

Logistic-based growth under resource limitation: equations, analytical solutions and applications

Alla N Seleznyova

The Horticulture and Food Research Institute of New Zealand Limited
Palmerston North Research Centre, Tennent Drive, Private Bag 11030
Palmerston North, 4474, NZ
aseleznyova@hortresearch.co.nz

Keywords: Logistic, model, growth, resource limitation, analytical solution, θ -logistic,

Introduction

Some recent functional-structural plant models (FSPMs) combine an explicit representation of plant architecture with a mechanistic approach to carbohydrate (C) allocation [1]. In this context, a plant is represented by a set of connected semi-autonomous modules and the C flow into the growing modules is determined by the intrinsic properties of the modules, environmental conditions and the sink/source interactions within the whole system [2]. While numerical methods for calculation of C flow within the plant are now available [3], there are no direct methods for dynamical modelling of resource limited growth of plant modules such as leaves and internodes. A logistic function [4]

$$a(t) = A(1 + \exp((t_0 - t)/\tau))^{-1}, \quad (1)$$

where t is time, A is an asymptote (final size of an organ/population), t_0 is an inflection point, and τ is a duration of rapid expansion phase, is often used for retrospective representation of the growth data and can be used in empirical modelling of growth. A differential equation (DE)

$$\frac{da(t)}{dt} = \frac{1}{\tau} a(t) \left(1 - \frac{a(t)}{A} \right), \quad (2)$$

often associated with logistic growth [5], is not suitable for use in mechanistic modelling, where the final size A is a result of the system dynamics and cannot be stated a priori. Thornley & France [6, 7] suggested modification of (2) for modelling limited growth

$$\frac{da_f(t)}{dt} = f_1 \cdot r \cdot a_f(t) \left(1 - \frac{a_f(t)}{A_f(t)} \right), \quad (3a)$$

where r is a parameter, $0 \leq f_1 \leq 1$ represents a degree of limitation on growth and $A_f(t)$ is a projected final size - a new state variable that can decrease depending on the growth limitation, according to the equation

$$\begin{cases} \frac{dA_f(t)}{dt} = -f_2 \cdot D(A_f(t) - a_f(t)) \\ A_f(0) = A \end{cases} \quad (3b)$$

where D is a parameter and $0 \leq f_2 \leq 1$ is interpreted as a degree of limitation of development and a maximum rate of development, respectively [7].

In the current paper I propose an alternative approach that is based on a single linear DE and does not include the notion of final size. I derive analytical solutions for growth responses to constant and pulse-like growth limiting conditions and show that this approach, although being simpler, is equivalent to the formulation of Thornley & France (3).

Linear equation for logistic growth

Derivation of equation (2), given in Thornley & Johnson [5], is based on three assumptions: 1) the growth machinery is proportional to current size $a(t)$, 2) the growth machinery works at a rate proportional to the amount of substrate $S(t)$, 3) there is no net gain or loss from the system, so that the current amount of substrate $S(t) = A - a(t)$, where A is an initial amount of the substrate. As a result, the growth is limited by the initial amount of substrate. The third assumption of this derivation does not hold for leaves and internodes of a growing shoot. These organs are connected to a common C pool; hence the amount of C available to each organ depends on the amount on photosynthesis and on competition with other organs. In addition, even when C is not limited, it does not result in indefinite growth of leaves and internodes; their growth curves can still be well approximated by the logistic function (1) [8]. According to experimental data on kiwifruit shoots, the parameter τ , which controls duration of expansion in these organs, depends mostly on temperature but not on C limitation [8]. Studies of leaf growth in wild-type and mutant of *Arabidopsis thaliana* under different light environments demonstrated a significant and robust negative correlation between the duration of expansion and the initial relative expansion rate [9]. Similar correlation, robust with respect to temperature, is established for kiwifruit growth under constant temperatures [8]. These results suggest the existence of an intrinsic growth pattern that originates within the organ and unfolds according to environmental conditions. This hypothesis is strongly supported by a controlled environment experiment on kiwifruit leaf growth under a set of step-wise changing temperature regimes (12/28/20 °C, 20/28/12 °C, etc.) [10]. The growth curves of leaves in this experiment plotted against time were not logistic and showed distinct changes in growth rates, corresponding to the step-wise temperature changes. However, when the measured leaf area data were plotted against a new variable

$$\varphi(t) = \int_0^t \frac{dz}{\tau(T(z))}, \quad (4)$$

where $T(t)$ is a time course of temperature, each growth curve was well fitted ($r^2 \cong 0.999$) by a logistic function $a(\varphi) = A(1 + \exp(\varphi - \varphi_0))^{-1}$, where $\varphi_0 = \varphi(t_0)$ is an inflection point. Apart from the final size, the growth curves for leaves grown under different temperature sequences differed only by the values of the inflection point φ_0 , which was determined by the time of leaf appearance.

Based on these results, I propose to represent the intrinsic growth pattern corresponding to logistic growth by a relative growth rate expressed as a function of organ developmental age, measured with respect to the inflection point, ($\alpha = \varphi - \varphi_0$). It follows from (4) that

$$\alpha = (t - t_0)/\tau \text{ for } T(t) = \text{const}. \quad (5)$$

For simplicity and for ease of comparison with existing results, in the following derivations I assume that $T(t) = \text{const}$ and use time rather than φ as an independent variable in equations. However these derivations can be generalised for the case of variable temperature using φ as an independent variable. From (1) relative growth rate can be expressed in a form that depends on α but not on the final size parameter A , leading to a linear DE for $a(t)$. Namely,

$$\frac{da(t)}{dt} = g(t)a(t), \quad (6a)$$

where

$$g(t) \equiv \frac{1}{\tau(1 + \exp((t - t_0)/\tau))} \quad (6b)$$

is a relative growth rate determined by the organ age (5). The solution of (6) with an initial condition $a(t_a)$, where t_a is a time of organ appearance, can be presented in the form

$$a(t) = a(t_a)G(t_a, t), \quad (7a)$$

where

$$G(t_1, t_2) = \exp\left(\int_{t_1}^{t_2} g(s) ds\right) = (1 + \exp((t_0 - t_1/\tau))(1 - \tau \cdot g(t_2))), \quad (7b)$$

is a function that propagates the solution from t_1 to t_2 . Formulation (6) corresponds to the case when the C is not limited and the growth is limited by an intrinsic growth rate depending on the organ age. Resource limitation on growth is modelled by introducing a multiplier $0 < f \leq 1$ into the right-hand side of (6a), namely

$$\frac{da_f(t)}{dt} = f \cdot a_f(t)g(t). \quad (8)$$

In the context of transport-resistance sink-source allocation models, f is interpreted as a sink response to C limitation and is usually represented by a non-linear function of C concentration in the vicinity of the sink [2, 3].

Analytical solutions and applications

Constant C limitation For $f = \text{const}$ (8) can be solved analytically using a substitution

$$a_f(t) = (y(t))^f \quad (9)$$

and noting that $y(t)$ satisfies (6a). This gives

$$a_f(t) = a(t_a)(G(t_a, t))^f = a(t)(G(t_a, t))^{f-1}. \quad (10)$$

The upper asymptote of this solution (the final size) $A_f = a(t_a)(G(t_a, \infty))^f$ can be expressed in terms of the final size $A = a(t_a)G(t_a, \infty)$ for unlimited growth, namely

$$A_f = (a(t_a))^{(1-f)} A^f. \quad (11)$$

This solution coincides with a particular case of the well-known Richards function [11] or θ -logistic [7]. Note that in the current formulation the final size is a function of the initial size, initial developmental age and the growing conditions. Hence the potential to reach a certain size is included via the initial conditions.

Fig. 1 shows the effects of growth limitation on the characteristics of the solution (10), time interval between appearance and inflection ($\mu_f = t_{0f} - t_a$), duration of growth defined as a time interval d_f between the organ appearance and reaching a fraction δ of final size (e.g. $\delta = 0.95$), $\rho_f = d_f - \mu_f$ and final A_f . In the vicinity of $f = 1$, the final size A_f is very sensitive to the value of f (Fig. 1b), while the effects on time characteristics are relatively small (Fig. 1a). The current analysis is in agreement with a recent study of leaf growth in kiwifruit [8] and explains that, even when leaf size was the most reduced by fruit presence, no deviation from logistic growth pattern was detected in the growth data. Indeed, the shape of the solution (10) is extremely robust in the vicinity of $f = 1$, e.g., for $f = 0.8$ the final size is considerably reduced, while the theoretical growth curve is practically undistinguishable from the fitted logistic (Fig. 1a).

Pulse-like C limitation. Note first that function G satisfies the following relationship,

$$G(t_1, t_2) \cdot G(t_2, t_3) = G(t_1, t_3) \quad (12)$$

graphically illustrated in Fig. 2a. A graphical solution of (8) for a pulse-like perturbation, where resources are limited $f < 1$ for a period of time (t_1, t_2) , is shown in Figs. 2b,c and gives

$$a_f(t) = (G(t_1, t_2))^{f-1} a(t) \quad (13)$$

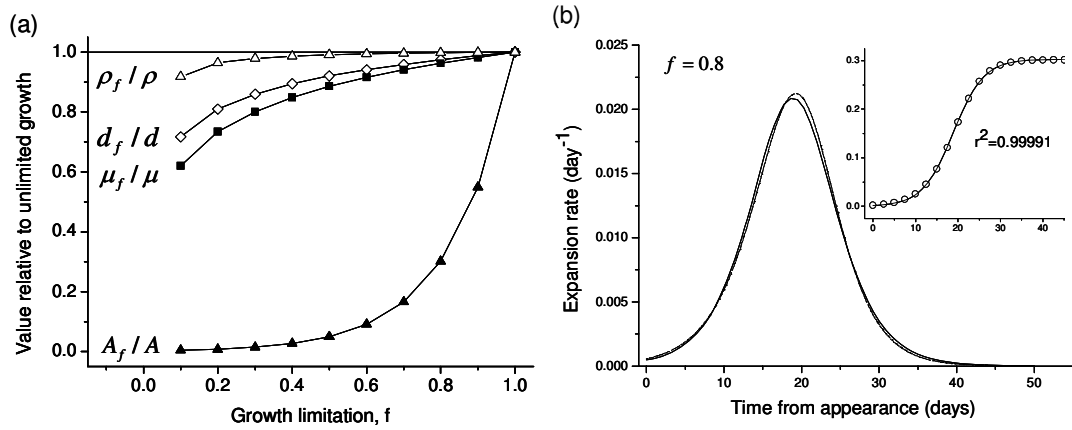


Figure 1. Properties of resource-limited growth (a) Effect of f on growth characteristics A_f , μ_f , d_f , and ρ_f (relative values of these variables with respect to values for unlimited growth A , μ , d , and ρ are shown) (b) Growth curve (open circles) and its derivative (dotted line) for $f = 0.8$, solid lines are the fitted logistic (1) (insert graph) and its derivative (main graph).

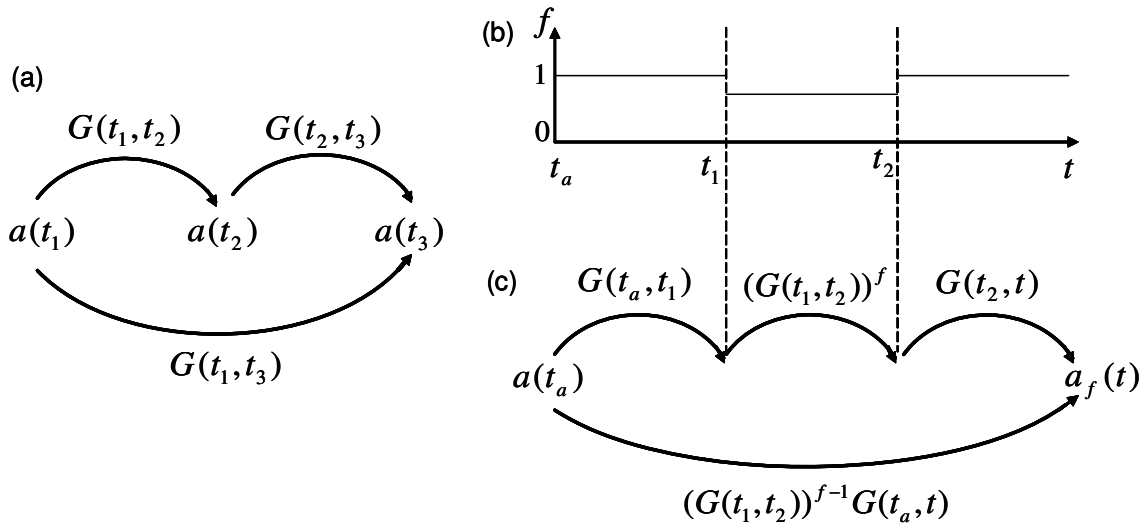


Figure 2. Growth under pulse-like perturbation of C supply (a) Schematic of the equation (12) (b) Pulse-like perturbation of C with $f < 1$ for $t_1 < t < t_2$ (c) Solution of (8) for this case.

Comparison with the approach by Thornley & France. Within the current approach, the projected final size variable $A_f(t)$, introduced by Thornley & France [6, 7], can be interpreted as an asymptote of the solution for the case where C limitation applies from the moment of appearance to the moment t , namely

$$A_f(t) = (G(t_a, t))^{f-1} A. \quad (14)$$

Substitution of $A_f(t)$ and $a_f(t)$ (10) into the system (3) and some rearrangements, show that these functions satisfy system (3) if and only if

$$f = \frac{f_1 \cdot r}{f_1 \cdot r + f_2 \cdot D} \quad \text{and} \quad \tau = \frac{1}{f_1 \cdot r + f_2 \cdot D}. \quad (15)$$

Although the approach by Thornley & France has four parameters, there are only two degrees of freedom in the parameter space, because the parameters enter equations (3) in the form of two products ($f_2 \cdot D$) and ($f_1 \cdot r$). For any given values of τ and f , the corresponding values of these products can be calculated from (15). Hence, the system (3) is equivalent to a single linear DE (8) with two parameters: τ - representing effects of environment (temperature) and f - representing effects of resource limitation.

Further extensions. Using variable φ (4), equation (8) can be generalised for the case of variable temperature. Taking advantage of linearity of this equation, analytical solution can be obtained for time-dependent $f = f(t)$. The present approach can be extended to the Boltzmann function that is also used in plant modelling [8] using a substitution $y(t) = a(t) - B$, where B is a lower asymptote of the Boltzmann function.

Conclusions

The simple linear DE proposed here allows intrinsic patterns of leaf and internode growth, temperature effects and C limitation to be taken into account. In the context of mechanistic modelling, C availability within the vicinity of each module is a result of the system dynamics, hence the equations describing the growth of individual modules are solved simultaneously and C distribution within the system is determined as a part of the solution process [2, 3]. Numerical solutions for such systems are not always easy to interpret. Analytical solutions provide an additional insight into the problem. They are more transparent and allow analysis of relationships between the system variables as well as comparisons with other systems. The linear DE proposed here is equivalent to a non-linear system (3) proposed previously by Thornley & France [6]. This DE can be also used as a linear DE corresponding to the Richards function [11], also known as θ -logistic or a “power-law logistic” [6, 7], allowing a mechanistic interpretation of these functions.

Acknowledgements

This study was supported by New Zealand Foundation for Science Research and Technology, contract C06X0202.

References

- [1] Godin C, Sinoquet H 2005. Functional-structural plant modelling. *New Phytologist* 166: 705-708.
- [2] Allen MT, Prusinkiewicz P, DeJong TM 2005. Using L-systems for modeling source-sink interactions, architecture and physiology of growing trees: the L-PEACH model. *New Phytologist* 166(3): 869-880.
- [3] Prusinkiewicz P, Allen MT, Escobar-Gutiérrez A, DeJong TM 2007. Numerical methods for transport-resistance sink-source allocation models. In: Vos J, Marcelis LFM, de Visser PHB, Struik PC, Evers JB ed. *Functional-structural plant modelling in crop production*. Berlin, Springer. Pp. 123-137.
- [4] Causton DR, Venus JR 1981. *The Biometry of Plant Growth*. London, Arnold
- [5] Thornley JHM, Johnson IR 1990. *Plant and crop modelling: a mathematical approach to plant and crop physiology*. Oxford, UK, Clarendon Press.
- [6] Thornley JHM and France J 2005. An open-ended logistic-based growth function. *Ecological Modelling* 184(2-4): 257-261.
- [7] Thornley JHM, Shepherd J, France J 2007. An open-ended logistic-based growth function: analytical solutions and the power-law logistic model. *Ecological Modelling*. 204 (3): 531-534.
- [8] Seleznyova AN, Greer DH 2007. Integrating developmental variables into process based modelling. Submitted for publication.
- [9] Cookson SJ, Lijsebetens MV, Granier C 2005. Correlation between leaf growth variables suggest intrinsic and early controls of leaf size in *Arabidopsis thaliana*. *Plant, Cell and Environment* 28(11): 1355-1366
- [10] Seleznyova AN, Halligan EA 2006. Modelling effect of temperature on area expansion at the leaf, the shoot and whole plant level. *Acta Horticulturae* 707: 167-174.
- [11] Richards FJ 1959. A flexible growth function for empirical use. *Journal of Experimental Botany* 10: 290-300.