

Modeling the growth of individuals in crowded plant populations

Christian Damgaard^{1,*} and Jacob Weiner²

¹ Department of Terrestrial Ecology, National Environmental Research Institute, University of Aarhus, DK-8600 Silkeborg, Denmark

² Department of Ecology, Faculty of Life Sciences, University of Copenhagen, Frederiksberg, Denmark and National Center for Ecological Analysis and Synthesis, Santa Barbara, CA 93101-5504, USA

*Correspondence address. Tel: +45-89201400; Fax: +45-89201414; cfd@dmu.dk

Abstract

Aims

We present an improved model for the growth of individuals in plant populations experiencing competition.

Methods

Individuals grow sigmoidally according to the Birch model, which is similar to the more commonly used Richards model, but has the advantage that initial plant growth is always exponential. The individual plant growth models are coupled so that there is a maximum total biomass for the population. The effects of size-asymmetric competition are modeled with a parameter that reflects the size advantage that larger individuals have over smaller individuals. We fit the model to data on individual growth in crowded populations of *Chenopodium album*.

Important Findings

When individual plant growth curves were not coupled, there was a negative or no correlation between initial growth rate

and final size, suggesting that competitive interactions were more important in determining final plant size than were plants' initial growth rates. The coupled growth equations fit the data better than individual, uncoupled growth models, even though the number of estimated parameters in the coupled competitive growth model was far fewer, indicating the importance of modeling competition and the degree of size-asymmetric growth explicitly. A quantitative understanding of stand development in terms of the growth of individuals, as altered by competition, is within reach.

Keywords: Birch model • growth curves • plant competition • Richards model • size-asymmetric competition

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Introduction

One of the goals of modern population ecology is to understand population phenomena in terms of the behavior of individuals. The development of a stand of plants results from the growth of individuals, as altered by interactions among these individuals. We know that plant growth is sigmoidal (Hunt 1982; Vanclay 1994), and several sigmoidal growth models with biologically interpretable parameters have been proposed to describe the growth of individual plants, such as the logistic and Gompertz models. In most sigmoid growth models, initial growth is exponential, and a negative term reduces the relative growth rate as size increases, resulting in an asymptotic maximum size (Zeide 1993). The main difference among different sigmoid growth models is the inflection point, the size at which the plant experiences its maximum absolute growth rate (Seber and Wild 1989). In the Richards model, this inflection point is not fixed but modeled by an additional parameter (Richards 1959). This makes the Richards growth model highly flexible and inclusive of most other sigmoid growth models.

The Richards growth model generally fits plant growth data well and has been widely used in plant ecology and forestry. Estimating the inflection point as a free parameter seems biologically reasonable since there is no general theory that predicts at what growth stage plants experience their maximum growth rate, and the inflection point has been shown to depend on density (Damgaard *et al.* 2002). One biologically undesirable feature of the Richards growth model is that when maximum growth rate is obtained early in plant growth, i.e. the growth curve has a low inflection point, initial growth is not exponential (Birch 1999). To address this problem, Birch (1999) proposed a growth model that has both initial exponential growth and an inflection point parameter. The degree of mathematical flexibility of the Birch growth model is comparable to that of the Richards model and both models have the same number of parameters, so it is expected that the Birch growth model will fit plant growth data as well as the Richards growth model. Furthermore, there are some problems with estimating the parameter estimation in the Richards growth model (Birch 1999; Ratkowsky 1983; Thornley, 2000; Zeide

1993), but since the Birch model does not include a power function of the current size relative to the maximum size, it is expected to have better estimation properties than the Richards model (Birch 1999).

In a previous study (Damgaard *et al.* 2002), we used the Richards growth model to analyze competition among individual plants by (i) coupling individual growth models such that the saturation term is based on the cumulative size of the whole population and (ii) including effects of size-asymmetric competition (Weiner 1990). Here we generalize the Birch growth model in a similar way and take advantage of the direct estimation of the initial growth rate in the Birch growth model. Furthermore, genetic differences in microhabitat and variation in local competition may cause variation in the shape of individual growth curves. Accounting for such variation among individuals is important to reduce biased and autocorrelated residuals, which may influence inferences made concerning the parameters of interest (Cam *et al.* 2002).

There is increasing interest in including the variation among individuals in the modeling of population growth with hierarchical models, in which some parameters are estimated at the level of the population, whereas other parameters are assumed to vary among individuals according to a specific distribution (e.g. a normal distribution), where the mean and the variance of the distribution can be estimated (Cam *et al.*, 2002; Clark *et al.*, 2004; Fox *et al.* 2001; Schneider *et al.*, 2006). In this study, we use a hierarchical population model, but instead of only estimating the summary statistics of some assumed distribution for parameters, all the individual growth parameters will be estimated for each individual, as suggested by Weiner *et al.* (1998). The estimates of the individual growth parameters will enable us to test hypotheses concerning the shape of the growth curves of plants at different positions within the size hierarchy. For example, is the fate of the plants that end up being large determined early on by factors of a non-competitive nature, e.g. early germination or a favorable microenvironment, or is an individual's position in the size hierarchy determined later on when the plants start to compete with each other? Using the Birch growth model, these two hypotheses can be tested by examining the estimates of the initial relative growth rate and the inflection point of the individual plants. Under the first hypothesis, it is expected that the plants that end up being the dominant ones has a relatively high initial relative growth rate, whereas under the second hypothesis, the dominant plants will have a relatively large inflection point.

Materials and Methods

Growth model

Birch (1999) proposed the following growth model:

$$\frac{dv(\tau)}{dt} = rv(\tau) \frac{w - v(\tau)}{w - v(\tau) + cv(\tau)}, \quad v \geq 0, r > 0, w > 0, c \geq 0, \quad (1)$$

where $v(\tau)$ is the plant size at time τ , r is the initial relative growth rate, w is the final plant size when growth stops and

c is a positive parameter that determine the inflection point. The Birch growth model is equivalent to the logistic equation for $c = 1$ and to exponential growth for $c = 0$. The maximum growth rate is $rw/(\sqrt{c}+1)^2$ when the plants have the size $w/(\sqrt{c}+1)$. When $c < 1$, the maximum growth rate occurs at $v > w/2$; when $c > 1$, the maximum growth rate occurs at $v < w/2$.

The Birch growth model may adequately describe the growth of a single plant or plant growth in a monoculture of identical plants. However, plants in a population are never identical. There may be variation in the time of germination, local neighbor conditions and microenvironment, resulting in size variation. If plant growth is limited by a resource that may be monopolized, e.g. light, then size-asymmetric competition may occur and larger plants will grow faster than smaller plants resulting in size-asymmetric growth. Size-asymmetric growth can be included by modeling individual plant growth as proportional to a power function of size (Damgaard 1999; Damgaard *et al.* 2002; Schwinning and Fox 1995; Wyszomirski *et al.* 1999):

$$f(v(\tau), a) = (v(\tau) + 1)^a - 1, \quad (2)$$

where the relationship between plant size and growth rate is expressed with a size-asymmetry coefficient, a , which measures the degree of curvature of the growth-size relationship within the population over the entire growth curve. The choice of a power function of plant size is somewhat arbitrary but may be motivated by the favorable scaling properties of the power function. If $a < 1$, the growth rate is less than proportional to the size of the plant. If $a = 1$ the growth rate is proportional to the size of the plant, and $a > 1$ means that the growth rate is more than proportional to plant size within the population (Schwinning and Weiner 1998; Weiner and Damgaard 2006).

In order to take the effect of plant size variation on the growth of individual plants into account, an individual-based Birch growth model may be formulated by generalizing equation (1) with respect to size-asymmetric growth equation (2). Assume a monoculture of n competitively interacting plants of variable size, then the growth of plant i at time t may be expressed by n coupled differential equations (here described by a single equation for plant i):

$$\frac{dv_i(\tau)}{d\tau} = \frac{r_i(v(\tau) + 1)^a - 1}{a} \frac{nw - \sum_{k=1}^n v_k(\tau)}{nw - (1 - c_i) \sum_{k=1}^n v_k(\tau)} \quad v \geq 0, \quad (3)$$

$$a \neq 0, r_i > 0, w > 0, c_i \geq 0,$$

where $v_i(\tau)$ is the size of plant i at time τ . In order to allow for individual growth curves, the two parameters that determine the initial relative growth rate, r_i , and the shape of the growth curve, c_i , were allowed to vary among plants, whereas the other two parameters, a , the size-asymmetry coefficient and the total biomass (nw , where n is the number of surviving individuals and w is the average plant size at the end of the growing season) were assumed to be fixed at the level of the population. Thus, the growth of each plant depends both on its own size

and the total size of all the plants in the population. Larger plants grow more, and growth is reduced by large total population biomass. When fitting the model, the biomass of dead plants was set to zero. Consequently, the biomass of dead plants is available for the continuing growth of living plants.

Similarly to the Birch growth model, the initial relative growth rate of plant i in the individual model (equation 3) is equal to r_i at the limit when all n plants are small, i.e. $\lim_{v_k \rightarrow 0} \frac{dv_i(\tau)}{d\tau} \frac{1}{v_i(\tau)} = r_i$.

At the limit, when $a = 0$, model (equation 3) is not defined but the growth curve is continuous in $a = 0$ with $\lim_{a \rightarrow 0} \frac{r_i(v(\tau)+1)^a - 1}{a} = r_i \log(v(\tau)+1)$.

The size where the plant i experience the maximum growth rate is the solution to $v_i''(\tau)=0$, which may be solved numerically in the simplifying case when $w=1, v_i=p$ and $\sum v_k \approx np$, where p is the size relative to w .

Growth data

Chenopodium album L. (*Chenopodiaceae*) is a broad-leaved summer annual weed that often colonizes open fertilized habitats (Grime *et al.* 1989). Growth of individuals in *C. album* populations at three densities was followed through the growing season. On 8 June 1990, the seeds, which had been collected from a natural population in a suburb of Tokyo in the previous year, were sown in three 1×1 m plots in the Botanical Gardens, Faculty of Science, University of Tokyo ($139^\circ 45'$ E, $35^\circ 43'$ N). Emergence was first observed on 13 June. The seedlings were thinned to one plant per sub-plot of 5×5 cm, which were used to establish populations at two plant densities, 400 plants m^{-2} (36 plants in 30×30 cm) and 800 plants m^{-2} (72 plants in 30×30 cm) on 28 June. Height and stem diameter of plants in the central area of the plots were measured non-destructively at intervals of 1–4 weeks until the end of the growing season. Height was measured from the soil surface to the terminal shoot apex, and diameter was measured just above the cotyledons. No fertilizer was applied because the fertility level seemed to be sufficient due to high organic matter from previous vegetation. The populations were watered almost daily throughout the experiments. The spatial distribution of the plants was not recorded. The individual plant biomass was estimated as height \times diameter². The biomass of dead plants was set to zero. For a complete description of the experimental methods, see Nagashima *et al.* (1995).

Parameter estimation

During the estimation procedure, the parameters r_i, w and c_i , all of which were assumed to be non-negative, were transformed to $\text{Exp}(r_i), \text{Exp}(w), \text{Exp}(c_i)$, but all results are reported after parameter values have been transformed back. In order to minimize autocorrelation among the residual variation, the growth model (equation 3) was fitted to the observed growth increments in plant size (Seber and Wild 1989). The expected sizes of the plants at time t were calculated using the observed plant sizes at time $t-1$ and a specific parameterization of the

growth model and compared to the observed plant sizes at time t :

$$V_i(t_j) = \int_{t_{j-1}}^{t_j} \frac{dV_i(\tau; \bar{V}(t_{j-1}), a, w, r_i, c_i)}{d\tau} d\tau + \varepsilon_{ij}, \quad (4)$$

$$i = 1, 2, \dots, n; j = 2, 3, \dots, m,$$

where m is the number of observed changes in plant size, $V_i(t_j)$ is the observed plant size at time t_j , $dV_i(\tau; \bar{V}(t_{j-1}), a, w, r_i, c_i)/d\tau$ is the expected plant growth of plant i at time τ calculated from (equation 3) using the NDSolve routine of Mathematica (Wolfram 2003) and where $\bar{V}(t_{j-1})$ is a vector of the observed plant sizes at time t_{j-1} . The residual error was assumed to increase proportionally with expected plant size and the time period of growth, i.e. $\varepsilon_{ij} \sim \text{normal}(0, (\sigma V_i(t_j)(t_j - t_{j-1}))^2)$ and the likelihood function of the stochastic model (equation 4) is

$$L = \prod_{j=2}^m \prod_{i=1}^n \frac{1}{\sqrt{2\pi}(t_j - t_{j-1}) \sigma X_{ij}} \exp\left(-\frac{(Y_{ij} - X_{ij})^2}{2(t_j - t_{j-1})^2 \sigma^2 X_{ij}^2}\right), \quad (5)$$

where Y_{ij} is the observed plant size and X_{ij} is the expected plant size as calculated by (equation 4).

The joint Bayesian posterior distribution of the parameters were simulated by an MCMC approach using the Metropolis Hastings algorithm, assuming uniform improper prior distributions of the location parameters and the square root of the inverse gamma distribution as the prior distribution of σ (Carlin and Louis 1996). The burn-in period was relatively long and the first 35 000 out of 100 000 simulations were discarded. The marginal posterior distribution of each parameter and the corresponding 95% credibility interval was constructed from the MCMC run.

We investigated the fitting properties of the growth model in the case where the model was parameterized with the maximum likelihood estimates of the parameters. The likelihood functions were maximized using the numerical NMaximize routine of Mathematica (Wolfram 2003). We checked the fit of the growth model by plotting the Pearson residuals $(Y_{ij} - X_{ij})/((t_j - t_{j-1})\sigma X_{ij})$ and with the Pearson χ^2 goodness-of-fit statistic. We looked for autocorrelation among the Pearson residuals by calculating the Durbin–Watson statistic. We investigated the biological significance of among-plant variability in growth curves parameters by analyzing relationships between parameter estimates for individual plants and their observed final mass.

Results

The growth model (equation 4) fitted the *C. album* growth data well. A visual inspection of the Pearson residuals of the maximum likelihood estimates demonstrated that the residual variation was homogenous among individual plants and for increasing expected values, and that the Pearson residuals were approximately normally distributed. The Pearson χ^2 goodness-of-fit statistic showed a non-significant deviation

from the expected residual variation (low density: $P = 0.49$; high density: $P = 0.12$). Furthermore, the Durbin–Watson statistic of the Pearson residuals was 1.86 and 1.76 at low and high plant density, respectively, which were not significantly different from the expected value of two in the case of residuals without autocorrelation.

To further examine the ecological relevance of the proposed coupled growth model (equation 4), where the growth rate of individual plants is expected to be influenced by the relative size of the plant and the degree of asymmetric competition, this model was compared to a model in which the growth of all plants was modeled individually by the Birch growth model (equation 1), with no coupling, and therefore no explicit modeling of interactions among individuals (Fig. 1). The coupled competitive growth model (equation 4) fitted better than the individual Birch growth model (equation 1) even though the number of estimated parameters in the coupled competitive growth model was fewer than in Birch growth model (Table 1).

In the coupled competitive growth model (equation 4), the individual growth parameters (c and r) showed a considerable among-plant variation (Fig. 2), and were positively correlated (Pearson correlation coefficient between the means of the posterior distributions; low density: $r = 0.72$, $P < 0.001$; high density: $r = 0.65$, $P < 0.001$). There was a significant negative correlation between the mean of the posterior distribution of the individual shape parameters, c_i , and the final size of the plants (Fig. 2): the plants that ended up being the larger individuals in the population reached the inflection point at a larger size. At low density, there was a negative correlation between initial growth rate (r_i) and final size (w_i) whereas at the highest density there was no significant correlation between initial relative growth rate and final size of the plants. This means that at both densities, plants that ended up being

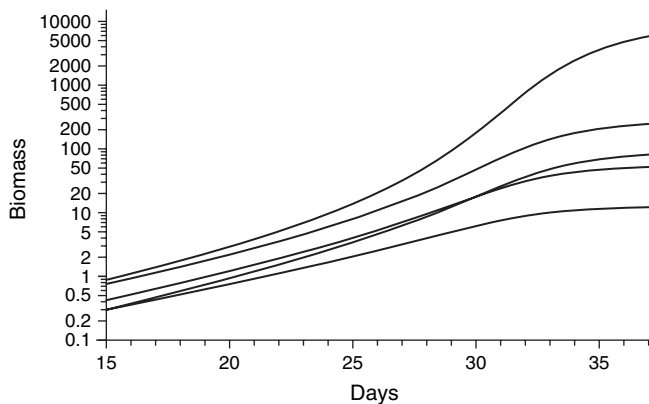


Fig. 1 individually fitted growth curves for five plants selected to cover a range of sizes, grown at low density. The growth curves are based on the estimated biomass after 11 days for the five plants and the corresponding maximum likelihood estimates of the growth parameters of the Birch model.

the largest in the population were not those with the highest initial relative growth rates.

The degree of size-asymmetric growth was significantly larger than one, indicating that the growth rate of the individual plants is more than proportional to the size of the plant relative to others in the population. The 95% credibility interval for a was 1.26–1.37 at the low density and 1.11–1.27 at the high density. Thus, the estimated degree of size-asymmetric growth was not significantly different at low versus high density.

Table 1 maximum likelihood value and number of parameters in the coupled competitive growth model and the individual Birch growth models

Density	Model	Maximum likelihood	Number of parameters
Low	Coupled competitive growth model	−1573	$35 \times 2 + 2 + 1 = 73$
	Individual growth models	−1658	$35 \times 4 + 1 = 141$
High	Coupled competitive growth model	−1221	$35 \times 2 + 2 + 1 = 73$
	Individual growth models	−2206	$35 \times 4 + 1 = 141$

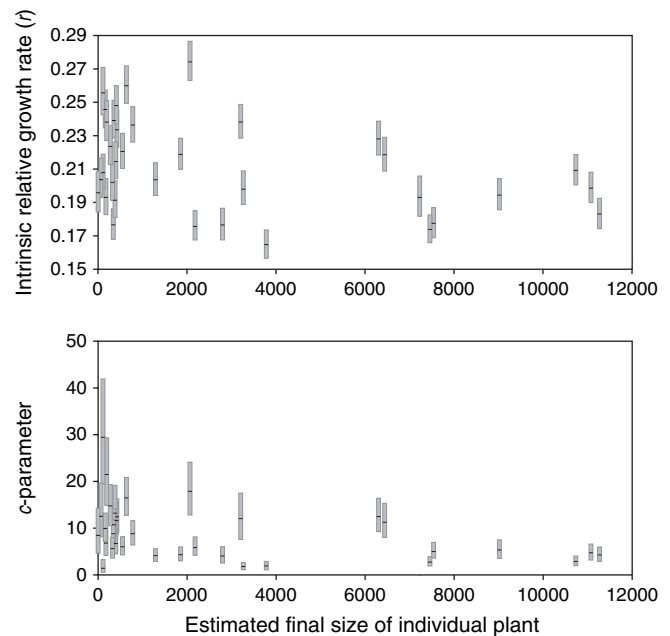


Fig. 2 the relationship between the observed final size of the plants grown at low density and the estimated initial relative growth rate of the individual plant growth curves, r_i (Pearson correlation coefficient between the mean of the posterior distributions and the final size: $r = -0.38$, $P = 0.025$), and the estimated inflection point of the individual plant growth curves, c_i (Pearson correlation coefficient between the mean of the posterior distributions and the final size: $r = -0.41$, $P = 0.013$). The estimates are shown by the 25, 50 and 75% percentiles of the posterior distributions of the parameters.

The estimated degree of size-asymmetric growth in the simple Birch growth model where r and c were assumed not to vary among plants did not differ significantly from the estimates obtained using a Richards growth model on the same data using a slightly different estimation procedure (Damgaard 1999; Damgaard *et al.* 2002; Schwinning and Fox 1995; Wyszomirski *et al.* 1999).

Discussion

There was either a negative or no correlation between initial growth rate and final size when individual, uncoupled growth curves were fit to each plant. This suggests that competitive interactions later in the course of growth were more important in determining final sizes than were the initial growth rates. This stands in contrast to numerous statements in the literature that a high initial growth rate is critical for an individual's competitive advantage. A negative correlation between initial growth rate and final size could even be interpreted as evidence for a trade-off between the ability to grow quickly before competition becomes important and the ability to compete.

The full coupled growth model (equation 4) fit the growth data better than individual, uncoupled growth models (equation 1) even though the number of estimated parameters in the coupled competitive growth model was fewer than in Birch growth model. This is a strong indication of the importance of (i) modeling competition explicitly and (ii) including the effects of size-asymmetric competition in the model.

The estimate of the degree of size-asymmetric growth seems to depend critically on whether or not the growth parameters are allowed to vary among plants. It has been demonstrated that such estimates can become highly biased if latent variability is ignored (Cam *et al.* 2002). It is also encouraging that the estimation of the degree of size-asymmetric growth was fairly robust across different flexible sigmoid growth models. We conclude that flexibility in the inflection point is important for modeling the growth of competing individuals, but that the specific formulation of this flexibility may not be critical. The main advantage of the Birch model is the biological interpretability of its parameters.

The degree of size-asymmetric growth has recently been modeled with a spatially explicit approach in which the sharing of resources within a zone-of-influence around each plant is described by a tanh function (Schneider *et al.* 2006). Inclusion of space requires much more complex data collection and modeling. While this may prove to be necessary in some situations, it is important to know how far non-spatial individually based models can take us (Weiner and Damgaard 2006). Models should be 'as simple as possible and as complicated as necessary', and the increased complexity of spatially explicit models may not be justified in many cases.

The estimation of all the individual parameters was possible in this case due to the relatively few competing plants. In larger populations, it may not be possible to estimate parameters for all individuals. In this case, it will be necessary to use a random

sample of individuals in the population. Another possibility would be to reduce the number of parameters by making assumptions about the distribution of individual growth parameters. Results to date, however, suggest that such distributions will be different under different competitive regimes, but further investigation is needed.

One result of our earlier analysis of these data (Damgaard *et al.* 2002) that the new analysis does not support was that the degree of size-asymmetric growth, i.e. the degree of curvature of the growth-size relationship (a), increased at higher density. In the current analysis, a was not significantly different at the two densities. We have no explanation for this change, and we can only conclude that this result is not robust across models.

We conclude that (i) the Birch model does offer advantages in interpretability over the Richards model in the modeling of individual growth in plant populations, (ii) competitive interactions are much more important than initial growth rates in determining final sizes in crowded plant stands and (iii) explicitly including competition and size-asymmetric growth (which is a result of size-asymmetric competition) into one large model improves model performance and interpretability. A quantitative understanding of stand development in terms of the growth of individual plants, as altered by competition, is within reach.

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