INTERNATIONAL JOURNAL OF AGRICULTURE & BIOLOGY
ISSN Print: 1560–8530; ISSN Online: 1814–9596
20–0164/2020/24–2–188–194
DOI: 10.17957/IJAB/15.1424
http://www.fspublishers.org

Full Length Article

The Role of Seed Morph and Water Availability in the Growth and Reproduction of Amphicarpic Plant *Amphicarpaea edgeworthii* (Fabaceae)

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Received 01 February 2020; Accepted 20 February 2020; Published 31 May 2020

Abstract

Amphicarpic plants produce both subterranean and aerial fruits on a single plant, which is a bet-hedging strategy for plant adaptation in the face of temporal and spatial variations in environmental conditions. *Amphicarpaea edgeworthii* (Leguminosae), an annual amphicarpic herb grows within wet to dry habitats, and exhibits considerable morphological variation. To understand the adaptation of *A. edgeworthii* to water availability, we studied plant growth and reproductive responses from subterranean seeds (SSP) and aerial seeds (ASP) from *A. edgeworthii* under 300, 450, 600, 750 and 900 mm of rainfall amounts. Vegetative biomass, plant height, leaf biomass, number of leaves, and number of branches in SSP were remarkably increased relative to those in ASP, while root / shoot biomass ratio was lower in SSP. With an increase in water availability, reproductive biomass, aerial reproductive biomass, and subterranean reproductive biomass gradually increased. Aerial reproductive biomass changed more significantly than subterranean reproductive biomass. SSP produced more seeds than ASP. With an increase in water availability, seed mass decreased. Results showed that *A. edgeworthii* exhibits potent plasticity to respond to the extent of water availability, which enhances the survival and reproductive capacities under uncertain environmental conditions. © 2020 Friends Science Publishers

Keywords: *Amphicarpaea edgeworthii*; Amphicarpy; Biomass allocation; Water availability; Reproductive strategy

Introduction

The essential resources for the growth of plant (including light, water and minerals) show heterogeneous distribution among the natural habitats (Heisler-White *et al.* 2008; Nicotra *et al.* 2010; Eziz *et al.* 2017; Shavrukov *et al.* 2017). Phenotypic plasticity is believed to be an important factor in the ability of plants to adapt to the environment (Matesanz *et al.* 2010; Molina-Montenegro *et al.* 2010). It enables a species to have a wider ecological niche, a greater tolerance for a variety of environmental conditions, and to occupy a broader geographic range (Pigliucci 2001). These plasticity responses cover morphological and physiological changes, genetic structure, demography and life history, which may be presented across generations or during the single individual lifespan (Molina-Montenegro *et al.* 2010). However, there are vicarious measures for managing the heterogeneity in environmental resource; among which, one is producing strongly contrasting reproductive structures, especially seeds, within the same plant, called seed heteromorphism. This strategy can help plants to bet-hedge their timing of germination in extremely stressful and unpredictable environments, such as dry, saline ecosystems (Cheplick 1987; 1994).

Amphicarpy is one of the extreme seed heteromorphism forms, wherein there is the production of subterranean and aerial fruits (seeds) by a single plant (Cheplick 1987; Barker 2005; Sadeh *et al.* 2009). Subterranean and aerial seeds from the amphicarpic species can be different in terms of various traits, such as the embryo mass/size (Cheplick 1987; Conterato *et al*. 2013; Zhang *et al*. 2015), class or level of dormancy (Baskin and Baskin 2014; Zhang *et al.* 2015; Conterato *et al.* 2019), dispersal mechanism and distance (Kumar *et al*. 2012; Auld and Rubio de Casas 2013; Hidalgo *et al*. 2016; Koontz *et al.* 2017) and ability to form a persistent seed bank. Additionally, plants that are raised from aerial and subterranean seeds may be different among numerous ways, such as growth and survival; competitive ability, as well as reproductive allocation (Zhang *et al.* 2017). With a decrease in amount of light, water and nutrients, aerial seeds are remarkably decreased compared with the subterranean ones in several amphicarpic species (Choo *et al*. 2014, 2015; Kim *et al* 2016; Nam *et al.* 2017; Zhang *et al.* 2017).

To cite this paper: Xiong Z, J Yang, K Zhang (2020). The role of seed morph and water availability in the growth and reproduction of amphicarpic plant *Amphicarpaea edgeworthii* (Fabaceae). *Intl J Agric Biol* 24:188–194

The fact that amphicarpic species change the proportion of offspring raised by different forms of the fruit to make their offspring become increasingly competitive in the presence of various environmental circumstances, may also be seen as a special kind of phenotypic plasticity. In stressful and drought ecosystems, production of subterranean seeds is more secure than aerial seeds (Cheplick 1994; Baskin and Baskin 2014). The subterranean seeds allow a species to avoid many hazards such as dehydration, terrestrial predators and fire (Baskin and Baskin 2014). For example, when the aboveground of an annual plant encounters devastating conditions (e.g. herbivory, fire), subterranean seeds allow the species to survive.

In terrestrial ecosystem, precipitation has been recognized as a crucial environmental factor that affects the growth of plant (Ogle and Reynolds 2008; Dai 2012). Patterns and annual amounts of precipitation serve as important factors in plant regeneration and survival as well as in other ecosystem functions (Ogle and Reynolds 2008). Moreover, precipitation shows direct effect on plant morphology, growth, and biomass accumulation (Nicotra *et al.* 2010; Eziz *et al.* 2017; Shavrukov *et al.* 2017). As the water availability decreases, the plant height, biomass accumulation rate, and seed production are reduced. Previous studies have shown that the plastic response of seedling growth (Ogle and Reynolds 2008), biomass allocation (Eziz *et al.* 2017), physiological characteristic (Ogle and Reynolds 2008; Dai 2012), phenology (Shavrukov *et al.* 2017) and seed production (Nicotra *et al.* 2010; Shavrukov *et al.* 2017) to variations in annual precipitation. The germination behavior of offspring may also be affected by changes in the timing or amount of annual precipitation (Nicotra *et al.* 2010). However, those adaptive mechanisms of amphicarpic species to variable precipitation remain largely unclear. In amphicarpic species, aerial seeded plants of *Amphicarpum purshii* have remarkably reduced seed production and total growth relative to those of subterranean plants in both dry and wet sites (Cheplick 1994).

Amphicarpaea edgeworthii is one of the amphicarpic herbal plants with wide distribution within the forest, stream and roadside in India, China, Korea, Japan, Vietnam and Russia (Sa and Michael 2010; Zhang *et al.* 2017). It can produce subterranean and aerial seeds, which are different with regard to morphological, physiological as well as ecological characteristics (Zhang *et al.* 2015). Aerial seeds are kidney-shaped and dark-brown in color, while the subterranean ones can be irregular spherical or kidney-shaped and are purple-brown in color (Zhang *et al.* 2015). Our field observation also found that plant of *A. edgeworthii* growing under moist and dry habitat varies considerably. Number, mass, together with subterranean-to-aerial seeds ratio also varies both within and among populations. However, it is unknown whether the differences of the number of seeds, mass, and subterranean-to-seed ratio are caused by different types of seeds or by soil moisture (i.e. phenotypic plasticity). We hypothesized that the plants raised from subterranean seeds (SSP) and aerial seeds (ASP) have different responses to water availability with regard to the reproductive and vegetative growth. In order to verify the above speculation, the present study was aimed at to compare: 1) the differences of reproductive and vegetative growth based on two seed morphs (ASP or SSP); and 2) the response of reproductive and vegetative growth for SSP and ASP under different water regimes.

Materials and Methods

Study area and seed collection

On 7–20 October 2017, the fresh *A. edgeworthii* mature seeds were obtained from a natural Beijing population. Seeds were collected from at least 500 individuals. The aerial seeds were subjected to 14 days of air-drying under room conditions (40–50% relative humidity, and 22–28°C). Afterwards, seeds were preserved within a paper bag at -18°C prior to use. At the same time, subterranean seeds were put into the natural soil-filling pots (with the soil water content of 15–18%, to simulate natural habitats maximum soil moisture), followed by preservation within the refrigerator at 4°C prior to use.

In this experiment, the area of study was located at the warm temperate monsoon climate zone, which had four distinct seasons consisting of dry winters and moist summers. Meanwhile, it had an annual mean temperature of 10–12°C. July weather is usually the hottest, and the mean temperature during the study period was 25–26°C, whereas January is coldest with a mean temperature during the experiment was -4 to -7°C. Besides, the extreme minimum and maximum temperatures were -27.4°C and 42°C, respectively, with an annual mean precipitation of ca. 600 mm, and approximately 75% of it was concentrated in June and August.

Seed germination and seedling transplantation

On April 08, 2018, five hundred subterranean and aerial seeds were randomly selected and germinated onto a 10 cm diameter Petri dish (25 seeds for each Petri dish), on the filter paper (two layers) humidified using distilled water (5 mL). Afterwards, the Petri dishes were sealed with parafilm and placed at 15/25°C with 12/12 h light/dark condition. Seed germination was scored every day and after 3 days of incubation, seedlings of SSP and ASP were transplanted to 200 pots. Each treatment had 20 pots and each pot contained five seedlings of ASP or SSP.

Effects of water availability on growth and reproduction

The present study used 24 cm diameter pots that were filled with 26.5 cm of soil from the natural habitat of this species.

Two layers of envelopes were used to avoid losing soil through the hole in the bottom of each pot. The time of transplanting time coincided with the emergence of *A. edgeworthii* seedlings in the wild in Beijing. Each pot contained five seedlings planted in the experimental garden; when they possessed four true leaves, the singular plants of uniform size as that of the remaining seedlings used for this experiment were chosen for experimentation; while other seedlings were eliminated. The experimental garden had glass windows on all four sides, which were left open to freely exchange air from outside. This kept the relative humidity (RH) inside and outside the greenhouse about the same. Pots were buried 20 cm deep to stabilize the soil temperature; soil was leveled in the pots with garden soil surface. Air temperature was recorded as a maximum of 38°C and a minimum of 7°C. The RH remained between 19–83%. Experiments were run from April 16 to October 20, 2018.

Water availability manipulation

The mean annual precipitation in Beijing from, 1995 to 2016 ranged from 318 mm in, 1969 to 919 mm in 2006, with an annual variation of ± 50%. According to the average total precipitation (600 mm), the gradient had been constructed, which treated values within such range of variation using 50, 75, 100, 125, or 150% of the total mean rainfall (600 mm) corresponding to 300, 450, 600, 750, and 900 mm, respectively. Plants in each treatment were watered every five days with 387, 581, 775, 968, 1162 mL, respectively, over a period of 175 days between 15 April and 7 October, 2018.

Plant harvests

We harvested all plants on October 10, 2018, when fruits were mature. Plant survival among various treatments was evaluated. Only one ASP and four SSP plant survived in 300 mm precipitation treatment, thus this treatment was ignored. Roots were collected and rinsed with the running tap-water. The whole plant was divided into roots, leaves, stems, as well as the reproductive organs (such as the subterranean and aerial fruits). Meanwhile, the branch and leaf numbers, plant height, together with biomass in root, shoot and leaf, were measured. Vegetative biomass was the sum of root, shoot and leaf biomass. Subterranean and aerial seed numbers in every plant were counted. We weighed 20 randomly chosen aerial seeds and subterranean seeds using analytical balance (Sartorius BP 221 Sartorius, Germany) for determining the seed weight. The aerial (subterranean) reproductive biomass was measured and S/(S+A) was calculated, where S is subterranean vegetative biomass, while S+A is total reproductive biomass.

Statistical analyses

In all our experiments plants were arranged in completely randomized block design (CRBD) with 20 replications of each seed type for each treatment. The SPSS 21.0 (SPSS Inc., Chicago, IL, USA) was used for analyzing data. If necessary, the values were subjected to log-transformation for improving the variance homogeneity and normality. The Two-way ANOVA was used for comparing main influences of water availability, plant type, as well as the interaction for vegetative biomass, fruit (and seed) number and mass ratios. Differences across different treatments were determined using Tukey's HSD test in the presence of data significance indicated by ANOVA ($P< 0.05$).

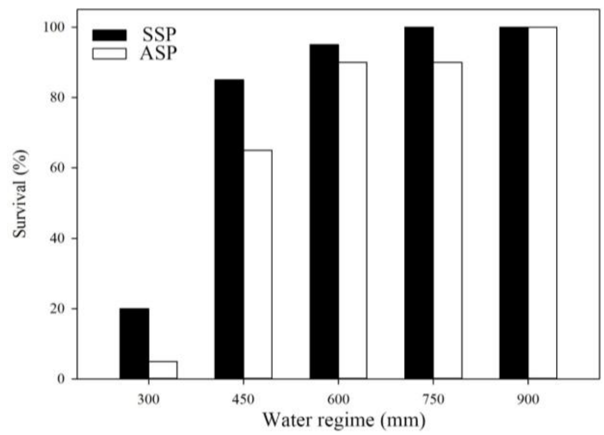

Fig. 1: Effect of plant type (ASP or SSP) and precipitation on plant survivorship of *A. edgeworthii* plants

Results

Plant survivorship

With an increase in water availability, plants survivorship of both ASP and SSP increased. SSP had higher survivorship when in 300, 450 and 600 mL water treatment. Only 5% plants from ASP survived in 300 mL water treatment, while the survivorship in SSP was 20% in 300 mL water treatment (Fig. 1).

Roles of water availability and plant type in plant vegetative traits

The plant height (Fig. 2A), vegetative biomass (Fig. 2B), biomass in leaves (Fig. 2C), number of leaves (Fig. 2D), as well as number of branches (Fig. 2E) in SSP were dramatically increased compared with those of ASP, while ASP had a great ratio of root to shoot mass relative to SSP (Fig. 2F). With an increase in water availability, plant height (Fig. 2A), leaf biomass (Fig. 2B), number of leaves (Fig. 2C), vegetative biomass increased, but root/shoot mass ratio decreased. The results of two-way ANOVA indicated that seed type, water availability and their interaction had significant effects on plant height, vegetative biomass, leaf biomass, number of leaves, and number of branches.

Table 1: Results of two-way ANOVA of effects of plant type, water availability and their interactions on vegetative and reproductive traits of *A. edgeworthii*

	Seed type		Treatment		Treatment × Seed type	
Variables	F	*P*	F	*P*	F	*P*
Height	17.382	< 0.05	12.274	< 0.05	3.003	< 0.05
Vegetative biomass	51.918	< 0.05	22.290	< 0.05	2.630	< 0.05
Leaf biomass	35.758	< 0.05	15.817	< 0.05	2.240	< 0.05
Number of leaves	47.122	< 0.05	16.467	< 0.05	3.005	< 0.05
Number of branches	23.504	< 0.05	13.465	< 0.05	2.198	< 0.05
Root / Shoot biomass ratio	4.297	< 0.05	6.538	< 0.05	0.749	0.560
Reproductive biomass	15.804	< 0.05	12.121	< 0.05	4.872	< 0.05
Aerial reproductive biomass	4.467	< 0.05	17.378	< 0.05	10.789	< 0.05
Subterranean reproductive biomass	9.276	< 0.05	0.515	0.725	0.112	0.978
S/(S+A)	1.635	0.203	9.587	< 0.05	3.467	< 0.05
Aerial seed number	57.692	< 0.05	35.509	< 0.05	5.519	< 0.05
Subterranean seed number	12.173	< 0.05	2.780	< 0.05	0.272	0.895
Single aerial seed mass	1.161	0.283	4.299	< 0.05	0.877	0.480
Single subterranean seed mass	0.027	0.870	2.238	< 0.05	0.510	0.728

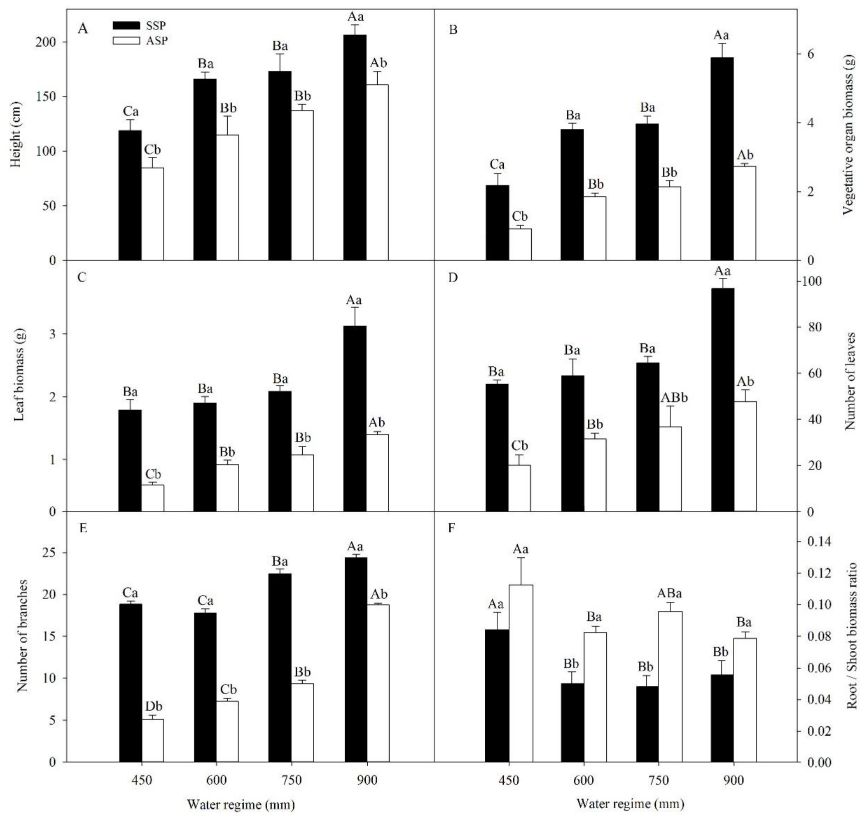

Fig. 2: Effect of plant type (ASP or SSP) and water availability on plant height (A), leaf biomass (B), number of leaf (C), vegetative biomass (D) root/shoot mass ratio (E) of *A. edgeworthii* plants. Black bars represent plants from subterranean seeds (SSP) and white bars plants from aerial seeds (ASP). For each kind of measurement, different uppercase letters indicate significant difference across all shading intensities and lowercase indicates significant difference between ASP and SSP in the same shading intensity (5 % level)

Root/shoot biomass ratio was effected by seed type and water availability, but their interactions (P = 0.560) were not found (Table 1).

Roles of water availability and plant type in plant reproductive biomass

Reproductive biomass (Fig. 3A), aerial reproductive biomass (Fig. 3B), subterranean reproductive biomass (Fig. 3C) and S/(S+A) (Fig. 3D) in SSP were remarkably increased compared with those in ASP. With an increase in water availability, reproductive biomass, aerial reproductive biomass, and subterranean reproductive biomass gradually increased, but S/(S+A) decreased. Reproductive biomass, aerial reproductive biomass were largely impacted by water availability, seed type, as well as the

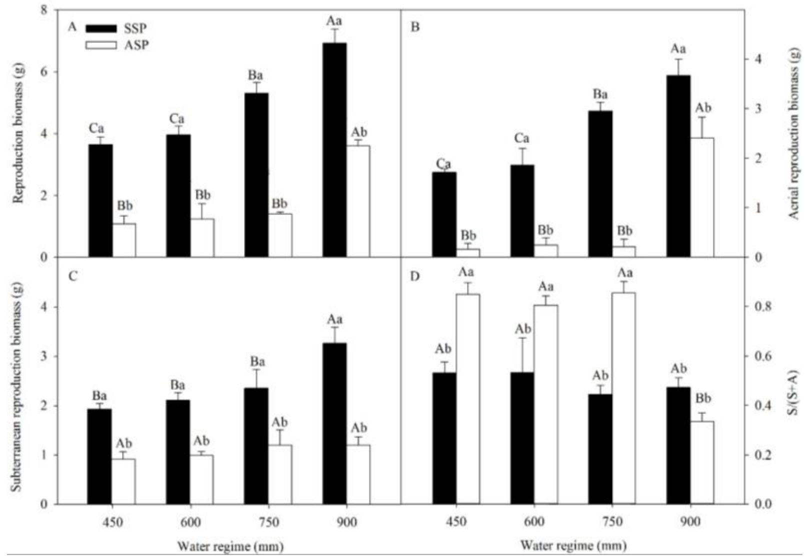

Fig. 3: Effect of plant type (ASP or SSP) and water availability on reproductive biomass (A), aerial reproductive biomass (B), subterranean reproductive biomass (C), and S/(S+A) (D) of *A. edgeworthii* plants. Black bars represent plants from subterranean seeds (SSP) and white bars plants from aerial seeds (ASP). For each kind of measurement, different uppercase letters indicate significant difference across all shading intensities and lowercase indicates significant difference between ASP and SSP in the same shading intensity (5 % level)

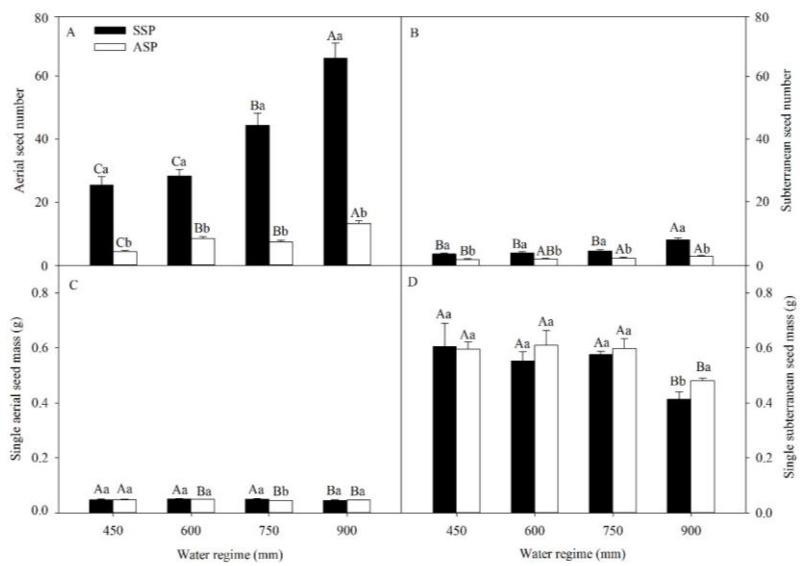

Fig. 4: Effect of plant type (ASP or SSP) and water availability on aerial seed number (A), subterranean seed number (B), single aerial seed mass (C), and single subterranean seed mass (D) of plants of *A. edgeworthii*. For each kind of measurement, different uppercase letters indicate significant difference across all shading intensities for the same plant type (ASP or SSP) and lowercase indicates significant difference between ASP and SSP in the same shading intensity (5 % level)

interaction between the two (Table 1). Subterranean reproductive biomass was under significantly influenced by the seed type, but not by water availability ($P = 0.064$) or their interactions ($P = 0.978$) of these factors (Table 1). The subterranean reproductive biomass/total reproductive biomass ratio had been under significant influence by water availability and seed type-water availability interaction, but not effected by seed type.

Roles of water availability and plants type in the number and size of seeds

SSP generated large amounts of subterranean and aerial seeds compared with those by ASP (Fig. 4A, B). With an increase in water availability, the subterranean and aerial seed numbers increased. The aerial and subterranean seed mass was lighter in 900 mm annual precipitation than 450, 600 and 750 mm (Fig. 4C, D). Two-way ANOVA showed that the seed number in each subterranean or aerial plant was significantly affected by water availability and seed type. However, interactions between seed type and water availability had significant effects on aerial seed number but not on subterranean seed number. Single aerial and subterranean seed mass were significantly affected by water availability, but not by seed type (Table 1).

Discussion

Response of plant morphology, physiology and development to resource availability is important for plants to survive and improve their competitiveness in heterogeneous habitats (Mokany *et al.* 2006; Nicotra *et al.* 2010; Eziz *et al.* 2017). With an increase in water availability, survival of *A. edgeeorthii* plant increased and SSP had higher survival than ASP. This might due to the difference in seed size. In *A. edgeworthii*, the mass of each aerial seed was 38.52 ± 0.14 mg, whereas that was 456.32 ± 12.53 mg for each subterranean seed (Zhang *et al.* 2015). Thus, seedlings raised from subterranean seeds have access to great amounts of resources compared with aerial ones. In amphicarpic species, plants from subterranean seeds often have the competitive superiority (Tan *et al*. 2010; Baskin and Baskin 2014; Speroni *et al*. 2014) than those from aerial seeds. In *Persicaria thunbergii*, subterranean and aerial seeds had analogous weight, and there was no difference in total biomass and biomass allocation in subterranean seeds- and aerial seeds-derived seedlings compared with their mother plants in terms of nutrient availability (Kim *et al.* 2016).

With a decrease in water availability, SSP and ASP in *A. edgeworthii* had been shorter and produced less biomass, less leaves and number of branches, but the root-to-shoot ratio was higher. This is a common response in other species (Mokany *et al.* 2006; Nicotra *et al.* 2010). SSP has higher plant height, biomass and number of branches than ASP. Plants that have increased biomass are associated with stronger competitive superiority to plants that have decreased biomass (Padilla *et al.* 2009; 2013). Therefore, SSP is better adapted to dry environments than ASP and ASP is better adapted to wet environments.

Seed size also influences post-seedling plant growth and reproductive output of amphicarpic species (Sonkoly *et al*. 2017; Larios and Venable 2018; Lázaro and Larrinaga 2018). With an increase in water availability, reproductive biomass increased and SSP produce more reproductive biomass than ASP. However, the production of aerial and subterranean reproductive biomass was different in ASP and SSP. Subterranean reproductive biomass was significantly enhanced in SSP as the water availability increased; however, the ASP was not changed. For aerial reproductive biomass, SSP and ASP were significantly improved as the water availability increased. In amphicarpic species, aerial seeds can be more flexibly produced, and they are more easily affected by biotic and abiotic environments, plant size and geographical location (Kim *et al*. 2016; Nam *et al.* 2017; Zhang *et al.* 2017).

With an increase in water availability, the biomass ratio of subterranean reproduction to total reproduction decreased, indicating that SSP and ASP from *A. edgeworthii* generated a great amount of aerial seeds under moist conditions relative to the subterranean seeds. In *A. edgeworthii* (Zhang *et al*. 2015) and *A. bracteata* (Trapp 1988), aerial seeds possess great dispersal capacity, which facilitates them reaching new sites at a farther areas from their mother plants, thus expanding the geographical area of the population. On the other hand, subterranean seeds are formed/placed in the vicinity of parental microsites, thus maintaining populations in the safe environment (Cheplick 1987, 1994; Zhang *et al*. 2017). Plants of *A. bracteata* grown in moist conditions produced more aerial seeds with a strong dispersal capacity. This enhances the species' ability to occupy new habitats. However, dry conditions causes' *A. bracteata* to increase the production of subterranean seeds that remain *in situ*, allowing them to achieve the goal of maintaining populations in the safe environment. These results indicate that *A. bracteata* modulates the fitness under uncertain environment.

A decrease in water availability leads to the increased weight of subterranean and aerial *A. bracteata* seeds; however, each plant produces less seeds. Such seed number and size trade-off plays an important role for plant propagation. A plant can weigh the benefits by producing small seed in large numbers or producing large seeds in few numbers, and such trade-off impact the life history of plant in various aspects; besides, it also affects the relationships between different species, as well as the community structure (Larios and Venable 2018). Big seed stores tremendous energy, which can allow the progeny growing in a shading environment to survive (Sonkoly *et al*. 2017), whereas the small seeds are advantageous in occupying different habitats (Larios and Venable, 2018; Lázaro and Larrinaga 2018).

Conclusion

Results in this study suggest that the subterranean and aerial seeds-derived *A. edgeworthii* plasticity allows for inhabitation in environments with low to high water availability. *A. bracteata* plant that grows from the subterranean and aerial seeds give the species a mixed reproductive strategy, allowing the species to cope with greater flexibility to different selective pressures.

Acknowledgments

The first author acknowledges the financial grant from the Kunshan Ecological Agriculture (KN1715), and the Northern Jiangsu Science and Technology (SZ-HA2017023).

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