

SOURCES OF VARIATION IN SEED MASS IN *ARUM ITALICUM*

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Models on seed size/number trade-off predict a uniform size of seeds and a decrease in seed size with an increase in seed number. However, substantial between- and within-plant variation in seed size has been found. This study examined the accommodation of *Arum italicum* to predictions of models. Seed mass variation at population, plant, fruit and within-fruit levels and the existence of a size/number trade-off were examined. Considerable within-plant variation was found in seed mass. Seeds in upper fruits were smaller than seeds in lower fruits and caused variation in seed size. An unequal mass partition between seeds in multiseeded fruits was another source of within-plant variation in seed size. Seed number per fruit is likely to be determined by resource or pollen limitation, not by seed-packaging costs. No size/number trade-off was found at the single plant level. Seedling performance was positively related to seed size. Nevertheless, a maximum seed size seems to exist in this species, instead of a minimum size.

Introduction

Size, usually measured as mass, of seeds has important consequences for fitness. A positive relationship has been found between seed mass and seedling performance (Wulff 1986; reviewed in McGinley et al. 1987). An important assumption of the theoretical analysis of life histories with regard to reproduction is that, because resources available for reproduction are limited, a trade-off must exist between offspring number and size (Roff 1992). Earliest models of offspring size/number trade-offs predicted a progeny uniform in size as optimal adaptation (Smith and Fretwell 1974). This seemed to be supported by the observation that seed size was the less variable component of yield (Harper et al. 1970). However, subsequent empirical evidence showed the existence of remarkable within- and between-plant variation in seed size (Thompson 1984; Wolf et al. 1986; Michaels et al. 1988).

Adaptive reasons, as the advantages of producing a more homogeneous seed shadow (Janzen 1977), adaptation to a heterogeneous environment (Capinera 1979), or different genetic quality among seeds (Temme 1986), could favor the production of seeds of different size. McGinley et al. (1987) modeled the effect for seed size of the spatial and temporal heterogeneity in environment as suggested by Capinera (1979). But they still found a uniform size for seeds as optimal solution in most cases (McGinley et al. 1987).

Other authors have proposed nonadaptive explanations for the variation observed (reviewed in McGinley et al. 1987): weak selection pressure or temporal variability in selection pressure (Pitelka et al. 1983; Thompson 1984), physiological constraints or pleiotropy (McGinley et al. 1987), seed size reduction from resource depletion during fruiting period (Cavers and Steel 1984), position effects of seeds on a plant or a fruit (McGinley et al. 1987; Lee 1988), environmental effects (Wulff 1986), or parent/offspring conflict settlement (Haig and Westoby 1988; Uma Shaanker et al. 1988).

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Manuscript received August 1996; revised manuscript received January 1997.

In this article, the seed mass variation in *Arum italicum* Miller (Araceae) is described as a part of a broader study on its reproductive biology (Méndez 1996). The extent to which this species meets predictions of the seed size/number trade-off theory is examined. Specific questions addressed are: (1) How variable is the seed mass both in absolute terms and with respect to other components of yield? (2) How is this variation partitioned among levels (population, plant, fruit, and within-fruit)? (3) What are the sources of within-plant variation in seed mass? and (4) Are the assumptions of a size/number trade-off and of a positive relationship between seed mass and seedling performance met?

Special attention is given to within-fruit variation in seed mass, poorly studied until now. In relation to this, some advantages and drawbacks of multiseeded fruit production are examined. In short, the number of seeds in a fruit could influence the relative cost per seed of protective structures (Mehlman 1993). Therefore, the variation in packaging cost for one-seeded and multiseeded fruits was also investigated.

Material and methods

Arum italicum is a perennial herbaceous geophyte distributed mainly in southern Europe, although reaching the Black Sea (Boyce 1993). In this species, clonal reproduction results in groups of independent ramets. During the flowering period (February–May), one to five monoecious inflorescences (spadices) are produced per fertile ramet. If pollinated, they become infructescences formed by a variable number of fleshy fruits, borne on verticils on a scape. Usually, only one to two infructescences are matured per ramet. The fruit pulp is red at maturity, although seeds can be mature even when the pulp of the fruit is still green. Fruits of *Arum maculatum* are mainly bird dispersed (Snow and Snow 1988), and probably the same is true for *A. italicum*.

Two populations were studied in the province of Asturias, northern Spain, where this species is common in riparian forests, hedgerows, roadsides, and other shaded, disturbed lowland sites. On July 20 and 29, 1993, a total of 26 mature infructescences, representing the whole yield of 25 ramets, were collected by a roadside in Ablaneda (43°30'N, 5°54'W). Infructescences retaining all or nearly all their fruits were chosen; only one ramet had two infructescences. The number of mature infructescences in Ablaneda was very

low in 1994, and the few infructescences found were used to test seed germination (see below). In 1994 the fruit production of plants in an experimental population in Avilés (43°31'N, 5°54'W) was studied. This experimental population was started from 67 tubers dug up from a natural population located in a riparian forest in Arlós (43°29'N, 5°54'W) in September 1992. Tubers were placed in pots with a 1:1 mix of perlite and peat and maintained outdoors at the University of Oviedo for a year. In July 1993, they were transplanted to the experimental site in Avilés. At this site, several treatments were imposed on plants; only the yield (18 infructescences) from 14 control plants was included in the study. One infructescence was excluded because of the production of abnormally small seeds.

For each infructescence, fruits were individually examined. The pulp of each fruit was removed, seed number was counted, and mass of each seed was obtained to the nearest 0.1 mg after oven-drying for 1 wk at 60°C. Because a clear-cut point was not evident among developed and aborted seeds, a limit was subjectively established at 10 mg. Below this mass, most seeds had a shriveled appearance and were probably nonviable. Exclusion of seeds below 10 mg did not alter the results qualitatively, because they represented a small fraction of the total seed pool.

At Ablaneda, the removed fruit pulp was also oven-dried and weighed to the nearest 0.1 mg, and its color (green or red) was noted. The packaging cost of seeds was measured as the proportion of total fruit mass allocated to the pulp. In addition, the position (upper, central, or lower) of each fruit in the infructescences was noted. The 10 uppermost, 10 lowermost, and a variable number (0–53) of fruits in the central portion of each infructescence were considered in an analysis of the effect of the position of fruits on seed mass. Eight infructescences were randomly chosen from each position in order to achieve data independence (Obeso 1993). Similar measurements were not possible for the experimental population infructescences because of temporal limitations.

The yield of plants in the experimental population was estimated as the total mass of seeds produced. This estimate was broken down according to the following expression: $TSM = NI \times FFPI \times FS \times SPF \times MSM$, where TSM is the total seed mass, NI is the number of inflorescences, $FFPI$ is the mean number of female flowers per inflorescence, FS is the fruit set (percentage of flowers becoming mature fruits), SPF is the mean number of seeds per fruit, and MSM is the mean seed mass. The relative importance of each component on the right side of the equation in determining total seed mass (TSM) was analyzed following the procedures specified by Mott (1966). Variance of each variable and covariance between each pair of variables were obtained on log-transformed data. After logarithmic transformation additivity is achieved, so that the variance in $\log(TSM)$ was equal to the sum of variances of the log-transformed right-side terms plus two times the covariance between each pair of terms (Mott 1966). Variances and covariances were standardized by expressing them as percentage of variance in $\log(TSM)$. The magnitude of standardized variance and covariance for each term estimates its contribution to between-plant variation in TSM .

Seeds for the germination test were collected on July 13, 1994, in Ablaneda. Fruits from three to four infructescences were mixed, and 30 with one seed and 30 with two to four seeds were randomly taken; a total of 100 seeds were used. Seeds were sown on August 3, 1994, in 3-cm-deep plastic trays filled with a 1:1 mix of perlite and peat. Twenty seeds were sown per tray. Until germination, trays were covered

in order to preserve moisture and to provide darkness. After germination, seeds and seedlings were exposed to ambient photoperiod (range: 9–11 h light per day) and temperature (range: 3°–19°C). Seeds and seedlings were watered four to five times per week throughout the study. Seeds were considered germinated when a radicle >1 mm in length was produced. Germination started October 4, 1994. Under the conditions of this test, no seedling survived beyond March 28, 1995, perhaps because the humidity of soil in trays was not high enough. Each seedling was weighed to the nearest 0.1 mg after wilting. Two measurements of seed mass were taken: (1) initial fresh mass of seed and (2) efficient seed mass, calculated as the difference between the initial fresh mass of the seed and the fresh mass of seed coat plus remaining endosperm left after germination. No sign of water absorption by seed coat and endosperm was observed, so fresh mass was used to obtain the efficient seed mass. This second measurement gives an idea of resources actually taken by the embryo during germination and early stages of seedling development. The seedling performance was measured as (1) the length of first leaf expanded, measured at the moment of unfolding, and (2) the mass of the seedling after wilting.

When parametric assumptions were met, differences between means were analyzed using ANOVA and “a posteriori” Student-Newman-Keuls tests. Otherwise, Mann-Whitney U (M-W) or Kruskal-Wallis (K-W) and a posteriori Dunn tests (Zar 1984) were used. The K-W test is sensitive to heteroscedasticity (Day and Quinn 1989). Thus, when logarithmic or square root transformations did not improve the homogeneity of variances, the significance level for this test was raised from 0.05 to 0.01 (N. Andrew, personal communication). To analyze the percentage of variance in seed mass because of population, plant, fruit, and within-fruit levels, nested ANOVA was used. It was not possible to include all these levels in a single analysis because of a substantial variation between plants in number of fruits and number of seeds per fruit. Thus, three sequential analyses were performed. A first analysis included the factors population and plant. A second analysis considered the factors plant and seediness of fruits. Finally, a third analysis studied the factors plant and fruit separately for fruits with a fixed number of seeds. A model II ANOVA (for one-seeded fruits) and nested type II ANOVA (for remaining analyses) were used. Sample size was balanced by randomly selecting fruits in plants with fruits sufficient to carry the analyses (see tables 2 and 3 for sample size). Masses are given as mean \pm standard deviation.

Results

RELATIVE AND ABSOLUTE VARIATION IN SEED MASS

Most variation among plants in yield resulted from differences in fruit set and from covariance between fruit set and seed number per fruit (table 1).

The mass of mature seeds had a normal distribution in both populations (Kolmogorov-Smirnov test: $Z = 0.799$, $n = 2246$, $P = 0.546$ for Ablaneda; $Z = 1.105$, $n = 1490$, $p = 0.174$ for the experimental population; fig. 1). Nevertheless, a significant bias to the left ($g_2 = -0.165$, $t = 2.619$, $p < 0.05$) in seed mass distribution was detected in the experimental population. In Ablaneda, the mean mass was 39.0 ± 7.6 mg and the coefficient of variation was 28.2%; the heaviest seed was 6.9 times heavier than the lightest one. In the ex-

Table 1

PERCENTAGE OF VARIANCE IN LOG (total seed mass) EXPLAINED BY DIFFERENT COMPONENTS OF YIELD FOR PLANTS OF *ARUM ITALICUM* IN AN EXPERIMENTAL POPULATION

	NI	FFPI	FS	SPF	MSM
No. of inflorescences (NI)	6.13				
Female flowers per inflorescence (FFPI)	2.79	0.09			
Fruit set (FS).....	-1.50	-1.78	48.27		
No. of seeds per fruit (SPF).....	-3.06	-2.16	32.21	7.63	
Mean seed mass (MSM).....	1.57	-0.14	6.20	1.81	0.10

Note. Variance (on diagonal) and covariance ($\times 2$) (below diagonal) of log-transformed data are shown.

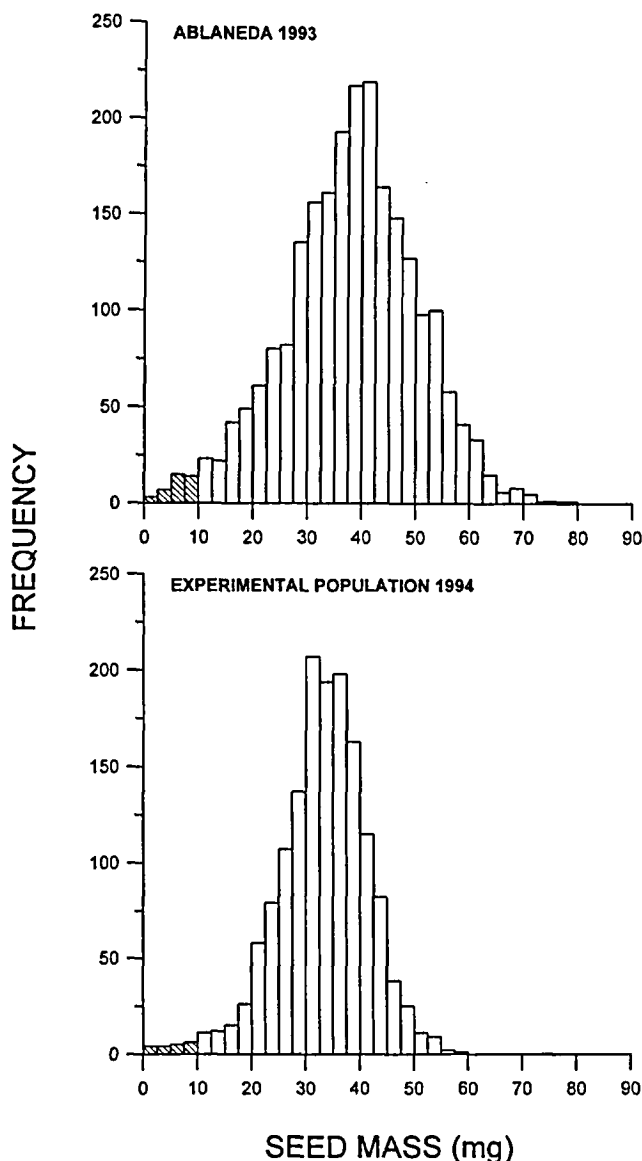


Fig. 1 Distribution of seed mass in two populations of *Arum italicum*. Shaded bars indicate seeds under 10 mg, considered aborted and excluded from analyses.

perimental population, mean mass was 33.6 ± 11.4 mg, the coefficient of variation was 21.6%, and heaviest to lightest seed weight ratio was 5.4. Mean overall seed mass was significantly lower in the experimental population than in Ablaneda (M-W test: $U = 117765$, $n = 3736$, $p < 0.0001$).

In the analysis considering population and plant levels, most variation was found within plants (table 2). When fruits with different seediness were considered, again within-plant variation was predominant (table 2). In both populations, most within-plant variation in this analysis was found within type of fruit (table 2). Differences between fruits with different seediness were significant in the experimental population (table 2).

In the analysis of fruits with a given number of seeds, a prevalence of between-plant variation was observed in Ablaneda (table 3). Overall within-plant variance increased with seed number per fruit but never exceeded between-plant variance. Variation among fruits within a plant was very low and was significant only in three-seeded fruits (table 3). In the experimental population, the highest variation was found within fruits. Among-fruit variation within a plant had little importance and was only significant in three-seeded fruits (table 3).

POSITION EFFECT ON SEED MASS

Seed mass was lower in the upper position of infructescences (table 4). Because of the effect of seed number per fruit on seed mass, this analysis was repeated independently for fruits with one to four seeds. A significant position effect remained at every fruit except for two-seeded fruits (table 4).

WITHIN-FRUIT VARIATION

Seed number per fruit varied between one and seven in Ablaneda and one and nine in the experimental population (fig. 2). In the experimental population a positive correlation was found between fruit set and fruit seediness ($R_s = 0.718$, $n = 16$, $p < 0.01$). A significant decrease in mean seed mass per fruit was observed in multiseeded fruits when compared to one-seeded fruits (K-W test: $\chi^2 = 54.212$, $n = 2145$, $p < 0.0001$ for Ablaneda; $\chi^2 = 49.012$, $n = 1471$, $p < 0.0001$ for the experimental population; fig. 3). Within a fruit, mass of the heaviest seed remained the same with an increase in seed number per fruit (K-W test: $\chi^2 = 7.488$,

Table 2

RESULTS OF TYPE II NESTED ANOVAS TESTING SEED MASS VARIATION IN *ARUM ITALICUM* FOR FACTORS POPULATION AND PLANT, AND PLANT AND FRUIT SEEDINESS

Sources of variation	Sums of squares	df	F	P	% variance
2 populations,					
7 plants per population,					
98 seeds per plant:					
Population	18,866.39	1	10.94	<0.01	23.4
Plant (population).....	20,685.14	12	26.65	<0.0001	15.9
Within plant	87,822.66	1,358			60.7
Ablaneda: 10 plants,					
3 types of fruits					
(1-3 seeds per fruit),					
7 seeds per type:					
Plant.....	11,707.87	9	14.51	<0.0001	38.4
Fruit type (plant).....	1,792.84	20	0.97	0.499	0.0
Within fruit type	16,613.38	180			61.6
Experimental population:					
4 plants, 4 types of fruits					
(1-3 and >3 seeds per					
fruit), 5 seeds per type:					
Plant.....	1,190.44	3	3.13	0.06	17.6
Fruit type (plant).....	1,523.76	12	2.68	<0.01	20.7
Within fruit type	3,033.94	64			61.7

Note. Percentage of variance explained by each factor is given in the last column.

$n = 1091$, $p = 0.114$ for Ablaneda; $\chi^2 = 8.582$, $n = 564$, $p = 0.198$ for the experimental population; fig. 4), while the mass of smallest ones was successively lower (K-W test: $\chi^2 = 206.049$, $n = 1091$, $p < 0.0001$ for Ablaneda; $\chi^2 = 123.962$, $n = 564$, $p < 0.0001$ for the experimental population; fig. 4).

PACKAGING COST OF SEEDS

In both green- and red-pulp fruits the packaging cost was significantly lower in multiseeded fruits (K-W test: $\chi^2 = 104.965$, $n = 476$, $p < 0.0001$ for green pulp; $\chi^2 = 110.306$, $n = 609$, $p < 0.0001$ for red pulp; fig. 5). For fruits with the same number of seeds, the percentage of pulp decreased with the increase in total seed mass per fruit (table 5).

SIZE/NUMBER TRADE-OFF

Seed number per plant ranged from 18 to 189 in Ablaneda and from 1 to 238 in the experimental population. No significant relationship was found between mean seed mass per plant and number of seeds per plant ($R^2 = 0\%$, $F_{1,18} = 0.001$, $p = 0.974$ for Ablaneda; $R^2 = 4.2\%$, $F_{1,12} = 0.529$, $p = 0.481$ for the experimental population).

SEED GERMINATION AND SEEDLING PERFORMANCE

Seed germination was 97%; 39.3% of the seeds from one-seeded fruits ($n = 28$ seeds) extended their first leaf, compared with 63.9% of the seeds from two-seeded fruits ($n = 36$ seeds) and 69% from three-seeded fruits ($n = 29$ seeds). These differences were not significant ($G_2 = 5.959$, $p = 0.051$).

There was no difference in initial seed mass between seeds germinated with or without their first

leaves extended (46.3 ± 8.3 vs. 43.5 ± 9.0 mg; ANOVA: $F_{1,95} = 2.379$, $p = 0.126$). Although there was a positive relationship between the effective seed mass and the initial seed mass ($R = 0.768$, $n = 62$, $p < 0.0001$), the former was a better predictor of seedling performance. Thus, the length of first leaf expanded at the moment of unfolding was not significantly related to the initial seed mass ($R^2 = 0.013$, $F_{1,56} = 0.755$, $p = 0.389$), while it was significantly related to the effective seed mass ($R^2 = 0.162$, $F_{1,56} = 10.820$, $p < 0.01$). Final seedling mass was related to initial seed mass ($R^2 = 0.068$, $F_{1,56} = 4.105$, $p < 0.05$), but the relationship with the effective seed mass explained a greater percentage of variance ($R^2 = 0.228$, $F_{1,56} = 16.559$, $p < 0.001$).

Discussion

RELATIVE AND ABSOLUTE VARIATION IN SEED MASS

Mean seed mass accounted for a small fraction of total variation in yield in *Arum italicum*, as proposed by Harper et al. (1970). Nevertheless, a minor importance of the relative variation in seed mass is not equivalent to a lack of absolute variation. In fact, variation in seed mass has been found for most species studied (Janzen 1977; Wolf et al. 1986; Wulff 1986; Ågren 1989; Winn 1991; Obeso 1993). *Arum italicum* also showed a variability in seed mass and was in agreement with the previously known range of variation.

The lack of data for Ablaneda in 1994 confounds the effects of year and of population. A proper interpretation of differences among populations in seed mass is then not possible. Between-plant differences were significant in most analyses. Sakai (1996) re-

Table 3

RESULTS OF TYPE II ANOVAS AND TYPE II NESTED ANOVAS TESTING SEED MASS VARIATION IN *ARUM ITALICUM* FOR FACTORS PLANT AND FRUIT (for a fixed fruit seediness)

Sources of variation	Sums of squares	df	F	P	% variance
Ablaneda, 1993:					
19 plants, 10 fruits per plant, 1 seed per fruit:					
Plant.....	36,871.70	18	27.76	<0.0001	72.8
Within plant.....	38,223.71	518			27.2
13 plants, 10 fruits per plant, 2 seeds per fruit:					
Plant.....	28,151.71	12	32.83	<0.0001	62.2
Fruit (plant).....	8,361.14	117	1.07	0.307	1.3
Within fruit.....	27,920.67	419			36.5
12 plants, 7 fruits per plant, 3 seeds per fruit:					
Plant.....	20,766.66	11	17.66	<0.0001	50.8
Fruit (plant).....	7,697.82	72	1.53	<0.01	7.4
Within fruit.....	23,910.56	343			41.8
Experimental population, 1994:					
7 plants, 10 fruits per plant, 1 seed per fruit:					
Plant.....	2,173.36	6	10.74	<0.0001	49.3
Within plant.....	2,124.66	63			50.7
5 plants, 9 fruits per plant, 2 seeds per fruit:					
Plant.....	1,005.36	4	3.42	<0.05	14.1
Fruit (plant).....	2,943.46	40	1.56	0.074	18.8
Within fruit.....	2,119.31	45			67.1
5 plants, 8 fruits per plant, 3 seeds per fruit:					
Plant.....	1,941.92	4	6.59	<0.0001	26.1
Fruit (plant).....	2,579.51	35	2.05	<0.001	19.2
Within fruit.....	2,873.77	80			54.7
3 plants, 8 fruits per plant, 4 seeds per fruit:					
Plant.....	957.78	2	6.10	<0.01	17.4
Fruit (plant).....	1,649.35	21	1.49	0.110	9.0
Within fruit.....	3,804.45	72			73.6

Note. Percentage of variance explained by each factor is given in the last column.

viewed possible causes for between-plant variation in seed mass: (1) size or resource level differences (Venable 1992), (2) variable inbreeding depression, (3) developmental or morphological constraints to increase in seed number, or (4) decreasing gains from an increase in seed number for plants with higher attractive structures (the fertilization efficiency hypothesis). Whatever the cause, variation between plants could blur the detection of a phenotypic size/number trade-off at the single plant level in *A. italicum*. Either positive (Klinkhamer et al. 1994; Stöcklin and Favre 1994) or nonsignificant (Michaels et al. 1988; Mehlman 1993) relationships have been found for other species.

Within-plant variation accounted for the highest percentage of variance in seed mass in most analyses performed. This is an usual finding (Thompson 1984; Wolf et al. 1986; Michaels et al. 1988; Winn 1991; Obeso 1993; Stöcklin and Favre 1994), although several species have been found to show little variation at this level and sometimes different populations of the

same species have different patterns of variation (Michaels et al. 1988).

The variation among fruits within a plant was small, both for fruits with different or with similar seediness. This result has been found in other species (Michaels et al. 1988) and it has been attributed to an equal energy allocation to each fruit (Winn 1991). However, in *A. italicum* differences between fruits were significant in several analyses.

WITHIN-PLANT VARIATION

Two sources of within-plant variation in seed mass were identified in *A. italicum*. First, a position effect on seed mass was found. Although in this article the variation accounted for by this factor was not explicitly addressed, it is a part of between-fruit variance (maximum of 27.2% for Ablaneda). In *Epilobium dodonaei*, the position effect explained 4.7% of variance in seed mass (Stöcklin and Favre 1994). Variation in seed mass with position of seeds along infructescences or stems has been found in several species (Lovett

Table 4

MEAN MASS (mg) AND STANDARD DEVIATION OF SEEDS OF *ARUM ITALICUM* AT DIFFERENT POSITIONS (upper, central, or lower) ON INFLORESCENCES

Seeds per fruit and position	Mass	<i>n</i>	<i>P</i>
One:			
Upper	39.1 ± 10.1 A	33	<0.05
Central	42.4 ± 13.0 A	42	
Lower	46.9 ± 9.2 B	30	
Two:			
Upper	38.1 ± 10.7 a	58	0.702
Central	39.3 ± 13.6 a	112	
Lower	39.2 ± 9.5 a	36	
Three:			
Upper	28.5 ± 9.8 A	18	<0.0001
Central	37.8 ± 10.8 B	96	
Lower	43.6 ± 10.5 C	30	
Four:			
Upper	26.5 ± 8.8 A	12	<0.0001
Central	38.5 ± 4.9 B	20	
Lower	41.9 ± 8.9 B	32	
Overall:			
Upper	35.0 ± 11.8 A	126	<0.0001
Central	39.3 ± 12.1 B	275	
Lower	42.4 ± 10.5 C	153	

Note. Means followed by the same letter are not significantly different at 0.05 level (ANOVA for uppercase, K-W for lowercase). Data correspond to Ablaneda, 1993.

Doust et al. 1986; Zimmerman and Aide 1989; Stöcklin and Favre 1994; Lokker and Cavers 1995). Position effects result from morphological limitations in the ability to send resources to fruits (Watson and Casper 1984) or from resource preemption by lower fruits (Lee 1988). In species with indeterminate growth, the position effect is usually linked to temporal effects of resource depletion (Stephenson 1981; Lee 1988), and it is difficult to differentiate between both factors (Winn 1991). In *A. italicum* the morphological limitation is the most likely cause, because all flowers in an inflorescence are pollinated within several hours, not days or weeks (Faegri and van der Pijl 1979). While certain temporal effect may remain, because upper fruits ripen approximately a week earlier than lower ones (M. Méndez, personal observation), this pattern could be seen as an effect of a lower resource input.

On the other hand, multiseeded fruits added variability to seed size, because higher seediness of a fruit did not affect mass of all seeds in the same way. A negative correlation between mean seed mass and number at fruit level is common (Harper et al. 1970; Wolf et al. 1986; Wulff 1986; Ågren 1989; Matthies 1990; Winn 1991; Obeso 1993) although not at all general (Michaels et al. 1988; Winn 1991; Obeso 1993; Lokker and Cavers 1995). The detection of such a negative relationship could be dependent on the specific resource partition among seeds between and within fruits. However, analyses of within-fruit seed mass have been neglected. Overlooked until now, an unequal mass partition among seeds in a fruit is probably

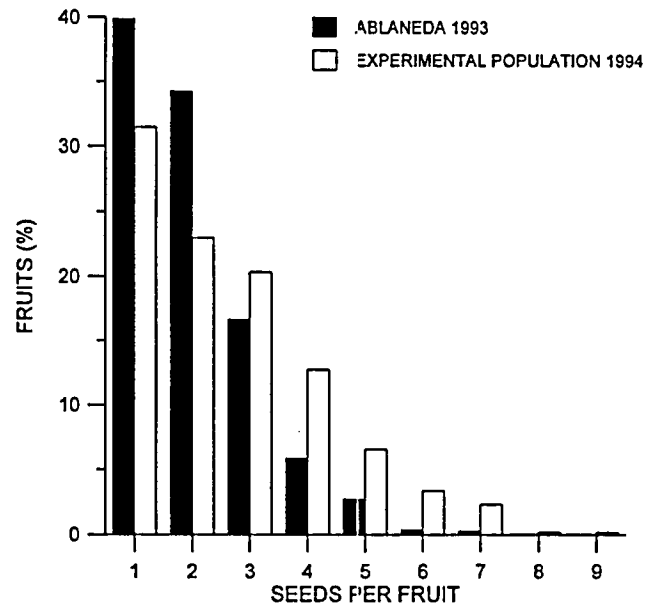


Fig. 2 Distribution of seed number per fruit (percentage) in two populations of *Arum italicum*.

very common in species with more than one ovule per carpel (J. R. Obeso, unpublished data). Differences in seed mass within a fruit could result from differential parental supply related to the genetic quality of seeds (Temme 1986), position effect within a fruit (Lee 1988), parent/offspring conflict (Lloyd 1992), or sibling rivalry (Uma Shaanker et al. 1988). Only the first of these possibilities entails a clear adaptive value for

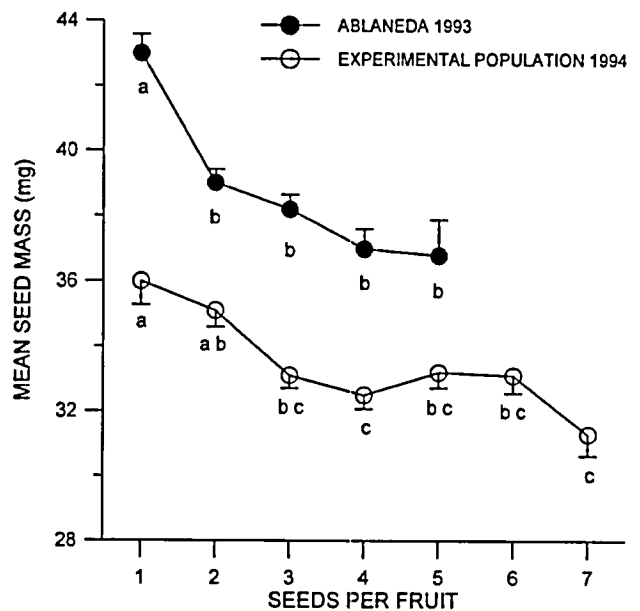


Fig. 3 Mean (\pm SE) seed mass per fruit with respect to the number of seeds per fruit, in two populations of *Arum italicum*. For each population, points with the same letter are not significantly different at 0.05 level (a posteriori Dunn test). Fruits with six to seven seeds in Ablaneda and with eight to nine seeds in the experimental population have been excluded because of small sample size.

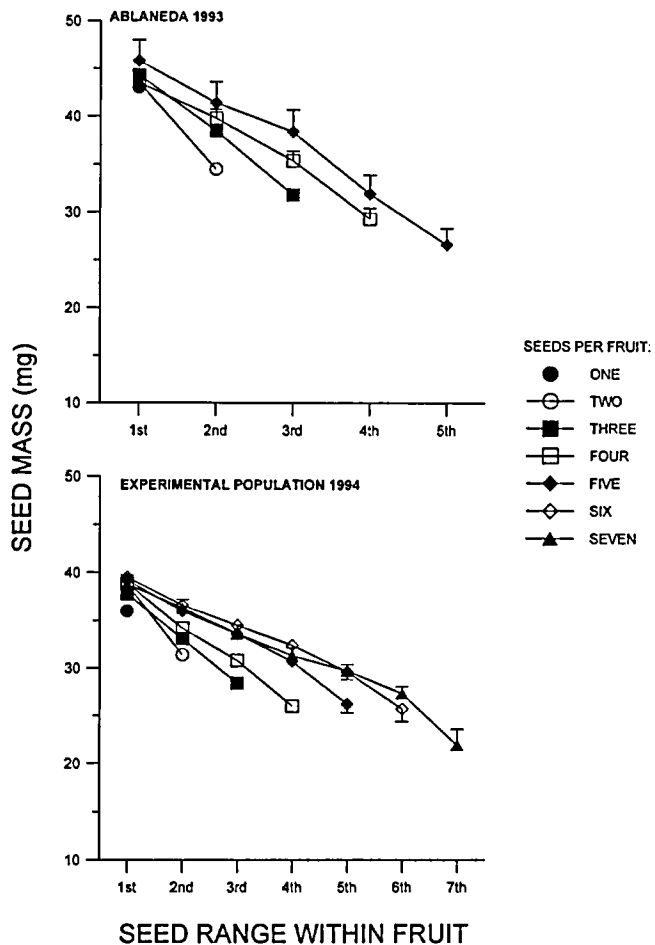


Fig. 4 Mean (\pm SE) seed mass with respect to range within a fruit, for fruits with one to seven seeds, in two populations of *Arum italicum*. Fruits with six to seven seeds in Ablaneda and with eight to nine seeds in the experimental population have been excluded because of small sample size.

parental fitness. Present data do not allow us to discern between these alternatives.

Several causes could influence the fruit seediness. The production of several seeds per fruit decreased the packaging cost in *A. italicum*, as found in other species (Hedge et al. 1991; Mehlman 1993). This could favor the production of multiseeded fruits. However, the positive relationship between fruit set and fruit seediness seems to point to resource or pollen limitation as causes for the prevalence of one-seeded fruits in both populations (Kelly 1984).

SEED GERMINATION AND SEEDLING PERFORMANCE

The within-fruit variation in seed size of *A. italicum* was not associated with differences in germination ability. This variability is not a case of seed heteromorphism, as found in other species (Rocha 1996). A positive relationship was found between seed mass and seedling performance. Models assume a threshold size for seeds below which seeds have zero fitness (Smith and Fretwell 1974; McGinley et al. 1987; Haig and Westoby 1988). All of these models predict that the

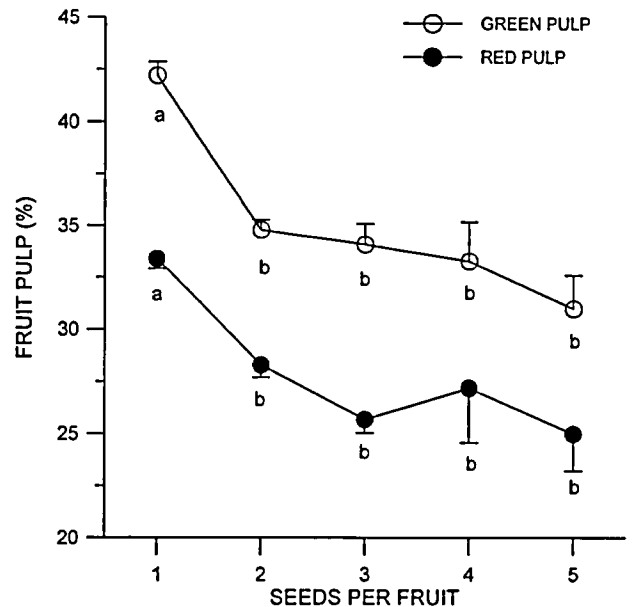


Fig. 5 Mean (\pm SE) percentage of fruit pulp with respect to different number of seeds in *Arum italicum* (Ablaneda, 1993). For each line, points with the same letter are not significantly different at 0.05 level (a posteriori Dunn test).

optimal seed size for parental plants is above this threshold size. However, an upper limit to seed mass seems to exist in *A. italicum* instead of a lower limit. This is consistent with the action on seed mass of factors not controlled by the plant.

The relationship between seedling performance and seed size was better when the partial use of seed stores was considered. Accordingly, initial seed mass could not be the best indicator of size. Events during germination, mediated by either genetic or environmental differences, also could be important.

Table 5

RESULTS OF THE REGRESSION BETWEEN THE PERCENTAGE OF PULP IN FRUITS OF *ARUM ITALICUM* AND TOTAL FRUIT MASS (pulp + seeds), FOR FRUITS WITH 1-5 SEEDS IN ABLANEDA, 1993

No. seeds per fruit	<i>r</i>	<i>df</i>	<i>F</i>	<i>P</i>
Green pulp:				
One.....	-0.35	1,169	24.254	<0.0001
Two.....	-0.28	1,155	13.381	<0.001
Three.....	-0.54	1,91	37.556	<0.0001
Four.....	0.10	1,30	0.328	0.571
Five.....	-0.58	1,21	10.727	<0.01
Red pulp:				
One.....	-0.34	1,261	34.791	<0.0001
Two.....	-0.31	1,215	22.840	<0.0001
Three.....	0.05	1,88	0.203	0.653
Four.....	-0.63	1,30	19.886	<0.001
Five.....	-0.82	1,5	10.253	<0.05

Note. Pearson's product-moment coefficient of correlation (*r*), degrees of freedom (*df*), *F* value, and significance (*P*) are shown.

Acknowledgments

José Ramón Obeso corrected earlier drafts of this article and discussed several aspects related with the within-fruit variation. Comments of two anonymous

referees substantially improved a previous draft of this article. I thank Neil Andrew for statistical advice, Carlos Herrera and Pedro Jordano for help with the bibliography, and José Rico for language corrections. This work was partially supported by an FICYT grant.

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