0.151 ^{ns}
Individual biomass (g)	16.686	0.004**	11.575	0.009**	3.312	0.106 ^{ns}
Aboveground biomass (%)	0.012	0.916 ^{ns}	0.084	0.780 ^{ns}	3.514	0.098 ^{ns}
Belowground biomass (%)	0.001	0.978 ^{ns}	0.096	0.764 ^{ns}	3.399	0.102 ^{ns}
AGB:BGB ratio	0.011	0.919 ^{ns}	0.133	0.725 ^{ns}	3.150	0.114 ^{ns}
Flower biomass (%)	33.238	0.0004***	2.684	0.140 ^{ns}	10.484	0.012**
Stem biomass (%)	9.638	0.0146*	1.361	0.277 ^{ns}	0.018	0.896 ^{ns}
Rhizome biomass (%)	0.864	0.380 ^{ns}	0.003	0.959 ^{ns}	0.196	0.670 ^{ns}
Tuber biomass (%)	0.196	0.670 ^{ns}	0.123	0.735 ^{ns}	2.629	0.144 ^{ns}
Root biomass (%)	0.998	0.347 ^{ns}	0.034	0.858 ^{ns}	0.037	0.853 ^{ns}
Density (shoot per pot)	0.551	0.479 ^{ns}	0.370	0.560 ^{ns}	1.515	0.253 ^{ns}
Shoot length (cm)	0.261	0.623 ^{ns}	3.813	0.087 ^{ns}	0.617	0.455 ^{ns}
Stem diameter (mm)	7.721	0.024*	0.097	0.763 ^{ns}	1.967	0.198 ^{ns}
Sum of rhizome length (cm)	5.293	0.050 ^{ns}	0.679	0.434 ^{ns}	2.070	0.188 ^{ns}
Flowering rate (%)	10.521	0.012*	5.364	0.049*	2.528	0.151 ^{ns}
Tuber number (per pot)	0.430	0.530 ^{ns}	1.621	0.239 ^{ns}	0.007	0.937 ^{ns}

Significance level: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns, $p \geq 0.05$.**Fig. 3.** Plastic growth responses of *Bolboschoenus planiculmis*. (a) Total biomass per pot, (b) individual biomass, (c) percentage of aboveground biomass (AGB), (d) percentage of belowground biomass (BGB), (e) AGB:BGB ratio, (f) density, (g) shoot length, (h) stem diameter, (i) sum of rhizome length, (j) flowering rate, and (k) tuber number. Different letters indicate significant differences among treatments according to Tukey's HSD test ($p < 0.05$). NT indicates non-tidal treatment; T indicates tidal treatment; NI indicates intraspecific interaction treatment; I indicates interspecific interaction treatment. Bars mean standard errors (n = 3).

treatment (0.80 g vs. 1.27 g); however, this effect was not significant ($p = 0.07$, $F = 4.42$). There was no interaction effect between tide and interaction treatments (i.e., $T \times I$). As a result, the total biomass of the control treatment (NT-NI) was higher than T-I treatment ($p = 0.04$, Fig. 3a). Similarly, the individual biomass was significantly reduced in tidal treatment (0.19 g) compared to non-tidal treatment (0.36 g) ($p = 0.004$, $F = 16.69$) and in interspecific interaction treatment (0.20 g) compared to intraspecific interaction treatment (0.35 g) ($p = 0.01$, $F = 11.58$), with no interaction effect. The individual biomass was significantly higher in the control treatment (NT-NI) than in T-I treatment ($p = 0.003$, Fig. 3b).

Allocation of biomass in *B. planiculmis* into aboveground (i.e., the percentage of aboveground biomass) was not significantly different between non-tidal treatment (68 %) and tidal treatment (67 %). It was

also not significantly different between interspecific interaction treatment and intraspecific interaction treatment (68 % vs. 67 %). There was no interaction effect between tide and interaction. Thus, the percentage of belowground biomass (mean and standard error, 33 ± 0.04 %) and AGB:BGB ratio (2.21 ± 0.42) were also not affected by the tidal treatments and interspecific interaction treatments.

Among biomass allocation to each organ, the percentage of flower biomass and stem biomass were significantly affected by tidal treatments (Fig. 4). A significant difference in the percentage of flower biomass was detected in tidal treatment (4 ± 2 %) compared to non-tidal treatment (19 ± 4 %) ($p = 0.0004$, $F = 33.24$). There was an interaction effect between tidal and interaction treatments in that percentage flower biomass in NT-NI was higher than in NT-I; however, percentage flower biomass of T-NI was not different from T-I ($p = 0.01$,

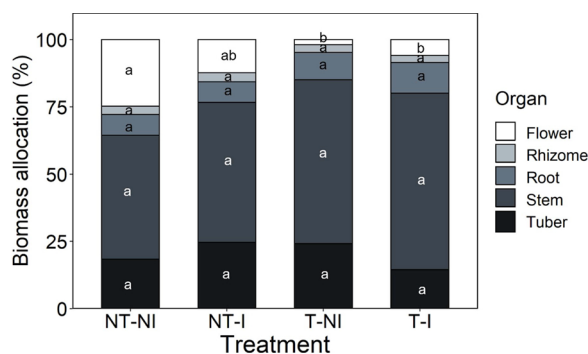


Fig. 4. Biomass allocation to each organ of *Bolboschoenus planiculmis* for various treatments. Different letters indicate a significant difference in the same organ among the treatments according to Tukey's HSD test ($p < 0.05$). NT indicates non-tidal treatment; T indicates tidal treatment; NI indicates intraspecific interaction treatment; I indicates interspecific interaction treatment. Bars mean standard errors ($n = 3$).

$F = 10.48$). In terms of the percentage of stem biomass, tidal treatment significantly increased compared to non-tidal treatment (63 % vs. 49 %) ($p = 0.01$, $F = 9.64$); however, the differences among treatments were not significant (Tukey's test). Allocation to rhizome, tuber, and root biomass was not affected by the tidal treatments, interaction treatments, or their interaction effect.

The density of *B. planiculmis* was on average 3.7 ± 0.3 (range 3–5) ramets per pot. There was no significant difference in density by the tidal treatments, interaction treatments, or their interaction effect. As a result, density in the control treatment (NT-NI) was not different from that in the other treatments (Fig. 3f). The mean shoot length was much shorter in interspecific interaction treatment (31.8 ± 5.4 cm) compared to intraspecific interaction treatment (41.8 ± 3.1 cm), although the difference was not significant due to small number of replicates ($p = 0.09$, $F = 3.81$). The tidal treatments influenced stem diameter ($p = 0.02$, $F = 7.72$), while the interspecific interaction treatments did not. The stems were thinner in the tidal treatment (1.7 ± 0.1 mm) than in the non-tidal treatment (2.1 ± 0.1 mm). T-NI treatment showed thinner stems compared to NT-NI; however, this difference was not significant (Tukey's test; Fig. 3h). The sum of rhizome lengths was on average 35.3 ± 6.2 cm without significant difference by tidal treatments, interaction treatments, and their interaction effect.

The flowering rate of *B. planiculmis* was influenced by the tidal treatments ($p = 0.01$, $F = 10.52$). A significant decrease in flowering rate was observed in tidal treatment (37 %) which was half of the non-tidal treatment (68 %). T-I and T-NI showed lower flowering rates than NT-NI (each $p = 0.02$; 0.04, Fig. 3i). The number of tubers (mean and standard error, 3.3 ± 0.7) was not different under the tidal treatments, interaction treatments, and their interaction effect.

3.3. Plastic growth responses of *C. Scabrifolia*

Supplementary table A1 summarizes the plastic growth response of neighboring species *C. scabrifolia* between tidal treatment and non-tidal treatment under the presence of *B. planiculmis*. A significant decrease in total biomass of *C. scabrifolia* appeared in tidal treatment (1.06 g) compared to non-tidal treatment (1.50 g) ($p = 0.04$, $t = 2.89$, Student's t -test). However, other plastic growth responses were not significantly different between tidal and non-tidal treatment.

4. Discussion

We found that the interspecific interaction between *B. planiculmis* and *C. scabrifolia* was competitive in the non-tidal treatment, compared to the intraspecific interaction in *B. planiculmis*. However, the interspecific interaction shifted to neutral in the tidal treatment, which

supports the first hypothesis that the interspecific interaction between the two species changes along a tidal stress gradient. The second hypothesis was also supported by altered growth responses of *B. planiculmis* that represented the avoidance strategy, and unchanged responses of *C. scabrifolia* to tidal stress.

4.1. Shift in interspecific interactions depending on tidal treatments

We detected negative RII for *B. planiculmis* in non-tidal treatment (i.e., non-stress condition) but neutral RII in the tidal condition (i.e., stress condition) (Fig. 2). This result was consistent with the SGH in that the interspecific interaction changed from competitive to neutral according to environmental stress gradients (He et al., 2013; Qi et al., 2018), even though facilitation was not observed in this study. The lack of facilitation in harsh environments is commonly observed depending on the stress type, species, and degree of stress (Choler et al., 2001; Maestre et al., 2009; Qi et al., 2018). The shift in RII has been explained that competition increases under non-stress condition where rapid resource acquisition is possible, while neutral interaction or facilitation can appear under severe stress condition due to the limited resource acquisition (Bertness and Callaway, 1994; Callaway and Walker, 1997). Others explained that this shift might be caused since different plant species have different levels of environmental tolerance (e.g., Zhou et al., 2018). Here, we focused on how differently *B. planiculmis* and *C. scabrifolia* responded to tidal stress on the basis of theories about avoidance and tolerance strategies.

4.2. Effects of tidal treatments on plastic growth responses

Tidal stress can reduce the biomass of diverse species (Szmeja, 1994; Doyle, 2001; Sun et al., 2002; Puijalon et al., 2008b); this is supported by the results of this study. The total biomass per pot and individual biomass of *B. planiculmis* and the total biomass per pot of *C. scabrifolia* in the tidal treatment were only half of those in the non-tidal treatment, indicating that tidal flooding was a major stressor to both species. However, they showed different tendencies regarding strategies against tidal stress.

For *B. planiculmis*, stem diameter became significantly smaller in the tidal treatment (Fig. 3h), supporting the hypothesis of the typical avoidance strategy. The thinner, smaller, and more flexible stems contribute to effective avoidance of wave stress by reducing the exposed surface (Puijalon et al., 2008a; Silinski et al., 2015, 2018). Other traits were not enough significant to support the avoidance strategy such as density, shoot length, and AGB:BGB ratio (Fig. 3). Some studies have revealed that these traits could be plastic or non-plastic under tidal stress, depending on the species (see Puijalon et al. (2008b) for density and shoot height, Szmeja (1994) for AGB:BGB ratio). In terms of sexual reproduction, the percentage of flower biomass and flowering ratio decreased under tidal stress (Fig. 3 and 4). Previous studies did not consider them as either avoidance strategy or tolerance strategy (Niklas, 1998; Puijalon et al., 2008b); however, they reported decreases in resource allocation to sexual reproduction under the tide or mechanical stress since plants cannot simultaneously maintain both environmental tolerance strategies and reproduction. The percentage to stem biomass of *B. planiculmis* increased in the tidal treatment (Fig. 4). This seems to contrast the predictions of avoidance strategy hypothesis; however, it might also be affected by other factors. First, the decreased percentage of flower biomass and unchanged percentage of above-ground biomass (i.e., flower biomass + stem biomass) would result in the increased percentage of stem biomass in the tidal treatment. Second, imitating the tidal flooding in the field may cause not only tide (mechanical) stress but also flooding stress simultaneously. Compared to the non-tidal treatment, plants in the tidal treatment were inundated (30 cm depth) less than two hours per day. Flooding stress can promote shoot elongation for some species to increase uptake of oxygen and light (Chen et al., 2011; Hattori et al., 2011). Further studies that

distinguish the flooding and tide effects will improve the understanding of strategies against environmental stress.

For *C. scabrifolia*, there was no clear tendency between avoidance strategy and tolerance strategy under tidal treatment (Table A1), indicating that it had limited ability to minimize the negative impact of tidal stress (Puijalon et al., 2011).

4.3. Effects of interspecific interactions on plastic growth responses

Interspecific interactions can affect growth, biomass allocation, and morphology of plants (Curt et al., 2005; Gratani, 2014). In this study, interspecific interactions between *B. planiculmis* and *C. scabrifolia* decreased the individual biomass of *B. planiculmis*. Interspecific interaction with *C. scabrifolia* tended to decrease the shoot length of *B. planiculmis*, regardless of the tidal treatment (Fig. 3g). This tendency was consistent with results of Costa et al. (2003), who found that interspecific interactions caused by a neighbor species reduce the maximum height of a target species.

4.4. Distributions in the field

In the field, *B. planiculmis* dominates lower elevations being exposed to more frequent tides, while *C. scabrifolia* favors higher elevation with rigid and dense rhizomes in estuaries (Bang et al., 2018). According to this study, frequent tides in lower elevation can be a major stressor to both species, reducing biomass. Interspecific interaction with *C. scabrifolia* was also another major stressor to *B. planiculmis* reducing biomass. However, the interspecific interaction between the two species was changed from competitive in non-tidal treatment to neutral to *B. planiculmis* under tidal exposure twice a day. More plastic growth responses in *B. planiculmis* would help it to avoid the tidal stress more effectively than *C. scabrifolia* which exhibited limited ability to avoid or tolerate the tide. Therefore, our results reflected species distributions in the field; the stress-tolerant species *B. planiculmis* adapts better to tidal stress (low elevations) than *C. scabrifolia* with more effective ability to avoid the tide, while it is outcompeted by *C. scabrifolia* in stable environments (high elevations).

5. Conclusion

In this study, simulated tide affected the interspecific interaction between *Bolboschoenus planiculmis* and *Carex scabrifolia*. In particular, *B. planiculmis* was at a disadvantage in the non-tidal treatment but the relationship became neutral in the tidal treatment. Both tide and interspecific interactions decreased the biomass of *B. planiculmis*. Tide induced thinner stems in *B. planiculmis*, supporting the hypothesis of avoidance strategy, and reduced sexual reproduction; however, other plastic growth responses were not observed. In contrast, *C. scabrifolia* did not exhibit any plastic abilities to respond to the tide effectively although it decreased biomass under tidal stress. These results can help to explain the real distribution of the two species in the field. *Bolboschoenus planiculmis* which can effectively avoid tidal stress would dominate at a low elevation; however, it may be outcompeted by the competitive species, *C. scabrifolia*, at a high elevation.

CRediT authorship contribution statement

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

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.flora.2020.151568>.

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