Seed mass variation in the perennial herb *Asphodelus albus*: sources of variation and position effect

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Abstract. Patterns of seed mass variation in the perennial herb *Asphodelus albus* (Liliaceae) were studied in one population over 3 years (1988–1990) and in three populations during 1989. Plant size, phenology and several components of plant fecundity showed no effect on mean seed mass per plant. Mean seed mass varied among populations and among plants within populations. Significant variation was also found among years and among plants within year, but most of the variation was accounted for by the within-plant component. Within-fruit variation may be as important as between fruits within plant. Fruit position within the plant influenced seed mass, being heavier the seeds at the bottom of the stalk. However, the plants markedly differed in the proportion of the variation accounted for by the position effect. The correlation between seed number per fruit and seed mass showed an interaction with fruit position. Seeds from small broods were heavier than those from large ones, but only in the lower part of the stalk. Decline in seed mass towards the top of the stalk may be attributed to seasonal reduction in resource availability. In addition, the change in the relationship between seed number and mass might be due to changes in the "resolution" of the parent-offspring conflict, also related to nutrient availability.

Key words: Seed mass variation – Position effect – Perennial herb – *Asphodelus albus* – Liliaceae

Many studies have shown that the size of seeds varies considerably within and among plants at a site (Thompson and Pellmyr 1989; Winn 1991) and at different places (Winn and Werner 1987; Ågren 1989). Many explanations have been proposed for these differences, including the following. The variation may be dependent on the trade-off in resource allocation between seed size and number (Smith and Fretwell 1974; Wilbur 1977; Winkler and Wallin 1987; Uma Shaanker et al. 1988; Venable 1992), or on variable genetic quality among offspring (Temme 1986). Another hypothesis suggests that variation may be favored in a heterogeneous environment (Janzen 1977). It has been also proposed that selection on seed mass may be weak or variable among years so that directional selection does not take place (e.g. Thompson 1984).

Seed size has been shown to be influenced by, for example, plant size (Aker 1982; Nakamura 1988), plant density (Matthies 1990), phenology (Roach 1986; Agren 1989), resource availability (Willson and Price 1980; Herrera 1990), defoliation (Bentley et al. 1980; Stephenson 1980; Crawley and Nachapong 1985), and maternal effect (Roach and Wulff 1987; Mazer 1989a, b; Schwaegerle and Levin 1990). The proportion of variance in seed mass explained by the within-plant component was usually high (Thompson 1984; Wolf et al. 1986), and these observations conflict with the models predicting a single optimum seed size (Smith and Fretwell 1974; Wilbur 1977). Sources that may contribute to within-individual variation in seed mass include the number of developing ovules within a fruit (Stanton 1984; Wulff 1986), phenology (Thompson and Pellmyr 1989; McGinley 1989), paternal effect (Antonovics and Schmitt 1986; Thompson and Pellmyr 1989; Andersson 1990; Richardson and Stephenson 1991). The position within the parent (Hendrix 1979; Nakamura 1986) or within the fruit (Schaal 1980; Nakamura 1988; Rocha and Stephenson 1990) may be another source of within plant variation.

This paper reports a field study of sources of variation in seed mass in the perennial herb *Asphodelus albus* Miller (Liliaceae). The observational study considered the effects of flowering phenology, a number of variables related to fruiting ecology and position on the parent plant. The effect of defoliation was investigated experimentally. The results are discussed in relation to the parent-offspring conflict.

Material and methods

The seeds were collected from three populations (Table 1) of *Asphodelus albus* located in northern Spain (Asturias province). The

Table 1. Variation in seed mass (mg) in three populations of *Asphodelus albus* in northern Spain

Naranco (forest, 540 m)	14.58 ± 2.77 (2162)
Ambás (meadow, 65 m)	17.31 ± 3.31 (830)
Moandi (pasture, 660 m)	15.35 ± 2.54 (550)
Naranco 1988	12.64 ± 3.50 (430)
Naranco 1989	14.58 ± 2.77 (2162)
Naranco 1990	12.63 ± 3.14 (1383)

The Naranco population was sampled from 1988 to 1990, and the remaining populations were sampled in 1989

Results are given ± SD, with *n* in parentheses

Naranco population was sampled from 1988 to 1990, and the other populations were sampled in 1989. At all sites *A. albus* was the most abundant species of the ground layer. The population at Naranco was from an area shaded by a chestnut forest, while the other populations were in open areas (meadows). At Naranco, 30–50 plants were tagged each year at the beginning of flowering and monitored for fruit and seed production. I visited this population at 5 to 10-day intervals until fruit maturation and the numbers of flowers and developing fruits were recorded. Tagged plants were collected at the time of fruit maturation (late June). The numbers of fruits, seeds and flowers (the peduncles or the flowering scars remain on the stalk) produced per plant were recorded. The dry weight of the overwintering structures (swollen root tubers) was determined. The seeds were dried at 50° C until a constant weight was obtained and were weighed individually to the nearest 0.1 mg.

To test whether phenological variables influenced mean seed mass I used the date of beginning and end of flowering relative to the rest of plants tagged. The difference between these variables was the flowering span or the total number of days a plant was in flower. The ratios of fruit to flower and seed to ovule were calculated, taking into account that each flower invariably produced six ovules.

In order to test the influence of nutrient availability on seed size, the nutrients available to plants were manipulated. Defoliations were performed at the timing of flowering (50 or 75% of the leaves were removed) on 30 plants at the Naranco site.

Results are expressed as mean weight per seed ± 1 SD, and the sample sizes are given in brackets. The differences between means were tested on untransformed data by ANOVA. In some analyses the design was not balanced, but the data were normally distributed and the variances were homogeneous. Nested ANOVAs with all effects treated as random were used to partition the variation among sources. Position effects on seed mass within the stalk were examined by simple linear regression, considering fruit position as a continuous variable. A two-factor ANOVA was used to test for

significant differences in seed mass due to fruit position and number of seeds per fruit. Taking into account that fruit position may influence seed mass, only the upper or the lower part of the stalk of any one plant was considered. Half of the plants were randomly assigned to upper position and the remaining plants were assigned to lower position, so data used to test both factors were independent. Seed mass refers to individual seed mass.

Results

In 1989, seed mass varied five-fold in the three populations taken together, from 6.1 to 29.5 mg. The overall mean was 15.35 ± 3.21 (3542). Seed mass varied up to four-fold within populations. Seed mass significantly varied between populations and between plants within population (Table 2). A nested ANOVA showed that 13% of the total observed variation was due to variation among populations, 31% was due to variation among plants within populations, and 56% was due to variation within plants. In the population at Naranco, seed mass varied significantly among years and among plants within years (Table 3). However, the total variance accounted for by the variation within plants was greater (61%) than either that among years or among plants within years. The lowest proportion of total variation was that among years.

Three nested analyses of variance, based on seed masses from the Naranco population in 1989, were used to test the relative contribution to variation in seed mass among and within plants (Table 4). In order to avoid the possible effect of number of seeds per fruit on mean seed mass per fruit, fruits with the same number of seeds were selected. The same number of fruits was used per plant. There were significant differences in the seed mass among plants and among fruits within plants. However, the percentage of the total variation accounted for by the sources of variation differed among analyses because they used different samples. Nevertheless, within-fruit variation may be as important as that between fruits within plants.

Taking into account the fact that position within the stalk affects fruit maturation (Obeso 1993) I tested for

Table 2. Proportion of the total variation in seed mass that was due to variation among populations, among plants within population and within individuals (error) of *A. albus*

Source of variation	df	MS	F	P	Percent of total
Population	2	94388.32	5.04	0.014	12.9
Plant (population)	27	18738.34	30.13	0.000	30.9
Within-plants	1588	621.98			56.2

Results from the random-effects nested ANOVA are also included

Table 3. Proportion of the total variation in mean seed mass that was due to variation among years, among plants within year and within plants (error) in the Naranco population

Source of variation	df	MS	F	P	Percent of total
Years	2	66492.75	3.63	0.038	7.57
Plants (year)	31	18295.34	31.21	0.000	33.35
Within-plants	1893	586.25			59.08

Results from the random-effects nested ANOVA are also included

Table 4. Results of the nested ANOVA for the variation in seed weight between plants and between fruits within plants, with the percentage of variation accounted for by each source of variation

Source of variation	df	MS	F	P	Percent of total
12 plants, 3 fruits per plant, 3 seeds per fruit					
Plants	11	3112.84	4.229	0.002	34.22
Fruits (plants)	24	736.03	1.870	0.022	14.79
Within fruits	72	393.55			50.99
6 plants, 2 fruits per plant, 4 seeds per fruit					
Plants	5	3329.90	9.294	0.009	66.78
Fruits (plant)	6	358.29	2.820	0.023	10.40
Within fruits	36	126.94			22.82
3 plants, 4 fruits per plant, 4 seeds per fruit					
Plants	2	6160.19	7.786	0.011	53.93
Fruits (plant)	9	791.24	6.679	0.000	27.03
Within fruits	36	118.47			19.04

Table 5. Relationship between seed weight and fruit position within the stalk (from bottom to top)

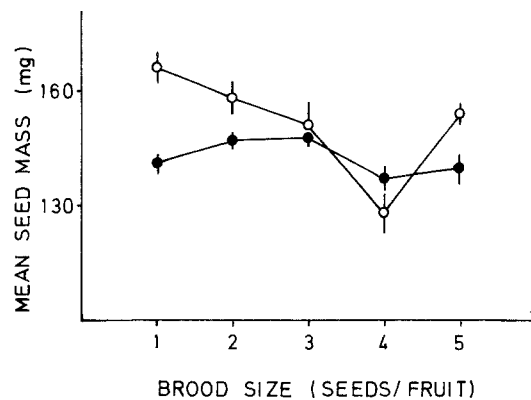| Plant number	Sign of b	r^2	F	df	P	
5	—	0.3075	15.982	1, 36	0.0003	***
6		0.0000	0.000	1, 111	0.9868	NS
7	—	0.4235	38.938	1, 53	0.0000	***
8	—	0.4042	29.174	1, 43	0.0000	***
9	—	0.5981	74.415	1, 50	0.0000	***
10	—	0.4970	33.594	1, 34	0.0000	***
12		0.0405	2.827	1, 67	0.0973	NS
15	—	0.1865	10.548	1, 46	0.0022	**
16	+	0.1537	7.083	1, 39	0.0112	*
17	—	0.1041	5.112	1, 44	0.0288	*
18	—	0.2608	7.056	1, 20	0.0152	*
19	—	0.4048	36.735	1, 54	0.0000	***
20		0.0154	1.501	1, 31	0.2297	NS
21	—	0.0531	4.599	1, 82	0.0349	*

Separate calculations were performed for 15 individual plants

Table 6. Results of the ANOVA considering the effects of fruit position (lower fruits vs. remaining fruits) and the number of seeds per fruit (one to four) on seed mass

Source of variation	df	MS	F	P
Fruit position	1	6562.896	6.212	0.013
Seeds per fruit	3	2955.151	2.797	0.026
Position × Number	3	14259.906	13.497	0.000
Residual	342	1056.543		
Total	349	24834.496		

The two levels of fruit position are dependent within individuals (see text), so upper and lower fruits were randomly taken from different plants to obtain independent cells

Fig. 1. Variation in mean mass of individual seeds according to brood size (seeds per fruit) and fruit position on the stalk (*open dots*, six lowest positions; *filled dots*, remaining fruits). *Vertical lines* are ±1 SE

position effects on seed mass by regression analyses of individual seed mass against fruit position within the stalk (from bottom to top). Since plants differ significantly in the mass of their seeds, separate calculations were performed for individual plants (Table 5). Most of the plants showed position effects and the mass of the seeds decreased towards the top of the stalk. However, the

plants differed in the proportion of the variance explained by the regression (r^2 ranged from 0.05 to 0.60) and some plants showed no position effect.

Some variation in seed mass per fruit might result from a negative relationship between seed mass and seed number. However, I found no relationship between mean seed mass per fruit and number of seeds per fruit. As a position effect had been demonstrated, I considered separately the six lowest fruits in the inflorescences and the remaining fruits. The results of the two-factor ANOVA showed that both seed number and fruit position had significant effect on seed mass (Table 6). There was also a significant interaction between the two factors. Mean seed mass decreased as seed number per fruit increased in the lower fruits of the inflorecences, but there was no variation in the remaining fruits (Fig. 1).

Defoliation had no effect on seed weight ($F_{(1,547)} = 2.4129$, $P = 0.1214$). Mean seed weight ±1 SD was 14.69 ± 3.39 (152) in control plants and 14.01 ± 3.16 (152) in plants defoliated.

No significant correlations were found between the mean seed mass per plant and a number of plant characteristics related to flowering and fruting in either of the three study years (Table 7).

Table 7. Pearson product-moment correlation coefficients between mean seed mass and a number of variables related to flowering and fruiting in the Naranco population from 1988 to 1990

	1988 ($n=14$)	1989 ($n=46$)	1990 ($n=27$)
Below-ground plant dry mass	0.1084	0.1265	0.2565
Number of flowers	-0.1413	-0.0875	-0.4229
Number of fruits	0.1846	0.1365	-0.3879
Number of seeds	0.1100	0.1226	-0.2977
Fr/Fl ratio	0.2968	0.1875	-0.3136
S/O ratio	-0.0555	-0.0840	0.2612
Beginning of flowering	-0.0362	0.3310	-0.2008
End of flowering	-0.0438	0.2129	-0.0164
Flowering span	-0.0124	-0.2544	0.2329

According to the sequential Bonferroni test none of the coefficients is significant ($P<0.05$)

Discussion

In *A. albus* a considerable variation in seed mass was observed within individuals and within fruits within individuals, indicating that parents do not provision all developing ovules (seeds) equally.

The fact that between-year differences were found in one population suggests that at least a proportion of the variation between localities may be due to environmental effects. However the variation between years was relatively low. Contrary to the findings of Ågren (1989) in *Rubus chamaemorus*, the shaded population (Naranco) of *A. albus* had the lowest mean seed mass. Seed mass variation due to individual differences was not as important as within-individual variation, despite genetic and microenvironmental differences among individual plants. Plant size, which is usually related to reproductive output (Weiner 1988; Kang and Primack 1991), had no effect on seed size in this species. On an individual plant basis, trade-off between seed number and seed mass was not demonstrated. Byrne and Mazer (1990) detected no trade-off between seed mass and number within infrutescences of *Phytolacca rivinoides*, although they suggested that the trade-off may be manifested at the level of an entire plant.

Other components of plant fecundity such as number of flowers or fruits showed no influence on mean seed mass per plant in *A. albus*. Flowering phenology of the individuals did not influence mean seed mass per plant. However, flowering phenology within individuals affected seed mass, since seeds from more basal fruits were derived from flowers opening earlier in the season and were heavier. Nevertheless, the proportion of variance accounted for by the position effect varied markedly between plants. Decline in mean seed mass over the season has been attributed to the parent plant tracking seasonal changes in resource availability (Cavers and Steele 1984; McGinley et al. 1987; Lalonde and Roitberg 1989; Kang and Primack 1991; Richardson and Stephenson 1991). However, in *Thlaspi arvense*, seeds produced later were heavier (Matthies 1990).

An alternative explanation might be that the parent-offspring conflict (Uma Shaanker et al. 1988) may be decided in favour of the offspring's interests early in the season (seeds from small broods were heavier than those from large ones). Later in the season, when the resources available for seed production decrease as the amount of resources committed to earlier fruit production increases, the conflict might be decided in favour of the parent plant's interests (seeds from few-seeded fruits were not heavier).

Nevertheless, variance within fruits may be proportionally important in both bottom and top fruits (most of the fruits used for calculations in Table 4 came from positions higher than sixth position in the stalk). Hence ovules were differentially provisioned, and this may be attributed to sibling competition (Uma Shaanker et al. 1988). However, the shortage of resources that is expected at the middle and top of the stalk did not reduce brood size ($F=2.898$; $df=1$, 999; $P=0.090$; 2.53 ± 1.39 (225) until the sixth fruit and 2.39 ± 1.12 (776) remaining fruits), as predicted by O'Connor (1978) and Uma Shaanker et al. (1988). This is possible if non-aborted seeds are provisioned at least until a minimum size to avoid late abortions and subsequent reallocation of resources to other seeds (Lloyd 1987). Thus, multi-seeded fruits should not exhibit a reduction in mean seed mass relative to one-seeded fruits, as observed in the present case. Furthermore, this is in agreement with the results of nutrient limitation by defoliation, which did not reduce mean seed mass. The fact that defoliation reduced fruit- and seed-set (Obeso 1993) fits the model of Harper et al. (1970) which suggests that stress should affect fruit and seed set before seed mass.

Seed mass is often positively correlated with progeny vigor, especially under competitive conditions (Schaal 1980; Gross and Soule 1981; Stanton 1984; Mazer 1987, 1989a, b). But offspring fitness is often influenced by other components such as dispersal efficiency (Ganeshaiah and Uma Shaanker 1991). The seeds of *A. albus* are autochorous and are individually dispersed. Hence it is expected that heavier seeds would have a lower dispersal distance, and hence would tend to be less successful in areas where parent clones are large. Additionally, Byrne and Mazer (1990) suggested that species in which seed dispersal distance is strongly associated with seed mass should exhibit greater seed mass variation than species in which dispersal is unrelated to seed size. Such variation might result in broader seed shadows, which may be favoured in heterogeneous environments (Janzen 1977, 1978).

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