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Cost of reproduction as reduced growth in genotypes of two congeneric species with contrasting life histories

E.G. Reekie[1] **and F.A. Bazzaz**[2]

[1] Department of Biology, Acadia University, Wolfville, N.S. Canada, BOP 1X0
[2] Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

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Summary. We examined the effect of reproduction on growth in 33 genotypes of *Plantago major* and 14 genotypes of *P. rugelii*. These two herbaceous perennials have contrasting life histories; *P. major* reproduces at a smaller size, and allocates a larger proportion of its biomass to reproduction, than *P. rugelii*. The effect of reproduction on growth was determined experimentally using photoperiod manipulations to control level of reproduction. The difference in growth between reproductive treatments was divided by the difference in capsule weight to produce a measure of reproductive cost per g of capsule for genotypes of the two species. In both species there was substantial variation among genotypes in the effect of reproduction on growth. Much of this variation could be correlated with differences among genotypes in the extent of reproductive investment and plant size. Cost in terms of reduction in growth per g of capsule increased with reproductive investment in *P. rugelii*, and with plant size in *P. major*. We suggest the differences between species in timing and extent of reproduction are related to the differences between species in effect of reproduction on growth. *Plantago rugelii* may reproduce to a lesser extent than *P. major* because cost per g of capsule in terms of reduced vegetative biomass, increases with reproductive output in the former species, but not in the latter. Similarly, *P. major* may reproduce earlier than *P. rugelii* because cost per g of capsule increases with plant size in *P. major*, but not in *P. rugelii*.

Key words: Time of reproduction – Size at reproduction – Reproductive effort – Reproductive output – Photoperiod

A crucial assumption of theories to explain differences among plants in extent of reproductive investment, is that there is a cost associated with reproduction (Harper 1977; Antonovics 1980). This cost is perhaps best measured by comparing the survivorship and future reproductive output of reproductive versus vegetative plants (Antonovics 1980). However, it also possible to get a measure of the cost of reproduction by examining the effect of reproduction upon growth. Reproduction in a given season cannot directly affect future survivorship or reproduction, but it does affect growth through its influence on resource uptake and allocation patterns (Reekie and Bazzaz 1987a, b). By affecting growth, reproduction influences plant size and this in turn helps determine the effect of reproduction on future survivorship and reproductive output. Plant size has been shown to be closely correlated with both survivorship and reproductive output (e.g. Werner 1975; Gross 1981). Therefore, by examining the effect of reproduction on growth we can predict how reproduction may affect both survivorship and future reproductive output, and gain some understanding as to why it does so.

There is a substantial body of anecdotal and correlative evidence concerning the effects of reproduction upon growth (see Harper 1977; Bazzaz et al. 1987). However, there are problems involved in using correlative evidence to assess the cost of reproduction (Antonovics 1980; Thompson and Stewart 1981; Bazzaz and Reekie 1985). In correlative studies the level of reproductive investment is usually confounded with both environmental and genetic differences; plants differing in level of reproductive investment can also differ in genotype and in environment. Therefore, differences between plants in growth cannot simply be attributed to differences in reproduction. There are methods to minimize these problems (eg. Primack and Antonovics 1982) but, experimental manipulations of reproduction are a potentially more powerful means of determining reproductive costs in those situations where they are practical.

It is only recently that controlled experiments have been used to critically assess the cost of reproduction in plants. Antonovics (1980) used photoperiod manipulations to control reproduction in *Plantago lanceolata*. He found that vegetative growth was reduced only at high

Offprint requests to: E.G. Reekie

levels of reproduction. Reekie and Bazzaz (1987a, b) using similar techniques, found the cost of reproduction in *Agropyron repens* was variable depending upon genotype and availability of light and nitrogen. In favorable environments with high light and nitrogen, reproduction did not reduce growth in some genotypes. Jurik (1985) used a model of carbon balance to examine cost of vegetative and sexual propagules in *Fragaria*. He found that cost per propagule was lowest in open habitats and highest in closed habitats. Horvitz and Schemske (1988) used flower bud removal to manipulate reproduction in the field in *Calathea ovandensis*, a tropical herb. They found reproduction did not reduce subsequent growth and survival under the conditions of this experiment. Enhancement of fruit set above natural levels by hand pollination results in reduced growth in several species of orchids (Snow and Whigham 1989; Ackerman and Montalvo 1990; Primack and Hall 1990). It appears that although reproduction may reduce vegetative growth, this effect is variable and, in some situations, negligible.

Current life history theory explains differences among plants in reproductive patterns in terms of the likely success of seedlings versus adults among habitats (for a review see Willson 1983). For example, in habitats where seedling survivorship is high relative to that of adults, those individuals that reproduce early and allocate a large proportion of resources to reproduction will have a selective advantage over those that do not. The fact that there is intraspecific variation in the cost of reproduction however, suggests an alternative explanation for differences among plants in reproductive patterns. We suggest differences among species in reproductive patterns can be related to differences in the cost of reproduction. There would be a selective advantage to modifying reproductive patterns to minimize cost per propagule. For example, plants that reproduce early may do so because it minimizes the detrimental effects of reproduction upon growth (and consequently, the detrimental effects of reproduction on future survivorship and reproductive output). Further, those plants that allocate only a small proportion of their resources to reproduction at any one time, may do so because cost per propagule increases with reproductive output. In such a situation, lifetime reproductive output may be maximised by reproducing many times, but producing only a few propagules each time.

We tested the above hypothesis by comparing cost of reproduction in two congeneric species: *Plantago major* L. and *Plantago rugelii* Decne. These species are similar in general morphology, but differ in several population and life history characteristics (Hawthorn 1974; Hawthorn and Cavers 1976, 1978; Primack 1979; Miao and Bazzaz 1990). *Plantago major* tends to occur where frequency of disturbance is higher, and reproduces at a smaller size and to a greater extent than *P. rugelii*. We will determine if it is possible to interpret the differences between these two species in reproductive patterns in terms of differences in the effect of reproduction on growth. We make two predictions: 1) Cost per propagule will increase with plant size in *P. major* but not in *P. rugelii*, or if so, to a lesser extent. 2) Cost per propagule will increase with extent of reproductive investment in *P. rugelii* but not in *P. major*, or if so, to a lesser extent. We tested these predictions by determining cost per g of capsule produced for individual genotypes of these two species, and examining to what extent these costs varied with size and reproductive output of the genotypes.

Methods

Seed of both species was collected in eastern Massachusetts, U.S.A., where the species are sympatric. Several populations were sampled to provide a bulk seed collection for each species. Seeds were germinated on moist vermiculite and, when well established, transplanted individually to 475 ml plastic pots filled with Turface[R]. Pots were placed in controlled environment chambers that provided a day/night temperature of 25/20° C, a 13 h photoperiod and a photon flux density of 300 μmoles $m^{-2}s^{-1}$ (400–700 nm). Plants were watered daily with tap water, and mineral nutrients were supplied by watering the plants once per week with 1/4 strength Hoaglands' nutrient solution.

After four months of growth, the caudex of each individual was cut into four equal pieces by splitting it along the vertical axis twice. Roots on each piece of the caudex were pruned to a uniform length of 2.5 cm and all leaves, except the two youngest, were removed. Each cutting was planted in a separate pot. Further growing conditions were as above with the exception of photoperiod. Plants were randomly assigned to one of two photoperiod treatments (13 or 15 h) with two replications of each genotype per photoperiod treatment. There were 33 genotypes of *P. major* and 14 genotypes of *P. rugelii*. Two growth chambers were used for each photoperiod treatment, for a total of four chambers with one cutting per genotype per chamber. Both short and long photoperiod treatments received 13 hours of high light (300 μmoles $m^{-2}s^{-1}$) but the long photoperiod plants received an additional two hours of low light (12 μmoles $m^{-2}s^{-1}$). Total light received in the period of low light amounted to less than 1% of the light received by the short photoperiod plants. To avoid confounding possible chamber effects with photoperiod treatments, plants with their respective treatments were rotated among chambers on a weekly basis.

The experiment was terminated five months after cuttings were transplanted into separate pots. By this time, all plants that flowered had mature seed capsules. Individual plants were divided into leaves, reproductive spikes (scape), seed capsules and roots (including caudex) and leaf area was determined. Plant material was dried at 50° C for > 48 h before weighing. Individual leaves that died over the course of the experiment remained attached to the stem base and were included as part of total biomass. The only plant parts not included in total biomass were the anthers which dehisced after pollination.

Cost of reproduction was determined in a manner similar to that described by Reekie and Bazzaz (1987b). Flowering was controlled experimentally by the photoperiod manipulations and plant growth in the two treatments compared. Both species are long-day plants with a critical photoperiod of 14 h (Hawthorn 1974). For *P. major*, and to a lesser extent in *P. rugelii*, plants flowered in the short as well as long photoperiod. However, the extent of flowering differed greatly between the two photoperiod treatments; all plants flowered in the long photoperiod treatment while only some flowered in the short photoperiod treatment, and those that did flower, produced fewer inflorescences. We calculated cost of reproduction in terms of lost growth per unit of capsule production (g/g) for each genotype using the following formula:

$$\frac{B_s - B_l}{C_l - C_s}$$

Table 1. Effect of reproduction on growth and allocation in *Plantago major* and *P. rugelii*. Low and high levels of reproductive investment were obtained experimentally by exposing plants to either short or long photoperiods. Error values represent two standard errors

	P. major		*P. rugelii*	
	Low *Reprod.*	High *Reprod.*	Low *Reprod.*	High *Reprod.*
Capsule Wt. (g)	0.69 ±0.18	1.46 ±0.12	0.03*	0.72 ±0.10
Vegetative Wt. (g)	5.44 ±0.42	3.38 ±0.42	6.70 ±0.74	7.45 ±0.78
Total Wt. (g)	6.37 ±0.34	5.69 ±0.36	6.76 ±0.78	8.48 ±0.74
Reproductive Ratio (g capsule/g total)	0.179±0.042	0.407±0.024	0.032*	0.119±0.016
Root: Shoot Ratio (g root/g shoot)	1.105±0.102	0.479±0.096	2.012±0.136	0.924±0.144
Leaf Area Ratio (cm^2 leaf/g total)	61.1 ±3.0	49.2 ±3.0	59.5 ±6.4	69.2 ±6.6

* Due to the large number of non-reproducing plants in this treatment a standard error was not calculated

Where: B_s = Biomass of plants in the short photoperiod treatment

B_l = Biomass of plants in the long photoperiod treatment

C_s = Capsule biomass in the short photoperiod treatment

C_l = Capsule biomass in the long photoperiod treatment

Costs were calculated in terms of both total biomass and vegetative biomass (i.e. biomass of leaves stems and roots). Cost assessed in terms of total biomass is useful in that it reflects the immediate effects of reproduction on the carbon gaining capacity of the plant. Cost measured in terms of vegetative biomass on the other hand, is perhaps a better measure of the effect of reproduction upon future growth.

In using capsule weight as a measure of reproductive output rather than seed weight we assume the species do not differ in the proportion of total capsule weight allocated to seeds. To test this assumption, we determined the seed fraction of total capsule weight for a subsample of 60 capsules. We found no difference ($p < 0.9337$) between *P. major* (63.5%) and *P. rugelii* (63.3%) in the seed fraction of total capsule weight. Average seed weight per capsule was 0.00166 and 0.00235 g for *P. major* and *P. rugelii* respectively. These values are similar to those of field grown plants (0.00147 and 0.00198 g, Hawthorn 1974) indicating level of seed set was normal.

Analysis of variance was used to determine the significance of differences between photoperiod treatments in overall biomass and allocation patterns. Separate analyses were conducted for each species. There were three factors in each analysis: photoperiod, genotype and the photoperiod × genotype interaction.

To confirm that the differences observed between species in the effect of reproduction on growth (see Table 1) were not an artifact of photoperiod manipulations, we also examined the cost of reproduction using correlative techniques (Primack and Antonovics 1982). Using plants from the long photoperiod treatment, we determined the correlation between total biomass or vegetative biomass (i.e., leaves, stems and roots) and either, reproductive output (g capsules), or reproductive ratio (biomass of capsules/total biomass). Due to the small number of reproductive plants in the short photoperiod treatment, a similar analysis could not be done for these plants. Separate analyses were conducted for each of the two species.

To determine the extent to which intraspecific variation in cost of reproduction was correlated with variation in plant size and extent of reproduction, we used regression analysis. Cost per g of capsule for each genotype was used as the dependent variable, and plant size (g total biomass) and reproductive output (g capsules) were used as possible independent variables. Plant size and reproductive output were the mean values for each genotype (i.e. values were averaged across treatment and replications). Similar results were obtained when separate values were used for the different photoperiod treatments. As plant size and reproductive output were partially correlated, multiple regression analysis was used. This procedure minimized the possibility of spurious correlations. Separate analyses were conducted for each species.

Results

The long photoperiod plants reproduced to a much greater extent than did the short photoperiod plants. This was true, regardless of whether reproductive output or proportional allocation to reproductive structures was used as a measure of reproduction (Table 1). In both short and long photoperiods, *P. major* reproduced to a greater extent than did *P. rugelii*. In the short photoperiod treatment where not all plants reproduced, the minimum size of reproductive plants was 1.0 for *P. major* compared to 3.6 g for *P. rugelii*.

Increasing level of reproduction in *P. major* (i.e. increasing photoperiod) caused a decrease in both total biomass and vegetative biomass, whereas increasing reproduction in *P. rugelii* did not affect vegetative growth and actually increased overall growth (Table 1). Both root/shoot ratio and leaf area ratio declined with reproduction in *P. major*. *Plantago rugelii* similarly exhibited a decrease in root/shoot ratio with reproduction, but, leaf area ratio increased with reproduction. Regard-

Table 2. Correlation between growth and level of reproductive investment among plants in the long photoperiod treatment. Growth was assesed as either total biomass or biomass of vegetative structures only. Capsule biomass and reproductive ratio (reproductive biomass/total biomass) were used as indicators of the level of reproductive investment. Values in parentheses are the level of significance for the correlation coefficient

	Total Growth	*Vegetative Growth*
Plantago major		
Capsule Weight	0.52 ($p < 0.0001$)	0.04 ($p < 0.7322$)
Reproductive Ratio	−0.02 ($p < 0.8533$)	−0.49 ($p < 0.0001$)
Plantago rugelii		
Capsule Weight	0.66 ($p < 0.0002$)	0.52 ($p < 0.0055$)
Reproductive Ratio	0.48 ($p < 0.0107$)	0.33 ($p < 0.0945$)

less of level of reproduction, root/shoot ratio was higher in *P. rugelii* than *P. major*. Leaf area ratio, total biomass and vegetative biomass of the two species were similar at low levels of reproduction, but lower in *P. major* at high levels of reproduction.

Correlations between reproductive ratio and various measures of plant growth in the long photoperiod treatment were in accord with results of the experimental manipulations; *P. major* experienced a greater reproductive cost than *P. rugelii* (Table 2). There was a negative correlation between reproductive ratio and vegetative weight for *P. major*, whereas there was no correlation for *P. rugelii*. Furthermore, there was a positive correlation between reproductive ratio and total biomass for *P. rugelii*, but not for *P. major*. The magnitude of the correlations differed when weight of capsules was used as a measure of reproductive investment rather than reproductive ratio, but the overall pattern (i.e. differences between species) remained the same.

Both species exhibited substantial intraspecific variation in cost per g of capsule. Costs for individual genotypes included negative as well as positive values, particularly when cost was expressed in terms of lost total growth rather than lost vegetative growth. On average, costs were lower for *P. rugelii* than *P. major* but, there was substantial overlap between species. A significant proportion of this intraspecific variation in cost was correlated with plant size and reproductive output but the relationships differed between species (Table 3). Cost per g of capsule increased with plant size in *P. major*, but not in *P. rugelii*. Variation in total biomass accounted for 26% of the variation in cost per g of capsule in *P. major* and only 6% of the variation in *P. rugelii*. Rather than varying with plant size, cost per g of capsule in *P. rugelii*

Table 3. Results of a stepwise regression analysis with cost/g capsule for individual genotypes as the dependent variable, and total biomass and capsule biomass as possible independent variables. Separate analyses were conducted for each species, and for cost measured in terms of lost total growth or lost vegetative growth

Species	Dependent Variable	Independent Variables	Coefficient of Determination	Level of Significance
P. major	Lost Total Growth/g Capsule	Total biomass	0.26	$p<0.0023$
		Capsule biomass	0.02	$p<0.4159$
P. rugelii	Lost Total Growth/g Capsule	Total biomass	0.06	$p<0.1005$
		Capsule biomass	0.75	$p<0.0001$
P. major	Lost Vegetative Growth/g Capsule	Total biomass	0.24	$p<0.0037$
		Capsule biomass	0.00	$p<0.7454$
P. rugelii	Lost Vegetative Growth/g Capsule	Total biomass	0.06	$p<0.0974$
		Capsule biomass	0.73	$p<0.0001$

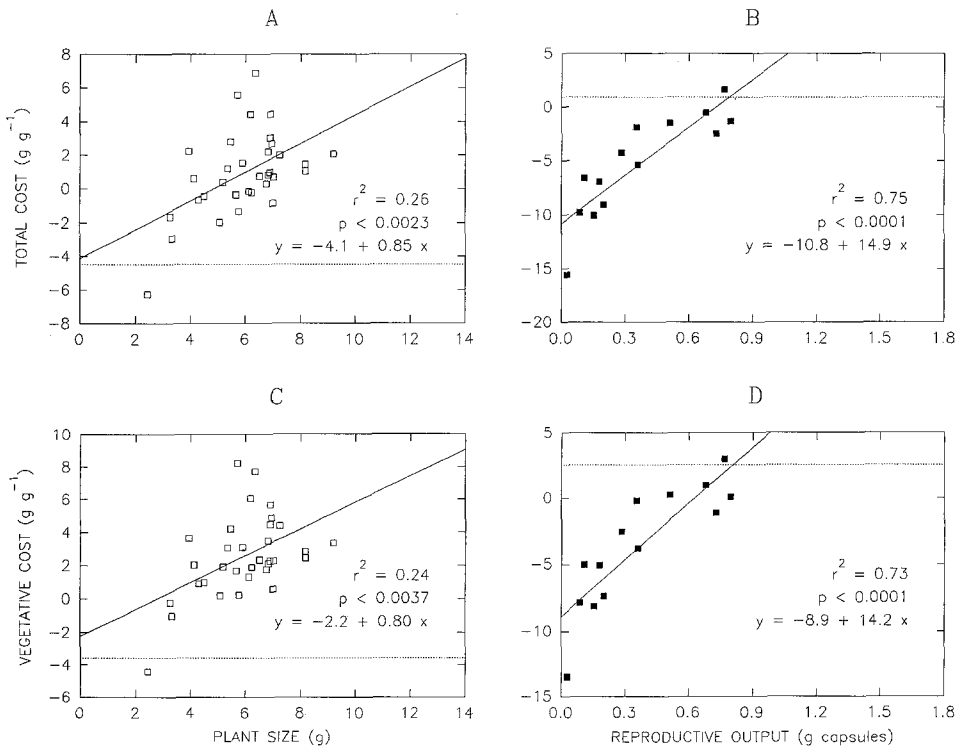

Fig 1A–D. Reproductive cost for genotypes of *P. major* expressed as function of plant size (*open symbols*, **A** and **C**), and reproductive cost for genotypes of *P. rugelii* expressed as a function of reproductive output (*closed symbols*, **B** and **D**). Reproductive cost represents the amount of lost growth per g of capsule produced. Cost was expressed in terms of either total (**A** and **B**), or vegetative growth (**C** and **D**). Solid lines represent the relationships fitted by stepwise regression analysis (see Table 3). There was no significant relationship between reproductive cost and plant size for *P. rugelii*, or between cost and reproductive output in *P. major* (Table 3). For the purposes of comparison between species, average cost per g of capsule for *P. rugelii* is plotted as a dotted line in graphs **A** and **D**, and for *P. major* in graphs **B** and **D**

increased with increases in reproductive output. Cost per g of capsule did not increase with reproductive output in *P. major*. Variation in capsule biomass accounted for 75% of the variation in cost per g of capsule in *P. rugelii* and for only 2% of the variation in *P. major*. Regardless of whether costs were expressed in terms of lost total growth or lost vegetative growth, similar results were obtained (Table 3).

The relationships between cost per g of capsule and either plant size or reproductive output are illustrated in Fig 1. Note that small genotypes of *P. major* experienced an increase in growth with reproduction similar that observed in *P. rugelii,* and that as plant size increased, cost in *P. major* increased relative to that experienced by *P. rugelii.* (Fig. 1A and C). Also note that although mean reproductive cost was lower in *P. rugelii* than in *P. major,* its cost increased rapidly with reproductive output. As a result, at a given level of reproductive output (eg. when reproductive output of the two species was 0.9 g capsules), cost in *P. rugelii* was similar to or greater than cost in *P. major* (Fig. 1B and D). Conclusions were the same regardless of whether costs were assessed in terms of lost total growth (Fig. 1A and B) or lost vegetative growth (Fig. 1C and D).

Discussion

Reproduction had marked effects upon growth in the two species. Averaged across genotypes, reproduction was associated with increased growth in *P. rugelii* and decreased growth in *P. major* (Table 1). It is concievable that photoperiod has a direct effect upon growth aside from its effect upon extent of reproduction. However, correlations between plant size and reproductive investment within the long photoperiod treatment revealed a similar pattern (Table 2). The difference in growth between photoperiod treatments was not an artifact of photoperiod manipulations. Rather, it was a reflection of the effect of reproduction on growth.

Although the positive effects of reproduction upon growth were more marked in *P. rugelii,* in both species there were some genotypes with a negative reproductive cost (Fig. 1). This was particularly true when cost was expressed in terms of total growth rather than vegetative growth. The idea of a negative reproductive cost (i.e. an increase in growth with reproduction) may at first glance be counter intuitive. However, it is in accord with current understanding of the effect of reproduction upon plant carbon balance. It also agrees with some of our previous work. Reproductive structures of many species are capable of photosynthesis and can supply a large proportion of the carbon required for reproduction (Bazzaz and Carlson 1979; Bazzaz et al. 1979; Werk and Ehleringer 1983; Jurik 1983). In addition, the developing reproductive structures constitute a very active sink for photosynthates, and increases in sink strength have been shown to increase leaf photosynthetic rates (Burt 1964; Nosberger and Humphries 1965; Neales and Incoll 1968). Both of these factors helped compensate for the cost of reproduction in *Agropyron repens* (Reekie and Bazzaz 1987a), and under favourable growing conditions, reproduction in this species also enhanced overall plant growth in some genotypes (Reekie and Bazzaz 1987b).

It seems likely that the same mechanisms that allow *Agropyron* to compensate for the cost of reproduction also operate in *Plantago.* We have no data on the effect of reproduction on leaf photosynthesis in *Plantago,* but the reproductive structures are green throughout their development and therefore, potentially capable of direct photosynthesis. In addition, we have shown that reproduction in *P. rugelii* increased leaf area ratio (Table 1). This increase in photosynthetic area relative to respiratory mass would further contribute to a positive effect of reproduction on plant carbon balance. It also helps explain why reproduction has less of a negative effect on growth in *P. rugelii* than in *P. major.* Future studies should examine the effect of reproduction on carbon balance in these two species to more fully explain why cost of reproduction differs between species, and why it varies with plant size in *P. major* and reproductive output in *P. rugelii.*

The differences observed between species in size at reproduction and in level of reproductive investment (Table 1), have previously been interpreted in terms of their different survivorship patterns (Hawthorn and Cavers 1976, 1978). Although these two species are often found in the same habitat, there is a tendency for *P. major* to be more common in sites where frequency of disturbance is greater. It has been suggested therefore, that in *P. major,* early reproduction and increased allocation to reproduction have been selected for as a consequence of the reduced life expectancy of the adults. However, it is also possible to interpret the differences in reproductive patterns between these two species in terms of the reproductive costs experienced by individuals of the two species.

In *P. major,* genotypes with a high reproductive output had the same cost per g of capsule as genotypes with a low reproductive output. On the other hand, genotypes of *P. rugelii* with a high reproductive output had a higher cost per g of capsule than genotypes with a low reproductive output. Thus in *P. rugelii,* there would be additional selection pressure over and above that experienced by *P.major,* to minimize investment in reproduction. This in itself could explain the lower reproductive investment of *P. rugelii* relative to *P. major.*

The difference in timing of reproduction between the two species (Hawthorn and Cavers 1976, 1978) can also be interpreted in terms of variation in reproductive cost (Table 3). The detrimental effect of reproduction on growth increased with plant size in *P. major* but, not in *P. rugelii.* Therefore, *P. major* may reproduce at a relatively small size to minimize the cost of reproduction. Postponing reproduction increases plant size at reproduction and as a result, increases cost per g of capsule. On the other hand, *P. rugelii* can postpone reproduction and reproduce at a large size without experiencing any increase in cost of reproduction. Therefore, the early reproduction of *P. major* relative to *P. rugelii* can be interpreted as a mechanism to minimize the detrimental effects of reproduction on growth.

The above explanations for differences between these two species in timing and extent of reproduction make no explicit assumptions concerning survivorship patterns of the two species Consequently, our explanation may account for some of the apparent exceptions (Willson 1983) to current theory.

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