Is reproductive allocation in *Senecio vulgaris* plastic?

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Abstract: Several purported cases of plasticity in plant allocation patterns appear to be the effects of size and allometric growth (''apparent plasticity''). To ask whether there is true plasticity (i.e., a change in the allometric trajectory) in reproductive allocation in *Senecio vulgaris* L., we grew *S. vulgaris* plants at high and low levels of water, nutrients, and competition, and analyzed the relationship between vegetative and seed biomass. Plant size was the major determinant of reproductive output, accounting for 83% of the variation in log (seed mass). There were also significant effects of the treatments that were not due to size, accounting for an additional 9% of the variation. The treatments affected the allometric coefficient (intercept), not the allometric exponent (slope) of the relationship, reflecting a small but significant shift in the efficiency of conversion of total plant biomass into reproductive biomass. In a second experiment, we grew *S. vulgaris* plants at three nutrient levels and allowed all individuals to complete their life cycles. Again, nutrient level had a small but significant effect on the allometric coefficient. Plasticity in reproductive allocation exists, but is very limited. The primary effects of the environment on the reproductive output of *S. vulgaris* occur via plant size.

Key words: allometry, common groundsel, plasticity, size effects.

Résumé : Plusieurs cas mis de l'avant de plasticité dans les patrons d'allocation semblent résulter de la dimension et de la croissance allométrique (« plasicité apparente »). Afin de vérifier s'il existe s'il existe une vraie plasticité (i.e. un changement de la trajectoire allométrique) dans l'allocation reproductive chez le *Seneciao vulgaris* L. les auteurs ont cultivé cette plante à des degrés élevés et faibles en eau, nutriments et compétition et ils ont analysé la relation entre la biomasse végétative et séminale. La dimension des plants constitue le déterminant majeur du produit de la reproduction, expliquant 83 % de la variation en log (masse séminale). On observe également des effets significatifs des traitements qui ne dépendent pas de la dimension expliquant un 9 % additionnel de la variation. Les traitements affectent le coefficient allométrique (interception), et non l'exposant allométrique (pente) de la relation, ce qui reflète un déplacement faible, mais significatif de l'efficacité de la conversion de la biomasse totale de la plante en biomasse reproductive. Dans une deuxième expérience, les auteurs ont cultivé des plants de *S. vulgaris* en présence de trois teneurs en nutriments et ont permis à tous les individus de compléter leurs cycles vitaux. Encore une fois la teneur en nutriments exerce un effet faible, mais significatif sur le coefficient allométrique. Il existe une plasticité dans l'allocation reproductive, mais elle est très limitée. Les effets primaires de l'environnement sur la productivité reproductive du *S. vulgaris* s'effectuent via la dimension de la plante.

Mots-clés : allométrie, senecio vulgaire, plasticité, effets des dimensions.

Introduction

Growth and reproduction are two of the most fundamental processes for plants. Reproduction is the currency of natural selection, but plants must grow to build the machinery to reproduce. After a plant produces biomass, it allocates this biomass to different functions and structures, including reproductive structures (Bazzaz and Reekie 1985). Because resources allocated to one function or organ are not available to other functions or organs, allocation implies trade-offs. Allocation patterns reflect evolved strategies that are the results of different selection pressures and constraints (Bonser and Aarssen 2001).

There is an emerging consensus among plant ecologists that allocation patterns, which we originally conceptualized and analyzed as ratios (e.g., root:shoot ratio) or percent allocation (e.g., ''reproductive effort'', defined as the percent of total biomass in reproductive structures; Tuomi et al. 1983) are better understood and analyzed allometrically (Jasienski and Bazzaz 1999; Weiner 2004). Plant allocation is usually allometric in the broad sense: it changes with size as plants grow. Therefore any factor that affects growth rate and therefore size will inevitably affect allocation, even if plant allocation at a given size is totally fixed (Coleman et al. 1994). Effects on allocation solely due to size and allometric growth have been referred to as ''apparent plasticity'' (Fig. 1*a*; McConnaughay and Coleman 1999; Weiner 2004),

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Fig. 1. Hypothetical example of (*a*) apparent vs. (*b*) true plasticity in reproductive allocation in response to nutrient level. In apparent plasticity (H_0), changes in allocation are due to the rate of growth along a fixed allometric trajectory. In true plasticity (broken lines), the slope (H_1) or the intercept (H_2) of the trajectory is altered by nutrient level.
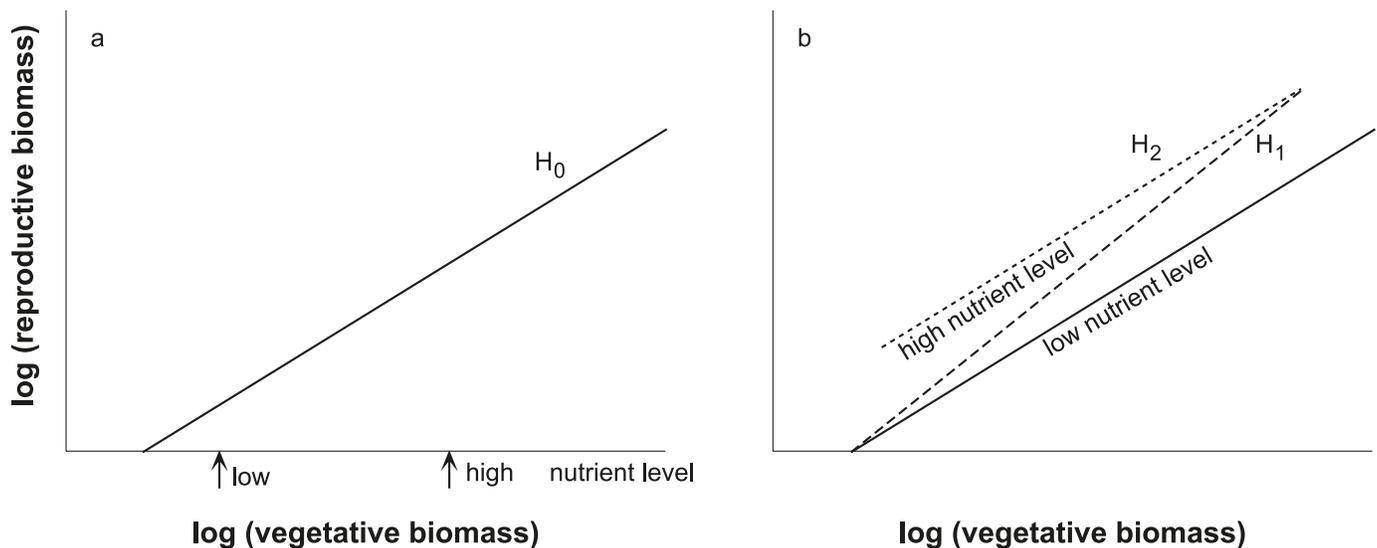
since true plasticity implies a change in an allometric growth trajectory (Fig. 1*b*), not only the speed at which a single trajectory is followed. Several patterns that were previously considered evidence for plasticity in allocation have been shown to be due to apparent plasticity (Coleman and McConnaughay 1995; Wright and McConnaughay 2002), whereas other plant traits show extensive true plasticity. Understanding which plant behaviors are plastic and which are fixed would be a major advance for plant ecology and evolution (Pigliucci and Preston 2004; Weiner 2004).

Here we address the simple and fundamental question: is reproductive allocation plastic, i.e., does the allometric relationship between reproductive and vegetative biomass change in different environments, or can the effects of the environment on allocation be understood in terms of size and a fixed allometric growth pattern? We grew the common cosmopolitan weed *Senecio vulgaris* L. under different levels of nutrients, water, and competition, and asked whether the relationship between seed mass and aboveground vegetative mass is affected by these treatments.

Materials and methods

Senecio vulgaris (Asteraceae) is a cosmopolitan annual herbaceous weed that grows up to 40 cm tall, has a thick taproot, and possesses an ephemeral strategy typical of many weedy species. A rosette phase of vegetative growth is followed by a more or less continuous period of seed production until the plant dies. There is, however, considerable variation in the pattern and timing of development. *Senecio vulgaris* was the subject of some of the earliest research on biomass allocation (Harper and Ogden 1970). This species shows very high rates of self-fertilization, and the degree of outcrossing is highly variable (Hull 1974).

We grew *S. vulgaris* plants in pots in the greenhouse of the Faculty of Life Sciences, University of Copenhagen, Frederiksberg, Denmark. Field-collected seed was purchased from Herbiseed (New Farm, Mire Lane, Twyford, Berkshire, UK).

Experiment 1

Plants were grown in 7.5 L pots filled with a mixture (*v*/*v*) of 15% vermiculite, 10% perlite, and 75% Pindstrup "Færdigblandining No. 1" (sphagnum with nutrients and lime, pH 6.8; Pindstrup Mosebrug A/S, DK-8550 Ryomgaard, Denmark). Several seeds were sown in each pot on 23 February 2006, and after germination they were randomly thinned to one or two individuals per pot, depending on the treatment. There were three factors in a full factorial design: (*i*) with and without competition; (*ii*) high vs. low nutrient (fertilizer); and (*iii*) high vs. low water level, giving eight treatment combinations. There were 12 replicate pots for all treatments without competition, and 4 replicate pots for all treatments with competition (see description of the competition treatment below). Thus, there were a total of 80 *S. vulgaris* individuals in 64 containers. Pots were arranged in 12 blocks. Each block included all treatments without competition, but only one or two of the four treatments with competition. Supplementary lighting was used to keep the day length at 18 h.

In the high water level treatment we kept the soil in the pots moist with osmotically demineralized water. In the low water treatment, pots were allowed to dry out. When the soil felt completely dry and leaves began to wilt, we added a small amount of water. One hundred millilitres was added at the beginning of the experiment, but as plants grew and transpiration demands increased, we increased the amount of water added. But water was only added after some wilting occurred.

For the high nutrient treatment we added 5 mL of liquid fertilizer [Hornum Pioner Næring, 5-1-4 + micronutrients (Brøste A/S, DK-2800 Lyngby, Denmark) in 500 mL water] once a week. In the low nutrient treatment, no fertilizer was added to the water throughout the course of the experiment. To avoid confounding of nutrient and water treatments, we added 500 mL of water to the low water – low nutrient treatment whenever we added fertilizer to the low water – high nutrient treatment.

In the competition treatment, two *Centaurea cyanus* L. plants grew in the pots together with two *S. vulgaris* plants. This was part of a larger design to look at both species, but few *C. cyanus* individuals flowered and very few seeds were produced, so results are presented only for *S. vulgaris*.

We collected all fruits produced by *S. vulgaris* plants as they matured. We also collected dead plant parts as they dried. All plants were harvested at the soil level on 17 May 2006, dried at 70 °C, and weighed. Fruits were dried at 25 °C for one day and weighed.

Experiment 2

Because plants were still growing and flowering when harvested, we performed a second experiment in which *S. vulgaris* plants were grown individually in small pots with only one factor (nutrient level); this allowed for the completion of the life cycle. Individual *S. vulgaris* plants were grown in 0.5 L pots at three different nutrient levels. The high nutrient level consisted of 100% Pindstrup "Færdigblandining No. 2" (Pindstrup Mosebrug A/S, DK-8550 Ryomgaard, Denmark), a commercial greenhouse sphagnum medium similar to that used in the first experiment but with higher nutrient levels. The middle nutrient level was 25% perlite, 25% vermiculite, and 50% of the commercial medium (v/v), and the low nutrient mixture 40% perlite, 40% vermiculite, and 20% of the commercial medium (v/v). There were 15 replicates of each, giving at total of 45 pots. Pots were organized on the greenhouse bench in groups of three, one of each treatment. Several *S. vulgaris* fruits were sown in each pot on 7 February 2007. Seedlings were thinned to three individuals one week later, and then one individual 2 weeks later. Plants were watered regularly and the soil kept moist. No additional nutrients were added throughout the course of the experiment, with one exception: owing to an error, the pots were watered once on 31 March with a very low concentration of the fertilizer solution used for regular watering in the greenhouse. All pots were heavily watered with deionized water immediately afterwards to minimize any effects. Mature fruits and dead parts were collected throughout the course of the experiments. All plants were dead by 5 June and the remaining plants were harvested on that day. Plant material and seeds were dried as in the first experiment. We attempted to harvest roots by separating them from the rooting medium, but we were not satisfied with our ability to do so.

Data and statistical analyses

We avoid the issue of defining structures with multiple functions as vegetative or reproductive (Bazzaz and Reekie 1985) by taking a very strict view of reproductive allocation: We consider total biomass of achenes produced by an individual as reproductive output (R) and all other biomass as vegetative (V). The values for both of these were log transformed. Total plant mass was also log transformed to homogenize variances for the analysis of total plant biomass in experiment 2.

The effect of treatments on total plant biomass was analyzed using ANOVA. Regression analysis was used to assess the relationship between $\log R$ and $\log V$ in both experiments and to ask (*i*) whether the treatments had significant effect on the $\log R - \log V$ relationship, and (*ii*) if so, how much additional variation in $\log R$ can their inclusion account for. In addition to analyzing each experiment independently, we also analyzed data pooled from both experiments to the degree possible given the different designs. In the combined analysis, the eight treatment combinations in experiment 1 and the three levels of nutrient in experiment 2 were nested within "experiment."

There is no general agreement among researchers concerning the best regression methods to analyze allometric relationships (Riska 1991). While reduced major axis and other orthogonal methods have the advantage of assuming error in both variables, they also present a series of disadvantages, especially in an experimental context with treatments and potential interactions. Like most researchers, we have used standard least-squares general linear models, in which $\log R$ is the dependent variable, $\log V$ is an independent variable, and treatments are nominal independent variables (factors). When analyzing only $\log R$ vs. $\log V$, without treatment effects, we also used reduced major axis regression. The differences between this and standard regression were very small. All analyses were performed with JMP statistical software (SAS Institute Inc. Cary, N.C.).

Results

Experiment 1

All three factors (nutrient level, water level, and competition) and all their interactions had significant effects on the biomass of *S. vulgaris* individuals in experiment 1 (Table 1). Low water level, low nutrient level, and competition all reduced plant size (Fig. 2).

Two extreme outliers were removed from the regression analyses of R vs. V, leaving 78 plants. Most of the variation in $\log R$ could be accounted for by variation in $\log V$ (Fig. 3). Simple least squares regression fit of $\log R$ on $\log V$ without inclusion of any factors was $\log R = -0.37 + 0.906 \log V$, $r^2 = 0.827$. The least squares slope was marginally significantly different from 1 ($P < 0.05$), but an orthogonal regression assuming variance in both $\log R$ and $\log V$ gave a slope of 0.995. When all three factors (nutrient level, water level, and competition), as well as $\log V$ were included in the analysis, they were all significant, but there were no significant interactions among them. Water limitation and competition had highly significant negative effects on $\log R$ (water: SS = 0.343; df = 1; F = 38.9; $P < 0.001$. Competition: SS = 0.358; df = 1; F = 40.6; $P < 0.001$), whereas low nutrient level had a marginally significant positive effect (SS = 0.044; df = 1; F = 4.90; $P = 0.03$). The complete model including $\log V$ and all three factors had an adjusted $r^2 = 0.915$. Thus, the inclusion of the three treatment factors in addition to $\log V$ increased r^2 by 0.088.
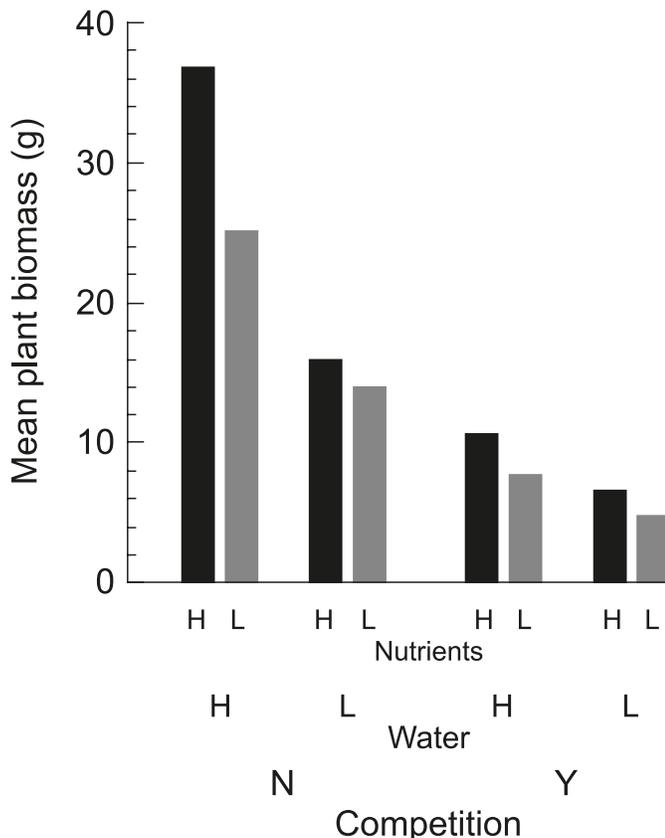
Experiment 2

Fertility level had a highly significant effect on log total plant biomass in a one-way ANOVA (SS = 4.09; df = 2; F = 288.7; $P < 0.0001$). While the difference between log biomass (in mg) at low and medium fertility levels (2.58 and 2.69, respectively) was quite small, plants grown at the highest fertility level were much larger (log biomass = 3.27). In least square means post-hoc tests on log total plant

Table 1. ANOVA of total plant mass of *Senecio vulgaris* individuals on the three factors in experiment 1.

Source	df	SS	*F*	*P*
Water	1	1781.4	154.3	<0.0001
Nutrients	1	395.8	34.3	<0.0001
Competition	1	4523.9	391.7	<0.0001
Water×nutrients	1	135.9	11.8	0.0010
Water×competition	1	746.5	64.6	<0.0001
Nutrients×competition	1	93.6	8.1	0.0058
Water×nutrients×competition	1	83.2	7.2	0.0091

Fig. 2. Mean total biomass of *Senecio vulgaris* individuals for the different treatments in experiment 1.

Fig. 3. Relationship between mass of seeds produced by *Senecio vulgaris* individuals and their vegetative biomass. Filled symbols, no competition; open symbols, competition; squares, water limitation; circles, no water limitation; black, low nutrients; gray, high nutrients. Single least-squares regression line (shown): $\log R = -0.37 + 0.906 \log V$, $r^2 = 0.83$.

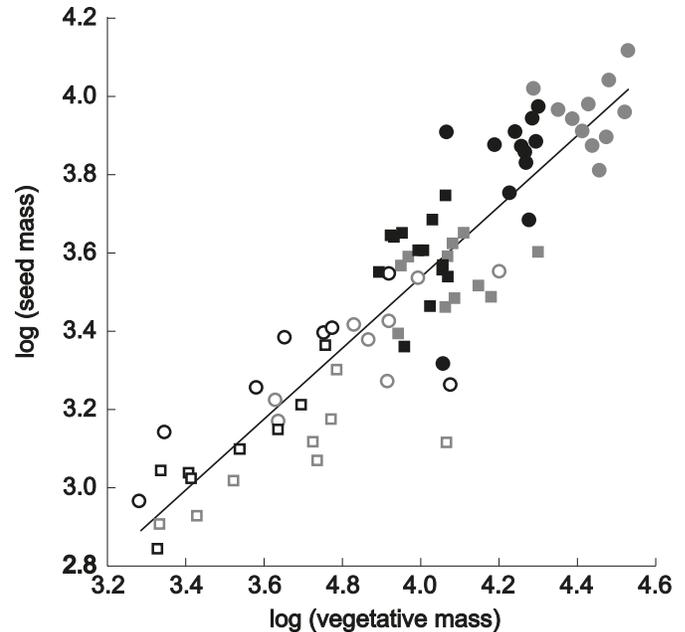biomass, all fertility levels were highly significantly different from each other ($P < 0.0001$).

Simple regression of $\log R$ on $\log V$ had an $r^2 = 0.915$. In an analysis with $\log V$ and nutrient level as independent variables, both were significant ($\log V$, SS = 0.443; df = 1; $P < 0.0001$. Nutrient level: SS = 0.061; df = 2; $P = 0.01$), with $r^2 = 0.956$ (Fig. 4).

Many plants had stopped reproducing and died by the beginning of May, 3 months after sowing, but some individuals produced new branches with flowers, resulting in a second wave of reproduction (Fig. 5).

Both experiments combined

In an analysis of the data from both experiments together, least squares regression of $\log R$ on $\log V$ was $\log R = -0.57 + 1.026 \log V$; $r^2 = 0.971$ (Fig. 6). In a more complete analysis

with $\log V$, experiment and treatment (factors) nested in experiment, all three variables were highly significant ($\log V$: SS = 0.801; df = 1; $P < 0.0001$. Experiment: SS = 0.430; df = 1; $P < 0.0001$. Treatment: SS = 0.808; df = 9; $P < 0.0001$), and $r^2 = 0.981$. There was no significant interaction between $\log V$ and experiment on $\log R$.

Discussion

Within and across both experiments, most of the variation in $\log R$ could be accounted for by variation in $\log V$. In addition, there were small but significant effects of the treatments on $\log R$ in both experiments, but no evidence of interactions among the treatments, or between the treatments and $\log V$. In other words, the treatments shifted the location (i.e., intercept, also called the allometric coefficient) of the allometric relationship between R and V slightly, but not the slope or the form of the relationship. The absence of significant interactions between $\log V$ and the treatments is consistent with the null hypothesis that the treatments do not affect the allometric slope of the R–V relationship. Inclusion of factors in addition to $\log V$ in the analyses improved the explanatory power of the statistical models by 1% to 9%. This means that there were small but significant additive effects of the treatments on reproductive output in addition to those mediated by size, but size-mediated effects of resources on reproductive output are much larger than non-size-mediated effects.

The slope of 1.0 for regression of $\log R$ on $\log V$ in the combined data set suggests that *S. vulgaris* has a very sim-

Fig. 4. Relationship between the mass of seeds produced by *Senecio vulgaris* individuals and their vegetative biomass in the experiment 2. Circles, low nutrient level; triangles, middle nutrient level; squares, high nutrient level. There was no difference between the low and medium nutrient levels in the least squares regression, but the estimate of the intercept was significantly different at the highest fertility level (lines shown).
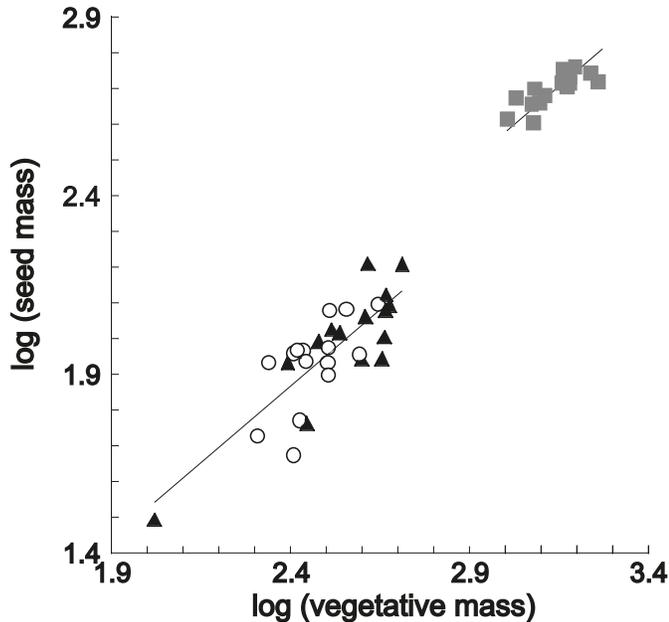
ple reproductive allocation strategy with relatively constant "reproductive effort", defined as $R/(V+R)$ (Tuomi et al. 1983; Bazzaz and Reekie 1985), over a large range of mature sizes. There was no evidence of a minimum size for reproduction. This is consistent with the opportunistic, weedy "r-selected" strategy of *S. vulgaris*, which emphasizes early reproduction. There were small but significant changes in this overall reproductive effort owing to resource levels. For example, almost all the points in the high fertility treatment in experiment 2 lie above the overall line from both experiments (Fig. 6, solid circles).

The observed changes in the $\log R - \log V$ relationship can perhaps be better interpreted in terms of constraints than adaptations (Weiner 1988). For example, water stress and competition in experiment 1 and lower nutrient levels in experiment 2 not only reduced plant size, but also slightly reduced reproductive output at a given size compared with individuals growing in more favorable environments. Similarly, competition resulted in smaller plants, and these plants produced slightly less reproductive biomass at a given size than did plants growing with less competition, as observed in a study on *Plantago major* growing at three densities (Weiner 2004). Plants grow as much as their environment permits, and they allocate resources to reproduction according to a relatively fixed allometric trajectory. In *S. vulgaris*, resource levels can alter the overall efficiency of this conversion (i.e., the allometric coefficient) slightly, but they do not seem to affect the form or slope of the relationship. Size and the allometric relationship between vegetative mass and reproductive output determine a plant's potential reproductive output. The rate of development determines whether or not this potential is

achieved, and variation in the rate or stage of development has been misinterpreted as variation in allometry (Clauss and Aarssen 1994; J. Weiner, L.G. Campbell, J. Pino, and L. Echarte, unpublished data).

The observed effects of resource levels on the intercept of the $R–V$ relationship would result if the concentration of different resources is more constrained in reproductive tissues than in vegetative tissues. For example, if a resource (e.g., nitrogen) is limiting plant growth, that resource may be in lower concentration in the plant's tissues than if it were more available. If the concentration of this resource in the seeds is physiologically constrained and therefore cannot be lowered to the same extent in the seeds produced as in vegetative parts, then the conversion of vegetative biomass into seeds will be at a lower overall rate when the resource is limiting than if the resource were more abundant. This would be reflected as change in the allometric coefficient, as observed here not the exponent. Our results for reproductive allocation are similar to those on root vs. shoot allocation in a study with 27 herbaceous species (Müller et al. 2000), in which nutrient level generally had no effect on root–shoot allometry or altered the allometric coefficient.

The one result that does not seem to fit this explanation is the slight and marginally significant increase in reproductive allocation (i.e., the allometric coefficient) at low fertility in experiment 1 (solid vs. gray symbols in Fig. 3). We attribute this to a "postponement effect" with increased nutrient levels. The higher fertility level resulted in more growth and more potential reproductive output, but it also postponed reproduction, and the experiment was concluded before this potential could be realized. This interpretation is supported by the results of the second experiment, in which all plants were allowed to complete their life cycles. Here there was a positive effect of increased nutrient levels on the $R–V$ allometric coefficient. The allometric approach focuses on size rather than time, but most studies collect data at given points in time (Coleman et al. 1994) so the available data are often far from ideal for allometric analyses. Effects of treatments on the timing of reproduction have been a major problem in analyzing and interpreting allometric data in studies that do not include the whole life cycle, and that is almost all studies.

Our analyses suggest that the factors determining a plant's size are much more complex than those determining its potential reproductive output, given the size achieved. Plant size in the first experiment was affected by all factors and all interactions among the factors were significant (Table 1). We do not yet understand how different resources and factors interact to determine plant growth. The allometric relationship between R and V, however, was only slightly affected by the factors and there were no significant interactions. Thus, the primary effects of the environment on a plant's reproductive output occur via plant size. Other effects are relatively small, although they could still be important under some circumstances.

Allocation to reproduction may be one of the least plastic of allocation patterns. Patterns of root vs. shoot allocation are functional, and plants can grow more by changing this allocation pattern (Gedroc et al. 1996). Reproduction in an annual plant involves the conversion of the maximum

Fig. 5. Temporal distribution of mature fruiting heads over time in experiment 2. Black bars, high fertility; dark gray, medium fertility; light gray, low fertility.
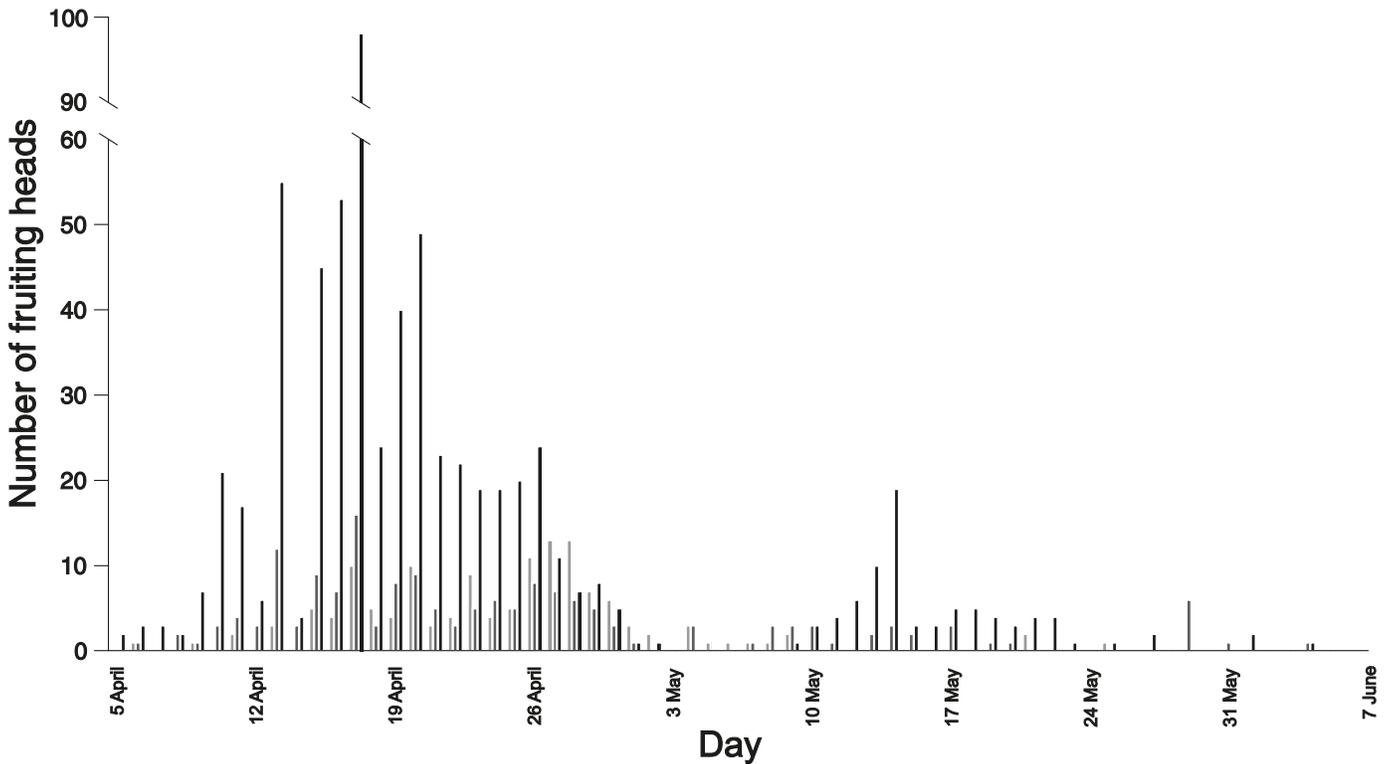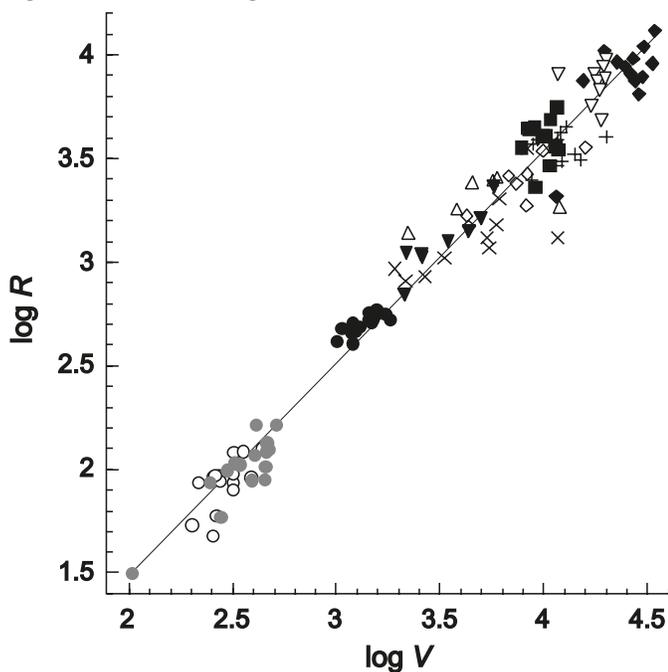

Fig. 6. Relationship between mass of seeds produced by *Senecio vulgaris* individuals and their vegetative biomass for both experiments combined. Circles indicate data from experiment 2, all other data are from experiment 1. Single regression line (shown): $\log R = -0.57 + 1.026 \log V$; $r^2 = 0.971$.

fully unfold, represents the limiting condition of how much the plant can reproduce, given its resources.

Although seed quality can be as important as seed number for plant reproduction, it is not clear how seed quality can be quantified and thus included in quantitative models of reproductive allocation. Most studies of plant fitness use seed production as the estimate of fitness, as we do here.

Most taxonomic sources describe *S. vulgaris* as monocarpic because it is an annual. This is a misconception. For the length of its life cycle, *S. vulgaris* starts reproducing quite early. In the second experiment most plants germinated around 12 February and most were dead by 24 May, giving an average life span of around 102 d. Most plants were flowering by 9 April, 56 d after emergence, and continued to do so until they died. Thus, plants were reproducing for around 45% of their lifespan, which can hardly be considered a monocarpic strategy. The opportunistic, annual, weedy strategy of *S. vulgaris* (Ollerton and Lack 1992; Leiss and Muller-Scharer 2001), growing as long and as much as the environment permits, means that seeds produced when an individual is young/small can germinate in the same growing season, thus fitting the demographic definition of iteroparous. Annuals should be considered monocarpic if they reproduce only towards the end of their lives.

The allometric approach focuses on size rather than time, but a more complete understanding of plant behavior must encompass size, time, and development. There was one major wave of reproduction in which all plants participated in experiment 2 (Fig. 5). Those individuals that continued to produce flowers and fruits after this period did not do so by extending this wave, but rather by producing a subsequent

amount of accumulated resources, which is reflected in its vegetative biomass, into reproduction. Given a plant's size and reproductive system, the *R–V* relationship, if allowed to

smaller wave of new shoots with flowers. There are several possible explanations for this pattern, which is often observed when plants are resource limited. One possibility is that the number of flowers (or in the case of *S. vulgaris*, inflorescences) to be produced by a shoot is determined before flowering starts, and the plant cannot adjust this upwards later (e.g., Inouye 1986). Individuals that have resources remaining after the first wave of reproduction is complete must make new shoots and flowers if they are to reproduce more. Alternatively, this behavior may be part of a bethedging strategy by relatively robust individuals to invest in a later reproductive episode rather than simply extending the current one. Such behavior can be seen as a step in the direction of perenniation, in which a generally senescent individual produces new "youthful" shoots. The size a plant achieves determines in large part its potential reproductive output, but the allometric relationship between reproductive output and size does not tell us the course of this reproduction over time.

Acknowledgements

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