An explanation for size-dependent reproductive allocation in *Plantago major*

Edward G. Reekie

Abstract: This study examined whether variation in reproductive allocation with size could be explained by differences in the trade-off between reproduction and growth. Seeds from 42 half-sibling families were collected from sites differing in mowing frequency and availability of light, nutrients, and water. Six seedlings from each family were grown in controlled environments and photoperiod manipulations were used to control reproduction and growth. Families collected from habitats with a tall canopy were larger and experienced a greater decrease in growth with reproduction than families from habitats where mowing maintained a short canopy. Reproductive output showed no relationship with size, while reproductive allocation (capsule mass to vegetative mass) decreased with size. This decrease may be a direct consequence of the increase in reproductive cost with size. The increase in cost can be partially explained by increased allocation to reproductive support structures; large individuals produce capsules on more elongate scapes and have a lower capsule to scape ratio. Differences in size and morphology among habitats are presumably the result of selection to avoid damage in mown sites and to avoid shade and ensure pollination in sites with a tall canopy and reduced wind movement.

Key words: allometry, life-history theory, size constraints, reproductive effort, reproductive cost.

Résumé : L'auteur a vérifié si la variation de l'allocation reproductive selon la dimension pourrait s'expliquer par des différences de répartition entre les appareils reproducteurs et végétatifs. Il a récolté les graines de 42 familles demi-soeurs, sur des sites différent selon la fréquence de tonte et selon la disponibilité de la lumière, des nutriments et de l'eau. Il a cultivé six plantules de chaque famille sous des conditions contrôlées, en variant la photopériode pour déterminer la reproduction. Il a comparé la masse de plantes végétatives et reproductives de la même famille afin d'évaluer la répartition entre les appareils végétatifs et reproducteurs. Les plantes des familles récoltées dans des habitats avec une canopée élevée sont plus grosses et subissent une plus forte diminution de croissance en cours de reproduction que les plantes dont la canopée est maintenue basse par la tonte. Le produit de la reproduction ne montre aucune relation avec la dimension alors que l'allocation reproductive (masse des capsules à masse végétative) diminue selon la dimension. Cette diminution pourrait s'expliquer partiellement par une augmentation du coût de la reproduction selon la dimension. L'augmentation du coût pourrait s'expliquer partiellement par une augmentation de l'allocation aux structures de support à la reproduction; les individus forts produisent des capsules sur des hampes plus longues et ont un ratio capsule à hampe plus faible. Les différences en dimension et en morphologie selon les habitats résultent présumément d'une sélection pour éviter les dommages sur les sites tondus, et pour éviter l'ombrage et assurer la pollinisation dans les sites avec une haute canopée et l'action réduit du vent.

Mots clés : allométrie, théorie du cycle vital, contraintes aux dimensions, effort de reproduction, coût de la reproduction.

[Traduit par la rédaction]

Introduction

There is much intraspecific variation in the proportion of total resources allocated to reproduction among plants from different habitats (e.g., Escarre and Thompson 1991; Nishitani and Kimura 1993; Ostertag and Menges 1994; Sans and Masalles 1994, see also references cited in Willson 1983). Until recently, differences among plants in reproductive allocation (RA) were most commonly interpreted as the result of selection in response to differences in survivorship schedules (Willson 1983; Lovett Doust 1989). However, this explanation

E.G. Reekie. Biology Department, Acadia University, Wolfville, NS B0P 1X0, Canada. e-mail: ereekie@ace.acadiau.ca

for much of the intraspecific variation in reproductive allocation has been challenged by studies that have examined the relationship between plant size and reproductive output (RO). Empirical data indicates that RA is often strongly correlated with size (Mendez and Obeso 1993; Shitaka and Hirose 1993; Zammit and Zedler 1993; Sans and Masalles 1994). Sampson and Werk (1986) explain this correlation by suggesting that RO increases with size because of underlying allometric constraints. For example, if flowers are borne in the axils of leaves, it is not possible to increase the number of flowers without increasing the number of leaves. They go on to argue that these allometric constraints will result in a linear relationship between RO and plant size. Given this linear relationship, it is mathematically inevitable that RA will increase, decrease, or remain constant with size depending upon whether the x intercept is positive, negative, or goes through the origin. As a result, it has been argued that size-dependent variation in RA

Received May 14, 1997.

is simply a consequence of allometric constraints and should be ignored when determining whether selection has occurred for different allocation patterns.

The suggestion that underlying allometric relationships may control how RA varies has a great deal of merit and may be widely applicable. Since plant size varies substantially among habitats, it is possible that much of the variation in reproductive allocation among habitats is simply a function of differences in size. This is particularly true in the case of environmentally induced variation in size (Weiner 1988), where plants of different size represent different developmental stages (Coleman and McConnaughay 1995). However, there is a danger in the blind application of this approach in that it is based on an empirical relationship to which a theoretical interpretation has been applied. This particular theoretical model predicts reproductive allocation varies with size because of morphological constraints. However with few exceptions (e.g., Schmid and Weiner 1993), there has been little attempt to test the model. It is conceivable, and in fact likely, that there are other theoretical models that would predict a similar relationship between reproductive output and plant size. For example, life-history theory predicts that low adult survivorship should select for high RA (Willson 1983). Assuming there is a trade-off between vegetative growth and reproduction, these plants will also be small. On the other hand, high adult survivorship and low juvenile survivorship will select for low RA, and as a consequence, plant size will be larger. In other words, life-history theory also predicts that RA should be strongly size dependent. This particular pattern of size dependency, i.e., decreasing RA with size is in fact commonly observed (Sampson and Werk 1986; Shipley and Dion 1992). Ignoring size-dependent RA can only be justified if indeed it is the result of allometric constraints rather than selection. Therefore, it is critical that the mechanistic basis for size-dependent variation is known.

The present study examines the mechanistic basis for sizedependent reproductive allocation in *Plantago major*. This species is an acaulescent, short-lived perennial that produces flowers on elongate spikes (Hawthorn 1974). It is a variable species that occupies a range of habitats differing in degree of disturbance and resource availability (Blom 1977; Van Dijk and Van Delden 1981; Van Dijk 1984). Therefore, it might be expected to display variation in reproductive allocation resulting from different selection pressures. Differences among *Plantago* populations in life-history traits have previously been interpreted in terms of strategies selected in response to survivorship patterns (Hawthorn and Cavers 1976, 1978; Primack and Antonovics 1982; Lotz 1990). It has also been shown that reproductive allocation in *P. major* is closely correlated with plant size (Weiner 1988).

The present study compares size and reproductive allocation of half-sibling families isolated from habitats that differ in disturbance regime (mowing frequency) and resource availability. Plants were grown in a common environment and reproduction was controlled using photoperiod manipulations. *Plantago major* is a long-day plant with a critical photoperiod of 15 h (Hawthorn 1974). Therefore, it was possible to experimentally assess the effect of reproduction on growth and allocation in plants of various sizes. A previous study (Reekie and Bazzaz 1992), found that the trade-off between reproduction and growth varied among genotypes of *P. major*. The current study adresses the question of whether variation in this tradeoff can explain changes in reproductive allocation with size. It also examines how the trade-off between reproduction and growth may vary among plants isolated from contrasting habitats and, therefore, addresses the question of whether the variation is the result of selection.

Materials and methods

Seed collection and description of sites

Seed was collected from 42 sites in Kings County, Nova Scotia. At each site, seed from a single individual was collected and stored dry in the laboratory until use. Since *P. major* is a predominantly self-fertilizing species, seed from each individual represents at least a half-sibling family, and most of the individuals will be full siblings. Because of this high degree of relatedness, comparisons of among-family variation to within-family variation provide a means of assessing degree of genetic variation in life-history parameters. To the extent that maternal environment may influence seedling performance (Miao et al. 1991), among-family comparisons will also include an environmental component.

Sites were classified into one of four habitat types based upon dominant vegetation and disturbance regime: (1) lawn (6 sites), more or less continuous grass cover mown at frequent intervals (i.e., 1- to 2-week intervals over course of growing season); (2) coarse turf (20 sites), herbaceous vegetation mown at infrequent intervals (i.e., 3- to 4-week intervals). (3) unmown (9 sites), herbaceous vegetation that is not mown or mown only rarely; and (4) forested (7 sites), areas having at least a partial tree cover and not subjected to mowing. To quantify site differences, the following variables were assessed: percentage of full sun reaching soil surface; red to far red light ratio; maximum available soil moisture; soil organic matter; soil pH; and soil content of P_2O_5 , K_2O , Ca, and Mg. Soil samples for laboratory analyses were collected at time of seed collection (October). Light penetration of canopy and red to far red ratio were determined at time of maximum standing crop (August).

Soil was sampled by taking two 5.7 cm diameter soil cores to a depth of 11 cm immediately adjacent to the sampled plant. One soil core was air-dried, ground, and sifted using a 2.0 mm mesh screen to remove any stones. The sifted soil was used for chemical analysis. Soil pH was determined from a 1:1 soil to water ratio, and percent organic matter content was determined by loss on ignition as outlined by the Council on Soil Testing and Plant Analysis handbook (1980). Soil phosphorous (P_2O_5), potassium (K_2O), calcium (Ca^{+2}), and magnesium (Mg⁺²) were extracted with Mehlich I and determined by inductively coupled plasma (ICP) as outlined by the Association of Official Analytical Chemists (1990). Soil organic matter and nutrient contents were expressed on a total soil weight basis (i.e., including the weight of any stones). Maximum available soil moisture was determined using the second soil core by calculating the difference in soil moisture between field capacity and permanent wilting point. Field capacity was obtained by wetting the intact core and allowing it to drain. Permanent wilting point was obtained by transplanting *Plantago* seedlings to the cores and allowing them to grow for a period of 8 weeks. At that time, watering ceased and the surface of the soil was sealed to prevent evaporation. Soil moisture was determined when the plants wilted and did not recover during the subsequent night.

Percentage of light penetration of the canopy was determined by measuring fluence rate (400–700 nm) with a quantum sensor (LI-18513, LI-COR, Lincoln, Neb.) Fluence rate at ground level was determined at five randomly located positions within a 1 m radius of the sampled plant. These five values were averaged and expressed as a proportion of fluence rate above the canopy. Red to far red ratio was determined using a narrow-band photometer (IL-150, International Light, Newburyport, Mass.). Measurements were made at five ran-

Table 1. Differences in environmental factors among habitats.

Variable	Lawn	Coarse turf	Unmown sites	Forested sites
Soil OM (%)	6.1 <i>ab</i>	3.8 <i>c</i>	5.6 <i>bc</i>	8.4 <i>a</i>
Soil pH	5.9 <i>a</i>	6.1 <i>a</i>	5.9 <i>a</i>	5.1b
$P_2O_5(g \cdot m^{-2})$	24.3 <i>a</i>	30.1 <i>a</i>	27.5 <i>a</i>	51.6 <i>a</i>
$K_2O(g \cdot m^{-2})$	35.3 <i>a</i>	26.8 <i>a</i>	40.8 <i>a</i>	30.4 <i>a</i>
$Ca (g \cdot m^{-2})$	254 <i>a</i>	213 <i>a</i>	209 <i>a</i>	139 <i>a</i>
$Mg (g \cdot m^{-2})$	34.6 <i>ab</i>	22.1b	45.3 <i>a</i>	26.9 <i>ab</i>
Available H_20 (%, v/v)	41 <i>a</i>	34 <i>a</i>	42 <i>a</i>	40 <i>a</i>
% Full sun	87 <i>a</i>	81 <i>a</i>	51 <i>b</i>	26b
Red to far red ratio	1.08 <i>ab</i>	1.16 <i>a</i>	0.87b	0.87b

Note: Sites were classified according to physiognomy of the dominant vegetation and management regime (see text). Means within a given row followed by the same letter were not significantly different from each other at the 0.05 level.

domly located positions with a 1 m radius of the sampled plant and averaged.

Plant culture

Seeds from each of the 42 families were germinated in moist vermiculite at a day:night temperature of 20:15°C. Six seedlings per family were transplanted to individual 400-mL pots filled with turface®. Pots were placed in one of two growth chambers maintained at a day:night temperature of 25:20°C. Light intensity was maintained at $800 \,\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ over a 13-h photoperiod. Nutrients were supplied by watering the plants once per week with a water-soluble fertilizer (10:6:16, N:P:K) at a concentration of 0.67 g·L⁻¹. Eight weeks after transplantation, the photoperiod in one of the chambers was extended to 15 h for a period of 6 weeks by the addition of 2 h of low light $(55 \,\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$ at the end of the normal photoperiod. The additional light received in the long-photoperiod treatment amounted to less than 0.5% of the total light received by the short-photoperiod plants over the course of the experiment. There were three plants per family in each of the photoperiod treatments. Plants with their respective treatments were rotated between chambers on a weekly basis to avoid confounding possible chamber effects with treatment.

Plants were harvested 20 weeks after transplantation. At this time, all plants that flowered (i.e., the long-photoperiod treatment) had set seed. Plants were divided into leaves, roots, caudex, scapes (i.e., reproductive stems), and capsules; dried at 50°C; and weighed.

Data analysis

The overall significance of differences among habitats in environment was assessed using multivariate analysis of variance. Dependent variables included the various environmental parameters assessed in this study (see Table 1), and the single independent variable was habitat type. Univariate analysis of variance was also performed for each of the dependent variables. Means were compared by means of Student–Newman–Keuls multiple-comparison procedure.

Proportional allocation to leaves, caudex, and roots was calculated by dividing mass of a given plant part by total mass. Reproductive allocation was calculated as capsule mass to vegetative mass. For the purpose of these analyses, vegetative structures included leaves, caudex, and roots. Partitioning of reproductive mass between capsules and scape was assessed by calculating the capsule to scape mass ratio. Differences among habitats in growth and allocation parameters of plants collected from these sites were assessed by means of univariate analysis of variance. In these analyses, families were nested within habitats and individuals within families. The among-family variance was used as the error term for the habitat effect, and the within-family variance was used to test the family effect. All proportional data were transformed prior to analysis by taking the arc sine of the square root

Table 2. Growth and allocation of vegetative and reproductive plants isolated from different habitats.

		Coarse	Unmown	Forested
Variable	Lawn	turf	sites	sites
Vegetative plants (short photope	riod)			
Total mass (g)	11.6 <i>a</i>	13.3 <i>a</i>	15.8 <i>b</i>	13.3 <i>a</i>
Stem allocation	0.14 <i>a</i>	0.15 <i>a</i>	0.14 <i>a</i>	0.15 <i>a</i>
Leaf allocation	0.57 <i>a</i>	0.54 <i>a</i>	0.55 <i>a</i>	0.54 <i>a</i>
Root allocation	0.28 <i>a</i>	0.30 <i>a</i>	0.31 <i>a</i>	0.30 <i>a</i>
Reproductive plants (long photop	period)			
Total mass (g)	13.4 <i>a</i>	14.4 <i>a</i>	14.9 <i>a</i>	14.8 <i>a</i>
Stem allocation	0.12 <i>a</i>	0.12 <i>a</i>	0.11 <i>a</i>	0.12 <i>a</i>
Leaf allocation	0.75b	0.71 <i>ab</i>	0.71 <i>ab</i>	0.69 <i>a</i>
Root allocation	0.13 <i>a</i>	0.17 <i>b</i>	0.18b	0.19 <i>b</i>
Vegetative mass (g)	8.6 <i>a</i>	8.9 <i>a</i>	9.3 <i>a</i>	9.2 <i>a</i>
Capsules (g)	3.02 <i>a</i>	3.21 <i>a</i>	3.12 <i>a</i>	3.30 <i>a</i>
Capsule to vegetative mass ratio	0.39 <i>a</i>	0.38 <i>a</i>	0.35 <i>a</i>	0.38 <i>a</i>
Capsule to scape mass ratio	2.34b	1.54 <i>a</i>	1.39 <i>a</i>	1.53 <i>a</i>

Note: Values for allocation parameters represent the untransformed proportions, but statistical analysis was performed on the arcsine transformed values. Within any one row, means followed by the same letter were not significantly different from each other at the 0.05 level.

of the proportion. Separate analyses were conducted for vegetative (short-photoperiod) and reproductive (long-photoperiod) plants.

The relationships between vegetative mass and capsule mass and between vegetative mass and reproductive allocation were examined by correlation analysis. These analyses included all reproductive plants (i.e., long-photoperiod plants) regardless of habitat. To assess the extent to which these patterns were a reflection of genetic differences among families, correlations were calculated using the data from both individual plants and family means in separate analyses. Analysis of covariance with habitat as a qualitative variable was used to determine whether individuals from the four habitats differed in these relationships.

The trade-off between reproduction and growth was assessed by calculating the difference between the mass of vegetative (short-photoperiod) plants and the vegetative mass of reproductive (long-photoperiod) plants. This measure is equivalent to the somatic cost of reproduction as defined by Tuomi et al. (1983). In the present study, however, rather than dividing this difference by the mass of the vegetative plants to get the relative somatic cost of reproduction (Tuomi et al. 1983), the difference in somatic growth between vegetative and reproductive individuals was divided by the capsule mass of the reproductive plants. This provides a measure of lost vegetative growth per gram of reproductive output. Least-squares regression was used to calculate these costs. Data from both vegetative (shortphotoperiod) and reproductive (long-photoperiod) treatments were combined for this analysis. Vegetative mass was the dependent variable, and capsule mass was the independent variable. The slope of this relationship represents the loss in vegetative mass per gram of capsule produced. Cost per gram of reproductive mass (i.e., capsule plus scape mass) was also calculated by substituting total reproductive mass for capsule mass in the analysis. Regressions were fitted using the general linear models (GLM) procedure of SAS (Statistical Analysis System). Family was entered as a categorical factor in this analysis, and separate slopes (costs) were obtained for each of the 42 families in the experiment. The significance of differences among families in cost was assessed using the heterogeneity of slopes model in the GLM procedure.

The relationship between reproductive cost and plant size was examined by dividing families into three equal groups on the basis of size. The family average for mass in the short-photoperiod treatment

Fig. 1. The relationship between capsule mass and vegetative mass (A and C) or between reproductive allocation and vegetative mass (B and D) for reproductive plants. Data are presented for individuals (A and B) and for family means (C and D). The correlation coefficient for each pair of variables (*r*) and the level of significance for the relationship (*p*) are presented in each graph. The different symbols represent plants isolated from: unmown (\bigcirc), lawn (\square), forested (\blacktriangle), and coarse turf (\square) sites. There were no differences among individuals from the four habitats in the relationship between reproductive output and size (*p* = 0.4506) or between reproductive allocation and size (*p* = 0.3806).



(i.e., vegetative plants) was used as the measure of plant size. Analysis of variance was then used to determine if there was any difference in cost among size categories. The effect of size on allocation patterns was examined in the same manner.

Analysis of variance was also used to determine if there were differences among habitats in cost of reproduction. To determine if variation in reproductive cost among habitats was due to variation in plant size, this analysis was repeated using plant size (family averages of vegetative mass) as a covariate.

Results

The four habitats sampled in this study differed substantially in their environmental characteristics (Table 1; p < 0.0001 for the habitat effect in a MANOVA). Soil organic matter was highest in the forested sites and lowest in coarse turf, with the other sites being intermediate. Soil pH was low in the forested sites (ca. 5) and somewhat higher (ca. 6) in the other sites. The Mg content of the soils was lowest in coarse turf and highest in the unmown sites, with the remaining sites being intermediate. Level of light and red to far red ratio were low in the forested and unmown sites relative to the coarse turf and lawn sites. There were no significant differences among habitats in the remaining variables (P₂O₅ content, K₂O content, Ca content, and available soil moisture).

Plants isolated from the four habitats were generally similar in terms of size and allocation parameters (Table 2). There were no differences in caudex allocation, reproductive allocation, or capsule production among families from the four habi-



tats. However, mass of vegetative plants was higher in the unmown sites than in any of the other three habitats. Reproductive plants from the lawn habitat also had a higher leaf allocation than plants from the forested sites and a lower root allocation and a higher capsule to scape ratio than plants from any of the other habitats. The general paucity of habitat differences in size and allocation parameters was not due to any lack of genetic variation. There were significant differences among families (p < 0.05 for the family effect) in all of the parameters examined.

There was a great deal of variation in both plant size and reproductive output among plants in this study. Vegetative mass of reproductive individuals ranged between 4 and 14 g, and capsule mass ranged between 1 and 5 g. In spite of this variation, there was no apparent relationship between reproductive output and size (Fig. 1A). Similar results were obtained when family means were used rather than individual plants (Fig. 1C). Reproductive allocation showed a marked size dependency, declining as plant size increased regardless of whether correlations were calculated using individuals (Fig. 1B) or family means (Fig. 1D). There were no differences among individuals from the different habitats in the relationship between reproductive output and size (p = 0.4506) or between reproductive allocation and size (p = 0.3806).

In general, reproduction resulted in an increase in total mass and a decrease in vegetative mass (Table 2). The one exception to this pattern were plants in the unmown sites; reproduction decreased total mass as well as vegetative mass in these plants. Fig. 2. Cost of reproduction assessed as lost vegetative growth per gram of capsule for families isolated from four different habitats. The individual lines represent the fitted relationships between vegetative mass and capsule mass for individual families. The mean slope (i.e., mean cost) ± 1 SE are presented for each habitat.





Cost of reproduction assessed in terms of lost vegetative growth per gram of capsule differed among families isolated from the different habitats (Fig. 2). Families from the unmown sites experienced a higher cost than families from the other three sites. The greatest difference was between the unmown sites and the lawn sites; the average cost for the unmown families was over twice as great as the cost for families from the mown sites. When costs were calculated as lost growth per gram of reproductive mass, differences among families decreased somewhat, but families isolated from the unmown sites still had a higher average cost (Fig. 3). Averaged across habitats, production of 1 g of capsule reduced vegetative growth by approximately 1.4 g, and the production of 1 g of reproductive mass reduced growth by 0.8 g.

Lost vegetative growth per gram of capsule increased as size of vegetative plants increased (Table 3). This correlation accounted for most of the differences in cost among habitats discussed above. When size of vegetative plants was entered as a covariate into the analysis of variance model, habitat no longer had a significant effect on reproductive cost (p = 0.0716). Plants from the tallgrass sites had a higher reproductive cost, because these plants were larger than plants from other habitats. Cost per gram of reproductive mass was also increased with plant size (Table 3).

Plants in the different size categories differed in their allocation patterns (Table 3). In the vegetative state, small plants allocated more to stem (caudex) than larger plants, but this difference disappeared in the reproductive state. Instead, small plants allocated more to leaves and less to roots when reproductive than larger plants. The ratio of capsule to vegetative mass and the ratio of capsule to scape mass was greater in small plants than in the larger size categories.

Discussion

Growth and allocation to vegetative organs

In spite of marked differences in disturbance regime and environment among habitats (Table 1), there were relatively few characters in which families isolated from the four habitats differed (Table 2). Plant size was one of these characters; families isolated from unmown sites were larger than families from other sites. Previous studies of life-history variation in P. major have also found marked genetic differences among populations in size-related parameters (Warwick and Briggs 1979, 1980; Lotz and Blom 1986; Lotz 1990). This size difference probably reflects selection to avoid mowing in mown sites, and selection to avoid shading in unmown sites. Small genotypes of P. major have been shown to have a higher reproductive output than larger genotypes in sites subjected to mowing (Warwick and Briggs 1980). On the other hand, competition for light will be more intense in unmown sites (Table 1), and this may select for increased size as a means to avoid shading. Forested sites also have low light availability (Table 1), but here shading is due to an overhead tree canopy. Since Plantago cannot effectively compete with a tree for light by increasing size, it is not surprising that large size was not selected for in these sites (Table 2).

There were also marked differences among families from the different habitats in capsule to scape ratio (Table 2). This effect was associated with the difference in plant size among

Fig. 3. Cost of reproduction assessed as lost vegetative growth per gram of spike for families isolated from four different habitats. The individual lines represent the fitted relationships between vegetative mass and spike mass for individual families. The mean slope (i.e., mean cost) ± 1 SE are presented for each habitat.



habitats (Table 3). The low capsule to scape ratio of large plants and the high capsule to scape ratio of small plants can be related to the contrasting habitats of small versus large plants. Small plants are found where canopy height is kept short by mowing, and large plants are found in sites with a tall herbaceous canopy (Table 2). As air movement is restricted within a tall canopy, there will be selection to increase the height at which flowers are displayed to facilitate pollination and seed dispersal by increasing the length of the scape below the flowers. On the other hand, there would be selection to decrease the length of the scape below the flowers in mown sites to reduce the chance that flowers would be removed by mowing. Data collected by Warwick and Briggs (1980) on the length of the capsule-bearing portion of the spike versus the length of the scape below the flowers in populations of P. major subject to different mowing regimes supports this suggestion.

The only other difference in allocation patterns among plants from the different habitats was the lower root and higher leaf allocation of plants from the lawn habitat when in the reproductive state (Table 2). Low root and high leaf allocation is often associated with high soil fertility (Chapin 1980). There is little evidence to suggest that the lawn sites were significantly more fertile than the other habitats (Table 1). However, it must be noted that nitrogen availability was not assessed.

Although there was no difference in caudex allocation among plants from the different habitats (Table 2), small plants allocated more to the caudex in the vegetative state than large plants (Table 3). As the caudex is largely a storage structure, this difference may be a direct consequence of their contrasting growth habits. Plants that allocate more to storage



(i.e., caudex) and less towards current growth (e.g., leaves) will grow more slowly and remain smaller than plants with a less conservative growth strategy.

The trade-off between reproduction and growth

The large size of plants isolated from unmown sites was associated with increased reproductive cost (Fig. 2, Table 3). One explanation for the increased cost of reproduction in larger plants and plants from the unmown sites is the low capsule to scape ratio of these plants (Tables 2 and 3). Since large plants produce more scape per gram of capsule, it follows that large plants should experience a greater decrease in growth per gram of capsule. This assumes that the production of the scape is a significant portion of total reproductive cost. The scape made up from 20 to 57% of total reproductive weight depending upon family, suggesting that it was a significant component of total cost. However, there were still significant differences among both habitats and size categories in cost per gram of spike (Fig. 3, Table 3). Therefore, differences in capsule to spike ratio cannot explain all the differences in cost among families and other explanations must be sought.

In the present study, plants were grown in a common environment, and variation in size was largely due to genetic differences. When plant size varies as a function of the environment, larger plants by definition have a larger resource base for reproductive activities to draw upon. However in discussing genetic variation in size, it does not follow that larger genotypes necessarily have a larger resource base. As discussed above, large genotypes may grow at a more rapid rate, because fewer nutrients are allocated to storage and more to current growth. If such is the case, the pool of resources avail-

Table 3. Effect of size on allocation patterns of vegetative and
reproductive plants and on cost of reproduction calculated as lost
growth per gram of capsule or lost growth per gram of spike.

	Size category					
Variable	Small	Medium	Large			
Vegetative plants (short photoperiod)						
Stem allocation	0.16b	0.14 <i>a</i>	0.14 <i>a</i>			
Leaf allocation	0.55 <i>a</i>	0.56 <i>a</i>	0.55 <i>a</i>			
Root allocation	0.30 <i>a</i>	0.29 <i>a</i>	0.31 <i>a</i>			
Reproductive plants (long photoperiod)						
Stem allocation	0.12 <i>a</i>	0.12 <i>a</i>	0.11 <i>a</i>			
Leaf allocation	0.74b	0.71 <i>ab</i>	0.69 <i>a</i>			
Root allocation	0.15 <i>a</i>	0.17 <i>b</i>	0.19 <i>c</i>			
Capsule to vegetative mass ratio	0.43 <i>b</i>	0.36 <i>a</i>	0.33 <i>a</i>			
Capsule to scape mass ratio	2.07b	1.45 <i>a</i>	1.35ia			
Lost growth per capsule (g/g)	1.03 <i>a</i>	1.34 <i>a</i>	1.74b			
Lost growth per spike (g/g)	0.68 <i>a</i>	0.76 <i>ab</i>	0.98 <i>b</i>			

Note: Values for allocation parameters represent the untransformed proportions, but statistical analysis was performed on the arcsine transformed values. Within any one row, means followed by the same letter were not significantly different from each other at the 0.05 level.

able for reproduction may be as large in a small plant that has a large pool of stored reserves. As a consequence, reproduction may well have a more deleterious effect upon growth of the large genotype.

Another reason why cost of reproduction varies among families are differences among habitats (Table 2) and size categories (Table 3) in how reproduction affects allocation. Reproduction resulted in increased leaf allocation at the expense of both caudex and root allocation. The increase in leaf allocation was more marked in the case of small plants and families from mown habitats because of their greater initial caudex mass in the vegetative state, and because of a more substantial decrease in root allocation with reproduction than in the other size categories. The large leaf allocation of these plants in the reproductive state means they will be better able to continue vegetative growth providing the root mass is sufficient to supply the leaves with water and nutrients.

Implications for the interpretation of size-dependent RA

Regardless of the reasons why cost per gram of capsule varies among families, the mere fact that it does has implications for understanding variation in reproductive output and reproductive allocation. The increase in RO with plant size that is often observed is a direct result of the increased resource base of the plant. However, if cost per gram of capsule also increases with plant size (Table 3), this will reduce or even negate the positive effect of any increase in the resource base. Therefore, the increase in cost per gram of capsule with plant size can explain the lack of a positive correlation between RO and plant size, and the negative correlation between RA and plant size (Fig. 1).

Given that variation in reproductive cost can modify the relationship between RO and plant size, this raises the question of how we should view size-dependent variation in RA. Are changes in RA with size simply a consequence of allometric constraints and, therefore, to be ignored in examining adaptation to different habitats, or are changes in RA with size adaptive and subject to selection? In the present study it is clear that RA in *P. major* is very much dependent upon size; RA decreases with plant size (Fig. 1, Table 3). It is also true that plant size differs substantially among families isolated from the different habitats. Does this mean that differences in RA among plants of different size are irrelevant to attempts to understand adaptation to different environments? Based upon the effect of reproduction on growth, I have suggested several possible explanations for why RA should vary with size. These explanations are based on trade-offs associated with growing in open versus closed canopies and are, therefore, directly relevant to an understanding of adaptation to these habitats.

Acknowledgements

This study was supported by a grant from the Natural Sciences and Engineering Research Council of Canada. Technical assistance was provided by R. Ives, and B. Harnish of the Nova Scotia Department of Agriculture and Marketing conducted the soil chemical analyses. D. Ackerly, S. Thomas, M.A. Maun, L. Hermanutz, and an anonymous reviewer provided helpful reviews of the manuscript.

References

- Association of Official Analytical Chemists. 1990. Official methods of analysis. Association of Official Analytical Chemists, Arlington, Va.
- Blom, C.W.P.M. 1977. Effects of trampling and soil compaction on the occurrence of some *Plantago* species in coastal sand dunes. 11. Trampling and seedling establishment. Oecol. Plant. **12**: 363–381.
- Chapin, F.S. 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. **11**: 233–260.
- Coleman, J.S., and McConnaughay, K.D.M. 1995. A non-functional interpretation of a classical optimal-partitioning example. Funct. Ecol. 9: 951–954.
- Council on Soil Testing and Plant Analysis. 1980. Handbook on reference methods for soil testing. University of Georgia, Athens, Ga.
- Escarre, J., and Thompson, J.D. 1991. The effects of successional habitat variation and time of flowering on seed production in *Rumex acetosella*. J. Ecol. **79**: 1099–1112.
- Hawthorn, W.R. 1974. The biology of Canadian weeds. 4. *Plantago* major and *P. rugelii*. Can. J. Plant Sci. 54: 383–396.
- Hawthorn, W.R., and Cavers, P.B. 1976. Population dynamics of the perennial herbs *Plantago major* L. and *P. rugelii* Decne. J. Ecol. 64: 511–527.
- Hawthorn, W.R., and Cavers, P.B. 1978. Resource allocation in young plants of two perennial species of *Plantago*. Can. J. Bot. 56: 2533–2537.
- Lotz, L.A.P. 1990. The relation between age and size at first flowering of *Plantago major* in various habitats. J. Ecol. **78**: 757–771.
- Lotz, L.A.P., and Blom, C.W.P.M. 1986. Plasticity in life history traits of *Plantago major* L. ssp. *pleiosperma* Pilger. Oecologia, 69: 25–30.
- Lovett Doust, J. 1989. Plant reproductive strategies and resource allocation. Trends Ecol. Evol. 4: 230–234.
- Mendez, M., and Obeso, J.R. 1993. Size-dependent reproductive and vegetative allocation in *Arum italicum* (Araceae). Can. J. Bot. 71: 309–314.
- Miao, S.L., Bazzaz, F.A., and Primack, R.B. 1991. Effects of maternal nutrient pulse on reproduction of two colonizing *Plantago* species. Ecology, **72**: 586–596.
- Nishitani, S., and Kimura, M. 1993. Resource allocation to sexual and vegetative reproduction in a forest herb *Syneilesis palmata* (Compositae). Ecol. Res. **8**: 173–183.
- Ostertag, R., and Menges, E.S. 1994. Patterns of reproductive effort

with time since last fire in Florida scrub plants. J. Veg. Sci. 5: 303–310.

- Primack, R.B., and Antonovics, J. 1982. Experimental ecological genetics in *Plantago*. VII. reproductive effort in populations of *P. lanceolata* L. Evolution, **34**: 742–752.
- Reekie, E.G., and Bazzaz, F.A. 1992. Cost of reproduction in genotypes of two congeneric plant species with contrasting life histories. Oecologia, **90**: 21–26.
- Samson, D.A., and Werk, K.S. 1986. Size-dependent effects in the analysis of reproductive effort in plants. Am. Nat. 127: 667–680.
- Sans, F.X., and Masalles, R.M. 1994. Life history variation in the annual arable weed *Diplotaxis erucoides* (Crucferae). Can. J. Bot. 72: 10–19.
- Schmid, B., and Weiner, J. 1993. Plastic relationships between reproductive and vegetative mass in *Solidago altissima*. Evolution, 47: 61–74.
- Shipley, B., and Dion, J. 1992. The allometry of seed production in herbaceous angiosperms. Am. Nat. **139**: 467–483.
- Shitaka, Y., and Hirose, T. 1993. Timing of seed germination and the reproductive effort of *Xanthium canadense*. Oecologia, 95: 334–339.
- Tuomi, J., Hakala, T., and Haukioja, E. 1983. Alternative concepts of reproductive effort, cost of reproduction, and selection in life history evolution. Am. Zool. 23: 25–34.

- Van Dijk, H. 1984. Genetic variability in *Plantago* species in relation to their ecology. II. quantitative characters and allozyme loci in *P. major*. Theor. Appl. Genet. **68**: 43–52.
- Van Dijk, H., and Van Delden, W. 1981. Genetic variability in *Plantago* species in relation to their ecology. I. Genetic analysis of the allozyme variation in *P. major* subspecies. Theor. Appl. Genet. **60**: 285–290.
- Warwick, S.L., and Briggs, D. 1979. The genecology of lawn weeds. III. Cultivation experiments with *Achillea millefolium L., Bellis perennis L., Plantago lanceolata L., Plantago major L.* and *Prunella vulgaris L.* collected from lawns and contrasting grassland habitats. New Phytol. 83: 509–536.
- Warwick, S.L., and Briggs, D. 1980. The genecology of lawn weeds.
 V. The adaptive significance of different growth habit in lawn and roadside populations of *Plantago major* L. New Phytol. 85: 289–300.
- Weiner, J. 1988. The influence of competition on plant reproduction. *In* Plant reproductive ecology: patterns and strategies. *Edited by* J.N. Lovett Doust and L. Lovett Doust. Oxford University Press, New York. pp. 228–245.

Willson, M.F. 1983. Plant reproductive ecology. Wiley, New York.

Zammit, C.A., and Zedler, P.H. 1993. Size structure and seed production in even aged populations of *Ceanothus gregii* in mixed chaparral. J. Ecol. 81: 499–511.