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교육학석사 학위논문

**Flooding effects on the amphicarpic seed production
of *Persicaria thunbergii* and differences of
two seed types in early life stage**

고마리의 이종과 생산에 대한 범람의 영향과
초기 생활사에서 두 종자 유형의 차이

2014년 2월

서울대학교 대학원
과학교육과 생물전공
추연희

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이 논문을 교육학 석사학위논문으로 제출함
2013년 12월

서울대학교 대학원
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추연희의 석사학위논문을 인준함
2014년 1월

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ABSTRACT

Flooding effects on the amphicarpic seed production of *Persicaria thunbergii* and differences of two seed types in early life stage

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To better understand the amphicarpy of *Persicaria thunbergii* as the reproductive strategy in stressful environment, I investigated the effects of flooding on the amphicarpic seed production and compared seed size and seedling stress response using a mesocosm experiment. First, I observed the effects of flooding on the amphicarpic seed production of *P. thunbergii*. To know the effect of the timing of the simple flooding, plants were submerged at a depth of 30cm during 2 weeks in June and August, respectively. To mimic severe damages by the flooding, 50% of the leaves were removed and the plants were shaded for 1 week in the late vegetative growth period (August). The results showed that the simple flooding in the both periods had no effects on the production of the amphicarpic seeds and the vegetative parts. However, the flooding with the damages tended to decrease the production of the seeds and the biomass. In particular, the production and the one seed weight of the subterranean seed were significantly decreased

with the biomass reduction under the strong disturbance. Also, the subterranean seeds were formed later than the aerial seeds. I can suggest that unlike other amphicarpic plants, *P. thunbergii* may not produce the subterranean seeds according to a pessimistic strategy and can reduce the production of the subterranean seeds when time and energy do not permit. The amphicarpic as evolutionary adaptations for *P. thunbergii* can have different ecological significance than for other amphicarpic plants.

Second, I compared aerial and subterranean seeds and seedlings in size, weight, and seedling stress response. The major axis and minor axis of the subterranean seeds were 22% and 17% longer than that of the aerial seeds, respectively. The subterranean seeds were 39% heavier than that of the aerial seeds. In the control group, the average stem length of the SS (seedling from subterranean seed) was 41% longer than that of the SA (seedling from aerial seed). Also, SS preponderated in leaf number, root length and overall dry weight over SA. In shaded group, the SS had 34% longer stem length and 99% wider leaf area than SA. Moreover, SS could grow stem length more rapidly to escape the water level than SA. The cause of producing superior subterranean seeds can be one of the strategies to survive in a negative environment in early life history. By producing not only the aerial seeds for dispersion but also subterranean seeds for survival, the *P. thunbergii*, which inhabit extreme riparian areas, seems to leave behind a community at its mother-site.

Keywords: amphicarpic, *Persicaria thunbergii*, flooding, seed size, young plant stress response

Student Number : 2012-21444

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INTRODUCTION

Amphicarpy is a unique trait of some plants, which form not only aerial seeds but also subterranean seeds on the same individual (Kaul et al., 2000). In general, aerial flowers are chasmogamous, and their seeds are produced by cross-pollination. The aerial seeds are greater in number, smaller, and lighter than the subterranean seeds. Thus, the aerial seeds can be a way for plants to keep genetic diversity and to disperse. On the other hand, subterranean flowers are cleistogamous and only self-pollinated, producing less, larger, and heavier seeds than the aerial seeds. The subterranean seeds are more likely to remain viable and can germinate and establish seedlings better than the aerial seeds even though they have a limited dispersibility due to their location under the soil surface (Cheplick, 1987; Kawano et al., 1990). There have been many suggestions regarding ecological and evolutionary significance of amphicarpy (Koller and Roth, 1964; Cheplick, 1983; Schnee and Waller, 1986; Masuda and Yahara, 1994; Sadeh et al., 2009); and possessing these two kinds of seeds provide the plants reproductive plasticity in order to adapt to frequent environmental changes (Koller and Roth, 1964; Weiss, 1980; Cheplick and Quinn, 1983). Subterranean flowers are formed earlier than or contemporaneous with aerial flowers in many amphicarpic plants (Cheplick and Quinn, 1982). Several studies have suggested that the earlier formation of more viable subterranean seeds, termed as pessimistic strategy, could be a key to producing the next stable generation in stressful situations (Zeide, 1978; Cheplick and Quinn, 1982; Cheplick, 1987). However, the specific response of amphicarpic plants to environmental stress can depend on plant species

and the environmental variables. Thus, in order to fully understand the amphicarpic trait, more information about specific results in amphicarpic responses of diverse plants under various stressful situations is needed.

Persicaria thunbergii (Siebold & Zucc.) H.Gross is an annual herb of Polygonaceae and a type of amphicarpic plants. *P. thunbergii* is one of the most dominant annual species in eastern Asia including Korea, China, Taiwan, Ussuri, and Japan (Kawano, 2008). They commonly inhabit riparian or water canals, where frequent water level fluctuations and hydrological disturbances create an unstable environment for plants (Cho, 1995; Song and Song, 1996; Kang and Kwak, 1998; Ahn and Song, 2003; Lee et al., 2004). The damage by flooding can lead to the change of amphicarpic flowering and seeding in the plants. Because flooding is one of the critical factors affecting the life history of wetland plants (Satake et al., 2001; Suzuki et al., 2007; Mony et al., 2010), flooding can impact the two kinds of seed production in amphicarpic plants like *P. thunbergii*. However, the effects of flooding on the reproduction of amphicarpic plants have never been examined even in other amphicarpic plants.

Also, early life history components, such as germination, seedling recruitment, and early establishment are momentous for wetland plant distribution (Weiher and Keddy, 1995; Nicol and Ganf, 2000), especially for annual plants like *P. thunbergii* (Noe and Zedler, 2001). In particular, the water level or moisture gradient is the most critical factor in wetlands because recurrent flooding is detrimental to seeds or seedlings (Keddy and Ellis, 1985; Kim et al., 2013). Light is also a highly heterogeneous environmental factor, influencing plant growth, survival, and competition

within the community (Canham et al., 1990). However, there is no study dealing with early life stage of *P. thunbergii* as the amphicarpic plant .

In order to understand the amphicarpic trait of *P. thunbergii* as a reproductive adaptation strategy, I conduct two mesocosm experiments. First experiment was aimed to investigate the effects of flooding on the amphicarpic property of *P. thunbergii*. The purpose of second experiment was to understand the advantages of the additional production of subterranean seeds in early life history within disturbed conditions by comparing the physical characteristics between two seed types, as well as investigating the stress response of the young plants from the two seed types under stressful conditions of shade and waterlogged.

REFERENCES

- Ahn Y.H., Song J.S., 2003. Occurrence of streamside flora in relation to environmental condition at Ansongchon creek. Korean J. Environ. Sci. 12, 573-582 (in Korean).
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20, 620-631.
- Cheplick, G.P., 1983. Differences between plants arising from aerial and subterranean seeds in the amphicarpic annual *Cardamine chenopodifolia* (Cruciferae). B. Torrey Bot. Club 110, 442-448.
- Cheplick, G.P., 1987. The ecology of amphicarpic plants. Trends Ecol. Evol.

2, 97-101.

- Cheplick, G.P., Quinn, J.A., 1982. *Amphicarpum purshii* and the “pessimistic strategy” in amphicarpic annuals with subterranean fruit. *Oecologia* 52, 327-332.
- Cheplick, G.P., Quinn, J.A., 1983. The shift in aerial/subterranean fruit ratio in *Amphicarpum purshii* : causes and significance. *Oecologia* 57, 374-379.
- Cho, D.S., 1995. A study on the distribution of streamside vegetation in Kyonganchon. *Korean J. Ecol.* 18, 55-62 (in Korean).
- Kang S. J., Kwak A. K., 1998. Changes of riparian vegetation in relation to disturbance of Musim-Chon stream, Cheongju. *Korean J. Ecol.* 21, 435-448 (in Korean).
- Kaul, V., Koul, A., Sharma, M., 2000. The underground flower. *Curr. Sci.* 78, 39-44.
- Kawano, S., 2008. 11: *Polygonum thunbergii* Sieb. et Zucc.(Polygonaceae). *Plant Spec. Biol.* 23, 222-227.
- Kawano, S., Hara, T., Hiratsuka, A., Matsuo, K., Hirota, I., 1990. Reproductive biology of an amphicarpic annual, *Polygonum thunbergii* (Polygonaceae): Spatio-temporal changes in growth, structure and reproductive components of a population over an environmental gradient. *Plant Spec. Biol.* 5, 97-120.
- Keddy, P.A., Ellis, T.H., 1985. Seedling recruitment of 11 wetland plant species along a water level gradient: Shared or distinct responses? *Can. J. Bot.* 63, 1876-1879.
- Kim, D.H., Kim, H.-T., Kim, J.G., 2013. Effects of water level and soil type

- on the survival and growth of *Persicaria thunbergii* during early growth stages. Ecol. Eng. 61, 90-93.
- Koller, D., Roth, N., 1964. Studies on the ecological and physiological significance of amphicarpy in *Gymnarrhena micrantha* (Compositae). Am. J. Bot. 51, 26-35.
- Lee K.B., Kim C.H., Lee D.B., Kim J.G., Park C.W., 2004. The flora and vegetation of the Dongjin river. Korean J. Environ. Agri. 23, 34-40 (in Korean).
- Masuda, M., Yahara, T., 1994. Reproductive ecology of a cleistogamous annual, *Impatiens noli-tangere* L., occurring under different environmental conditions. Ecol. Res. 9, 67-75.
- Mony, C., Mercier, E., Bonis, A., Bouzillé, J.B., 2010. Reproductive strategies may explain plant tolerance to inundation: a mesocosm experiment using six marsh species. Aquat. Bot. 92, 99-104.
- Nicol, J.M., Ganf, G.G., 2000. Water regimes, seedling recruitment and establishment in three wetland plant species. Mar. Freshw. Res. 51, 305-309.
- Noe, G.B., Zedler, J.B., 2001. Spatio-temporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment. J. Veg. Sci. 12, 61-74.
- Sadeh, A., Guterman, H., Gersani, M., Ovadia, O., 2009. Plastic bet-hedging in an amphicarpic annual: An integrated strategy under variable conditions. Evol. Ecol. 23, 373-388.
- Satake, A., Sasaki, A., Iwasa, Y., 2001. Variable timing of reproduction in unpredictable environments: Adaption of flood plain plants.

- Theor. Popul. Biol. 60, 1-15.
- Schnee, B.K., Waller, D.M., 1986. Reproductive behavior of *Amphicarpaea bracteata* (Leguminosae), an Amphicarpic Annual. Am. J. Bot. 73, 376-386.
- Song J.S., Song S.D., 1996. A phytosociological study on the riverside vegetation around Hanchon, and upper stream of Nak-tong river. Korean J. Ecol. 19, 431-451 (in Korean).
- Suzuki, M., Kaya, Y., Ishida, T.A., Hattori, K., Miki, K., Nakamura, T., Kimura, M.T., 2007. Flowering phenology and survival of two annual plants *Impatiens noli-tangere* and *Persicaria thunbergii* co-occurring in streamside environments. Ecol. Res. 22, 496-501.
- Weiher, E., Keddy, P.A., 1995. The assembly of experimental wetland plant communities. Oikos 73, 323-335.
- Weiss, P.W., 1980. Germination, reproduction and interference in the amphicarpic annual *Emex spinosa* (L.) Campd. Oecologia 45, 244-251.
- Zeide, B., 1978. Reproductive behavior of plants in time. Am. Nat. 112, 636-639.

Chapter 1.

Flooding effects on the seed production of amphicarpic plant, *Persicaria thunbergii**

Abstract

The study was aimed to investigate the effects of flooding on the amphicarpic seed production of *P. thunbergii* using a mesocosm experiment. The plants for the effect of the timing of the simple flooding were subjected to 2 week's inundation at a depth of 30 cm in June and August, respectively. To mimic severe damages by the flooding, 50% of the leaves were removed and the plants were shaded for 1 week. The results showed that the simple flooding in the period of the early vegetative growth and the late vegetative growth had no effects on the production of the amphicarpic seeds and the vegetative parts. The amphicarpic seeds of *P. thunbergii* do not show any changes under the stress like the inundation level reaching approximately the plant height. However, the flooding with the damages in the late vegetative growth tended to decrease the production of the seeds and the biomass. In particular, the production and the one seed weight of the subterranean seed were significantly decreased with the biomass reduction under the strong disturbance. The subterranean seeds were formed later than the aerial seeds. I can suggest that unlike other amphicarpic plants, *P. thunbergii* may not produce the subterranean seeds according to a

* This manuscript was submitted to Aquatic Botany

pessimistic strategy and can reduce the production of the subterranean seeds when time and energy do not permit. The amphicarpy as evolutionary adaptations for *P. thunbergii* can have different ecological significance than expected (or for other amphicarpic plants).

Keywords: amphicarpic plant, flooding, leaf loss, shading, *Persicaria thunbergii*

1. Introduction

Amphicarpy is a unique trait of some plants, which form subterranean seeds with aerial seeds on the same individual (Kaul et al., 2000). The trait is found in a few species, and there have been many suggestions regarding its ecological and evolutionary significance (Koller and Roth, 1964; Cheplick, 1983; Schnee and Waller, 1986; Masuda and Yahara, 1994; Sadeh et al., 2009). Previous studies have shown that amphicarpic seeds differ from aerial seeds in their development and functions. In general, aerial flowers are chasmogamous, and their seeds are produced by cross-pollination. The aerial seeds are greater in number, smaller, and lighter than the subterranean seeds. Thus, the aerial seeds can be a way for plants to keep genetic diversity and to disperse. On the other hand, subterranean flowers are cleistogamous and only self-pollinated, producing less, larger, and heavier seeds than the aerial seeds. However, the subterranean seeds are more likely to remain viable and can germinate and establish seedlings better than the aerial seeds even though they have a limited dispersibility due to their location under the soil surface (Cheplick,

1987; Cheplick, 1994).

Although producing larger subterranean seeds along with aerial seeds may require plants to invest additional energy for seed production, it can be a beneficial reproductive strategy. Most amphicarpic plant species inhabit stressful environments like deserts and riparian wetlands, where disturbances such as drought and flooding can affect the survival of their seeds. Having two kinds of seeds can give the plants reproductive plasticity adapted to frequent environmental changes (Koller and Roth, 1964; Masuda and Yahara, 1994; Sadeh et al., 2009).

In addition to the difference in their location and functions, the formation period of the flowers could be different. Subterranean flowers are formed earlier than or contemporaneous with aerial flowers in many amphicarpic plants such as *Commelina benghalensis* L., *Catananche lutea* L., *Gymnarrhena micrantha* Desf., *Cardamine chenopodifolia* Pers., *Pisum fulvum* Sibth. & Sm. var. *amphicarpum* Warb. & Eig, *Vicia sativa* subsp. *amphicarpa* (Dorth.) Aschers. & Graebn., *Amphicarpum purshii* Kunth, *Emex spinosa* (L.) Campd. (Cheplick and Quinn, 1982). Several studies have suggested that the earlier formation of more viable subterranean seeds, termed as pessimistic strategy, could be a key to producing the next stable generation in stressful situations (Zeide, 1978; Cheplick and Quinn, 1982; Cheplick, 1987). However, the specific response of amphicarpic plants to environmental stress can depend on plant species and the environmental variables. Thus, in order to fully understand the amphicarpic trait as an adaptive strategy of plants, more information about specific results in amphicarpic responses of diverse plants under various stressful situations is

needed.

Persicaria thunbergii (Siebold & Zucc.) H.Gross is an annual herb of Polygonaceae and a type of amphicarpic plants. Its aerial flowers, developed at the shoot tips, are chasmogamous and self-pollinated or cross-pollinated by insect pollinators such as flies, wasps and flower-visiting bees, producing more and smaller seeds than the subterranean flowers (Suzuki et al. 2007). The subterranean flowers are formed at the tips that stretch from the creeping stem toward the soil layers and are cleistogamous and only self-pollinated, producing a few larger seeds (Kawano et al., 1990).

P. thunbergii community commonly occurs at watery areas such as riparian zones and lakesides in eastern Asia including Korea, China, Taiwan, Ussuri, and Japan (Kawano, 2008). In particular, riparian vegetation including *P. thunbergii* faces harsh floods which occur almost every year (Naiman and Decamps, 1997; Cho and Cho, 2005). Thus, the aerial parts of *P. thunbergii* are also damaged by the flooding during the rainy season (Kim et al., 2012). The damage by flooding can lead to the change of amphicarpic flowering and seeding in the plants. The effects of flooding on seed production can also depend on the period and intensity of flooding (Satake et al., 2001; Suzuki et al., 2007; Mony et al., 2010).

While many researches have been conducted to investigate reproductive responses of amphicarpic plants to the change of environmental variables such as light, nutrients, soil moisture, density, and the depth of seed burial (Weiss, 1980; Cheplick and Quinn, 1982, 1983; Trapp and Hendrix, 1988; Masuda and Yahara, 1994), the difference in how the level of light and nutrient impact the amphicarpy of *P. thunbergii* was

investigated by Kawano et al. (1990). However, the effects of flooding on the reproduction of amphicarpic plants have never been examined. Because flooding is one of the critical factors affecting the life history of *P. thunbergii* (Kim et al., 2013), flooding can also be a potential factor causing the change of the amphicarpic seeds in *P. thunbergii*. Therefore, in order to understand the amphicarpic trait of *P. thunbergii* as a reproductive adaptation strategy, I need to observe the seed formation change in a flooding situation.

The present study was aimed to investigate the effects of flooding on the amphicarpic property of *P. thunbergii* under mesocosm settings. The study results may present basic information for understanding the reproductive adaptation of amphicarpic plants to frequent and more detrimental flooding from strong rainfalls.

2. Materials and methods

2.1. Mesocosm experiment

The experiment was conducted at Seoul National University, Korea from May to November 2012. The oval rubber pots (70 cm (W) × 100 cm (L) × 35 cm (H)) were filled 5cm depth with sand. The general management and the number of *P. thunbergii* per pot were based on the preliminary experiment and field survey conducted in 2011. In the mesocosms, NH_4^+ , NO_3^- , and PO_4^- showed 4.4 ± 2.8 , 1.3 ± 0.5 , and 3.8 ± 0.8 mg/kg, respectively in May and about 5 g of composite fertilizer (N 11%, P 10%, K 8%; Dongbuhitech, Korea) were given four times during the experiment period. At first, two young plants of *P. thunbergii* were

transplanted per pot, but only the young plant reaching approximately 18 cm in height was kept per pot and the other young plant was removed.

There were five experimental treatments and each treatment had four pots. The treatments included no flooding, two treatments of one simple flooding in June or August, flooding with 50% leaf removal, and flooding with 50% leaf removal and shading (Table 1). The water level of 30 cm in the simple flooding treatments was determined based on my observation for several years that on average, the water level in streams increased by 30~40 cm during the growing season. To investigate the effects of the timing of simple flooding, I chose June and August. The treatment flooded for two weeks in June (Group 6F) indicated the flooding in the early vegetative growth stage when the vigorous branching of *P. thunbergii* occurred. The two-week flooded treatment in August (Group 8F) was for the flooding in the late vegetative growth stage right before the formation of the floral buds was begun. The flooding water level (30 cm) was higher than the plants' height in June, but reached about 63% of their height in August.

Table 1
Monthly treatment of five groups in mesocosm.

Group	June	August
Control		
6F	inundation	
8F		inundation
8D		inundation + leaf loss
8M		inundation + leaf loss + shading

Inundation water level was 30 cm and inundation duration was two weeks. Leaf loss included 50% leaf removal and pressing. The pressing and shading was maintained for a week.

The treatments with the leaf removal and shading indicated the disturbance that could be caused by strong currents and muddy waters when torrential flooding occurred. The damages caused by the flooding can lead to the loss of the living leaves and shading. The decrease of the dried leaf weight by 50% was observed in flooded area compared with non-flooded area in my field survey (not published data). In addition, I confirmed that muddy water can transmit just about 5% of sunlight. Consequently, the treatment for the leaf loss caused by flooding (Group 8D) adopted the removal of about 50% of the living leaves followed by the one-week's pressure of 990.2 Pa using plastic baskets and bricks to represent water pressure caused by a swift current during the early two-week's flooding in August. The treatment for flooding with the leaf loss and shading (Group 8M) was covered with three layers of black polyester nets for one week during the early two-week's flooding in August. The water level in the treatment without flooding was maintained between 0 and 3 cm in depth during the whole experiment period.

When the aerial flowers began to bloom, nets with 2 millimeter-sized holes were placed around the aerial shoots to collect the aerial seeds and the fallen seeds were monitored daily. The experiment was finished with all biomass harvested on 15 November when the temperature fell below zero. The ratio of the living parts to the biomass was investigated to compare the plant growth status among the treatments at the end of the life cycle. Therefore, the harvested parts were classified into the shoots with green living leaves, the shoots with withered leaves, and the roots, followed by drying at 80°C for over 48 hours. During the classification, the aerial

and subterranean seeds remaining on the shoots were collected. The sand in the pots was sieved using a 2 mm-mesh sieve to collect the subterranean seeds. Both of the collected seeds were stored in dark and humid conditions. After 80 days, the number and weight of both seeds and the germination rate per pot were investigated for the mature seeds. To show the allocation of energy and resource to both seeds, the ratio of each seed weight to the plant total dry weight was measured.

Statistical analyses were performed using one-way analysis of variance without transformation and Duncan's post hoc test at the 5% significance level using SPSS ver. 20.0 (SPSS, Inc., Chicago, IL, USA).

2.2. Pot experiment for investigation of formation timing of the flowers

While conducting the 2012 experiment, I found that the subterranean flowers might be formed simultaneously or later than the aerial flowers. To confirm the observation, several *P. thunbergii* were planted in oval rubber pots and prepared just like the 2012 experiment at Seoul National University in 2013. Acrylic plate was placed to divide the pot into two subplots. The water level was maintained to a depth of no more than 3 cm and the general management was applied according to the previous experiment. When the first aerial flowers began to bloom at 13rd, September, I harvested the total aerial and subterranean shoots to investigate the formation of the floral buds. The harvested shoots were classified into the shoot tips with floral buds and without floral buds.

3. Results

3.1 Effects of simple flooding

The productions of the aerial and subterranean seeds in the plots with only flooding in each June (Group 6F) and August (Group 8F) did not significantly differ from the control corresponding to the plots with no flooding (Table 2). For the number and weight of seed per individual, one seed weight, and the germination rate for the both of aerial and subterranean seeds, the plots with simple flooding did not show significant differences from the control. In allocation of the aerial and subterranean seeds, significant differences were not found among the plots (Fig. 1). Total dry weight and the ratio of the weight of living green shoot to the weight of total shoot were not significantly different (Table 3).

The aerial seeds were greater in the total number and higher in the total weight than the subterranean seeds, but for the one seed weight and the germination rate, the subterranean seeds were higher than the aerial seeds in all the plots (Table 2).

Table 2Effects of flooding period on production of the aerial and subterranean seeds, mean (\pm standard error)

Condition	Number of seeds per individual		Weight of seeds per individual (g)		One seed weight (mg)		Germination rate (%)	
	Aerial	Sub	Aerial	Sub	Aerial	Sub	Aerial	Sub
Control	1042 (\pm 138) ^a	558 (\pm 39) ^a	12.1 (\pm 1.4) ^a	8.3 (\pm 0.3) ^a	11.7 (\pm 0.3) ^a	15.0 (\pm 0.6) ^a	6.3 (\pm 2.4) ^a	43.3 (\pm 5.2) ^a
6F	1049 (\pm 79) ^a	652 (\pm 62) ^a	11.9 (\pm 1.0) ^a	9.9 (\pm 0.9) ^a	11.3 (\pm 0.3) ^a	15.2 (\pm 0.6) ^a	11.7 (\pm 4.8) ^a	39.9 (\pm 8.5) ^a
8F	1069 (\pm 81) ^a	605 (\pm 60) ^a	12.4 (\pm 1.6) ^a	8.5 (\pm 0.9) ^a	11.5 (\pm 0.8) ^a	14.2 (\pm 1.2) ^a	4.9 (\pm 2.6) ^a	35.8 (\pm 11.8) ^a

Aerial : aerial seed; Sub : subterranean seed; 6F : simple flooding in June; 8F : simple flooding in August. Means of both aerial seeds and subterranean seeds were not significantly different at the 0.05 level (n = 4).

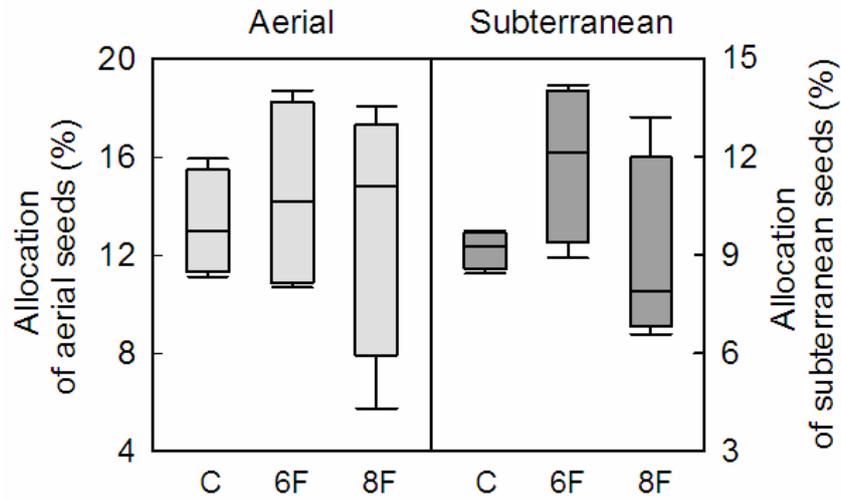


Fig. 1. Effects of flooding period on allocation of aerial and subterranean seeds. C : Control; 6F : simple flooding in June; 8F : simple flooding in August; n = 4.

Table 3

Effects of flooding period on growth, mean (\pm standard error)

Condition	Total dry weight (g)	Green shoot / total shoot (%)
Control	90.65 (\pm 4.98) a	3.52 (\pm 1.86) a
6F	84.32 (\pm 7.00) a	5.40 (\pm 2.07) a
8F	99.74 (\pm 11.45) a	9.67 (\pm 4.54) a

Means were not significantly different at the 0.05 level. 6F : simple flooding in June; 8F : simple flooding in August; n = 4.

3.2. Effects of leaf removal and shading

Flooding with the leaf removal and shading was likely to have more impact on the seed production than just with the leaf removal (Table 4). All variables concerning the aerial seeds did not show significant differences among the plots, but the decreasing trend was shown in the total number and weight of the seed. Although, as for the subterranean seeds, the plot with the leaf loss (Group 8D) did not significantly differ with the control; the total number and weight per the individual, the one seed weight, and the germination rate from the plot with the leaf loss and shading (Group 8M) significantly decreased. Furthermore, the one seed weight and the germination rate showed the decreasing pattern.

The allocation of the aerial and subterranean seeds did not show a significant difference among the plots. However, the allocation of the subterranean seeds in the Group 8M plot seemed to be likely to decrease (Fig. 2). Although the total dry weight in the Group 8M plot was just significantly different from in the other plots, the decreasing pattern was observed (Table 5). The ratios of the weight of living green shoot to the total dry weight in the plots of Group 8D and 8M were significantly different from the control plot, with the value increased.

In comparison with the aerial seeds, the subterranean seeds had the lower total number and total weight of the seed, but higher one seed weight and germination rate (Table 4).

Table 4Effects of flooding with damage on production of the aerial and subterranean seeds, mean (\pm standard error)

Condition	Number of seeds per individual		Weight of seeds per individual (g)		One seed weight (mg)		Germination rate (%)	
	Aerial	Sub	Aerial	Sub	Aerial	Sub	Aerial	Sub
Control	1042 (± 138) ^a	558 (± 39) ^a	12.1 (± 1.4) ^a	8.3 (± 0.3) ^a	11.7 (± 0.3) ^a	15.0 (± 0.6) ^a	6.3 (± 2.4) ^a	43.3 (± 5.2) ^a
8D	854 (± 57) ^a	580 (± 93) ^a	9.7 (± 0.8) ^a	7.9 (± 1.6) ^a	11.3 (± 0.4) ^a	13.3 (± 0.7) ^{ab}	3.0 (± 2.9) ^a	28.1 (± 8.6) ^{ab}
8M	678 (± 199) ^a	274 (± 50) ^b	7.2 (± 2.1) ^a	3.2 (± 0.7) ^b	10.7 (± 0.2) ^a	11.6 (± 0.2) ^b	11.1 (± 3.5) ^a	16.2 (± 3.6) ^b

Aerial : aerial seed; Sub : subterranean seed; 8D : flooding with 50% leaf removal; 8M : flooding with 50% leaf removal and shading. Only means of subterranean seeds are significantly different ($p \leq 0.05$) by one-way analysis of variance and Duncan's test are followed by different letters (n = 4).

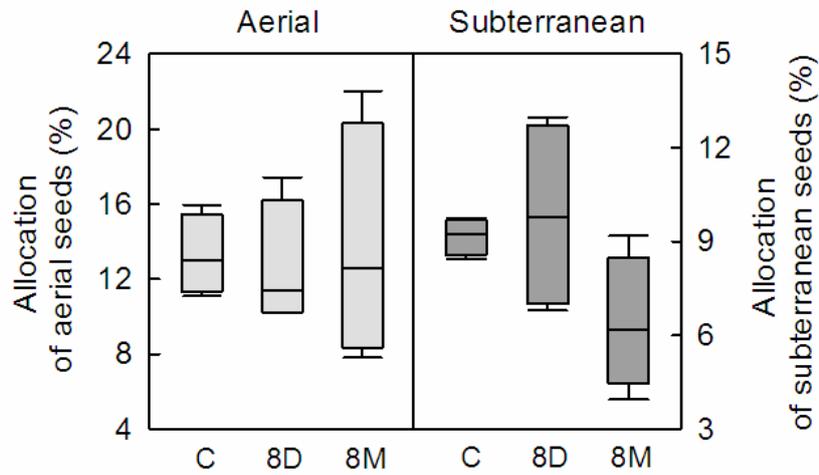


Fig. 2. Effects of flooding with damage on allocation of aerial and subterranean seeds. C : Control; 8D : flooding with 50% leaf removal; 8M : flooding with 50% leaf removal and shading; n = 4.

Table 5

Effects of flooding with damage on growth, mean (\pm standard error)

Condition	Total dry weight (g)	Green shoot / total shoot (%)
Control	90.65 (\pm 4.98) a	3.52 (\pm 1.86) a
8D	78.74 (\pm 6.30) a	24.99 (\pm 5.62) b
8M	50.24 (\pm 3.74) b	37.76 (\pm 5.47) b

8D : flooding with 50% leaf removal; 8M : flooding with 50% leaf removal and shading. Means (n = 4) that are significantly different ($p \leq 0.05$) by one-way analysis of variance and Duncan's test are followed by different letters.

3.3. Formation timing of the aerial and subterranean flowers

When the shoots above the soil surface were preparing to form the aerial flowers, the subterranean flowers were not found in the shoots below the soil surface (Fig. 3). The numbers of the aerial shoots with the floral buds and without floral buds were 48 and 22, respectively, which indicates that the aerial shoots were ready to bloom. In contrast, even though about 348 shoots that had a potential to form the subterranean flowers were identified below the soil surface, no subterranean flowers and seeds were found in the subterranean shoots.

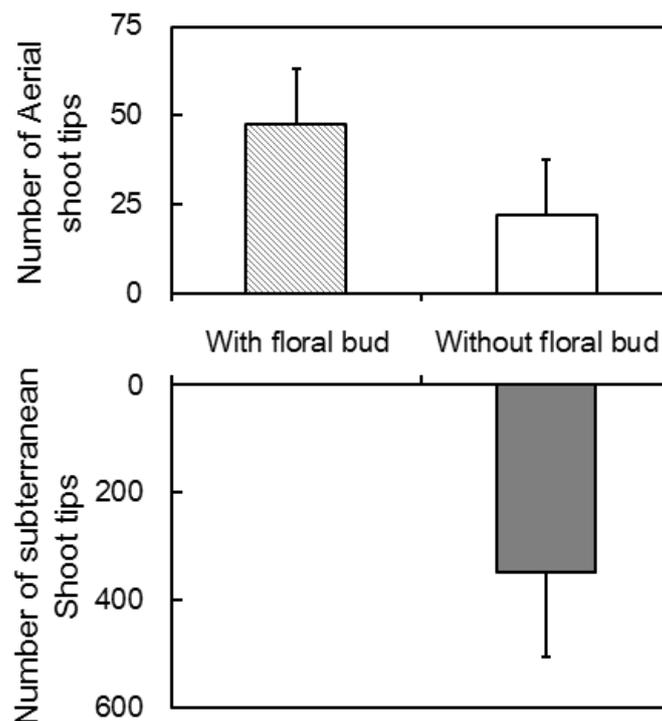


Fig. 3. The difference of the formation timing of the floral buds at the aerial and subterranean shoot tips. Vertical bars show standard error ($n = 2$). While there were many aerial floral buds, there was no subterranean floral bud.

4. Discussion

4.1 Effects of flooding timing on amphicarpy of *P. thunbergii*

In Korea, the *P. thunbergii* living in streamside can be flooded during the vegetative and reproductive growth period. The ramification period corresponds with the rainy season and the period forming the floral buds can face the flooding caused by typhoons. Wetland plants adapt to frequently flooded habitats through sexual and asexual reproductive strategies (Mony et al., 2010). Simple flooding can also be a stress to the wetland plants, and the increased duration of inundation can promote the increased total mass and the reproductive production (Mony et al., 2010). Thus, the subterranean seeds developed from cleistogamous flowers of *P. thunbergii* can respond to change of water regime. However, the present results showed that the simple flooding during each ramification and reproductive growth periods did not impact the formation of aerial and subterranean seeds, as well as the vegetative production of the plant. According to the model of Satake et al. (2001), annual plants living in riverine habitats can adapt to unpredictable environmental disturbances using the bold strategy where they reproduce only when they are fully grown. The experiment for rapid current and submergence after heavy rainfall showed high survival of *P. thunbergii*, suggesting that the plant is likely to evolve a bold strategy (Suzuki et al., 2007). The results of present study also support that although their habitats like streamside make the *P. thunbergii* frequently face flooding, the plant as a bold strategist blooms and produces its seed over a period from September to November. Additionally, the simple and slight increase of water level during the period from June to

August does not hamper the life history and the production of the biomass and the seed.

4.2 Effects of flooding with biomass loss and shading

Simple two week's flooding causing the partial submergence of *P. thunbergii* is less likely to affect the total biomass and reproductive production. However, if the flooding causes the loss of green leaves and the subsequent shading, the biomass productions of *P. thunbergii* are likely to decrease. The seed production can be also affected. The flooding accompanying the leaf loss and the shading can critically inhibit the growth with the significantly lowered photosynthetic activity, leading to the decreased production. The speculation of growth delay caused by the flooding damages can be proved by the comparison of the ratio of living parts. When the onset of senescence was observed in November and the plants were harvested, the green parts relatively maintained more in the plants under the damages (Table 6). These green living parts may have resulted from compensatory growth triggered by the harsh flooding accompanying the growth delay. Based on the difference in the total dry weight and the ratio of living parts, the disturbance impact seems to have been higher in the plot with the additional shading than without the shading. I can assume that they might not be fully grown for the perfect reproductive production when they had to cease their life history because of sub-zero temperatures. When time and growth conditions allow sufficient energy resources to accumulate in the plant body, aerial seeds are formed and their production generally depends on plant biomass (Zeide, 1978; Weiss, 1980;

Cheplick, 1987). Therefore, the decrease of the seed production may be primarily due to the insufficient energy production caused by the disturbance like the loss of photosynthetic parts and the inhibition of photosynthesis.

In response to the relative decrease of light regime in the natural habitat, *P. thunbergii* showed the decrease of the aerial reproductive components, while the subterranean components were less variable (Kawano et al., 1990). However, the production and the one seed weight of the subterranean seeds are likely to decrease under the severe damages. The discrepancy in the response of the amphicarpic seeds to the environmental factors can be due to the difference of the environmental impact on the plant. Although the limitation of resource availability (light and nutrient etc.) could also be a stress that inhibited the growth, the plant seemed to produce the sufficient biomass for their reproductive investment to the aerial flowers because the production of the aerial seeds from chasmogamous flowers was likely to depend on the biomass (Kawano et al., 1990). It was suggested that an increase in plant size results in an increase in chasmogamous flowers and cleistogamous flowers are preferred when resources are abundant (Diaz and Macnair, 1998). Although *P. thunbergii* suffered from a short-term disturbance like a harsh flooding caused by a heavy rainfall in field, the plant rapidly recovered from the biomass loss and showed no decrease of the aerial seed production (Kim et al., 2012). However, if the disturbance like the biomass loss and the subsequent shading is so severe, enough to inhibit the sufficient production for the reproductive growth, the response of the amphicarpic seed production can be different.

4.3 Amphicarpic of P. thunbergii as a reproductive strategy

The decreased production of the subterranean seed in *P. thunbergii* unlike other amphicarpic plants requires that the amphicarpic of *P. thunbergii* in terms of a reproductive strategy should be reconsidered. Most amphicarpic plants show that the production of subterranean fruits tends to precede that of aerial fruits (Cheplick and Quinn, 1982). Amphicarpic plants inhabiting highly disturbed regions where completing growing is uncertain are said to have an optimistic strategy and a pessimistic strategy at the same time (Zeide, 1978). As a pessimistic strategy, they form subterranean flowers early and produce the fruits as early as possible (Cheplick and Quinn, 1982; Cheplick, 1987). However, the subterranean seeds of *P. thunbergii* were reported to occur almost simultaneously with the aerial seeds (Kawano et al., 1990). In this study, the subterranean flowers were not formed when the aerial flowers were observed. The subterranean seeds were not formed earlier than the aerial seeds and rather are likely to occur later. In addition, the decrease of the one seed weight seems to be more significant in the subterranean seeds than in the aerial seeds. Larger seeds need to allow more time for being mature (Primack, 1987). Even though the plant grows again late after the disturbance to recover from the delayed growth, sub-zero temperatures cause the *P. thunbergii* not to live a full life span, leading to greater impact on the production of the subterranean seeds than the aerial seeds. Therefore, the present results suggest that *P. thunbergii* may not apply perfectly the pessimistic strategy to the production of the subterranean seeds, if their produced energy is below a threshold for the perfect reproductive production.

In amphicarpic species that follow the pessimistic strategy for the production of subterranean seeds, it has been known that subterranean seed output is less changeable than aerial seed output and is less likely to be affected by environmental conditions (Schemske, 1978; Cheplick and Quinn, 1987). Because amphicarpic plants mostly inhabit places where the favorable environment is very limited, they steadily produce large subterranean seeds in smaller amount for successful regeneration, and only vigorous individuals usually produce mature light aerial seeds for distribution (Cheplick, 1994). Under difficult conditions, the latter can sometimes not be produced at all (Zeide, 1978). It was suggested that the failure of the resource allocation to aerial seeds could be attributed to the variable and unpredictable length of their growing periods (Cheplick and Quinn, 1982). These plants show the early allocation of the reproductive effort to large subterranean propagules and then to smaller aerial propagules when time and energy permit (Cheplick and Quinn, 1982).

Like other amphicarpic plants studied, *P. thunbergii* certainly have low number of heavy subterranean seeds and a greater number of lightweight aerial seeds, and a high germination rate for subterranean seeds relative to aerial seeds. However, my results showed that the responses of amphicarpic seeds of *P. thunbergii* to environmental impact like damage and subsequently delayed vegetative growth are likely to differ from other amphicarpic plants. Subterranean seed production has evolved independently in phylogenetically diverse taxa and the relevant selection pressure can be different among the species (Cheplick, 1987). Although amphicarpic plants are simultaneously r-strategists with aerial seeds and K-

strategists with subterranean seeds (Zeide, 1978), my results suggest that the importance of subterranean seeds could differ among the plant species. It is known that wetland plant utilizing both r-strategy and K-strategy adjust their allocation of energy depending on environmental impact (McNaughton, 1975). If the amphicarpic plants produce subterranean seeds according to the perfect pessimistic strategy regardless of the biomass and environmental impacts, I can say that the subterranean seeds could function as obligate insurance for reproduction because subterranean seeds can settle more successfully than aerial seeds in locally favorable habitats among harsh environment like deserts (Cheplick, 1987). In contrast, the subterranean seeds in *P. thunbergii* can be referred to as facultative insurance in terms of reproductive investment because they can be reduced when the plants face environmental conditions where time and energy is insufficient because of high disturbance such as damage in the study (Mony et al., 2010).

References

- Cheplick, G.P., 1983. Differences between plants arising from aerial and subterranean seeds in the amphicarpic annual *Cardamine chenopodifolia* (Cruciferae). B. Torrey Bot. Club 110, 442-448.
- Cheplick, G.P., 1987. The ecology of amphicarpic plants. Trends Ecol. Evol. 2, 97-101.
- Cheplick, G.P., 1994. Life history evolution in amphicarpic plants. Plant Spec. Biol. 9, 119-131.
- Cheplick, G.P., Quinn, J.A., 1982. *Amphicarpum purshii* and the “pessimistic strategy” in amphicarpic annuals with subterranean

- fruit. *Oecologia* 52, 327-332.
- Cheplick, G.P., Quinn, J.A., 1983. The shift in aerial/subterranean fruit ratio in *Amphicarpum purshii* : causes and significance. *Oecologia* 57, 374-379.
- Cheplick, G.P., Quinn, J.A., 1987. The role of seed depth, litter, and fire in the seedling establishment of amphicarpic peanutgrass (*Amphicarpum purshii*). *Oecologia* 73, 459-464.
- Cho, H.J., Cho, K.H., 2005. Responses of riparian vegetation to flooding disturbance in a sand stream. *KSCE J. Civ. Eng.* 9, 49-53.
- Diaz, A., Macnair, M., 1998. The effect of plant size on the expression of cleistogamy in *Mimulus nasutus*. *Funct. Ecol.* 12, 92-98.
- Trapp, E.J., Hendrix, S.D., 1988. Consequences of a mixed reproductive system in the hog peanut, *Amphicarpaea bracteata*, (Fabaceae). *Oecologia* 75, 285-290.
- Kaul, V., Koul, A., Sharma, M., 2000. The underground flower. *Curr. Sci.* 78, 39-44.
- Kawano, S., 2008. 11: *Polygonum thunbergii* Sieb. et Zucc.(Polygonaceae). *Plant Spec. Biol.* 23, 222-227.
- Kawano, S., Hara, T., Hiratsuka, A., Matsuo, K., Hirota, I., 1990. Reproductive biology of an amphicarpic annual, *Polygonum thunbergii* (Polygonaceae): Spatio-temporal changes in growth, structure and reproductive components of a population over an environmental gradient. *Plant Spec. Biol.* 5, 97-120.
- Kim, D.H., Choi, H., Kim, J.G., 2012. Occupational strategy of *Persicaria thunbergii* in riparian area: rapid recovery after harsh flooding

- disturbance. *J. Plant Biol.* 55, 226-232.
- Kim, D.H., Kim, H.-T., Kim, J.G., 2013. Effects of water level and soil type on the survival and growth of *Persicaria thunbergii* during early growth stages. *Ecol. Eng.* 61, 90-93.
- Koller, D., Roth, N., 1964. Studies on the ecological and physiological significance of amphicarp in *Gymnarrhena micrantha* (Compositae). *Am. J. Bot.* 51, 26-35.
- Masuda, M., Yahara, T., 1994. Reproductive ecology of a cleistogamous annual, *Impatiens noli-tangere* L., occurring under different environmental conditions. *Ecol. Res.* 9, 67-75.
- McNaughton, S.J. 1975. r- and K-Selection in *Typha*. *Am. Nat.* 109, 251-261.
- Mony, C., Mercier, E., Bonis, A., Bouzillé, J.B., 2010. Reproductive strategies may explain plant tolerance to inundation: a mesocosm experiment using six marsh species. *Aquat. Bot.* 92, 99-104.
- Naiman, R.J., Decamps, H., 1997. The ecology of interfaces: Riparian zones. *Annu. Rev. Ecol. Syst.* 28, 621-658.
- Primack, R.B., 1987. Relationships among flowers, fruits, and seeds. *Annu. Rev. Ecol. Syst.* 18, 409-430.
- Sadeh, A., Guterman, H., Gersani, M., Ovadia, O., 2009. Plastic bet-hedging in an amphicarpic annual: An integrated strategy under variable conditions. *Evol. Ecol.* 23, 373-388.
- Satake, A., Sasaki, A., Iwasa, Y., 2001. Variable timing of reproduction in unpredictable environments: Adaption of flood plain plants. *Theor. Popul. Biol.* 60, 1-15.
- Schemske, D.W., 1978. Evolution of reproductive characteristics in

- Impatiens* (Balsaminaceae): The significance of cleistogamy and chasmogamy. *Ecology*, 596-613.
- Schnee, B.K., Waller, D.M., 1986. Reproductive behavior of *Amphicarpaea bracteata* (Leguminosae), an Amphicarpic Annual. *Am. J. Bot.* 73, 376-386.
- Suzuki, M., Kaya, Y., Ishida, T.A., Hattori, K., Miki, K., Nakamura, T., Kimura, M.T., 2007. Flowering phenology and survival of two annual plants *Impatiens noli-tangere* and *Persicaria thunbergii* co-occurring in streamside environments. *Ecol. Res.* 22, 496-501.
- Weiss, P.W., 1980. Germination, reproduction and interference in the amphicarpic annual *Emex spinosa* (L.) Campd. *Oecologia* 45, 244-251.
- Zeide, B., 1978. Reproductive behavior of plants in time. *Am. Nat.* 112, 636-639.

Chapter 2.

Advantages of the subterranean seeds production of amphicarpic *Persicaria thunbergii* in early life history

Abstract

To understand the advantages of the additional subterranean seeds production of amphicarpic *P. thunbergii* in early life history, I compared aerial and subterranean seeds and young plants in seed size, weight, and young plant stress response in shaded and waterlogged condition using a mesocosm experiment. The major axis and minor axis of the subterranean seeds were 22% and 17% longer than that of the aerial seeds, respectively. The subterranean seeds were 39% heavier than that of the aerial seeds. In the control group, the average stem length of the young plant from subterranean seed (SS) was 41% longer than that of the young plant from aerial seed (SA). Also, SS preponderated in leaf number, root length and overall dry weight over SA. In the shaded group, the SS had 34% longer stem length and 99% wider leaf area than SA. Moreover, SS could grow stem length more rapidly to escape the water level than SA. The cause of producing superior subterranean seeds can be one of the strategies to survive in a negative environment in early life history. By producing not only the aerial seeds for dispersion but also subterranean seeds for survival, the *P. thunbergii*, which inhabit extreme riparian areas, seems to leave behind a community at its mother-site.

Keywords: Amphicarpy, Seed size, Young plant, Shaded stress, Waterlogged stress, Stress Response

1. Introduction

The diverse wetland plants have similar optimal range for distribution, but various plant communities can be developed and maintained in a similar environment (Lee et al., 2007). This means that early life history components, such as germination, seedling recruitment, and early establishment are momentous for wetland plant distribution (Weiher and Keddy, 1995; Nicol and Ganf, 2000), especially for annual plants (Noe and Zedler, 2001). In the young plant seasons, seedlings having low confrontation ability could be more influenced by microhabitat (Franco and Nobel, 1989; Ohlson and Zackrisson, 1992). In particular, the water level or moisture gradient is the most critical factor in wetlands because recurrent flooding is detrimental to seeds or seedlings (Kim et al., 2013). Light is also a highly heterogeneous environmental factor, influencing plant growth, survival, and competition within the community (Canham et al., 1990). Thus, shade tolerance could also be a key factor in population maintenance (Valladares and Niinemets, 2008).

Persicaria thunbergii (Siebold & Zucc) H. Gross ex Nakai is a Polygonaceae annual herb and one of the most dominant annual species found in the Korean wetlands. They commonly inhabit riparian or water canals, where frequent water level fluctuations and hydrological disturbances create an unstable environment for plants (Cho, 1995; Song and Song, 1996; Kang and Kwak, 1998; Ahn and Song, 2003; Lee et al., 2004). Thus, plants that inhabit riparian areas have developed special strategies to overcome such unfavorable conditions. In regards to the *P. thunbergii*, one of those strategies could be amphicarpy.

Amphicarpy is a unique trait of some plants, where subterranean seeds form on the same individual as aerial seeds (Kaul et al., 2000). Possessing these two kinds of seeds provide the plants reproductive plasticity in order to adapt to frequent environmental changes (Koller and Roth, 1964; Weiss, 1980; Cheplick and Quinn, 1983; Masuda and Yahara, 1994; Sadeh et al., 2009). In many amphicarpic plants, subterranean seeds are heavier and larger than aerial seeds, and are also more favorable in early life-history (Cheplick, 1987). In *Amphicarpum purshii*, which is an amphicarpic plant, survivability of seedlings from subterranean seeds were greater in both dry and wet sites as well as at low and high densities than that of seedlings from aerial seeds (Cheplick and Quinn, 1982). Like this, *P. thunbergii* might be utilizing this survival strategy – producing a subterranean seed in addition to an aerial seed – to overcome environmental stress in early life history.

However, studies regarding the amphicarpic traits of the *P. thunbergii* are difficult to find, although there have been many studies on the *P. thunbergii* as a water purification plant (Woo et al., 1996; Kang and Kim, 1997; Kang et al., 2000), or as one of the wetland vegetation components (Cho, 1995; Lee et al., 2007; Yoon et al., 2011). While other studies have focused on its ecological characteristics (Araki and Washitani, 2000; Konuma and Terauchi, 2001; Kawano, 2008; Kim et al., 2012), only one study focused on the amphicarpic trait of the *P. thunbergii* (Kawano et al., 1990). Even then, the study did not investigate its early stages, which is an important timeframe for maintaining the community of annual species.

The purpose of this study was to understand the advantages of the

additional production of subterranean seeds in early life history within disturbed conditions. I tried to find the advantages of subterranean seeds production by comparing the physical characteristics of aerial seeds and subterranean seeds of the *P. thunbergii*, as well as by investigating the stress response of the seedlings from the two seed types under stressful conditions of shading and waterlogging.

2. Materials and methods

2.1. Comparing physical characteristics of two types seeds

In order to compare the physical characteristics of the two seed types, the size and weight of the seeds were measured. The *P. thunbergii* seeds were collected in October 2011 in Boonwon-ri, Namjong-myon, Gwangju, Gyeonggi-do, Korea. The Boonwon-ri is an abandoned rice paddy field possesses a stable, non-flooding environment. Among the collected seeds, 34 aerial and 31 subterranean seeds were randomly sampled and measured. The length of the major and minor axes of seed was measured with an Olympus SZX stereomicroscope (Olympus Model SZX-ST, Tokyo, Japan) (8× magnification). Also, the dry weight of the seeds after drying at 60°C, over 48h, was weighed on an Ohaus electronic scale (Ohaus Model EPG 214C, Pine Brook, New Jersey, USA).

Statistical analyses were performed using t-test without transformation, with SPSS ver. 20.0 (SPSS, Inc., Chicago, IL, USA).

2.2. Comparing stress response

The growth in shaded or waterlogged stress conditions was compared between seedlings from aerial seed (SA) and seedlings from subterranean seed (SS) between May and July 2012 by a mesocosm experiment at Seoul National University in South Korea.

The naturally germinated 33 SA and 31 SS were planted in plastic pots ($\Phi=10$ cm, H=9 cm), filled 6.5 cm deep with sand. For the waterlogged condition, the water level was twice as high as the height of the tallest plant of each group. In the shaded condition, only about 25% of light was penetrated through the two layers of black polyester nets that enclosed the set of pots. Conversely, the control group maintained 0 cm of water without shade during the whole experiment period. There were 10~11 replicas (pots) of each condition. When the experiment began, the average SA stem length was 54.4 mm, and the average SS stem length was 58.5 mm. In May, the nutrient level of the sand that the seedlings were planted in was $\text{NH}_4\text{-N}$ 6.9 (± 3.3) mg/kg, $\text{NO}_3\text{-N}$ 1.1 (± 0.4) mg/kg, $\text{PO}_4\text{-P}$ 0.3 (± 0.1) mg/kg.

The stem length was measured every four days, and the experiment concluded when all of the waterlogged SA or SS were dead (July). The individuals without green leaf were classified as dead plants. At the end of the experiment, every plant in both the shaded and waterlogged conditions was harvested; and five individuals in the control group (1st, 3rd, 5th, 7th, and 9th individual in the order of stem length) were harvested. I measured the number of leaves, root length, as well as the dry weight of the leaf, stem, and root of the plants; and the leaf area was detected with a portable area meter (Li-3000, Li-COR, USA) in both the control and shaded

group. In contrast, the waterlogged plants were measured only by the root length and root dry weight because they did not have measurable leaves and stems by the end of the experiment. The dry weights of the leaf, stem, and root were measured after being dried at 60 °C for over 48 hours.

Statistical analyses were performed using t-test without transformation, with SPSS ver. 20.0 (SPSS, Inc., Chicago, IL, USA).

3. Results

The length of the major and minor axes of the subterranean seeds were significantly longer than that of aerial seeds; also, the weight of the subterranean seeds were significantly heavier than that of the aerial seeds (Fig 1). The average major axis of the subterranean seeds was 22% longer than that of the aerial seeds, and the average minor axis of the subterranean seeds was 17% longer than that of the aerial seeds. The average subterranean seeds weight was 39% heavier than that of the aerial seeds.

In all conditions, the SS showed a longer stem length (Fig 2). In the control group, the stem length difference between the SA and SS appeared after 20 days from the start of the experiment (June 20, $p < 0.05$). Thereafter, the difference became larger and more apparent ($p < 0.01$). In the end, the average stem length of SS was 41% longer than that of SA. In the shaded group, the stem length growth of both the SA and SS was faster than the control group. Also, the SS showed longer stem length ($0.063 < p < 0.092$). Due to the individual differences in stress response, it is possible that the significance is less apparent in the shaded group than in the control group. Finally, the average stem length of SS was 34% longer than that of

SA in the shaded group. For the waterlogged group, early stem length growth of both the SA and SS was fastest in all groups; and the stem length difference between the SA and SS was earliest in all groups (after 12 days from the start of the experiment). Moreover, that difference increased during the experimental time period because the SA stopped growing after the 8th day, while the SS continued to grow. The plants that overcome the water level appeared after the 8-day mark. However, the stems could not support the plant vertically, and the majority of the leaves were submerged. The plant death in the waterlogged group began after 24 days, and nearly all of the plants were dead after 28 days (10 SA individuals, and 4 SS individuals died). Therefore, due to the difference in plant survival between the groups, a statistical comparison could not be made. By the 32-day mark, all SA had died and only one SS had survived. However, even the surviving SS was in a weakened state.

All of the measured dry weight (leaf, stem, and root) of the SS was heavier than the SA in the control group (Fig 3). In the control group, the leaf and root dry weight of SS were significantly heavier than these of SA. Although the stem dry weight of the SS and SA did not show a significant difference, the stem dry weight of SS seemed to be heavier than that of SA. In the shaded group, the total dry weight of both the SA and SS decreased. Also, there was not a significant difference in the dry weight of each component between SA and SS, due to the larger decrease of dry weight in SS, which had shown a significantly heavier dry weight than SA in the control group.

In the control group, the leaf number of SS was significantly more

than that of SA. Although the leaf area did not show a significant difference between seed types, the average leaf area of SS seemed to be wider than that of SA (Fig 4). The length of the SS root was significantly longer. In the shaded group, although SS showed greater decrease in dryweight, SS possessed a significantly larger number of leaves as well as a wider leaf area than SA; and the SS weight per area of the leaf, which indicated thickness or density, was significantly lighter than the SA. This means that the SS developed thinner and wider leaves than SA in the shaded group. The root length, which showed a disparity in the control group, did not show a significant difference.

In the waterlogged group, the root dry weight did not show a meaningful difference between SA and SS-SA $10(\pm 1)$ mg, SS $11(\pm 2)$ mg- and the root length also did not show a noteworthy difference between SA and SS-SA $116(\pm 12)$ mm, SS $110(\pm 12)$ mm.

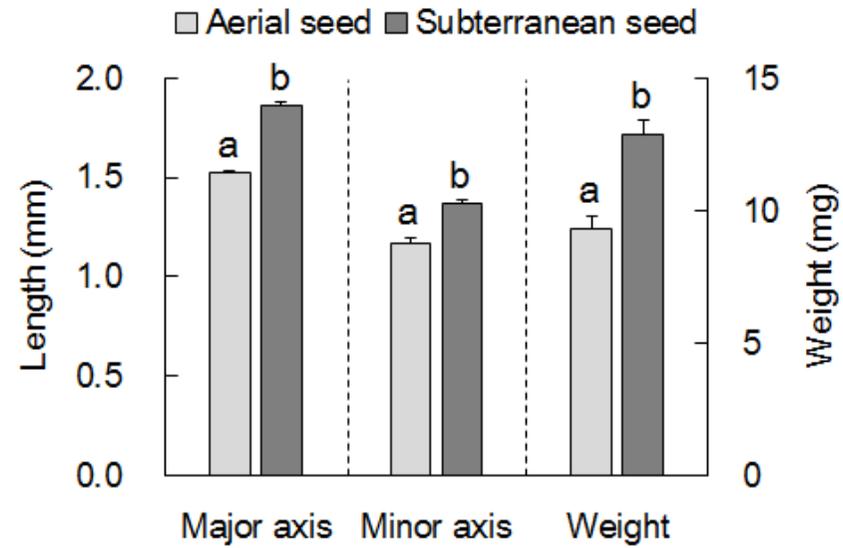


Fig 1. Size and weight of aerial seed and subterranean seed. Means that are significantly different ($p \leq 0.05$) by one-way analysis of variance and Duncan's test are followed by different letters. Vertical bars show standard error (aerial seed: $n = 34$, subterranean seed: $n = 31$).

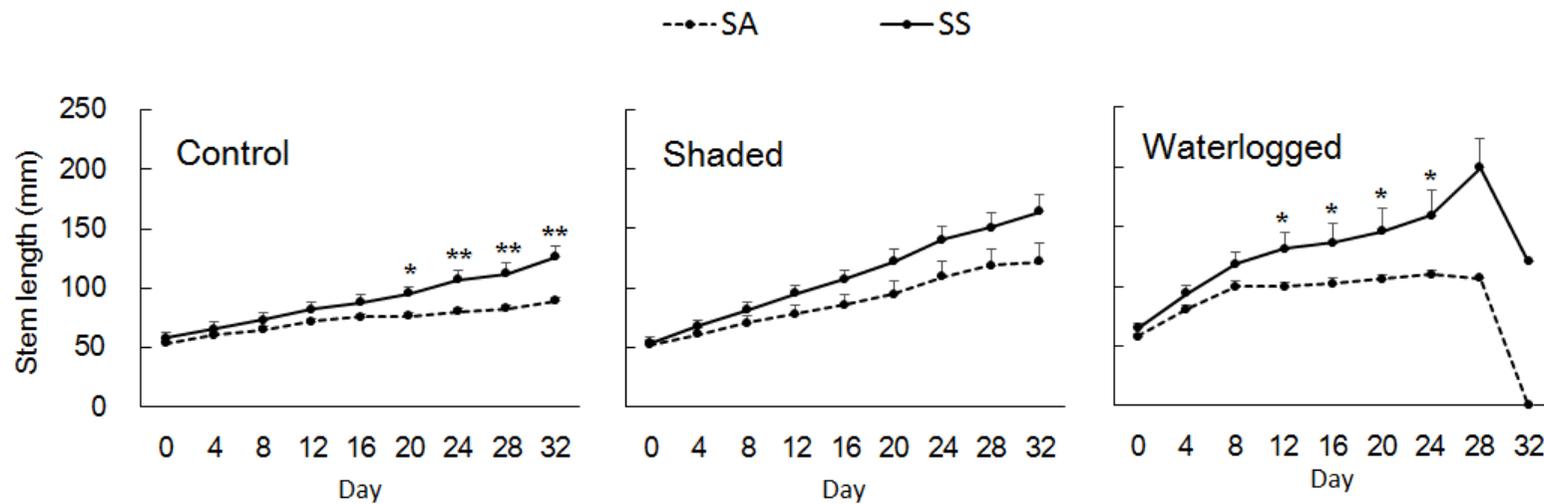


Fig 2. Change of stem length of SA and SS in each group. SA : seedlings from aerial seed; SS : seedlings from subterranean seed. Means that are significantly different by one-way analysis of variance and Duncan's test are followed by asterisk (* : $0.01 < p \leq 0.05$, ** : $p \leq 0.01$). Vertical bars show standard error (n = 10~11).

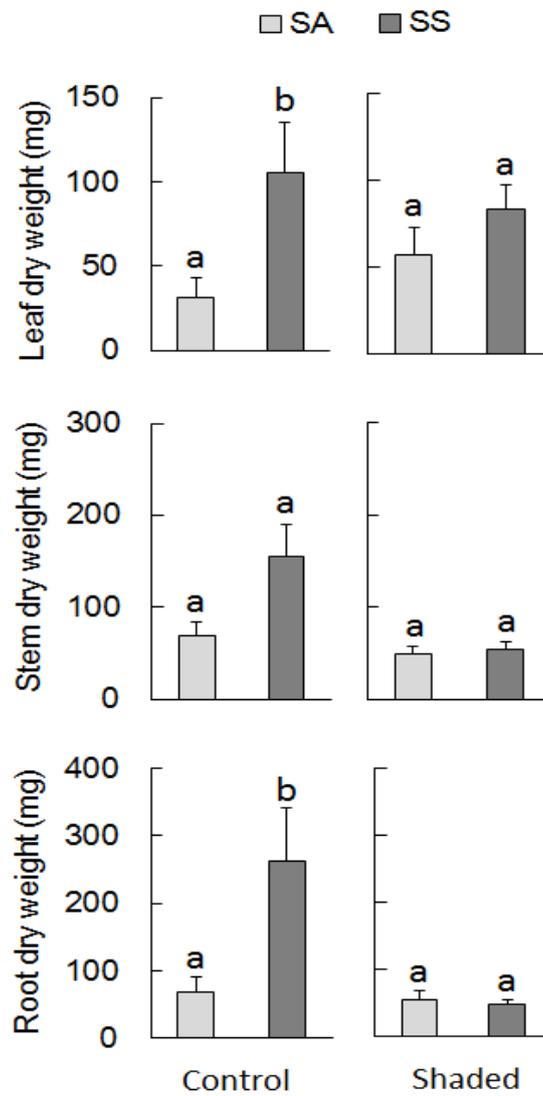


Fig 3. Dry weight (leaf, stem, and root) of SA and SS. SA : seedlings from aerial seed; SS : seedlings from subterranean seed. Means that are significantly different ($p \leq 0.05$) by one-way analysis of variance and Duncan's test are followed by different letters. Vertical bars show standard error (control group : $n = 5$, shaded group : $n = 10 \sim 11$).

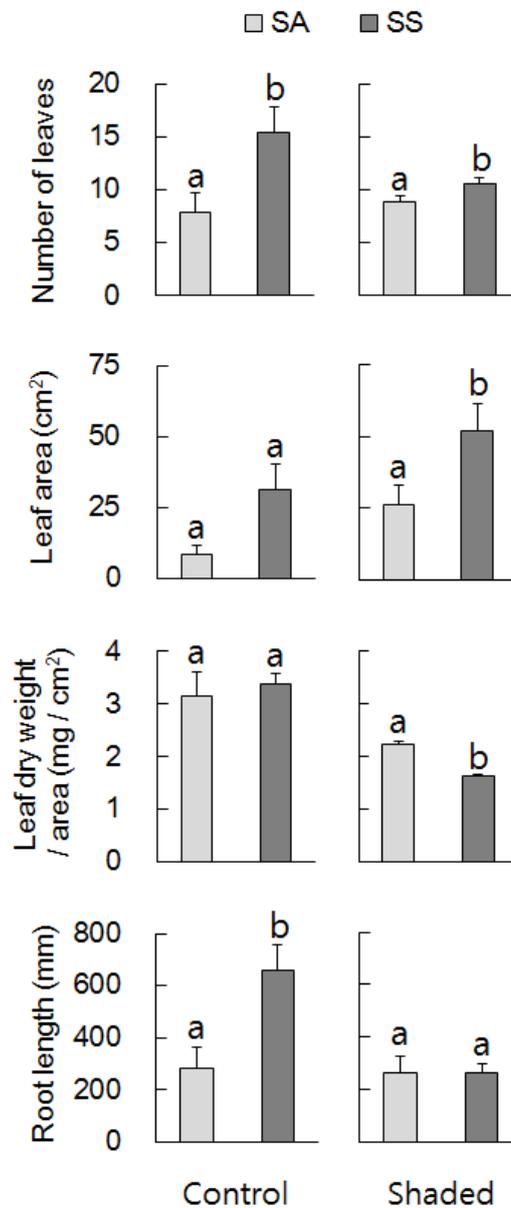


Fig 4. Leaf number, total leaf area, leaf weight per area, root length of SA and SS. SA : seedlings from aerial seed; SS : seedlings from subterranean seed. Means that are significantly different ($p \leq 0.05$) by one-way analysis of variance and Duncan's test are followed by different letters. Vertical bars show standard error (control group : $n = 5$, shaded group : $n = 10 \sim 11$).

4. Discussion

It is well known that seed size is a crucial factor for germination and early stages of growth (Stanton, 1984; Wulff, 1986; Primack, 1987; Walters and Reich, 2000). When comparing the two types of *P. thunbergii* seeds, the size and weight of the subterranean seeds were significantly longer and heavier than those of aerial seeds. Seed size is directly proportional to its reserved substances; therefore, the larger subterranean seeds could use its reserved substances to have larger leaf area, root weight, root length, and overall seedling dry weight in its early stages (Wulff, 1986; Primack, 1987). When considering the overall characteristics of the 26 amphicarpic plant types, subterranean seeds are generally large and heavy, and seedlings from subterranean seeds have high survivorship, competitive ability, stress tolerance, and fitness (Cheplick, 1987). In this regard, the *P. thunbergii* also showed a similar tendency in this study. Particularly regarding importance of early life stage of annual plants (Bartolome, 1979), the subterranean seeds may have more survival potential than the aerial seeds do.

In a favorable condition—no shading, no waterlogging—during early seedling season, the SS from larger seeds preponderated in leaf number, root length, and overall seedling dry weight over the SA from smaller seeds as in preceding studies. Additionally, the average stem length of SS was longer than that of SA, and over the course of the experimental period, the gap became increasingly apparent. The difference of stem length and dry weight means that SS has a higher height and sturdier plant body in the seedling season than SA when they germinate simultaneously.

Consequently, in stressless environments, SS may have more intraspecific and interspecific competitiveness in the early growth stage than SA does.

The microhabitat can affect the germination or growth. Especially, seedlings, which have low confrontation ability, can be more influenced by microhabitat (Franco and Nobel, 1989; Ohlson and Zackrisson, 1992; Gul et al., 2007). In this study, when comparing the SA and SS, the shaded or waterlogged stress responses of SS were much clearer. SS could efficiently endure shade or waterlogged conditions and grow stem length more rapidly than SA. During the seedling season, the shading condition could be caused by intraspecific and interspecific competition as well as habitat characteristics. Shading can cause dry weight decrease (Groninger et al., 1996) because of the decrease of energy for photosynthesis (Groninger et al., 1996), and relative root growth decline (Fitter and Ashmore, 1974). Shade tolerance is proportional to survival for population maintenance (Walters and Reich, 2000) and shading can stimulate stem elongation for shade evasion (Méthy et al., 1990; Aphalo and Ballaré, 1995; Collins and Wein, 2000). Water depth and water fluctuation are clearly of greater importance than other factors for wetland plants, especially during germination and establishment phases (Weiher and Keddy, 1995). Also, it was clear that the water level was the most critical factor for survival to *P. thunbergii* seedlings (Kim et al., 2013). Because the plants could not overcome water levels that were two times the height of the tallest plant (Kim et al., 2013), almost every individual used during the experiment died. Because the longer stem length provides a strong chance to escape from the shaded or waterlogged conditions, SS is more competitive than SA in such pessimistic

environments. Also, shading can cause leaf area expansion (Fitter and Ashmore, 1974; Méthy et al., 1990), which caused plants to increase their potential for light acquisition, were shown clearer in the SS than in the SA of the shaded group. This means that SS may be more competitive than SA in a shaded condition because the leaf area expansion is a way to endure the shaded condition.

Therefore, SS was more favorable to survival in all three conditions than SA. Furthermore, subterranean seeds have a better chance for germination and survival because their micro-habitat creates adequate conditions for life cycle completion, and they are already in the soil that provides them with suitable conditions for germination and survival. Consequentially, seedling from larger seeds had more of an advantage than seedling from smaller seeds during the early stages of growth. Seedling from larger seeds also had more chances to succeed in growth, and seedlings from larger seeds may be favored over those from smaller seeds if both types are grown in competition (Wulff, 1986; Primack, 1987).

5. Conclusion

The cause of producing subterranean seeds, which is definitely superior, can be one of the strategies to survive in a pessimistic environment (Cheplick and Quinn, 1982). By producing both the aerial seeds for dispersion along with the high energy cost and un-transferable, but highly survivable subterranean seeds, the *P. thunbergii*, which inhabit extreme riparian areas, seems to leave behind a community at its mother-site.

References

- Ahn Y.H., Song J.S., 2003. Occurrence of streamside flora in relation to environmental condition at Ansongchon creek. Korean J. Environ. Sci. 12, 573-582 (in Korean).
- Aphalo, P.J., Ballaré, C.L., 1995. On the importance of information-acquiring systems in plant-plant interactions. *Funct. Ecol.* 9, 5-14.
- Araki, S., Washitani, I., 2000. Seed dormancy/germination traits of seven *Persicaria* species and their implication in soil seed-bank strategy. *Ecol. Res.* 15, 33-46.
- Bartolome, J.W., 1979. Germination and Seedling Establishment in California Annual Grassland. *J. Ecol.* 67, 273-281.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20, 620-631.
- Cheplick, G.P., 1987. The ecology of amphicarpic plants. *Trends Ecol. Evol.* 2, 97-101.
- Cheplick, G.P., Quinn, J.A., 1982. *Amphicarpum purshii* and the “pessimistic strategy” in amphicarpic annuals with subterranean fruit. *Oecologia* 52, 327-332.
- Cheplick, G.P., Quinn, J.A., 1983. The shift in aerial/subterranean fruit ratio in *Amphicarpum purshii* : causes and significance. *Oecologia* 57, 374-379.
- Cho, D.S., 1995. A study on the distribution of streamside vegetation in Kyonganchon. Korean J. Ecol. 18, 55-62 (in Korean).

- Collins, B., Wein, G., 2000. Stem elongation response to neighbour shade in sprawling and upright *Polygonum* species. *Ann. Bot.* 86, 739-744.
- Fitter, A., Ashmore, C., 1974. Response of two *Veronica* species to a simulated woodland light climate. *New Phytol.* 73, 997-1001.
- Franco, A.C., Nobel, P.S., 1989. Effect of nurse plants on the microhabitat and growth of Cacti. *J. Ecol.* 77, 870-886.
- Groninger, J.W., Seiler, J.R., Peterson, J.A., Kreh, R.E., 1996. Growth and photosynthetic responses of four Virginia Piedmont tree species to shade. *Tree Physiol.* 16, 773-778.
- Gul, S., Ahmad, S., Achakzai, A.K.K., Islam, M., 2007. Impact of microhabitat on survival of *Seriphidium quettense* seedlings. *Pak. J. Bot.* 39, 1717-1724.
- Kang K.H., Kim I.S., 1997. The relationship of Cu content and phytochelatins in *Persicaria thunbergii*. *Korean J. Environ. Biol.* 15, 157-164 (in Korean).
- Kang K. H., Kim I. S., Koo J. S., 2000. The study on absorption of Cd²⁺ and Pb²⁺ by *Persicaria thunbergii* and *Rumex crispus*, and their phytochelatins. *Korean J. Environ. Biol.* 18, 269-277 (in Korean).
- Kang S. J., Kwak A. K., 1998. Changes of riparian vegetation in relation to disturbance of Musim-Chon stream, Cheongju. *Korean J. Ecol.* 21, 435-448 (in Korean).
- Kaul, V., Koul, A., Sharma, M., 2000. The underground flower. *Curr. Sci.* 78, 39-44.
- Kawano, S., 2008. 11: *Polygonum thunbergii* Sieb. et Zucc. (Polygonaceae). *Plant Spec. Biol.* 23, 222-227.

- Kawano, S., Hara, T., Hiratsuka, A., Matsuo, K., Hirota, I., 1990. Reproductive biology of an amphicarpic annual, *Polygonum thunbergii* (Polygonaceae): Spatio-temporal changes in growth, structure and reproductive components of a population over an environmental gradient. *Plant Spec. Biol.* 5, 97-120.
- Kim, D.H., Choi, H., Kim, J.G., 2012. Occupational strategy of *Persicaria thunbergii* in riparian area: Rapid recovery after harsh flooding disturbance. *J. Plant Biol.* 55, 226-232.
- Kim, D.H., Kim, H.T., Kim, J.G., 2013. Effects of water level and soil type on the survival and growth of *Persicaria thunbergii* during early growth stages. *Ecol. Eng.* 61, Part A, 90-93.
- Koller, D., Roth, N., 1964. Studies on the ecological and physiological significance of amphicarpy in *Gymnarrhena micrantha* (Compositae). *Am. J. Bot.* 51, 26-35.
- Konuma, A., Terauchi, R., 2001. Population genetic structure of the self-compatible annual herb; *Polygonum thunbergii* (Polygonaceae) detected by multilocus DNA fingerprinting. *The Am. Midl. Nat.* 146, 122-127.
- Lee B.A., Kwon G.J., Kim J.G., 2007. The optimal environmental ranges for wetland plants:II. *Scirpus tabernaemontani* and *Typha latifolia*. *J. Ecol. Field Biol.* 30, 151-159
- Lee K.B., Kim C.H., Lee D.B., Kim J.G., Park C.W., 2004. The flora and vegetation of the Dongjin river. *Korean J. Environ. Agri.* 23, 34-40 (in Korean).
- Méthy, M., Alpert, P., Roy, J., 1990. Effects of light quality and quantity on

- growth of the clonal plant *Eichhornia crassipes*. *Oecologia* 84, 265-271.
- Masuda, M., Yahara, T., 1994. Reproductive ecology of a cleistogamous annual, *Impatiens noli-tangere* L., occurring under different environmental conditions. *Ecol. Res.* 9, 67-75.
- Nicol, J.M., Ganf, G.G., 2000. Water regimes, seedling recruitment and establishment in three wetland plant species. *Mar. Freshw. Res.* 51, 305-309.
- Noe, G.B., Zedler, J.B., 2001. Spatio-temporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment. *J. Veg. Sci.* 12, 61-74.
- Ohlson, M., Zackrisson, O., 1992. Tree establishment and microhabitat relationships in north Swedish peatlands. *Can. J. For. Res.* 22, 1869-1877.
- Primack, R.B., 1987. Relationships among flowers, fruits, and seeds. *Annu. Rev. Ecol. Syst.* 18, 409-430.
- Sadeh, A., Guterman, H., Gersani, M., Ovadia, O., 2009. Plastic bet-hedging in an amphicarpic annual: An integrated strategy under variable conditions. *Evol. Ecol.* 23, 373-388.
- Song J.S., Song S.D., 1996. A phytosociological study on the riverside vegetation around Hanchon, and upper stream of Nak-tong river. *Korean J. Ecol.* 19, 431-451 (in Korean).
- Stanton, M.L., 1984. Seed variation in *Wild Radish*: Effect of seed size on components of seedling and adult fitness. *Ecology* 65, 1105-1112.
- Valladares, F., Niinemets, Ü., 2008. Shade tolerance, a key plant feature of

- complex nature and consequences. *Annu. Rev. Ecol. Evol. Syst.* 39, 237.
- Walters, M.B., Reich, P.B., 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology* 81, 1887-1901.
- Weiher, E., Keddy, P.A., 1995. The assembly of experimental wetland plant communities. *Oikos* 73, 323-335.
- Weiss, P.W., 1980. Germination, reproduction and interference in the amphicarpic annual *Emex spinosa* (L.) Campd. *Oecologia* 45, 244-251.
- Woo Y.K., Park E.J., Lee K.S., Lee D., 1996. Effects of *Persicaria thunbergii* on nitrogen retention and loss in wetland microcosm. *Korean J. Ecol.* 19, 179-189 (in Korean).
- Wulff, R.D., 1986. Seed size variation in *Desmodium paniculatum*: II. Effects on seedling growth and physiological performance. *J. Ecol.* 74, 99-114.
- Yoon J.H., Kim H.T., Nam J.M., Kim J.G., 2011. Optimal environmental range for *Juncus effusus*, an important plant species in an endangered insect species (*Nannopya pygmaea*) habitat in Korea. *J. Ecol. Field Biol.* 34, 223-235.

국 문 초 록

본 연구에서는 스트레스 환경에서의 생식 전략으로써 고마리 (*Persicaria thunbergii*)의 이종과 형성을 이해하기 위해 두 가지 메조코즘 실험을 수행하였다. 첫째, 고마리가 가장 흔히 접하는 교란인 범람시의 고마리의 이종과 형성에 관한 실험을 수행하였다. 단순 수위 변동의 시기에 따른 효과를 알아보려고 6월과 8월에 각각 30cm의 수위를 2주간 처리하였다. 범람에 의한 훼손을 가정한 실험구는 8월에 50%의 잎을 제거하고 1주간 990.2 Pa의 압력을 가하고 차광 처리 하였다. 실험 결과 초기 영양생장기(6월)와 후기 영양생장기(8월) 모두 단순한 수위 변동은 생장과 종자 생장에 영향을 미치지 못했다. 그러나 훼손을 동반한 범람은 종자의 생산과 건중량을 감소시켰다. 강력한 교란 상황에서 특히 지하부 종자의 생산과 종자 하나당 무게가 유의하게 감소하였다. 또한 지하부 종자는 지상부 종자보다 늦게 형성되었다. 그러므로 고마리는 다른 이종과 형성종과는 달리 지상부 종자에 앞서 튼실한 지하부 종자를 형성하여 교란을 대비하는 ‘pessimistic strategy’를 완전히 따르지 않는 것으로 보이고, 시간과 에너지가 불충분할 경우 지하부 종자를 형성을 줄일 수 있다. 결과적으로, 고마리의 이종과 형성은 다른 이종과 형성종과 다른 생태적 중요성을 가질 수 있다.

둘째, 초기 생활사에서의 두 종자 유형을 비교하기 위해 지상부와 지하부의 종자(무게, 크기), 유묘의 스트레스 반응을 비교하였다. 지하부 종자가 지상부 종자에 비해 장축은 22%, 단축은 17% 길었으며, 무게는 39% 더 무거웠다. 대조군에서 SA (지상부 종자로부터 발생한 어린 개체)보다 SS (지하부 종자로부터 발생한 어린 개체)의 평균 줄기 길이가 41% 길었다. 또한 SA에 비해 SS는 잎 수가 많고, 뿌리 길이가

길고, 전반적인 견중량이 컸다. 차광 실험군에서, SA에 비해 SS는 줄기 길이가 34% 더 길고, 잎면적이 99% 더 넓었다. 또한 SA에 비해 SS가 수위를 극복하기 위해 더 빠르게 줄기를 신장시켰다. 더 우월한 지하부 종자를 생산하는 것은 부정적인 환경에서 살아남기 위한 하나의 전략일 수 있다. 분산을 위한 지상부 종자를 생산할 뿐만 아니라 생존을 위한 지하부 종자를 생산함으로써 교란이 심한 수변에 서식하는 고마리가 기존 서식지를 유지할 수 있는 것으로 보인다.

Keywords : 이종과 형성, 고마리, 범람, 종자의 크기, 유묘의 스트레스 반응

Student Number : 2012-21444