

Effects of nutrient availability on the amphicarpic traits of *Pericaria thunbergii*



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ABSTRACT

Environmental factors affecting the expression of amphicarpic traits in *Pericaria thunbergii* are not well studied. We thus performed to investigate the effects of nutrients on the amphicarpic traits of *P. thunbergii* in a mesocosm experiment. Three nutrient levels were applied using different intervals between fertilization: no fertilization (low nutrient), fertilization at eight-week intervals (medium), and at four-week intervals (high). We compared the relative stem length growth rates (RGR_{ST}) and biomass allocation of seedlings from aerial seeds (SA) and subterranean seeds (SS), and then investigated the flowering time and the seed production traits of *P. thunbergii* according to nutrient level. The results showed that RGR_{ST}, biomass allocation and total biomass were not different between SA and SS at all levels. Aerial flowering started earlier than subterranean flowering, in contrast to other amphicarpic plants. Subterranean seed allocation and the number of subterranean seeds were stable regardless of nutrient levels whereas aerial seed allocation decreased with increasing nutrient level. The number of aerial seeds per biomass with low nutrient was significantly higher than that at other levels. *P. thunbergii* showed a different trait of seed production: subterranean seeds appeared to play a role in retaining the mother-site while aerial seeds can escape the site conditions at low nutrient levels. In conclusion, the reproductive strategy of *P. thunbergii* on aerial propagule was changeable but not subterranean propagule under various nutrient conditions. SA and SS were similar about growth responses. Those characteristics would increase survivability of *P. thunbergii*. Evolutionary drivers might explain the differences of life-history strategies in flowering time between the aquatic *P. thunbergii* and other arid amphicarpic plants.

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1. Introduction

Amphicarpic plant are able to form above-ground and below-ground flowers and fruits (Cheplick, 1987). Amphicarpic plants can survive under variable environmental conditions using two seed types with different modes of development, function and strategy. (1) Aerial flowers are chasmogamous and are usually cross-pollinated, resulting in seeds that are smaller and lighter than subterranean seeds. Therefore, aerial seeds appear suitable for genetic exchange and dispersal. (2) Subterranean flowers are cleistogamous and only self-pollinated, and also have fewer, larger, and heavier seeds than aerial flowers (Koller and Roth, 1964; Cheplick, 1983; Schnee and Waller, 1986; Masuda and Yahara,

1994; Kaul et al., 2000; Barker, 2005). Subterranean seed production evolved independently in phylogenetically diverse taxa, and the relevant selective pressure can be different among species (Cheplick, 1987). The specific responses of amphicarpic plants to disturbances depend on the species and environmental variables. Thus, to fully understand the amphicarpic trait as an adaptive strategy, more information about specific amphicarpic responses of diverse plants under various environments situations is needed.

Pericaria thunbergii (Siebold & Zucc.) H. Gross belongs to the Polygonaceae and is an annual amphicarpic plant, easily occupying wetland areas such as riparian zones and lakesides (Kawano, 2008; Kim et al., 2012). *P. thunbergii* has similar characteristics to other amphicarpic plants. The aerial flowers, which develop at the tips of shoot, are usually chasmogamous and the subterranean flowers, which develop at the tips of decumbent stem toward the ground, are cleistogamous (Kawano et al., 1990; Suzuki et al., 2007).

The environment affects the nutrient allocation pattern (Brouwer, 1962; Bloom et al., 1985). In addition, the capability

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of plants to obtain nutrients is determined by allocation patterns, competition with other species and seed production (Abrahamson and Gadgil, 1973; Tilman, 1988; Poorter et al., 1990; Schmid and Weiner, 1993; Grime, 2006). Overall, the most important concept in plant life-history theory is resource allocation (Gadgil and Bossert, 1970; Iwasa and Roughgarden, 1984; Gedroc et al., 1996). Earlier studies on *P. thunbergii* dealt with various environmental factors that affect the population, such as light, which affects allocation patterns and seed outputs (Kawano et al., 1990), as well as flooding, which influences plant height and biomass (Kim et al., 2013). A mesocosm experiment on flooding and physical damage determined that *P. thunbergii* changed the allocation to aerial seeds and subterranean seeds (Choo et al., 2014). Especially, Choo et al. (2015) reported that seedlings from subterranean seeds (SS) in the early life history would have greater ability to escape water-logged and shaded conditions and an advantage in retaking the mother-site because of higher and faster germination rates than seedlings from aerial seeds (SA). Thus, they suggested that different seedling types would have different allocation patterns under unfavorable conditions. In addition, Choo et al. (2014) suggested that *P. thunbergii* has a reproductive strategy distinct from those of other amphicarpic plants. Accordingly, *P. thunbergii* would not fully satisfy the pessimistic strategy observed in other amphicarpic plants, in which the productivity of subterranean seeds decreases when flooding occurs.

In this study, we aimed to understand the amphicarpic traits of *P. thunbergii* under different soil nutrient conditions. The hypotheses are that 1) the leaf, stem, root and seed biomass allocation of two types of seedlings would differ according to nutrient levels, 2) flowering time would be faster under high nutrient conditions, and aerial flowering would be faster than subterranean flowering, 3) aerial seeds would be more productive per biomass at poor nutrient conditions to facilitate dispersal, and 4) aerial seeds exhibited a plastic reproductive allocation at different nutrient conditions, different to that found in subterranean seeds.

2. Methods

2.1. Nutrient conditions

The experiment was conducted outdoors at Seoul National University, Korea from May to November 2014. The average temperature was 19.8 ± 6.3 °C during the experimental period. Thirty oval rubber pots (70 cm W \times 100 cm L \times 35 cm H) were filled to a depth of 5 cm with sandy soil. Fertilization was performed using 5 g of an 18:2:10 (N:P:K) solid fertilizer (Dongbu-Hannong, Korea). The low nutrient level was soil without fertilizer addition. Medium and high nutrient levels were achieved by macronutrient addition every 4 or 8 weeks. Microelement fertilizer (Plant Nutrition Res. Inst., Daeyu, Korea) containing boron (2%), zinc (0.6%), manganese (0.4%), copper (0.05%), iron (0.1%) and molybdenum (0.0005%) was performed once in September.

Ninety subterranean seedlings and 90 aerial seedlings of similar stem length (SA: 5.0 ± 1.1 cm, SS: 5.0 ± 0.6 cm) ($p=0.831$) were selected, and three subterranean seedlings and three aerial seedlings were planted in a pot on 15 May (Fig. 1). We supplied distilled water; the water level was maintained at a depth of no more than 3 cm through drainage via a hole drilled at the appropriate height.

2.2. Measurement

Stem length was measured biweekly from 15 May to 30 June. We evaluated the blooming time for each condition every day. At the beginning of flowering, we installed a net at 15 cm above

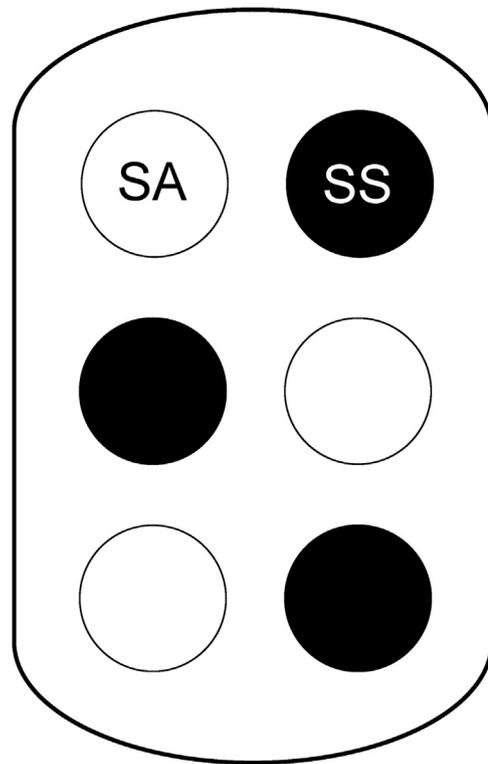


Fig. 1. Diagram of seedling arrangement in pot. SA, seedling from aerial seed. SS, seedling from subterranean seed.

the soil to separate aerial from subterranean seeds. Subterranean flowering was observed as the growth of the tip of the creeping stem of up to 10–15 cm on the soil. Harvesting was performed twice: on 25 July with 15 pots (5 pots per nutrient level) and on 3 November, when the plant foliage had withered, with 15 pots. The plants harvested on 25 July (first harvest) were separated into three organ parts (leaf, root and stem) and those are assorted again as seedling from subterranean and aerial seed. For the second harvest, plants were separated into four organs (leaf, root, stem and seed). Aerial seeds were gathered from the net, and subterranean seeds from soil. Finally, the organs were dried in an oven for 48 h at 80 °C. We calculated relative stem length growth rates (RGR_{st}) ($\text{cm/day} = (\ln x_2 - \ln x_1) / (t_2 - t_1)$), where x_1 is the stem length at t_1 time and x_2 is the stem length at t_2 time. To evaluate biomass allocation, we used stem mass fraction (SMF), leaf mass fraction (LMF) and root mass fraction (RMF) ($\text{SMF or LMF or RMF} = \text{stem or leaf or root dry mass/total dry mass; g/g}^{-1}$). As a reproductive allocation pattern, we calculated aerial seed allocation, subterranean seed allocation (g/g^{-1}) (aerial or subterranean allocation = aerial or subterranean seed dry mass/total biomass).

2.3. Analysis of soil nutrient

Soil was sampled 1 week after each fertilization and sieved using a 2 mm mesh sieve. $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ in soil were extracted with a 2 M KCl solution (Kim et al., 2004), and $\text{PO}_4\text{-P}$ was extracted with Bray No. 1 solution (Bray and Kurtz, 1945). $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and $\text{PO}_4\text{-P}$ in water and in the extracted soil solution 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.

2.4. Statistical analysis

Data were statistically analyzed using the statistical software environment R (R Development Core Team, 2014) for two-way ANOVA and one-way ANOVA with post hoc test Tukey HSD (honestly significant difference) and PERMANOVA with 999 permutations. The reproduction allocation data were log-transformed and evaluated by ANOVA with Tukey's post hoc HSD test. Differences in soil nutrient levels from May to September were assessed using repeated measured ANOVA with Greenhouse-Geisser to adjust degrees of freedom. In addition, we used the pair-wise permutational *t*-test after PERMANOVA. Standardized major axis (SMA) regression was used to describe the relationship between each combination of traits in seedlings from aerial and subterranean seeds after log-transformation. The SMA method is appropriate when the purpose of the study is to describe the relationships between variables (Warton et al., 2006).

3. Results

3.1. Changes in soil nutrient conditions

Before treatment, the $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and $\text{PO}_4\text{-P}$ levels were 2.9 ± 0.7 , 1.7 ± 0.5 , and 24.5 ± 1.7 mg/kg, respectively (Fig. 2). The $\text{PO}_4\text{-P}$ level decreased significantly during the experiment (repeated measured ANOVA, $F_{4,24} = 4.050$, $p = 0.012$). There was no interaction between nutrient levels and time ($F_{8,24} = 1.126$, $p = 0.382$). There was no significant difference between nutrient levels ($F_{2,6} = 0.047$, $p = 0.955$). The $\text{NO}_3\text{-N}$ level decreased significantly during the experiment (repeated measures ANOVA, Greenhouse-Geisser adjusted $F_{1,16,6,93} = 56.067$, $p = 0.004$). There was an interaction between nutrient levels and time (Greenhouse-Geisser adjusted $F_{2,31,6,93} = 8.493$, $p = 0.012$). Nutrient levels differed significantly ($F_{2,6} = 30.876$, $p = 0.001$). The $\text{NH}_4\text{-N}$ level decreased significantly during the experiment (repeated measured ANOVA, Greenhouse-Geisser adjusted $F_{1,46,8,77} = 19.262$, $p = 0.001$). There was an interaction between nutrient levels and time (Greenhouse-Geisser adjusted $F_{2,92,8,77} = 3.960$, $p = 0.05$). There was no significant difference between nutrient levels ($F_{2,6} = 2.692$, $p = 0.146$).

3.2. Growth responses to nutrient

The RGR_{ST} was not different between seedling types but was affected by nutrient levels. RGR_{ST} in May differed significantly between high and medium-low level (two-way ANOVA, $F_{2,174} = 53.04$, $p < 0.02$), but not between seedling types ($F_{1,174} = 0.010$, $p = 0.919$), and there was no interaction between nutrient level and seedling type ($F_{2,174} = 0.016$, $p = 0.852$). RGR_{ST} in June was significantly different among the nutrient levels (two-way ANOVA, $F_{2,174} = 46.812$, $p < 0.001$), but there was no significant difference between seedling types ($F_{1,174} = 0.067$, $p = 0.796$), and no significant interaction between nutrient level and seedling type ($F_{2,174} = 0.119$, $p < 0.888$).

The mean total biomass of SA and SS in late July was 1.11 ± 0.77 g and 1.03 ± 0.80 g under low-nutrient conditions, 12.49 ± 5.81 g and 11.35 ± 5.96 g under medium nutrient conditions, and 22.66 ± 7.02 g and 27 ± 8.03 g under high-nutrient conditions, respectively. There was no significant difference between seedling types (PERMANOVA, $F_{1,86} = 0.77$, $p = 0.391$) and no significant interaction between nutrient levels and type ($F_{2,86} = 2.13$, $p = 0.127$), but there were significant differences among nutrient levels ($F_{2,86} = 205.49$, $p < 0.001$).

For the LMF of high, medium and low nutrient levels, the individual slopes for SA and SS were not significantly different (high: $p = 0.30$, medium: $p = 0.94$, low: $p = 0.60$) and negatively corre-

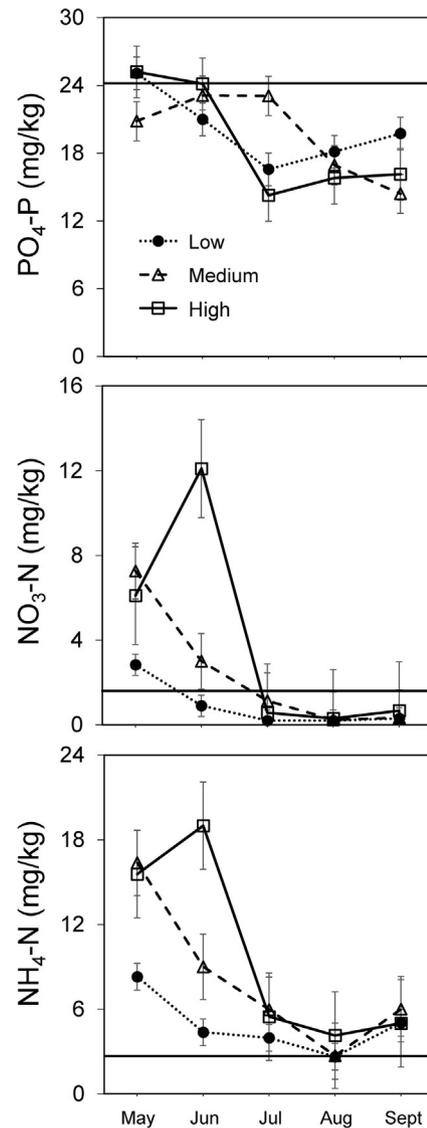


Fig. 2. Changes in soil nutrient contents. Horizontal solid line (—), initial soil nutrient condition.

lated with total biomass (high: common slope = -1.48 , medium: common slope = -2.74 , low: common slope = -2.75) (Table 1). LMF differed significantly between nutrient levels (two-way ANOVA, $F_{2,84} = 14.771$, $p < 0.0001$) but not between seedling types ($F_{1,84} = 0.191$, $p = 0.664$), and there was no interaction between nutrient level and seedling type ($F_{2,84} = 0.726$, $p = 0.485$) (Table 3).

For RMF at high, medium and low nutrient levels, the individual slopes for SA and SS were not significantly different (high: $p = 0.98$, medium: $p = 0.98$, low: $p = 0.32$) and positively correlated with total biomass (high: common slope = 1.83 , medium: common slope = 2.27 , low: common slope = 1.56) (Table 1). RMF was not significantly different between seedling types (PERMANOVA, $F_{1,84} = 1.746$, $p = 0.177$), but was significantly different between nutrient levels ($F_{2,84} = 5.400$, $p < 0.001$). There was no interaction between seedling type and nutrient level ($F_{2,84} = 1.239$, $p = 0.308$).

For SMF at the high, medium and low nutrient levels, the individual slopes for SA and SS were not significantly different (high: $p = 0.51$, medium: $p = 0.29$, low: $p = 0.41$). SMF at the high and medium levels was positively correlated with total biomass (high: common slope = 2.60 , medium: common slope = 4.83) but at the low level was negatively correlated with total biomass (common slope = -3.69). SMF was not significantly different between

Table 1
Standardized major axis (SMA) regression for LMF, RMF and SMF with seedling types and fertility level in the first collected data. T, seedling type. L, fertility level. C slope, common slope. Ci, 95% confidence interval.

Trait Y(X)	T	L	Slope	r ²	SMA Pval	Ci	C slope
LMF (total biomass)	SA	High	-0.083	0.023	0.30	-2.14	-1.03
	SS		-0.458	0.338			
	SA	Medium	-0.256	0.483	0.94	-3.55	-2.12
	SS		-0.294	0.659			
	SA	Low	-0.208	0.275	0.60	-3.91	-1.93
	SS		0.142	0.185			
RMF (total biomass)	SA	High	-0.096	0.047	0.12	1.24	2.66
	SS		0.217	0.383			
	SA	Medium	0.173	0.797	0.98	1.53	3.38
	SS		0.16	0.397			
	SA	Low	-0.149	0.229	0.32	1.09	2.24
	SS		-0.055	0.058			
SMF (total biomass)	SA	High	-0.066	0.008	0.51	1.82	3.68
	SS		0.234	0.296			
	SA	Medium	<0.005	<0.005	0.29	3.80	6.05
	SS		0.031	0.234			
	SA	Low	0.451	0.372	0.41	-5.37	-2.54
	SS		-0.039	0.006			

seedling types (two-way ANOVA, $F_{1,84} = 1.150$, $p = 0.287$), and there was no interaction between nutrient level and seedling type ($F_{2,84} = 0.823$, $p = 0.443$), but there was a significant difference between nutrient levels ($F_{2,86} = 4.609$, $p = 0.016$).

3.3. Effect of nutrient level on flowering time and seed production of *P. thunbergii*

The first flower was observed on 8 September. Flowering time was affected by nutrient level and differed between aerial and subterranean flowers (Fig. 3). Initial flowering at the high nutrient level occurred earlier than at the other levels. Aerial flowers appeared more rapidly than subterranean flowers (Fig. 3).

The number of subterranean seeds was significantly higher than that of aerial seeds (two-way ANOVA, $F_{1,24} = 6.342$, $p < 0.05$), and the number of seeds increased significantly with increasing nutrient level ($F_{2,24} = 110.881$, $p < 0.001$). There was no interaction between seedling type and nutrient level ($F_{2,24} = 1.080$, $p = 0.355$) (Table 2). The weight of subterranean seeds was significantly greater than that of aerial seeds (PERMANOVA, $F_{1,24} = 5.173$, $p < 0.05$), and seed weight significantly increased with increasing nutrient level ($F_{2,24} = 77.836$, $p < 0.001$). There was no interaction between seedling type and nutrient level ($F_{2,24} = 0.839$, $p = 0.447$) (Table 2).

The number of seeds per biomass differed significantly among nutrient levels for aerial seeds (ANOVA, $F_{2,12} = 25.500$, $p < 0.001$) but not for subterranean seeds ($F_{2,12} = 0.435$, $p = 0.657$) (Fig. 4a and 4b). At low levels, the number of aerial seeds per biomass was higher than that under the other conditions ($p < 0.05$, Tukey HSD). Aerial seed allocation was significantly increased with increasing nutrient level (ANOVA, $F_{2,12} = 4.646$, $p < 0.05$) but not subterranean seed allocation ($F_{2,12} = 0.213$, $p = 0.811$). This was due to the dissimilar low (1.2%) and high (0.8%) nutrient levels ($p < 0.05$, Tukey HSD) (Fig. 4c and d).

4. Discussion

P. thunbergii showed a decrease in LMF and an increase SMF and RMF with total biomass, thus during plant growth. This characteristic is similar to that of other plants (Poorter et al., 2012). RGR_{ST} did not differ between seedling types in the different nutrient treatments, which contradicts our initial hypothesis. We had argued that irrespective of seedling type *P. thunbergii* would be similar to other plant species, which are incapable of high RGR_{ST} at low nutri-

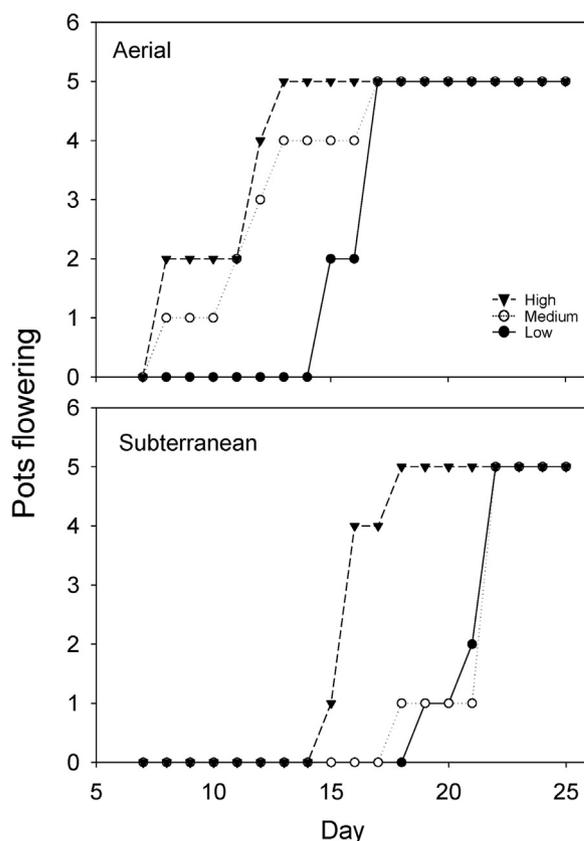


Fig. 3. *Persicaria thunbergii* flowering time according to nutrient levels. The date on which flowering was observed in the pot was recorded.

ent levels (Chapin, 1980). Choo et al. (2015) reported that biomass allocation differed between SS and SA under flooding and shading conditions. Our results show that biomass allocation to SS and SA did not differ in the different nutrient treatments. Thus, soil nutrient levels apparently had little influence on biomass allocation to SS and SA.

In the annual amphycaptic plant *Amphicarpum purshii*, Cheplick and Quinn (1982) suggested that the allocation to different plant parts differed between the two seedling types according to soil moisture level, and that these differences were responsible for

Table 2

Number and weight of seeds in a pot according to nutrient level (average ± SE, Tukey or permutational pair-wise test; $p < 0.05$).

	Type	High level (n=5)	Medium level (n=5)	Low level (n=5)
Number	Aerial seeds	1330.8 (±135.55) ^a	648.4 (±34.79) ^b	48.2 (±12.76) ^c
	Subterranean seeds	1543.4 (±166.48) ^a	959.0 (±54.68) ^b	91.8 (±14.50) ^c
Weight	Total aerial seeds	16.379 (±1.513) ^a	7.169 (±0.647) ^b	0.418 (±0.134) ^c
	Total subterranean seeds	19.197 (±2.665) ^a	11.319 (±1.157) ^b	1.062 (±0.189) ^c

Table 3

SA and SS of LMF, RMF and SMF according to nutrient level (average ± SE, Tukey or permutational pair-wise test; $p < 0.05$).

	High		Medium		Low	
	SA	SS	SA	SS	SA	SS
LMF	0.27 ± 0.02 0.26 ± 0.01 ^b	0.25 ± 0.02	0.33 ± 0.03 0.34 ± 0.01 ^a	0.34 ± 0.03	0.27 ± 0.03 0.27 ± 0.01 ^b	0.28 ± 0.02
RMF	0.2 ± 0.02 0.21 ± 0.01 ^b	0.2 ± 0.02	0.18 ± 0.02 0.18 ± 0.01 ^b	0.18 ± 0.02	0.26 ± 0.05 0.23 ± 0.02 ^a	0.21 ± 0.03
SMF	0.53 ± 0.03 0.54 ± 0.01 ^a	0.55 ± 0.02	0.49 ± 0.02 0.49 ± 0.01 ^b	0.48 ± 0.04	0.47 ± 0.04 0.49 ± 0.01 ^{ab}	0.52 ± 0.03

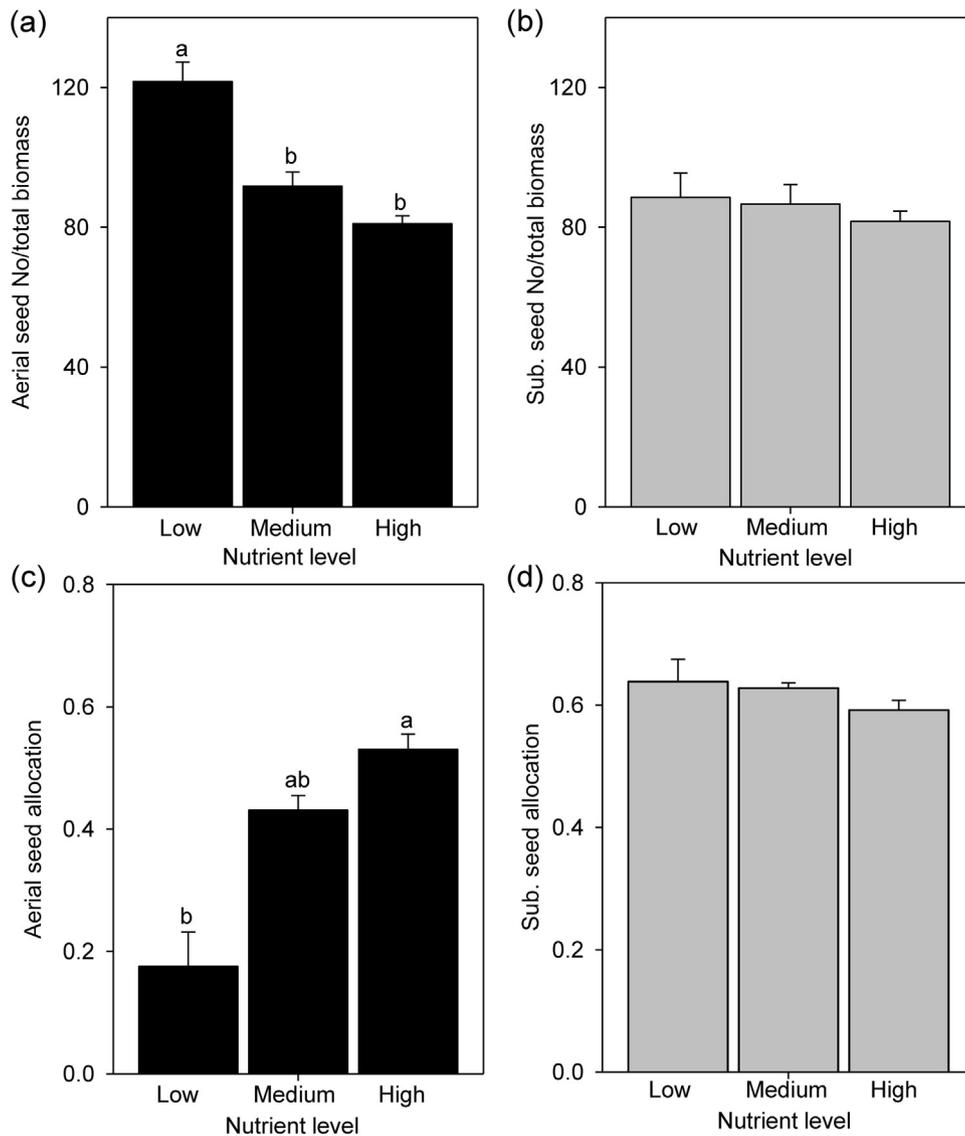


Fig. 4. Aerial and subterranean seed production at three nutrient levels. (a) Number of aerial seeds per biomass (number/g), (b) number of subterranean seeds per biomass (number/g), (c) aerial seed allocation, and (d) subterranean seed allocation.

seedlings from subterranean seeds having greater survivorship than seedlings from aerial seeds. *P. thunbergii* seedlings from subterranean seeds in early growth stages had a survival advantage and a greater number of leaves (Choo et al., 2015). In our study, however, the different seedling types showed similar RGR_{ST} and total biomass values at first harvest. Thus, the ability to survive or compete under various nutrient conditions did not differ between SA and SS. In addition, this result showed that SA and SS would have similar productivity because plant productivity depends on plant size (Gadgil and Bossert, 1970; Abrahamson and Gadgil, 1973). Amphicarpic plants exhibit a close relationship between the amphicarp ratio (aerial propagule: subterranean propagule) and the total biomass (Trapp and Hendrix, 1988; Kawano et al., 1990).

Kawano et al. (1990) suggested that soil nutrient and moisture exerted only slight effects on allocation pattern in field *P. thunbergii*. However, in our study the number and weight of the two types of seed increased with increasing nutrient levels; moreover, aerial seed allocation increased with increasing nutrient level in *P. thunbergii*. The previous study (Kawano et al., 1990) was conducted in the field, which complicates determination of the effect of nutrients on reproduction. Habitat conditions, such as nutrient availability, may modulate the amphicarp trade-off. The observed decline in allocation to aerial seeds combined to the higher number of small aerial seeds produced per biomass under nutrient limitation might reflect a specific plant response that can increase the probability of escape in a detrimental habitat (Cheplick, 1987, 1994). The stability of the subterranean seed allocation and the number of seeds per biomass at all three nutrient levels might reflect a specific plant response that source dispersal increases the likelihood of maintaining mother sites even under unfavorable conditions (Urbanska, 1997).

Most amphicarpic plants developed early to subterranean propagules or flower under various conditions (Zeide, 1978; Cheplick and Quinn, 1982; Cheplick, 1983). In addition, aerial plant biomass production was more dynamic and plastic than subterranean reproductive organ production (Cheplick, 1994). Flooding changed the allocation in *P. thunbergii* to earlier aerial flowering, with potential impacts on the population (Choo et al., 2014). In our study, subterranean flowers did not form earlier than the aerial ones. It is thus more congruent with the findings by Kawano et al. (1990) than those of Choo et al. (2014). We suggested that different evolutionary drivers acted on seed allocation in aquatic amphicarpic (*P. thunbergii*) and arid amphicarpic plants.

5. Conclusion

P. thunbergii has an efficient reproductive strategy in insufficient nutrient habitats, which increases the probability of being retained in its mother site using stable productive traits with subterranean seeds and escaping insufficient nutrient habitats by changing the productive traits of aerial seeds. These characteristics would increase the ability of survival at insufficient nutrient conditions. This life-history strategy of *P. thunbergii* is thus different from amphicarpic plants in arid or semi-arid habitats.

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