

Effects of Sexual Reproduction on Growth and Vegetative Propagation in the Perennial Geophyte *Arum italicum* (Araceae)

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Abstract: The influences of sexual reproduction on growth and vegetative propagation were analysed in three populations of the geophyte *Arum italicum* Miller (Araceae). In an observational study using multiple regression, a negative influence of reproduction on tuber mass was detected for two populations. In an experimental study, "control" and "inflorescence removal" treatments were imposed on plants from one of the populations. Tuber growth was significantly lower in "control" plants than in "removal" plants, indicating the existence of a somatic cost of reproduction. The somatic cost of reproduction was decreased by an increasing degree of temporal coincidence between leaves and reproductive structures on the plant. Neither the observational nor the experimental studies showed any negative effect of sexual reproduction on vegetative propagation.

Key words: Somatic cost of reproduction, *Arum italicum*, vegetative propagation, compensation.

Introduction

The cost of reproduction consists of a negative effect on organism performance due to the investment of limited resources or time in current reproduction (Williams, 1966^[32]). This cost can be expressed as lower somatic growth (somatic cost) and/or as a decrease in subsequent individual survival, sexual reproduction or vegetative propagation (demographic costs) (Bell, 1980^[4]; Kozłowski, 1991^[18]). Whether reproduction has some detrimental consequences for organisms is still a matter of dispute (Jönsson and Tuomi, 1994^[17]). For example, Tuomi et al. (1983^[30]) proposed that organisms can have mechanisms that partially or totally compensate for costs incurred during reproduction.

Geophytes are plants in which the perennating bud is borne on a subterranean storage organ (Dafni et al., 1981^[10]). Their annual growth cycle usually includes a dormant period (Pate and Dixon, 1982^[22]). Reserves in the storage organ support leaf growth at the beginning of the season (Zimmerman and Whigham, 1992^[34]) and, to a varying degree, also reproduction (Cha-

pin et al., 1990^[8]). Seasonal patterns of reserve use and allocation of geophytes have been classified by Dafni et al. (1981^[10]) according to the annual or perennial nature of the storage organ and to temporal coincidence (synanthly) or separation (hysteranthly) of leaf and flower presence on the plant. Differences in the sequence of events (production, storage, flowering) determine the importance of reserves for reproduction (Dafni et al., 1981^[10]). In addition, such differences have potential consequences for both somatic and demographic costs of reproduction (Jönsson, 1997^[16]).

A somatic cost of reproduction is likely to be found in geophytes with tubers or bulbs, where both size decreases and increases between successive growth seasons have been found (Barkham, 1980^[3]; Bierzychudek, 1982^[5]; Calvo, 1990^[7]; reviewed in Silvertown et al., 1993^[27]). Demographic costs are also suggested because reduction of fecundity or survival is supposedly mediated by a decrease in growth (Kozłowski, 1991^[18]; Silvertown et al., 1993^[27]). In this paper, the influence of sexual reproduction on resource allocation to tuber growth and vegetative propagation is analysed in the perennial, tuberous, synanthous *Arum italicum* Miller (Araceae), using both correlative and experimental approaches. Temporal coincidence between productive (leaves) and reproductive (flowers, fruits) structures on a plant is studied in relation to compensation for the cost of reproduction. Specific questions addressed are: 1) Does sexual reproduction have a negative effect on tuber mass or growth?, 2) If so, is this negative effect reduced by an increasing temporal coincidence between leaves and reproductive organs? 3) Is vegetative propagation reduced in sexually reproductive plants?

Materials and Methods

The species

Arum italicum is a perennial geophyte distributed mainly in southern Europe (Boyce, 1993^[6]). The underground tuber is the only portion of the plant that remains from one growth season to the next, because plants usually shed their leaves shortly after the reproductive structures appear. During every growth season, however, the tuber is totally or partially replaced by a new tuber. Thus, tuber mass can be considered as an integrative measure of the seasonal allocation pattern, and it makes this structure suitable for measuring growth of the plant. Concurrent with new tuber development, plants pro-

duce a variable number of daughter tubers attached to it. These daughter tubers will become independent in the next season, contributing to vegetative propagation. Leaves begin to appear in September–October and wilt in June. Their presence on the plant partially coincides with production of inflorescences (spadices) and infructescences during February–May. Infructescences consist of berries borne in verticils on a scape and remain as the only above-ground portion of the plant until their complete maturation in August–September.

Study sites and variables measured

Reproduction in *A. italicum* was studied in Asturias province, northern Spain, where this species is frequent in riparian forests, hedgerows, roadsides and other shaded, disturbed lowland sites. One experimental and two natural populations were utilized. The experimental population was started in September 1992, using 67 tubers dug up from a natural population in a riparian forest in Arlós (43°29'N, 5°54'W). Tubers were planted singly in 21 pots filled with a 1:1 mix of perlite and peat. Pots were maintained outdoors at the University of Oviedo for one year. That year many plants did not flower and none produced fruits. In July 1993, these tubers were replanted in an experimental garden in Avilés (43°31'N, 5°54'W). Plants were arranged within a rectangular plot, spaced approximately 30 cm apart. Competing grasses were periodically removed.

In addition, plants were randomly selected and tagged in two natural populations near Avilés. Twenty plants were studied on a roadside in Ablaneda (43°30'N, 5°54'W). Another 39 plants were examined in a riparian forest in Tamón (43°31'N, 5°52'W).

All populations were monitored once a week from August–November 1993 to the full ripening of final infructescences in August 1994. At every visit, the number of leaves, inflorescences, and infructescences was recorded. All wilted aboveground parts of plants were harvested, separated into fractions and then oven-dried for a week at 60°C and weighed. For eight plants, one or two leaves were lost before harvest and these missing values were substituted using the average mass of remaining leaves on the plant. In Avilés, initial and final masses of each tuber were measured to the nearest 0.01 g. Tubers lose water when they are not in soil; thus, they were put in paper bags and weighed 18 days after collection. After this period, water loss reached an asymptote (pers. obs. on a previous sample of tubers). In Ablaneda and Tamón only final tuber mass was measured, after oven-drying it at 60°C for a week. Daughter tubers were counted and their mass obtained in the same way as for parental tubers. Time of development of infructescences was estimated as the number of weeks that infructescences remained on a plant between anthesis and maturation or abortion. Where several infructescences developed in the same plant, the time between pollination of first inflorescence and ripening (or abortion) of the last infructescence was taken. Temporal coincidence between the presence of leaves and reproductive structures (inflorescences or infructescences) on a plant was calculated as:

$(\text{Date of first appearance of inflorescence} - \text{Date of loss of last leaf}) \times 100 / \text{No. days of development of the inflorescence.}$

This index had values higher than 100% when leaves remained after abscission or maturation of infructescences. Such values were allowed because they have an obvious biological meaning, i.e., refilling of the tuber after reproduction.

Observational study of the effect of sexual reproduction

For every population, plants showing a natural range of reproductive allocation were included in a multiple regression to study the effect of several variables on final tuber mass (see Statistical analyses below). In Avilés, only "Control" plants and three naturally vegetative plants (not included in the experimental study, see below) were considered. Initial tuber mass (where available), total leaf mass, reproductive mass, daughter tuber mass and time with infructescences were the variables considered. These variables were chosen to represent the different processes involved in the annual resource allocation pattern.

The effect of sexual reproduction on allocation to daughter tubers was also explored using multiple regression. In this case, daughter tuber mass was the dependent variable and initial tuber mass (where available), reproductive mass, total leaf mass and time with infructescences were used as independent variables.

In every case, a significantly negative coefficient of partial correlation of reproductive mass would indicate a cost of reproduction.

Experimental study of the effect of sexual reproduction

When flowering began in Avilés, an experiment was conducted to determine the effect of two treatments: control and removal of inflorescence buds. Twenty plants were randomly allocated to each treatment.

The somatic cost of reproduction was estimated as differences between treatments in tuber growth, i.e., the difference between initial and final tuber mass.

Statistical analyses

Multiple regression was utilized in the observational study. Assumptions of the regression were checked by examining the residuals of regression. In some cases (see Table 1), log-transformation of independent and dependent variables expressed as mass improved either linearity or behaviour of residuals. No strong co-linearity was detected between independent variables, according to the condition index (< 30 in all cases) or the variance inflation factor (< 10 in all cases) (cf. Philippi, 1993^[23]). To further avoid artifacts due to co-linearity between independent variables, all variables were simultaneously introduced into the model. This gives information on the sign and absolute values of all partial regression coefficients in the equation, not just those entering significantly.

In the experimental study, normality (Kolmogorov-Smirnov test) and homogeneity of variances (Bartlett's test) were tested and ANOVA was utilized to analyse differences among treatments when assumptions were met. Heteroscedastic variables were log-transformed. Throughout the text, means are indicated with their standard deviation.

Table 1 Variables influencing final tuber mass in three populations of *Arum italicum*. Proportion of variance explained (R^2) and ANOVA results are given for the multiple regression model. For every variable, partial regression coefficient, b , \pm standard error, t -value and significance (p) are shown

Population/Variable	$b \pm SE$	t	p
Ablaneda ($R^2 = 0.954$, $F_{4,15} = 78.125$, $p < 0.0001$)			
\log_{10} (Daughter tuber mass + 1)	0.698 ± 0.110	6.334	<0.0001
\log_{10} (Total leaf mass)	0.645 ± 0.151	4.269	<0.001
\log_{10} (Reproductive mass + 1)	-0.188 ± 0.154	-1.226	0.239
Time with inflorescences	-0.001 ± 0.001	-0.799	0.436
Avilés ($R^2 = 0.742$, $F_{5,10} = 5.749$, $p < 0.01$)			
\log_{10} (Daughter tuber mass + 1)	0.511 ± 0.198	2.581	<0.05
\log_{10} (Reproductive mass + 1)	-0.676 ± 0.283	-2.388	<0.05
\log_{10} (Total leaf mass)	0.729 ± 0.326	2.240	<0.05
Time with inflorescences	0.003 ± 0.002	1.276	0.230
\log_{10} (Initial tuber mass)	0.017 ± 0.317	0.055	0.957
Tamón ($R^2 = 0.719$, $F_{4,29} = 18.573$, $p < 0.0001$)			
Total leaf mass	1.720 ± 0.252	6.830	<0.0001
Reproductive mass	-0.927 ± 0.310	-2.993	<0.01
Time with inflorescences	-0.009 ± 0.008	-0.147	0.292
Daughter tuber mass	-0.002 ± 0.818	-0.003	0.998

Results

Somatic cost of reproduction

Observational study. In Avilés, independent variables included in the multiple regression explained 74% of variance in logarithm of final tuber mass (Table 1). Total leaf mass and daughter tuber mass (log-transformed) had a significantly positive effect on the dependent variable, while reproductive mass (log-transformed) had a significantly negative influence on final tuber mass (Table 1). In Ablaneda, total variables explained 95% of variance in logarithm of final tuber mass (Table 1). Both daughter tuber mass and total leaf mass (log-transformed), had a significant positive influence on the dependent variable (Table 1). In Tamón, independent variables accounted for 72% of variance in final tuber mass (Table 1). The influence of total leaf mass was significantly positive (Table 1) and the influence of reproductive mass was significantly negative (Table 1).

In Avilés and Tamón both vegetative and reproductive plants were included in the data set. These analyses were repeated excluding vegetative plants to ascertain whether it was the fact of being reproductive or the amount of reproductive mass produced that was important for detection of a cost. In Avilés, the multiple regression model became non-significant when only reproductive plants were considered ($R^2 = 0.67$, $F_{5,7} = 2.804$, $p = 0.106$), although reproductive mass was still the variable closest to significance ($p = 0.088$). In Tamón, results remained unchanged when only reproductive plants were considered in the multiple regression analysis (results not shown).

Experimental study. Treatments did not differ in initial tuber mass and total leaf mass produced (Table 2). Mean reproductive mass was lower in "removal" plants than in "control" ones (Table 2). All tubers except one increased in mass (range: -0.16

to 88.09 g; $n = 32$). Although mean final tuber mass was not significantly different between treatments (Table 2), there were significant differences between treatments in tuber growth (Table 2). Tubers of plants in the "control" treatment showed significantly lower growth than those in "removal" treatments (Table 2). Overall, "control" plants grew 30% less than "removal" ones.

There was much variation in the time leaves were kept after flowering onset in Avilés. Some (two in the "control" and three in the "removal" treatment) plants retained leaves until the final harvest in August. For "control" plants, a positive relationship was found between the degree of temporal coincidence between leaves and infructescences and tuber growth (Fig. 1).

Effect on vegetative propagation

Observational study. In Avilés, independent variables accounted for 56% in the variance of daughter tuber mass (Table 3). Total leaf mass had a significant positive effect on daughter tuber mass (Table 3). In Ablaneda, variables considered explained 90% of variance in daughter tuber mass (Table 3). Total leaf mass showed the only significant partial correlation coefficient and had a positive influence on daughter tuber mass (Table 3). In Tamón, none of the independent variables used had a significant influence on daughter tuber mass and variance explained was only 14% (Table 3).

Experimental study. No difference between treatments was found in either number or mass of daughter tubers (Table 2). Differences remained non-significant when ANCOVA was used with final tuber mass as covariate ($F_{1,29} = 0.20$, $p = 0.685$). The effect of the covariate was highly significant ($F_{1,29} = 13.09$, $p < 0.001$) but the covariate \times treatment interaction was not significant ($F_{1,28} = 0.03$, $p = 0.866$).

