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An experimental field study of the cost of reproduction in *Plantago major* L.[1]

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Abstract: Plantago major is a variable species that occupies a wide range of open habitats with a herbaceous canopy. Previous studies have shown that individuals from habitats where the canopy is kept short by mowing have a higher reproductive allocation than individuals from habitats with a tall canopy. The present study was conducted to determine whether or not the cost of reproduction differed between these two habitats. Fifteen half-sibling families, selected from a range of habitats differing in canopy height, were grown in the laboratory. Reproduction was controlled experimentally by photoperiod manipulations, and vegetative and reproductive plants of each family were transplanted to either a mown (short canopy) or unmown (tall canopy) grass sward in the fall of the first year. Number of leaves, length and width of largest leaf, and capsule production were monitored over the next 18 months. Total shoot biomass was determined at the end of this period. Cost of reproduction was assessed in three ways, by *i*) comparing the subsequent performance of vegetative and reproductive individuals, *ii*) calculating the phenotypic correlation between reproductive output in the first year of growth and subsequent performance using only those individuals that reproduced in the first year, and *iii*) calculating the above correlations at the among family level. Regardless of method used, cost of reproduction was smaller in the mown than in the unmown plots, suggesting that differences in cost among habitats may be involved in selecting for different allocation patterns.
Keywords: reproductive effort, life history theory, reproductive allocation, disturbance, r- *versus* K-selection.

Résumé: Plantago major est une espèce variable qui occupe toute une gamme d'habitats ouverts composés de plantes herbacées. Des études précédentes ont montré que les individus poussant dans des habitats où le couvert est maintenu relativement bas par la fauche montre une allocation à la reproduction plus élevée que les individus poussant dans des habitats à couvert plus haut. La présente étude a été menée pour déterminer si le coût de la reproduction diffère entre les deux habitats. Des graines provenant de quinze familles maternelles, sélectionnées dans des habitats ayant différentes hauteurs de couvert, ont été semées en laboratoire. La reproduction a été contrôlée expérimentalement en modulant la photopériode et des individus végétatifs et reproducteurs ont été transplantés dans une pelouse fauchée (couvert bas) ou non (couvert haut), à l'automne de la première année. Le nombre de feuilles, leur longueur et largeur et la production de capsules ont été suivi durant les 18 mois suivants. La biomasse totale de la partie aérienne a été déterminée à la fin de cette période. Le coût de la reproduction a été estimé de 3 façons différentes, soit *i*) en comparant les performances ultérieures des individus végétatifs et reproducteurs, *ii*) en calculant une corrélation phénotypique entre le rendement reproductif de la première année de croissance et les performances subséquentes, en ne considérant que les individus qui se sont reproduits la première année et *iii*) en calculant les corrélations précédentes mais en tenant compte des familles. Indépendamment de la méthode utilisée, le coût de la reproduction était toujours plus faible chez les individus provenant des parcelles fauchées que chez les individus provenant des parcelles non fauchées. Ceci suggère que des coûts différents entre les milieux peuvent être impliqués dans la sélection de patrons d'allocation différents.
Mots-clés: effort reproducteur, théorie du cycle vital, allocation à la reproduction, perturbation, sélection r *versus* k.

Introduction

A number of studies have shown that the cost of reproduction in plants is highly variable depending upon environmental conditions (Jurik, 1985; Reekie & Bazzaz, 1987a,b; Primack & Hall, 1990; Zimmerman, 1991; Reekie & Reekie, 1991; Saulnier & Reekie, 1995; Thoren, Hemborg & Karlsson, 1996). This variation is significant in that it may influence the evolution of life history characters (Svensson *et al.*, 1993; Obeso, 1993; Syrjanen & Lehtila, 1993). For example, variation in the relative cost of seeds *versus* vegetative propagules among environments may influence the resources allocated to these two modes of propagation (Reekie, 1991). Although this suggestion has merit, the conclusions are tentative in that there are serious difficulties involved in accurately assessing reproductive costs in terms that are relevant to evolution (Stearns, 1989). Four basic approaches have been used to measure the cost of reproduction: *i*) phenotypic correlations, *ii*) experimental manipulations of reproductive output, *iii*) genetic correlations, and *iv*) selection experiments.

Studies that examine the correlation between reproductive output (RO) and some measure of subsequent performance (*e.g.*, survival or future RO) have been widely used to assess the phenotypic cost of reproduction under field conditions (Law, 1979; Piñero, Sarukhán & Alberdi, 1982). However, differences in RO are confounded with environmental differences and spurious correlations may result (Fox & Stevens, 1991). For example, an individual in a particularly favourable microhabitat might have a high reproductive output. This same plant may also have a high subsequent growth rate compared to individuals growing in less favourable habitats which reproduced to a lesser extent. Phenotypic correlations in this case will underestimate the cost of reproduction.

Experiments that control level of reproduction using photoperiod manipulations, growth regulator applications or removal of inflorescences (Reekie & Bazzaz, 1992; Reekie

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& Reekie, 1991; Thoren, Karlsson & Tuomi, 1996) have a major advantage over correlative methods in that level of reproduction is not confounded with environmental differences. Experimental manipulations of RO provide an estimate of the phenotypic cost of reproduction which is relevant to questions of how an individual should allocate its resources to reproduction in different environments; *i.e.*, it can explain phenotypic plasticity in allocation (see Reekie, 1997). However, it provides no direct information on the genetic tradeoffs associated with reproduction, and therefore, on the evolution of different allocation patterns (Reznick, 1985). If similar physiological mechanisms are involved, it may be possible to infer genetic costs from phenotypic costs, but it would be unwise to simply assume that they are similar.

Genetic correlations between RO and subsequent performance (*e.g.*, Geber, 1990) provide an estimate of the cost of reproduction that is directly relevant to evolutionary questions. However, genetic correlations will only give an accurate estimate if there is sufficient variation in RO within the population. Given that RO is likely subject to strong selection, many populations will contain little variation (Bailey, 1992). In this situation, there would be no measureable correlation between RO and subsequent performance and it would be (incorrectly) concluded that reproduction has no cost. Another potential problem is the presence of genotype × environment interactions. As discussed above, reproduction may have very different consequences in different environments. Therefore, if genetic correlations are determined in the field where the environment may be variable, genotype × environment interactions could obscure or bias the genetic correlations. On the other hand, if correlations are determined in the laboratory where the environment can be controlled, the correlations may not reflect what occurs in the field where the environment may differ substantially from that simulated in the laboratory.

Experiments in which low or high RO is selected for, and the tradeoffs which result from this selection quantified, perhaps provide the most satisfying estimate of the cost of reproduction from an evolutionary perspective (Reznick, 1985; Stearns, 1989). This method suffers from the same drawbacks as an examination of genetic correlations. There must be sufficient genetic variation in RO within the population to allow selection; the tradeoffs that result will likely vary depending upon the environment and therefore must be assessed in realistic field environments.

The present study examines cost of reproduction in *Plantago major* in two contrasting field environments: *i*) a closely mowed lawn and *ii*) an unmown grass sward. A previous study (Warwick & Briggs, 1980) found that reproductive allocation as assessed by the ratio between reproductive and vegetative mass is more than twice as great in individuals isolated from mown sites than in individuals from unmown sites when grown in a common environment. Although size differs between individuals isolated from mown *versus* unmown sites, these differences in reproductive allocation are not simply related to size constraints (see Sampson & Werk, 1986; Weiner, 1988) as the relationship between size and reproductive output differs between individuals isolated from the two habitats (Reekie, unpubl. data). One possible explanation for these different allocation patterns are differences in the cost of reproduction among habitats, *i.e.*, if the cost of reproduction is low, this may select for a higher reproductive allocation. The present study examines this possibility by estimating the cost of reproduction under field conditions using three different approaches. Experimentally manipulated reproductive and vegetative plants belonging to 15 different half-sibling families were transplanted to mown *versus* unmown plots and their subsequent performance monitored for the next 18 months. Cost of reproduction was estimated by: *i*) comparing size of vegetative *versus* reproductive plants across the two treatments, *ii*) calculating the phenotypic correlation between reproduction and subsequent performance among the reproductive individuals, and *iii*) calculating the genetic correlation between reproduction and subsequent performance among the reproductive individuals.

Material and methods

THE SPECIES

Plantago major L. is a short-lived iterocarpic perennial found in a wide variety of habitats differing in disturbance regime and resource availability (Hawthorn & Cavers, 1976; Blom, 1977; Van Dijk & Van Delden, 1981; Van Dijk, 1984; Lotz, 1990). It forms an acaulescent rosette in the vegetative state and leafless elongate spikes are formed when reproduction occurs. The flowers are inconspicuous and primarily self-pollinated (Hawthorn, 1974). The spikes, flowers and developing capsules are green and therefore at least potentially photosynthetic and may supply a portion of their own carbon requirement. Reproduction is photoperiod dependent requiring long days with a critical photoperiod of approximately 15 hours (Hawthorn, 1974).

SEED COLLECTION

Seed was collected from 15 sites in Kings County, Nova Scotia (45° 06' N, 64° 24' W). Sites were selected to sample the range of habitats in which *P. major* is found within this area. Habitats included closely mown lawns, coarse turf, forest margins and hay fields. At each site, seed from a single individual was collected. Each site, therefore, represents at least a half-sib family, and because *P. major* is predominantly self-fertilizing, most of the individuals within a family will be full siblings. The different families were included within the study to provide a sample of the genetic variation within the species. To the extent that maternal environment may influence seedling performance (Miao, Bazzaz & Primack, 1991), among family comparisons may also include an environmental component.

PLANT CULTURE AND EXPERIMENTAL DESIGN

Seeds were germinated in moist vermiculite and transplanted when each seedling had at least two true leaves into 250 ml pots containing a commercial, peat-based potting soil (ASB-Greenworld Ltd., Point Sapin, New Brunswick). Transplanting took place on July 23, 1990. There were 36 plants in each of the 15 families for a total of 540 pots. Pots were placed in one of two plant growth chambers which provided a day/night temperature of 25/20°C and a photosynthetic photon flux (PPF) of 300 μmol m^{-2} s^{1} (400-700 nm) supplied by a mixture of cool-white fluorescent and

incandescent lamps (62.5% and 37.5% input wattage respectively) for 13 hours. In one of the chambers, this was supplemented by an additional 2 hours of 8.5 μmol m^{-2} s^{-1} PPF (60.3% input wattage fluorescent and 39.7% incandescent) immediately prior to the high light period to provide a photoperiod of 15 hours. The period of low light extension in the long photoperiod treatment was continued for a period of six weeks, at that time the photoperiod in both chambers was reduced to 12 hours of high light and temperature was reduced to 20/15°C. After two weeks, photoperiod was further reduced to 11 hours and temperature to 15/10°C for a two week period and finally to 10 hours and 10/5°C for another two week period. The extra light received by plants in the long photoperiod treatment was less than 0.3% of the light received in the short photoperiod treatment. Plants with their respective photoperiod treatments were rotated between chambers on a weekly basis to avoid confounding possible chamber effects with photoperiod treatments.

On October 24, 1990, after a total of 12 weeks growth, plants were transplanted to experimental field plots. The field site was a 6 m × 10 m grass sward heavily dominated by *Poa pratensis*. The grass sward was established on September 21, 1990 using commercially available sod. The site was located in an experimental garden and was surrounded by a large buffer zone of cultivated soil and mown lawn. The site was level with good drainage and soil type was a Wolfville clay loam. There were no obvious environmental gradients within the site. Plants were transplanted into the grass sward on an 18 × 30 plant grid. Each plant was 30 cm from the nearest neighbour and at least 30 cm from the edge of the grass sward. The site was divided into two 3 m × 10 m sub plots. Each plot contained 270 plants: nine replications of each family × photoperiod combination. Within plots, placement of plants was at random. At time of transplantation, plants in the long photoperiod treatment had flowered and had immature capsules. Capsules were collected from these plants as they matured in the field. Plants were checked for mature capsules on a weekly basis and all capsules had matured and were collected by mid-November.

Starting on May 16, 1991, one of the plots was mowed on a weekly basis with a rotary lawn mower set at a height of 7 cm. Mowing removed reproductive spikes but, otherwise had little direct effect upon *Plantago*. Plants in the mowed plots formed flat rosettes with most leaves below 7 cm height. The remaining plot was left unmown and reached a maximum canopy height of approximately 50 cm. Plants were censused on June 25 and August 20 in 1991. At each census, number of leaves and length and maximum width of the largest leaf were recorded for each plant. These data were used to generate a plant size index by multiplying the number of leaves by length and width of the largest leaf. This size index is closely correlated with leaf biomass (Lotz & Blom, 1986). Capsules were collected as they matured for plants in the unmown plots by checking plants on a weekly basis in the late summer and fall. Capsules were not collected from plants in the mown plots as the mowing procedure removed many of the reproductive spikes before they matured. Plants were harvested on May 19, 1992. The caudex and attached leaves of each plant were removed, dried at 60°C for longer than 48 hours and weighed.

DATA ANALYSIS

Analysis of variance was used to examine how differences in level of reproduction between photoperiod treatments affected growth and capsule production in the subsequent year. The general linear models (GLM) procedure of SAS (Statistical Analysis System, Cary, North Carolina) was used for this analysis. Dependent variables included plant size indices for June and August of 1991, capsule production in 1991 and shoot biomass in May of 1992. Family, mowing treatment and photoperiod treatment were independent categorical variables. Plants that died were excluded from the analyses. Only 10% of the plants died over the course of the experiment and mortality was not associated with treatment.

Cost of reproduction was also assessed by examining the correlation between reproductive output in 1990 and (*i*) plant size indices for June and August of 1991, (*ii*) capsule production in 1991, and (*iii*) shoot biomass in May of 1992. These analyses included all reproductive individuals regardless of family, but excluded plants which were vegetative in 1990 (*i.e.*, short photoperiod plants). Separate analyses were conducted for the two mowing treatments. To assess the extent to which these phenotypic correlations may reflect genetic correlations, the analyses were repeated using family means (Thomas & Bazzaz, 1993). Although the resulting estimates do include a component of environmental effects, this bias is relatively small given reasonably large sample sizes (Geber, 1990).

Results

REPRODUCTIVE COST AS DETERMINED BY EXPERIMENTAL MANIPULATION

All individuals in the long photoperiod treatment flowered in 1990, while none of the individuals in the short photoperiod treatment flowered.

Reproduction in 1990 decreased plant size in June and August of 1991 as well as shoot biomass in May of 1992 in both the mown and unmown plots, but the magnitude of this effect differed between mowing treatments, *i.e.*, a significant reproduction × mowing treatment interaction (Table I). The decrease in plant size was always less in the mown than in the unmown plots (Figure 1). In the case of final shoot biomass, reproduction decreased growth by 19% in the mown plot compared to 36% in the unmown plot. There were marked differences among families in all of the size characters examined (Table I). Families that performed well in one habitat, however, did not necessarily perform well in the other; there was an interaction between family and mowing treatment for the size index in August and for final mass (Table I). There were no differences among families in the effect of reproduction on plant size the following year in either the mown or unmown plots, *i.e.*, the interaction term was never significant (Table I).

Reproduction in the previous year decreased capsule production in the unmown plots in 1991 (Table I). Averaged across families, plants that were vegetative in 1990 produced 1.16 g of capsules in 1991, compared to 0.70 g for plants that reproduced in 1990. This represents a decrease of 0.8 g capsule for every 1 g of capsule produced the

previous year. There were no differences among families in this relationship, nor did average capsule mass in 1991 differ among families (Table I).

Correlative measures of reproductive cost

Among individuals in the long photoperiod treatment (*i.e.*, reproductive plants), capsule production in 1990 ranged between 0 (individuals that flowered but did not set seed) and 1.03 g. There were weak negative correlations between capsule mass in 1990 and the various measures of plant size in 1991-1992 in the unmown plot. Individuals having a high capsule mass in 1990 tended to be smaller than individuals with a lower capsule mass (Figure 2). These correlations were not always significant at the 0.05 level, but were significant at the 0.1 level. In contrast, there was no evidence of any correlation between capsule mass and subsequent size in the mown plots, regardless of when size was assessed (Figure 3). Capsule production in 1991 was not correlated with capsule production the previous year in the unmown plots (Figure 4). It was not possible to assess this correlation in the case of the mown plots because mowing removed many of the reproductive spikes before capsules matured.

There was also a great deal of variation among families in 1990 capsule production. Family means ranged between 0.27 and 0.72 g. Correlations between capsule production in 1990 and the various measures of subsequent performance showed essentially the same pattern as correlations at the individual level (Figures 2, 3 & 4). In the unmown plots there were negative correlations with plant size index in August, 1991 and with shoot biomass in May 1992. There were no significant correlations in the case of the mown plots, nor was there any correlation with capsule production in 1991.

Table I. Level of significance for the effects of reproductive state (R), mowing treatment (M), family (F) and their interactions on plant size in 1991 and 1992 and reproductive output in 1991. Reproductive output was not determined for plants in the mown plots. Degrees of freedom (df) for each effect are provided in the table. The error term had 480 df for all variables except capsule mass which had 210

Effect	df	Size index June, 1991	Size index Aug., 1991	Capsule mass 1991	Shoot mass May, 1992
R	1	0.0001	0.0001	0.0001	0.0001
M	1	0.0001	0.0001		0.0001
F	14	0.0036	0.0074	0.0895	0.0001
R × M	1	0.0014	0.0011		0.0005
M × F	14	0.1799	0.0319		0.0007
R × F	14	0.7755	0.3938	0.9298	0.5538
R × M × F	14	0.9434	0.8097		0.9650

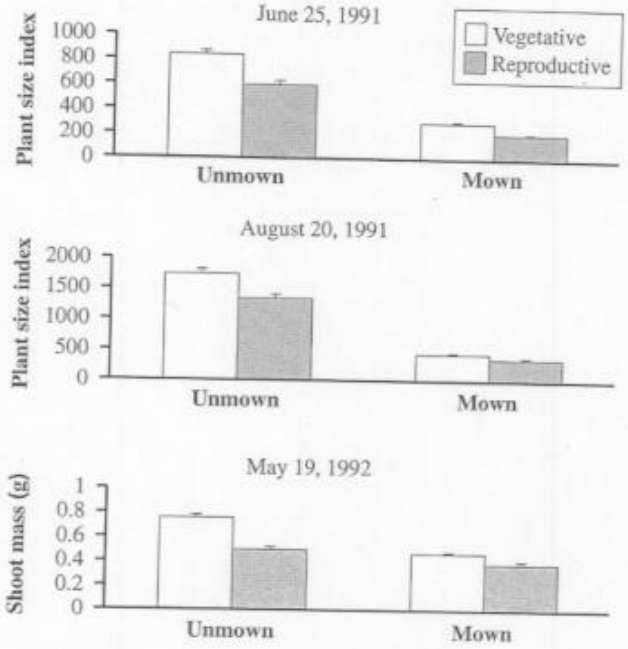

Figure 1. Effect of reproduction in 1990 on plant size assessed on June 25, 1991, August 20, 1991 and May 19, 1992 in mown *versus* unmown plots. Error bars represent one standard error.

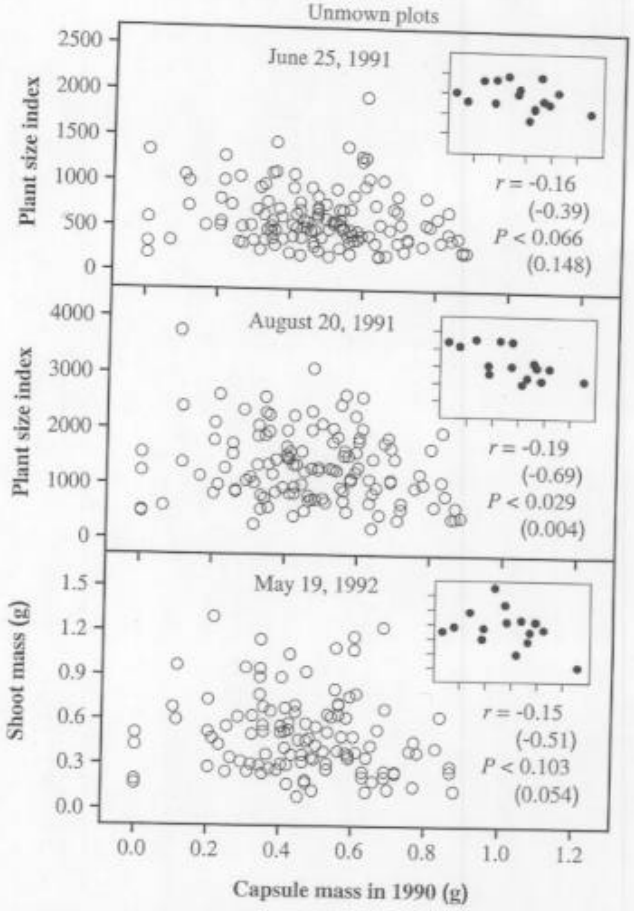

Figure 2. Relationship between capsule production in 1990 and plant size assessed on June 25, 1991, August 20, 1991 and May 19, 1992 in unmown plots. Open symbols represent individual plants while the closed symbols in the inserts represent family means. Pearson's correlation coefficient (r) and the level of significance for the correlation (P) are given for the individual data and in parentheses, for the family means.

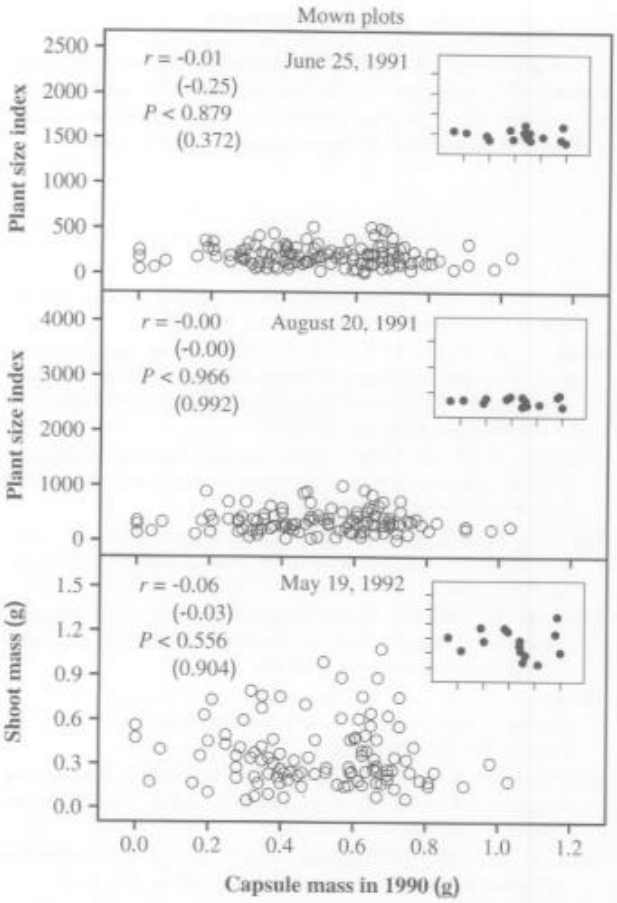

FIGURE 3. Relationship between capsule production in 1990 and plant size assessed on June 25, 1991, August 20, 1991 and May 19, 1992 in mown plots. Open symbols represent individual plants while the closed symbols in the inserts represent family means. Pearson's correlation coefficient (r) and the level of significance for the correlation (P) are given for the individual data and in parentheses, for the family means.

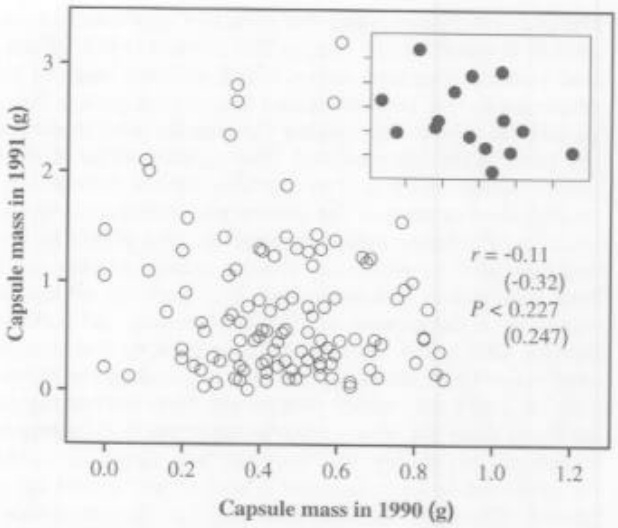

FIGURE 4. Relationship between capsule production in 1990 and capsule production in 1991 for plants in unmown plots. Open symbols represent individual plants while the closed symbols in the inserts represent family means. Pearsonís correlation coefficient (r) and the level of significance for the correlation (p) are given for the individual data and in parentheses, for the family means.

Discussion

Although all three methods used to assess the cost of reproduction found a negative relationship between reproduction and subsequent growth, there were differences among methods in the strength of the relationships. The relationships were stronger and more frequently statistically significant in the case of experimental manipulations followed by phenotypic correlations then among family correlations. Further, experimental manipulation was the only method that revealed a negative relationship between reproduction in year one and reproductive output in year two. Given the nature of these three methods, this is to be expected. Experimental manipulation provides two distinct groups that differ only in level of reproduction, making it relatively easy to detect the effects of reproduction. Correlative methods, on the other hand, deal with smaller differences in level of reproduction and these are confounded with other, possibly unrelated differences among plants. The among family correlations have a further disadvantage relative to phenotypic correlations in that sample size is smaller and therefore tests have less statistical power to detect effects. However, from the point of view of explaining the evolution of life history characteristics, correlations at the among family level are clearly more relevant as they are a direct measure of the tradeoffs experienced among the pool of genotypes which are subject to selection. As suggested by Stearns (1989), perhaps the best approach to this dilemma is to assess the cost of reproduction using a variety of techniques while being aware that the different approaches are not completely equivalent.

In spite of the fact that the three methods differ in the extent to which they can detect reproductive costs, all three methods suggest that reproductive cost was higher in the unmown plots than in the mown plots. This raises the question of why the cost of reproduction should differ between these two habitats.

Plants in the mown *versus* unmown plots exhibited clear differences in morphology. In the unmown plots, plants were substantially taller due to increases in the length of both the petiole and leaf blade as well as changes in the angle with which the leaf was held relative to the ground surface (data not presented). These differences in morphology between plants grown in mown *versus* unmown sites have previously been described in this species (Warwick & Briggs, 1980) as well as in other rosette forming species (Warwick & Briggs, 1979). These differences have been interpreted as the result of selection to avoid mowing in the case of the mown plots and to avoid shade in the unmown plots. More generally, it is also well established that plants grown under shade conditions exhibit increased specific leaf area, leaf allocation and leaf area ratio and decreased root allocation (Crawford, 1989). Such differences in morphology and allocation patterns are likely to have significant consequences for reproductive costs. A previous study (Reekie &

Bazzaz, 1992) examined the effect of reproduction on growth in two *Plantago* species that differed in their allocation patterns. *Plantago major*, which allocates more of its resources to leaf production and less to root growth compared to *P. rugelii*, experienced a greater decrease in growth per gram of capsule produced. This apparent effect of allocation pattern on the cost of reproduction can perhaps best be explained in terms of the nutrient requirements for reproduction. *Plantago major* in general, and plants in the unmown plots in particular, allocate a large proportion of total resources to leaf production. This high leaf allocation would be at the expense of allocation to roots and perhaps storage. Due to the lower root uptake capacity and storage reserves of these plants, the nutrient requirements of reproduction could not be met without extensive scavenging of nutrients from the photosynthetic apparatus (*e.g.*, nitrogen in rubisco and chorophyll). Reproduction, therefore, would be expected to have more of a detrimental effect upon growth. This hypothesis has been tested in *Oenothera biennis*, a herbaceous monocarpic perennial that accumulates nutrient reserves with age and can be found in a range of sites differing in soil fertility. The negative effects of reproduction on growth decrease with plant age as nutrient reserves accumulate and decrease as level of soil nutrient availability increase. These effects are correlated with the effect of reproduction upon photosynthesis and the chlorophyll and nitrogen content of the leaves (Reekie & Reekie, 1991; Saulnier & Reekie, 1995).

Another factor that may be involved in reducing the cost of reproduction in the mown plots is the removal of a significant proportion of inflorescences in subsequent years by mowing. Although these inflorescences were replaced by new inflorescences, which likely involves a significant cost to the plant, a relatively small proportion of these inflorescences survived long enough to produce mature capsules. If the cost of producing new inflorescences to replace those removed by mowing is small relative to the cost of producing mature seed, this may increase the resources available for survival and growth.

Given that the cost of reproduction is lower in mown than in unmown sites, there are clear consequences for selection in these two contrasting habitats. There will be stronger selection for genotypes with a high reproductive allocation in the mown sites than in the unmown sites. As reproductive allocation is indeed higher in populations adapted to mowing (Warwick & Briggs, 1980), this lends support to the notion that environmentally induced variation in reproductive cost is an important factor influencing selection on reproductive allocation. It should be noted, however, that there are other factors that may be involved in selecting for higher reproductive allocation in these populations. For example, if mowing increases adult mortality, conventional life history theory predicts that this would select for high reproductive allocation (Willson, 1983). These proposed explanations are not mutually exclusive, and both may operate together, making it difficult to determine their relative importance. Nevertheless, the wide variation observed in the cost of reproduction among environments strongly suggests that it must be considered in any attempt to understand the evolution of life history characteristics.

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