

## Size-dependent reproductive output in agricultural weeds<sup>1</sup>

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Data on reproductive and vegetative weights of individuals from five species of agricultural weeds (*Apera spica-venti* L., *Datura stramonium* L., *Abutilon theophrasti* Medic., *Sorghum halepense* (L.) Pers., and *Panicum miliaceum* L.) were used to test Weiner's (1988) model of linear size-dependent reproductive output in plants. In general, the populations showed strong evidence ( $P < 0.001$ ) of linear relationships between reproductive and vegetative weight. Linearity was most pronounced in cases where size differences were primarily due to competition. Generally, the linear relationships were consistent from population to population within a species. Many of the populations also showed positive  $x$ -intercepts, indicating a threshold size for reproduction. However, there were a number of populations with no apparent relationship between reproductive and vegetative weight, with departures from linearity, or with positive  $y$ -intercepts (negative  $x$ -intercepts).

*Key words*: reproductive weight, vegetative weight, agricultural weeds, size-dependent reproduction.

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Les auteurs ont utilisé les données pondérales des parties végétatives et reproductives de cinq espèces de mauvaises herbes agricoles (*Apera spica-venti* L., *Datura stramonium* L., *Abutilon theophrasti* Medic., *Sorghum halepense* (L.) Pers. et *Panicum miliaceum* L.) afin de vérifier la justesse du modèle de Weiner (1988) pour la relation linéaire pondérale des structures de reproduction. En général, les populations montrent une forte relation linéaire ( $P < 0,001$ ) entre les poids de l'appareil reproducteur et de l'appareil végétatif. La linéarité est la plus prononcée dans les cas où les différences de grosseur sont attribuables surtout à la compétition. Généralement, les relations linéaires sont constantes d'une population à l'autre, pour une espèce donnée. Plusieurs populations montrent également des interceptions positives avec l'axe  $x$ , ce qui indique l'existence d'une dimension minimale pour assurer la reproduction. Cependant, on trouve un certain nombre de populations qui ne montrent pas de relation entre les données pondérales en poids secs des parties végétatives et reproductives ou avec des écarts à partir de la linéarité avec des interceptions positives avec l'axe  $y$  (interceptions négatives avec  $x$ ).

*Mots clés* : poids de l'appareil reproducteur, poids de l'appareil végétatif, mauvaises herbes agricoles, dépendance de la reproduction sur la grosseur.

[Traduit par la rédaction]

### Introduction

Weiner (1988) presented a simple linear model of size-dependent reproductive output to explain the decrease in reproductive allocation in plants grown at high densities. He suggested that plants must reach a certain size before they can devote energy to reproductive biomass. Above this threshold size, many plants may allocate a constant proportion of additional biomass to reproductive tissues. Thus, a plot of reproductive output against size would be linear, with a positive slope and a positive  $x$ -intercept. Weiner looked at two weedy species, *Plantago major* L. and *Verbascum thapsus* L., and found that the data supported his model. However, in two of his three data sets, Weiner only had population means available: it may be preferable to work with data from individual plants within a population to avoid complications arising from differences among populations.

Samson and Werk (1986) described the three possible models of linear size-dependent reproductive output in plants. They used data from several species of desert annuals to support the hypothesis that reproductive output shows a linear relationship with plant size. Ohlson (1988) found linear relationships between seed production and vegetative mass in several populations of *Saxifraga hirculus* L. Rees and Crawley (1989) assumed that the relationship between size and reproductive output in plants is linear, and they argued that plants generally do not have threshold sizes for reproduction. In support of this claim, they presented  $y$ -intercepts for regressions of reproductive output on plant size for 11 unpublished and 5 published studies. They also presented slopes (allometric exponents) for 12 regressions of log reproductive output on log plant size, although the value of allometric exponents as evidence for intercepts is questionable. Several species, including *Dipsacus fullonum* L. (Werner 1975), *Verbascum thapsus* L., *Oenothera biennis* L., *Daucus carota* L., *Tragopogon dubius* Scop. (Gross 1981), and *Heterotheca subaxillaris* (Lam.) Britt. & Rusby (Couvét et al. 1990), have been shown to have a minimum size for reproduction when the probability of flowering (rather than the reproductive output) has been viewed as size dependent.

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Over the past few years, Agriculture Canada researchers have studied a number of weedy species that are undergoing rapid northern range expansion in eastern North America (see review by Warwick 1990). These researchers have collected much data on individual plants in numerous populations, including samples from both annual and overwintering species. In this paper, we use some of these data to test two predictions of the models described above: (i) that the relationship between size and reproductive weight is linear (Samson and Werk 1986; Weiner 1988) and (ii) that there is a threshold size for reproduction (Weiner 1988).

### Materials and methods

The data used here were obtained from five earlier studies. Because the details concerning methods are described in the respective publications, only a brief summary of the experiments is included below.

#### *Apera spica-venti* L., silky bentgrass (Warwick et al. 1987)

This study included 15 populations, 9 from various locations in Ontario, Canada, and 6 from Europe. Fifteen plants were grown from most populations, but only 11 were grown from three of the Canadian populations.

#### *Datura stramonium* L., jimson weed (Weaver et al. 1985)

This study involved populations from five localities, two in the United States and three in Ontario, Canada. In general, 60 plants were grown from each population.

#### *Sorghum halepense* (L.) Pers., johnsongrass (Warwick et al. 1984)

In this study, there were 13 populations, 12 with 16 plants and 1 with 8 plants. To keep sample sizes as large as possible and to maintain equal numbers for each population, the small population was excluded from the analyses. Of the remaining 12 populations, 3 represented the overwintering biotype and 9 the nonoverwintering biotype. These biotypes differ in resource allocation patterns, with the former producing more rhizome, particularly at greater depths, accounting for its ability to overwinter under Canadian conditions. Furthermore, the overwintering biotype produces less seed than the nonoverwintering biotype.

#### *Abutilon theophrasti* Medic., velvetleaf (Warwick and Black 1986)

This study involved four plants from each of 39 populations.

#### *Panicum miliaceum* L., proso millet (Warwick and Thompson 1987)

In this study, five biotypes were tested at each of five densities: 1 plant per pot and 15, 32, 64, and 132 plants per flat. In the first case, there were 15 separate pots for each biotype, while two replicates were grown under each of the other four densities. There were differences in survival rates among biotypes with two (golden and white) having considerably lower survivability than the others. Few survivors failed to flower at any density.

All species were grown under standard greenhouse conditions individually in spaced pots, except *A. theophrasti*, which was grown outside in a common field plot. The reproductive dry weights for the grasses, *A. spica-venti*, *S. halepense*, and *P. miliaceum*, consisted of the entire inflorescence or panicle, including peduncle. For *D. stramonium* and *A. theophrasti*, total reproductive weight included weights of immature inflorescences, short peduncles, and fruit (capsules) including seed.

For each study, the relationship between reproductive weight (dry mass of reproductive parts) and vegetative weight (dry mass of above-ground nonreproductive parts) was considered (Klinkhamer et al. 1990). This is more valid statistically than analyzing the relationship between reproductive and total weight (Samson and Werk 1986; Weiner 1988). Since principal components analysis (PCA) is a more appropriate method of estimating the regression line than the standard linear regression method when there is no clear-cut dependent or inde-

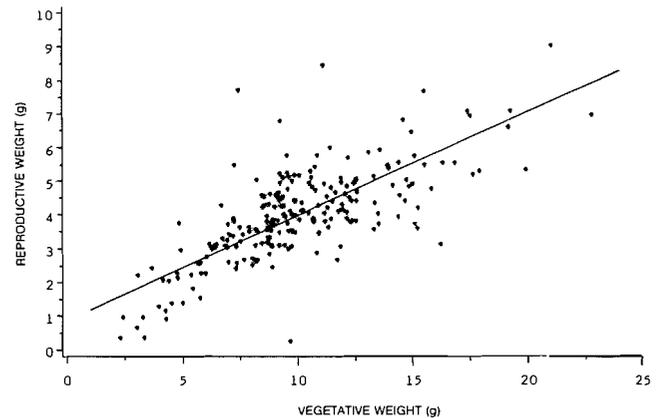


FIG. 1. Plot of reproductive weight against vegetative weight for nine Canadian and five European populations of *Apera spica-venti* (Warwick et al. 1987). Values are deviations from population means, with the overall means added. The regression line based on first principal axis is shown as a solid line.

pendent variable (SAS Institute Inc. 1985), the equations presented are those of the first principal axis. However, we performed statistical tests with standard linear regression, because the tests for regression are well defined and available in statistical software. The test for the significance of a slope in linear regression is equivalent to that for the significance of a correlation coefficient. Estimates of intercepts, on the other hand, will differ between analyses and consequently the tests will not correspond for PCA and standard regression. However, when the correlation between variables is high, PCA and regression yield similar results. Furthermore, regression will yield a smaller  $x$ -intercept than PCA, so that  $x$ -intercepts that are significantly positive on the basis of regression will certainly be positive in PCA.

All statistical analyses were performed on untransformed vegetative and reproductive weights. Departures from linearity were tested in two ways. First, we used regression of log reproductive weight on log vegetative weight. A slope significantly ( $P < 0.05$ ) different from 1.0 was considered evidence that the relationship is not linear. This test can produce a significant result if the relationship is linear, but the intercept is appreciably different from 0. Therefore, we also used second- and third-order polynomial regression when considering nonlinearity. Significance of second- or third-order terms was considered evidence for nonlinearity.

When several populations are shown in a single figure, the data plotted are

$$z_{ij} = y_{ij} - \bar{y}_i + \bar{y}.$$

where  $y_{ij}$  is the  $j$ th observation from the  $i$ th population,  $\bar{y}_i$  is the mean of the  $i$ th population, and  $\bar{y}$  is the overall mean. The population means have been subtracted from the original observations to remove variation among populations from the figure. The overall mean has been added to make the plotted data comparable in magnitude with those in other figures and tables; this step has no effect on the orientation of the data in the figure.

### Results and discussion

#### *Apera spica-venti* (Warwick et al. 1987)

There was no evidence of differences among populations in means, slopes, or intercepts ( $P > 0.05$ ). Twelve of the populations had  $y$ -intercepts significantly ( $P < 0.05$ ) greater than 0. The plot of deviations from population means (Fig. 1) shows a positive slope ( $\beta = 0.28$ ;  $r^2 = 0.46$ ) and a positive ( $P < 0.001$ )  $y$ -intercept.

A positive  $y$ -intercept (or equivalently a negative  $x$ -intercept) would imply a plant with reproductive output, but no

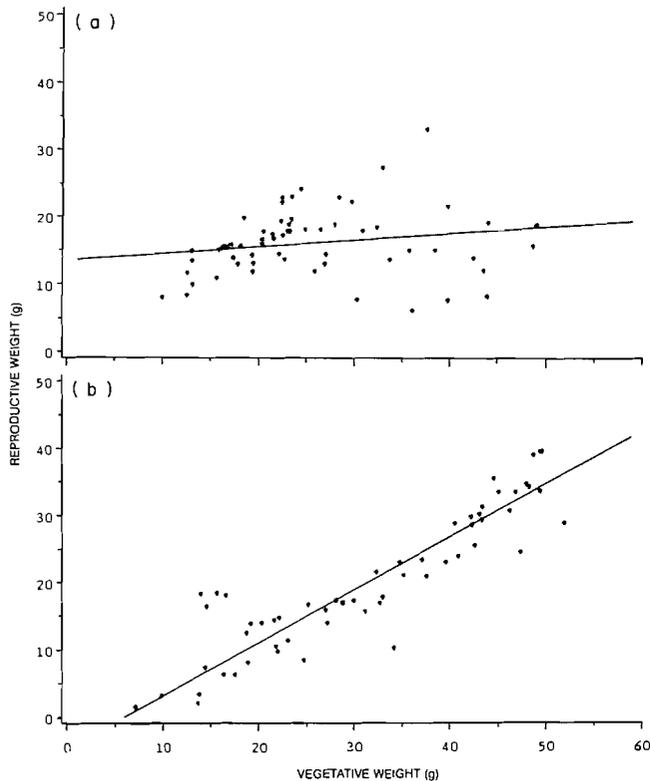


FIG. 2. Plots of reproductive weight against vegetative weight for *Datura stramonium* from two populations: (a) Kent county, Ont., Canada; and (b) Michigan state, MI, U.S.A. (Weaver et al. 1985). The regression line based on first principal axis is shown as a solid line.

vegetative material, which is biologically impossible. Consequently, the trend line must bend towards the origin as plant size approaches 0. The data (Fig. 1) suggest that the relationship between reproductive weight and plant size is not linear; the reproductive output of the smallest plants tends to be lower than predicted by the linear model. Both regression of log reproductive weight on log vegetative weight and polynomial regression of reproductive weight on vegetative weight indicated a significant ( $P < 0.05$ ) departure from linearity. The data from the smallest plants suggest a positive  $x$ -intercept, that is, a threshold plant size below which there is no reproductive output.

#### *Datura stramonium* (Weaver et al. 1985)

There were great differences among populations in the regression slopes ( $P < 0.01$ ). Two of the populations, those from Kent (Fig. 2a;  $r^2 = 0.02$ ) and Essex counties ( $r^2 = 0.001$ ), showed no relationship between vegetative and reproductive weights. The Michigan population, on the other hand, showed a strong linear relationship between the two variables (Fig. 2b;  $\beta = 0.73$ ;  $r^2 = 0.83$ ). The other two populations fell between these extremes.

The differences among these populations were most likely due to differences in the phenological status of the plants. Plants in the Michigan population were more advanced phenologically by the time of harvest (10 weeks after first emergence). It is almost certain that some of the larger plants in the Kent population (Fig. 2a) had not reached full reproductive potential by the time of harvest. The presence of individuals

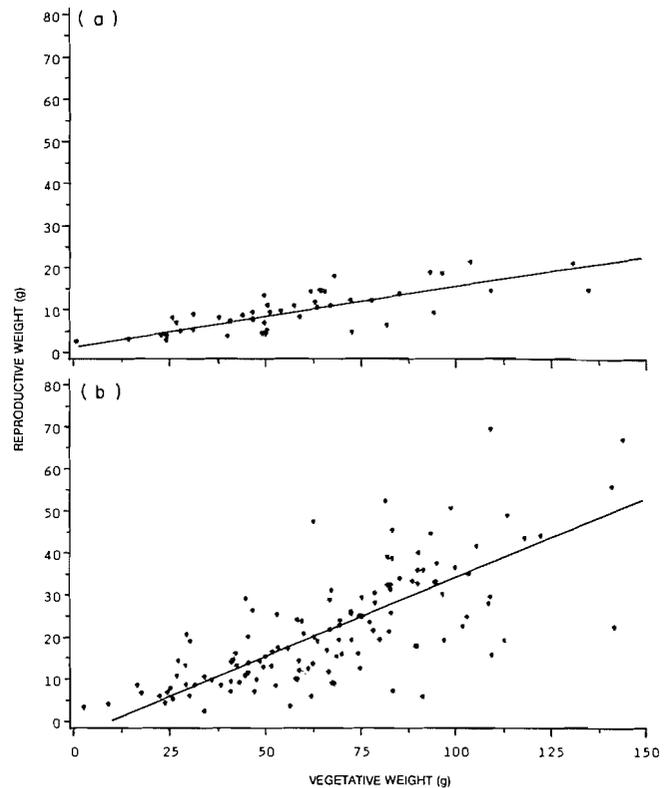


FIG. 3. Plots of reproductive weight against vegetative weight for (a) three overwintering and (b) nine nonoverwintering populations of *Sorghum halepense* (Warwick et al. 1984). Values are deviations from population and replicate means, with the overall means added. The regression line based on first principal axis is shown as a solid line.

that are large and will reproduce, but have not yet done so (or are just beginning), will have the effect of reducing the slope, decreasing the  $x$ -intercept, and increasing the variation in the data. Ideally, the relationship between size and reproduction should be studied when all plants have completed their life cycle, although this is rarely feasible in plants with indeterminate growth patterns, where reproduction stops because of changing environmental conditions such as killing frosts.

It is meaningless in the case of weak relationships to evaluate estimated intercepts. The one close relationship, the Michigan population, does follow the pattern suggested by Weiner: a linear trend with a positive slope and a positive ( $P < 0.07$ )  $x$ -intercept.

#### *Sorghum halepense* (Warwick et al. 1984)

There was considerable evidence of difference in slopes among the 12 populations ( $P < 0.005$ ). Much of the variation was attributable to differences between the overwintering and nonoverwintering biotypes. The slopes of the three overwintering populations (Fig. 3a) were not significantly different, the pooled estimate of slope being positive and the  $x$ -intercept negative, though not significant ( $P > 0.30$ ).

The slopes of the nonoverwintering populations were significantly different ( $P < 0.05$ ), mainly because of one of the populations. The slopes of the remaining eight populations were not significantly different. The pooled estimate of slope for the nonoverwintering populations ( $\beta = 0.38$ ; Fig. 3b) was much greater than that for the overwintering populations

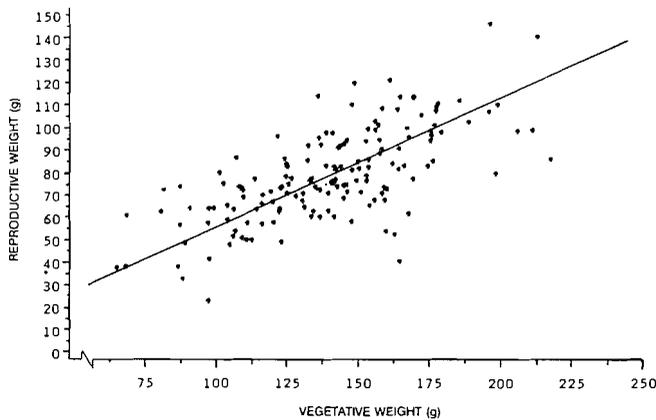


FIG. 4. Plot of reproductive weight against vegetative weight for *Abutilon theophrasti* (Warwick and Black 1986). Values are deviations from 39 populations and four replicate means, with the overall means added. The regression line based on first principal axis is shown as a solid line.

( $\beta = 0.15$ ) and the  $x$ -intercept was positive but not significantly so ( $P > 0.50$ ).

The data from the nonoverwintering populations showed a tendency towards greater variation in reproductive weights for larger plants. Regression of log reproductive weight against log vegetative weight indicated nonlinearity, perhaps because of the wide range of plant sizes showing little reproductive output.

#### *Abutilon theophrasti* (Warwick and Black 1986)

There was no evidence ( $P > 0.05$ ) of differences in slopes among populations. The data (Fig. 4), with replicate and populations means removed, were consistent with Weiner's linear model as both slope ( $\beta = 0.46$ ;  $r^2 = 0.46$ ) and  $x$ -intercept were positive, though the latter was not significant ( $P > 0.50$ ). With so few observations on each population, little of value can be learned about the  $x$ -intercepts of each population.

#### *Panicum miliaceum* (Warwick and Thompson 1987)

There was strong evidence of linear relationships for each biotype, and the linearity held over a very wide range of sizes. For the five biotypes, the  $x$ -intercepts were small and positive but highly significant ( $P < 0.001$ ). The slopes of the biotypes ranged ( $P < 0.001$ ) from a maximum of  $\beta = 0.56$  (crown, Fig. 5a), through three intermediate values, including golden (Fig. 5b), to a minimum of  $\beta = 0.20$  (black, Fig. 5c). All conformed closely with the model proposed by Weiner (1988). Possible explanations for the two extreme slopes are suggested by biological considerations: crown is a small, early flowering biotype, so almost all reproductive material will have been collected; black, on the other hand, has inflorescences that shatter, so some reproductive material will certainly have been lost before collection, thus biasing the results.

It is interesting that the regressions for specific densities (Table 1) were essentially the same as the overall regression, especially for the golden and black biotypes. As Weiner (1988) argued, differences in density do not introduce any new functional relationships but simply alter the range of plant sizes; the same linear model holds throughout. The results for this species support Weiner's (1988) contention that linear relationships with positive  $x$ -intercepts are most likely when competition is the cause of size differences.

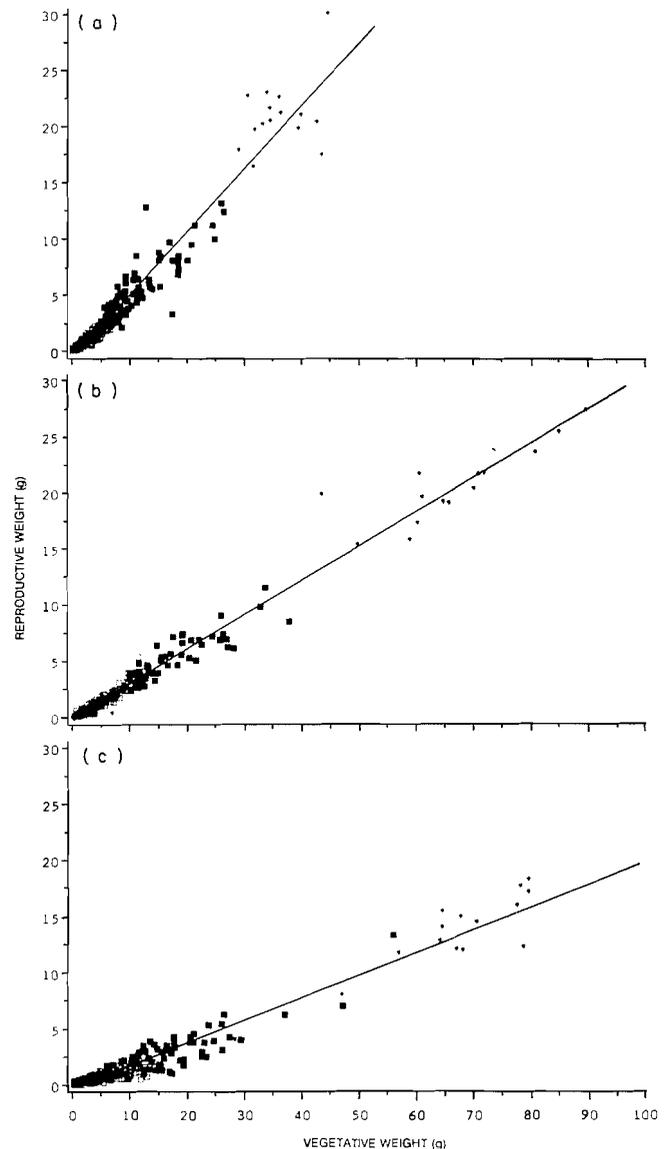


FIG. 5. Plot of reproductive weight against vegetative weight for three biotypes of *Panicum miliaceum* (Warwick and Thompson 1987): (a) crown; (b) golden; and (c) black. The regression line based on first principal axis is shown as a solid line. \*, plants grown individually in pots; ■, plants grown in flats.

#### General

For the most part, the data from the five agricultural weed species were consistent with the model of linear size-dependent reproductive output, although for one species (*A. spicaventi*) there was some evidence of nonlinearity. Strongest support for the model occurred when size differences were caused by competition.

A number of factors will influence the linear relationship between vegetative and reproductive weights. One such factor is indeterminate and determinate flowering and fruiting behaviour. With indeterminate flowering plants, there is a tendency to underestimate reproductive growth because some reproductive structures will have been lost by the time of harvest. This is particularly evident for the black biotype of *P. miliaceum*, which is essentially indeterminate, leading to a lower regression slope relative to biotypes with more determinate growth such as golden. Flowering in *D. stramonium* and *A. theo-*

TABLE 1. The slopes,  $x$ -intercepts, and correlations of the regressions of reproductive weight against vegetative weight at different densities for three biotypes of *Panicum miliaceum* (data from Warwick and Thompson 1987)

Density (plants/flat)	Biotypes								
	Crown			Golden			Black		
	Slope	Inter	Corr	Slope	Inter	Corr	Slope	Inter	Corr
1	0.36	-22.2	0.37	0.29	-2.6	0.90	0.24	11.5	0.94
15	0.38	-4.4	0.72	0.26	-2.6	0.89	0.20	2.8	0.89
32	0.44	-0.5	0.83	0.31	0.5	0.93	0.15	-1.0	0.74
64	0.42	0.4	0.85	0.34	1.0	0.95	0.10	-1.2	0.74
132	0.37	0.1	0.92	0.34	0.5	0.88	0.12	-0.1	0.83
Overall	0.56	0.9	0.97	0.31	0.4	0.99	0.20	1.5	0.98

NOTE: In the table, the correlation 0.37 is not significant ( $P > 0.05$ ); the correlation 0.72 is significant at the 1% level; all other correlations are significant at the 0.1% level. Inter,  $x$ -intercepts; Corr, correlations.

*phrastii* are markedly indeterminate; the selection of a single harvest date would certainly result in an underestimate of total reproductive capacity. Among the taxa studied, *A. spica-venti* exhibited a determinate growth pattern and hence the estimates of potential reproductive weight should be more reasonable.

Another factor affecting the regression of reproductive weight on vegetative weight is population variation in maturity or phenological status of the plants at time of harvest, which will tend to mask the underlying relationship between the two variables. This was evident with *D. stramonium* where data from two of the late-flowering populations failed to show any relationship between vegetative and reproductive weight. Since these plants were less mature at the time of harvest, the reproductive weights were severely underestimated in these populations.

In the literature, evidence for a threshold size prior to flowering for reproduction is contradictory. For example, in studies of three biennial species, two of the taxa, *Dipsacus sylvestris* L. (Werner 1975) and *Barbarea vulgaris* R. Br. (MacDonald 1977), demonstrated a threshold requirement for vernalization (and subsequent flowering) regardless of age, while *Alliaria petiolata* (M. Bieb.) Cavara Grande (Cavers et al. 1979) did not. Rees and Crawley (1989) argue that annual plants do not generally have a threshold size for reproduction.

The data from the species considered here also provide contradictory evidence with respect to the hypothesis of a threshold size for reproducing. Two species, *D. stramonium* and *P. miliaceum*, gave significant positive  $x$ -intercepts, that is, support for the hypothesis of a threshold size. Two other species, *S. halepense* and *A. theophrasti*, had intercepts that did not differ significantly from zero. With these two species, estimates of intercept required considerable extrapolation, since there were few, if any, small plants in the samples. Experiments where the plants are placed under stress, such as that with *P. miliaceum*, may be needed to obtain reliable estimates of intercepts for the two species. In the one species in which the relationship between reproductive and vegetative weight appeared to be nonlinear (*A. spica-venti*), the data suggest a threshold size for reproduction, although a much more complex model would be needed to test this hypothesis.

The hypotheses of linear size-dependent reproductive output and reproductive thresholds warrant further tests, and it would be worth looking for the mechanisms that determine whether or not these models are appropriate, that is, why some populations show linear relationships between size and fecundity while others do not.

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