Size-dependent reproductive and vegetative allocation in *Arum italicum* (Araceae)

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The proportional allocation of plant total resources for growth, reproduction, vegetative propagation, and the balance between them were examined in *Arum italicum*. A minimum threshold dry mass (2.5 g) was found in this species before reproduction could occur, but above 10 g of dry mass, all individuals in a sample of 151 produced at least one inflorescence. Resource allocation for vegetative growth, sexual reproduction, and vegetative propagation significantly increased as dry mass of the plant increased. Increases in plant size resulted in increased proportional allocation to sexual reproduction, and relative decreases in both vegetative growth and vegetative propagation. Mass ratios between sexual reproductive structures and new tuber, and between sexual reproductive structures and organs of clonal growth increased with plant size. Allocation of resources to reproduction occurred at the expense of vegetative growth. In reproductive plants, the cost of reproduction, measured as relative reduction in vegetative growth was approximately 24% and was estimated by comparing growth in nonreproductive plants.

Key words: *Arum italicum*, Araceae, cost of reproduction, reproductive allocation, vegetative growth, vegetative propagation.

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Les auteurs ont examiné la proportion des allocations des ressources totales de la plante à la croissance, à la reproduction, à la propagation végétative et à la balance entre ces paramètres, chez l'*Arum italicum*. On observe chez cette espèce une masse critique minimale (2,5 g) qui doit être atteinte avant que la reproduction s'effectue, mais au delà de 10 g de masse sèche, tous les individus d'une population de 151 individus ont produit au moins une inflorescence. L'allocation des ressources pour la croissance végétative, la reproduction sexuelle et la propagation végétative augmentent de façon significative à mesure que la masse sèche de la plante augmente. Une augmentation de la dimension de la plante se traduit par une augmentation de l'allocation proportionnelle à la reproduction sexuelle et des diminutions relatives de celle allouée à la croissance végétative ainsi qu'à la propagation végétative. Les rapports de masses entre les structures de reproduction sexuelle et le nouveau tubercule, et entre les structures de reproduction sexuelles et les organes de croissance clonale augmentent avec la dimension de la plante. L'allocation des ressources à la reproduction s'effectue aux dépens de la croissance végétative. Chez les plantes en reproduction, le coût de la reproduction, mesuré en tant que réduction de la croissance végétative, est d'environ 24%, comparativement aux plantes qui ne sont pas en reproduction.

Mots clés : *Arum italicum*, Araceae, coût de la reproduction, allocation à la reproduction, croissance végétative, propagation végétative.

[Traduit par la rédaction]

Introduction

Many empirical and theoretical studies have focused on sexual and vegetative reproductive efforts (SRE and VRE, respectively) of plants, because these can influence plant fitness in natural populations (Armstrong 1982; Loehle 1987; Reekie and Bazzaz 1987*a*, 1987*b*, 1987*c*). Within a species, SRE values were shown to vary markedly within and among populations (e.g., Douglas 1981; Ashmun et al. 1985; Karlsson 1986; Hartnett 1990) and between years (Ohlson 1988). However, much of the variation in SRE can be accounted for by size-dependent reproductive allocation, rather than external effects (Samson and Werk 1986; Weiner 1988).

A trade-off between growth, sexual reproduction, and vegetative propagation was proposed for clonal polycarpic perennials (Abrahamson 1980; Hartnett 1987, 1990; Lovett-Doust 1989; cf. Pitelka et al. 1980; Reekie 1991). Therefore, SRE, VRE, and the balance between them are expected to be size dependent. However, the question of size dependency on variation in VRE has scarcely been studied, and results from empirical studies are inconsistent. For example, Douglas (1981) found that the proportion of energy allocation to VRE increased as total plant biomass increased in *Mimulus primuloides*. Conversely, Hartnett (1990) found no significant relationship between VRE and ramet size in four composites.

According to the model of Samson and Werk (1986), reproductive allocation is expected to increase allometrically with increasing plant size, while the SRE may either increase or decrease monotonically. Therefore, it may be predicted that VRE variations with plant size should exhibit a trend opposite to that of SRE. In this study, we examined the influence of plant size on patterns of biomass allocation in *Arum italicum* Miller (Araceae), and we investigated the following: whether VRE and SRE varied among populations, whether VRE varied with plant size, and whether the patterns of VRE variation were consistent with SRE variation with respect to the trade-off between them.

Material and methods

Arum italicum is a polycarpic herbaceous perennial that inhabits humid forests and hedgerows of western Europe and the western Mediterranean region (Tutin et al. 1980). Growth begins in autumn when the stem tuber develops new leaves and a new stem tuber. The new tuber grows from the old one, which is progressively absorbed. There are no secondary structures in these plants. The new tuber produces lateral daughter tubers, and growth finishes in July, marked by the total absorption of the old tuber and the shedding of leaves. Most daughter tubers become independent from the stem tuber during the same growing season, but a small number remain attached to the stem tuber during winter and become independent in the next growing

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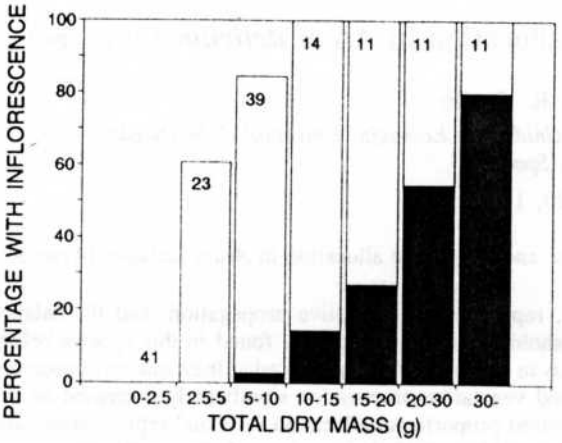

FIG. 1. Percentage of plants of *Arum italicum* showing sexual reproduction as a function of plant dry weight. Shaded histograms show individuals with two inflorescences. White histograms show individuals with one inflorescence. The number above each bar represents the sample size.

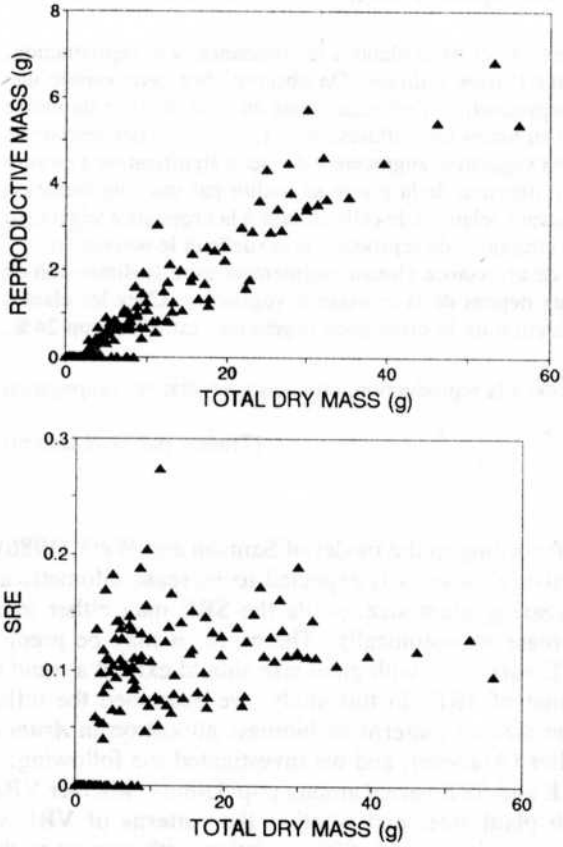

FIG. 2. Resource allocation to sexual reproduction as a function of plant dry mass. Upper graph represents absolute allocation, and lower graph represents allocation relative to plant mass. SRE, sexual reproductive effort.

season. This vegetative propagation produces clumps of completely independent ramets. Flower primordia are also laid down during the same growing season, and by late April to late May most of the plants have produced one or two inflorescences (monoic spadix, type III B of Grayum 1990). The fleshy fruits ripen in August and September and are dispersed by birds (personal observation). Details of the pollination, reproduction, and dispersal in the closely related species *Arum maculatum* were described by Prime (1960), Faegri and Van der Pijl (1973), and Snow and Snow (1987).

TABLE 1. Mean, SD, and *N* of sexual and vegetative reproductive effort (SRE and VRE), relative vegetative growth (RVG) and the ratios of SRE to RVG and SRE to VRE for study sites including the results of the ANCOVAS for comparisons among sites

Variable and site	Mean	SD	*N*	*F*	df	*p*
SRE				2.658	3, 146	0.051
1	0.09	0.07	30			
2	0.06	0.06	43			
3	0.07	0.07	32			
4	0.07	0.05	46			
RVG				3.441	3, 146	0.000
1	0.63	0.12	30			
2	0.68	0.10	43			
3	0.63	0.15	32			
4	0.67	0.14	46			
VRE				6.752	3, 134	0.019
1	1.36	1.98	28			
2	1.82	1.78	43			
3	1.81	3.08	30			
4	0.77	0.74	38			
SRE/RVG				3.378	3, 146	0.020
1	0.16	0.17	30			
2	0.10	0.11	43			
3	0.13	0.12	32			
4	0.12	0.11	46			
SRE/VRE				1.462	3, 88	0.230
1	0.27	0.36	21			
2	0.20	0.50	23			
3	0.16	0.19	20			
4	0.17	0.18	29			

NOTE: Plant dry mass was used as a covariate to avoid size effect; the highly significant effect of the covariate was omitted from the table.

Study sites and methods

The following four sites were chosen as the most representative habitats in which the species occurs in northern Spain (Asturias Province): (*i*) site 1: Arlós (43°29′N, 5°54′W), a riparian forest (dominated by *Alnus glutinosa*) on frequently flooded clay soils; (*ii*) site 2: Espinaredo (43°17′N, 5°21′W), a riparian forest (dominated by *Alnus glutinosa*) in the highlands adjacent to a stream where flooding is infrequent; (*iii*) site 3: Carbayín (43°20′N, 5°38′W), a chestnut (*Castanea sativa*) forest edge in which the soils are relatively dry (*iv*) site 4: Xagó (43°37′N, 5°53′W), a stand of *Eucalyptus globulus* on fixed coastal dunes, which has the lowest soil moisture.

Sixteen genets, each with a variable number of ramets, were sampled at each site at the peak of flowering in mid to late May 1991. The number of ramets collected from each site ranged from 32 to 47. Ramets were separated into shoots, reproductive structures (including the scapes), old tubers (including previous-year daughter tubers), and new tubers (including the new daughter tubers). The components were oven-dried at 70°C for 1 week and then weighed to the nearest 0.1 mg.

SRE was calculated as the ratio of mass of sexual structures to total plant mass. VRE was calculated as the ratio of the number of new daughter tubers produced (the new stem tuber was not included) to the total plant mass. We preferred as an indication of VRE to calculate the number instead of the mass of new daughter tubers because the latter is dependent on phenology. At the time of flowering all daughter tubers were developing, and no small ones were found at fruiting. The use of the mass of the daughter tubers should be more reliable at the end of the growing season but not at flowering. Unfortunately, at the end of the season when all daughter tubers are fully developed, most of them are independent, and it is very difficult to assign them to one ramet in the field. Relative vegetative growth (RVG) was estimated as the ratio of overwintering structures (new stem tubers) to total plant mass.

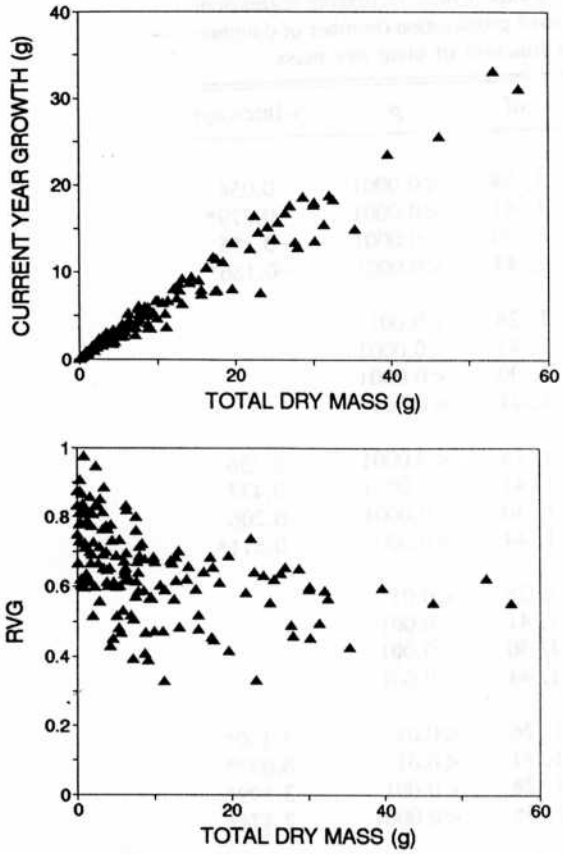

FIG. 3. Resource allocation to vegetative growth as a function of dry mass. Upper graph represents absolute allocation, and lower graph represents allocation relative to plant mass. RVG, relative vegetative growth.

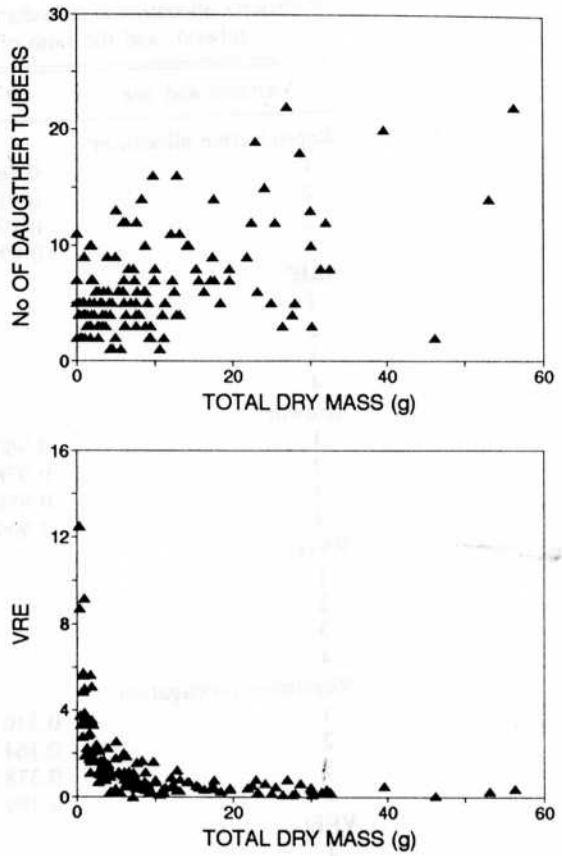

FIG. 4. Resource allocation to vegetative propagation as a function of plant dry mass. Upper graph represents absolute allocation, and lower graph represents allocation relative to plant mass. VRE, vegetative reproductive effort.

Dry mass was used as an integral measure of allocation. Total plant mass was used as the independent variable because the reproductive mass was only 7.1 ± 6.3% ($\bar{X} \pm$ SD, $n = 151$) of the total. Although the use of total plant mass as the independent variable results in artificial autocorrelation, the effect is negligible when the reproductive allocation is only a small proportion of the total plant mass (Samson and Werk 1986). Another possibly confounding variable might have been the time when measurements of reproductive allocation were taken. We chose to sample tissue of flowering plants because at flowering the plants bear all their inflorescences, whereas at fruiting the male flowers and the spadix appendix have already been shed and have therefore lost mass. In addition, most of the plants lose their second inflorescence before fruiting. Thus, we obtained the highest estimates of SRE at flowering.

The allocation of resources to sexual reproduction may occur at the expense of future vegetative growth, and this has been referred to as the somatic cost of reproduction (Tuomi et al. 1983). The somatic cost in individuals that sexually reproduce, relative to those that vegetatively reproduce, was calculated using equal-sized pairs of reproductive and nonreproductive individuals, according to the procedure of Karlsson et al. (1990). The relative somatic cost (RSC) was calculated as $(V - S)/V$, where V is the resource pool in overwintering organs of vegetative plants and S is the resource pool in overwintering organs of reproductive plants. The calculations were based on 10 pairs selected from all populations combined, although both plants in each pair were from the same population. Within the pairs, differences in total plant mass between reproductive and vegetative individuals ranged between 1 and 3.4%.

All computer analyses were done using the SPSS and BMDP statistical packages. Changes in dry mass allocation with plant size were fitted by means of nonlinear regressions, which were performed according to the method of Mead and Curnow (1983). ANCOVA was used to compare sites, using total plant mass as the covariate to avoid plant size effects. The results did not differ using original or log-transformed data, so original data were used. A one-way ANOVA was used to test differences among total dry masses of plants that produced different numbers of inflorescences. Heterogeneous data were cube-root transformed.

Results

Reproduction appeared to be closely linked to plant size in the total sample (Fig. 1). Individuals with masses less than 2.5 g did not produce any inflorescences, but all individuals heavier than 10.0 g produced at least one. There were significant differences in mass among individuals having none (2.1 ± 2.0 g; $N = 56$), one (10.5 ± 6.9 g; $N = 73$), or two (28.1 ± 13.3 g; $N = 20$) inflorescences ($F = 148.981$; df = 2, 146; $p < 0.001$; and $p < 0.05$ S−N−K test).

VRE, RVG, and the ratio of SRE to RVG differed significantly among sites in the ANCOVA (Table 1), but differences among sites were only nearly significant for SRE ($p = 0.051$). Ratios of SRE to VRE did not differ significantly between sites (Table 1). To summarize, we used all ramets combined because the size-dependent patterns of variation were similar for all sites (Table 2).

Data from combined samples showed that dry mass of the reproductive structures significantly increased with total plant mass (Fig. 2; $R^2 = 0.901$; $F = 1350.421$; df = 1, 141; $p < 0.0001$). The linear regression had a negative y-intercept. A significant linear relationship between SRE and plant mass was found ($R^2 = 0.292$; $F = 61.382$; $p < 0.001$), but an exponential regression gave a better fit ($F = 191.647$; $p < 0.001$; and lower residual sum of squares).

A highly significant linear regression was found between the

TABLE 2. Test of the linear, exponential increasing, and exponential decreasing regressions of resource allocation to reproduction, growth, vegetative propagation (number of daughter tubers), and the ratio of SRE to VRE as a function of plant dry mass

Variable and site	R^2	F	df	p	y-Intercept
Reproductive allocation[a]					
1	0.863	176.647	1, 28	<0.0001	0.054
2	0.915	442.576	1, 41	<0.0001	−0.279*
3	0.895	256.246	1, 30	<0.0001	−0.155
4	0.924	536.483	1, 44	<0.0001	−0.186*
SRE[b]					
1		38.009	1, 28	<0.001	
2		58.048	1, 41	<0.0001	
3		46.474	1, 30	<0.0001	
4		50.124	1, 44	<0.001	
Growth[a]					
1	0.980	1402.645	1, 28	<0.0001	0.336
2	0.978	1853.005	1, 41	<0.0001	0.437
3	0.958	683.229	1, 30	<0.0001	0.206
4	0.909	440.376	1, 44	<0.0001	0.611*
RVG[c]					
1		8.030	1, 28	<0.01	
2		10.353	1, 41	<0.001	
3		20.801	1, 30	<0.001	
4		16.012	1, 44	<0.001	
Vegetative propagation[c]					
1	0.310	11.688	1, 26	<0.01	5.160*
2	0.164	8.029	1, 41	<0.01	6.037*
3	0.378	16.987	1, 28	<0.001	3.599*
4	0.489	34.394	1, 36	<0.0001	2.474*
VRE[c]					
1		99.160	1, 26	<0.001	
2		60.161	1, 41	<0.0001	
3		594.642	1, 28	<0.0001	
4		94.896	1, 36	<0.001	
SRE/RVG[b]					
1		15.755	1, 28	<0.001	
2		47.983	1, 41	<0.0001	
3		50.096	1, 30	<0.0001	
4		38.876	1, 44	<0.001	
SRE/VRE[a]					
1	0.104	3.028	1, 26	0.093	0.009
2	0.450	33.493	1, 41	<0.0001	−0.092
3	0.586	39.622	1, 28	<0.0001	0.006
4	0.339	18.441	1, 36	<0.001	0.055

[a]Linear regression.
[b]Exponential increasing regression.
[c]Exponential decreasing regression.
*y-intercept significantly different from zero at $p < 0.05$.

dry mass of new tubers and plant mass (Fig. 3; $R^2 = 0.960$; $F = 3610.994$; $p < 0.0001$). The regression of the RVG on plant mass was negative and significant ($F = 41.258$; $p < 0.001$). The number of daughter tubers produced increased as plant mass increased (Fig. 4; $R^2 = 0.288$; $F = 55.517$; df = 1, 137; $p < 0.001$), but their relative number (VRE) fitted a nonlinear decreasing regression ($F = 269.655$; $p < 0.001$).

Plant mass had a significant effect on the ratio of mass of reproductive structures to the mass of new tubers (SRE/RVG), showing a significant nonlinear regression (Fig. 5A; $F = 132.356$; df = 1, 149; $p < 0.001$). The ratio of SRE to VRE increased linearly with plant mass increases (Fig. 5B; $R^2 = 0.329$; $F = 67.104$; df = 1, 137; $p < 0.001$).

Estimated RSC for individuals producing one inflorescence was 23.6 ± 10.5% ($N = 10$ pairs), but its value was not affected by SRE ($R^2 = 0.001$; $F = 0.008$; df = 1, 8; $p = 0.929$), the ratio of reproductive structures to the new tuber mass ($R^2 = 0.001$; $F = 0.007$; $p = 0.937$), or total plant mass ($R^2 = 0.002$; $F = 0.019$; $p = 0.893$).

Discussion

As for many perennial plants, *A. italicum* needs to grow to a minimum size before sexual reproduction occurs. Similar findings have been found in *Viola* spp. (Thompson and Beattie 1981), *Plantago* spp. (Antonovics and Primack 1982), *Saxifraga hirculus* (Ohlson 1988), and *Cypripedium acaule* (Primack and Hall 1990). This delay in reproduction was attributed to several causes. Weiner (1988) proposed allometric constraints as one possibility, while other authors (Peterson and Bazzaz 1978; Tissue and Nobel 1990) suggested the need to accumulate a certain amount of energy for reproduction. Similarly, the carbon

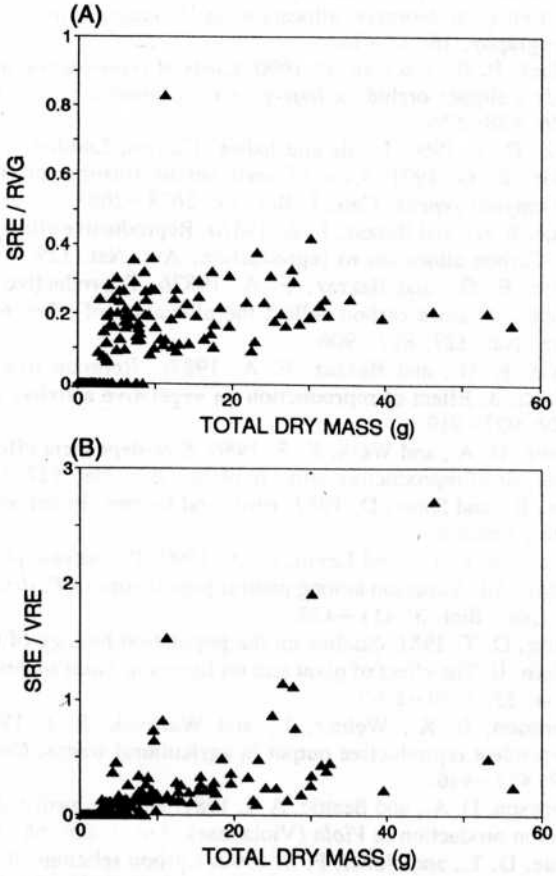

FIG. 5. (A) Ratio of reproductive structures to vegetative growth (new tuber mass) and (B) ratio of reproductive structures to vegetative reproduction (number of small new tubers) as a function of plant dry mass.

balance (Mooney and Chiariello 1984), the requirement of vernalization (De Jong et al. 1986), or the existence of different leaf morphologies for young and reproductive individuals (Valerio 1988) were also proposed. Ramets of *A. italicum* that are above a minimum size of 2.5 g do not flower regularly until they reach approximately 10.0 g. However, in other herbaceous perennials, even the larger plants do not reproduce sexually with regularity (Herrera 1988; Inghe and Tamm 1988; Primack and Hall 1990; Obeso and Villalba 1991). This may indicate the existence of a reproductive cost as suggested by Karlsson et al. (1990) and Eggert (1992). Nevertheless, *A. italicum* exhibited positive RSC, and ramets reproduced in successive years. The RSC was calculated using pairs of plants with masses less than 10 g (there were no vegetative individuals above the mass) and therefore the RSC may vary in larger plants. We found no relationship between RSC and the SRE, as suggested by Karlsson et al. (1990), but no conclusions can be drawn because of the limited data available. A high RSC may result in a shortage of resources allocated to successive reproductive sessions, which may be responsible for the low reproductive effort found in *A. italicum*. This provides the theoretical framework for asymtotic limitation of SRE, despite plants increasing in size. Accordingly, *A. italicum* showed low values of SRE compared with a number of forest perennial herbs ranging from 5 to 56% (Barrett and Helenurm 1987; Van Baalen et al. 1990). Furthermore, the closely related species, *Arisaema triphyllum*, does not reproduce regularly (Lovett-Doust and Cavers 1982) and exhibited higher SRE at flowering than *A. italicum*.

In *A. italicum*, resource allocation to different plant activities increased with increasing plant size; however, the relative allocations showed different patterns. Variations in SRE with plant size fit the model of Samson and Werk (1986) and were determined by the negative *y*-intercept of the regression line. Higher values of SRE in larger plants were predicted by Weiner (1988) and demonstrated in many experimental studies (e.g., Hartnett 1990; Thompson et al. 1991). Even within a species this relationship may vary among populations or between years (Ohlson 1988) and may be dependent on experimental treatments (Antonovics and Primack 1982). Patterns of biomass allocation may depend on soil moisture, nutrient availability, and light intensity (Zimmerman and Lechovicz 1982; Bell and Quinn 1987; Van Baalen et al. 1990; Dunn and Sharitz 1991; Reekie 1991; Powelson and Lieffers 1992). It is expected that plastic responses in resource allocation should be common in species inhabiting heterogeneous environments (Pitelka 1977; Vitale and Freeman 1986; Schlichting and Levin 1990). However, in *A. italicum*, despite the characteristics of our sites differing markedly, there were no clear differences among sites with respect to SRE.

Relative allocation to vegetative structures decreased as plant size increased. Other herbaceous perennials have shown either variable (Van Baalen et al. 1990) or fixed VRE (Ogden 1974; Van Andel and Vera 1977). Douglas (1981) found a positive relationship between VRE and plant size in *Mimulus primuloides*, while Hartnett (1990) found no relationship in four members of the Compositae. Decreasing VRE with increasing plant size may be attributed to the trade-off between allocation to sexual and vegetative reproduction (Solbrig 1981, Lovett-Doust 1989). In *A. italicum* the fact that the SRE to VRE ratio did not differ among populations, but vegetative growth patterns did, may indicate a fixed relationship. However, there is an alternative hypothesis. Clonal growth in *A. italicum* is of the "phalanx" type (Lovett-Doust 1981). The daughter tubers are close to the parent tuber and the ramets in the middle of a genet are larger than their surrounding ramets. Larger ramets had greater increases in SRE than smaller ramets, but the vegetative growth and propagation could be limited by space. This explains the increasing the SRE to VRE ratio as plant size increased and corresponds to a flexible reproductive strategy (Waller 1988). Furthermore, this pattern fits the model of Abrahamson (1980) that predicts increases in SRE as density increases.

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