

Modelling individual growth and competition in plant populations: growth curves of *Chenopodium album* at two densities

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Summary

1 We modelled the growth in estimated biomass of individuals in experimental populations of *Chenopodium album* grown at two densities and measured sequentially nine times over 128 days. Competition is modelled by coupling individual growth equations and, within the population, the growth rate of a plant at any point in time is a function of its size to the power a , a measure of the degree of size-asymmetry of competition.

2 The growth of individuals in these crowded populations was significantly better fit by a Richards growth model than by models with one fewer parameter (e.g. logistic or Gompertz growth models). The additional parameter determines the location of the inflection point and provides great flexibility in fitting growth curves. Density had a significant effect on this parameter.

3 At the higher density, the maximum size that plants achieved was decreased and the exponential phase of growth was reduced. The estimate of the size-asymmetry parameter a was always greater than 1 and it increased significantly at the higher density. Growth was reduced and the number of very small individuals increased at the higher density, although a few plants still achieved a large size.

4 Our approach combines several recent innovations in the modelling of stand development, including (a) modelling of individual growth with biologically meaningful growth models and (b) modelling the relationship between size and growth of individuals within the population. Sequential, non-destructive data on the growth of individuals over time, in combination with modern statistical computing techniques, can lead to major advances in the modelling of plant population development, providing powerful tools for exploring variation in individual growth and for testing a wide range of hypotheses.

Key-words: density effects, growth equations, individual-based models, Richards model, sequential measurements

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Introduction

The last two decades have seen major advances in the description and modelling of the development of crowded plant populations. The study of plant competition began with the study of density-dependence: the analysis of the relationship between mean plant yield and density at one point in time (Bleasdale & Nelder 1960; Watkinson 1980; Vandermeer 1984; Damgaard

1998). The characterization of density–yield relationships has led to some important general patterns, but such models are quite limited because (i) they are usually based on a single harvest and therefore reflect a static view of competition and (ii) they describe competition only in terms of mean performance, ignoring variation within the population. To address the first problem, growth curves have been used to describe the growth of an average individual over time (Evans 1972; Causton & Venus 1981; Hunt 1982).

Already in the 1970s researchers had realized that describing plant populations only in terms of mean

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behaviour was not adequate to address the most interesting questions in plant population biology or in applied fields such as forestry and agriculture, and researchers began to investigate variation within populations. The first step was the analysis of plant size distributions (Obeid *et al.* 1967; Ogden 1970; Turner & Rabinowitz 1983; Weiner 1985). It soon became clear that there are numerous possible interpretations for any static size distribution. Plant population processes are often better reflected in the changes that occur in size distributions over time than in the distributions themselves (Westoby 1982). One method for studying changes in size distributions is to analyse the relationship between the sizes of plants within a population at a point in time (t) and their growth over a subsequent interval ($t \rightarrow t + x$). We refer generally to such models as 'size-growth' models. Westoby (1982) called the relationship between size and subsequent growth increment (absolute growth rate) the 'distribution-modifying function' (DMF), because the relationship describes how the size distribution changes over an interval. Hara (1984) expanded the DMF approach into a full diffusion model, adding a diffusion term ($D[t, x]$) to describe the variation in growth rate to the DMF or mean change term ($G[t, x]$). Very large sample sizes are needed to get a sufficient characterization of the $D[t, x]$ function and its interpretation has proved problematic (Hara 1988), so most researchers have looked only at DMF/ $G[t, x]$ relationships and considered variation in the growth rate at a given size to be random. The 'size-growth' or DMF approach represented a major advance in the modelling of plant population developments, in that stand development was now seen and modelled as a dynamic process.

'Size-growth' approaches have been criticized because each time interval is treated separately: no assumptions are made about the time course of plant growth beyond the single growth interval analysed (Weiner *et al.* 1998). Empirical studies following the growth of individuals (Stoll *et al.* 1994; Nagashima *et al.* 1995; Weiner 1995a) have provided compelling evidence for the advantages of looking at stand development in terms of the growth of individuals over time, rather than as a series of independent 'snapshots' or growth increments. Models of stand development based on explicit growth equations permit both increased biological content and stronger statistical inferences (Stoll *et al.* 1994; Weiner *et al.* 1998). Biological content is increased because we can look at the influence of different factors or treatments on model parameters that have clear biological interpretations. Stronger statistical inferences are possible because we can apply what we know about individual plant growth curves, rather than making no assumptions at all about plant growth.

Until now the individual growth modelling approach has not explicitly modelled the interactions among individuals. Individual growth modelling has allowed us to look at the distribution of growth parameters among individuals, and at the effects of

different treatments or factors on these distributions, but the growth of each individual is modelled independently of the others. We can see the effects of competition among individuals, but we do not model these effects. Linking or coupling the growth equations of individual plants can achieve this.

An early attempt to link growth equations for individual plants was based on the classical Lotka–Volterra equations, which were originally developed to study intra- and interspecific competition in microorganisms and animals. Weiner & Thomas (1986) modified the Lotka–Volterra model such that individual plants (which can be considered populations of modules) grow logistically in the absence of competition, thus reflecting 'intraindividual competition', i.e. the sigmoidal nature of plant growth. In such a model, individuals compete with each other in basically the same way that they 'compete' internally, and competition coefficients are used to translate the effects of one unit of biomass of another individual into the equivalent effects of one unit of biomass of an individual on itself. Weiner and Thomas (1986) used coupled equations to show that such a simple 'size-symmetric' model of competition, in which the effect of competitors is proportional to their size, predicts decreased or unchanged size inequality in populations grown at higher densities.

Damgaard (1999) took this approach further, coupling the growth of individuals, but also assuming that, within the population, a plant's growth rate at any point in time is a function of its size to the power a (Hara & Wyszomirski 1994; Schwinning & Fox 1995; Wyszomirski *et al.* 1999). In crowded populations, this parameter is a measure of the degree of 'size-asymmetry' of competition (Weiner 1990; Schwinning & Weiner 1998). Although size-asymmetry is usually defined as a disproportionate access to contested resources by larger individuals (Weiner 1990; Schwinning & Weiner 1998; Berntson & Wayne 2000), it is usually observed in terms of variation in growth. Inferring resource acquisition from growth, Weiner (1990) argued that if, within a crowded population of plants at a point in time, plants' growth rates are proportional to their sizes (Fig. 1, curve for $a = 1$), this would be consistent with the hypotheses of no competition or size-symmetric competition. A convex relationship between the absolute growth rate (AGR) and size (Fig. 1, $a = 2$) is consistent with size-asymmetric, but not size-symmetric, competition, because it implies a positive relationship between relative growth rate (RGR) and size, and this is considered evidence for size-asymmetric competition (Schmitt *et al.* 1987). Damgaard (1999) used a measure of the curvature of the AGR-size relationship over all time intervals as an estimate of the degree of size-asymmetry of competition. Thus, the model offers the possibility of combining the 'growth-size' and the 'individual growth' approaches to the modelling of plant population development, assuming that the growth of individual plants could be adequately described by a logistic growth function multiplied by

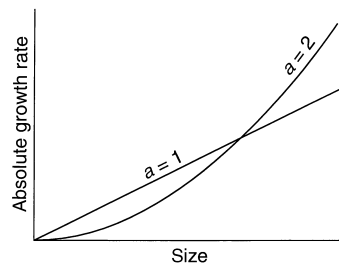


Fig. 1 The relationship between size and subsequent growth (distribution modifying function (Westoby 1982) or $G[t, x]$ function (Hara 1984)) within a plant population for two values of the asymmetry parameter (a). A curvilinear relationship with an increasing slope is considered evidence for size-asymmetric competition, and the parameter a is a measure of the degree of curvature.

the power function of individual plant weights. Here, we relax the assumption of logistic growth and generalize the individual plant growth model to a Richards growth function (Richards 1959; Seber & Wild 1989) multiplied by the power function of individual plant weight. We used the model to analyse the growth of *Chenopodium album* populations grown at two densities, and asked the following questions:

- Can coupled equations provide a reasonable description of population development as a process of individual growth as modified by competition?
- What type of growth equation is sufficient to provide an adequate general description of individual growth of populations at different densities?
- How does a change in density affect the growth curves of individuals?
- Is competition size-asymmetric in crowded *Chenopodium album* populations? If so, does the size-asymmetry of competition increase with density?

Materials and methods

Chenopodium album L. (Chenopodiaceae) is a broad-leaved summer annual that often colonizes in open fertilized habitats (Grime *et al.* 1989). Growth of individuals in *C. album* populations was followed at three densities 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 1, 2 and 7–10 plants per subplot of 5×5 cm to make the plant densities 400, 800 and 3600 plants m^{-2} , respectively, on 28 June. For plants in the central 30×30 cm portion of the plots, height and diameter of the stems were measured non-destructively at intervals of 1–4 weeks until the end of the growing season (i.e. a total of 36 and 72 plants for densities 400 and 800 m^{-2} , respectively; for the highest density, 135 plants were measured in the central 15×25 cm). 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 estimates of biomass at the first measurement for the most crowded population (3600 plants m^{-2}) were not considered to be accurate enough for the present purposes, so our analyses are restricted to the two lower densities. For a complete description of the experimental methods see Nagashima *et al.* (1995).

MODEL

The growth of n competitively interacting plants is modelled by n coupled differential equations. The growth of an individual plant (i) is assumed to be adequately described by the Richards growth model (Richards 1959; Seber & Wild 1989), where the growth rate is assumed to be a function of plant size:

$$\frac{dv_i(t)}{dt} = \begin{cases} \frac{\kappa}{1-\delta} f(v_i(t), a) \left(\left(\frac{1}{n\alpha} \sum_{j=1}^n v_j(t) \right)^{\delta-1} - 1 \right) & \delta \neq 1 \\ \kappa f(v_i(t), a) \left(\log(n\alpha) - \log \left(\sum_{j=1}^n v_j(t) \right) \right) & \delta = 1 \end{cases} \quad \text{eqn 1}$$

$(t \geq 0, \kappa > 0, \alpha > 0)$

$v_i(t)$ is the dimensionless size (estimated biomass) of plant i at time t , $n\alpha$ is the maximum cumulative size of the n plants, and κ , δ and $f(v_i(t), a)$ determine the absolute growth rate of the plant. The initial growth rate is $\frac{\kappa\alpha}{(\delta-1)}$. The shape of the growth curve is mainly

determined by δ . If $\delta > 0$, then the growth curve is sigmoidal, and the slope of the tangent at the point of inflexion decreases with δ (Richards 1959; Seber & Wild 1989). The Richards growth model is flexible and includes the monomolecular ($\delta = 0$), von Bertalanffy ($\delta = 2/3$), Gompertz ($\delta = 1$) and logistic models ($\delta = 2$) as special cases (Richards 1959; Seber & Wild 1989). Thus, the Richards model can be considered hierarchical and therefore can be tested against these simpler growth models.

The saturating term, $\left(\left(\frac{1}{n\alpha} \sum_{j=1}^n v_j(t) \right)^{\delta-1} - 1 \right)$ or $\left(\log(n\alpha) - \log \left(\sum_{j=1}^n v_j(t) \right) \right)$ if $\delta = 0$, measures the decrease in plant growth due to the size and competitive effects of the n interacting plants. The saturation term is equal for all n plants at a given time. The saturation term reduces as the plants grow and, when $\sum_{j=1}^n v_j(t) = n\alpha$, the saturation term equals zero and growth stops. The saturation term is analogous to the competition term in

the logistic model of population growth of individuals towards a carrying capacity.

We assume that the growth of individual plants is proportional to a power function of their size (Schwinning & Fox 1995; Damgaard 1999; Wyszomirski *et al.* 1999) and, following the terminology of Schwinning & Weiner (1998), we define the power function as:

$$f(v_i(t), a) = \begin{cases} 1 & a = 0 \\ v_i(t)^a & a > 0 \\ 1 \text{ (large plants) or } 0 \text{ (small plants)} & a = \infty \end{cases} \quad \text{eqn 2}$$

where the effect of plant size on growth is summarized by the size-asymmetry parameter, a , taking values between 0 and ∞ . If $a = 0$, all plants have the same growth rate irrespective of their size (complete symmetry). If $0 < a < 1$, the growth rate is less than proportional to the size of the plant (partial size symmetry). If $a = 1$, the growth rate is proportional to the size of the plant (perfect size symmetry; Fig. 1). If $a > 1$, the growth rate is more than proportional to the size of the plant (varying degrees of size asymmetry, as for $a = 2$ in Fig. 1). If $a = \infty$, only the largest plants grow at all (complete size asymmetry). In the special case of perfect size symmetry ($a = 1$) and logistic growth ($\delta = 2$) the growth model (equation 1) reduces to Weiner & Thomas's (1986) model with all intraspecific competition coefficients set to one. The parameter a measures the degree of curvature of the size-growth relationship among individuals over the entire growth curve. If the hypothesis of complete symmetry is not rejected (i.e. a is not significantly different from zero), then modelling growth as a function of size does not result in a significant improvement over a simpler, mean field growth model.

STATISTICAL FIT OF THE MODEL

In order to describe adequately the growth of a plant with a dimensionless size less than one, the power function in equation 2 was modified to the following expressions:

$$f(v_i(t), a) = \begin{cases} 1 & a = 0 \\ (v_i(t) + 1)^a - 1 & a > 0 \\ 1 \text{ (large plants) or } 0 \text{ (small plants)} & a = \infty \end{cases} \quad \text{eqn 3}$$

because this gives a monotonic increasing function of both size and the parameter a , for all $v_i(t) > 0$, while still passing through the origin (John & Draper 1980; Damgaard 1999).

The individual plant biomass was estimated as height \times diameter². Plants that died no longer contribute to the population's biomass (i.e. they no longer compete with living plants).

The coupled differential equations (1) cannot be solved analytically, and were therefore solved numerically using the NDSolve routine of Mathematica (Wolfram 1999), after the equations had been reparameterized ($\theta_1 = \log(\kappa)$, $\theta_2 = \log(a)$, $\theta_3 = \log(\alpha)$) to ensure that all

parameters are strictly positive (parameter estimates presented below have been back transformed). In order to avoid auto-correlated errors, the model was fitted to the growth increments in plant size. The residual variance was homogenized with a Box-Cox transformation, which gave residuals that were approximately normally distributed. The log-likelihood of a specific parameter combination was calculated from the transformed predicted sizes and transformed observed sizes of all observed increments for all n plants.

The maximum likelihood estimates of the parameter values, and the profile log-likelihood curve of the asymmetric competition parameter (a) and the shape parameter (δ), were found using the FindMinimum routine of Mathematica (Wolfram 1999). Using the profile log-likelihood curves, the Bayesian posterior probability distributions of the asymmetric competition parameter and the shape parameter were calculated assuming an uninformative prior distribution. Statistical inferences were based on the 95% credibility intervals (2.5% percentile to 97.5% percentile of the posterior distribution) of the parameters. Parameters were concluded to be significantly different if the 2.5% percentile of the high parameter was higher than the 97.5% percentile of the lower parameter.

Results

Our estimate of individual plant biomass, height \times diameter², accounted for 98% of the variation in final biomass. The numerical fitting method was successful in fitting the growth model (equation 1) to the *C. album* data (Table 1). A visual inspection of the data (Fig. 2) clearly indicates that the plants have stopped growing by the last measurement. As expected, the estimated maximum size of plants (α) decreased at the higher density (Table 1).

The use of the Richards growth model, which includes the additional shape parameter (δ) improved the fit of the model significantly ($P < 0.001$ for both densities; likelihood ratio tests against the logistic growth model). The shape of the growth curve was different at the two densities (Table 1), so that no simpler growth model with a fixed shape parameter satisfactorily described the growth curve over both densities. In both cases the hypothesis of logistic growth ($\delta = 2$) was rejected (Table 1).

The maximum likelihood estimate of the degree of asymmetric competition (a) was significantly greater than one at both densities and was significantly larger at the higher density (Table 1).

Discussion

Increased density reduced both the maximum size that plants could achieve, and the size at which plant growth began to deviate from exponential.

Competition among *Chenopodium album* individuals was always partially size-asymmetric. This seems to be the most common form of competition among

Table 1 Maximum likelihood estimates and 95% credibility intervals of the parameters in the individual-based Richards growth model (equations 1 and 3) fitted to the *Chenopodium album* growth data. The biomass of plants was assumed to be proportional to height (stem diameter²). Plants that died no longer contribute to the population's biomass (i.e. they no longer compete with living plants)

Plant density (plants m ⁻²)	κ	a	α	δ
400	0.0160 (0.0104–0.0324)	1.16 (1.07–1.22)	2460 (2200–2780)	0.80 (0.72–0.95)
800	0.0046 (0.0023–0.0062)	1.31 (1.27–1.39)	1070 (1030–1110)	0.43 (0.33–0.55)

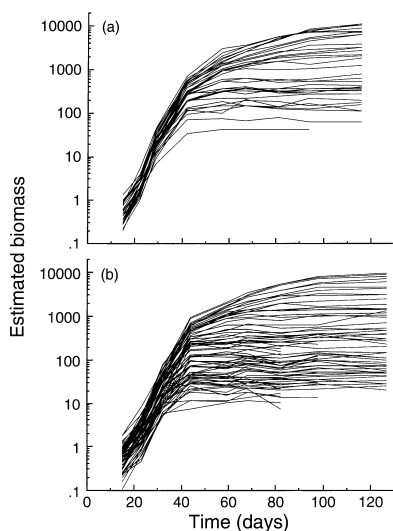


Fig. 2 Growth in estimated biomass (height \times diameter², arbitrary units, log scale) for the individual plants grown at 400 (a) and 800 (b) plants m⁻².

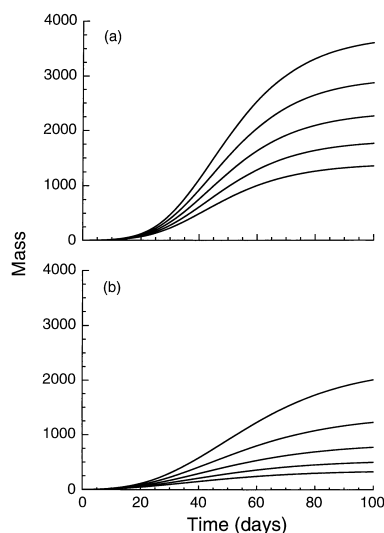


Fig. 3 Fit Richards curves for plants of five initial sizes (0.50, 0.55, 0.60, 0.65, 0.70) at 400 (a) and 800 (b) plants m⁻². A linear scale is used to show the effects of density clearly.

plants. Our data also provide support for the hypothesis that the degree of size-asymmetry increases with density. The advantage of being larger than other plants increases as the density increases (Fig. 3), i.e. the relationship between size and subsequent growth

(DMF or $G[t, x]$ function; Fig. 1) becomes more upwardly curved at higher densities.

Hara and Wyszomirski (1994) argued that including a measure of the degree of asymmetry as a parameter in a model cannot provide reliable empirical estimates of the degree of asymmetry in real populations, because models always improve in fit when an additional parameter is added. Modern statistical methods, such as the hierarchical models we use here, or Akaike's information criterion (Burnham & Anderson 1998) allow us to compare models with different numbers of parameters (e.g. models with and without an asymmetry parameter). In contrast to Hara and Wyszomirski, we argue that the inclusion of an asymmetry parameter is an important step in the modelling of plant stand development (Schwinning & Fox 1995).

Spatial models are becoming increasingly popular in plant ecology (e.g. Weiner & Conte 1981; Pacala & Deutschman 1995) and spatial models will be of increasing importance in the coming years (Tilman & Kareiva 1998). But in addition to the huge analytical obstacles confronting spatial modellers (Dieckmann *et al.* 2000), the collection of spatial data is itself extremely demanding and often impossible. It is important to develop alternative approaches, and to ask how far we can go in modelling plant population development without explicitly including space. We believe that the methods presented here represent an important step in this direction. It is possible that some of the effects demonstrated here are a result of the spatial pattern, but that must be considered an hypothesis at this point. It is possible to extend the present model to include spatial effects by including a term that describes the decrease in the competitive effect of plants on their neighbours with distance. The form of the distance decay can be described by a parameter that can be estimated, and alternative distance-decay models can be compared (C. Damgaard, unpublished data).

New computer-intensive statistical methods enable us to build and fit more biologically based models, i.e. models in which the parameters have biological meaning, and are therefore explanatory as well as predictive (Loehle 1983; Weiner 1995b). Such models can be used to explore the effects of different treatments on plant growth and competition, as well as to test specific hypotheses, as we have done here. In a classical statistical analysis of plant growth data, we ask if a treatment has a statistically significant effect, and, if so, how large

is its effect. This is sufficient for many scientific questions, e.g. does a treatment increase growth? In this classical 'statistical' approach the criteria for an analysis are sensitivity and statistical power. As scientific understanding develops further, one can begin to build quantitative models that reflect underlying biological processes. In this second approach, the criteria have more to do with biological information and explanation. One could liken the classical statistical approach to plant population development to showing that the acceleration of an object increases with the force applied to it. The second approach is more like testing the model that force equals mass times acceleration. New methods allow us to combine these two approaches, providing statistical tests for biologically meaningful parameters, thus giving us increased predictive power, while also increasing our mechanistic understanding of the biological processes involved.

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