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Establishment strategy of a rare wetland species *Sparganium erectum* in Korea

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Abstract

Background: To reveal establishment strategy of *Sparganium erectum*, we tried to find realized niche of adults through field survey and effects of water level on the establishment process through mesocosm experiments.

Results: In the field survey, the height and coverage of community living in deeper water were greater than those of community living in shallow water. There was no statistically significant difference ($p > 0.05$) in the means of water and soil properties between the two communities. In mesocosm experiments, we found no correlation between water levels and germination rates, but *S. erectum* seedlings have characteristics of post germination seedling buoyancy when *S. erectum* seeds germinated in inundation conditions. Shoot height, total leaf length, and survival rates of sinking seedlings in shallow water levels at -5, 0, and 5 cm were higher than those in deeper water levels at 10 and 20 cm. Floating seedlings established in water levels of 3 and 6 cm only. The seedlings could live up to 6 weeks in floating state but died if they were unable to establish.

Conclusions: The water level around adult *S. erectum* communities in the field were different from the water level at which *S. erectum* seedlings can survive in the mesocosm experiments. The findings provided not only understanding of *S. erectum* habitat characteristics but also evidence to connect historical links between the early seedlings stage and adult habitat conditions. We suggested the logical establishment strategy of *S. erectum* based on the data.

Keywords: Adult niche, Habitat environment, Macrophyte, Regeneration niche, Seedling establishment

Background

Most macrophytes are capable of both sexual and asexual reproduction (Yang and Kim 2016). Sexual reproduction is important for the colonization and maintenance of macrophyte populations. Vegetative reproduction is also important because populations are usually maintained by this method rather than by seed production. The environmental ranges of living adults and establishing seedlings have been emphasized because the range determines species distribution and abundance in vegetation (Grubb 1977; Grime 2006; Jeong and Kim 2017). Grubb (1977) stated that the environmental gradient affecting seed dispersal, germination, and seedling survival is the regeneration niche, while the environmental gradient affecting adult survival is the habitat niche. These two niches are not mutually exclusive. Thus, habitat and regeneration

niches must be analyzed simultaneously to understand the relationships between plants and their habitat environments (Collins and Good 1987, Yang and Kim 2017).

Various environmental factors including water depth, salinity, light, temperature, and nutrient concentration influence different plant stages (Clarke and Allaway 1993; Coops and van der Velde 1995; Kim et al. 2013). Above all, water depth is the most important factor affecting seedling establishment and growth for submerged and amphibious plants (Seebloom et al. 1998; Kwon et al. 2007). Water depth can create favorable or unfavorable conditions for the germination and establishment of various species (Eriksson 1989; Kim et al. 2013). Each species has diverse properties that enable them to establish, survive, and colonize according to the water depth (Grace 1987). Thus water depth is important for seedling establishment and growth to sustain the species populations.

Sparganium erectum L., a perennial macrophyte, is widely distributed in Europe but is designated as a vulnerable species in South Korea and an endangered

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species in Japan (Cook 1962; National Institute of Biological Resources 2012; National Museum of Nature and Science 2017). *S. erectum* is mainly distributed in banks of river and canals and forms a continuous belt (DeKlerk et al. 1997; Whitton et al. 1998; Takahashi et al. 2000). This plant prefers slow water flow and fine sediment in riverine areas. Also, *S. erectum* grows from on wet mud to in water to a depth of 100 cm (Cook 1962; Asaeda et al. 2010; Kaneko and Jinguji 2012). Persisting necrotic leaves and stems of *S. erectum* during winter can accumulate fine sediments that influence both the physical environment of habitats and the retention of seeds (Pollen-Bankhead et al. 2011; O'Hare et al. 2012). These could be exploited to create mesohabitats for other plants and animals and they contribute to physical and biological habitat diversification in rivers (Friedman et al. 1996; Abbe and Montgomery 2003). Thus, *S. erectum* is worthy as an ecosystem engineer in riverine areas (Gurnell et al. 2006; Gurnell 2007; Asaeda et al. 2010; Liffen et al. 2011; O'Hare et al. 2012).

Habitat niche of species living in shallow water such as *Pericaria thunbergii* and *Cicuta virosa* are similar for adult and seedling (Kim et al. 2013; Shin and Kim 2013; Shin et al. 2013). However, many species such as *Typha* and *Phragmites* spp. that live in deep water adopt different strategies over their lifetime (Shipley et al. 1989; Kwon et al. 2006; Hong et al. 2012). Adults of these species can live in deep water, but seedlings can only endure shallow water. The water depth for *S. erectum* adults shares similar habitat environments as these emergent plants. Therefore, it was predicted to differ from the water depth for seedlings of the plant. *S. erectum* mainly reproduces using rhizomes regardless of water level, but most seeds can be only produced at stable water levels (Cook 1962). Seeds of *S. erectum* usually fall into the water and disperse by hydrochory (Pollux et al. 2009). *Sparganium* spp. produce two types of seeds: short floating seeds that sink within 4 weeks (approximately 71% of all seeds), and long floating seeds that float for at least 6 months (approximately 28% of all seeds) (Pollux et al. 2009). Thus, *S. erectum* germination and seedling growth require an underwater or

saturated germination environment (Cook 1962). *Sparganium* spp. are also considered to exhibit different growth forms depending mainly on water depth and is especially reported to change their growth form from submerged to emergent during the early seedling phase (Kankaala et al. 2000; Riis et al. 2000; Asaeda et al. 2010; Kim and Kim 2015). However, the effects of water depth on seed germination and seedling establishment as well as growth are unknown.

In this study, we surveyed the water level, accompanying species, and water and soil environments in habitats. We also evaluated the effect of water level on the early life stages through mesocosm experiments. To know the germination condition, seed germination experiments were done with different seed storage conditions, temperatures, photoperiods, and water levels. We also investigated how the water level influences growth responses (growth, mortality, and stand development) of two seedling types (planted versus floating) when water level was the only environmental factor controlled.

Methods

Field study

Vegetation survey

We searched *S. erectum* habitats through literature and field surveys in South Korea and selected the largest habitat of *S. erectum* in South Korea at the Gosancheon stream of the Mankyong river in Wanju (N 35° 56' 36.8" E 127° 10' 18.9", altitude 42 m). We could not find any more habitats where *S. erectum* was dominant species.

We investigated three habitats of *S. erectum* for environment evaluations. *S. erectum* communities grouped into two based on coverage of *S. erectum*: communities A and B. The coverage of *S. erectum* was over 50% in community A and mingled with other species, mainly with *Leersia japonica*, *Typha orientalis*, and *Pericaria thunbergii*. Community A had the lowest water depth and there was no inflow of river water except during floods. Community A was not directly connected to the main stream of the Mankyong river and had no direct exposure to waves (Fig. 1). Community B was monospecific

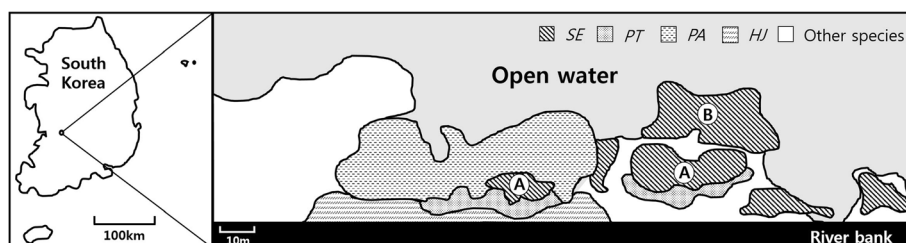


Fig. 1 Habitat of *S. erectum* at Gosancheon in Mankyong River, South Korea. The figure on the right represents a magnification of the figure on the left. A and B show *S. erectum* communities. Community A lives in shallow water and community B lives in deep water. Community A was dominated by *S. erectum* and other species were *Leersia japonica*, *Typha orientalis*, and *Pericaria thunbergii*. Community B was a pure stand of *S. erectum*. SE: *Sparganium erectum* community, PT: *Pericaria thunbergii* community, PA: *Phragmites australis* community, HJ: *Humulus japonicus* community

stands of *S. erectum* and formed a belt and rarely had accompanying species. Community B extended to the main stream but the velocity of the moving water was so slow that it rarely affected the population.

Plant sociological analysis including coverage, density, and height was performed at 30 quadrats of 1 m × 1 m (10 quadrats in community A and 20 quadrats in B) based on a modification of the Braun-Blanquet method (Mueller-Dombois and Ellenberg 2003; Kim et al. 2004). We measured water depth at each quadrat using a 1-m stick ruler.

Analyses of water and soil properties

We collected eight and three water samples for communities A and B, respectively, and sampled twice in July and September before and after flooding. pH was measured with a pH meter (model AP 63; Fisher, USA) and electron conductivity (EC) was measured with a conductivity meter (Corning Checkmate model 311; Corning, USA) in the field. NO₃-N, NH₄-N, and PO₄-P were analyzed by the hydrazine method (Kamphake et al. 1967), indo-phenol method (Murphy and Riley 1962), and ascorbic acid reduction method (Solorzano 1969), respectively. K⁺, Ca²⁺, Na⁺, and Mg²⁺ were measured using an atomic absorption spectrometer (Model AA240FS; Varian, USA).

We collected eight and three soil samples for communities A and B, respectively, when the plants reached maximum growth. We sampled submerged bed sediments until 3 cm below the surface of the sediments. Soil organic matter contents were analyzed by the loss on ignition method (Boyle 2004). NO₃-N and PO₄-P analyses were performed by the same method of water analysis (Kamphake et al. 1967, Solorzano 1969).

Statistical analysis

To compare habitat environmental characteristics, water and soil properties were analyzed and statistical analysis was performed with *t*-test at the 5% significance level, using SPSS ver. 20.0 software (SPSS, Inc., Chicago, IL, USA).

Mesocosm experiments

Germination experiment

Seeds were collected on August 2 in 2012. After collection, the seeds were cleaned with distilled water. Two third of them were stored in wet condition (a sealed plastic bag filled with wet cotton) and one third were dried in room temperature for 1 week and stored in dry condition. In each condition, seeds were divided into three groups and stored in three temperatures (−20 °C, 4 °C, 25 °C). Germination rate was calculated after 30-day incubation and germination criterion was the exposure of longer cotyledon than 0.1 cm.

To know the effect of storage period on germination, germination tests were done in growth chamber with 35 °C/light for 12 h and 25 °C/dark for 12 h by sowing

three replicates of 20 seeds on Petri dishes containing three pieces of filter paper (Baskin and Baskin 1998). Average light intensity in the chamber was 127(±16.5) μmol/m².

To know the effect of temperature and photoperiod on germination, germination tests were conducted under alternating temperature regime at 12-h intervals (35/25, 30/20, 25/15, 20/10, 15/5 °C), at different photoperiods (12 h light/12 h dark and 24 h dark). Each condition has 10 seeds stored in 4 °C/wet condition and repeated three times.

To know the effect of the water level, we selected the seeds that sank, thus germination occurred in inundation (water level, 20 cm) or waterlogged conditions (water level, 0 cm). This experiment was conducted in a greenhouse in June 2013, using a stainless steel tank (150 cm × 80 cm × 50 cm). We compared germination rates and germination characteristics between the two conditions. For each water condition, 10 pots were prepared. Each pot (Φ 15 cm; height 9 cm) was surrounded by plastic film to prevent moving out of seedling after germination and contained 20 seeds. Germination responses were recorded after 2 weeks. A seed was considered to have germinated if any part of the leaf had emerged from the seed coat. We calculated germination rate and seedling (after germination) buoyancy rate in the inundation condition.

Seedling establishments

Seeds used for seedling establishment experiments were collected on September 5, 2013, in the Mankyong river, South Korea (N35° 56' 36.8" E 127° 10' 18.9", 42 m). They were stored in a sealed plastic bag filled with wet cotton at 4 °C in the dark until February 2014, representing 5 months of wet and cold stratification for breaking seed dormancy. The seedling establishment experiments were divided into two types according to seedling types (floating seedlings and sinking seedlings). Seeds germinated and grew in the greenhouse until they became seedlings of 4 ± 1 cm length. In both experiments, the water levels were based on a preliminary experiment and field survey conducted in 2012. The water levels in these treatments were maintained by weekly additions of tap water. We monitored growth responses such as the shoot height, total leaf length, survival rate, and total dry mass. We measured the early response in the first 2 months every 2~3 days, then measured once every week or two for the next 2 months. Algae is lethal to *S. erectum* seedlings, therefore, any algal growth was carefully removed with a plankton net. Plants were harvested in October when the seeds were mature and the total plant dry mass was measured. To compare plant growth differences among the treatments at the end of the life cycle, the harvested parts were classified into

shoots and roots then dried at 60 °C for over 48 h. Afterward, the plants' total dry weights were measured.

Sinking seedling experiments After germination, only the seedlings that sank were used for the sinking seedling experiments. Sinking seedlings were planted in plastic pots (Φ 15 cm; height 9 cm) and the evaluations were adjusted to account for 1 week of transplant stress. The experimental water level gradient included treatments in which the water levels were -5, 0, 5, 10, and 20 cm, with 10 replicates of each water level for a total of 50 pots. The water level gradients were made by plastic stairs in a stainless steel tank (150 cm × 80 cm × 50 cm) and ten pots were located at each water level gradient. 1350 g of soil comprised of 1:8 mixtures of nursery soil (NH₄-N 350 mg/kg, PO₄-P 400 mg/kg; Pungnong, Korea) and sand was added to each pot.

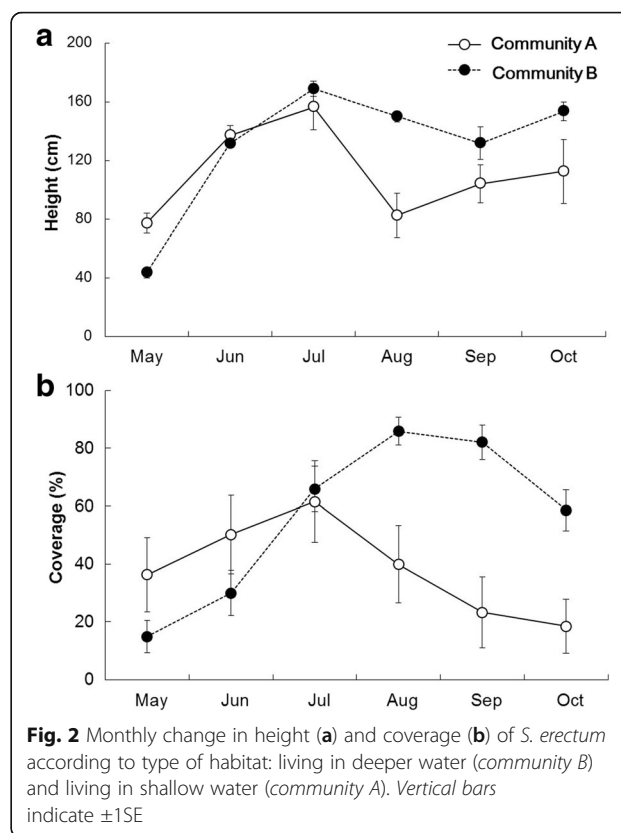
Floating seedling establishments After germination, only the seedlings that floated were used for the floating seedling experiments. Floating seedlings were placed in plastic pots (Φ 15 cm; height 9 cm) surrounded by plastic film. Soil comprised of 1:8 mixtures of nursery soil (NH₄-N 350 mg/kg, PO₄-P 400 mg/kg; Pungnong, Korea) and sand was added up to 3 cm thick in each pot. The experimental water level gradient included treatments in which the water levels were 3, 6, 9, and 12 cm, with 18 replicates for each water level, and a total of 72 pots. We placed six pots in each plastic container, with holes drilled in the containers to maintain the water level. The seedling establishment standard stipulated that seedlings remain stationary despite water flow. A seedling was considered dead if no part of the leaf was green.

Statistical analysis Statistical analyses were performed with *t*-test at the 5% significance level in the germination experiments. We performed one-way ANOVA at the 5% level based on Duncan's test in the seedling experiments. We used SPSS ver. 20.0 software for all statistical analyses (SPSS, Inc.; Chicago, IL, USA).

Results

Field study

S. erectum germinated in early May. Flowers were produced in June and July and the plants bore fruit in August and September. The average height was highest during the flowering periods and gradually declined over the months the seeds ripened in most of the quadrats (Fig. 2a). Coverage of community A was higher than that of community B in the early growing season, but coverage of community B increased and surpassed community A after July (Fig. 2b). Coverage of community B in October remained higher than that of community A because *S. erectum* shoots reemerge throughout the year except



in winter and can survive under water. Height and coverage of community B were also higher than those of community A after August, beyond the maximum growth months.

The water depth of community B was deeper than that of community A year round (Fig. 3). Water depths in community A and B in August increased simultaneously compared to other months because of a lot of rain during the investigation period.

Mean water and soil environmental properties at *S. erectum* habitats are shown in Tables 1 and 2. There were no significant differences between the two communities in all investigated soil environmental factors at *p* ≤ 0.05. Water

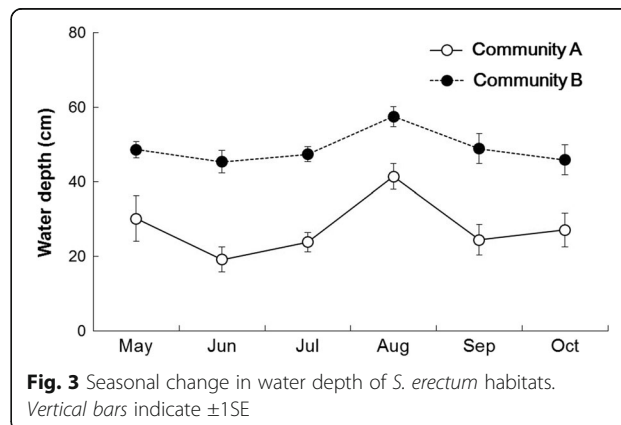


Fig. 3 Seasonal change in water depth of *S. erectum* habitats. Vertical bars indicate ±1SE

Table 1 Soil environmental properties at *S. erectum* habitats in June 2013 (A, $n = 8$; B, $n = 3$)

Factor	Community A	Community B	p value	t value
Soil texture	Sandy loam	Sandy loam	–	–
Loss-On-Ignition (%)	0.2 (0.2)	0.1 (0.1)	0.180	1.452
NO ₃ -N (mg/kg)	4.6 (1.7)	5.2 (1.1)	0.584	–0.569
PO ₄ -P (mg/kg)	28.5 (16.0)	24.0 (13.3)	0.677	0.430

Values are means (S.D.)

environmental factors in the two communities showed no significant differences at $p \leq 0.05$, with the exception of pH and EC before the flooding in July. The pH value of community B, in the deeper water depth areas, was higher, whereas the EC of community B was lower than that of community A. pH, EC, and cation contents in community B were significantly different in September after flooding. EC and cation contents in community A were higher than those of community B due to inflow of muddy water.

Mesocosm experiments

Germination experiments

When the *S. erectum* seeds were collected, they floated on the water surface. However, most of the seeds (98.1%) sank after exposure to cold and wet conditions for 3 months. Germination rate was 0% in all seeds stored in dry condition. Among seed stored in wet condition, only seeds stored in 4 °C were germinated and others were not. Germination rate of seeds stored for 3 months was 100 and 44.4% for 1 month stored and 82.3% for 2 months stored (Fig. 4).

Seeds were germinated only in three conditions (30/20/12, 25/15/12, 20/10/12) of temperature and photoperiod (Fig. 5). The highest germination rate was in the condition of 30/20(°C)/12. There was no germination under high temperature of 20 °C or 24 h dark condition.

Two weeks after sowing, the cumulative germination rate and post germination seedling buoyancy at each water level were recorded (Table 3). Cumulative germination rates between inundation and waterlogged treatments were not different ($p = 0.207$). 38.4% of *S. erectum* seedlings have characteristics of post germination seedling buoyancy when germinated in inundation conditions.

Effects of water level on seedling establishment

Sinking seedling experiment Clear differences in the effects of water levels on seedling growth were observed (Fig. 6 and Table 4). Leaf extension was very rapid in submerged conditions compared with other conditions during the first 3 weeks. After 3 weeks, early height growth rate at 0 cm water level was higher than at other water levels and seedlings at 0 cm water level reached maximum shoot height first. The same tendency was seen in seedlings at 5 and –5 cm. The early height growth was delayed in water level groups over 10 cm until the seedlings emerged from below the water surface. The deeper the water level, the later the seedlings broke the water surface (Table 4). However, the shoot height at each water level eventually reached a maximum.

Total leaf length representing growth quantity differed at each water level (Fig. 6b). Total leaf length at 5 cm water level regimes was higher than at other water regimes. After seedlings emerged from below the water surface, they reached their maximum heights and tillering began (Table 4). Tillering began at water levels over 10 cm for seedlings that had yet to reach their maximum height. Tillering tended to occur later in inundation conditions. After tillering, the total leaf length increased considerably at each water level.

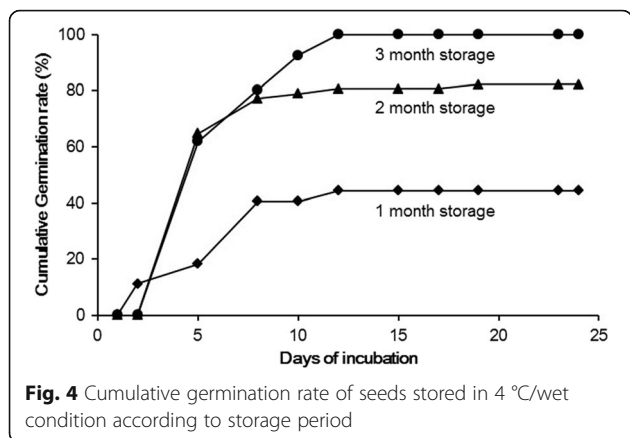
Survival rate was 100% for the first 10 weeks, then fell to 90% at the water level of 10 cm. The survival rates at

Table 2 Water environmental properties in *S. erectum* habitats in July and September 2013 (A, $n = 8$; B, $n = 3$)

Region	July				September			
	Community A	Community B	p value	t value	Community A	Community B	p value	t value
pH	6.15 (0.11)	6.54 (0.10)	***	–5.402	6.30 (0.23)	6.82 (0.15)	**	–3.625
EC (µs/cm)	192.9 (25.7)	101.6 (10.9)	***	5.806	269.3 (117.5)	86.0 (1.6)	*	2.611
Turbidity (NTU)	2.2 (1.5)	1.0 (0.3)	n.s.	1.364	22.1 (53.3)	1.2 (0.2)	n.s.	0.672
NO ₃ -N (mg/L)	6.2 (3.4)	1.8 (0.08)	n.s.	2.155	4.2 (4.0)	1.4 (0.6)	n.s.	1.918
NH ₄ -N (mg/L)	0.1 (0.1)	0.1 (0.0)	n.s.	0.502	0.5 (0.9)	0.0 (0.0)	n.s.	0.906
PO ₄ -P (mg/L)	0.0 (0.0)	0.0 (0.0)	n.s.	0.358	0.0 (0.0)	0.0 (0.0)	n.s.	1.528
K ⁺ (mg/L)	16.6 (9.7)	8.2 (1.2)	n.s.	1.439	26.3 (8.4)	8.1 (2.7)	**	3.587
Na ⁺ (mg/L)	8.8 (4.2)	5.4 (0.9)	n.s.	1.371	10.9 (1.9)	4.7 (1.6)	***	4.933
Ca ²⁺ (mg/L)	19.5 (8.1)	13.4 (1.4)	n.s.	1.245	35.8 (12.9)	15.5 (3.1)	*	2.628
Mg ²⁺ (mg/L)	4.5 (2.2)	1.6 (0.5)	n.s.	2.126	3.7 (1.8)	0.0 (0.0)	***	5.651

Values are means (S.D.)

***, $p < 0.001$; **, $0.001 < p < 0.01$; *, $0.01 < p < 0.05$; n.s. = no significance, $0.05 < p$



-5 and 0 cm fell to 50% within 3 weeks thereafter and remained at that level. Survival rate at 20 cm remained at 100% for 5 weeks before dropping to 10% by 12 weeks. Seedling survival rates in submergence treatments (water level 5, 10, and 20 cm) were higher than those in non-submergence treatments. The long submerged leaves were very fragile and thin and could not survive when exposed to air conditions. When leaves were exposed to air conditions as floating leaves spread on the water surface, the seedlings began to produce erect and thick leaves and their growth rates increased.

The total biomasses of the planted seedlings differed among water levels (Fig. 7). Although the total dry masses at -5, 0, and 5 cm showed no statistical differences, the total dry mass at the 0 cm water level (19.73 ± 5.40 g) was higher than at others. The total dry mass at submerged conditions with 10 and 20 cm water level were significantly lower than the others ($p < 0.05$). Overall, total growth was higher at water levels near the water surface compared with deeper water levels.

Floating seedling experiment After seedlings rooted in substrate, the total leaf length increased (Fig. 8a). However,

there was a difference in total leaf length at 3 and 6 cm water levels. Survival rates decreased at all water levels within 2 weeks of seedling establishment (Fig. 8b). If seedlings could not rooted in substrate, they all died. After 6 weeks, the respective survival rates were 39 and 17% at water levels of 3 and 6 cm. All seedlings unable to establish at these water levels died. All seedlings at water levels of 9 and 12 cm died. The maximum water level for the survival of floating seedlings was approximately 6 cm.

Total dry masses at 9 and 12 cm water level regimes were not measured because all seedlings died. There was no statistically significant difference between the total dry mass associated with 3 and 6 cm water levels ($p > 0.05$) (Fig. 9).

Discussion

Multiple plant species have the potential to coexist at a given location along environmental gradients because each species differs in their adult niche (Whittaker 1960; Shreve 1922; Byun et al. 2008; Hong and Kim, 2014). Therefore, environmental factors have an impact on the distribution of species in wetlands. However, abiotic factors alone cannot fully dictate species distributions. Many species have limited movement between locations and prior occupation affects species distributions and community structure (Grace 1987; Cornell and Lawton 1992; Tilman 1997). Thus, identifying the abiotic conditions in areas where the species live and simultaneously identifying environmental conditions at suitable habitats available for establishment are important as these reflect the current environmental conditions as well as historical recruitment events (Seabloom et al. 2001).

This study showed the range of the soil and water properties of *S. erectum* habitat. Except for water depth, the chemical characteristics in *S. erectum* habitats were similar to those of common coexisting species, *Typha*, *Phragmites*, *Persicaria*, and *Humulus* spp. in Korean wetlands (Kang and Joo 1999; Kwon et al. 2006; Lee et

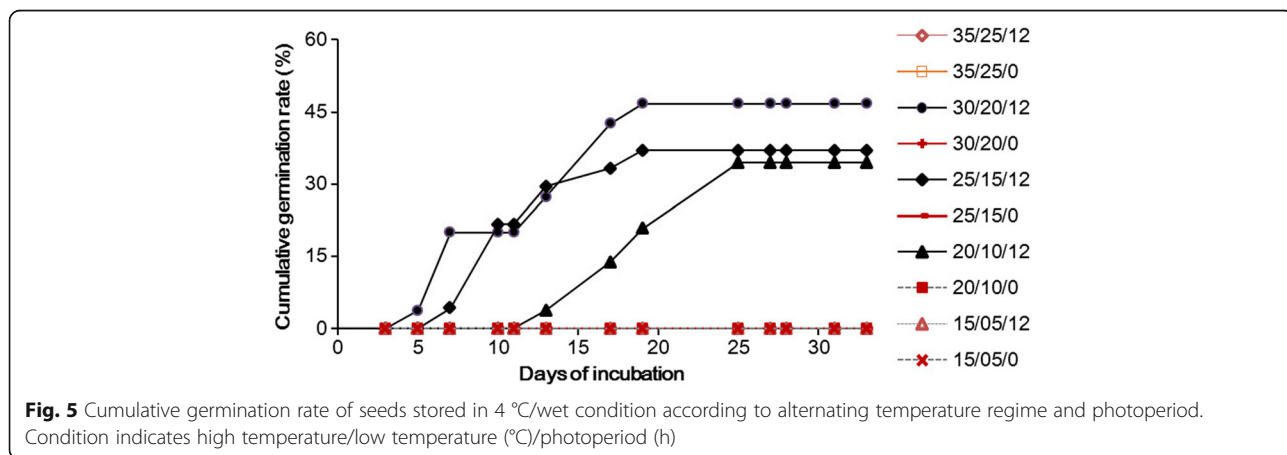


Table 3 Effects of water conditions on the germination (%) and post germination seedling buoyancy (%) (0 cm, n = 10; 20 cm, n = 10)

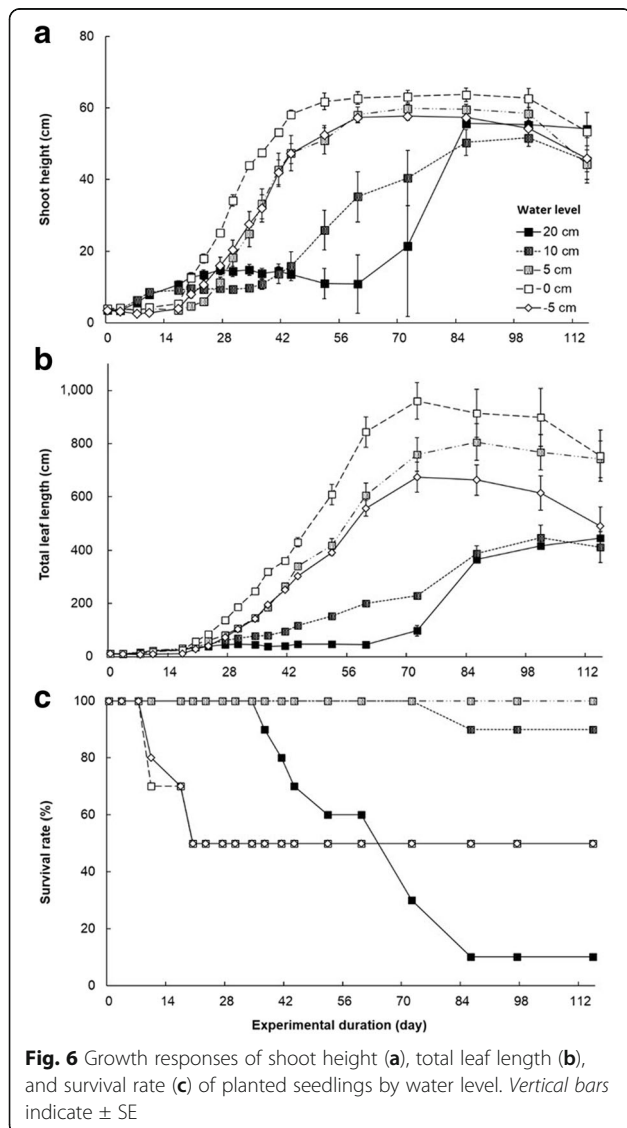
Water level	Waterlogged condition (0 cm)	Inundation condition (20 cm)	p value	t value
Cumulative germination rate (%)	65 ± 5.2	71 ± 4.3	n.s	0.885
Post germination seedling buoyancy (%)	–	38.4 ± 4.9	–	–

Values are means ± S.D.
n.s = no significance, 0.05 < p

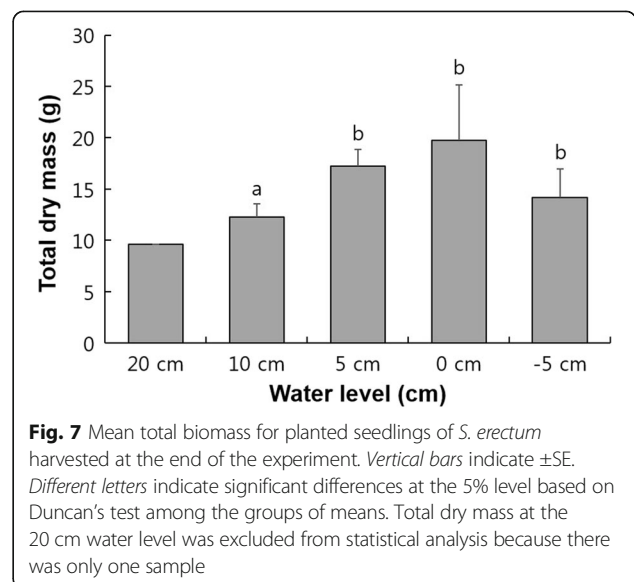
Table 4 The dates that seedlings overcame the water surface, reached maximum height, and started tillering in the planted seedling experiment

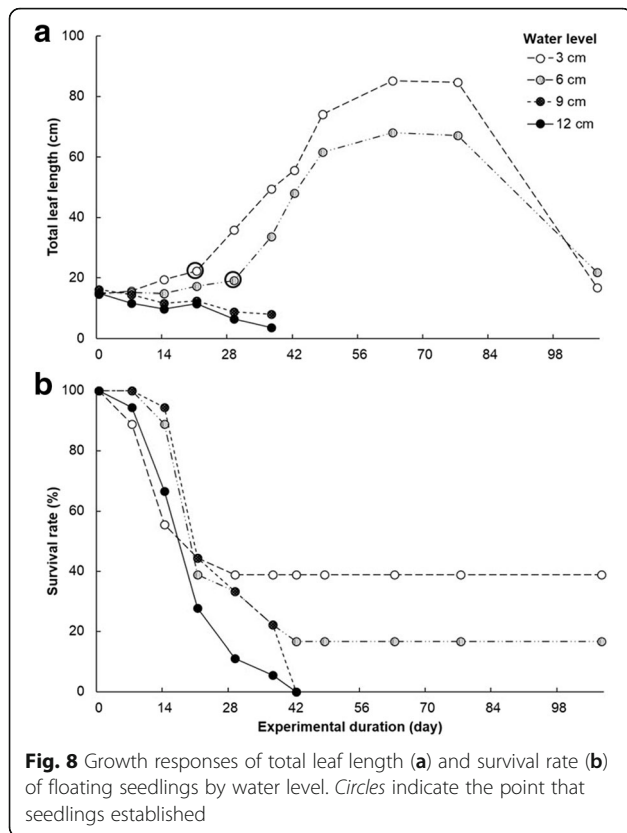
Water level	Date that seedlings overcome water surface	Date that seedlings reach maximum height	Date that seedlings start tillering
20 cm	53.0	73.0	85.0
10 cm	42.9 ± 1.5	80.0 ± 6.2 ^a	88.5 ± 3.5 ^a
5 cm	25.0 ± 2.3	70.4 ± 5.2 ^b	58.1 ± 4.4 ^b
0 cm	–	56.2 ± 2.0 ^c	39.0 ± 1.0 ^c
-5 cm	–	61.0 ± 0.0 ^{bc}	47.8 ± 1.1 ^{bc}

Values are means ± S.D. Different letters in the table indicate significant differences at the 5% level based on Duncan's test among groups of means. 20 cm water level was excluded from statistical analysis because there was only one sample from that water level

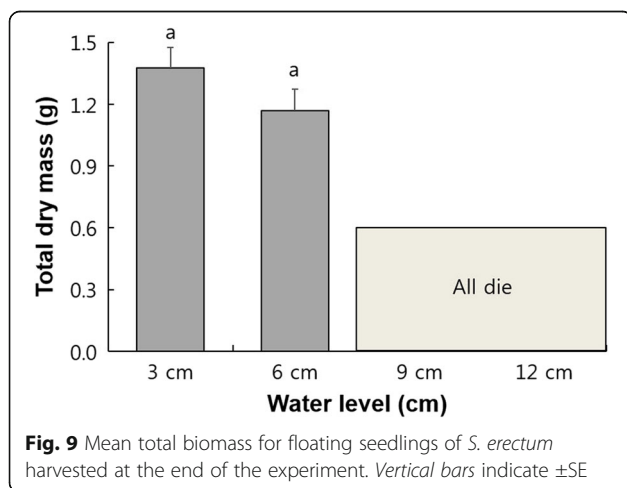


al. 2007; Kim and Kim 2009; Kim et al. 2012). This is in agreement with previous reports that the distribution of adult wetland plants is dominated by a single environmental gradient of water depth (Spence 1982). *S. erectum* was mainly distributed at deeper water depth than the other species. Although water level depends on precipitation, *S. erectum* was not distributed at and had low coverage at shallow water depths (-10~10 cm) where species abundance was high as many species live and are distributed at -20~30 cm water depths (Coops et al. 1996; Kang and Joo 1999; Kim et al. 2013; Kwon et al. 2006, Jeon et al. 2013). This suggests that shallow water depths were quickly occupied by early starting annual plant species and adult *S. erectum* lagged far behind the annual plant species.





We observed that plant height and coverage of *S. erectum* community in shallow water decreased more rapidly in deep water with time. Adults of *S. erectum* are mainly distributed in deep waters and the seeds fall in deep waters after ripening. Therefore, seeds are dispersed by hydrochory. Our results indicated that germination potential of seeds was very low at dry condition. Also, most seeds sink into the bottom of water after floating for 3 months. However, seeds buried in bottom soil could not germinate because of darkness. Once the seeds



started to germinate in inundation conditions, a number of the seedlings began to float. Thus, the floating seedlings move through the water flow while sinking seedlings establish where they fall. Our finding that seedlings float after germination is not surprising. Previous studies have shown that amphibious plant seedlings like *Triglochin procerum*, *Philydrum lanuginosum*, and *Helmholtzia glaberrima* float after germinating underwater (Nicol and Ganf 2000; Prentis et al. 2006). Some amphibious species have flexible seed germination strategies for two reasons. First, seeds can germinate under both flooded and non-flooded conditions like the family *Pontederiaceae* (Pons 1982). Second, when water depths fluctuate according to seasonal variations and different periods of time, germination is not seriously affected (Prentis et al. 2006).

After germination, floating seedlings survived for 1 or 1.5 months with prolonged floatation. Stable water depths increased the overall submergence of the seedlings, reducing CO_2 and O_2 availability and providing stress in the form of phytotoxicity and hypoxia. This resulted in seedlings with depleted carbohydrates, which prevents rhizome growth and leads to reduced shoot growth (Rea 1996). Therefore, stable water depths also obstruct regeneration from seed (Sand-Jensen et al. 1992; Clevering et al. 1995; Rea 1996). *S. erectum* seedlings could not establish below 6 cm water levels and most of them were able to establish from 3 to 6 cm. The rate of seedling establishment was 20~40% and the seedlings grew after successful establishment. The amount of post germination seedling buoyancy indicates that a high percentage of seedlings can establish if the water level stabilizes. These seedlings are often at the water surface in flooded conditions, which may be advantageous to reduce inundation stress (van der Valk 1981). Also, they have the ability to move to more favorable conditions for establishment (Nicol and Ganf 2000).

After germination, sinking seedlings have modified morphological traits such as leaf elongation and increased shoot: root ratios in response to the total submergence period (Cooling et al. 2001). This can increase the percentage that reaches the water surface. If seedlings cannot reach the water surface, plant growth decreases (Haslam 1970; Waters and Shay 1992; Coops et al. 1996). But once seedlings grew taller than the water surface, establishment, survival rates, and total leaf length were higher than for floating seedlings. With sinking seedlings, the seeds move to hydrochory, fall in the water column and germinate where they sink. The survival rate and growth rate of *S. erectum* is higher than other plants such as *Typha* and *Phragmites* spp. Survival rates at water logged conditions were lower than at other water levels, but the total dry mass was higher. Seedlings of major accompanying species of *S. erectum*

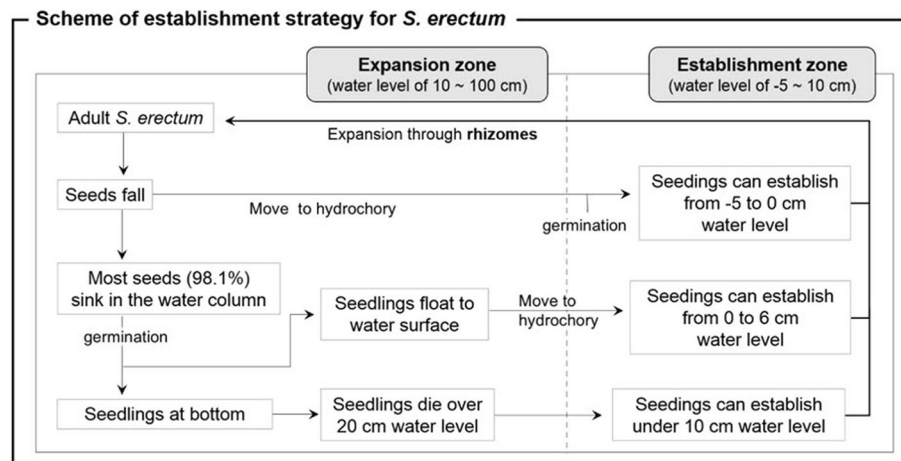


Fig. 10 Scheme of establishment strategy of *S. erectum*

such as *P. thunbergii*, *P. australis*, and *H. japonicus* grow well in water logged conditions but seedling survival rates and growth rates are reduced at water levels more than twice their heights (Mauchamp et al. 2001; Kim et al. 2013; Choo et al. 2015). It seems that *S. erectum* is more competitive than its major accompanying species, particularly in inundation conditions as opposed to waterlogged condition.

Conclusions

The water level around adult *S. erectum* populations in the field were different from the level in which the seedlings survived in the mesocosm experiments. Adult *S. erectum* live at deeper water depths than other species that share the same habitat niche, while seedlings of *S. erectum* can establish only at shallow water levels regardless of the seedling type (Fig. 10). This means that the survival strategies differ at each life stage and advance the process of establishment and growth. After floating on the water surface, then reaching and establishing on favorable conditions such as exposed mudflats and sediment topographies, the seedlings cannot survive in competition with other species such as annual plant species at shallow water levels where those species are greater. Consequently, *S. erectum* living in shallow water eventually die out and only *S. erectum* that can regenerate through rhizomes and live at deeper water depths survive. These results not only explain *S. erectum* habitat characteristics but also provide evidence to connect life-historical links between the early seedling stage and adult habitat conditions. When *S. erectum* is planted at shallow water depths in wetlands, the wetlands cannot maintain the landscape and there is a possibility the species will die out at shallow water levels. Finally, this study contributes practical information for the life cycle of *S. erectum* in wetland.

Abbreviation

EC: Electron conductivity

Acknowledgements

The authors would like to thank Eunguk Kim for assistance in mesocosm experiments.

Funding

This study was funded by the Korea Ministry of Environment (MOE) as "public technology program based on Environmental Policy" (2016000210003) and by the Basic Science Research Program through the National Research Foundation of Korea (NRF-2015R1D1A1A01057373).

Availability of data and materials

The datasets during and/or analyzed during the current study available from the corresponding author on reasonable request.

Authors' contributions

KSH participated in the design of the study, carried out field study, mesocosm experiments, and data analyses, and wrote the manuscript draft. KJG conceived the study, participated in the design of the study, edited manuscript draft, and secured funding. NJM participated in field work. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Received: 4 July 2017 Accepted: 21 July 2017

Published online: 01 August 2017

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