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Effects of water level on the establishment and growth of *Sparganium erectum*

수위가 흑삼릉 정착과 생장에 미치는 영향

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ABSTRACT

Effects of water level on the establishment and growth of *Sparganium erectum*

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Habitat environmental conditions for identifying the adult niche of *Sparganium erectum* were investigated in a field survey. The effect of water level on germination, establishment and growth of *S. erectum* seedlings was evaluated to identify the early life cycle in mesocosm experiments. In a field survey, the height and coverage of population B (living in deeper water) were greater than those of population A (living in shallow water). Means of water and soil environmental properties were not significant at $p \leq 0.05$ between the two populations. In mesocosm experiments, I found no correlation between water levels and germination rates, but *S. erectum* seedlings have characteristics of post germination seedling buoyancy when 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 six weeks but died if they were unable to establish. I concluded that the water level around adult *S. erectum* populations 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.

Keywords: adult niche, habitat environment, regeneration niche, seedling establishment.

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1. Introduction

Most macrohydrophytes are capable of both sexual and asexual reproduction. Sexual reproduction is important for colonization and the maintenance of populations of macrohydrophytes. 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). 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).

Various environmental factors including water depth, salinity, light, temperature and nutrient concentration influence different plant stages (Clarke and Allaway 1993; Coops and Velde 1995; Kim et al. 2013). Above all, the most important factor affecting seedling establishment and growth for submerged and amphibious plants is water depth (Seebloom et al. 1998). 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 wetland plant, is widely distributed in Europe but is designated as vulnerable in South Korea and endangered in Japan (Cook 1962; National Institute of Biological Resources 2012; Japanese Wildlife Research Association 2015). *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 is preferred for slow flow and fine sediment in riverine areas. 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 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).

Species that live in shallow water such as *Persicaria thunburgii* and *Cicuta virosa* represent both adult and regeneration niches (Kim et al. 2013; Shin and Kim 2013; Sine et al. 2013). However, many species such as *Typha* and *Phramites* spp. that live in deep water adopt different strategies over their lifetime (Kwon et al. 2006; Shipley et al. 1989). Adults of these species can live in deep water, but seedlings can only endure shallow water. The water depth for living *S. erectum* adults shares similar habitat environments as these emergent plants. Therefore, it was predicted to differ from the water depth of living seedlings of the plant. *S. erectum* mainly reproduces using rhizomes, but seeds can be produced at stable water levels (Cook 1962). Seeds of *S. erectum* usually fall into the water and disperse by hydrochory. *Sparganium* spp. produces 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. is also considered to exhibit different growth forms depending mainly on water depth and is especially reported to change its growth form from submerged to emergent during the early seedling phase (Kankaala et al. 2000; Riis et al. 2000; Asaeda et al. 2010). However, the effects of water depth on seed germination and seedling establishment as well as growth and historical links between the adult and regeneration niches of *S. erectum* are unknown.

In this study, I investigated habitat environmental conditions to identify the adult niche of *S. erectum* through a field survey. I also evaluated the effect of water depth on germination, establishment and growth of *S. erectum* seedlings to investigate the early life cycle in mesocosm experiments. In the mesocosm experiment, I investigated how differences in water level influence germination responses (germination rate, post germination seedling buoyancy).

I also investigated how the water level influences growth responses (growth, mortality and stand development) of two seedling types (planted versus floating) when water depth was the only environmental factor controlled.

2. MATERIALS AND METHODS

2.1 Field study

2.1.1 Vegetation Survey

I investigated *S. erectum* habitats through literature searches and field surveys in South Korea and selected the largest habitat of *S. erectum* in South Korea at the Gosancheon stream of the Mankyeong river in Wanju (N 35°56'36.8'' E 127°10'18.9'', altitude 42 m).

There were a total of six populations and we selected three for habitat environment evaluations. *S. erectum* population A clumped and mingled with other species, mainly with annual plants. Population A had the lowest water depth and there was no inflow of river water except during floods. Population A was not directly

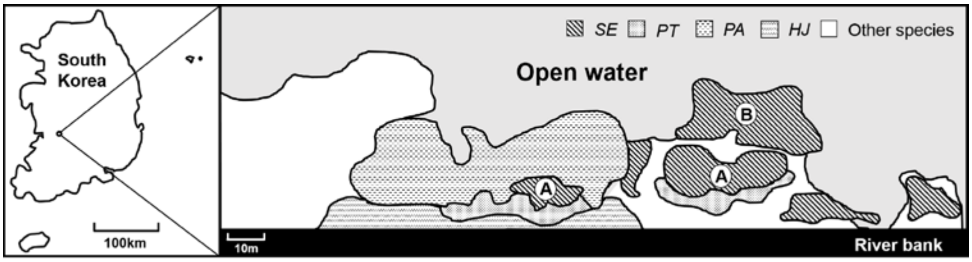

Figure 1 Habitat of *S. erectum* at Gosancheon in Mankyeong River, South Korea. The figure on the right represents a magnification of the figure on the left. A and B show populations of *S. erectum*; population A lives in shallow water and population B lives in deep water. *SE*: *Sparganium erectum*, *PT*: *Persicaria thunbergii*, *PA*: *Phragmites australis*, *HJ*: *Humulus japonicus*.

connected to the main stream of the Mankyeong river and had no direct exposure to waves (Figure 1). *S. erectum* population B formed a belt and rarely had accompanying species. Population 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 permanent quadrats of 1 m × 1 m (10 quadrats in population A and 20 quadrats in B) based on a modification of the Braun−Blanquet method (Mueller−Dombois and Ellenberg 1974; Kim et al. 2004). I measured water depth at each quadrat using a 1 m stick ruler and compared it with habitat environment conditions of other species.

2.1.2 Analyses of water and soil properties

I collected eight and three water samples for populations 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 conductivity was measured with a conductivity meter (Corning Checkmate model 311; Corning, USA) in the field. NO_3−N, NH_4−N and PO_4−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^+, Ca^{2+}, Na^+ and Mg^{2+} were measured using an atomic absorption spectrometer (Model AA240FS; Varian, USA).

I collected eight and three soil samples for populations A and B, respectively, when the plants reached maximum growth. Soil organic matter contents were analyzed by the loss on ignition method (Boyle 2004). NO_3−N and PO_4−P analysis were performed by the same method of water analysis (Kamphake et al. 1967, Solorzano 1969).

2.1.3 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).

2.2 Mesocosm experiments

2.2.1 Germination experiment

Seeds were collected on August 2 in 2012. After collection, the seeds were cleaned with distilled water (DW) and stored in a sealed plastic bag filled with wet cotton and DW at 4℃ in the dark until the germination experiment. This experiment was conducted in a greenhouse in June 2013, using a stainless steel tank (150 cm × 80 cm × 50 cm). After a few months, most of the *S. erectum* seeds sank. I selected only the seeds that sank for further study, thus germination occurred in inundation (water level, 20 cm) or waterlogged conditions (water level, 0 cm). I 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 and contained 10 seeds. Germination responses were recorded after two weeks. A seed was considered to have germinated if any part of the leaf had emerged from the seed coat. I calculated post germination seedling buoyancy rates for only the germinating seeds in the inundation condition.

2.2.2 Seedling establishments

Seeds used for seedling establishment experiments were collected on September 5, 2013 in the Mankyeong river, South Korea (N 35°56'36.8" E 127°10'18.9", 42 m). They were stored in a sealed plastic bag filled with wet cotton at 4℃ in the dark until February 2014, representing five months of wet and cold stratification for breaking seed dormancy. Seeds germinated and grew in the field until they became seedlings of 4 ± 1 cm length. After germination, two types of seedlings were observed in 2012: sinking or floating. Thus, the seedling experiments were divided into two types according to seedling types.

After germination, only the seedlings that sank were used for the sinking seedling experiments. Sinking seedlings were planted in flowerpots (Φ 15 cm; height 9 cm) and the evaluations were adjusted to account for one 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. 1,350 g of soil comprised of 1 : 8 mixtures of nursery soil (NH_4−N 350 mg/kg, PO_4−P 400 mg/kg; Pungnong, Korea) and sand was added to each pot.

After germination, only the seedlings that floated were used for the floating seedling experiments. Floating seedlings were placed in flowerpots (Φ 15 cm; height 9 cm) surrounded by plastic film. Soil comprised of 1 : 8 mixtures of nursery soil (NH_4-N 350 mg/kg, PO_4-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. I 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.

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. I monitored growth responses such as the shoot height, total leaf length, survival rate and total dry mass. I measured the early response in the first two months every 2 ~ 3 days, then measured once every week or two for the next two months. Algae is lethal to *S. erectum* seedlings, therefore, any algal growth was carefully removed. 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℃ for over 48 h. Afterward, the plants' total dry weights were measured.

2.2.3 Statistical analysis

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

3. Results

3.1 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 (Figure 2a). Coverage of population A was higher than that of population B in the early growing season, but coverage of population B increased and surpassed population A after July (Figure 2b). Coverage of population B in October remained higher than that of population A because *S. erectum* shoots reemerge throughout the year except in winter and can survive under water. Population B's height and coverage were also higher than those of population A after August, beyond the maximum growth months.

The water depth of population B was higher than that of population A year round (Figure 3). Water depths in population A and B in August increased simultaneously compared to other months because it rained a lot during the investigation period.

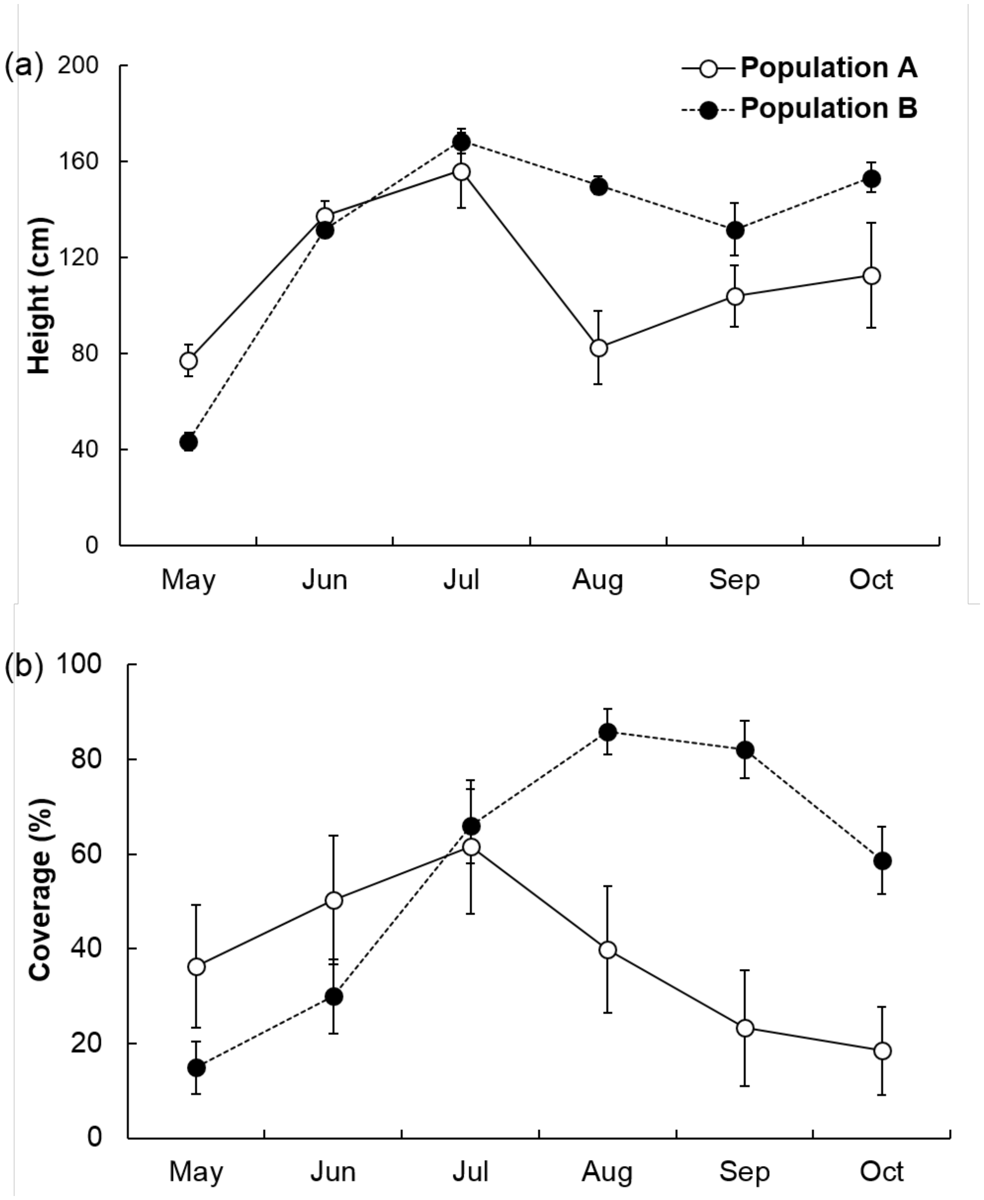

Figure 2 Monthly change in height (a) and coverage (b) of *S. erectum* according to type of habitat: living in deeper water (population B) and living in shallow water (population A). Vertical bars in Figure 2 (a) and (b) indicate ± SE.

Mean water and soil environmental properties at *S. erectum* habitats are shown in Table 1 and Table 2. There were no significant differences between the two populations in all investigated soil environmental factors at $p \leq 0.05$. Water environmental factors in the two populations 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 population B, in the deeper water depth areas, was higher, whereas the EC of population B was lower than that of population A. pH, EC and the amount of cations in population B were significantly different in September after flooding. EC and the amount of cations in population A were higher than those of population B due to inflow of muddy water.

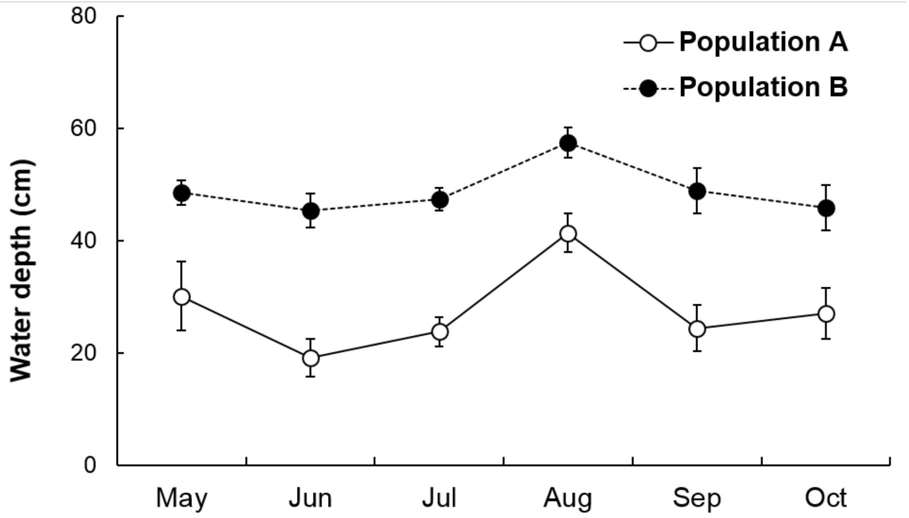

Figure 3 Seasonal change in water depth of *S. erectum* habitats. Vertical bars indicate ± SE.

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

Factor	A	B	*p*-value	t-value
Soil texture	Sandy loam	Sandy loam	-	-
LOI (%)	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

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

	July				September			
Region	A	B	*p*-value	t-value	A	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 (0.8)	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

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

3.2 Mesocosm experiments

3.2.1 Effects of water level on germination

When the *S. erectum* seeds were collected, they floated on the water surface. However, most of the seeds sank after exposure to cold and wet conditions for five months. Two weeks after sowing, the cumulative germination rate and post germination seedling buoyancy at each water level were recorded. Cumulative germination rates in the water treatments were not significantly different (p = 0.207). Thus, the germination rates with inundation and waterlogged treatments in this experiment were similar. *S. erectum* seedlings have characteristics of post germination seedling buoyancy when germinated in inundation conditions.

3.2.1 Effects of water level on establishment

3.2.2.1 Planted seedlings

Clear differences in the effects of water levels on seedling growth were observed (Figure 4 and Table 4). Leaf extension was very rapid in submerged conditions compared with other conditions during the first three weeks. After three 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 (Figure 5b). 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 ten weeks, then fell to 90% at the water level of 10cm. The survival rates at −5 and 0 cm fell to 50% within three weeks thereafter and remained at that level. Survival rate at 20 cm remained at 100% for five weeks before dropping to 10% by twelve 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

Table 3 Effects of water conditions on the germination (%) and post germination seedling buoyancy (%) (0 cm, n = 10; 20 cm, n = 10). Values are means ± S.D.

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	-	-

n.s = no significance, 0.05 < *p*

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. 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 depths 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.

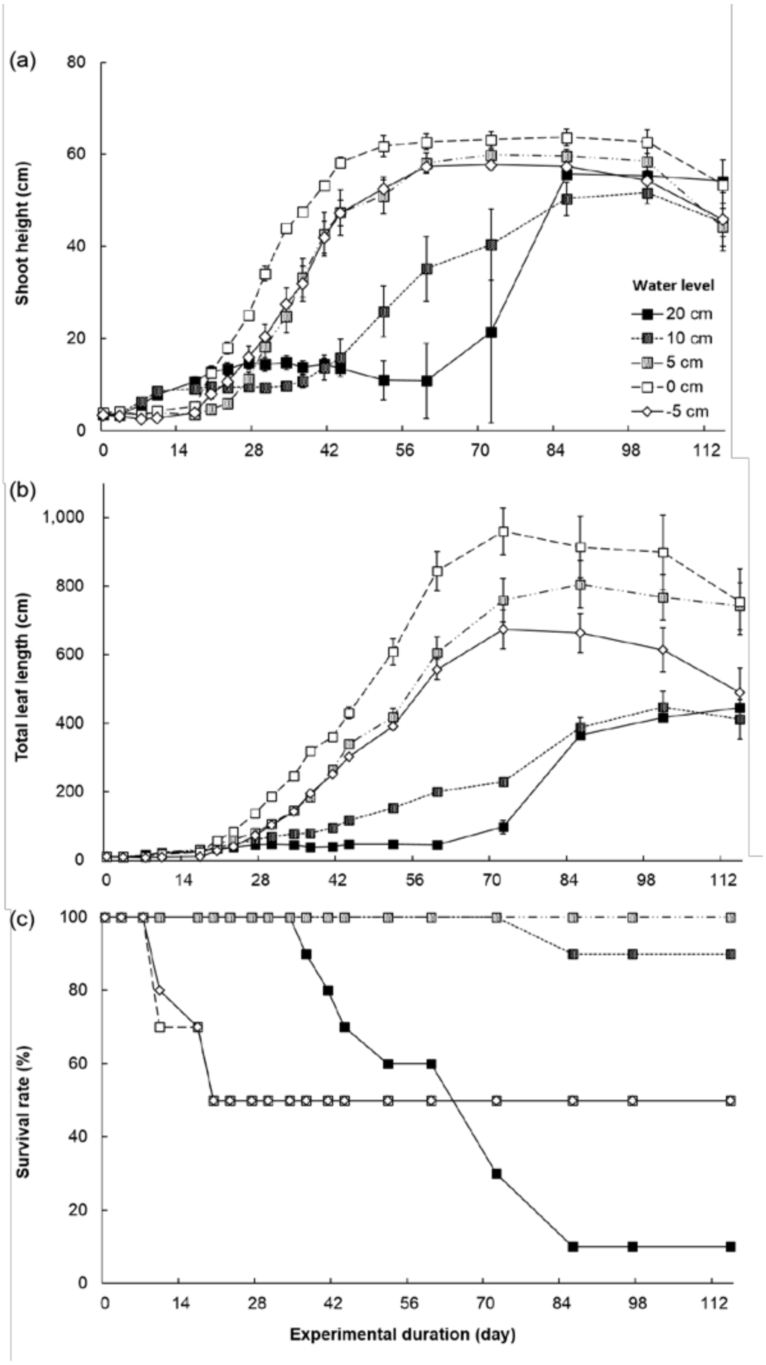

Figure 4 Growth responses (shoot height (a), total leaf length (b), survival rate (c)) of planted seedlings by water level. Vertical bars indicate ± S.E.

3.2.2.2 Floating seedlings

After seedling establishment, the total leaf length increased (Figure 7a). However, there was a difference in total leaf length at 3 cm and 6 cm water levels. Survival rates decreased at all water levels within two weeks of seedling establishment (Figure 7b). If seedlings could not establish, they all died. After six weeks, the respective survival rates were 39% and 17% at water levels of 3 cm 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.

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

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 ± 1.4 bc

Total dry masses at 9 and 12 cm water level regimes were not measured because all seedlings died. The total dry masses at 3 and 6 cm were not statically significant (Figure 7).

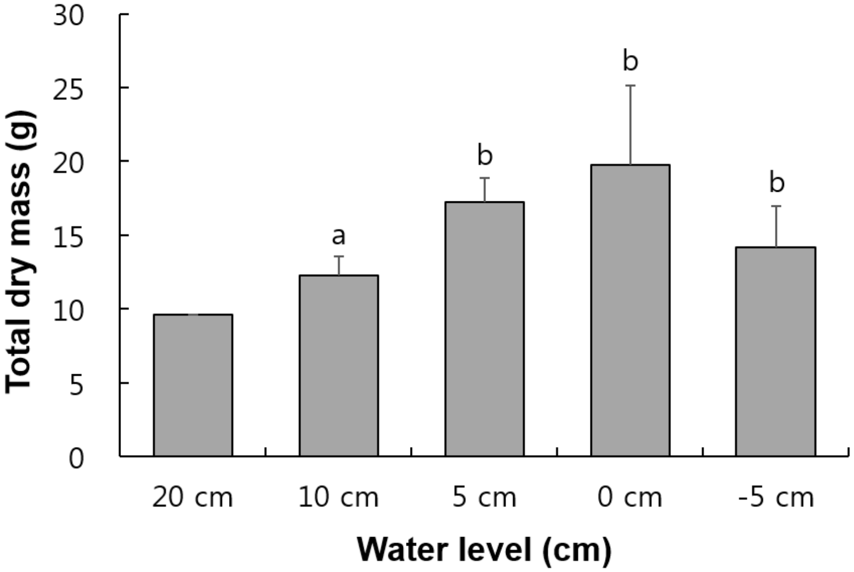

Figure 5 Mean total biomass for planted seedlings of *S. erectum* harvested at the end of the experiment. Vertical bars indicate ± SE. Different letters indicate significant differences at the 5% level at the 20 cm water level was excluded from statistical analysis because there was only one sample.

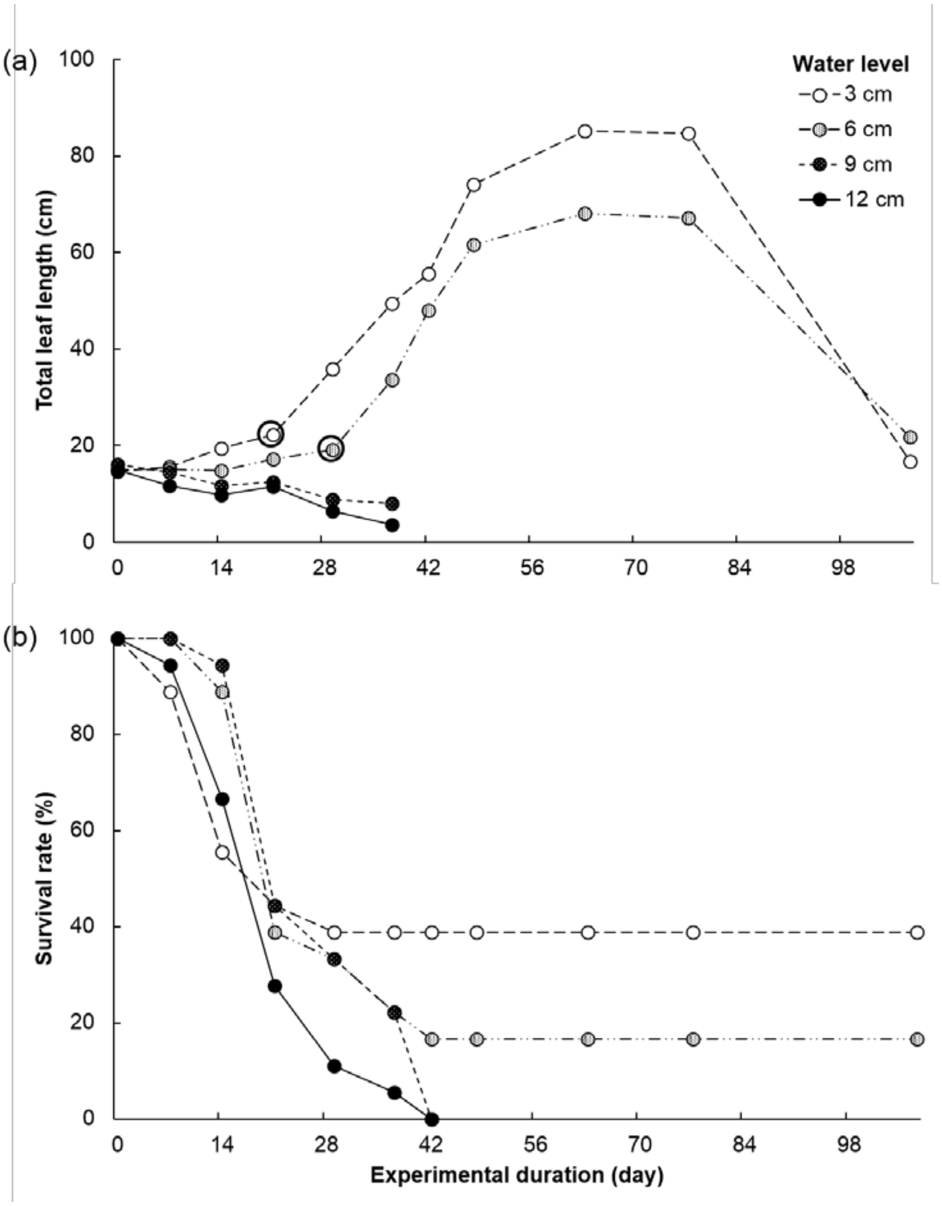

Figure 6 Growth responses (total leaf length (a), survival rate (b)) of floating seedlings by water level. Circles indicate the point that seedlings established.

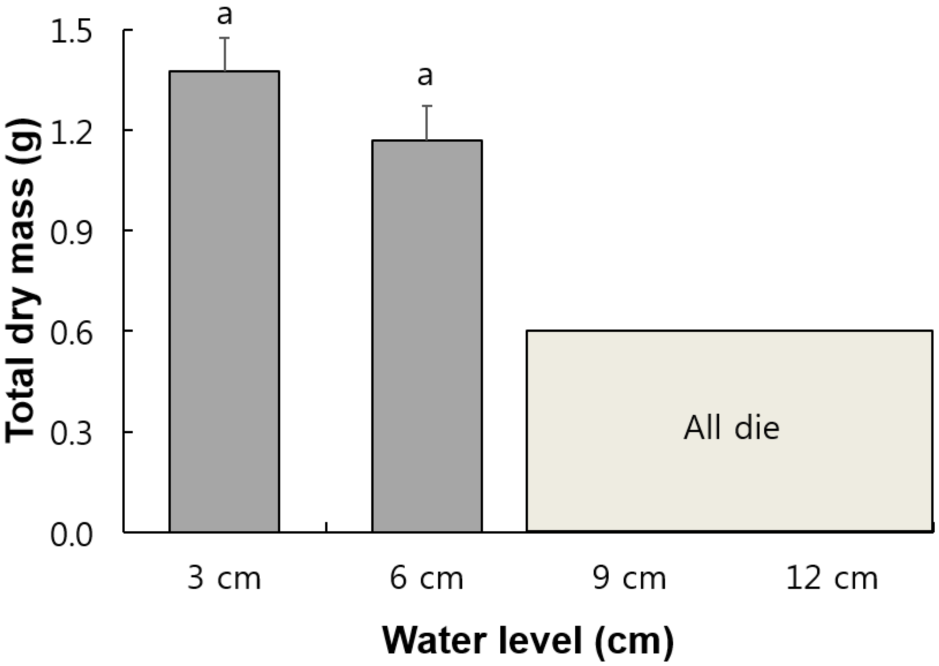

Figure 7 Mean total biomass for floating seedlings of *S. erectum* harvested at the end of the experiment. Vertical bars indicate ± SE.

4. Discussion

Multiple plant species have the potential to coexist at a given location along environmental gradients because each species differs in their adult niche (Shreve 1922; Whittaker 1960). 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 2006; 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 1996; Kim et al. 2013; Kwon 2006, Jeon 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.

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. Most *S. erectum* seeds sink and germinate in inundation and waterlogged conditions. The cumulative germination rates were not significant depending on water levels. *S. erectum* seedlings have characteristics of post germination seedling buoyancy when germinated in inundation conditions. Once the seeds started to germinate, 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 due to undernourishment and most of them were able to establish from 3 cm 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 (Arber 1920; Funke and Bartels 1937; 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; Grace and Wetzel 1981; Lieffers and Shay 1981; Hultgren 1989; Waters and Shay 1990; Waters and Shay 1992; Van den Brink et al. 1995; 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, Phramites* 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* 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). It seems that *S. erectum* is more competitive than its major accompanying species, particularly in inundation conditions as opposed to waterlogged condition.

5. 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 (Figure 8). 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 seedlings 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 use of *S. erectum* in wetland restoration.

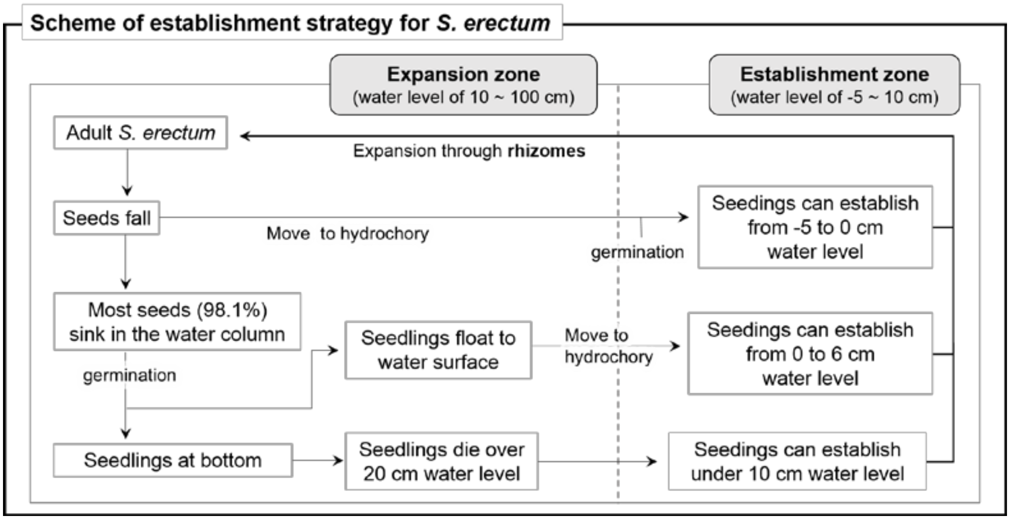

Figure 8 Scheme of establishment strategy for *S. erectum*.

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국문 초록

흑삼릉(*Sparganium erectum*)의 adult niche를 알아보기 위하여 야외에서의 서식지 환경 조건을 조사하였다. 종자 분산, 발아, 유묘 생존에 영향을 미치는 환경인자인 Regeneration niche를 알아보기 위하여 서식지 환경 조사 결과 가장 중요한 영향을 미친다고 판단되는 수위가 흑삼릉 유묘의 발아, 정착, 생장에 미치는 영향에 대해 메조코즘 실험을 하였다. 야외조사에서 비교적 깊은 물에 사는 흑삼릉 군락(population B)이 얕은 물에 사는 흑삼릉 군락(population A)의 초고와 피도보다 더 높았다. 두 군집 의 수환경과 토양환경의 평균값들은 유의수준 0.05보다 낮았다. 메조코즘 실험 중 발아실험에서, 수위와 발아율은 상관관계를 보이지 않았지만 침수환경에서 발아할 경우 흑삼릉 유묘가 수면 위로 뜨는 현상(post germination seedling buoyancy)을 보였다. 유묘 실험 중 가라앉는 유묘 실험에서는 −5, 0, 5 cm 의 얕은 수위에서 깊은 수위인 10, 20 cm 보다 평균 초고, 전체 잎 길이, 생존율이 높았다. 뜨는 유묘 실험에서는 3, 6 cm 수위에서만 정착을 하였고, 6주까지는 생존하였으나 정착하지 못한 유묘는 모두 죽었다. 위의 결과를 토대로 야외에서 수위가 흑삼릉 성체 군집에 미치는 영향과 메조코즘 실험에서 흑삼릉 유묘가 살 수 있는 수위는 서로 다르다는 것을 알 수 있었다. 이러한 결과는 흑삼릉 서식지 특성을 이해하는 것뿐 만 아니라 흑삼릉 초기 유묘 단계에서 살 수 있는 환경과 성체 서식지 조건을 연결하는 연결고리로서 정보를 제공할 수 있을 것이다.

주요어 : 발아, 서식지 환경, 수위, 유묘 정착

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