The costs and benefits of fast living

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Abstract

Growth rates play a fundamental role in many areas of biology (Q. Rev. Biol., 67, 1992, 283; Life History Invariants. Some Explorations of Symmetry in Evolutionary Biology, 1993; Philos. Trans. R. Soc. Lond. B Biol. Sci., 351, 1996, 1341; Plant Strategies, Vegetation Processes, and Ecosystem Properties, 2002; Trends Ecol. Evol., 18, 2003, 471; Q. Rev. Biol., 78, 2003, 23; J. Ecol., 95, 2007, 926.) but the cost and benefits of different growth rates are notoriously difficult to quantify (Q. Rev. Biol., 72, 1997, 149; Funct. Ecol., 17, 2003, 328). This is because (1) growth rate typically declines with size and yet the most widely used growth measure - relative growth rate or RGR (conventionally measured as the log of the ratio of successive sizes divided by the time interval) - is not size-corrected and so confounds growth and size, (2) organisms have access to different amounts of resource and (3) it is essential to allow for the long-term benefits of larger size. Here we experimentally demonstrate delayed costs and benefits of rapid growth in seven plant species using a novel method to calculate size-corrected RGR. In control treatments, fast-growing plants benefited from increased reproduction the following year; however, fast-growing plants subjected to an experimental stress treatment (defoliation) showed strongly reduced survival and reproduction the following year. Importantly, when growth was estimated using the classical RGR measure, no costs or benefits were found. These results support the idea that life-history trade-offs have a dominant role in life-history and ecological theory and that the widespread failure to detect them is partly due to methodological shortcomings.
The Costs and Benefits of Fast Living

By

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Letter
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Abstract

Growth rates play a fundamental role in many areas of biology (Herms & Mattson 1992; Charnov 1993; Franco & Silvertown 1996; Grime 2002; Metcalf et al. 2003; Stamp 2003; Rees & Venable 2007), but the cost and benefits of different growth rates are notoriously difficult to quantify (Arendt 1997, 2003). This is because 1) growth rate typically declines with size and yet the most widely used growth measure – relative growth rate or RGR (conventionally measured as the log of the ratio of successive sizes divided by the time interval) – is not size-corrected and so confounds growth and size, 2) organisms have access to different amounts of resource and 3) it is essential to allow for the long-term benefits of larger size. Here we experimentally demonstrate delayed costs and benefits of rapid growth in seven plant species using a novel method to calculate size-corrected RGR. In control treatments, fast-growing plants benefited from increased reproduction the following year; however, fast-growing plants subjected to an experimental stress treatment (defoliation) showed strongly reduced survival and reproduction the following year. Importantly, when growth was estimated using the classical RGR measure, no costs or benefits were found. These results support the idea that life-history trade-offs have a dominant role in life-history and ecological theory and that the widespread failure to detect them is partly due to methodological shortcomings.

Introduction

Characterising growth rates for an individual or species is notoriously difficult. Growth is environmentally sensitive and changes continuously as an organism ages, confounding any attempt to capture species growth rates in a single parameter. As a result, our understanding of the evolution of growth rates remains rudimentary (Arendt 1997, 2003). This is particularly problematic as growth rate provides a fundamental axis along which both plant and animal species are differentiated (Charnov 1993; Franco & Silvertown 1996; Grime 2002) and influences the evolution of numerous plant traits, e.g. offspring provisioning (Rees & Venable 2007), maturation time (Roff 1992), and herbivore defence (Herms & Mattson 1992; Stamp 2003). Recent work has emphasised that growth rates are typically well below their physiological maxima in many taxa (Arendt 1997; Munch & Conover 2004) although most fitness components increase with size, implying there must be substantial costs
to rapid growth. However, although such costs are widely assumed in theoretical studies (Perrin & Sibly 1993; Iwasa 2000), quantifying the costs and benefits of rapid growth with real organisms has been less easy (Arendt 1997, 2003), leaving some to assume that this theory is flawed (discussed in Reznick et al. (2000)).

There are several reasons why the costs of rapid growth are hard to measure. First, relative growth rate (RGR) typically declines as organisms get larger (Hunt 1982; West et al. 2001) making it difficult to separate the effects of growth rate and size. Second, because larger organisms have higher survival and reproductive rates (Blanckenhorn 2000; Metcalf et al. 2003), it is essential to allow for the long-term benefits of larger size that accrue from rapid growth. Third, individuals have access to different amounts of resources and so can differ in both acquisition and allocation (van Noordwijk & de Jong 1986) allowing organisms to potentially grow fast and survive well so masking the cost of fast growth (Reznick et al. 2000). Finally, because relative growth rate or RGR typically decreases with size, classical growth analysis – based on comparing individuals at two points in time – cannot distinguish between individuals that grow slowly because they are large and individuals that grow slowly because they are pursuing a slow growth strategy (Turnbull et al. 2008). Thus, unless individuals are identically sized, classical growth analysis using RGR does not allow fair comparisons among individuals or species.

Here we describe a novel approach to this problem, in which we fit individual growth curves using non-linear mixed-effects models and calculate a size-corrected growth rate for each individual at a common reference size. We use non-linear mixed-effects models for several reasons. First it allows us to fit a single model to the entire dataset and so estimate parameters efficiently, and second it accounts for the structure of the data (i.e. repeated non-destructive size measurements on individual plants; (Gelman & Hill 2007)). We used this approach to quantify the cost of rapid growth in seven common monocarpic perennial plant species in a randomised block experiment with a defoliation treatment. Monocarpic plants are ideal subjects for evolutionary experiments as reproduction is always fatal, and therefore the cost of reproduction is known. We predict that initially fast-growing individuals achieve larger sizes and so have higher probabilities of survival and reproduction when undisturbed; however, because they invest in growth at the expense of storage (Poorter and Kitajima 2007), they will show the greatest sensitivity to stress and are therefore the least likely to survive and reproduce following a defoliation treatment. We also predict that the costs
will only be evident when growth rates are corrected for individual size. In other words, we predict that classical RGR analysis will fail to identify the costs of rapid growth due to the failure of RGR to correct for differences in individual size.

**Methods**

Seeds of *Arctium minus* L. (burdock), *Carduus nutans* L. (musk thistle), *Cirsium vulgare* Savi (spear thistle) and *Senecio jacobaea* L. (common ragwort), all Compositae, and *Digitalis purpurea* L. (foxglove), *Verbascum blattaria* L. (moth mullein), and *Verbascum thapsus* L. (great mullein), all Scrophulariaceae, were collected from naturally occurring local populations. On the 15 - 21 March 2007, approximately 120 seeds per species (n = 842 plants) were sown individually into 7 cm diameter biodegradable pots filled with a mix of sand, M3 compost and medium vermiculite (in the proportions 9:1:1 by volume). These plants were later transplanted into larger (2.2 L volume) pots filled with the same soil mix and arranged into 8 outdoor blocks, with roughly equal numbers of each species per block. To calculate growth rates, size was recorded for each individual as the length of the longest leaf (mm) throughout the spring and early summer on the following dates (census number): 10/04/2007 (1), 17/04/2007 (2), 24/04/2007 (3), 01/05/2007 (4), 12/06/2007 (5), 19/06/2007 (6). Plants were randomly assigned to control (n = 5 per species per block) or defoliation treatments (n = 9 per species per block). Treatment plants were completely defoliated by removing all leaf material (30/6/07) and ~ 50% of these plants were then completely defoliated a second time (07/08/07). Control plants were left untouched. A small number of plants died in the first few weeks of the experiment, and these were removed from the analysis. The experiment was left uncovered throughout the winter with no additional watering. The survival and reproductive status of all plants was recorded a further seven times over the year following the defoliation treatments so that we could link early growth rates to later survival and reproductive success. At the last measurement date (week 61) reproductive individuals of all species except *Arctium* were present. Table 1 illustrates the timing of censuses and treatments.
Fitting mixed models

We characterised the growth curve of each individual early in the first year so that we could estimate its growth rate at a common size. We then used this growth rate to predict its fate during the winter and in the following year. There were six non-destructive size measurements before the first defoliation treatment was applied, and these were used to fit 3-parameter von Bertalanffy growth curves (von Bertalanffy 1957), of the form

\[ L_i(t) = L_{\infty,i}(1 - \exp[-k_i(t - t_{0,i})]) \]  

where \( L_i(t) \) is log size of the \( i \)th plant at time \( t \), \( L_{\infty,i} \) is the asymptotic size, \( k_i \) a rate parameter, and \( t_{0,i} \) the time at which \( L_i(t) = 0 \) so \( t - t_{0,i} \) is plant age from emergence; these growth models are widely used in studies of life-history evolution (Roff 1992; Stearns 1992; Mangel 1996; Rees et al. 2000). The time required to reach some standard size \( L_c \) is

\[ t(L_c) = t_{0,i} - \frac{1}{k_i} \log \left[ \frac{L_c}{L_{\infty,i}} \right] \]  

In the statistical model \( L_i(t) \) is log size and so \( RGR = dL_i(t) / dt \). Calculating \( dL_i(t) / dt \) and substituting for \( t(L_c) \) gives the size-corrected RGR for the \( i \)th individual

\[ k_i(L_{\infty,i} - L_c) \]  

which declines linearly with log size \( L_c \). Note that because individuals grow at different rates they will achieve the reference size, \( L_c \), at different ages (given by equation 2); this corresponds to the asynchronous approach advocated by Nicieza & Alvarez (2009) for the detection of compensatory growth. For other growth curves (e.g. Gompertz and Logistic) a similar approach can be used to calculate the size-corrected RGR, although equation 3 will differ depending on the growth curve fitted.

The growth curves (Eqn 1) were fitted as non-linear mixed-effects models using the \textit{nlme} package in R with a self-starting nonlinear regression function, \textit{SSasympOff} (Pinheiro & Bates 2000). The self-starting routine finds sensible initial parameter estimates for the model and hence aids convergence and model fitting. The final model retained all three parameters \( (t_{0,i}, L_{\infty,i}, k_i) \) fitted as individual-specific random
effects and assumed a general positive, definite variance-covariance matrix. This means that each individual grows according to equation 1 with its own individual-specific parameters \((t_{0,i}, L_{0,i}, k_i)\) drawn from a multivariate normal distribution. Approximate 95% confidence intervals on the correlations between the random effects suggested that the random effects were not independent. The model with correlated random effects (AIC = 7309) was clearly better than the one with independent random effects (AIC = 7372). We extracted the individual-specific random effects using the `ranef` function in the `nlme` package and used these to predict RGR for each individual using equation 3. This method allows us to compare growth rates among individuals of different sizes: if all individuals follow the same growth curve they will all have the same size-corrected RGR, decoupling the effects of size and growth rate. The individual RGRs were then used as explanatory variables in binomial generalized linear models to predict both an individual’s fate (survived or died) and reproductive decision (flowered or remained vegetative). We explored the effect of growth rate on three demographic transitions: 1) survival over winter, 2) survival from spring to summer conditional on survival over winter – individuals that died over winter were removed, and 3) the probability of flowering conditional on survival to the end of the experiment – individuals that died over winter or during the spring were removed from the analysis.

We calculated classical RGR as the log of the ratio of plant sizes in the current (2, 4 or 6) and previous censuses, divided by the number of days between censuses. For size-corrected RGR we used the mean plant size at censuses 2, 4 and 6 as a reference size \((L_c)\) and estimated RGR at that size using Eqn 3.

**Results**

Survival over winter was unaffected by either classical or size-corrected RGR, or defoliation treatment \((p > 0.1\) for all terms, Fig. 1a). However, in the analysis of survival from spring to summer in the following year there was a significant interaction between size-corrected RGR and defoliation treatment with both main effects also being highly significant (Table 2). With all species’ data combined, this interaction means (Fig. 1b) that in a favourable environment (Control) there is no survival cost to fast growth. However, there is a substantial survival cost to fast growth in the defoliation treatments: survival drops from ~ 95% in the Control to ~
85% with a single defoliation and ~ 60% with two defoliations. Only size-corrected RGR calculated immediately prior to defoliation (census 6) was significant (Table 2), growth rates calculated earlier than this (censuses 2 and 4) did not predict subsequent survival. When using classical RGR we found no effect of growth rate at any census on subsequent survival (Table 2). In the analysis of flowering probability there was again a highly significant size-corrected RGR by treatment interaction (Table 3, Fig. 1c), demonstrating that fast growth increased the probability of flowering in the Control group, but decreased the probability of flowering in the defoliation treatments. These effects were again substantial: the probability of flowering for fast-growing individuals drops from ~60% in the control to ~40% with a single defoliation and ~20% with two defoliations. As in the survival analysis we found no significant effect of classical RGR on the probability of flowering (Table 3). Likewise, only size-corrected RGR estimated immediately prior to defoliation (census 6) significantly explained variance in flowering success (Table 3), growth rates calculated earlier than this (censuses 2 and 4) had no significant effect. Hence, unless otherwise stated, both size-corrected and classical RGR now refer explicitly to growth between census 5 and 6.

For both survival and reproduction, size-corrected RGR is a better predictor than either classical RGR or indeed absolute size. For example we can compare models using growth rates from the 6th census date using the AIC (Akaike’s information criteria). Differences in AIC of 4-7 units indicate clearly distinguishable models, and differences of 10 units indicate that the model with the lower score is substantially better (Burnham and Anderson 2002). In each case the size or growth measure was fitted as an interaction with the defoliation treatment. For survival from spring to summer the AIC values were 341.6 using size-corrected RGR, 357.4 using classical RGR and 356.17 using log size at census 6. For the probability of flowering we obtain similar results yielding AIC values of 708.4 using size-corrected RGR, 723.5 using classical RGR and 717.8 using log size at census 6. These results strongly suggest that the size-corrected RGR models are better.

In the experiment we used plants from seven different species to generate a range of growth rates. It is therefore important to determine whether the results are a consequence of having one species that is very different from the others; in fact we selected the species from only two families and all with the same life history to minimise this problem. For size-corrected RGR at the 6th census species differences
account for 26% of the variation in the data, suggesting that species difference are important but not dominant source of variation in RGR (differences between individuals accounted for the remaining 74%). Mixed effect models with species as a random effect failed to converge because of the huge number of parameters being estimated, so to explore the patterns of variation in growth rate further we superimposed density plots for each species (Figure 2), which clearly shows there is considerable overlap in the individual RGRs of the different species. Also note there are a small number of plants that are getting smaller (RGR<0), however, exclusion of these individuals had no effect on the conclusions of the analysis. In both the spring to summer survival analysis and flowering analysis there were highly significant species effects (P<0.001) after fitting the effects of size-corrected RGR, suggesting that in addition to their growth rates, species differed in other important ways.

Discussion

In this experiment we have demonstrated both the benefits and potential costs of rapid growth in early life. In a benign environment there were no measurable survival costs of fast growth and a considerable benefit in terms of an increase in the probability of flowering. However, when subjected to environmental stress (defoliation) rapidly-growing plants survive less well and have a lower chance of reproduction compared to their slower-growing counterparts. Including appropriate treatments and long-term monitoring are therefore essential to uncovering the costs and benefits of different life-history strategies. Importantly, these effects were only detected when RGR was measured in a size-corrected way; we found no negative effects of rapid growth on fitness using classical RGR analysis.

Our analysis based on size-corrected RGR implicitly assumes that size rather than age is a better predictor of individual fate. This seems reasonable as numerous studies have shown that growth, survival and reproduction are generally size-dependent in plants – particularly in monocarpic perennials – whereas age is a poor predictor of plant fate (Metcalf et al. 2003). This is mainly because growth is highly variable among individuals in natural populations and so individuals of a given age have highly variable sizes. Several physiological studies have also demonstrated a size-dependent threshold for the initiation of flowering (contingent on vernalization, e.g. de Jong et al. 1998) which accounts for the increase in flowering probability
observed for fast-growing plants in the control treatments: fast-growing individuals are more likely to achieve the threshold size and so have a higher probability of flowering compared with slow-growing ones. Despite needing to achieve a critical size in order to initiate flowering, early growth rate is a better predictor of flowering probability than early absolute size. This probably reflects the fact that absolute size early in the growing season also depends on other factors such as germination time and seed size, and hence early growth rate is a better predictor of whether the plant achieves the threshold size later in the year. Interestingly it is only size-corrected RGR immediately before the first defoliation that influences survival and reproduction (Tables 2 and 3), which suggests that characterising species by their RGRs at arbitrary sizes may be problematic because growth rates change continuously as individuals grow.

Life-history trade-offs are often looked for in vain, leading to the conclusion that they are unimportant or that in fact species are essentially the same (Hubbell 2001). Here we show that, even in closely related species with similar biology, life-history trade-offs still offer the best explanation for why a single species cannot do it all. The trade-off described here reveals why: in years or locations where herbivory levels are high and defoliation likely, slow-growing species have an advantage; however, where herbivory levels are low and defoliation is unlikely, the fast-growing species are more likely to both survive and reproduce. By offering different species the advantage in different locations or years, this trade-off provides a potentially powerful stabilising mechanism (Chesson et al. 2004). We believe that the new methods described here support the idea that size-correction will lead to the discovery of similar trade-offs in other groups of species (e.g. Turnbull et al. 2008) and supports the conclusion that such stabilising mechanisms are probably ubiquitous in ecological communities (Chesson 2000).

Acknowledgements
We would like to thank Andrew Beckerman for comments on the manuscript. KER and MR were funded by NERC grant NER/A/S/2000/01326. RLA was funded by a NERC PhD Studentship and LAT by grant 31-65224.01 from the Swiss National Science Foundation. Steve Ellin provided technical support.
Figure 1. The effects of size-corrected RGR on the probability of a) over-winter survival and b) spring to summer survival (2008), and c) flowering (summer 2008), for control plants (light grey), single defoliation plants (dark grey) and double defoliation plants (black). For graphical presentation of binary data we divided the data into 6 equal sizes groups per treatment level and calculated the mean RGR and probability of survival or flowering for each group (note that each point summarizes data for multiple species). Statistical analysis was performed on the binary data. The size-corrected RGR is calculated for an average-sized plant at census 6 (19/06/07) immediately prior to the first defoliation.
Figure 2. Density plot for size-corrected RGR for an average sized individuals at the 6th census. Points at the bottom are the jittered individual data points.
Table 1. Schematic of the schedule of measurement dates (referred to as census 1-13) and how these were distributed through the seasons. Winter was defined as the period between census 11 and 12, and Spring 2008 was the period between census 12 and 13. The defoliation treatments, highlighted by the two bold lines, were applied between census 6-7 (exact dates, 29/06 – 01/07) and 9-10 (exact date, 07/08).

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Table 2. Analysis of deviance results for the probability of plant survival through spring (17/03/08 to 22/05/08) using treatment (defoliated once/ defoliated twice/ not defoliated control), classical RGR and size-corrected RGR; based on a binomial generalized linear model with logit link function. Classical RGR was calculated as the log of the ratio of plant sizes in the current (2, 4 or 6) and previous censuses, divided by the number of days between censuses. For size-corrected RGR we used the mean plant size at censuses 2, 4 and 6 as a reference size ($L_c$) and predicted RGR at that size; Fig.1b shows the results estimated from census 6. (* p<0.05, ** p<0.01, *** p<0.001).

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Table 3. Analysis of deviance results for the probability of flowering (summer 2008) conditional on survival to the end of the experiment, using treatment (defoliated once/defoliated twice/not defoliated control), classical RGR and size-corrected RGR; based on a binomial generalized linear with logit link function. Classical RGR was calculated as the log of the ratio of plant sizes in the current (2, 4 or 6) and previous censuses, divided by the number of day between censuses. For size-corrected RGR we used the mean plant size at censuses 2, 4 and 6 as a reference size ($L_c$) and predicted RGR at that size; Fig. 1c shows the results estimated from census 6. (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

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References


