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On the analysis of size-dependent reproductive output in plants

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Summary

1. A general model is presented to analyse size-dependent reproductive output in plants. The model formulation makes it possible to test for both a minimum size for reproduction and a non-linear relationship between size and reproductive output.
2. The model is statistically analysed with the likelihood-ratio test. In contrast to previously proposed models, this model admits a hump-shaped relationship between reproductive effort (RE) and plant size.
3. Data for three species analysed here show that RE is not always monotonically increasing or decreasing with plant size.
4. For a realistic data set the statistically required sample size is calculated.

Key-words: Carlina vulgaris, Ipomopsis aggregata, maximum-likelihood analysis, reproductive effort, *Saxifraga hirculus*

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Introduction

The way a plant apportions its resources, including its accumulated biomass, to different structures is a fundamental aspect of its biology (Begon, Harper & Townsend 1986). Life-history theory has put special emphasis on the allocation of biomass to reproductive structures, especially offspring themselves. The qualitative relationship between reproductive output and plant size or investment in reproduction is of fundamental importance in many life-history models. The statistical analysis of the relationship between reproductive output and plant size still shows, however, some major shortcomings.

Traditionally, reproductive effort (RE) has been considered as the proportion of biomass in reproductive structures $[R/(V+R)]$, where V=mass of vegetative structures, and R=mass of reproductive structures or mass of seeds produced (Reekie & Bazzaz 1987). However, the observation that RE in plants is often size dependent has led several researchers to propose that reproductive effort is better analysed allometrically (in the broad sense, *sensu* Gould 1966), as the relationship between reproductive biomass and vegetative biomass (Samson & Werk 1986; Weiner 1988; Klinkhamer, de Jong & Meelis 1990). A major problem is that to characterize a mathematical relationship in a bivariate situation, one needs to use the statistical approach of the functional relationship rather than regression. This is not straightforward even in the linear case, so regression forms a convenient approximate model. Before proceeding any further it is necessary to discuss two further statistical problems concerning the analysis of the relationship between size and reproductive output.

1. Many authors have correlated RE with plant weight. Because these variables share a common term (with included measurement error) this may lead to 'spurious correlations' ['spurious relationship' would perhaps be a better term (J.A. Nelder, personal communication)]. For this reason Samson & Werk (1986), Weiner (1988) and Klinkhamer *et al.* (1990) argued that it is better to statistically analyse the relationship between reproductive mass (R) and vegetative mass (V) than the relationship between R and total plant weight ($V+R$). While Prairie & Bird (1989) argued that the problem of spurious correlation has been exaggerated, this is not the consensus among biologists and statisticians (Jackson & Somers 1991; Kenney 1991). The statistical analyses of several variables which are arithmetically related have been extensively described in the literature of econometrics, where they are referred to as 'simultaneous equation systems' (Stewart 1984; Kelejian & Oates 1989). Contrary to Prairie & Bird, econometric statisticians have concluded that it is an important problem, whose solution in a particular case depends upon scientific more than mathematical reasoning (Stewart 1984, p. 230). For the statistical analysis of size effects on reproductive output, Klinkhamer *et al.* (1990) showed that tests based on the correlation coefficient between RE [defined as: $R/(V+R)$ or R/V] and $(V+R)$ or V were clearly inferior to F-tests based on the relationship between reproductive weight R and vegetative weight V, both in terms of type I and type II errors. We conclude that statistical analysis should be performed on R *vs* V, and we limit our discussion below to this analysis. Similarly, following Samson & Werk (1986) we define reproductive effort (RE) as R/V. For convenience we use total biomass of seeds produced by a plant (reproductive output) as our R, although the same arguments can be applied to any measure of R, e.g. the biomass of reproductive tissues.

2. The independent variable in standard regression analysis is considered to be fixed, but weights of plants collected from natural populations are subject to error (including true biological variation as well as sampling and measurement errors, or damage to the plants before sampling, e.g. by herbivory). This introduces an extra error into the estimate of the regression coefficient and this may lead to loss of power in the test used. Using Monte Carlo simulations, Klinkhamer *et al.* (1990) showed that despite the fact that the V-values are random variables rather than fixed, the F-test has very good power properties compared to correlation tests. Because the F-test is a transformation of the likelihood-ratio test (LR-test, e.g. Sokal & Rohlf 1981), it is to be expected that the more generally applicable LR-test has the same favourable properties. In the remainder of this paper we use this test to study a general model for analysing size-dependent reproductive output in plants.

Several models of size-dependent reproductive effort in plants have been proposed:

MODEL 0

Linear relationship between R and V, without a minimum size for seed production:

$$R_i = aV_i + E_i, \qquad i = 1 \,.\,.\,.\,.\,.\,.\,.\, n$$

where E_i is an error term and n denotes the total number of observations and where $a>0$ (Samson & Werk 1986, model A; minimal model without size dependency).

MODEL 1

Linear relationship between R and V, with a minimum size for seed production (b):

$$R_i = a(V_i - b) + E_i, \qquad i = 1 \,.\,.\,.\,.\,.\,.\,.\, n$$

where $a>0$ and $b>0$ (Samson & Werk 1986, model B; Weiner 1988). (Samson & Werk also discuss this model with $b<0$, but because this would imply that plants without vegetative weight can produce seeds we consider this model unrealistic.)

MODEL 2

Classical 'allometric' (in the narrow sense) relationship between R and V, without a minimum size for seed production. $R_i = aV_i^c$, i.e. the relative increase of the reproductive biomass is proportional to the relative increase of the vegetative biomass. This model is usually analysed as:

$$\log R_i = \log a + c \log V_i + E_i$$

(Reiss 1989; Klinkhamer *et al.* 1990).

In model 0, RE is constant over all sizes. In model 1, RE increases above the minimum size for seed production, approaching an asymptote. In model 2, RE increases with size if $c>1$ and decreases with size if $c<1$.

While model 0 can be considered mathematically as a special case or a reduced model of either models 1 and 2, statistical analyses of data in terms of models 1 and 2 are incompatible.

Following Klinkhamer *et al.* (1990), linear regression of R on V (H_0, model 0; H_1, model 1):

$$R_i = a(V_i - b) + E_i, \qquad i = 1 \,.\,.\,.\,.\,.\,.\,.\, n$$

with E_i normally and independently distributed with mean zero and common variance σ^2, allows one to test whether the intercept b with the V-axes differs significantly from zero or not, while it is assumed that the relationship between R and V is linear. When a log-linear relation is tested the regression of R on V (H_0, model 0; H_1, model 2) is:

$$\log R_i = a' + c \log V_i + E_i, \qquad i = 1 \,.\,.\,.\,.\,.\,.\,.\, n$$

($a' = \log a$) with E_i as above. This allows one to test whether the exponent is significantly different from 1, while it is assumed that the intercept (on linear scale) is 0.

The fact that analysing data in terms of either models 1 or 2 makes the assumption that the other is not appropriate has led to confusion. For example Rees & Crawley (1989) used model 2 to analyse several sets of data and found a slope greater than 1 in some of the regressions on log-transformed variables. Their interpretation of this result as evidence for a minimum size requirement is statistically incorrect.

Several species have been shown to have a minimum size for the transition from the vegetative to the generative phase (below a certain size plants do not flower) (e.g. Werner 1975; van der Meijden & van der Waals-Kooi 1979; Gross 1981; Klinkhamer, de Jong and Meelis 1987a,b 1991). In these species plants that do flower may or may not have a minimum size for actual seed production. In models with a minimum size for reproduction, $R=0$ for $V<V_{min}$ and $R>0$ for $V>V_{min}$, where V_{min} is the minimum size for reproduction. Because of this discontinuity, it is possible that some plants may have a minimum size for flowering, yet the R *vs* V relationship for those plants which do reproduce could pass through the origin if extrapolated (Fig. 1). In this paper we will only consider plants that flowered.

Weiner (1988) argued that a positive V-intercept in

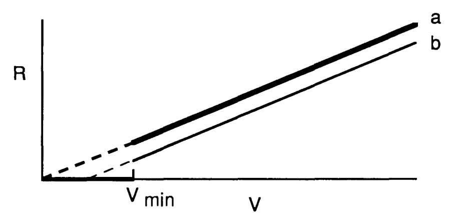

Fig. 1. Two possible relationships between reproductive output (R) and vegetative plant weight (V) for plants with a minimum size for flowering (V_{min}). The R-V relationship for those plants which do reproduce ($V>V_{\mathrm{min}}$) may (a) or may not (b) pass through the origin after extrapolation. For convenience we assume a linear relationship for plants with $V>V_{\mathrm{min}}$.

model 1 is to be expected because of developmental constraints (fixed minimum costs for reproduction), especially when size differences are caused by competition. An exponent greater than 1 in model 2 might occur if there are economies of scale in the production of seeds or reproductive structures, e.g. if large plants attract disproportionally more pollinators and seed set is pollen limited, or if large plants have a disproportional access to resources required for reproduction. An exponent smaller than 1 in model 2 (a decreasing slope in the relationship between size and reproductive output) might arise if biochemical constraints require that large plants invest an increasing proportion of their resources in supportive tissues. Since the biological bases for models 1 and 2 are different and not exclusive, it is possible that plants may show both a positive V-intercept and a non-linear relationship between R and V. Indeed, data of *Saxifraga hirculus* (Ohlson 1988) and *Apera spica-venti* (Thomson, Weiner & Warwick 1990) suggest such a relationship. Below we describe a method to test for both a minimum size for seed production and a non-linear relationship between size and reproductive output.

A general model

MODEL 3

We propose the following model (model 3), as a logical extension of models 1 and 2:

$$R_i=a(V_i-b)^c+E_i, \qquad i=1\,.\,.\,.\,.\,.\,.\,.\,n$$

where $R_i=$ reproductive biomass of plant i; $V_i=$ vegetative biomass of plant i; $E_i=$ error term. The E_i are mutually independent and normally distributed random variables with expectation zero and variance σ^2 [$E_i=N(0, \sigma^2)$]. Furthermore it is assumed that E_i are stochastically independent of the V_i.

The intercept with the V-axis is determined by parameter b. Parameter c determines the degree of non-linearity (Fig. 2). Because plants without vegetative mass cannot produce seeds, only positive values of b are biologically meaningful. When $c=1$ and $b=0$ (equivalent to model 0), RE is independent of plant size (Fig. 2b). When $c=1$ and $b>0$ (this is equivalent to model 1), RE increases with plant size. When $b=0$ (this is equivalent to model 2), values of $c<1$ produce a decreasing RE with size (Fig. 2a), whereas values of $c>1$ produce an increasing RE with size (Fig. 2c). Because values of $b>0$ give rise to an increasing RE with plant size while values of $c<1$ give rise to a decreasing RE with plant size, the combination leads to a hump-shaped relationship between RE and plant size (Fig. 2a). It can easily be shown that for the combination of $b>0$ and $c<1$, the maximum value of RE is attained at $V_{max}=b/(1-c)$.

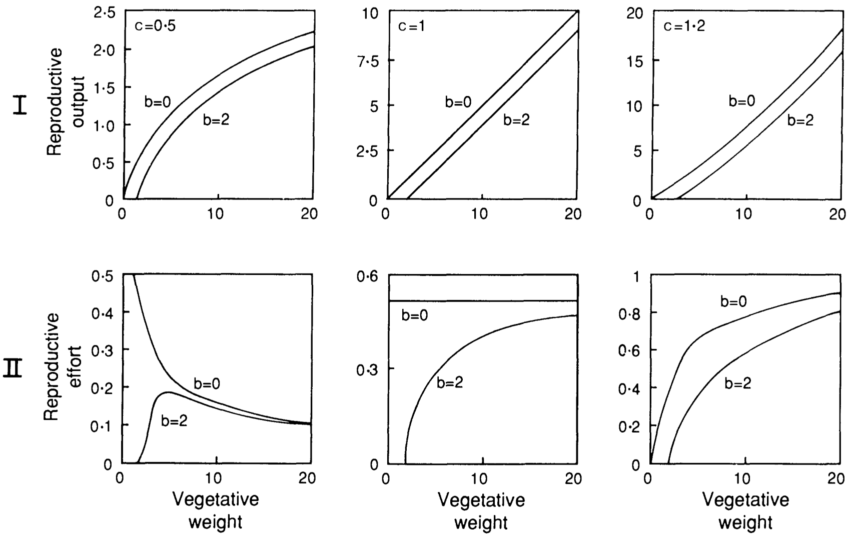

Fig. 2. (I) The relationship between reproductive output (R) and vegetative plant weight (V), using the model $R=a(V-b)^c$. In all cases $a=0{\cdot}5$. (II) The corresponding proportional allocation functions ($RE=R/V$) for the lines in I.

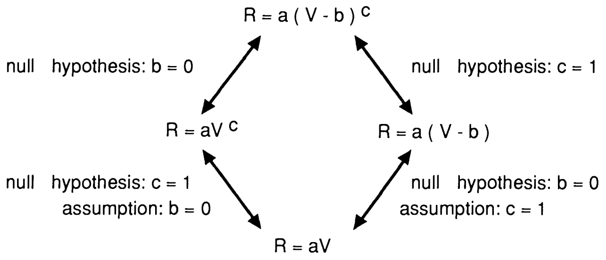

Fig. 3. Two routes of testing the relationship between reproductive output (R) and vegetative plant weight (V). For further explanation see text.

ESTIMATING AND TESTING THE PARAMETERS OF MODEL 3

In our previous paper (Klinkhamer *et al.* 1990) we used the F-test to test the parameters of model 1 [see Jongman, Ter Braak & van Togeren (1987) for a description of this test, see also Sokal & Rohlf (1981) for a statistical textbook for biologists]. We showed that despite the fact that the V-values are not fixed, the F-test has very good power properties. However, we cannot use the F-test for analysing this generalized model. The F-test is a transformation of the LR-test (Sokal & Rohlf 1981). Therefore it is a logical step to use the more widely applicable LR-test in this more general case.

The tests are performed on the condition that $V_i=v_i$. Hence:

$$R_i=a(v_i-b)^c+E_i, \qquad \text{where } E_i=N(0, \sigma^2).$$

The log-likelihood function is then defined by:

$$L=\log \prod_{i=1}^{n} \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left\{-\tfrac{1}{2}\frac{[r_i-a(v_i-b)^c]^2}{\sigma^2}\right\}$$

$$=-\tfrac{1}{2}n \log 2\pi-\tfrac{1}{2}n \log \sigma^2-\tfrac{1}{2} \sum_{i=1}^{n} \frac{[r_i-a(v_i-b)^c]^2}{\sigma^2}$$

The unknown parameters a, b, c and σ^2 are estimated by $\hat{a}$, $\hat{b}$, $\hat{c}$ and s^2, those values for which the minimum of L is attained. The estimates were obtained by applying a numerical minimization procedure, the method of steepest descent, on:

$$\sum_{i=1}^{n} [r_i-a(v_i-b)^c]^2$$

(see Stoer & Bulirsch 1980). The variance σ^2 is estimated by:

$$s^2=1/n \sum_{i=1}^{n} [r_i-a(v_i-b)^c]^2$$

Hence:

$$L(\hat{a}, \hat{b}, \hat{c}, s^2)=\min_{a, b, c, \sigma^2} L(a, b, c, \sigma^2)$$

The likelihood ratio test, e.g. for testing H_0: $b=0$ against H_1: $b\neq 0$ is based on the statistic:

$$\Lambda=2\,[L(\hat{a}, \hat{b}, \hat{c}, s^2)-L(a^*, c^*, s^{*2})]=n\log (s^{*2}/s^2)$$

where $\hat{a}$, $\hat{b}$, $\hat{c}$, s^2 denote the estimates under H_1 and a^*, c^*, s^{*2} under H_0, which can be obtained in the same way as under H_1. For large n, Λ follows a χ^2 distribution with 1df. Parameter estimates and values of s^2 and s^{*2} and hence $n\log (s^{*2}/s^2)$ can be obtained by most major statistical software packages (e.g. SAS, PROCEDURE NLIN, METHOD=GAUSS or MARQUARDT, CONVERGE=10^{-12}).

When applying the model on a data set, one has to make a choice between two possible routes of testing (Fig. 3). Starting, e.g., at the bottom in Fig. 3 one may first test H_0: $c=1$ under the assumption $b=0$ and then test H_0: $b=0$. Alternatively, one may first test H_0: $b=0$ under the assumption $c=1$ and then test H_0: $c=1$. Within each route the two tests are independent from each other for large n. The two routes, however, may lead to different results. The route of testing should be chosen beforehand. Ideally, the choice is based on explorative data. Without such data, it depends on one's biological knowledge or intuition (see suggested mechanisms in the Introduction). Sometimes the route is indicated by the test results themselves if one of the routes leads to biologically unreasonable results. For instance, when in the full model $b>0$ and $c<1$, testing the null hypothesis $b=0$ under the assumption $c=1$ may lead to negative values of b.

THE ANALYSIS OF EMPIRICAL DATA

The model was used to analyse three experimental data sets. One on seed number and vegetative plant weight of *Saxifraga hirculus* from a rich-fen area in Sweden in 1984 (data from Ohlson 1988). The second contains data on seed weight and vegetative weight of *Carlina vulgaris* (T.J. de Jong & P.G.L. Klinkhamer, unpublished results, data collected on natural plants in a coastal dune area at Meyendel near the Hague, The Netherlands). The third data set is on seed weight and vegetative weight of *Ipomopsis aggregata* from a natural population in Colorado, USA (T.J. de Jong, unpublished results).

Saxifraga hirculus

Using data from Ohlson's (1988) Fig. 1, the relationship between seed number and vegetative weight of

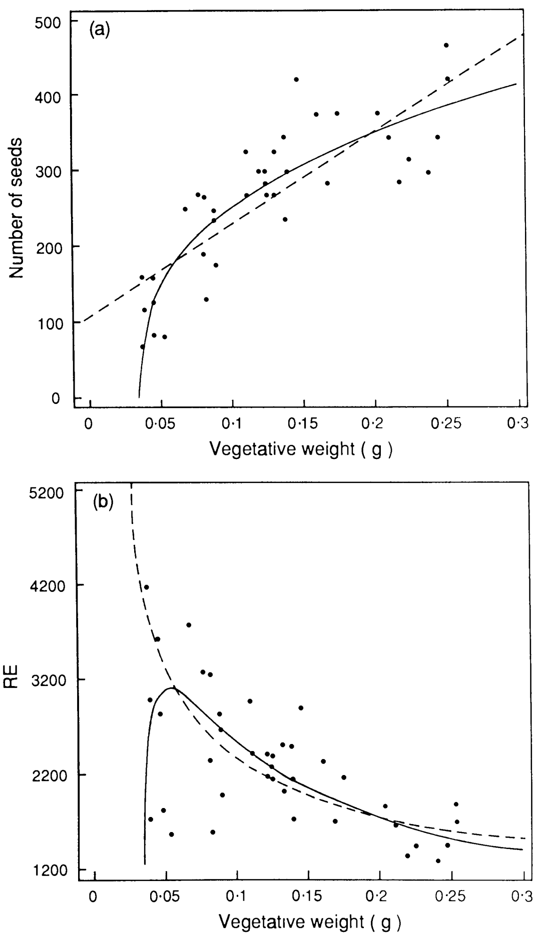

Fig. 4. (a) The relationship between the number of seeds (R) and vegetative plant weight (V) in *Saxifraga hirculus*. (b) The relationship between reproductive effort ($RE=R/V$) and vegetative plant weight using the model $R=a(V-b)^c$. (—) $c=0{\cdot}365$; (- - -) $c=1$. Note that statistical analysis showed that c is significantly different from 1 (Fig. 5).

S. hirculus is plotted in Fig. 4. Ohlson analysed his data by calculating a linear regression between seed number and vegetative plant weight. Linear regression results in a negative intercept with the V-axis (Fig. 5). Such an intercept gives a decreasing RE with plant size. Because a negative intercept is biologically unrealistic, this analysis is not satisfactory. The results of our generalized regression model show that there is a significant positive intercept with the V-axis ($b>0$), and that the relationship is non-linear ($c<1$; Fig. 5). At low plant weights RE sharply increases with increasing plant weight; at larger plant weights RE decreases (Fig. 4).

Carlina vulgaris

In *C. vulgaris* too, we find a negative intercept if we first test the null hypothesis $b=0$ under the condition $c=1$ (i.e. if we use a linear model). Therefore the other route must be taken (Figs. 6 and 7). If we first test the null hypothesis $c=1$ under the condition $b=1$, we find that c is significantly smaller than 1. If we then test the null hypothesis $b=0$, we find that this null hypothesis cannot be rejected. Therefore, the V-intercept is not significantly different from 0. Accordingly RE is decreasing with plant size. It should be noted, however, that the number of sampled plants is rather low for this kind of analysis (see next section). Visual inspection of the plot of RE *vs* plant size suggests that in *C. vulgaris*, a humped shaped relationship between RE and plant size may be likely.

Ipomopsis aggregata

Again, if we first test the null hypothesis $b=0$ under the condition $c=1$, we find a negative intercept with the V-axis (Figs. 8 and 9). We therefore take the other route. Under the condition $b=0$, we cannot reject the null hypothesis $c=1$. However, the full model gives a significant improvement, showing that we have to reject the null hypothesis $b=0$. Because under the condition $c=1$ we get an unrealistic negative estimate of b, we must assume that $c\neq 1$.

As in the other two species, RE sharply increases with v at low plant weights, while RE decreases at larger plant weights (Fig. 8).

THE REQUIRED SAMPLE SIZE

We can use the covariance matrix F and the estimated values of a, b, c to calculate the probability of

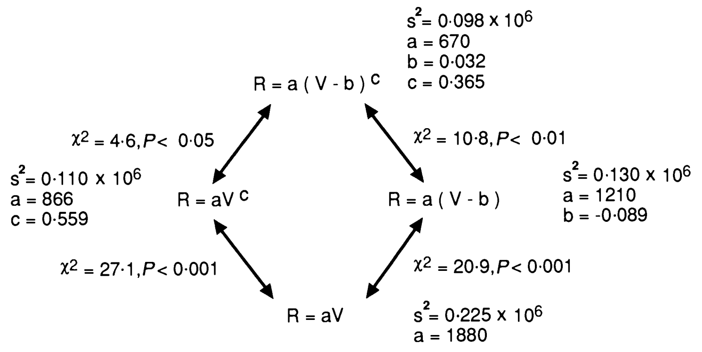

Fig. 5. Statistical analysis of the relationship between the number of seeds (R) and vegetative plant weight (V) in *Saxifraga hirculus*.

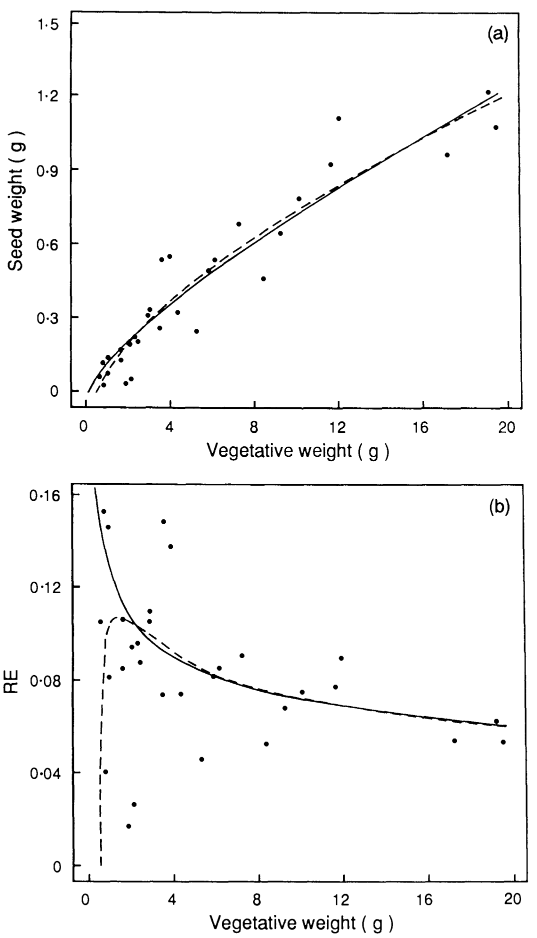

Fig. 6. (a) The relationship between seed weight (R) and vegetative plant weight (V) in *Carlina vulgaris*. (b) The relationship between reproductive effort ($\mathrm{RE}=R/V$) and vegetative plant weight using the model $R=a(V-b)^c$. (—) $b=0$; (- - -) $b=0{\cdot}417$. Note that statistical analysis showed that b is not significantly different from 0 (Fig. 7).

rejecting the null hypothesis $b=0$ (see Appendix). This probability depends on the level of significance, the true value of b, and on the sample size (n).

For a data set with a structure similar to the one of *S. hirculus* and the level of significance equal to 0·05, the chance of rejecting H_0: $b=0$ is approximately 0·25 when $n=40$ and $b=0{\cdot}0317$. To raise this probability to, e.g., 0·9, a sample size of about 200 is required (Fig. 10).

In a similar way, it is possible to calculate the probability of rejecting the null hypothesis $c=1$. However, it appeared that the covariance matrix strongly depends on the value of c. The outcome of such a calculation would, therefore, strongly depend on our assumptions about this matrix. Because we have no a priori information of this covariance matrix we cannot calculate the sample size required to obtain a specific probability of rejecting H_0 for a relevant value of $c\neq1$.

Discussion

The advantage of the proposed approach is that it allows us to ask about two aspects of the relationship between plant size and reproductive output which have been incompatible in previous methods of analysis. Plants may have a minimum size for reproduction and the relationship between size and reproductive output may not be linear. Before we can compare the reproductive allometries of different populations, and thus gain insight into their ecological causes and implications, we must be able to characterize adequately these allometries.

The model discussed in this paper appears to be a useful generalization of the two most commonly used models to analyse size dependency in the reproductive output of plants. In the case of *S. hirculus* and *I. aggregata*, the results are qualitatively different from the results of a linear model. Since raw data are not usually published, it is difficult to reanalyse data and to present a general picture of the relationship between RE and plant size. The three data sets analysed in this paper show that non-linear relationships are not uncommon. Furthermore, the data of *Saxifraga* and *Ipomopsis* show that RE is not always monotonically increasing or decreasing with plant size; more complicated relationships can occur in nature.

In the model we assumed E_i to be normally distributed, $E_i=N(0,\ \sigma^2)$. This assumption seems reasonable for the three data sets tested in this paper.

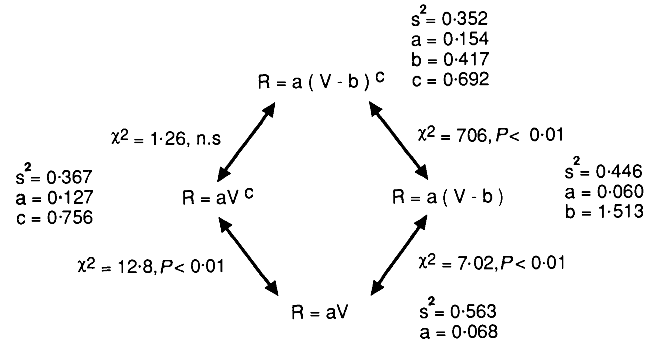

Fig. 7. Statistical analysis of the relationship between seed weight (R) and vegetative plant weight (V) in *Carlina vulgaris*.

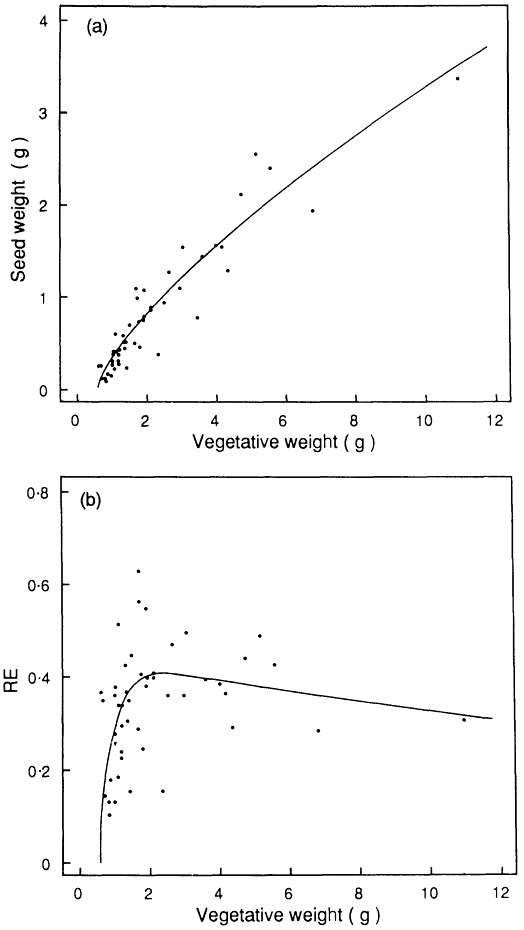

Fig. 8. (a) The relationship between seed weight (R) and vegetative plant weight (V) in *Ipomopsis aggregata*. (b) The relationship between reproductive effort ($\mathrm{RE}=R/V$) and vegetative plant weight using the model $R=a(V-b)^c$. For statistical analysis see Fig. 9.

In other cases this assumption may not be met. It is a well-known property of the F-test that it is insensitive to departures of the data from the normal distribution (Scheffé 1964). Because the F-test is a special case of the test we consider here, we expect the same to hold true for the LR-test.

A more serious problem presented by the formulation of model 3 (and model 1) is that the estimated value of b cannot be larger than the smallest value of v_i [otherwise we get negative estimates of r (model 1) or we cannot calculate $(v_t-b)^c$ (model 3)]. The models 1 and 3 are relationships with a discontinuous first derivative at $v=b$, with $r=0$ for $v<b$ and r increasing with v for $v>b$. Weiner (1988) suggests the use of plants with $r>0$ only when fitting a regression line. Plants with $r=0$ can provide additional evidence for the existence of an intercept by comparing the v_t of plants with $r_i=0$ and those with $r_i>0$ (J. Weiner, E. Weber & B. Schmid, submitted for publication). If after omitting such data points the analysis indicates that b should be larger than the smallest value of v_t, we might proceed by taking the average value of v_t for a small group of plants with small v_i. To avoid the problem as best as possible it is necessary to reduce all possible errors in the estimates of v_t (especially when v_t is small). Some of these 'errors' in statistical sense will, however, reflect true biological variation. Clearly this problem needs further investigation.

Our results show that for realistic values of b a large data set is required to obtain a sufficiently high probability of rejecting the null hypothesis $b=0$. In addition, a wide range of v_i is important. Small values of v_i are required to estimate b accurately and large values of v_i improve the estimate of d. It may be worthwhile to sample more small plants when collecting data if one wants a good test for the intercept with the V-axis.

It would be interesting to re-examine some of the data that have been analysed previously with different models or tests. It would be even better to collect new data. When collecting data it should be kept in mind that more complex models will require larger data sets.

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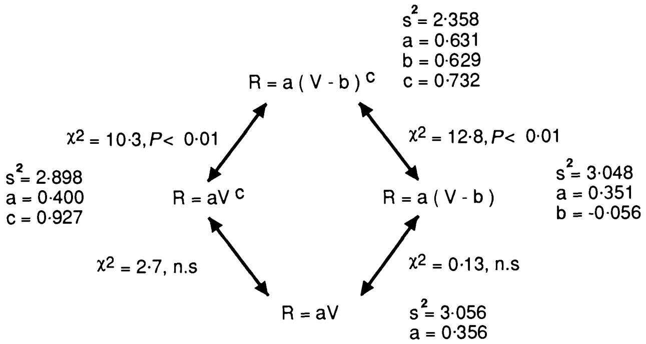

Fig. 9. Statistical analysis of the relationship between seed weight (R) and vegetative plant weight (V) in *Ipomopsis aggregata*.

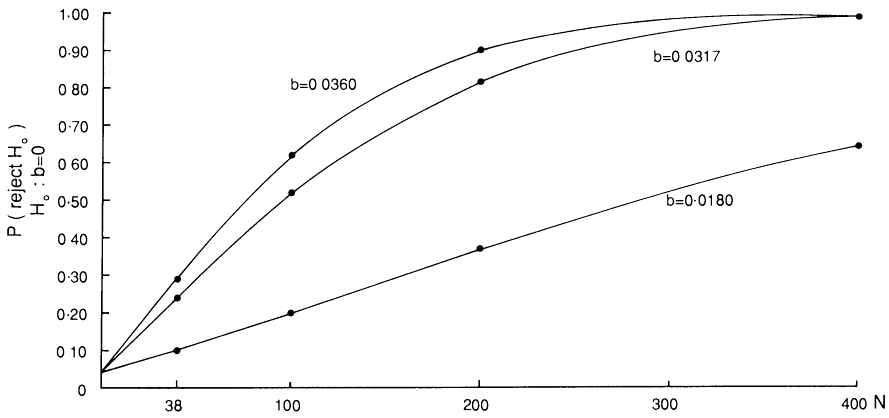

Fig. 10. The relationship between the probability of rejecting the null hypothesis $b=0$ and the number of data points for a data matrix similar to the one of *Saxifraga hirculus*. The level of significance $P=0{\cdot}05$; for further explanation see text.

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Appendix

The determination of the sample size necessary to detect relevant departures from H_0, e.g. $b=0$, with a specified probability is based on the fact that Λ has a non-central χ^2 distribution under H_1 with 1df and a non-centrality parameter:

$$\sigma^2=n\,b^2\,(F_{bb}-F_{b\Theta}\times F_{\Theta\Theta}{}^{-1}\times F_{\Theta b})$$

where b is a relevant parameter value and the F are partitions of the information matrix, the covariance matrix F of the vector (b, a, c, σ^2) and Θ denotes (a, c, σ^2):

$$F = \begin{vmatrix} F_{bb} & F_{b\Theta} \\ F_{\Theta b} & F_{\Theta\Theta} \end{vmatrix}$$

For the full details we refer to mathematical statistical textbooks, e.g. Cox & Hinkley (1974).

Given b and estimated values for the covariance matrix F the value of σ^2 can be manipulated by altering n, the sample size. Since the mean of the non-central χ^2 distribution shifts to the right if n increases, n can be chosen in such a way that the probability of rejecting H_0 is, e.g., 0·9 if b is the true parameter value.

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