

How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists

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Summary

1. Plant growth is a fundamental ecological process, integrating across scales from physiology to community dynamics and ecosystem properties. Recent improvements in plant growth modelling have allowed deeper understanding and more accurate predictions for a wide range of ecological issues, including competition among plants, plant–herbivore interactions and ecosystem functioning.

2. One challenge in modelling plant growth is that, for a variety of reasons, relative growth rate (RGR) almost universally decreases with increasing size, although traditional calculations assume that RGR is constant. Nonlinear growth models are flexible enough to account for varying growth rates.

3. We demonstrate a variety of nonlinear models that are appropriate for modelling plant growth and, for each, show how to calculate function-derived growth rates, which allow unbiased comparisons among species at a common time or size. We show how to propagate uncertainty in estimated parameters to express uncertainty in growth rates. Fitting nonlinear models can be challenging, so we present extensive worked examples and practical recommendations, all implemented in R.

4. The use of nonlinear models coupled with function-derived growth rates can facilitate the testing of novel hypotheses in population and community ecology. For example, the use of such techniques has allowed better understanding of the components of RGR, the costs of rapid growth and the linkage between host and parasite growth rates. We hope this contribution will demystify nonlinear modelling and persuade more ecologists to use these techniques.

Key-words: mixed-effects models, nonlinear regression, relative growth rate, R language

Motivation

The purpose of this contribution is to update ecologists regarding recent advances in plant growth modelling, which allow a deeper understanding of ecological processes than was possible with traditional approaches. The methods we develop are general and may be applied to a wide range of organisms. The advance they represent is made evident by the insight they have provided into a wide variety of ecological subjects. Recent applications of these techniques include assessing the relationship between seed size and growth rates (Turnbull *et al.* 2008), documenting trade-offs between growth and survival (Rose *et al.* 2009), quantifying the costs of investment in chemical

defence (Paul-Victor *et al.* 2010; Züst *et al.* 2011), assessing the effects of hemi-parasitic plants on their hosts (Hautier *et al.* 2010) and partitioning the components of relative growth rate (RGR) (Rees *et al.* 2010). These studies illustrate particular aspects of the approach advocated in this contribution, but here, we synthesize them to provide a general framework suitable for many applications.

Three factors make the time ripe for a review of nonlinear growth models. There is a growing consensus that traditional approaches to modelling growth, rooted as they are in linear and exponential models, are inadequate. Statistical software has matured to the point that implementation of nonlinear models is increasingly within the grasp of ecologists. Finally, the relevance of metabolic theory, the only widely accepted theoretical model of plant growth (West, Brown & Enquist 1999), continues to be actively debated (e.g. Muller-Landau

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et al. 2006). Thus, there is a pressing need to fit empirical models, particularly nonlinear ones. We hope through this contribution to encourage more ecologists to take advantage of nonlinear models for growth.

Background

Growth, the ontogenetic change in the biomass of an organism, links scales of biology from physiology and metabolism to community dynamics (McMahon & Bonner 1983). An understanding of growth is therefore essential to understand a host of ecological processes, including competition, plant–herbivore interactions, interactions between plants and their abiotic environment and local community dynamics (Kobe 1999; Tanner *et al.* 2005; Muller-Landau *et al.* 2006). The details of plant growth tend, however, to be ignored in many ecological studies. Most dynamic global vegetation models, for example, leap from resource availability to ecosystem processes, with little consideration of how individual physiology or height-structured competition for light affect the conversion of those resources into biomass (Purves & Pacala 2008).

Traditional analyses of growth are rooted in the statistics of linear regression, which limits the range of models that can be fit (Causton & Venus 1981; Hunt 1982; Charles-Edwards, Doley & Rimmington 1986; Poorter 1989). Linear models assume constant absolute growth rate (AGR, g day^{-1}), and exponential (loglinear) models assume constant RGR ($\text{g g}^{-1} \text{day}^{-1}$). These assumptions limit their utility, as both AGR and RGR vary with environmental conditions and over ontogeny. Many studies of plant growth rates dispense with curve fitting entirely and calculate absolute and RGRs directly from a small number of observations of biomass. AGR is traditionally calculated as $(M_t - M_{t-\Delta t})/\Delta t$, and RGR as $\ln(M_t/M_{t-\Delta t})/\Delta t$, where M indicates biomass at successive times t (Hoffmann & Poorter 2002), and only two observations per species are required. When measurements are available at more than two time points, RGR can be estimated as the slope of a linear regression of log-transformed size vs. time. These

calculations have been widely used in ecology (for one of many examples, see Paine *et al.* 2008), but are predicated on the rarely tenable assumption that growth is exponential. Traditional calculations confound RGR with initial size and fail to capture the temporal dynamics of growth (Rees *et al.* 2010).

In particular, growth models need to account for the universal decrease in RGR that occurs as plants increase in biomass. This decrease results from a combination of factors, including an accumulation of non-photosynthetic biomass in the form of stems and roots, self-shading of leaves and decreases in local concentrations of soil nutrients. In broad terms, respiration cost scales with whole-plant biomass, whereas carbon acquisition scales with photosynthetic biomass. Thus, the rate of biomass accumulation, as a fraction of total biomass, slows as plants grow (Hunt 1982; South 1995). Only when light is plentiful and nutrients are continually replenished, such as algae growing in a chemostat, would RGR not be expected to slow through time. To maintain a constant RGR, as an organism grows would require an ever-increasing AGR, which is made impractical by limitations of available resources and by geometrical considerations. Contrastingly, AGR can remain constant or even increase (e.g. Sillett *et al.* 2010), although not at a rate that would allow a constant or increasing RGR.

We illustrate two cases of slowing growth, and the inadequacy of traditional calculations of RGR, in Fig. 1. Applying an exponential model of growth, the slopes of the line segments indicate RGR on these semi-log plots. The solid line segments indicate the slopes that would be inferred were these plants to grow exponentially during every census interval. The heavy dashed lines indicate the constant RGR that would be inferred by fitting a model of exponential growth to all of the data. It is evident from the differences in slopes among census intervals that the traditional approach fails to capture the decrease in RGR through time. Traditional calculations of growth rates should not be used when temporal growth dynamics are of interest, or initial sizes vary among experimental units. The best way to accommodate temporal variation in growth rates is with nonlinear growth models.

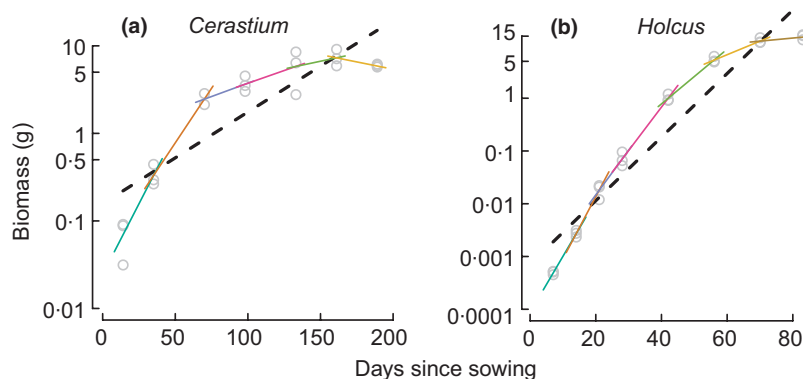


Fig. 1. The traditional calculation of relative growth rate, $\ln(M_t/M_{t-\Delta t})/\Delta t$ is predicated on an assumption of exponential growth and is inappropriate in most circumstances. Line segments indicate the growth trajectory assumed by the traditional calculation, fitted for each census interval for (a) *Cerastium diffusum* and (b) *Holcus lanatus*. Their colours are arbitrary, but vary to highlight the different growth rates among intervals. The dashed lines indicate the growth trajectory assumed by an exponential model of growth. Neither of the traditional approaches captures the temporal variation in growth rates. Note that the Y-axes are log transformed. See text ('Data sets') for details of the underlying data.

Many of the complexities of plant growth have long been appreciated, and nonlinear growth models, therefore, have a long history (Gompertz 1825; von Bertalanffy 1938; Blackman 1919; Hunt 1982). Only recently, however, have statistical software and nonlinear model fitting advanced to the point, where a wide range of models can be explored in realistically complex experiments (Pinheiro & Bates 2000; Ritz & Streibig 2008). Using nonlinear models does not preclude calculating growth rates. Rather, AGR is the derivative with respect to time of the function used to predict biomass, and RGR is simply AGR divided by current biomass (Table 1). Growth rates calculated in this way have the attractive property of capturing age- and size-dependent growth. In this paper, we show how growth rates can be derived from any differentiable growth function and expressed as functions of time or biomass.

We begin with a brief survey of some of the functional forms commonly used for growth analysis, updating earlier reviews (Hunt 1981, 1982; Heinen 1999; Thornley & France 2007). We do not attempt to enumerate all conceivable models, but rather we concentrate on the basic forms at the core of the most popular models (Table 1). They balance, to varying degrees, the objectives of realism, predictability and generality and also vary in the data necessary for their parameterization (Hilborn & Mangel 1997). These models can be applied to the growth of any organism (Ricklefs 2010), but we emphasize botanical examples, as we are ecologists mostly working with plants. We do not discuss the relationships among models (Causton & Venus 1981; Tjørve & Tjørve 2010) nor the techniques of fitting fixed and random effects in them, as these topics are elegantly presented elsewhere (Pinheiro & Bates 2000; Bolker 2008; Ritz & Streibig 2008; Bolker *et al.* 2009). We present the models in continuous-time formulations, although discrete-time versions exist for many (Thornley & France 2007). To facilitate their implementation, we demonstrate how to obtain the best-fit parameters for all models using nonlinear least squares. We then show, for all functional forms, how AGR and RGR can be calculated as functions of both time and mass, including uncertainty in our estimates of those rates. We use biomass as a response variable, although any response variable allometrically related to biomass can be analysed in the same framework. These techniques are implemented in the *nls*, *gnls* and *nlsList* functions of the R statistical language and environment (R Development Core Team 2011; Pinheiro *et al.* 2009). Several of the more flexible model forms are difficult to fit to noisy ecological data, often requiring *ad hoc* modifications to the fitting routines. In the interest of making this contribution as useful as possible, we illustrate extensive troubleshooting techniques. The approach we recommend is documented in an R script (Appendix S1).

Data sets

We illustrate the various functional forms and approaches using two data sets (Fig. 1). In the first, Turnbull *et al.* (2008) grew nine species of sand-dune annuals from seed under five dilutions of fertilizer. All seeds were grown outdoors initially, with half transferred to a cool glasshouse after 5 weeks. Three

individuals per treatment combination were sacrificed and individual biomass measured at each of seven census intervals over the course of 198 days. In this study, we focus on the growth of *Cerastium diffusum* L. (Caryophyllaceae) in unfertilized greenhouse conditions. We also compare the growth of *Cerastium* with that of *Geranium molle* L. (Geraniaceae). Because the growth of these plants in the unfertilized treatment showed a clear asymptote at the end of the growing season, we use these data to illustrate the asymptotic models.

As part of a study on parasitic plants, Hautier *et al.* (2010) grew nine species of grass from seed as host plants in a glasshouse under three levels of shading. Three replicate plants were sacrificed at eight time points over the course of 83 days. In this study, we use the aboveground biomass of *Holcus lanatus* L. (Poaceae) grown under unshaded conditions. We use these data to illustrate the non-asymptotic forms, and, after log-transforming biomass, also use them to fit asymptotic models. Species are henceforth, referred to by their generic names.

Types of growth models








Growth models can be classified under two broad headings: those that assume that an asymptotic final size exists and those that do not. The idea of asymptotic final size is somewhat problematic for individual plants (Hunt 1982), but is well-established in zoology and for the resource-limited growth of populations (McMahon & Bonner 1983). Plant size may approach an asymptote because of limiting belowground resources or ontogenetic changes, such as the onset of flowering. Choosing between asymptotic and non-asymptotic functional forms depends in part upon the response variable of interest and the time scale of the study. For example, canopy trees may be considered to grow asymptotically in terms of height, even as their girth and biomass may increase without limit (Thomas 1996; Chave *et al.* 2003; Muller-Landau *et al.* 2006; Sillett *et al.* 2010). Asymptotic models are also appropriate for analyses that include the entire lifespan, as is frequently the case for studies of annual plants. Non-asymptotic models make the implicit (and in the extreme case, unrealistic) assumption that growth continues indefinitely. Even so, they can be appropriate for modelling the initial stages of the lifespan, such as seedlings of long-lived trees. This is not an absolute dichotomy, however. Biomass can be log transformed, allowing non-asymptotic forms to be fit, usually with the added benefit of reducing heteroscedasticity (Fig. 1, e.g. Rees *et al.* 2010). We include models that can be fitted within a linear model framework for completeness and to illustrate that their performance is frequently poor. We provide details of all model forms in Table 1, and a table of alternative parameterizations in Appendix S2.

Linear forms – non-asymptotic

(LOG-) LINEAR MODELS

In linear models, AGR is constant, i.e. the same quantity of biomass is added in each unit of time (Table 1, Fig. 2a). Thus,

Table 1. Basic functional forms for plant growth modelling. The models are autonomous first-order differential equations expressing the change in biomass, M , as a function of time, t . The solution of each differential equation provides an expression for M at any time t . Absolute growth rate (AGR) is the derivative of M with respect to time. Relative growth rate (RGR) can be expressed either as a function of mass or as a function of time. Note that in the linear model, AGR is constant with respect to time, and in the exponential model, RGR is constant with respect to both time and mass. Also it is to be noted that if log-transformed biomass $M' = \ln(M)$ is modelled, RGR is simply $d(M')/dt$, because $d \ln(F(t))/dt = (1/F(t))dF(t)/dt$. AGR is, correspondingly, $\exp(M') \cdot (d(M')/dt)$, because $d \exp(F(t))/dt = \exp(F(t)) dF(t)/dt$. These models may be parameterized in many ways, and we have chosen naming conventions that facilitate comparisons among models. The parameters L and K indicate lower and upper horizontal asymptotes, respectively. A table of equivalent parameterizations is provided in Appendix S2

Name	Form	Model dM/dt	Biomass M time basis	AGR dM/dt time basis	RGR (dM/dt)/ M time basis	RGR (dM/dt)/ M mass basis
Linear		r	$M_0 + rt$	r	$\frac{r}{M_0 + rt}$	$\frac{r}{M}$
Exponential		rM	M_0e^{rt}	rM_0e^{rt}	r	r
Power law		rM^β	$(M_0^{1-\beta} + rt(1-\beta))^{1/1-\beta}$	$r(M_0^{1-\beta} + rt(1-\beta))^{\beta/1-\beta}$	$r(M_0^{1-\beta} + rt(1-\beta))^{-1}$	$rM^{\beta-1}$
Monomolecular		$r(K - M)$	$K - e^{-rt}(K - M_0)$	$re^{-rt}(K - M_0)$	$\frac{r(K - M_0)}{M_0 + K(e^{rt} - 1)}$	$\frac{r(K - M)}{M}$
Three-parameter logistic		$rM\left(1 - \frac{M}{K}\right)$	$\frac{M_0K}{M_0 + (K - M_0)e^{-rt}}$	$\frac{rM_0Ke^{-rt}(K - M_0)}{(M_0 + e^{-rt}(K - M_0))^2}$	$\frac{re^{-rt}(K - M_0)}{M_0 + e^{-rt}(K - M_0)}$	$r\left(1 - \frac{M}{K}\right)$
Four-parameter logistic*		$r(M - L)\left(\frac{K - M}{K - L}\right)$	$L + \frac{M_0(K - L)}{M_0 + Pe^{-rt}}$	$\frac{rM_0(K - L)Pe^{-rt}}{(M_0 + Pe^{-rt})^2}$	$\frac{rM_0(K - L)Pe^{-rt}}{(M_0 + Pe^{-rt})(LPe^{-rt} + M_0K)}$	$\frac{r(M - L)}{M} \left(\frac{K - M}{K - L}\right)$
Gompertz		$rM\left(\ln \frac{K}{M}\right)$	$K\left(\frac{M_0}{K}\right)^{e^{-rt}}$	$rKe^{-rt}\left(\frac{M_0}{K}\right)^{e^{-rt}} \ln \frac{K}{M_0}$	$re^{-rt} \ln \frac{K}{M_0}$	$r \ln \frac{K}{M}$

* $P = K - L - M_0$.

biomass acquisition is independent of current biomass. This assumption is implausible, as biomass acquisition should depend on leaf area, and hence biomass at least initially, when resources are unlikely to be limiting. There are two parameters in the linear model: M_0 , initial biomass, and r , the absolute increase in biomass per unit time. A problem with the standard linear model is that it frequently predicts negative biomass at early time points (Fig. 2a). This biologically impossible prediction may be avoided by constraining the intercept to pass through the origin ($M_0 = 0$). In such a 'no-intercept' linear model, biomass is always positive (Fig. 2a), and seed mass is implicitly ignored. With only one parameter, r , the no-intercept model is less flexible than the standard linear model, so it is no surprise that it fits the data even less well. In this example, the no-intercept model has lower R^2 and higher Akaike Information Criterion (AIC) than does the linear model, even as it retains the implausible assumption that the rate of biomass acquisition remains constant over time. Owing to their notable defects, linear models appear rarely in the current growth-analysis literature and are included here primarily for completeness.

Fitting a linear regression to the logarithm of biomass yields the exponential (loglinear) model, in which the rate of biomass acquisition is proportional to current biomass (Blackman 1919). In the unlikely event that neither environmental nor physiological factors slow the rate of biomass acquisition, the exponential model may be appropriate (for example, in the initial portion of a plant's lifespan). There are two parameters: M_0 , initial biomass, and r , the relative growth rate. The exponential model is the only one, in which the estimated parameter r is equivalent to RGR, and constant with respect to time and biomass (Fig. 2g,j). The AIC and R^2 of the exponential model are far superior to either of the linear fits (Fig. 2a). However, the exponential model is only appropriate when growth is unconstrained (e.g. algal blooms) and is not flexible enough to account for the slowing of biomass acquisition that can occur with increasing structural biomass. In contrast to the linear models, exponential models are frequently used to analyse growth data. Although they may be useful in cases where growth is authentically exponential, we generally discourage their use in favour of more flexible nonlinear models.

POLYNOMIAL

In the polynomial model, growth follows a smooth curve, potentially of great complexity (Poorter 1989; Heinen 1999). They were once widely used because they can be fit in a linear model framework. However, polynomial functions tend to make spurious upward or downward predictions, especially at the extremes of the data. Furthermore, it is difficult to determine the proper order of polynomial to use and to interpret the model parameters. We discourage the use of polynomial models and present no results for them.

Nonlinear forms – non-asymptotic

POWER LAW (AKA ALLOMETRY)

A power-law model allows RGR to slow with increasing time and biomass, according to the value of the exponent β (Fig. 2g,j). $\beta = 0$ yields the linear model, $0 > \beta > 1$ corresponds to progressive decreases in RGR, $\beta = 1$ yields the exponential model (RGR is constant through time), and $\beta > 1$ corresponds to the case of RGR increasing with increasing biomass. Recently, the metabolic theory of ecology has focused attention on power-law functions for their ability to predict relationships among many aspects of individual survival and growth. Specifically, it predicts that biomass AGR should scale with (biomass)^{3/4} and that diameter AGR should scale with (diameter)^{1/3} (West, Brown & Enquist 1999). A test of these predictions was conducted in 10 tropical rainforests, encompassing > 1.7 million trees, but were only upheld in one forest (Muller-Landau *et al.* 2006). Among the non-asymptotic models, the power law is preferred in terms of R^2 and AIC. It effectively captures the rapid initial growth and the slowing over time (Fig. 2a). Despite continuing discussion regarding the value of the exponent β to be expected from theory, the power law is frequently useful for non-asymptotic data, as it allows RGR to decrease as biomass increases.

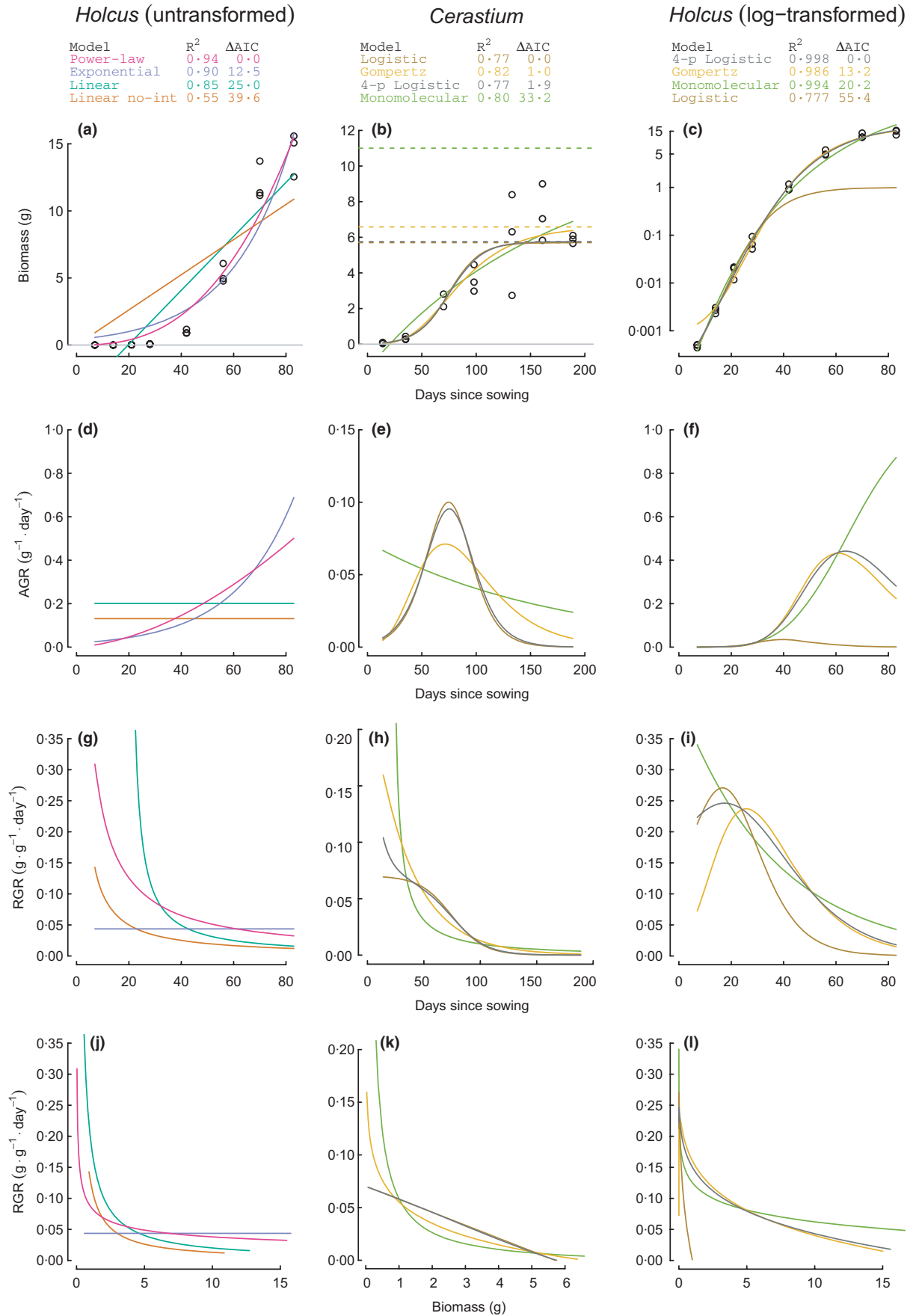
Nonlinear forms – asymptotic

MONOMOLECULAR (AKA MITSCHERLICH)

The monomolecular model was originally derived from physical chemistry, where it describes the progress of first-order chemical reactions (Richards 1959; Zeide 1993; Heinen 1999). There is no point of inflection; unlike the other asymptotic forms it is always concave-down. Correspondingly, AGR is fastest initially, and slows thereafter (Fig. 2e). It can be appropriate, therefore, for log-transformed data (Fig. 2c) but it can predict negative biomass at early time points for untransformed data (Fig. 2b). In the limit, as the asymptotic mass (K) approaches zero, the monomolecular becomes the exponential. It has been occasionally applied to plant growth (Scanlan & Burrows 1990; Paul-Victor *et al.* 2010) and is implemented in R with the *SSasympt* function (Pinheiro & Bates 2000).

THREE-PARAMETER LOGISTIC (AKA VERHULST, AUTOCATALYTIC GROWTH) AND FOUR-PARAMETER LOGISTIC

The logistic is the most commonly utilized asymptotic form (Winsor 1932; Fresco 1973; Hunt 1982; Zeide 1993; Heinen 1999). In the three-parameter version, the lower horizontal asymptote is fixed at 0 and the inflection point – the time at which AGR is maximized – falls rigidly at $M = K/2$. Four-parameter versions loosen one or the other of these strictures (Nelder 1961; R function *SSfpl* in Pinheiro & Bates 2000). The



five-parameter version provides maximum flexibility and alleviating both restrictions (Gottschalk & Dunn 2005; Appendix S2). The three-parameter version collapses to the exponential in the limit as K approaches infinity. For some data sets, the additional flexibility of the four-parameter version greatly increases the variance explained by the model (Fig. 2c), although the three-parameter version provides a more parsimonious and equally adequate fit in other situations (Fig. 2b). The three- and four-parameter logistic models are implemented in R with the *SSlogis* and *SSfppl* functions, respectively (Pinheiro & Bates 2000).

GOMPERTZ

In the Gompertz model, RGR declines exponentially over time (Fig. 2e, Heinen 1999; Gompertz 1825; Winsor 1932; Zeide 1993). The Gompertz model differs from the three-parameter logistic in that the inflection point of the former occurs at approximately 37% of the asymptotic mass K (Winsor 1932), whereas in the latter, the inflection point occurs at one-half the maximal biomass (Fig. 2e, Hunt 1982). The Gompertz and logistic models provide similar fits to the *Cerastium* data. The three-parameter logistic is preferred on the basis of AIC, whereas the Gompertz is preferred on the basis of R^2 (Fig. 2b). Like the logistic, the Gompertz model can be generalized to allow non-zero initial masses and variation in the inflection point (Winsor 1932). It is implemented in R with the *SSgompertz* function (Pinheiro & Bates 2000).

Calculating and comparing growth rates

Many ecological analyses require estimations of absolute and relative growth rates. Once the best functional form has been selected, AGR and RGR can be calculated on the basis of time or mass (Table 1). For proper inference, the uncertainty surrounding the estimated growth rates must be quantified. If experimental groups (such as species or treatment levels) only vary in a single parameter, then the standard error of the growth rate is simply the standard error for that parameter, and comparisons are easily made. However, if groups vary in two or more parameters, then the covariance among parameters must be accounted for to generate confidence intervals for the growth rates. We present the method of population prediction intervals, which is easily implemented and is considered reliable, although it lacks a strong statistical justification. Bolker (2008) reviews this and other techniques of error propagation, including the delta method.

To calculate population prediction intervals, we first examine the square-root transformed likelihood profiles for each parameter to check that they are approximately V-shaped, and thus that the corresponding sampling intervals are approximately multivariate normal (Appendix S1). If this is the case, we randomly draw parameter combinations from a multivariate normal distribution centred on the maximum-likelihood parameter estimates and variance-covariance estimates (as determined by the R functions *nls*, *gnls* or *nlsList*). These sets of parameter combinations are used to calculate replicates of the desired growth rate using the expressions in Table 1. Confidence intervals for a significance threshold α can be extracted by taking the $\alpha/2$ and $(1 - \alpha)/2$ quantiles at every point in time (or biomass). For comparisons among experimental groups, for example between a wild type and various mutants, it is frequently more interpretable to calculate the difference in growth rates and compare that difference to zero, corresponding to the null expectation of no difference between groups (see Züst *et al.* 2011). This can be accomplished with population prediction intervals, except that one calculates differences in growth rates between groups, rather than the growth rates themselves.

The fluctuating nature of growth rates derived from nonlinear growth models encourages a reconsideration of comparisons of growth rates (whether AGR or RGR) among experimental groups. Rather than comparing point estimates of growth rates, one compares time-(or biomass-) specific functions. For example, the best form for modelling *Cerastium* and *Geranium* growth was the three-parameter logistic. Using the traditional approach, one could hypothesize that their growth rates would differ. Using function-derived growth rates, we can refine this hypothesis, testing the degree to which they differ in terms of the timing and magnitude of peak AGR and RGR. To visualize these comparisons, we plot biomass, AGR and RGR as functions of time and mass for both species (Fig. 3). In this case, the peak AGR of *Geranium* precedes that of *Cerastium* by 46 days and is 29% greater in magnitude (Fig. 3b). In the middle of the growing season, *Cerastium* has a 37% greater RGR than does *Geranium* (Fig. 3c). The differences in magnitude are significant, as the confidence intervals around the differences in AGR and RGR between species do not overlap zero (Appendix S3). Time-based comparisons of RGR can be misleading, however, as physiological and environmental conditions change over time, and experimental groups may vary widely in initial size (Britt *et al.* 1991). Differences in initial size among groups are especially common when comparisons are made among species (Turnbull *et al.* 2008;

Fig. 2. Biomass trajectories predicted by the non-asymptotic models for (a) untransformed *Holcus lanatus* and by asymptotic models for (b) *Cerastium diffusum* and (c) log-transformed *Holcus lanatus*. The dashed lines in (b) indicate the predicted asymptotic biomass for each model. For the *Cerastium* data, the predictions from the three- and four-parameter logistic models are almost equivalent. Models are sorted by Δ AIC. Absolute and relative growth rates (RGRs) are derived from functions given in Table 1. (d) Absolute growth rate (AGR) is constant for linear models and increases monotonically for exponential and power-law models. (e, f) AGR is concave-down for logistic and Gompertz functions, and monotonically decreasing (*Cerastium*) or increasing (*Holcus*) for monomolecular. RGR may be expressed as a function of (g–i) time or (j–l) biomass. For the exponential function, RGR is constant with respect to (h) time and (k) biomass, whereas RGR varies with time and biomass for all other functions. For the three- and four-parameter logistic functions, (j) RGR decreases linearly with biomass. Growth rates for linear and monomolecular models, both of which predict negative biomass at early time points, are shown only for positive biomass.

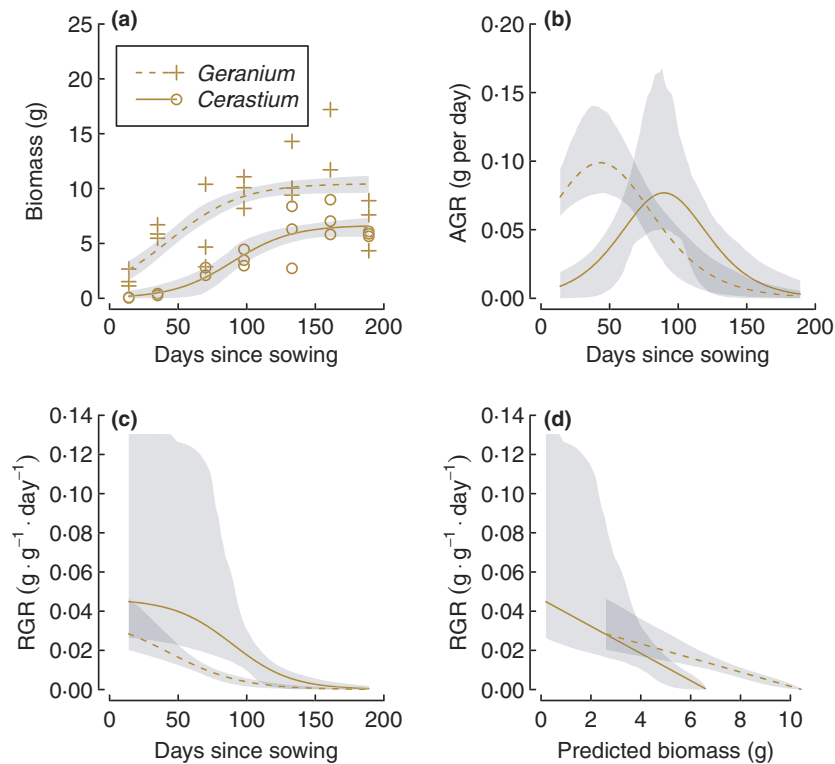


Fig. 3. Observed and predicted values from a three-parameter logistic model for (a) biomass, (b) absolute growth rate (AGR), (c) relative growth rate (RGR) on a time basis and (d) RGR on a biomass basis of *Cerastium diffusum* and *Geranium molle*. Grey curves indicate 95% confidence bands for biomass and growth rates, as derived from population prediction intervals. Confidence bounds can be generated for any growth function (Appendix S1), but are suppressed for clarity in other figures.

Rees *et al.* 2010). Thus, it can be more illuminating to express RGR on the basis of biomass, rather than that of time. Standardized for mass, *Geranium* has a significantly greater RGR than does *Cerastium* (Fig. 3d, Appendix S3). Analysing RGR on a biomass basis corrects for variation in initial size, which can be substantial.

It is important to carefully select the times or biomasses at which growth rates are compared among experimental groups. For example, Paul-Victor *et al.* (2010) compared RGR among inbred recombinant lines of *Arabidopsis thaliana* at the average mass of plants half-way through their experiment, whereas Rees *et al.* (2010) compared growth rates at the smallest size common to all studied species. Here, at a common size of 5 g, *Geranium* has a greater RGR than does *Cerastium* (Fig. 3d, Appendix S3). The choice of comparison times is particularly important when values of two or more model parameters differ among experimental groups, because crossovers in growth rates among experimental units may then occur (e.g. Hautier *et al.* 2010). For example, *Cerastium* and *Geranium* differ in both initial and asymptotic biomass (M_0 and K , respectively), and their AGR trajectories correspondingly intersect (Fig. 3b). Comparisons performed at different times would therefore lead to different conclusions. Compared at day 75, *Geranium* had significantly greater AGR, whereas at day 100, *Cerastium*'s AGR was significantly greater (Fig. 3b, Appendix S3). These patterns are not obvious in the trajectory of biomass through time (Fig. 3a). For these reasons, we recommend plot-

ting AGR and RGR against time or biomass to allow a more holistic understanding of the variation in growth rates as time passes and biomass increases (Heinen 1999; Hautier *et al.* 2010).

Troubleshooting

The approach we advocate for modelling growth does not differ substantially from that for any other statistical analysis, but fitting nonlinear models is rather more involved than fitting linear models. In this section, we describe some techniques that can be used to avoid common pitfalls. The steps we describe are implemented in an R script (Appendix S1).

STUDY DESIGN

In planning your study, several simple considerations can facilitate the subsequent analysis. Frequently, measures of biomass (or allometrically related variables, such as height or diameter, Muller-Landau *et al.* 2006) are made on many individuals at relatively few time points (e.g., Paine *et al.* 2008). One of the easiest ways to increase the reliability of parameter estimates is to take the opposite approach: measure relatively few individuals at each of many time points, particularly during times of rapid changes in growth. For example, more frequent measurements in the early stages of the *Cerastium* study may have reduced our uncertainty in

the estimate of RGR during that period (Fig. 3c,d). Just as important, however, is that the number of individuals sampled at any time point be sufficient to capture the variation in sizes at that time, and that, they be drawn in such a way (e.g. randomly) to be representative of that variation. When nondestructive measurements are used, individuals are often measured repeatedly through time and should be, therefore, represented by a random-effects term in the model. In such studies, the number of individuals sampled at each time should be large enough to provide a reasonable number of groups for this term. Note that the examples in this contribution were derived from destructively harvested plants. Accordingly, each individual was observed only once, mooting the issue of correlated observations on individuals through time. Balancing number of sampling times with the number of individuals to sample at each time is a topic in study design that deserves careful consideration. Finally, the timing of observations should be tailored to the expected growth rates of the plants studied, as well as the error inherent to the measurement technique. For example, more frequent measurements of diameter growth of large trees can be made with dendrometer bands than with tape measures, owing to their greater precision.

Recommendation

To enhance reliability in parameter estimation, measure relatively few individuals per time point and use relatively many time points, while sampling individuals representatively and adhering to the requirements of mixed-effects models. Make observations more frequently in periods of rapid changes in growth.

GET TO KNOW THE DATA

Plotting the data, understanding the natural history of the system and considering the attributes of the various functional forms are essential to select an appropriate model (South 1995). Carefully examine the raw data before selecting a growth model. Together with knowledge of the study system, graphics can indicate which model(s) is most appropriate for the data. Examination of diagnostic plots can aid in identifying mis-specified models (Appendix S3; Fig. 2). Log-transforming biomass permits the application of a wide variety of additional models (Fig. 2c). Generalized additive models can also be applied when the biomass trajectory conforms to no simple parametric form (Katsanevakis 2007; Wood 2006), and the use of the *predict.gam* function in the package *mgcv* can permit the calculation of function-derived growth rates.

Recommendation

Make graphs early and often. The importance of this step cannot be overstated. Avoid polynomial functions (too difficult to interpret parameters) and linear or exponential functions (too simplistic). Use flexible nonlinear forms, such as the power-law or four-parameter logistic. Consider log-transforming biomass when growth rates are of primary interest.

CHOOSE AMONG MODELS

Through experience, we have found that inappropriate functional forms often fail to converge or yield unreasonable parameter estimates. A common pitfall is to attempt to fit overly complicated models. The smaller or noisier the data set, the simpler the model should be: i.e. avoid over-parameterization. Exploring different model specifications is essential for selecting the most parsimonious model. The ‘params’ and ‘fixed’ arguments of the *gnls* and *nlme* functions, respectively, provide important tools for model selection, as they can specify which parameters are to vary among treatment groups and which are to be global. Several different models may be almost equally good, particularly if the data are noisy. It is frequently desirable to choose a model with biologically interpretable parameters. The models presented here include only very basic forms, however. Given sufficient data, these models may be combined with others to test more elaborate ecological hypotheses. As examples, Godoy, Monterubbianesi & Tognetti (2008) combined Gompertz models to model the biphasic double-sigmoid growth of highbush blueberries (*Vaccinium corymbosum* L.), and Damgaard & Weiner (2008) model the growth of *Chenopodium album* L. (Chenopodiaceae) with the Birch function, a generalization of the logistic that allows initially exponential growth to slow.

Recommendation

Use the simplest possible model that captures the essence of your data. For models with roughly equal fits, use biological relevance to arbitrate.

HETEROSCEDASTICITY

Because growth is essentially a multiplicative process, variation in genetic and environmental conditions increases the variation among individuals in biomass through time. Thus, heteroscedasticity is a frequent problem in modelling plant growth. There are two principal approaches to reduce heteroscedasticity. The first is to model the logarithm of biomass, rather than biomass itself. A logarithmic transformation will often reduce heteroscedasticity, because multiplicative relationships become additive following transformation (Fig. 2b,c). Log transformation, however, can complicate the biological interpretation of some model parameters, although if the estimation of growth rates is the main objective, this does not pose a major problem. It is to be noted that models fit to transformed and untransformed data cannot be compared unless appropriate steps are taken to accommodate the change in scale (Burnham & Anderson 2002; Weiss 2010). An alternative approach to reducing heteroscedasticity is to model the variance in biomass explicitly, for example as a power or exponential function of the mean (Pinheiro & Bates 2000). In fitting curves to the *Cerastium* data, we modelled the variance in biomass as an exponential function of predicted biomass. This reduced, although did not entirely eliminate, heteroscedasticity (Appendix S3). If many nondestructive measures are made on the

same individuals, then the error structure of the model fit must take this into account. One can fit a mixed-effect model for repeated-measures data with the function *nlme*, specifying individuals as a random effect, and indicating the within-group correlation structure with the 'correlation' argument (see Pinheiro & Bates 2000 for details).

Recommendation

Account for heteroscedasticity in your data and/or repeated measures with an appropriate transformation and/or variance modelling (Pinheiro & Bates 2000).

CONVERGENCE FAILURE

Even appropriate models sometimes fail to converge on reasonable parameter estimates. The easiest way to avoid problems is to use a nonlinear model for which self-starting routines exist. These routines, which are available in R for the majority of models presented here, facilitate model convergence by selecting sensible starting estimates for parameters and computing derivatives analytically (Pinheiro & Bates 2000). Fitting routines will fail if parameter values lead to non-numeric predictions. For example, in the Gompertz model, as asymptotic biomass (K) approaches zero, divide-by-zero errors become common. Some errors of this type may be avoided by bounding parameter values away from zero. Care should be taken when using bounded methods, however, that the estimated parameter values are not at, or close to, the bounded limits. Such a situation usually indicates a mis-specified model or bounds. In some models, certain parameters may take only positive values (such as the power law, where β , biologically, should be > 0). This can be achieved by exponentiating the parameter in the model, then subsequently log transforming the best-fit parameter value. R's *grofit* package may facilitate model fitting in certain cases, and for some mixed-effects models, the functions in the *lme4* package converge more readily than do those of *nlme* (Kahm *et al.* 2010; Bates, Maechler & Bolker 2011).

Further problem-solving techniques may be called for in extreme cases, particularly for the power-law model, which seems particularly prone to convergence failures. The first is to fix the value of one parameter, typically the initial mass M_0 , and fit only the rate and scaling exponent, r and β . This technique was employed in the original analysis of the *Holcus* data set, where the value of M_0 was determined by germinating a large sample of seeds on filter paper and using the average initial seedling biomass as the mass on day 0 (0.0606 mg, Hautier *et al.* 2010). This approach can also be used in the linear model to avoid predictions of negative biomass. Another option is to use a brute-force search to determine the most likely combination of parameters, given the data. In this technique, the likelihood of all possible parameter combinations within a plausible volume of parameter space is evaluated (Fig. 4). Brute-force searches can be iterated to generate parameter estimates of any desired precision, but are prohibitively slow for parameter-rich models.

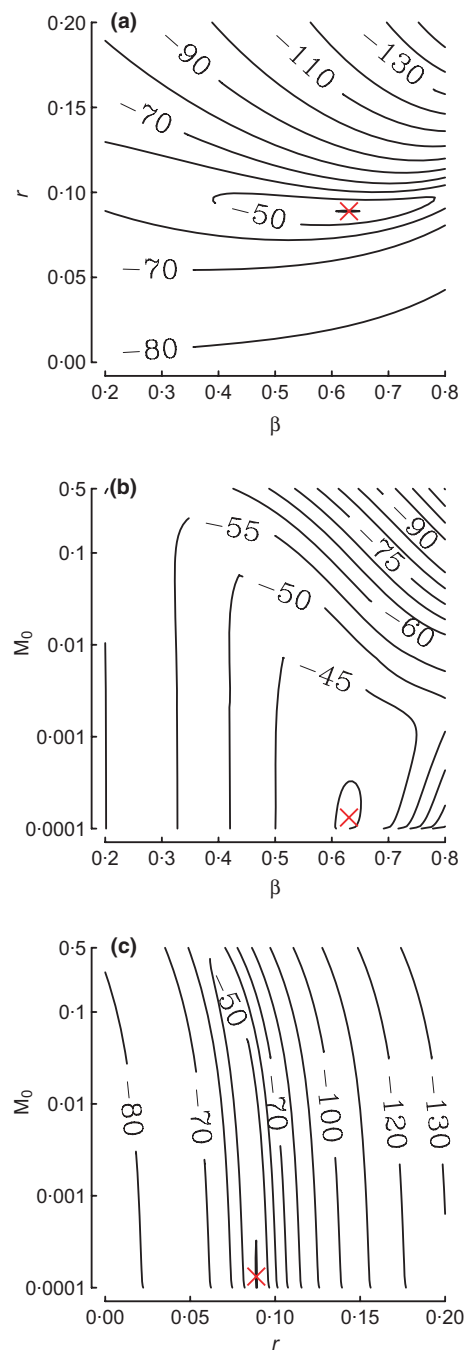


Fig. 4. Three slices through the three-dimensional volume of parameter space for the power-law model showing the likelihood surface for each of pairwise combination of parameters, as determined through an iterated brute-force search. Contour lines indicate the likelihood of each parameter combination, given the data and the specified model. The 'X's indicate the most likely combination of parameters. Note that the Y-axes in panels (b) and (c) are log transformed.

A third option is to use general-purpose optimization methods, such as that implemented in the R function *nlminb*. As *nlminb* has convergence criteria that differ from those in *nlm*, the former sometimes converges in cases where the latter fails. We used these techniques after *nlm* failed to converge

for the power-law model and arrived at parameter estimates that differed by no more than 2.3%. The grid search also illuminated one possible cause of the failure of *nls* to converge: substantial uncertainty in the estimate of β (Fig. 4a).

Recommendation

Be persistent. Use these hints to determine the most likely parameter values, given your data and model. The payoff, in terms of biological plausibility and additional insight, will be worth it.

PROPAGATE UNCERTAINTY

The ecological significance of a model frequently lies in the growth rates it predicts, rather than the parameter values themselves. In these circumstances, it is essential that growth rates be properly calculated.

Recommendation

Derive absolute and RGRs from fitted nonlinear functions. Propagate uncertainty from the parameter estimates to the function-derived growth rates. Allow ecological hypotheses and natural history to guide your choice of times and biomass for comparison of growth rates among experimental groups.

Future directions

The models presented in this contribution may be extended in many ways. One objective is the development of fitting routines for highly flexible forms, such as those pioneered by von Bertalanffy (1938, 1957) and others (see Thornley & France 2007). With four parameters, the von Bertalanffy model allows rapid initial growth to slow, without imposing strict asymptotic conditions. This model is also valued because its parameters are biologically interpretable (Thornley & France 2007). There are two components – one for anabolism (i.e. synthesis, taken to follow a power law) and one for catabolism (i.e. degradation, taken as exponential, Appendix S2). Furthermore, the von Bertalanffy model collapses to all the other models presented here, depending upon the values of its parameters (Tjørve & Tjørve 2010). In theory, therefore, a von Bertalanffy model could fit a wide variety of growth data sets. However, it is so flexible that it can be very difficult to fit to data, because different combinations of parameter values can produce very similar growth curves. Markov chain Monte Carlo (MCMC) or similar methods may be necessary to obtain reliable parameter estimates for this model (Hilborn & Mangel 1997; Bolker 2008; Lichstein *et al.* 2010), but this is beyond the scope of this contribution.

An active avenue of research is in the development of mechanistic models of plant growth. These models consider growth algorithmically or as an iterative process of carbon acquisition, allocation to various compartments and biomass gain (Tilman 1988; Grimm & Railsback 2005). They

are set up as a system of (potentially nonlinear) equations. This allows for an enormously flexible framework that can accommodate multiple compartments (e.g. roots, stems and leaves), changes in environmental conditions, latent variables such as the rate of photosynthate allocation to roots and leaves, and losses of biomass through time (Turnbull *et al.* 2008). These aspects cannot easily be accommodated in the nonlinear regression framework we advocate. The development of individual-based mechanistic models is described in detail by Grimm & Railsback (2005). Such models generally require the use of MCMC for parameter estimation and should be more widely employed, as they become easier to implement.

Conclusion

The analysis of plant growth and the determination of robust estimates of parameter values and growth rates are an important area of ecological research. Advice on the mechanics of curve fitting is, however, dispersed throughout the academic literature and progressing quickly, as new statistical techniques become available. Updating earlier reviews with practical advice, we have briefly summarized some of the basic functional forms for growth, discussed the derivation of growth rates from functional forms and advocated the propagation of uncertainty from model parameters to estimated growth rates. We hope that the methodological review and synthesis presented here will facilitate the study of growth rates by ecologists.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. R script.

Appendix S2. Table of equivalent parameterizations of functions.

Appendix S3. Supplemental figures.

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