

ESSAY REVIEW

The allometry of reproduction within plant populations

Jacob Weiner^{1,2*}, Lesley G. Campbell³, Joan Pino⁴ and Laura Echarte⁵

¹National Center for Ecological Analysis and Synthesis, Santa Barbara, CA 93101, USA; ²Department of Agriculture and Ecology, University of Copenhagen, DK-1958 Frederiksberg, Denmark; ³Department of Ecology and Evolutionary Biology, Rice University, Houston, TX 77005, USA; ⁴Center for Ecological Research and Forestry Applications, Autonomous University of Barcelona, E-08193 Bellaterra, Spain; and ⁵National Research Council of Argentina (CONICET), CC 276, 7620 Balcarce, Argentina

Summary

1. The quantitative relationship between size and reproductive output is a central aspect of a plant's strategy: the conversion of growth into fitness. As plant allocation is allometric in the broad sense, i.e. it changes with size, we take an allometric perspective and review existing data on the relationship between individual vegetative (V , x -axis) and reproductive (R , y -axis) biomass within plant populations, rather than analysing biomass ratios such as reproductive effort ($R/(R+V)$).

2. The allometric relationship between R and V among individuals within a population is most informative when cumulative at senescence (total R – V relationship), as this represents the potential reproductive output of individuals given their biomass. Earlier measurements may be misleading if plants are at different developmental stages and therefore have not achieved the full reproductive output their size permits. Much of the data that have been considered evidence for plasticity in reproductive allometry are actually evidence for plasticity in the rate of growth and development.

3. Although a positive x -intercept implies a minimum size for reproducing, a plant can have a threshold size for reproducing without having a positive x -intercept.

4. Most of the available data are for annual and monocarpic species whereas allometric data on long-lived iteroparous plants are scarce. We find three common total R – V patterns: short-lived, herbaceous plants and clonal plants usually show a simple, linear relationship, either (i) passing through the origin or (ii) with a positive x -intercept, whereas larger and longer-lived plants often exhibit (iii) classical log–log allometric relationships with slope < 1 . While the determinants of plant size are numerous and interact with one another, the potential reproductive output of an individual is primarily determined by its size and allometric programme, although this potential is not always achieved.

5. *Synthesis.* The total R – V relationship for a genotype appears to be a relatively fixed-boundary condition. Below this boundary, a plant can increase its reproductive output by: (i) moving towards the boundary: allocating more of its resources to reproduction, or (ii) growing more to increase its potential reproductive output. At the boundary, the plant cannot increase its reproductive output without growing more first. Analysing size-dependent reproduction is the first step in understanding plant reproductive allocation, but more integrative models must include time and environmental cues, i.e. development.

Key-words: allometric growth, biomass allocation, partitioning, plant life history, reproductive allocation, reproductive strategy, size dependence

Introduction

Growth and reproduction are two of the most fundamental processes in plants. After a plant produces biomass, it allocates

this biomass to various structures and functions, among them reproduction (Bazzaz & Reekie 1985). Offspring are the currency of natural selection, but plants must first accumulate resources and build reproductive machinery via growth. Because resources allocated to one function or organ are unavailable for other functions or organs, allocation requires

*Correspondence author. E-mail: jw@life.ku.dk

investment trade-offs. Ultimately, allocation patterns reflect strategies that are the product of both selection and constraints. This relationship between the accumulation of biomass and its allocation to structures and functions is the core of plant life-history strategies.

Traditionally, allocation has been considered to be a ratio-driven process: 'partitioning'. According to this perspective, a plant with a given amount of resources at any point in time partitions them among different structures or activities (Klinkhamer, de Jong & Meelis 1990). This has led to the concept of 'reproductive effort' (RE = reproductive biomass/total biomass), which has been the measure of reproductive allocation in many studies. But the 'partitioning' perspective and the analysis of RE are difficult to reconcile with the observation that plant allocation is allometric in the broad sense, i.e. it changes with size. The ratio-based perspective of allocation is size independent, whereas almost all observed plant allocation patterns are size dependent (McConnaughay & Coleman 1999; Weiner 2004). There is an emerging consensus among researchers that we should be analysing and interpreting allometric patterns, not allocation ratios such as RE (Jasienski & Bazzaz 1999; Müller, Schmid & Weiner 2000; Karlsson & Méndez 2005).

While there may be no single unified concept of size for plants (Weiner & Thomas 1992), dry mass is a widely used measure for many purposes. Plants are primarily composed of carbohydrates, so the dry biomass of a plant is usually proportional to the plant's energy content (Hickman & Pitelka 1975). A portion of this energy is mobile, e.g. sugars and starches, and can be used to produce reproductive structures. Thus, a plant's biomass tells us something about the energy potentially available for reproduction, and it generally reflects other resources available to an individual (Reekie & Bazzaz 1987).

THREE DIFFERENT KINDS OF ALLOMETRIC RELATIONSHIPS

Before addressing allometric patterns within plant populations, it is important to distinguish among three fundamentally different kinds of allometric relationships, which address very different questions, but have been conflated throughout much of the literature:

- 1 Broad interspecific allometric scaling relationships, usually based on adults. This has been a recent focus of research, and important scaling relationships have emerged (Niklas 1994; West, Brown & Enquist 1999; Enquist & Niklas 2002), including patterns of reproductive allocation (Shiple & Dion 1992; Niklas & Enquist 2003).
- 2 Static intraspecific allometric relationships among individuals within a species, usually at one point in time (e.g. Vega *et al.* 2000; Wang *et al.* 2006).
- 3 Allometric growth of individuals (e.g. Weiner & Thomas 1992; Bonser & Aarssen 2001, 2003).

There is no basis for assuming, as many researchers have, that relationships among individuals within a population or

the allometric growth trajectories of individuals are similar to the broad interspecific relationships that have been documented. For example, larger species have a lower shoot : root ratio than smaller species (Enquist & Niklas 2002; Zens & Webb 2002), but shoot : root ratio increases as a plant grows (Müller, Schmid & Weiner 2000). Similarly, large K-selected species have lower RE than small r-selected species (Begon, Harper & Townsend 2006), but within a population, larger individuals often have greater RE than smaller individuals (Weiner 1988). Allometric relationships among individuals within a population at one point in time (or over a short interval) do not usually reflect the allometric growth patterns of these individuals. Although there have been several attempts to clear up this confusion (Weller 1989; Klingenberg & Zimmermann 1992; Weiner & Thomas 1992), it still plagues the analysis and interpretation of allometric relationships. Here we address (2) and (3) above, not (1).

MODELS OF SIZE-DEPENDENT REPRODUCTIVE OUTPUT

What pattern or patterns of size-dependent reproductive output within populations would one predict from basic principles? As plants are modular and reproductive output is clearly related to module number, the null model is usually that plants allocate a simple proportion of their biomass to reproduction (Fig. 1, model a). An alternative model, based on a micro-economic analogy between a biological plant and an industrial plant (Weiner 1988), predicts a minimum size for reproduction and a linear relationship between biomass and reproductive output above that size (Fig. 1, model b). Capital investment to build the factory is necessary before any products (seeds) can be produced, and this corresponds to a threshold size for reproduction. After this initial investment, there are fixed costs for materials, maintenance, etc. resulting in a linear increase in reproductive output with size. This relationship appears to hold for many annual herbaceous species (e.g. Hartnett 1990; Thompson, Weiner & Warwick 1991; Aarssen & Taylor 1992; Schmid & Weiner 1993; Echarte & Andrade 2003).

A minimum size for reproduction has been erroneously considered identical to a positive x -intercept on a graph of reproductive output (y -axis) versus size (x -axis). To clarify the potential difference between a positive x -intercept and minimum size for reproduction, let us consider a schematic plant that grows several, for instance four, leaves without flowering. The fifth and all subsequent leaves have a single flower, which becomes a single fruit with a fixed number of seeds, in the axil. Such behaviour would result in the simple relationship shown in model b in Fig. 1, where the positive x -intercept and minimum size for reproduction are one and the same. Alternatively, one can imagine a modification of our schematic plant, in which five leaves are necessary for flowering to occur, but flowers are then formed in all five leaf axils. In such a case there would still be a minimum size for reproduction, but the (extrapolated) x -intercept would be the origin (Fig. 1, model a; Samson & Werk 1986): the relationship between R and V is discontinuous, with a step occurring at the minimum size for

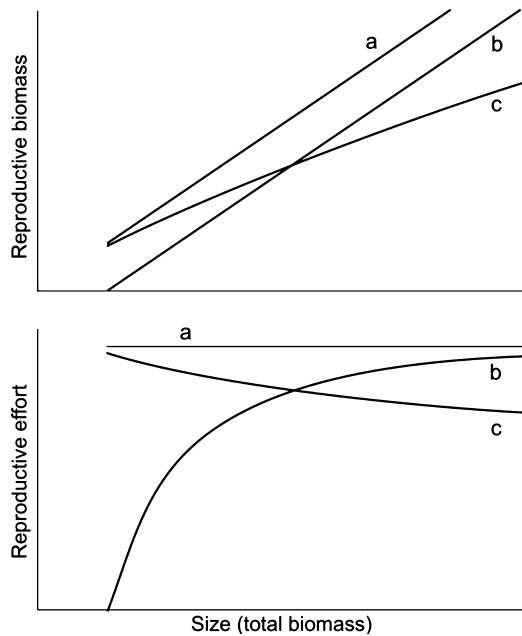


Fig. 1. The relationship between total (or vegetative) and reproductive biomass can alter 'reproductive effort' (reproductive biomass/total biomass). In model a, reproductive effort is size independent. In model b, there is a minimum size for reproduction and a linear relationship between biomass and reproduction above that size. In this case reproductive effort increases with size (Crawley 1983; Samson & Werk 1986; Weiner 1988). Although biologically unlikely, it is theoretically possible for an extrapolated x -intercept to be negative, which would result in decreasing reproductive effort with increasing size. In model c, there is a classical 'allometric' relationship between reproductive (R) and total (T) biomass ($R = aT^b$), which is linear with slope = b on log–log scale. If $b < 1$, as shown, then reproductive effort decreases with size.

reproduction. Although they seem improbable biologically, other algorithms can result in a negative x -intercept. For example, if we further modify our schematic plant such that one or more of the leaves below the threshold number form two flowers in the axil whereas those above the threshold have only one, then there will be a positive y -intercept (and a negative x -intercept) in the extrapolated linear R – V relationship. Thus, a minimum size for reproduction does not necessarily require a positive x -intercept on the R – V relationship, but the latter does imply the former.

Our schematic plants also help us to define plasticity in the R – V relationship. A change in RE with density has been interpreted as an example of plasticity, but it is usually an effect of size and allometric growth: 'apparent plasticity' (McConnaughey & Coleman 1999). At higher densities plants are smaller, and if there is a positive x -intercept on the R – V relationship, plants will be closer to, or even below, this intercept, which means lower or even zero RE. 'True' plasticity in allocation can be defined as a change in the allometric relationship itself, rather than a change in the rate of growth (Weiner 2004). For example, if our schematic plant were to produce a flower and then fruit in every leaf axil starting with the fifth under some conditions, but only one flower in every second leaf axil under

other conditions, this would represent true plasticity in reproductive allocation.

The simple models a and b illustrated in Fig. 1 and by our first two schematic plants may be reasonable hypotheses for herbaceous plants, such as annual crops and weeds, but as size increases further we would not expect reproductive output to remain a simple linear function of size. Increased per-unit-size costs of biomechanical support and internal transport, and, in woody plants, an increase in the proportion of non-living structural tissues, may result in a decrease in the slope of the R – V relationship (model c). In such cases, the classical allometric approach based on the 'allometric equation' ($Y = ax^b$, usually fit as $\log Y = \log a + b \log X$) is often useful. It is also possible to model both a positive x -intercept and an allometric relationship above this intercept (Klinkhamer *et al.* 1992).

Here, we explore allocation trends in published data on herbaceous plants and ask the following questions: (i) Are there one or a few general patterns of size-dependent reproductive output within plant populations? (ii) Is there evidence for a non-trivial positive x -intercept in the R – V relationship, which is strong evidence for a minimum size for reproduction, in most plant populations? (iii) Is there evidence for extensive plasticity in the R – V relationship? We hope our review of R – V relationships within herbaceous plant populations will serve as an alternative to the analysis of biomass ratios such as RE, and thus contribute to an allometric approach to reproductive allocation.

Materials and methods

We limited our review to herbaceous plants, both because of the problem of defining size for long-lived organisms that build up dead tissues and because of the lack of data on lifetime R and V for woody plants. We reviewed all published relevant data we could find, with special emphasis on figures showing individual data or data made available to us by researchers. Our requirements for inclusion of studies included (i) accurate measurement of above-ground (or above- and below-ground) vegetative biomass and (ii) biomass of reproductive structures or seed production that reflect cumulative R – V relationships for genets or at least whole ramets. In addition to searching the literature, we also requested relevant data from all members of the Plant Population Biology Section of the Ecological Society of America and the Ecological Section of the Botanical Society of America via E-mail. All data we found that fit our criteria were included. Although we may have missed some published results, we are confident that we have compiled the majority of the peer-reviewed scientific literature available on this topic.

There has been much discussion about how to distinguish between vegetative and reproductive structures, as many supporting structures, such as leafy bracts, pedicels and calices, have both vegetative and reproductive functions (Bazzaz & Reekie 1985; Reekie & Bazzaz 2005). Previous studies have shown that all measures of reproductive biomass are highly correlated within a population (e.g. Bazzaz, Ackerly & Reekie 2000), so we included studies that used different definitions of reproductive structures, as long as these were consistently applied within a study. We included studies that presented estimates of reproductive output only when these estimates were based on extensive measurements and were calibrated with harvest data. As mean size of seeds produced by an individual is known to be among the least plastic of

plant traits, we also include studies in which the number of seed produced was estimated with a high degree of accuracy.

In our search, we found 44 publications, involving 97 experimental or descriptive studies on 76 species (Table 1)*. From each publication, we collected information on plant life history, experimental sample size, the timing of experimental harvest and the proportion of variation (r^2) explained by a simple R - V relationship. We report relevant published results, and we reanalysed the data when doing so was desirable and possible. Because our goal here is to look for general patterns, we employ simple least-square linear models (log-transformed when this improved the residual structure), rather than more sophisticated methods (e.g. Klinkhamer *et al.* 1992; Brophy *et al.* 2007). This allows us to use and compare all previous studies, including those in which data is not available for reanalysis, as simple regression results are always presented, even in the oldest studies. We take a 'common sense' approach to reviewing published studies: reporting all published results, evaluating data visually when possible while giving more weight to statistical tests when presented or when we could perform them ourselves, and keeping our own analyses relatively simple so that older and more recent studies can be compared.

To determine how many general patterns of size-dependent reproductive output within plant populations exist, we assessed whether a study presented evidence for nonlinearity in the R - V relationship, i.e. log-log slope significantly different from 1. To determine whether there is evidence for a non-trivial minimum size for reproduction in most plant populations, we recorded the sign of the x -intercept in each publication or our own analyses. Finally, to search for evidence of extensive plasticity in the reproductive R - V relationship, we tested for effects of different treatments on the R - V relationship. Patterns within each publication were classified as significant or non-significant.

There has been much debate about whether one should analyse the relationship between reproductive biomass (R) and vegetative (i.e. non-reproductive, V) biomass, or whether it is more appropriate to analyse the relationship between reproductive biomass and total ($T = V + R$) biomass. As total biomass includes reproductive biomass, it has been argued that this can result in a 'spurious correlation' (Brett 2004). Other researchers have argued that the problem is insoluble or non-existent, as none of the three variables is independent from the other two (Prairie & Bird 1989). Although this debate has not been resolved to the satisfaction of all researchers and is beyond the scope of this paper, we think it is most appropriate to analyse reproductive biomass (R) versus vegetative biomass (V) when possible. When R is measured or estimated as fecundity (number of seeds produced) then we see no clear advantage of V over T as a measure of size.

Results

Reproductive allocation studies within populations have been performed on a wide range of plant species (Table 1), with experimental ($n = 37$) and descriptive ($n = 60$) data sets over a wide range of conditions. Of these, there were 33 annual, nine monocarpic, 16 polycarpic and 18 clonal perennial species (two species, *Arum italicum* and *Pinguicula vulgaris*, which can reproduce by gemmae but clonal ramets do not remain physically attached to the parent plant, are considered non-clonal here). There were three common forms of the R - V relationship, corresponding to the three models described in the Introduction:

- (a) a linear relationship passing through the origin (e.g. *Senecio vulgaris*, Fig. 2);
- (b) a linear relationship with a positive x -intercept (e.g. *Zea mays*, Fig. 3);
- (c) a classical 'simple allometric' relationship (Seim & Sæther 1983), i.e. linear on a log-log scale, with a slope < 1 (e.g. *Raphanus raphanistrum*, *Rumex obtusifolius*; Figs 4 and 5).

We found 48 data sets conforming to R - V relationship of type (a) (no evidence of a positive x -intercept and no evidence of nonlinearity), 25 data sets conforming to type (b) (evidence for a positive x -intercept but no evidence for nonlinearity), and five conforming to the third type (c) (evidence for nonlinearity and residual structure consistent with log-log transformation). The remaining 19 data sets did not conform to any type of R - V relationship. Although variation in V accounted for most of the variation in R in most studies, there were also several studies in which the r^2 for the R - V relationship was very low (e.g. four studies had $r^2 < 0.1$) and therefore did not fit any of the above models.

In many cases in which data were available, there was a cloud of points below the R - V line, likely representing plants that had not yet completed their reproduction at the time of harvest (e.g. Fig. 4). In 21% of the species (18% of cases), we found evidence that the plants had been harvested prior to maturity.

Overall 27.6% (21 of 76 species; 24.7% – 24 of 97 cases) of the species showed strong evidence for, and 32.9% of species had strong evidence against (25 of 76 species, 30.0% – 29 of 97 cases) a positive x -intercept (Table 1). Evidence for a positive x -intercept size was less common in clonal perennials than annuals ($\chi^2 = 3.477$, d.f. = 1, $P = 0.062$ (species-level analysis); $\chi^2 = 4.61$, d.f. = 1, $P = 0.032$ (case-level analysis)).

For most studies (86 of 97 of cases and 68 of 76 species), the R - V relationship was linear (i.e. the residual structure of the linear regression on untransformed data was good and/or the log R -log V slope was not significantly different from 1). In the remaining studies, the R - V relationship was nonlinear (i.e. the log R -log V slope was significantly different from 1). In all the cases of nonlinearity, the log R -log V slope was < 1 (i.e. RE decreased with size). There was no difference among life histories in the frequency of species exhibiting nonlinear relationships ($\chi^2 = 5.37$, d.f. = 3, $P = 0.147$ (species-level analysis); $\chi^2 = 4.90$, d.f. = 3, $P = 0.177$ (case-level analysis)).

Twenty-five studies (across 19 species) investigated potential plasticity in the R - V relationship, nine cases of which (nine species) provided statistically significant support for the existence of plasticity. In those cases that demonstrated plasticity, the effects were very small compared to the effects of size alone. For example, in experiments on *Arabidopsis thaliana* (Clauss & Aarssen 1994b), in which siliques were counted as the measure of R , variation in log V alone accounted for 94.4% of the variation in log R , and inclusion of treatment effects increased this to 96.6%. In *Triticum aestivum* (wheat)

*[Correction added on 15 September 2009, after first online publication: 90 changed to 97 and 71 changed to 76 for experiments and species, respectively].

Table 1. Summary of reproductive output (R , reproductive biomass or fecundity, y -axis) versus size (V , vegetative or total biomass, x -axis) relationships within plant populations collected for 71 species from 44 sources from both experimental (E) and descriptive (D) studies. The r^2 reported is for a simple, linear regression or linear on a log-log scale (noted as L-L), determined by the residual structure (when the data were available for analysis) or as reported. ni, not investigated; nr, not reported; y, weak (ns) evidence for pattern; Y, strong (significant) evidence for pattern; n, weak evidence against a pattern (no evidence, but low statistical power); N, strong evidence against a pattern (no evidence, high statistical power); c, calculated from published data; d, calculated from original data provided by researchers; all other results as reported in publications.

Species	n	Evidence for positive x -intercept?	Evidence for nonlinearity in $R-V$ relationship?	Evidence for plasticity in $R-V$ relationship?	r^2 for linear $R-V$ (or log R -log V) relationship	Plants harvested at full maturity?	Type of study	Reference
Annual								
<i>Abutilon theophrasti</i>	156	N	N	ni	0.46	nr	D	Thompson, Weiner & Warwick 1991
<i>Abutilon theophrasti</i>	373	Y	Y	Y	0.91	Y	E	Sugiyama & Bazzaz 1998
<i>Amaranthus retroflexus</i>	20 or 30 per treatment	n	Y	N	0.73-0.95	N & Y	E	Wang <i>et al.</i> 2006
<i>Amaranthus retroflexus</i>	12	Y	N	ni	0.98	N	E	McLachlan <i>et al.</i> 1995
<i>Amaranthus retroflexus</i>	20	n	N	ni	0.95	N	E	McLachlan <i>et al.</i> 1995
<i>Amsinckia tessellata</i>	10	n	N	ni	0.92	nr	D	Samson & Werk 1986
<i>Anoda cristata</i>	14, 40	N	N	N	0.078	N	E	Puricelli <i>et al.</i> 2004
<i>Apera spica-venti</i>	213	n	Y	ni	0.46	n	E	Thompson, Weiner & Warwick 1991
<i>Arabidopsis thaliana</i>	20/pop	N	N	ni	0.56-0.98	N	E	Aarssen & Clauss 1992
<i>Arabidopsis thaliana</i>	108	N	N	N	nr	N & Y	E	Clauss & Aarssen 1994a
<i>Arabidopsis thaliana</i>	15/pop, 3 genotypes, 3 treatments with several levels	N	N	Y	0.51-0.97 ^d	Y	E	Clauss & Aarssen 1994b
<i>Bromus rubens</i>	10	n	n	ni	0.94	nr	D	Samson & Werk 1986
<i>Caulanthus lasiophyllus</i>	10	n	n	ni	0.98	nr	D	Samson & Werk 1986
<i>Chaenactis fremontii</i>	10	n	n	ni	0.90	nr	D	Samson & Werk 1986
<i>Chenopodium album</i>	50	n	N	ni	0.95	Y	D	Aarssen & Taylor 1992
<i>Chenopodium album</i>	240	N	N	N	0.93	Y	E	Grundy, Mead & Overs 2004
<i>Cryptantha pterocarya</i>	10	n	n	ni	0.98	nr	D	Samson & Werk 1986
<i>Datura stramonium</i>	60	N	N	ni	0.00	nr	E	Thompson, Weiner & Warwick 1991
<i>Datura stramonium</i>	60	Y	N	ni	0.83	nr	E	Thompson, Weiner & Warwick 1991
<i>Descurania pinnata</i>	8	n	n	ni	1.00	nr	D	Samson & Werk 1986
<i>Echinochloa crus-galli</i>	15	N	N	ni	0.99	Y	D	Martinková & Honek 1992
<i>Eschscholzia minutiflora</i>	10	n	n	ni	0.84	nr	D	Samson & Werk 1986
<i>Gilia minor</i>	10	n	n	ni	0.59	nr	D	Samson & Werk 1986
<i>Glycine max</i>	20-72	y	y	Y	0.93-0.98	Y	E	Nagai & Kawano 1986
<i>Glycine max</i>	322, 77	Y	y	n	0.95, 0.98	Y	E	Vega <i>et al.</i> 2000

Table 1. (Continued)

Species	<i>n</i>	Evidence for positive <i>x</i> -intercept?	Evidence for nonlinearity in <i>R-V</i> relationship?	Evidence for plasticity in <i>R-V</i> relationship?	<i>r</i> ² for linear <i>R-V</i> (or log <i>R</i> -log <i>V</i>) relationship	Plants harvested at full maturity?	Type of study	Reference
<i>Helianthus annuus</i>	37–117	N	y	Y	0.82–0.90 (L-L)	Y	E	Kawano & Nagai 1986
<i>Helianthus annuus</i>	258, 60	Y	y	y	0.98, 0.97	Y	E	Vega <i>et al.</i> 2000
<i>Lotus humistratus</i>	10	y	n	ni	0.93	nr	D	Samson & Werk 1986
<i>Malacothrix coulteri</i>	10	n	n	ni	0.85	nr	D	Samson & Werk 1986
<i>Mentzelia congesta</i>	10	n	n	ni	0.95	nr	D	Samson & Werk 1986
<i>Panicum miliaceum</i>	243	N	y	N	0.94–0.98	nr	E	Thompson, Weiner & Warwick 1991
<i>Phacelia fremontii</i>	10	n	n	ni	0.85	nr	D	Samson & Werk 1986
<i>P. tanacetifolia</i>	10	n	n	ni	0.94	nr	D	Samson & Werk 1986
<i>Raphanus raphanistrum</i>	200	N	Y	y	0.61 (L-L) ^d	Y	E	Campbell & Snow 2007
<i>R. raphanistrum</i> × <i>R. sativus</i>	155	N	Y	y	0.55 (L-L) ^d	Y (with some exceptions)	E	Campbell & Snow 2007
<i>Schismus barbatus</i>	10	n	n	ni	0.95	nr	D	Samson & Werk 1986
<i>Senecio vulgaris</i>	117	N	N	y	0.97 (L-L)	Y	E	Weiner <i>et al.</i> 2009
<i>Setaria glauca</i>	50	n	N	ni	0.93	Y	D	Aarssen & Taylor 1992
<i>Sinapis arvensis</i>	256	ni	n	Y	nr, analysis L-L	N	E	Brophy <i>et al.</i> 2008
<i>Thlaspi arvense</i>	50	n	y	ni	0.98	Y	D	Aarssen & Taylor 1992
<i>Triticum aestivum</i>	50 per pop.	Y	N	N	0.89–0.96 ^d	Y	E	Pan <i>et al.</i> 2003a
<i>Triticum aestivum</i>	50 or 60	Y	n	N	nr	Y	E	Pan <i>et al.</i> 2003b
<i>Triticum aestivum</i>	552	y	N	Y	0.97 ^d	N	E	Liu <i>et al.</i> 2008
<i>Xanthium canadense</i>	26	Y	N	ni	0.96 ^c	Y	E	Matsumoto <i>et al.</i> 2008
<i>Zea mays</i>	298, 287	Y	n	y	0.94, 0.97	Y	E	Vega <i>et al.</i> 2000
<i>Zea mays</i>	200 per variety	Y	N	ni	0.93–0.95 ^d	Y	E	Echarte & Andrade 2003
Clonal perennial								
<i>Artemisia halodendron</i>	118, 118	n	n	ni	0.32, 0.35	Y	D	Li <i>et al.</i> 2005
<i>Aster lanceolatus</i>	42, 39	Y	n	ni	0.85, 0.88	Y	E	Schmid, Bazzaz & Weiner 1995
<i>Erythronium americanum</i>	50	n	n	ni	0.19	Y	D	Aarssen & Taylor 1992
<i>E. americanum</i>	25	N	N	ni	0.77	N	D	Wolfe 1983
<i>Matanthemum canadensis</i>	50	N	n	ni	0.02	Y	D	Aarssen & Taylor 1992
<i>Pistia stratiotes</i>	195	Y	N	ni	0.81	nr	D	Coelho, Deboni & Lopes 2005
<i>Pityopsis graminifolia</i>	31	Y	N	ni	0.76	nr	D	Hartnett 1990
<i>Ranunculus muelleri</i>	50	N	n	ni	0.42	N	D	Pickering 1994
<i>R. dissectifolius</i>	83	N	n	ni	0.34	N	D	Pickering 1994
<i>R. graniticola</i>	92	N	n	ni	0.34	N	D	Pickering 1994
<i>R. niphophilus</i>	46	N	n	ni	0.11	N	D	Pickering 1994
<i>Saxifraga hirculus</i>	23–45	N	n	ni	nr	ni	D	Ohlson 1988

Table 1. (Continued)

Species	<i>n</i>	Evidence for positive <i>x</i> -intercept?	Evidence for nonlinearity in <i>R</i> - <i>V</i> relationship?	Evidence for plasticity in <i>R</i> - <i>V</i> relationship?	<i>r</i> ² for linear <i>R</i> - <i>V</i> (or log <i>R</i> -log <i>V</i>) relationship	Plants harvested at full maturity?	Type of study	Reference
<i>Silphium speciosum</i>	56	Y	N	ni	0.85	Y	D	Hartnett 1990
<i>Solidago altissima</i>	24 families	Y	N	Y	0.71–0.91	N	D	Schmid & Weiner 1993
<i>S. canadensis</i>	35	Y	N	ni	0.71	Y	D	Hartnett 1990
<i>S. canadensis</i>	48, 48	Y	n	ni	0.80, 0.78	Y	E	Schmid, Bazzaz & Weiner 1995
<i>Sorghum halepense</i>	48	N	N	ni	na	nr	D	Thompson, Weiner & Warwick 1991
<i>Sorghum halepense</i>	136	Y	N	ni	na	nr	E	Thompson, Weiner & Warwick 1991
<i>Trillium grandiflorum</i>	50	Y	N	ni	0.95	Y	D	Aarssen & Taylor 1992
<i>Veronia baldwinii</i>	33	Y	N	ni	0.90	Y	D	Hartnett 1990
<i>Viola pubescens</i>	50	n	n	ni	0.73	Y	D	Aarssen & Taylor 1992
Monocarpic biennial or perennial								
<i>Althaea officinalis</i>	50	n	y	ni	0.86	Y	D	Aarssen & Taylor 1992
<i>Barbarea vulgaris</i>	50	y	n	ni	0.72	Y	D	Aarssen & Taylor 1992
<i>Cynoglossum officinale</i>	21–54	N	N	n	0.58–0.94	Y	D	Klinkhamer & de Jong 1987
<i>Cynoglossum officinale</i>	20	N	y	ni	0.89–0.95 (L-L)	N	E	de Jong & Klinkhamer 1989
<i>Diploxaxis erucoides</i>	88	y	y	ni	nr	N	D	Sans & Masalles 1994
<i>Erodium cicutarium</i>	10	n	n	ni	0.83	nr	D	Samsom & Werk 1986
<i>Gossypium hirsutum</i>	104	n	Y	Y	0.81	N & Y	E	Sadras, Bange & Milroy 1997
<i>Lepidium campestre</i>	50	N	Y	ni	0.97	Y	D	Aarssen & Taylor 1992
<i>Lesquerella fendleri</i>	33	N	N	N	0.58, 0.75 (provided by author)	Y	E	Ploschuk, Slafer & Ravetta 2005
<i>Melilotus alba</i>	50	n	N	ni	0.89	Y	D	Aarssen & Taylor 1992
Polycarpic, non-clonal perennial								
<i>Arum italicum</i>	151	Y	N	ni	0.90 ^d	N	D	Méndez & Obeso (1993)
<i>Chrysanthemum leucanthemum</i>	50	n	Y	ni	0.76	Y	D	Aarssen & Taylor (1992)
<i>Cichorium intybus</i>	50	n	N	ni	0.88	Y	D	Aarssen & Taylor (1992)
<i>Hesperis matronalis</i>	50	n	N	ni	0.60	Y	D	Aarssen & Taylor (1992)
<i>Hordeum jubatum</i>	50	n	Y	ni	0.96	Y	D	Aarssen & Taylor (1992)
<i>Lesquerella mendocina</i>	40	N	N	N	0.67, 0.73 (provided by author)	Y	E	Ploschuk, Slafer & Ravetta (2005)
<i>Mitella diphylla</i>	50	n	n	ni	0.47	Y	D	Aarssen & Taylor (1992)
<i>Pinguicula vulgaris</i>	49–51 per pop.	N	ni	ni	0.27–0.75	N	D	Méndez & Karlsson (2004)
<i>Plantago major</i>	130	Y	N	Y	0.72	Y	E	Weiner (1988)
<i>Plantago major</i>	252 total	n	n	ni	0.02, 0.03 (ns) ^d	Y	E	Reekie (1998)
<i>Potentilla recta</i>	50	y	N	ni	0.94	Y	D	Aarssen & Taylor (1992)
<i>Potentilla recta</i>	6	y	n	ni	0.86	nr	D	Soutle & Werner (1981)

Table 1. (Continued)

Species	<i>n</i>	Evidence for positive <i>x</i> -intercept?	Evidence for nonlinearity in <i>R-V</i> relationship?	Evidence for plasticity in <i>R-V</i> relationship?	<i>r</i> ² for linear <i>R-V</i> (or log <i>R</i> -log <i>V</i>) relationship	Plants harvested at full maturity?	Type of study	Reference
<i>Quercus serrata</i>	29	Y	Y	ni	nr	N	D	Nakashizuka, Takahashi & Kawaguchi (1997)
<i>Rumex crispus</i>	50	n	N	ni	0.59	Y	D	Aarssen & Taylor (1992)
<i>R. obtusifolius</i>	181	N	Y	ni	0.81 (L-L) ^d	Y	E	Pino, Sams & Masalles (2002)
<i>Taraxacum officinale</i>	50	n	n	ni	0.58	Y	D	Aarssen & Taylor (1992)
<i>Taraxacum officinale</i>	32	y	n	ni	0.92	ni	D	Welham & Setter (1998)
<i>Taraxacum officinale</i>	39	n	n	ni	0.66	ni	D	Welham & Setter (1998)
<i>Thalictrum dioicum</i>	50	Y	y	ni	0.82	Y	D	Aarssen & Taylor (1992)
<i>Tragopogon pratensis</i>	50	N	y	ni	0.35	Y	D	Aarssen & Taylor (1992)

populations grown at five densities (Liu *et al.* 2008), log *V*, density and the log *V* × density interactions all had significant effects on log (spike mass). Log *V* alone accounted for 97.4% of the variation in log (spike mass), and inclusion of density and the interaction term increased this to 98.4%.

There is much evidence for genetic variation in the *R-V* relationship within and among populations, i.e. different genotypes have significantly different *R-V* relationships (Aarssen & Clauss 1992; Schmid & Weiner 1993; Reekie 1998). There is also evidence for developmental effects in clonal perennials; *Solidago altissima* plants grown from seeds had different *R-V* relationships than plants grown from vegetative organs (Schmid & Weiner 1993).

Discussion

Our review of the available data yielded (i) evidence for three general patterns of size-dependent reproduction in plant populations, corresponding to models a, b and c described in the Introduction. There was also (ii) evidence for a positive *x*-intercept in 29% of the cases, which is strong support for a minimum size for reproduction in these cases, but this pattern is by no means universal. Finally, we document (iii) plasticity in the *R-V* relationship in 37% of the species for which relevant data were collected, but the effects of plasticity were always very small compared to the effects of size alone. Below we address the implications of our findings for our understanding of reproductive allocation within plant populations.

AN ALLOMETRIC APPROACH TO REPRODUCTIVE STRATEGIES

Allometric effects on allocation are still analysed and interpreted in terms of ratios such as RE (e.g. Cheplick 2005), but our results and recent studies (Jasienski & Bazzaz 1999; Müller, Schmid & Weiner 2000; Weiner 2004; Karlsson & Méndez 2005) argue convincingly that the converse is more useful. It is the *R-V* relationship that is selected, and RE results from this. We urge researchers to interpret *R-V* allometric relationships themselves, rather than interpreting allometric phenomena in terms of the resultant ratios. Fitness is closely related to reproductive output, not to reproductive effort, so interpreting such ratios can be misleading biologically (Jasienski & Bazzaz 1999).

We have implicitly defined the *R-V* relationship as cumulative over the life of the plant. This idea is intuitive for monocarpic plants, which are much easier to study in this context, so it is not surprising that most of the currently available data are for annual and monocarpic species. To apply this approach to iteroparous species, such as woody perennials, the minimal allometric model would be that allocation is a function of production, and we propose this as a null hypothesis for future investigations. According to this model, a plant produces biomass and allocates it to different organs and structures according to a relatively fixed allometric programme. Some of this biomass (a) remains in living tissue, (b) becomes dead but structural tissue or (c) is shed (including leaves, bark, dead branches, etc.). (It is important to remember that production

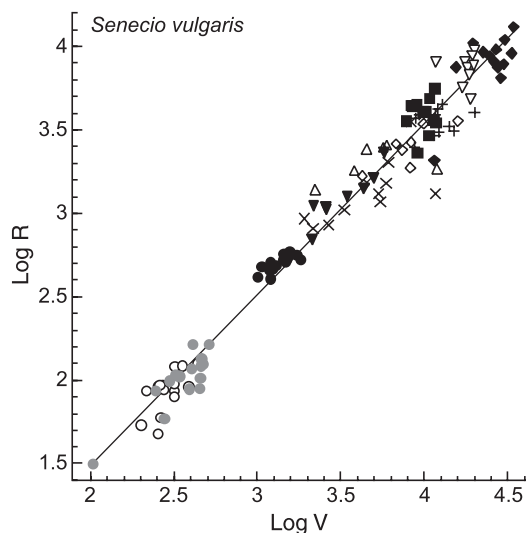


Fig. 2. Relationship between mass of seeds (actually fruits) produced by *Senecio vulgaris* individuals and their vegetative biomass in two glasshouse experiments. Circles are from experiment 2 (shading represents different fertility levels), all other data from experiment 1 (symbols represent different treatment combinations of water, nutrients and competition). Single regression line (shown): $\log R = -0.57 + 1.026 \log V$; $r^2 = 0.971$ (Weiner *et al.* 2009). Data are shown and analysed here on log–log scale because the residual structure is not consistent with regression on a linear scale, but a log R –log V slope = 1 is equivalent to model a: $R \propto V$. There were small but significant effects of the treatments on the intercept, but not the slope, of the log R –log V relationship.

allocated to (d) reproductive structures (fruits and seeds), is also shed.) Thus, using biomass production, which in practice means including dead and shed structures in V , is one solution to defining size in R – V relationships for iteroparous plants. The best way to investigate the total R – V relationship is to collect all the seeds produced by an individual throughout its life (Fig. 2; Weiner *et al.* 2009). Information from any single harvest or bout of reproduction will not reflect the total R – V relationship.

As the allometric exponent of dead structural tissue (b) versus ((a) + (c) + (d)) will be greater than unity for large upright plants due to biomechanical constraints, and for iteroparous herbaceous perennials if storage organs are included in V , we would expect the allometric exponent of reproductive structures (d) versus ((a) + (b) + (c)) to be < 1 , assuming the proportion of structures that are shed as dead (c) is relatively constant. This argument may not be relevant for short-lived herbaceous plants but valid for long-lived woody plants. This may explain why short-lived herbaceous plants tend to show linear R – V relationships, whereas longer-lived organisms with more structural tissue or storage organs (such as *Raphanus raphanistrum* (Fig. 4) and *Rumex obtusifolius* (Fig. 5)) show log R –log V slopes < 1 .

Plant life-history theory would benefit from an allometric perspective. For example, according to optimal allocation theory, to maximize seed production, plants should reinvest all resources into further growth (stems, leaves and roots), 100% vegetative investment and 0% reproductive allocation,

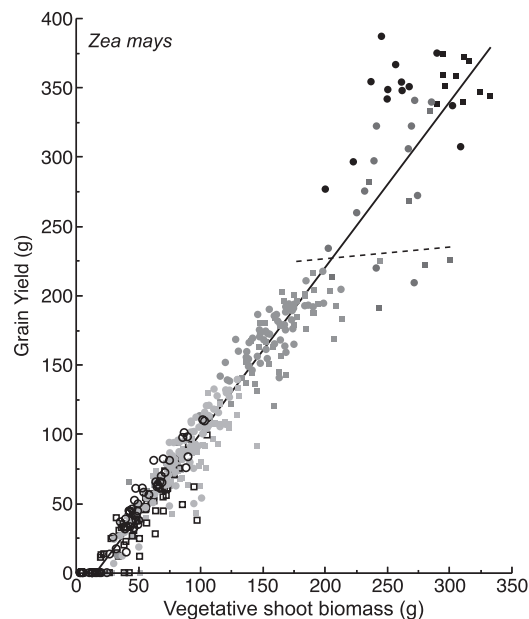


Fig. 3. Individual plant grain yield versus shoot biomass for maize (*Zea mays* cv. DK752) in two experiments (circles, squares) at five densities (2 plants m^{-2} : black, 4 plants m^{-2} : dark grey, 8 plants m^{-2} : middle grey, 16 plants m^{-2} : light grey and 30 plants m^{-2} : empty symbol). Two features of these data illustrate the importance of reproductive morphology for the R – V relationship: (i) because there is a minimum size for an ear, there is clear evidence of a minimum size for reproduction; (ii) plants above the dotted line have more than one ear. Relatively large individuals that only make one ear cannot fully utilize their size to produce more yield. Overall $r^2 = 0.941$. When experiment and density are added as variables $r^2 = 0.952$; with all interactions $r^2 = 0.966$. Thus, although plasticity can be detected, its effects are very small (after Echarte & Andrade 2003).

for most of their lives, and then switch at a certain time to investing all resources into reproduction, 0% further vegetative investment, 100% reproductive investment: a monocarpic strategy (Cohen 1968; Ellner 1987). In the allometric view, this means that the plant should grow along the x -axis and then switch to growth in the y -variable (Fig. 6). If plants do not succeed in completing their potential reproduction, the R – V graph will lie below the line. In such a case, the allometric growth trajectory is distinct from the static, inter-individual allometric relationship (Clauss & Aarssen 1994a). For example, the static inter-individual allometric slope of estimated R versus estimated V for tropical trees was much > 1 (Thomas 1996). This would occur if the individuals were distributed along the optimal strategy line in Fig. 6. An extreme example would be a monocarpic species, in which an individual does not produce fruits and seeds until the end of its life. The R – V relationship among individuals in a population cannot reflect the developmental trajectory for a plant that only flowers at the end of its life. The other extreme is a plant such as *Senecio vulgaris*, an ‘iteroparous annual’ that starts flowering at a very small size and continues growing and reproducing until it dies (Weiner *et al.* 2009). In this case, the total R – V relationship among individuals does reflect the developmental trajectory.

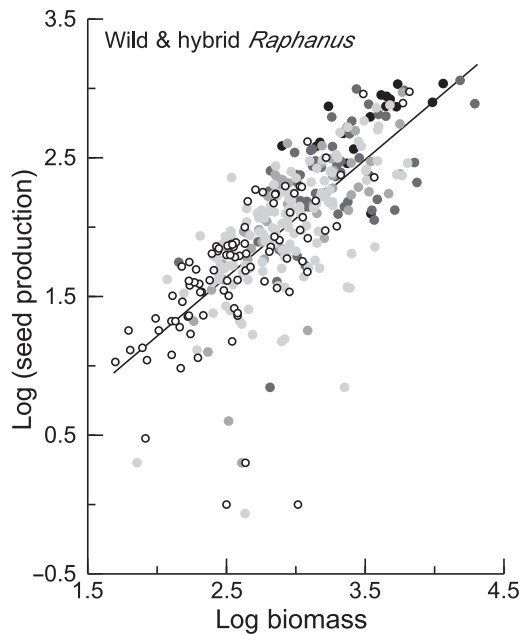


Fig. 4. Log seed production versus log biomass for wild *Raphanus raphanistrum* and hybrid (*R. raphanistrum* × *R. sativus*) grown in pots at densities of 1 (●), 2 (●), 3 (○), 4 (○) and 8 (○) plants per pot. General linear model: log biomass, SS = 30.6, d.f. = 1, $P < 0.0001$; density level, SS = 1.8, d.f. = 4 $P = 0.006$, $r^2 = 0.55$. These data show several of the common patterns in R - V (or, as here, fecundity-size) relationships: (i) a classical allometric relationship with slope < 1 (here 0.85), (ii) a cloud of points below the line, representing plants that have not completed reproduction (in this case hybrids that have obtained genes that delay maturation from the crop), (iii) weak or no evidence of plasticity in the allometric relationship, but (iv) clear effects of treatments on size and the rate of development, and therefore reproductive output (after Campbell & Snow 2007).

Of course plant behaviour is not solely a function of size, but we argue the role of size relative to the other factors has been under-appreciated and many effects attributed to time are actually due to size (e.g. Weiner & Thomas 2001). This may be because time is more central to our daily and scientific thinking: ontological processes are usually described in terms of time, experiments are completed and plants harvested at one point in time (Coleman, McConnaughay & Ackerly 1994), and classic demographic models are based on age rather than size. A complete understanding of plant behaviour must encompass time, size, environmental signals and genotype.

New statistical methods allow us to include values of $R = 0$ when fitting a line to an R - V relationship (Schmid *et al.* 1994; Brophy *et al.* 2007), thus improving our ability to estimate the x -intercept and slope of an R - V relationship when a population contains plants that have not reproduced at all, but we also need methods that allow us to estimate the total R - V relationship when there are individuals far below the line but with R greater than zero (e.g. Figs 4 and 7). We need methods that can exclude points that lie below a presumed limiting relationship, using reasonable assumptions and criteria. In some cases (e.g. Fig. 7, $t = 1$), there may not be enough information in the data to estimate the total R - V relationship, but in other cases (e.g. Fig. 7, $t = 2$) it should be possible. Potential methods include frontier production function models (Aigner, Lovell &

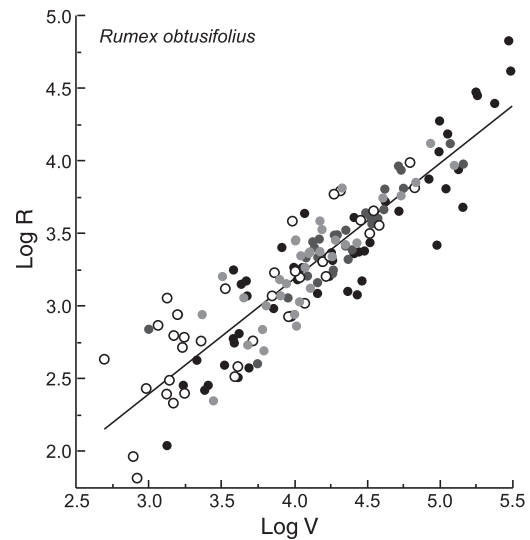


Fig. 5. Log R -log V relationship for *Rumex obtusifolius* growing in a *Medicago sativa* crop and harvested on four dates over 2 years (represented by different colours). Least-squares regression line is $\log R = -0.0026 + 0.795 \log V$, $r^2 = 0.81$. The slope is significantly < 1 . There was no effect of harvest date on the relationship, although data from a later harvest, when taproots were being depleted and there was large variation among individuals in developmental stage, did not fit this pattern. All points, however, were near or below the line shown (after Pino, Sans & Masalles 2002).

Schmidt 1977) and quantile regression (Cade & Noon 2003; Koener 2005). We encourage statistically oriented ecologists to address this issue and suggest the best tools for this purpose.

HOW PLASTIC IS THE TOTAL R - V RELATIONSHIP?

In the allometric view, plasticity in allocation is defined as a change in an allometric trajectory, not a change in the speed with which a trajectory is followed (Weiner 2004). Although there was clear evidence for plasticity in the total R - V relationship (statistically significant in 9 of 25 cases and 7 of 19 species; Table 1), in every case the effects were very small in comparison to the effects of size and developmental stage (see below). Meristems can have alternative fates and this suggests that plasticity in the R - V relationship is possible, yet attempts to find evidence for plasticity in allocation of meristems to reproductive versus other functions have been unsuccessful to date (Lehtilä & Larsson 2005; Zhang *et al.* 2008). This leads to the hypothesis that the total R - V relationship is, along with mean size of seeds produced by an individual, one of the least plastic plant attributes. According to this hypothesis, plant size is influenced by a myriad of factors and interactions, but at a given size, a plant's potential reproductive output is relatively fixed. A weaker version of this hypothesis is that this generalization holds for annual and monocarpic plants, which should allocate all available (i.e. mobile) resources to reproduction at maturity, but that iteroparous perennial species will show much more plasticity in their total R - V relationship. The available data are strongly biased toward annuals and monocarpic perennials, so it would be premature to generalize at this point. Tests of these hypotheses are needed. Simple allometric growth

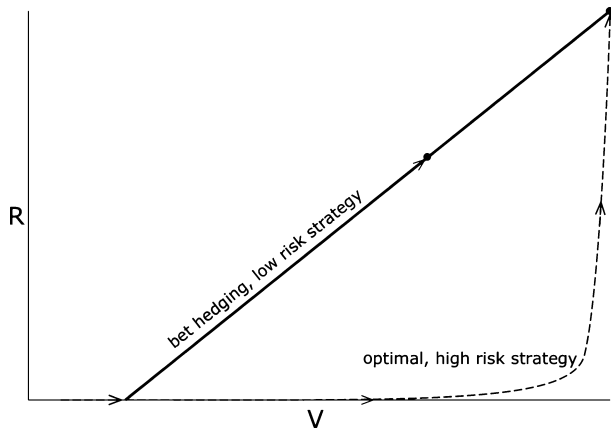


Fig. 6. Illustration of the relationship between a total R - V relationship (dark line), and two potential developmental trajectories (lines with arrows). The simple linear R - V relationship with positive x -intercept (model b) was chosen for convenience, the point applies to any R - V relationship. In the low-risk, bet-hedging strategy, the developmental trajectory follows the total R - V relationship, and the plant starts reproducing as soon as it has reached the minimum size for reproduction. This strategy assures that the plant will produce seeds as long as it is above the threshold size, but there is a cost in growth and therefore size achieved, because resources allocated to reproductive structures do not contribute to further growth. In the high-risk 'optimal' strategy, the plant invests all resources into growth until it has reached a specific size or age or receives necessary environmental cues (Thomas 1996). After a given period of growth, the optimal strategist will be larger than the bet-hedging strategist, and it will also produce more seeds if it has the time necessary to complete its reproduction, but its risk of very low or zero seed production is much greater if it stops growing or dies before completing reproduction.

should be the null or minimal hypothesis, while support for true plasticity requires that we can reject the simple allometric model (Weiner 2004).

The available data suggest that the total R - V relationship of a genotype is not very plastic, but there can be much genetic variation in the total R - V relationship within a population, especially among local populations of a species (Aarssen & Clauss 1992; Schmid & Weiner 1993; Reekie 1998). The results of Echarte & Andrade (2003; Fig. 3) on *Zea mays* are especially relevant here, because cultivars are genetically homogeneous. Echarte & Andrade grew one variety for 2 years at five densities. Ninety-four percent of the variation in R could be explained by variation in V . Inclusion of year, density and all interactions increased this by 2.5%. Other varieties, which were only tested in 1 year, showed slightly different x -intercepts and slopes, but the general R - V pattern was the same for all varieties. If a population's R - V relationship is primarily due to genetic rather than environmental variation, there is no reason to expect any of the three general R - V patterns described here. Indeed, there may be no clear relationship between R and V , as observed among genotypes of *Plantago major* (Reekie 1998).

SIZE, TIME, DEVELOPMENT AND REPRODUCTIVE OUTPUT – RECONCILING PHENOLOGY AND ALLOMETRY

According to our allometric model, the total R - V relationship can be seen as a boundary condition below which reproductive

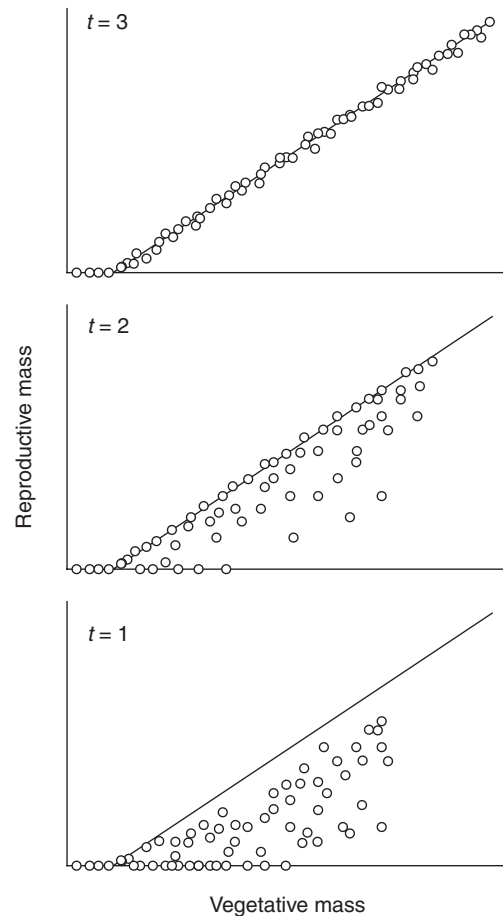


Fig. 7. Some commonly observed variation in R - V patterns can be understood in the context of developmental time (t) and a total R - V relationship (line). These patterns can also occur at the same time from different treatments that affect the rate of development. A linear relationship with a positive x -intercept (model b) is chosen for convenience, the point applies to any total R - V relationship.

behaviour takes place. The total R - V relationship for a genotype does not explain all of its reproductive behaviour, but it reframes plant reproductive behaviour in terms of allometry + development. Like a self-thinning trajectory, the total R - V relationship sets a limit, and although there is much room for variation in behaviour below this limit, it often dominates behaviour. In this view, a plant can increase its reproductive output in one of two ways: (i) by converting more of its current biomass into reproductive biomass and/or (ii) by increasing its size and therefore its potential reproductive output. The former is constrained by the total R - V relationship, whereas the latter is only limited by the maximum size a genotype can achieve. If a plant is at or near the total R - V boundary, it can only increase its reproductive output by growing more first.

Reproductive behaviour can be extremely plastic even if there is little plasticity in the total R - V relationship. As many gardeners know, if one over-fertilizes tomato plants with nitrogen, growth and therefore size will increase greatly, as does potential fruit production, but this fruit production may be postponed. Many inexperienced gardeners, who are overenthusiastic with nitrogen fertilizer, observe huge but non-flowering

tomato plants as the end of the growing season approaches. Such a postponement in reproduction can be interpreted as developmental plasticity in the direction predicted by optimal allocation theory, which predicts that plants should devote 100% of their resources towards growth, and then switch to 100% allocation to reproduction (Cohen 1968; Ellner 1987). A high level of nitrogen may be a signal that much more growth is possible, and therefore the switch should be postponed to take advantage of the increased potential reproductive output. Thus, increased nutrient levels can give the impression of reduced reproductive output if plants do not have time to complete their life cycles. What appears to be plasticity in the R - V relationship is often plasticity in the rate of growth and development (Fig. 7; Bonser & Aarssen 2009).

Plant size affects the probability of a plant flowering as well as the magnitude of reproductive success once it occurs. However, our review and previous work (e.g. Schmitt 1983) suggest that size determines the potential amount of reproduction more tightly than it determines the probability of reproduction. Although the probability of reproducing increases with size, specific triggering mechanisms, such as photoperiod or vernalization, are sometimes required to induce flowering. In the original research by Garner & Allard (1920) on photoperiodism in *Nicotiana tabacum* (tobacco), it was noted that only plants above a certain size threshold could respond to night length cues by flowering.

REPRODUCTIVE MORPHOLOGY AND REPRODUCTIVE ALLOMETRY

A clear relationship between reproductive morphology and allometry is shown in the results from *Zea mays* (Fig. 3; Echarte & Andrade 2003). A maize plant must reach a certain biomass before it can produce an ear, presumably because an ear itself cannot be below a certain size. Above this threshold, grain yield per plant is a linear function of V . There is a maximum, as well as a minimum, yield per ear, so there is an upper limit on R for plants that do not produce a second ear ('non-prolific' individuals), whereas the R - V relationship continues its linear increase for plants that do produce a second ear ('prolific' individuals; Fig. 3). The same pattern is found in every variety and experiment in the study. The microeconomic analogy suggests the hypothesis of a positive correlation between the x -intercept and R - V slope: greater capital investment (larger minimum size for reproduction) could lead to decreased per-unit cost above the minimum size (increased slope), but there was no evidence for this among the varieties of *Z. mays* or genotypes of *Solidago altissima* (Schmid & Weiner 1993).

IMPLICATIONS OF THE MOST COMMON R - V PATTERNS

When reproductive output is proportional to vegetative biomass (model a), an individual's fitness is more closely related to the total biomass produced by its offspring than to the number of surviving offspring. When the total R - V relationship has a positive x -intercept (model b), then the effect of size on

reproductive output is more than proportional. In this case, achieving a large size is even more important for fitness than if there is no positive intercept. A plant with such reproductive allometry may have higher fitness if it produces a few large offspring than many small ones with the same total offspring biomass, so this strategy could lead to the evolution of larger seed size (Venable & Rees 2009). This is also the type of relationship that can produce oscillations in population dynamics models with density dependence (Rees & Crawley 1989), because the population's total seed production will decrease at high density, even if total population biomass does not.

In the third type of R - V relationship, a classical log-log allometric relationship with slope < 1 (model c), the efficiency of the conversion of biomass production to reproductive output decreases with size. Although this pattern was not as common as the other two within the data sets we surveyed, we predict that it will prove to be much more common as more larger and long-lived species are investigated. This pattern is consistent with the hypothesis that smaller species are more 'reproductively economical' than larger species (Aarssen 2008). An individual's fitness will be higher if it produces many small rather than few large offspring, and inequality in fitness will be lower than inequality in size within the population.

Conclusions

The study of reproductive allocation in plants will benefit from an allometric approach, rather than an emphasis on ratios such as reproductive effort, which still dominate research in this area. It is important not to conflate the three kinds of allometric relationships. The hypothesis that a genotype has a genetically determined and relatively fixed total R - V relationship, below which allometric growth and variation occur, is a useful starting point for interpreting reproductive behaviour. The effects of size are a good place to begin, but a deeper understanding of plant reproductive behaviour and reproductive strategies must also include time and triggering mechanisms, in short, development.

Acknowledgements

This work was supported by a Sabbatical Fellowship from the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0553768), the University of California, Santa Barbara, and the State of California, and by the Danish Natural Science Research Council (Grant nr. 21-04-0421). We thank Maria Clauss, Jing Liu, Marcos Méndez, Edmundo Ploschuk and Gen-Xuan Wang for providing us with data, and Stephen Bonser, Marcos Méndez, and an anonymous referee for comments. Special thanks to Ed Reekie for critical comments and discussion.

References

- Aarssen, L.W. (2008) Death without sex – the 'problem of the small' and selection for reproductive economy in flowering plants. *Evolutionary Ecology*, **22**, 279–298.
- Aarssen, L.W. & Clauss, M.J. (1992) Genotypic variation in fecundity allocation in *Arabidopsis thaliana*. *Journal of Ecology*, **80**, 109–114.
- Aarssen, L.W. & Taylor, D.R. (1992) Fecundity allocation in herbaceous plants. *Oikos*, **65**, 225–232.

- Aigner, D., Lovell, C.A.K. & Schmidt, P. (1977) Formulation and estimation of stochastic frontier production function models. *Journal of Econometrics*, **6**, 21–37.
- Bazzaz, F.A., Ackerly, D.D. & Reekie, E.G. (2000) Reproductive allocation in plants. *Seeds: The Ecology of Regeneration in Plant Communities* (ed. M. Fenner), pp. 1–30. CABI Publishing, Wallingford.
- Bazzaz, F.A. & Reekie, E.G. (1985) The meaning and measurement of reproductive effort in plants. *Studies on Plant Demography* (ed. J. White), pp. 373–387. Academic Press, London.
- Begon, M., Harper, J.L. & Townsend, C.R. (2006) *Ecology: Individuals, Populations and Communities*, 4th edn. Blackwell Scientific Publications, Oxford.
- Bonsler, S.P. & Aarssen, L.W. (2001) Allometry and plasticity of meristem allocation throughout development in *Arabidopsis thaliana*. *Journal of Ecology*, **89**, 72–79.
- Bonsler, S.P. & Aarssen, L.W. (2003) Allometry and development in herbaceous plants: functional responses of meristem allocation to light and nutrient availability. *American Journal of Botany*, **90**, 404–412.
- Bonsler, S.P. & Aarssen, L.W. (2009) Interpreting reproductive allometry: individual strategies of allocation explain size-dependent reproduction in plant populations. *Perspectives in Plant Ecology, Evolution and Systematics*, **11**, 31–40.
- Brett, M.T. (2004) When is a correlation between non-independent variables “spurious”? *Oikos*, **105**, 647–656.
- Brophy, C., Gibson, D.J., Wayne, P.M. & Connolly, J. (2007) A modelling framework for analysing the reproductive output of individual plants grown in monoculture. *Ecological Modelling*, **207**, 99–108.
- Brophy, C., Gibson, D.J., Wayne, P.M. & Connolly, J. (2008) How reproductive allocation and flowering probability of individuals in plant populations are affected by position in stand size hierarchy, plant size and CO₂ regime. *Journal of Plant Ecology*, **1**, 207–215.
- Cade, B.S. & Noon, B.R. (2003) A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, **1**, 412–420.
- Campbell, L.G. & Snow, A.A. (2007) Competition alters life history and increases the relative fecundity of crop-wild radish hybrids (*Raphanus* spp.). *New Phytologist*, **173**, 648–660.
- Cheplick, G.P. (2005) The allometry of reproductive allocation. *Reproductive Allocation in Plants* (eds E.G. Reekie & F.A. Bazzaz), pp. 94–125. Elsevier, Amsterdam, the Netherlands.
- Clauss, M.J. & Aarssen, L.W. (1994a) Patterns of reproductive effort in *Arabidopsis thaliana*: confounding effects of size and developmental stage. *Ecoscience*, **1**, 153–159.
- Clauss, M.J. & Aarssen, L.W. (1994b) Phenotypic plasticity of size-fecundity relationships in *Arabidopsis thaliana*. *Journal of Ecology*, **82**, 447–455.
- Coelho, F.F., Deboni, L. & Lopes, F.S. (2005) Density-dependent reproductive and vegetative allocation in the aquatic plant *Pistia stratiotes* (Araceae). *Revista de Biologia Tropical*, **53**, 369–376.
- Cohen, D. (1968) A general model of optimal reproduction in a randomly varying environment. *Journal of Ecology*, **56**, 219–228.
- Coleman, J.S., McConnaughay, K.D.M. & Ackerly, D.D. (1994) Interpreting phenotypic variation in plants. *Trends in Ecology and Evolution*, **9**, 187–191.
- Crawley, M.J. (1983) *Herbivory*. University of California Press, Berkeley, CA, USA.
- Echarte, L. & Andrade, F.H. (2003) Harvest index stability of Argentinean maize hybrids released between 1965 and 1993. *Field Crops Research*, **82**, 1–12.
- Ellner, S. (1987) Alternate plant life-history strategies and coexistence in randomly varying environments. *Vegetatio*, **69**, 199–208.
- Enquist, B.J. & Niklas, K.J. (2002) Global allocation rules for patterns of biomass partitioning in seed plants. *Science*, **295**, 1517–1520.
- Garner, W.W. & Allard, H.A. (1920) Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *Journal of Agricultural Research*, **18**, 1920.
- Grundy, A.C., Mead, A.S.B. & Overs, T. (2004) Seed production of *Chenopodium album* in competition with field vegetables. *Weed Research*, **44**, 271–281.
- Hartnett, D.C. (1990) Size-dependent allocation to sexual and vegetative reproduction in four clonal species. *Oecologia*, **84**, 254–259.
- Hickman, J.C. & Pitelka, L.F. (1975) Dry weight indicates energy allocation in ecological strategy analysis of plants. *Oecologia*, **21**, 117–121.
- Jasienski, M. & Bazzaz, F.A. (1999) The fallacy of ratios and the testability of models in biology. *Oikos*, **84**, 321–326.
- de Jong, T.J. & Klinkhamer, P.G.L. (1989) Limiting factors for seed production in *Cynoglossum officinale* L. *Oecologia*, **80**, 167–172.
- Karlsson, P.S. & Méndez, M. (2005) The resource economy of plant reproduction. *Reproductive Allocation in Plants* (eds E.G. Reekie & F.A. Bazzaz), pp. 1–49. Elsevier, Amsterdam, the Netherlands.
- Kawano, S. & Nagai, Y. (1986) Regulatory mechanisms of reproductive effort in plants: I. Plasticity in reproductive energy allocation and propagule output of *Helianthus annuus* L. (Compositae) cultivated at varying densities and nitrogen levels. *Plant Species Biology*, **1**, 1–18.
- Klingenberg, C.P. & Zimmermann, M. (1992) Static, ontogenic, and evolutionary allometry – a multivariate comparison in 9 species of water-striders. *The American Naturalist*, **140**, 601–620.
- Klinkhamer, P.G.L. & de Jong, T.J. (1987) Plant size and seed production in the monocarpic perennial *Cynoglossum officinale* L. *New Phytologist*, **106**, 773–783.
- Klinkhamer, P.G.L., de Jong, T.J. & Meelis, E. (1990) How to test for proportionality in the reproductive effort of plants. *The American Naturalist*, **135**, 291–300.
- Klinkhamer, P.G.L., Meelis, E., de Jong, T.J. & Weiner, J. (1992) On the analysis of size-dependent reproductive output in plants. *Functional Ecology*, **6**, 308–316.
- Koenker, R. (2005) *Quantile Regression*. Cambridge University Press, Cambridge.
- Lehtilä, K. & Larsson, A.S. (2005) Meristem allocation as a means of assessing reproductive allocation. *Reproductive Allocation in Plants* (eds E.G. Reekie & F.A. Bazzaz), pp. 51–75. Elsevier, Amsterdam, the Netherlands.
- Li, F.-R., Zhang, A.-S., Duan, S.-S. & Kang, L.-F. (2005) Patterns of reproductive allocation in *Artemisia halodendron* inhabiting two contrasting habitats. *Acta Oecologica*, **28**, 57–64.
- Liu, J., Wang, G.-X., Wei, L. & Wang, C.M. (2008) Reproductive allocation patterns in different density populations of spring wheat. *Journal of Integrative Plant Biology*, **50**, 141–146.
- Martinková, Z. & Honek, A. (1992) Effect of plant size on the number of caryopses in barnyard grass, *Echinochloa crus-galli* (Poaceae). *Preslia*, **64**, 171–176.
- Matsumoto, Y., Oikawa, S., Yasumura, Y., Hirose, T. & Hikosaka, H. (2008) Reproductive yield of individuals competing for light in a dense stand of an annual, *Xanthium canadense*. *Oecologia*, **157**, 185–195.
- McConnaughay, K.D.M. & Coleman, J.S. (1999) Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Oecologia*, **113**, 447–455.
- McLachlan, S.M., Murphy, S.D., Tollenaar, M., Weise, S.F. & Swanton, C.J. (1995) Light limitation of reproduction and variation in the allometric relationship between reproductive and vegetative biomass in *Amaranthus retroflexus* (Redroot Pigweed). *Journal of Applied Ecology*, **32**, 157–165.
- Méndez, M. & Karlsson, P.S. (2004) Between-population variation in size-dependent reproduction and reproductive allocation in *Pinguicula vulgaris* (Lentibulariaceae) and its environmental correlates. *Oikos*, **104**, 59–70.
- Méndez, M. & Obeso, J.R. (1993) Size-dependent reproductive and vegetative allocation in *Arum italicum* (Araceae). *Canadian Journal of Botany*, **71**, 309–315.
- Müller, I., Schmid, B. & Weiner, J. (2000) The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 115–127.
- Nagai, Y. & Kawano, S. (1986) Regulatory mechanisms of reproductive effort in plants: II. Plasticity in reproductive energy allocation and propagule output of *Glycine max* Merr. (Leguminosae) cultivated at varying densities and nitrogen levels. *Plant Species Biology*, **1**, 181–194.
- Nakashizuka, T., Takahashi, Y. & Kawaguchi, H. (1997) Production-dependent reproductive allocation of a tall tree species *Quercus serrata*. *Journal of Plant Research*, **110**, 7–13.
- Niklas, K.J. (1994) *Allometry of Plants: The Scaling of Form and Process*. University of Chicago Press, Chicago, IL, USA.
- Niklas, K.J. & Enquist, B.J. (2003) An allometric model for seed plant reproduction. *Evolutionary Ecology Research*, **5**, 79–88.
- Ohlson, M. (1988) Size-dependent reproductive effort in three populations of *Saxifraga hirculus* in Sweden. *Journal of Ecology*, **76**, 1007–1016.
- Pan, X.-Y., Wang, G.-X., Chen, J.K. & Wei, X.-P. (2003a) Elevated growth redundancy and size inequality in spring wheat populations mulched with clear plastic film. *Journal of Agricultural Science*, **140**, 193–204.
- Pan, X.-Y., Wang, G.-X., Yang, H.-M. & Wei, X.-P. (2003b) Effect of water deficits on within-plot variability in growth and grain yield of spring wheat in northwest China. *Field Crops Research*, **80**, 195–205.
- Pickering, C.M. (1994) Size-dependent reproduction in Australian alpine *Rumex crispus*. *Australian Journal of Ecology*, **19**, 336–344.
- Pino, J., Sans, F.X. & Masalles, R.M. (2002) Size-dependent reproductive pattern and short-term reproductive cost in *Rumex obtusifolius* L. *Acta Oecologica*, **23**, 321–328.
- Ploschuk, E.L., Slafer, G.A. & Ravetta, D.A. (2005) Reproductive allocation of biomass and nitrogen in annual and perennial *Lesquerella* crops. *Annals of Botany*, **96**, 127–135.

- Prairie, Y.T. & Bird, D.F. (1989) Some misconceptions about the spurious correlation problem in the ecological literature. *Oecologia*, **81**, 285–288.
- Puricelli, E., Faccini, D., Orioli, G. & Sabbatini, M.R. (2004) *Anoda cristata* control with glyphosate in narrow- and wide-row soyabean. *Weed Research*, **44**, 150–156.
- Reekie, E.G. (1998) An explanation for size-dependent reproductive allocation in *Plantago major*. *Canadian Journal of Botany*, **76**, 42–50.
- Reekie, E.G. & Bazzaz, F.A. (1987) Reproductive effort in plants. 2. Does carbon reflect allocation of other resources? *The American Naturalist*, **129**, 897–906.
- Reekie, E.G. & Bazzaz, F.A., eds. (2005) *Reproductive Allocation in Plants*. Elsevier, Amsterdam, the Netherlands.
- Rees, M. & Crawley, M.J. (1989) Growth, reproduction and population dynamics. *Functional Ecology*, **3**, 645–653.
- Sadras, V.O., Bange, M.P. & Milroy, S.P. (1997) Reproductive allocation of cotton in response to plant and environmental factors. *Annals of Botany*, **80**, 75–81.
- Samson, D.A. & Werk, K.S. (1986) Size-dependent effects in the analysis of reproductive effort in plants. *The American Naturalist*, **127**, 667–680.
- Sans, F.X. & Masalles, R.M. (1994) Life-history variation in the annual arable weed *Diploaxis erucoides* (Cruciferae). *Canadian Journal of Botany*, **72**, 10–19.
- Schmid, B., Bazzaz, F.A. & Weiner, J. (1995) Size dependence of sexual reproduction and of clonal growth in two perennial plants. *Canadian Journal of Botany*, **73**, 1831–1837.
- Schmid, B. & Weiner, J. (1993) Plastic relationships between reproductive and vegetative mass in *Solidago altissima*. *Evolution*, **47**, 61–74.
- Schmid, B., Polasek, W., Weiner, J., Krause, A. & Stoll, P. (1994) Modelling of discontinuous relationships in biology with censored regression. *The American Naturalist*, **143**, 494–507.
- Schmitt, J. (1983) Individual flowering phenology, plant size, and reproductive success in *Linanthus androsaceus*, a California annual. *Oecologia*, **59**, 135–140.
- Seim, E. & Sæther, B.-E. (1983) On rethinking allometry: which regression model to use? *Journal of Theoretical Biology*, **104**, 161–168.
- Shiple, B. & Dion, J. (1992) The allometry of seed production in herbaceous angiosperms. *The American Naturalist*, **139**, 467–483.
- Soule, J.D. & Werner, P.A. (1981) Patterns of resource allocation in plants, with special reference to *Potentilla recta* L. *Bulletin of the Torrey Botanical Club*, **108**, 311–319.
- Sugiyama, S. & Bazzaz, F.A. (1998) Size dependence of reproductive allocation: the influence of resource availability, competition and genetic identity. *Functional Ecology*, **12**, 280–288.
- Thomas, S.C. (1996) Reproductive allometry in Malaysian rain forest trees: biomechanics vs. optimal allocation. *Evolutionary Ecology*, **10**, 517–530.
- Thompson, B.K., Weiner, J. & Warwick, S.I. (1991) Size-dependent reproductive output in agricultural weeds. *Canadian Journal of Botany*, **69**, 442–446.
- Vega, C.R.C., Sadras, V.O., Andrade, F.H. & Uhart, S.A. (2000) Reproductive allometry in soybean, maize and sunflower. *Annals of Botany*, **85**, 461–468.
- Venable, D.L. & Rees, M. (2009) The scaling of seed size. *Journal of Ecology*, **97**, 27–31.
- Wang, T., Zhou, D., Wang, P. & Zhang, H. (2006) Size-dependent reproductive effort in *Amaranthus retroflexus*: the influence of planting density and sowing date. *Canadian Journal of Botany*, **84**, 485–492.
- Weiner, J. (1988) The influence of competition on plant reproduction. *Plant Reproductive Ecology: Patterns and Strategies* (eds J. Lovett Doust & L. Lovett Doust), pp. 228–245. Oxford University Press, New York.
- Weiner, J. (2004) Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 207–215.
- Weiner, J. & Thomas, S.C. (1992) Competition and allometry in three species of annual plants. *Ecology*, **73**, 648–656.
- Weiner, J. & Thomas, S.C. (2001) The nature of tree growth and the “age-related decline in forest productivity”. *Oikos*, **94**, 374–376.
- Weiner, J., Rosenmeier, L., Massoni, E.S., Vera, J.N., Hernández Plaza, E. & Sebastia, M.T. (2009) Is reproductive allocation in *Senecio vulgaris* plastic? *Botany*, **87**, 475–481.
- Welham, C.V.J. & Setter, R.A. (1998) Comparison of size-dependent reproductive effort in two dandelion (*Taraxacum officinale*) populations. *Canadian Journal of Botany*, **76**, 166–173.
- Weller, D.E. (1989) The interspecific size-density relationship among crowded plant stands and its implications for the -3/2 power rule of self-thinning. *The American Naturalist*, **133**, 20–41.
- West, G.B., Brown, J.H. & Enquist, B.J. (1999) A general model for the structure and allometry of plant vascular systems. *Nature*, **400**, 664–667.
- Wolfe, L.M. (1983) The effect of plant size on reproductive characteristics in *Erythronium americanum* (Liliaceae). *Canadian Journal of Botany*, **61**, 3489–3493.
- Zens, M.S. & Webb, C.O. (2002) Sizing up the shape of life. *Science*, **295**, 1475–1476.
- Zhang, H., Zhou, D., Huang, Y., Japhet, W. & Sun, D. (2008) Plasticity and allometry of meristem allocation in response to density in three annual plants with different architecture. *Botany*, **86**, 1291–1298.

Received 2 December 2008; accepted 23 July 2009
 Handling Editor: David Gibson