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Effect of native *Suaeda japonica* structure on the initial seed settlement of an invasive plant *Spartina anglica*

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ABSTRACT

The relationships between native halophytes and initial seed settlement of *Spartina anglica* in the field are not well-studied. We therefore investigated the effect of the native halophyte *Suaeda japonica* on initial settlement of the invasive *Spartina anglica* on a tidal flat. The seed bank among native vegetation was compared with an unvegetated mudflat, and the effects of inundation on seed germination were tested. Five flooding duration treatments were compared: moistened, permanently-inundated, and inundated for 1, 2, or 3 h per day. Seed bank density was significantly higher where native vegetation (7.1 ± 1.3 seeds m^{-2}) than on the unvegetated mudflat (0.6 ± 0.3 seeds m^{-2}). Seed germination tests showed no significant differences among inundation treatments (log-rank test, $p > 0.05$). The broad range of conditions in which seeds can germinate allow *Spartina anglica* to become established widely in mudflat environments. Results suggest that native halophytes may function as an effective seed trap promoting initial settlement and establishment of the invasive *Spartina anglica*.

1. Introduction

Wetland plant species exhibit several seed dispersal modes, of which water-mediated dispersal is the most common in many wetland systems (Schneider and Sharitz, 1988; Smits et al., 1989; Cappers, 1993). The seed dispersal and germination strategy is different for each wetland plant. In case of *Persicaria thunbergii*, seeds are produced and spread at different positions (Choo et al., 2014). The seed of *Sparganium stoloniferum* are floated and sink, then becoming seedlings, they are floated again and disperse as seedlings (Kim et al., 2017). The seed dispersal and germination strategy are one of the most important factors in wetland plant populations maintenance. With respect to ecosystem management, seed dispersal of invasive plants is an important issue (An et al., 2007), and an understanding of initial settlement processes is essential for successful management. Seed spreading of invasive species increases the likelihood of settlement not only in the near area but also in a remote area as well as in common plant seed dispersal (Cain et al., 2000). For this reason, studies on seed dispersion and settlement of invasive species are important.

The grass *Spartina anglica* C.E. Hubbard (Family Poaceae) (Raybould et al., 1991; Hedge et al., 2003) is believed to have arisen by hybridization between *Spartina alterniflora* Louiseleur from the north-eastern United States and *Spartina maritima* Fernald, a species native to the southern coast of England (Raybould et al., 1991; Baumel et al., 2002). *Spartina* spp. has been introduced into several countries for stabilization of embankments and coastlines (Hubbard and Partridge, 1981; Chung, 1993; Ayres and Strong, 2002). The dense underground root and rhizome networks of *S. anglica* can have a negative influence on biodiversity of tidal flats and other wetlands (Marks and Truscott, 1985; Xiao et al., 2016), and establishment of the species can lead to significant changes in habitat conditions (Ehrenfeld, 2003). *Spartina anglica* has rapidly become established on mudflats in China and populations have proved difficult to control (An et al., 2007).

Kim et al. (2015) identified *Spartina anglica* on the tidal flat near Dongmak Beach, on the west coast of Korea, where it was first reported in 2012. The potential negative impacts of *S. anglica* on tidal flat biodiversity have engaged the attention of ecologists in Korea. Introduction of *S. anglica* occurred at least 5 years ago, and the Donggeom-ri (near the Dongmak Beach) has been suggested as an initial settlement site. At this site, very small patches of *S. anglica* (diameter < 1 m) occur among beds of the native halophyte *Suaeda japonica* (Fig. 1). Understanding the mechanisms promoting initial settlement of *S. anglica* may be a critical factor for successful management of the species before it becomes more widespread on Korean shores.

Spartina anglica can form vast monotypic colonies, and seeds are dispersed by floating on the water surface (Strong and Ayres, 2009).

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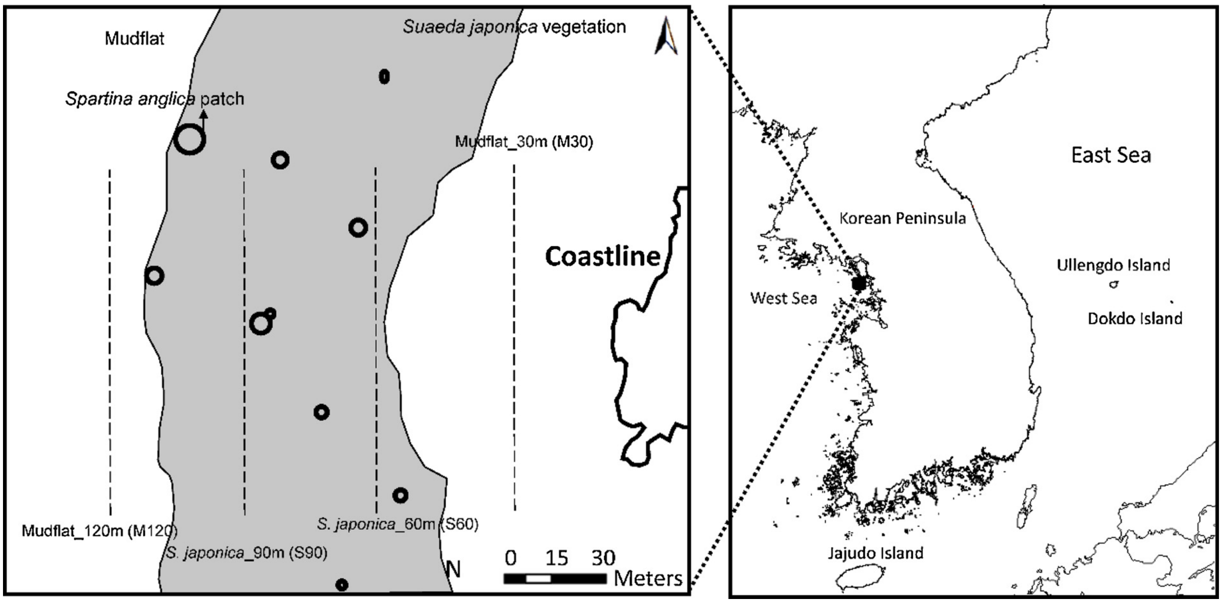

Fig. 1. *Suaeda japonica* vegetation colonized by *Spartina anglica* at Donggeom-ri, Ganghwa Island, Korea. The gray area represents *S. japonica* vegetation. Circles represent *S. anglica* patches. Dashed lines represent sampling transects.

Huiskes et al. (1995) reported that a large proportion of *S. anglica* seed was caught in standing and in floating nets. However, the initial settlement process and the effects of other plants are not known.

In this study, our hypothesis is that the initial seed settlement of *Spartina anglica* is influenced by the structure and environment condition of native halophytes such as *Suaeda japonica*. We investigated seed bank of *S. anglica* in mudflat, and soil physicochemical condition and water inundation time in the habitat of *S. japonica* to determine their influence on the early settlement of *S. anglica* seeds.

2. Methods

2.1. Study area

The study was carried out in the tidal marsh in the western part of Donggeom-ri (37°35´16.72´´N; 126°30´44.46´´E), Ganghwa Island, Korea. *Suaeda japonica* Makino and *Phragmites communis* Trinius are two common marsh plants in this area. *Suaeda japonica* occurs in a band approximately 50–100 m away from the coastline (Fig. 1). Patches of *Spartina anglica* are found among the *S. japonica* vegetation. Mean annual temperature is 11.7 °C, with minimum and maximum mean monthly values of −7.5 and 28.7 °C. Mean total annual precipitation is 787 mm, mean wind velocity is 2.02 m s^{-1}, and total annual duration of sunshine is 2274 h based on 2017 data from Ganghwa weather station (Korean Meteorological Administration, 2018).

2.2. Initial seed settlement of Spartina anglica

2.2.1. Survey of the native plant Suaeda japonica

The *Spartina anglica* seed survey was conducted in March since dispersal has been reported to peak in this month (Huiskes et al., 1995). The effect of *Suaeda japonica* on seed settlement was measured using 0.5 m × 0.5 m quadrats sampled along four line transects of 120 m perpendicular to the shoreline, with 20 replicate quadrats per line. Each line was separated from the next by ≥ 30 m (Located in Mudflat, 30 m from the shoreline (M30), located in *S. japonica*, 60 m from the shoreline (S60), located in *S. japonica*, 90 m from the shoreline (S90), located at Mudflat, 120 m from the shoreline (M120)), with 5 m between replicate quadrats (Fig. 1). Height, density, and percentage cover of *S. japonica* were recorded in each quadrat. Aboveground biomass of *S. japonica* in each replicate quadrat was harvested and measured after drying at 80 °C for 48 h.

2.2.2. Seed bank among native vegetation

Soil samples were collected from surface to 3–5 cm in each replicate quadrat by 50*50*3 cm square-shaped soil sampler in March 2017 and stored in a refrigerator at 4 °C. Soil samples were washed through a 1 mm mesh sieve to recover and count the seeds of *Spartina anglica*.

2.3. Environmental conditions

2.3.1. Soil analysis

A 300 g sub-sample was taken from each soil sample and mixed by hand. Water content was determined by drying 5 g at 105 °C for 24 h (Topp, 1993). The dry soil was then ashed at 550 °C for 4 h to determine organic content (Boyle, 2004). Salinity and pH of a mixture of 1 part soil and 5 parts distilled water were measured using a salinity and pH meter (PC-2700, Thermo Euthec, Singapore). NH_4–N in soil was extracted with a 2 M KCl solution, and PO_4–P was extracted with Bray No. 1 solution (Bray and Kurtz, 1945). NH_4–N and PO_4–P in water and the extracted soil solution were analyzed using the indo-phenol (Murphy and Riley, 1962) and ascorbic acid reduction methods (Solorzano, 1969), respectively.

2.3.2. Measurement of flooding duration

The speed (m h^{-1}) of tidal fluctuation and estimated mean flooding duration were calculated at each shore sampling line. Water speed was ~67.96 m h^{-1} and flooding durations were ~53, ~106, ~159, and ~212 min per tidal cycle at the four sampling lines (M30, S60, S90, and M120; Fig. 1, Table S1). Lee et al. (2006) showed that the elevation gradient of the study site was low, such that the slope of the shore would have only a minor effect on flooding duration.

2.4. Seed germination test

A seed germination test, focusing on the effect of water, was performed to determine the conditions promoting initial settlement of *Spartina anglica*. Five experimental treatments were selected based on the field data (Table S1): moistened and flooding conditions into 1, 2, 3, and 24 h per day. The water depth for the flooding condition was

~2 cm. All seeds were immersed in water before the test. Thirty seeds were placed on moistened filter paper with distilled water in a petri dish (diameter: 9 cm) with three replicates. Conditions in the growth chamber were set at 25/15 °C with 12 h photoperiod and light intensity of 100–110 μmol m^{-2} (HB-301L Hanbaek Scientific Co., Korea). Germinated seeds were counted daily for 50 days. Germination was defined by appearance of the radicle.

2.5. Statistical analysis

Seed number, vegetation, and environmental variables were analyzed with one-way ANOVA and Tukey's HSD test, or Kruskal-Wallis and Pairwise *t*-tests. Normality tests and homogeneity tests were performed before all statistics were performed. Due to censured data (no germination), a semi-parametric time-to-event analysis was conducted (McNair et al., 2012). The number of germinated seeds was counted and the data log-ranked to compare survival. The semi-parametric Cox proportional-hazard model was used to determine the probability of germination within the experiment period (50 days). The first and second days when all the seeds failed to germinate were excluded to reduce the error in the Cox model (Scott et al., 1984). All statistics were analyzed in the R 3.4.0 (R Development Core Team, 2015).

3. Results

3.1. Distribution of the native plant Suaeda japonica

There was no significant difference in density, percentage cover, or aboveground biomass between the S60 and S90. However, the height of *Suaeda japonica* plants on the S60 was significantly higher than at S90. Mean density, percentage cover, height, and aboveground biomass were 43.2 ± 3.2 ind. m^{-2}, 42.0 ± 2.2 % m^{-2}, 20.11 ± 0.11 cm, and 38.95 ± 8.95 g m^{-2} respectively (Table 1).

3.2. Comparison of seed banks

Seeds of *Spartina anglica* were significantly more abundant when *Suaeda japonica* was present than on unvegetated mudflat lines (Fig. 2a). Seed densities on the two mudflat lines (M30 and M120) were not significantly different. Seed densities also did not differ significantly between the two lines in the *S. japonica* vegetation band (S60 and S90) (Fig. 2b). Mean density of *S. anglica* seeds among *S. japonica* was 7.1 ± 1.3 seeds m^{-2} compared with 0.6 ± 0.3 seeds m^{-2} on the unvegetated mudflat. Spearman correlation analysis showed no significant correlations between *S. anglica* seed density and the density (r = 0.084, $p > 0.05$), cover (r = 0.091, $p > 0.05$), height (r = 0.043, $p > 0.05$), or aboveground biomass of *S. japonica* (r = 0.285, $p > 0.05$).

3.3. Soil condition in the tidal flat

Electrical conductivity (EC), water content (WC), and organic matter (OM) tended to decrease with distance from the coastline, in contrast to pH and NH_4^+ (Table 2). However, there were no significant differences between the lines. This suggests a relatively homogenous environment along this stretch of coast. Mean values for soil conditions at the study site were as follows: pH 7.76 ± 0.11; EC 6.89 ± 1.12 mS cm^{-1}; WC 37.96 ± 0.34 %; OM 3.90 ± 0.05 %; PO_4^-–P 27.90 ± 0.92 mg kg^{-1}; NH_4^+–N 51.00 ± 4.39 mg kg^{-1} (Table 2).

Table 1
Comparison of *Suaeda japonica* vegetation at 60 m (S60) and 90 m (S90) distance from the coastline at Donggeom-ri. Ganghwa Island, Korea.

Line	Density (ind. m^{-2})	Cover (%)	Height (cm)	Biomass (g m^{-2})
M30	N/A	N/A	N/A	N/A
S60 (n = 20)	44.6 ± 4.6^a	42.5 ± 2.5^a	20.98 ± 0.98^a	37.40 ± 3.24^a
S90 (n = 20)	41.8 ± 1.8^a	41.5 ± 1.5^a	19.24 ± 9.24^b	40.50 ± 0.54^a
M120	N/A	N/A	N/A	N/A
Total	43.2 ± 3.2	42.0 ± 2.2	20.11 ± 0.11	38.95 ± 8.95

Means with different superscript letters within a column are significantly different at $p < 0.05$ using Tukey's honestly significant difference (HSD) test.

3.4. Germination model and hazard ratios

Seed germination began from Day 3 in the experimental treatments. In the flooding condition 1, 2, and 3 h, final germination rate was < 32 %, with the lowest rate seen in the 1 h flooding condition. In addition, seeds in the flooding treatments took fewer days to reach 50 % final germination than those in the moistened and 24 h flooding condition (Table 3).

The overall Cox proportional-hazard model suggested that flooding conditions had no significant effect on germination probability (Fig. 3, Table S2). There were also no significant differences among the different flooding duration treatments.

4. Discussion

Seed availability and dispersal processes are important factors affecting recruitment patterns (Eriksson and Ehrlén, 1992; Rand, 2000). Although there have been some studies of seed dispersal in tidal marshes (Huiskes et al., 1995; Rand, 2000), there is very little information on initial seed settlement of invasive plants relevant to the management of these species. In this study, we set out to test the hypothesis that the presence of the native plant *Suaeda japonica*, and the environment it creates, will facilitate initial seed settlement of the invasive *Spartina anglica*.

The seed bank has important effects on the composition of growing vegetation (Hutchings and Russell, 1989). To test whether the presence of *S. japonica* affects seed settlement of *S. anglica*, we compared the *S. anglica* seed bank in the presence and absence of *S. japonica*. Our results showed a significant difference in *S. anglica* seed density between sites with and without *S. japonica*. However, the numbers of seeds at the two *S. japonica* sites (M60 and M90) were not significantly different. The presence or absence of mudflat vegetation can affect the abundance of some species in the seed bank (Parker and Leck, 1985; Baldwin et al., 1996). A positive association between existing vegetation and seed bank composition has been observed, and many propagules may be trapped in the vegetation (Parker and Leck, 1985; Huiskes et al., 1995; Neff and Baldwin, 2005). This pattern has also been found in mangrove communities (Rabinowitz, 1978). In our study, the abundance of seeds (7.1 ± 1.3 seeds m^{-2}) among *S. japonica* vegetation was similar to that recorded in the seed trap on the mudflat at Paulinapolder in the Netherlands (Zhu et al., 2014). These results support the hypothesis that the presence of *S. japonica* played a role as the seed trap of *S. anglica*. Similar results were obtained in previous studies. Sher et al. (2002) showed that the native species *Populus* and *Salix* affect the establishment of exotic seedlings. In addition, in our study site where *S. anglica* has been established for less than 5 years, *S. anglica* patches occurred only where *S. japonica* vegetation was already present. It indicates that native halophyte plants may promote seed settlement and establishment of *S. anglica*. In other words, native plants may be involved in the settlement of exotic species, eventually leading to ecological succession in salt marsh (Prach and Walker, 2011).

Soil environment and water depth may be correlated with seed bank species composition (Wilson et al., 1993). Soil conditions such as salinity and water flooding duration are also crucial factors affecting germination and seedling establishment of wetland plants (Ungar, 1978; Shumway and Bertness, 1992; Kellogg et al., 2003; Li et al., 2010). Our hypothesis was that the environmental conditions favoring native

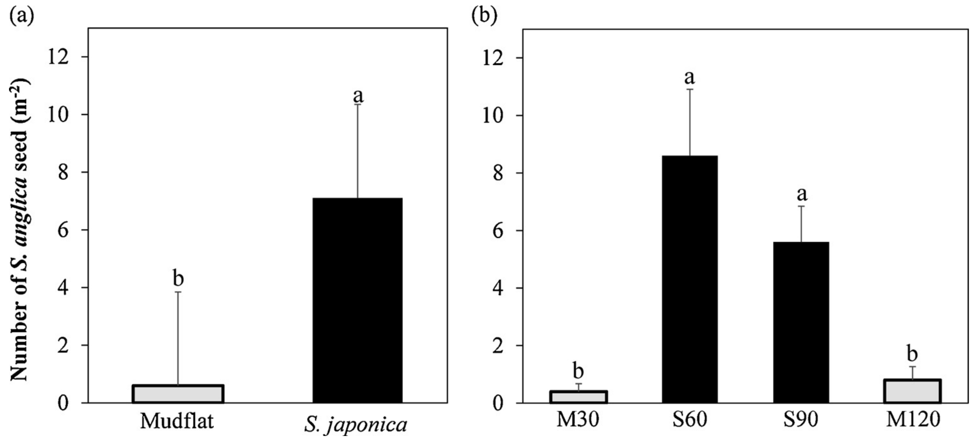

Fig. 2. Abundance (m^{-2}) of *Spartina anglica* seeds in the soil seed bank. (a) Seed number on the four transect lines. (b) Total seed number on the unvegetated mudflat and among *Suaeda japonica* vegetation (Kruskal-Wallis test and pairwise *t*-test, $p < 0.05$).

Table 2
Environmental variables recorded on the west coast of Donggeom-ri, Ganghwa Island, Korea. M30: Mudflat 30 m distant from shoreline; *S*60: *Suaeda japonica* 60 m distant; *S*90: *S. japonica* 90 m distant; M120: Mudflat 120 m distant (n = 20); EC (mS cm^{-1}); WC (% weight); OM (% weight); PO_4–P (mg kg^{-1}); NH_4^+-N (mg kg^{-1}) (mean ± SE).

	pH	EC	WC	OM	PO_4^--P	NH_4^+-N
M30	7.41 ± 0.01^a	7.55 ± 0.24^a	40.65 ± 0.63^a	4.43 ± 0.09^a	28.55 ± 1.54^a	56.32 ± 1.79^a
S60	7.58 ± 0.03^b	6.97 ± 0.25^{ab}	30.00 ± 0.53^b	3.84 ± 0.08^b	29.64 ± 2.79^a	42.84 ± 4.18^{ab}
S90	7.60 ± 0.01^b	6.74 ± 0.22^{ab}	36.38 ± 0.55^b	3.80 ± 0.07^b	26.52 ± 2.23^a	31.12 ± 8.49^b
M120	7.60 ± 0.02^b	6.30 ± 0.21^b	36.89 ± 0.58^b	3.54 ± 0.09^b	26.98 ± 1.81^a	73.66 ± 7.22^a
p-value	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p > 0.05$	$p < 0.001$

Means with different superscript letters within a column are significantly different at $p < 0.05$ using Tukey's honestly significant difference (HSD) test.

Table 3
Seed germination rates, mean number of days to reach 50 % germination and final germination rates in five experimental treatments (moistened, flooded 1, 2, 3, 24 h flooding/day). Experimental duration: 50 days. Data represent mean ± SE.

Treatment	Final germination rate (%)	Mean number of days	
		50 % germination	Final germination
Moistened	68.89 ± 13.65	21.50 ± 8.50	39.33 ± 4.37
1 hour flooding/ day	47.78 ± 23.28	10.00 ± 5.85	24.00 ± 7.81
2 hour flooding/ day	63.33 ± 20.00	11.00 ± 7.89	32.33 ± 5.04
3 hour flooding/ day	63.33 ± 15.28	10.50 ± 1.50	31.00 ± 7.09
24 hour flooding/ day	67.78 ± 12.37	21.00 ± 6.00	37.33 ± 1.20
p-value	$p > 0.05$	$p > 0.05$	$p > 0.05$
F-value	0.236	0.662	1.145
Degree of freedom	4	4	4

Final germination percentage ± SE is the mean of 90 seeds divided equally among three petri dishes.

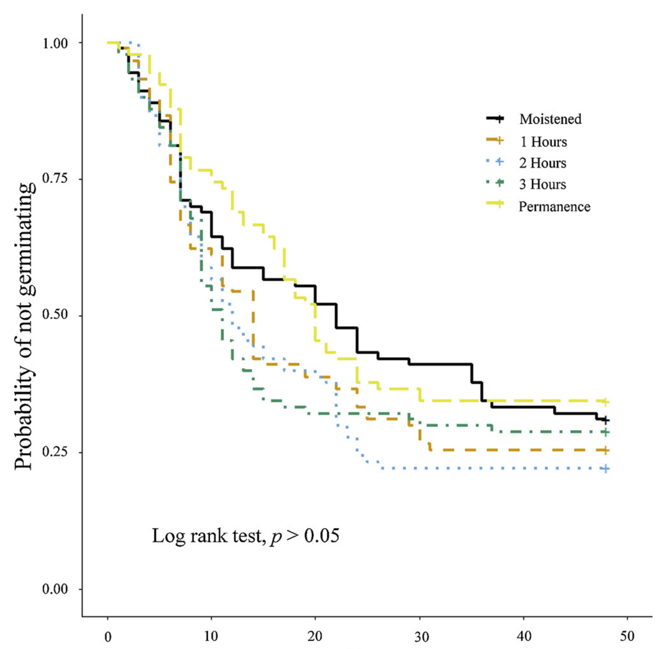

Fig. 3. Kaplan-Meier survivor main effects curves for *Spartina anglica* seeds. Five experimental treatments are shown: Moistened, 1 h, 2 h, 3 h (daily flooding duration), and Permanence (permanently waterlogged).

halophytes would enhance the seed germination of *Spartina anglica*. Plant recruitment in different marsh zones may be affected by environmental conditions related to tidal elevation (Rand, 2000). However, at our site, differences in salinity were not significant (there was a small difference in the mudflat 30 m distant from the coastline). Our results showed that the salinity gradient within 120 m from the coastline would have only a small impact on germination (Li et al., 2010). Flooding duration is the principal factor affecting germination in wetland and tidal flat environments. Many studies have shown that halophytes have higher germination rates in moist conditions than in waterlogged or flooded environments (Baldwin et al., 1996; Casanova and Brock, 2000; Elsey-Quirk et al., 2009; Yu et al., 2012). However, in our study, the Cox Proportional-Hazard Model showed that inundation had a lower impact on the germination of *S. anglica* seeds. These results suggest that *S. anglica* is well-adapted to field conditions and is likely to occur within at least 120 m from the coastline in Korea, as in other countries (Ayres and Strong, 2002; An et al., 2007; Strong and Ayres, 2009).

In summary, our study provides insight into the pattern of seed arrival and germination of *Spartina anglica*. Native species such as *Suaeda japonica* may affect seed settlement of *S. anglica* to a greater extent than other environmental gradients. This mechanism is a critical factor affecting establishment on a tidal flat, and may be applied to the management of invasive plants in this environment. Traps mimicking native species could be applied as a management tool to limit seed dispersal of invasive plants.

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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.aquabot.2019.103175.

References

An, S.Q., Gu, B.H., Zhou, C.F., Wang, Z.S., Deng, Z.F., Zhi, Y.B., Li, H.L., Chen, L., Yu, D.H., Liu, Y.H., 2007. *Spartina* invasion in China: implications for invasive species management and future research. Weed Res. 47, 183–191.

Ayres, D., Strong, D., 2002. The *Spartina* invasion of San Francisco Bay. Aquat. Nuis. Species Dig. 4, 37–39.

Baldwin, A.H., McKee, K.L., Mendelssohn, I.A., 1996. The influence of vegetation, salinity, and inundation on seed banks of oligohaline coastal marshes. Am. J. Bot. 83, 470–479.

Baumel, A., Ainouche, M., Kalendar, R., Schulman, A.H., 2002. Retrotransposons and genomic stability in populations of the young allopolyploid species *Spartina anglica* CE Hubbard (Poaceae). Mol. Biol. Evol. 19, 1218–1227.

Boyle, J.F., 2004. A comparison of two methods for estimating the organic matter content of sediments. J. Paleolimnol. 31, 125–127.

Bray, R.H., Kurtz, L.T., 1945. Determination of total, organic, and available forms of phosphorus is soils. Soil Sci. 59, 39–45.

Cain, M.L., Milligan, B.G., Strand, A.E., 2000. Long-distance seed dispersal in plant populations. Am. J. Bot. 87, 1217–1227.

Cappers, R.T.G., 1993. Seed dispersal by water: a contribution to the interpretation of seed assemblages. Veg. Hist. Archaeobot. 2, 173–186.

Casanova, M.T., Brock, M.A., 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? Plant Ecol. 147, 237–250.

Choo, Y.H., Kim, H.T., Nam, J.M., Kim, J.G., 2014. Flooding effects on seed production of the amphicarpic plant *Persicaria thunbergii*. Aquat. Bot. 119, 15–19.

Chung, C.H., 1993. Thirty years of ecological engineering with *Spartina* plantations in China. Ecol. Eng. 2, 261–289.

Ehrenfeld, J.G., 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6, 503–523.

Elsey-Quirk, T., Middleton, B.A., Proffitt, C.E., 2009. Seed flotation and germination of salt marsh plants: the effects of stratification, salinity, and/or inundation regime. Aquat. Bot. 91, 40–46.

Eriksson, O., Ehrlén, J., 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91, 360–364.

Hedge, P., Kriwoken, L.K., Patten, K., 2003. A review of *Spartina* management in Washington State, US. J. Aquat. Plant Manage. 41, 82–90.

Hubbard, J.C.E., Partridge, T.R., 1981. Tidal immersion and the growth of *Spartina anglica* marshes in the Waihopai River Estuary, New Zealand. New Zeal. J. Bot. 19, 115–121.

Huiskes, A.H.L., Koutstaal, B.P., Herman, P.M.J., Beeftink, W.G., Markusse, M.M., De Munck, W., 1995. Seed dispersal of halophytes in tidal salt marshes. J. Ecol. 83, 559–567.

Hutchings, M.J., Russell, P.J., 1989. The seed regeneration dynamics of an emergent salt marsh. J. Ecol. 77, 615–637.

Kellogg, C.H., Bridgham, S.D., Leicht, S.A., 2003. Effects of water level, shade and time on germination and growth of freshwater marsh plants along a simulated successional gradient. J. Ecol. 91, 274–282.

Kim, E.K., Kil, J.H., Joo, Y.K., Jung, Y.S., 2015. Distribution and botanical characteristics of unrecorded alien weed *Spartina anglica* in Korea. Weed Turfgrass Sci. 4, 65–70 (in Korean with English Abstract).

Korean Meteorological Administration, 2018. Searching Climate Condition Information (Accessed on 17 August 2017). https://data.kma.go.kr/climate/RankState/selectRankStatisticsDivisionList.do?pgmNo = 179.

Kim, S.H., Nam, J.M., Kim, J.G., 2017. Establishment strategy of a rare wetland species *Sparganium erectum* in Korea. J. Ecol. Environ. 41, 27.

Lee, Y.K., Ryu, J.H., Hong, S.H., Won, J.S., Yoo, H.R., 2006. A study of DEM generation in the Ganghwado southern intertidal flat using waterline method and InSAR. J. Korean Wetlands Sci. 8, 29–38 (in Korean with English Abstract).

Li, R., Shi, F., Fukuda, K., 2010. Interactive effects of salt and alkali stresses on seed germination, germination recovery, and seedling growth of a halophyte *Spartina alterniflora* (Poaceae). S. Afr. J. Bot. 76, 380–387.

Marks, T.C., Truscott, A.J., 1985. Variation in seed production and germination of *Spartina anglica* within a zoned saltmarsh. J. Ecol. 73, 695–705.

McNair, J.N., Sunkara, A., Frobish, D., 2012. How to analyse seed germination data using statistical time-to-event analysis: non-parametric and semi-parametric methods. Seed Sci. Res. 22, 77–95.

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.

Neff, K.P., Baldwin, A.H., 2005. Seed dispersal into wetlands: techniques and results for a restored tidal freshwater marsh. Wetlands 25, 392–404.

Parker, V.T., Leck, M.A., 1985. Relationships of seed banks to plant distribution patterns in a freshwater tidal wetland. Am. J. Bot. 72, 161–174.

Prach, K., Walker, L.R., 2011. Four opportunities for studies of ecological succession. Trends Ecol. Evol. 26, 119–123.

Rabinowitz, D., 1978. Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationship of dispersal and zonation. J. Biogeogr. 5, 113–133.

Rand, T.A., 2000. Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient. J. Ecol. 88, 608–621.

Raybould, A.F., Gray, A.J., Lawrence, M.J., Marshall, D.F., 1991. The evolution of *Spartina anglica* CE Hubbard (Gramineae): origin and genetic variability. Biol. J. Linn. Soc. 43, 111–126.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Schneider, R.L., Sharitz, R.R., 1988. Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. Ecology 69, 1055–1063.

Scott, S.J., Jones, R.A., Williams, W.A., 1984. Review of data analysis methods for seed germination. Crop Sci. 24, 1192–1199.

Sher, A.A., Marshall, D.L., Taylor, J.P., 2002. Establishment patterns of native Populus and Salix in the presence of invasive nonnative Tamarix. Ecol. Appl. 12, 760–772.

Shumway, S.W., Bertness, M.D., 1992. Salt stress limitation of seedling recruitment in a salt marsh plant community. Oecologia 92, 490–497.

Smits, A., Van Ruremonde, R., Van der Velde, G., 1989. Seed dispersal of three nymphaeid macrophytes. Aquat. Bot. 35, 167–180.

Solorzano, L., 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. Lett. 14, 799–801.

Strong, D., Ayres, D., 2009. *Spartina* introductions and Consequences in Salt Marshes. University of California Press, Berkeley and Los Angeles.

Topp, G.C., 1993. Soil sampling and Methods of Analysis. Lewis Publishers for the Canadian Society of Soil Science, pp. 541–549.

Ungar, I.A., 1978. Halophyte seed germination. Bot. Rev. 44, 233–264.

Wilson, S.D., Moore, D.R.J., Keddy, P.A., 1993. Relationships of marsh seed banks to vegetation patterns along environmental gradients. Freshw. Rev. 29, 361–370.

Xiao, D., Zhang, C., Zhang, L., Zhu, Z., Tian, K., Gao, W., 2016. Seed dispersal capacity and post-dispersal fate of the invasive *Spartina alterniflora* in saltmarshes of the Yangtze Estuary. Estuar. Coast. Shelf Sci. 169, 158–163.

Yu, J., Wang, X., Ning, K., Li, Y., Wu, H., Fu, Y., Zhou, D., Guan, B., Lin, Q., 2012. Effects of salinity and water depth on germination of *Phragmites australis* in coastal wetland of the Yellow River Delta. Clean 40, 1154–1158.

Zhu, Z., Bouma, T.J., Ysebaert, T., Zhang, L., Herman, P.M., 2014. Seed arrival and persistence at the tidal mudflat: identifying key processes for pioneer seedling establishment in salt marshes. Mar. Ecol. Prog. Ser. 513, 97–109.