



The characteristics of seed production in an *Adonis multiflora* (Ranunculaceae) population

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Abstract

A natural population of *Adonis multiflora*, a spring ephemeral herb growing in temperate deciduous forests, was studied to determine the seed production characteristics. Plant size, flowering time, and seed number were monitored from February 2009 to May 2011 in main growing season (i.e., from March through May). The biomass rates of the shoot and the root in the *A. multiflora* population were 22-24% and 76-78%, respectively, and the biomass of the root was proportional to that of the shoot. The flowering rate was 60% in the plants with 1 to 2 g of shoot biomass, and 100% in the plants with >2 g of shoot biomass. In the plants with root biomass between 4 and 6 g, the flowering rate was 43% and, in the plants with the root biomass over 8 g, it was 100%. The shoot biomass was a better predictor of the flower production probability than the root biomass. The number of flowers and seeds was closely correlated to shoot biomass at 1% significance level. The size of the plant that produced seed excessively instead of the shoot biomass in one year typically decreased in the next year and *vice versa*. The flowering time and its duration were closely related to the number of faithful seeds but not to that of total seeds. The number of faithful seeds was proportionate to flowering duration and inversely proportionate to flowering time (year day, YD). In a plant, the number of faithful seeds noticeably decreased with the inflorescence (i.e., order of flower in a plant), and this difference between the two successive flowers was significant at the 1% level between the first and the third flower in 2009 and 2011 but not between the third and the fourth. However, the number of total seeds was mostly similar in the first through the fourth flower for all three years.

Key words: *Anonis multiflora*, biomass, flowering time, seed production, shoot, spring ephemeral

INTRODUCTION

Spring-flowering ephemerals of northern hardwood forests have a specific life-history trait; shoot growth and seed production occur simultaneously during a period from snowmelt to canopy closure (Schemske et al. 1978, Nault and Gagnon 1993, Gutjahr and Lapointe 2008). Because of a relatively short epigeous growth period (40-60 days), most of these species are clonal and perennial (Lapointe 2001, Whigham 2004). One way to cope with a short life cycle is early-season growth. This strategy means potentially high risk of encountering weather conditions

unsuitable for plant growth and for pollinator activity, so it is not always profitable (Schemske et al. 1978). Another way would be a late-season growth. However, this strategy is not applicable because spring ephemerals have typical 'sun-plant' photosynthetic characteristics, having high light-saturated rate of photosynthesis and light compensation points (Pearcy and Sims 1994, Rothstein and Zak 2001, Horibata et al. 2007). Moreover, a shortened bright period due to early canopy closure effectively restricts carbon assimilation, which greatly reduced subsequent re-

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productive output due to low photosynthetic production for fruit development and small carbon storage for future reproduction (Lapointe 2001). Spring ephemerals fix the solar energy for survival and reproduction for a short growing period. As a result, the photosynthetic products are not sufficient under unsuitable environment. Nonetheless, small finite carbohydrates must be allocated to two strategies of survival and reproduction. Thus, the correlation between reproduction and storage within plants becomes increasingly negative. Available empirical work indicates that allocation to reproduction vs. storage can be inversely related (Sohn and Policansky 1977). Moreover, the allocation of resources to current reproduction at the expense of survival and future reproduction possibly reflects the selective effects of unpredictable availability of pollinators for this spring ephemeral (Lubbers and Lechowicz 1989).

On the other hand, factors affecting reproduction of plants are very diverse. Physical factors like day length, air temperature, soil water potential, and minerals are important to annual plants' reproduction. However, not only physical factors but also biological factors like age or size are important to perennial plants (Klinkhamer et al. 1992). Especially, plant size is very important for reproduction (Wesselingh et al. 1997). The reproductive potential depends upon the number of pollinated flowers, the number of fertilized ovules, fruit/seed predation, weather conditions, and the ability of the maternal parent to provide the necessary resources for development (Stephenson 1984). Considering the finite photosynthetic products and two strategies mentioned above, reproduction is often a lethal or semi-lethal activity. Many flowers and fruits are green, and a fraction of the energy and carbon might be obtained by direct photosynthesis within these structures (Biscoe et al. 1975, Bazzaz et al. 1979). In most plants, it is difficult to estimate the energy needed for survival separately from reproduction. First, photosynthetic products can be transferred in diverse organs or directions. Second, the reproductive period and whole growing season are largely overlapping. Third, allocation patterns of photosynthetic products between current reproduction and storage for next season should be a crucial life-history strategy (Lubbers and Lechowicz 1989, McKenna and Houle 2000).

Spring ephemerals are a common element of the herb layer and have a short life cycle. Thus, spring ephemerals are worthy of study at a population and community level. In Korea, there were reports on *Corydalis* L. at the population level (Fumariaceae) (Min 2003a, 2003b, Kim et al. 2006) and a study on the life cycle of several ephemerals

in deciduous forest was published as well (Cho 1998). However, studies about spring ephemerals are largely insufficient. *Adonis multiflora* produces several bisexual flowers, which lack the nectar gland in perianth (Lee et al. 2003). This plant species is pollinated by the fly, so there is no limitation on pollinators at cool air temperature in early season (Kudo et al. 2004).

The aim of the present study was to examine the seed production in a natural *A. multiflora* population in relationship with plant size and look at other factors that affect seed production in this plant species.

MATERIALS AND METHODS

Study area, study period and plants studied were as previously reported (Min 2014). When all petals (corolla) fell, fruit was wrapped in nylon mesh to prevent loss of the seed. When half of the leaves was changed to yellow in late growing season (15-25 May), the shoots of all plants surveyed (including receptacle and peduncle) were harvested. Except for seeds, the shoot was oven-dried at 85°C for 48 h and weighed. Seeds were divided into two groups according to their length and then counted. Seeds over 3 mm and globular were faithful, and those under 3 mm and flattened were insufficient. However, the insufficient seeds were mostly below 2 mm in length and the size difference between the two groups was clear. To check the biomass of its shoot and root, 94 plants were excavated on May 15, 2009. The sample was classified into two groups of flowering and non-flowering plants regardless of number of flowers. The samples were then divided into shoot and root. All samples were oven-dried at 85°C for 48 h and weighed. Over-flower (i.e., flower = faithful seed) and under-flower product plants were classified as follows: in over-flower product plant, the plant's shoot biomass was smaller than y ($y = ax + b$; y = shoot biomass; x = number of flowers or faithful seeds each year); in under-flower product plant, the plant's shoot biomass was larger than y ($y = ax + b$; y = shoot biomass; x = number of flowers or faithful seeds each year).

RESULTS AND DISCUSSION

Plant size and seed production

In 94 plants, the biomasses of shoot and root were in the range of 0.014–6.538 g and 0.005–12.038 g, respectively. Thus, the range of sizes was broader in the latter than

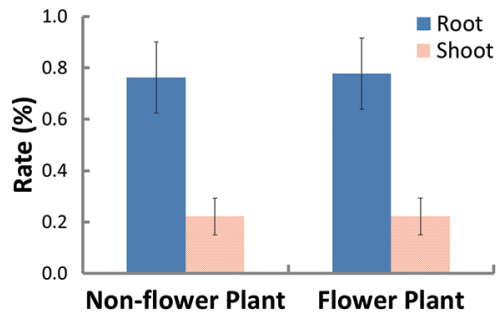


Fig. 1. Rates of the shoot biomass and root biomass to the total biomass.

in the former. The rates of shoot and root were 22% and 78% in non-flowering plants, and 24% and 76% in flowering ones, respectively (Fig. 1). Thus, biomass was larger in the root than in the shoot, regardless of flower production. The biomass of the root was closely related to that of the shoot or total plant (Fig. 2). Correlation coefficients (CC) between the two biomass elements of the shoot, root, and total plant were over 0.6 and significant at the 1% level, except for the CC between shoot/root rate and total plant (Table 1). CCs were higher in the biomass elements of non-flowering plants than in those of flowering

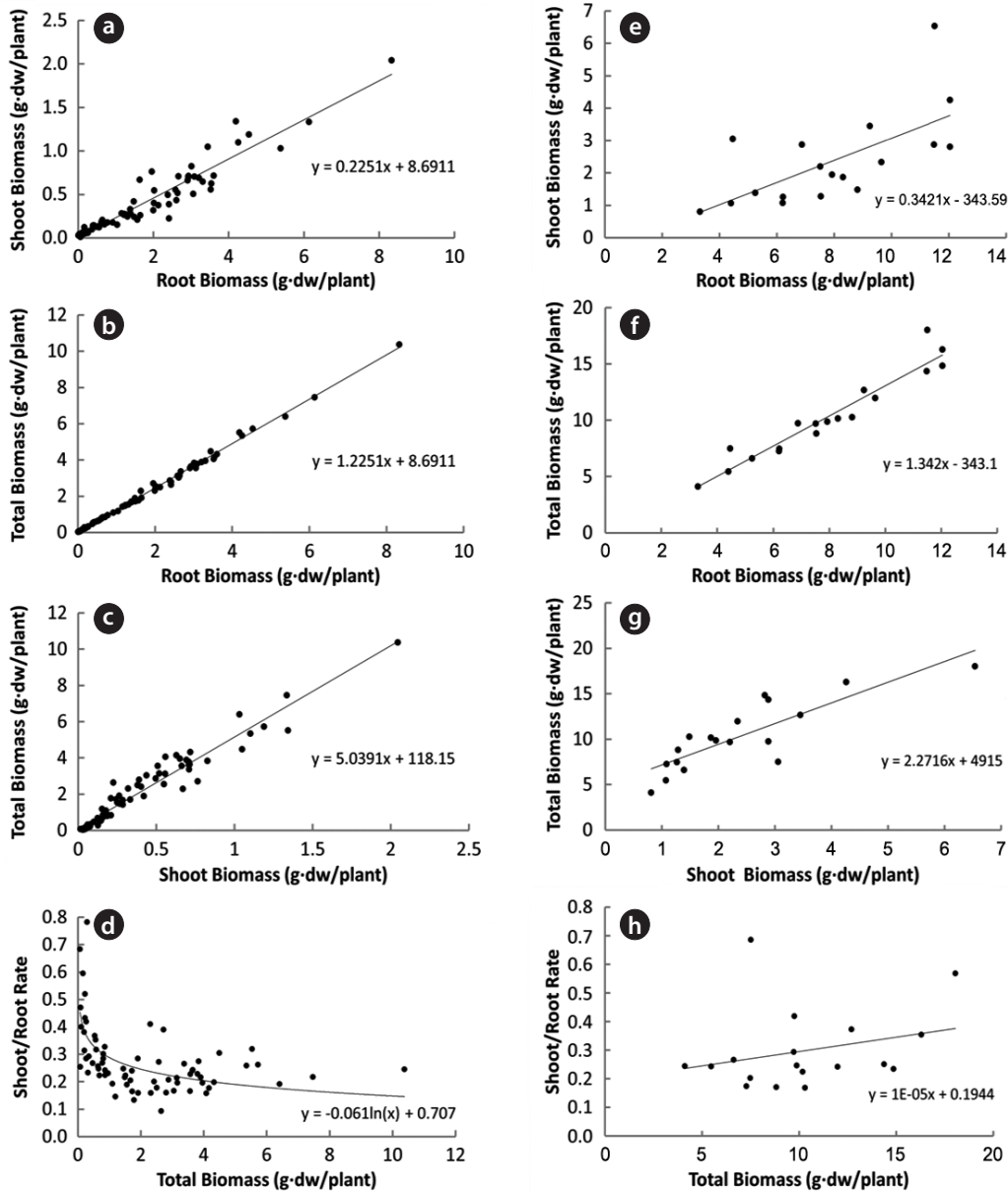


Fig. 2. Relationship between the biomass of shoot, root, or total plant and root/shoot rate in flowering (a-d) and non-flowering (e-h) plant. (a,e) root biomass and shoot biomass, (b, f) root biomass and total biomass, (c, g) shoot biomass and total biomass, and (d, h) total biomass and shoot/root rate. The unit "g-dw" represents "g dry weight".

ones. CC between root and total plant biomasses of non-flowering plants was the highest while CC between shoot and root biomasses in flowering plants was relatively low. However, in non-flowering plant, shoot/root rate was reversely proportionate to the total biomass with the regression line between these two elements being a curve rather than a line. Three conclusions could be drawn from these

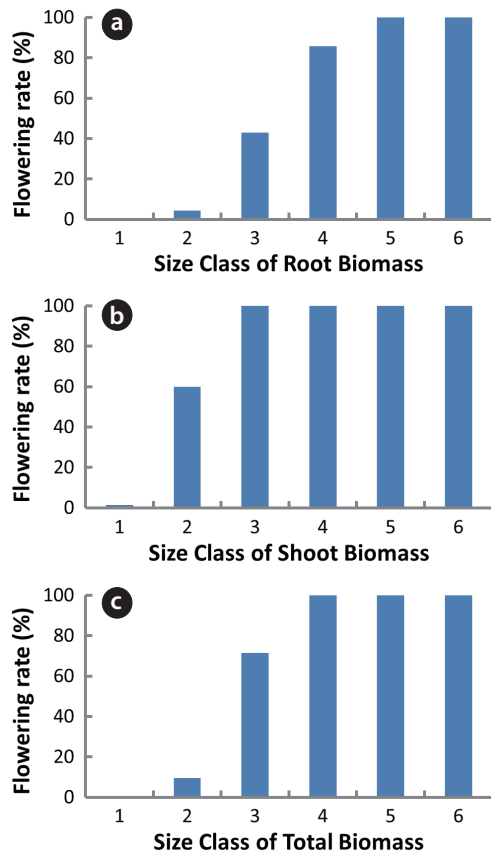


Fig. 3. Flowering rate based on the size class of the (a) root biomass, (b) shoot biomass, and (c) total biomass. Root size classes (a) were determined by their biomass as follow: 1, <2.0 g; 2, 2.0-4.0 g; 3, 4.0-6.0 g; 4, 6.0-8.0 g; 5, 8.0-10.0 g; 6, >10.0 g. Shoot size classes (b) as follows: 1, <1.0 g; 2, 1.0-2.0 g; 3, 2.0-3.0 g; 4, 3.0-4.0 g; 5, 4.0-5.0 g; 6, >5.0 g. Total size classes (c) as follow: 1, <3.0 g; 2, 3.0-6.0 g; 3, 6.0-9.0 g; 4, 9.0-12.0 g; 5, 12.0-15.0 g; 6, >15.0 g. The gram (g) unit is g dry weight.

Table 1. Correlation coefficients between the two biomass factors of the shoot (S), the root (R), the shoot/the root rate (S/R) and the total plant (T) of *Adonis multiflora*

Plant status	Organ (dry weight)			
	S-R	R-T	S-T	(S/R)-T
Non-Flowering (n = 76)	0.954*	0.998*	0.970*	-0.618*
Flowering (n = 34)	0.660*	0.960*	0.843*	0.274

*indicates significantly different at the 1% level; n = number of plants which were dug out in the field and analyzed.

results. First, *A. multiflora* allocated the energy to the root more than to the shoot. Spring ephemerals largely store current foliage photosynthetic products in the below-ground parts for survival and future growth (Horibata et al. 2007), so *A. multiflora* was thought to behave similarly. Second, the flower production changed the energy allocation or shoot/root ratio in the plants. This might be a result of excessive energy investment into reproductive organs in flowering plants. Third, the shoot/root biomass rate was relatively large in young plants and small in mature ones. These findings imply that the carbohydrates of the root at early-growing season and photosynthetic products of leaves at late-growing season move to reproductive organs instead of the leaves or root.

Ninety-four plants were also divided into 6 classes based on shoot, root and total biomasses and the flowering rate of each class was calculated (Fig. 3). In the 2.0-4.0 g root biomass, flowering rate was 5% while it was 100% in the root biomass over 8 g. In the shoot biomass below 1 g, the flowering rate was under 1%; in 1.0-2.0 g of the shoot biomass, the flowering rate was 60%; and over 2 g of the shoot biomass, it was 100%. In the 3-6 g of total plant biomass, the flowering rate was 10%; in 6-9 g, 71%; and over 12 g, 100%. Thus, the flowering rates increased with the increase in all biomasses. However, the increasing trend was gentle with root biomass, but it was steep with shoot or total biomass. Thus, the shoot biomass was the best predictor of flower-producing ability of a plant. A minimum plant size is required before sexual reproduction occurs (Thompson et al. 1991, Schmid and Weiner 1993). Thus, our results in *A. multiflora*'s population are in agreement with other plants.

During the three years, the number of fruits, faithful seeds, and total seeds were proportionate to the shoot biomass (Fig. 4). The CCs were significant at the 1% level for all three years (Table 2). Thus, the relationship between the biomass elements and reproductive factors were highly positive. However, considering faithful seeds and other reproductive elements separately, the shoot biomass and number of fruits were more closely related to the number of total seeds than that of faithful ones. Thus, shoot size, number of flowers, and total seeds appear to be determined by the same factors, and the faithful seeds might be analyzed by other methods. The former was mostly fixed before germination and might be affected by root biomass, genetic factors, or embryological properties. Shoot embryos of spring ephemerals are completed in the previous year's autumn and the maximum number of ovaries in a fruit is genetically fixed (Lapointe and Lerat 2006). The shoot growth in early season was affected by

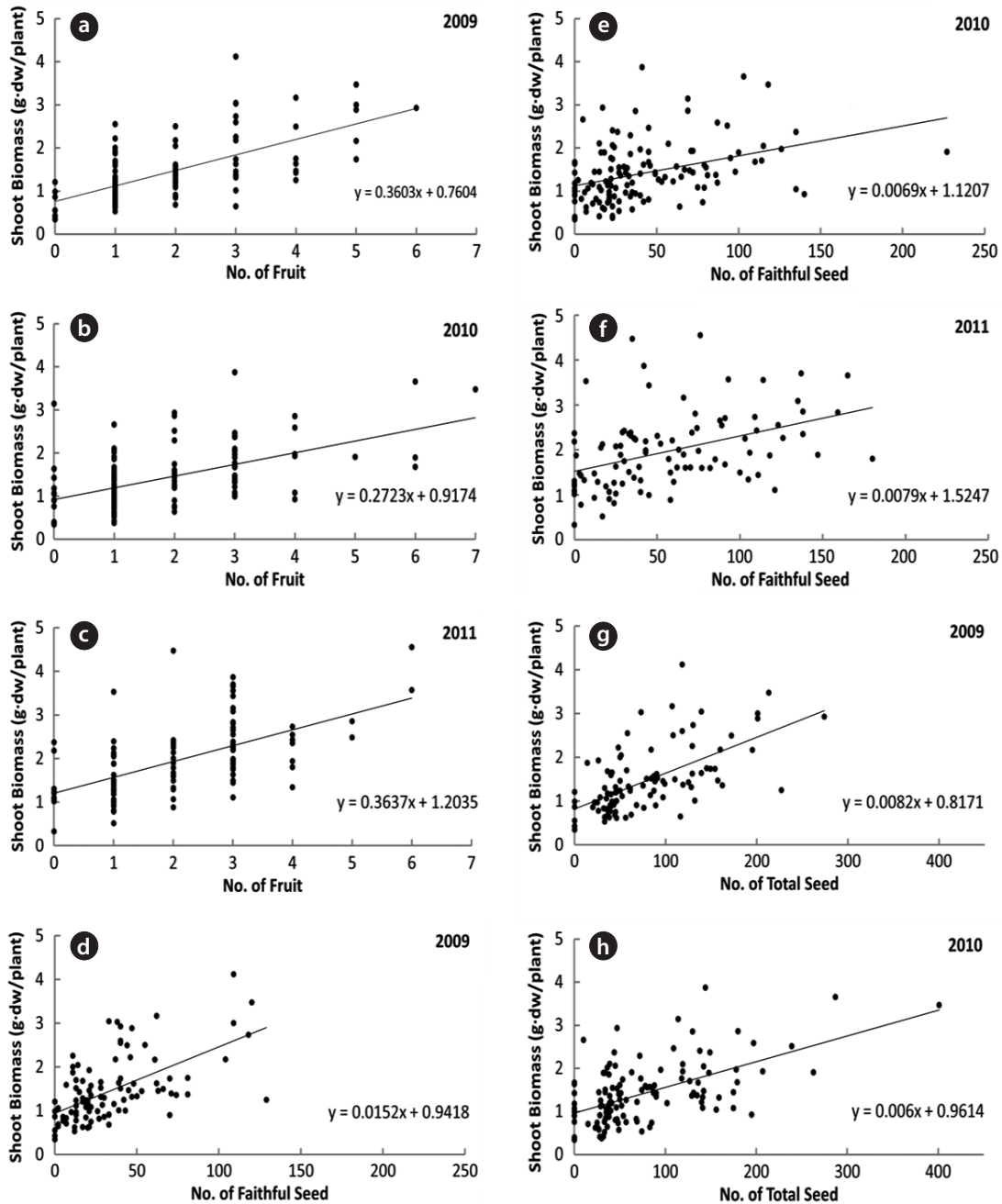


Fig. 4. Relationship between the plant size and the number of fruits or seeds produced for three years (2009–2011). Relationship between the number of fruit and shoot biomass (a–c), number of faithful seed and shoot biomass (d–f), number of total seed and shoot biomass (g–i), number of fruit and faithful seed (j–l), and numbers of fruit and total seed number (m–o). The unit “g-dw” represents “g dry weight”.

Table 2. Correlation coefficients between the two factors of number of seed, number of fruit and shoot biomass

Year	Shoot biomass			No. of fruit	
	No. of fruit	No. of faithful seed	No. of total seed	No. of faithful seed	No. of total seed
2009 ($n = 100$)	0.643	0.588	0.620	0.651	0.950
2010 ($n = 130$)	0.537	0.379	0.573	0.751	0.864
2011 ($n = 99$)	0.579	0.422	0.540	0.739	0.903

All numbers are significantly different at the 1% level; n = number of plants.

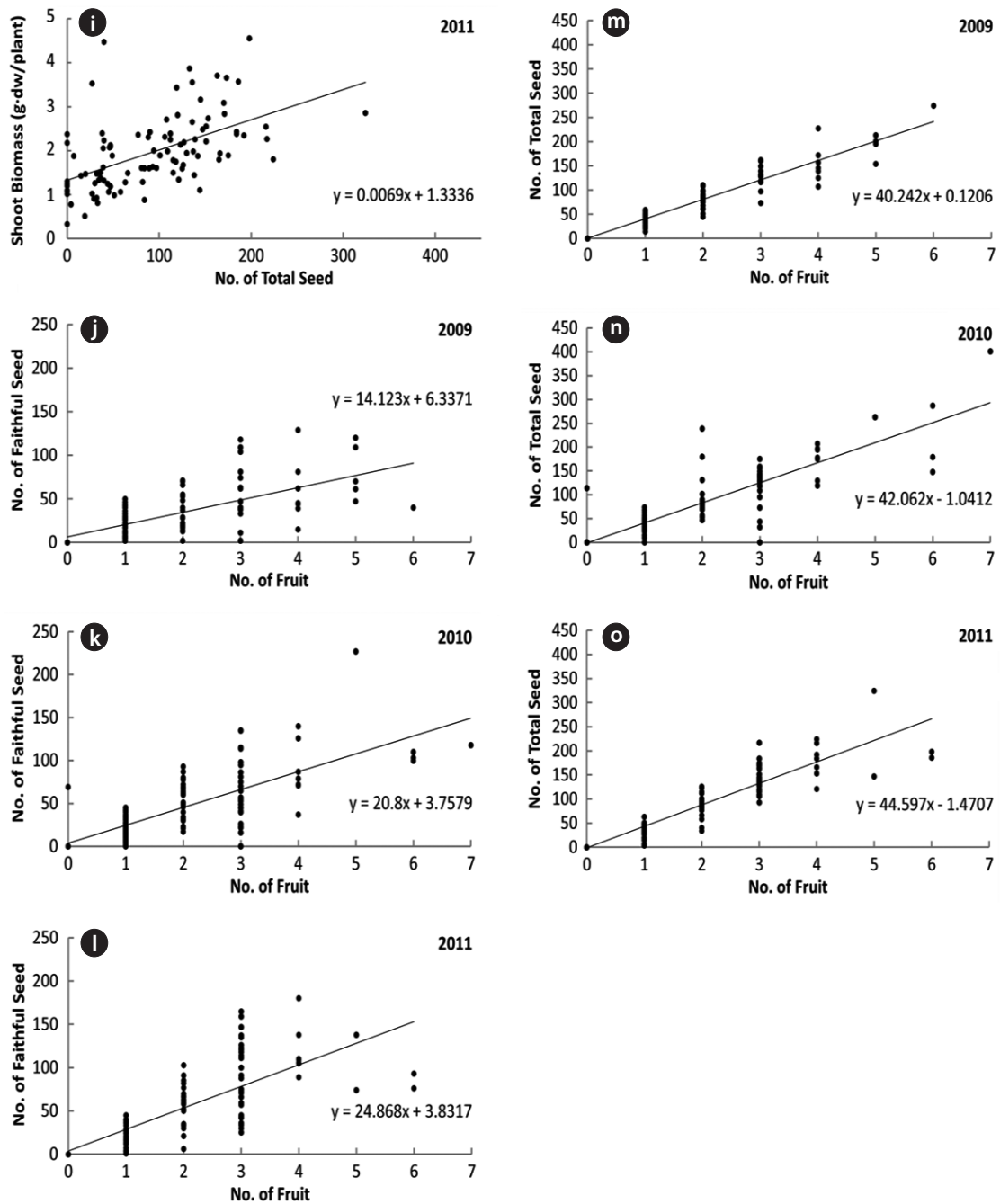


Fig. 4. continued.

the energy stored in root. However, the faithful seeds were provided the energy from photosynthetic organs during the current growing season. Thus, the number of faithful seeds seems to be influenced by photosynthetic products during the fruiting period. A strong positive correlation between plant size and reproductive output were revealed by many authors (Klinkhamer et al. 1992, Schmid

and Weiner 1993, Obeso 2002), but the relationship between plant size and reproductive effort has received little attention (Verburg et al. 1996).

Seed production and other properties

In the flowering plants for two consecutive years, the

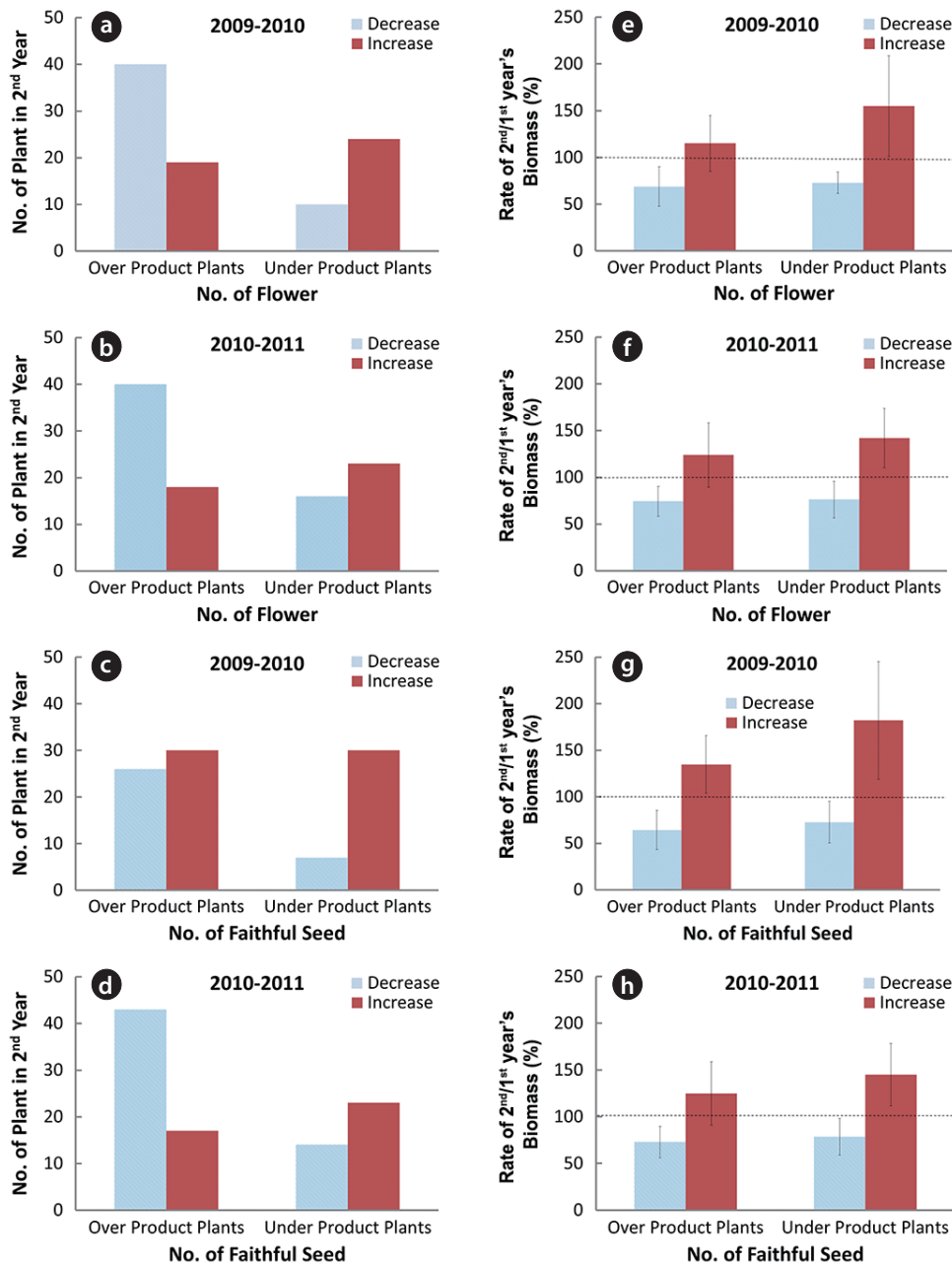


Fig. 5. The change of shoot biomass between the two years, 2009-2010 and 2010-2011. Over product plants are smaller than average shoot size plant; under product plants are larger than average plant. Dotted line indicates 100%, i.e., average size of plant. Relationship between the number of plant and reproductive organs (a-d), the rate of plant biomass and reproductive organs (e-g), the number of flower and amount of plant (a, b, e, f), and the number of faithful seed and amount of plant (c, d, g, h).

relative shoot biomass changes between over-flower (faithful seed) product plant and under-flower (faithful seed) one were prominent. The over-flower product plant in one year showed mostly small shoot biomass in the next year and *vice versa* (Fig. 5). The number of over-flower product plants in 2009 was 59, and their shoot biomass was small in 40 plants and large in 19 plants in 2010. The

number of over-flower product plants in 2010 was 58, and their shoot biomass was small in 40 plants and large in 18 plants in 2011. However, the number of under-flower production plants in 2009 was 34, and their shoot biomass was small in 10 plants and large in 24 plants in 2010. The number of under-flower production plants in 2010 was 39, and their shoot biomass was small in 16 plants

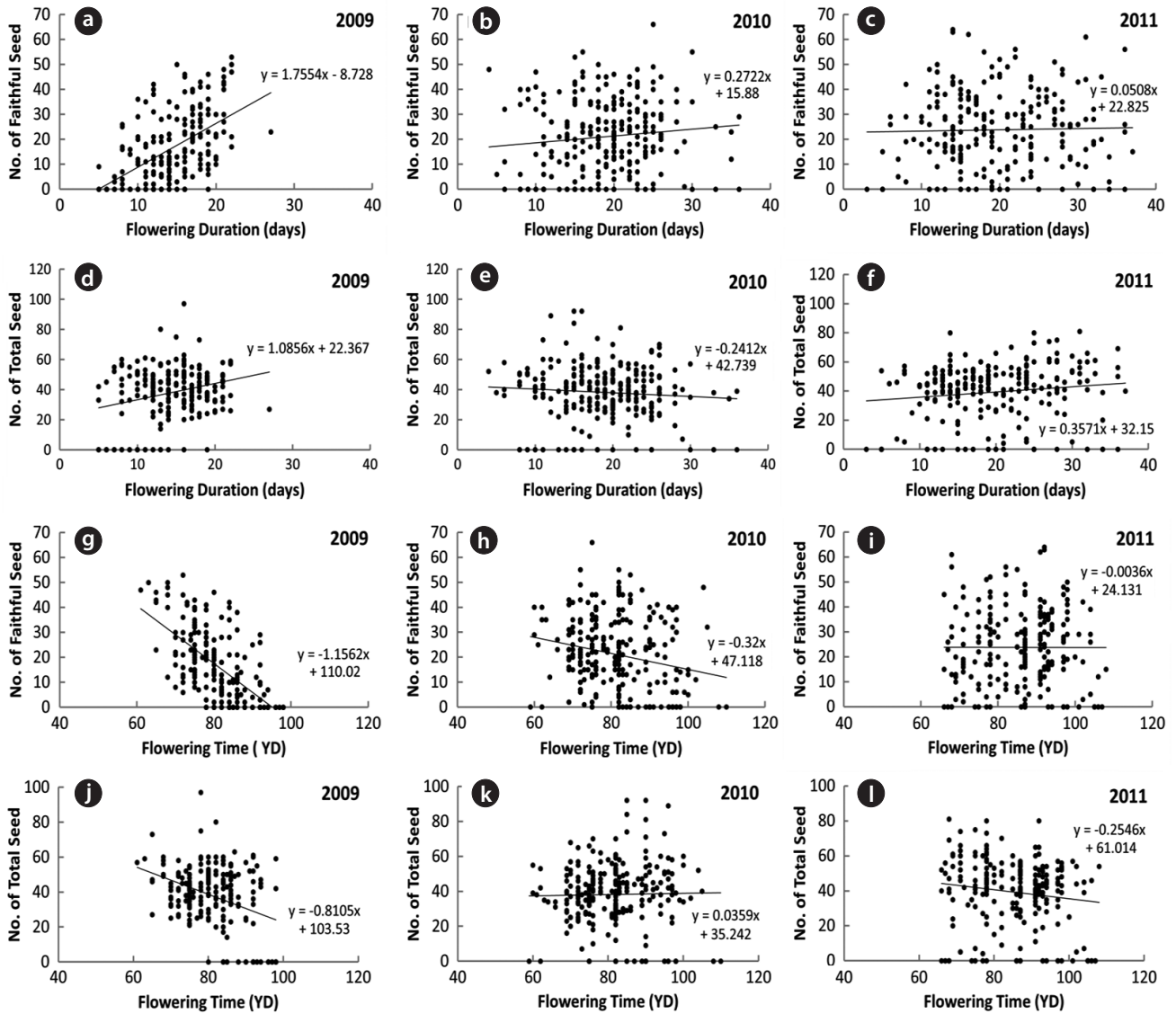


Fig. 6. Relationship between the flowering duration, flowering time and seed production. (a-c) flowering duration (day) and the number of faithful seed, (d-f) flowering duration and the number of total seed, (g-i) flowering time and the number of faithful seed, and (j-l) flowering time and the number of total seed.

and large in 23 plants in 2011. The results of faithful seeds were similar to those of flowers. On the other hand, the percentage of over-flower product plants (mean ± SD) in 2009 changed into 68.8 ± 21.2 in small plant and 115.0 ± 29.8 in large plant in 2010. The percentage of under-flower product plants in 2009 changed into 72.9 ± 11.4 in small plant and 154.8 ± 53.9 in large plant in 2010. Thus, the rate of shoot biomass clearly decreased in over-flower product plants (32.2%) and increased in under-flower ones (54.8%).

Based on these results, *A. multiflora*'s production of flowers and faithful seeds in one year appears to affect its shoot biomass in the next year. Flowering in plants

increases the risk of mortality and the cost of fruit production is evident in terms of small leaf area in subsequent years (Primack and Stacy 1998). When the leaves of *Trillium grandiflorum* were removed, the number of seeds production was not affected, however, the survival rate and plant size noticeably decreased in the following year (Lubbers and Lechowicz 1989). However, when the flowers of *Adonis ramosa* received insufficient sunlight, the number of seeds produced severely decreased, while plant did not change its size (Horibata et al. 2007). Thus, between reproductive and vegetative organs, one that is more affected by restriction in photosynthetic products availability is different in the same *Adonis* along the spe-

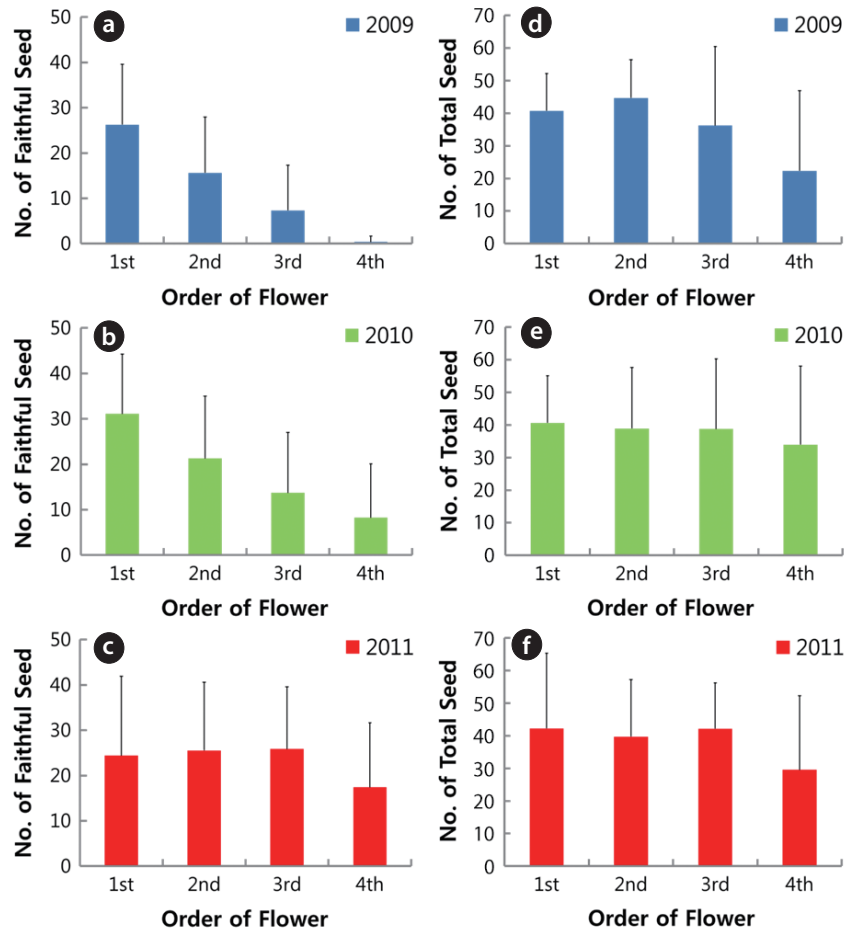


Fig. 7. Seed production based on the order of the flower in a plant for three years (2009-2011). Faithful seed production (left, a-c) and total seed production (right, d-f).

cies. The change of *A. multiflora*'s shoot biomass in the next year seems to be closely related to reproduction. However, the organ most severely affected by reproduction in *A. multiflora* population was not surveyed and this subject needs further studies.

The number of seeds (faithful and total) produced was related to flowering duration in 2009 (Fig. 6). The longer the flowering duration lasted, the more seeds were produced. CC between the number of seeds and flowering duration was significant at the 1% level. However, there was no significant relationship between flowering duration and seed production in 2010 and 2011 (Table 3). Thus, the number of seeds produced was only partly related to the flowering duration. On the other hand, the flowering time affected the number of seeds (faithful and total) in 2009 with CCs between the two factors significant at the 1% level. The earlier flowering time started, the more seeds were produced. However, the relationship between the flowering time and the number of seeds was not evi-

dent in 2010 and 2011. Thus, as for flowering duration, the relationship between the flowering times and the number of seeds was not clear. As previously reported, low air temperatures below 0°C lasted for several days in mid-March of 2010 and 2011, but not in 2009. These low temperatures appear to severely affect the time and duration of flow-

Table 3. Correlation coefficients between the number of seed and the flowering factors

Flowering Factor	Year	No. of seed	
		Faithful seed	Total seed
Flowering duration (day)	2009 ($n = 202$)	0.534*	0.267*
	2010 ($n = 252$)	0.109	-0.079
	2011 ($n = 232$)	0.025	0.137
Flowering time (YD)	2009 ($n = 202$)	-0.640*	-0.363*
	2010 ($n = 252$)	-0.211*	0.019
	2011 ($n = 232$)	0.002	-0.134

* indicates significantly different at the 1% level; n = number of flowers.

ering. Typically, the natural flowering time maximizes the reproductive output and long flowering duration is favorable to fruiting (Shitaka and Hirose 1998). In spring ephemerals, the earlier flowering time started, the longer flowering duration lasted. However, in early-flowering populations, the low activity of pollinators may result in a quantitative pollen limitation due to low visit frequency under cool conditions, so that flowering in early-season is not always advantageous (Kudo 1993). Flowers with longer duration could receive more energy than those with the short duration ones. Thus, the flowering duration is important in the seed production of spring ephemerals, whose life cycle is short (McKenna and Houle 2000, Rothstein and Zak 2001).

The number of faithful seeds was closely related to inflorescence (the order of flower in a plant), except in 2011 (Fig. 7). The numbers of faithful seeds from first to fourth flower were 26.2 ± 13.4 , 15.6 ± 12.3 , 7.3 ± 10.0 , and 0.4 ± 1.3 , respectively, in 2009; and 31.1 ± 13.2 , 21.3 ± 13.7 , 13.7 ± 13.3 and 8.2 ± 11.9 , respectively, in 2010. The differences in seed number between the two consecutive inflorescences from first to fourth flower were significant at the 1% level. However, the total seeds were similar in the first through fourth flowers and the differences in the inflorescence were not significant at the 1% level, except for the result in 2009. Based on this, the number of ovule per flower of *A. multiflora* appears to be generally fixed. However, the energy invested in reproductive organs decreased with growing season, so that the first flower received a good deal of energy, while the last one did not. The first flowers to open have a very high probability of initiating fruit, but the last flowers almost never set (Stephenson 1981). Moreover, to cope with the energy shortage, the floral photosynthetic energy moves and is stored to seeds in various herbs, including *A. ramosa* and *Spiranthes cernua* (Bazzaz et al. 1979, Antlfinger and Wendel 1997, Guido and Hardy 2003, Horibata et al. 2007). Accordingly with the shortage of energy, the total number of seeds produced per plant does not increase with the number of flowers under natural conditions (Nishikawa 1998). However, removal of leaf or floral bract tissues did not affect mean seed set, but leaf removal did reduce allocation of biomass and nonstructural carbohydrates to rhizomes in *T. grandiflorum* (Lubbers and Lechowicz 1989). As for *A. ramosa* above-mentioned, further studies are needed to see whether the floral photosynthetic products are stored in seed in *A. multiflora* as well.

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