Analytical growth equations and their Genstat 5 equivalents

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Abstract

This paper compares two ways of representing some of the existing growth functions, i.e., the exponential, the monomolecular or Mitscherlich, the logistic or autocatalytic, the Gompertz, and the Richards equations. A second order exponential polynomial will be discussed as well. In the first expression growth is expressed in the parameters mass at time zero W_0, mass at time infinity W_f, and a measure for the relative growth rate k. In the second expression different parameters are used because of robust parameter optimization (e.g., by the statistical software package Genstat). This paper shows the relationships between these fitted parameters and the parameters W_0, W_f and k. This paper addresses the properties of these models, such as physical meaning of the parameters, properties at the point of inflection (if existing), and the growth rate in the limit $W \rightarrow 0$. The second order exponential polynomial is rewritten in such way that use is made of a proportionality constant, being equal to the relative growth rate at point of inflection. Application of the growth models is demonstrated using data of lettuce grown on nutrient film. Finally, it is shown that, except for the exponential polynomial, all growth equations originate from one single equation.

Keywords: growth rate, relative growth rate, analytical growth equation, exponential growth, monomolecular or Mitscherlich growth, logistic or autocatalytic growth, Gompertz growth, Richards or general logistic growth, exponential polynomial growth, point of inflection

Introduction

Growth of a crop involves uptake of water and nutrients. Because nutrients are taken up by the plant to be incorporated in new plant material, study of the increase in plant mass gives a first idea of the need of nutrients by the plant. In case a nutrient constitutes a constant fraction of the plant mass, the uptake rate is proportional to the growth rate of the plant.

Descriptions of growth rate, i.e. increase in plant mass with time, can be given either by physiological mechanistic models or by empirical or mathematical functions. Mechanistic models are mostly used to predict growth, while mathematical functions are mostly used to describe afterwards observed increase in mass. By fitting the observed data to the relatively simple mathematical functions, the parameters appear-

ing in these functions are optimized. It appears that there are several ways to represent the same mathematical function. That means that the parameters appearing in each representation of the same function are linked to each other. This paper describes a few mathematical growth functions that appear in the literature. These functions are formulated using parameters with a physiological meaning that can be identified as mass at time zero, mass at time infinity, and a proportionality constant that is a measure for the relative growth rate. These functions appear also in a specific statistical package (i.c. Genstat 5; Anon., 1993), but then they are formulated in a different way, for reasons of robust parameter optimization. The aim of this paper is to show how the parameters appearing in the two descriptions of the same mathematical function are related, and to show some of the properties of these functions. As a demonstration, examples of fitting growth and nutrient uptake data to some of these functions are presented. Finally it is shown that most of the growth functions used in this paper belong to one family of equations. This paper is not meant to give a review of existing growth functions; such reviews can be found in existing handbooks (e.g., Charles-Edwards *et al.*, 1986; France and Thornley, 1984; Hunt, 1978, 1982).

Mathematical growth models

All growth models considered in this study explicitly express the plant mass as a function of time. They are, however, empirical models, i.e., growth is not explained in terms of physiological processes. Only later the parameters of these growth equations can be given a physiological meaning. For this study use is made of standard references (Charles-Edwards *et al.*, 1986; France and Thornley, 1984; Hunt, 1978, 1982).

In general, the growth rate will be the starting point, i.e. the change in plant mass W (M) with time t (T) dW/dt, or the growth rate per unit plant mass $(1/W)(dW/dt)$, known as the relative or specific growth rate or sometimes proportional growth rate. Here growth is considered to be a function of the plant mass already formed:

$$\frac{dW}{dt} = f(W). \tag{1}$$

Now the question remains how this function $f(W)$, which relates dW/dt and W, looks like. Several functions $f(W)$ will be considered, typically those that are present in Genstat 5 (Anon., 1993). For each of the functions the following expressions and properties will be determined.

A The main part of the model is the expression for $W(t)$, which is obtained by integrating the expression for dW/dt between the limits $t = 0$, $W = W_0$ and $t = t$, $W = W$. The main parameters appearing in these equations are given a physiological meaning, such as the weight W_0 at $t = 0$, the weight W_f at $t \rightarrow \infty$, and the growth rate proportionality constant k, which is a measure for the relative growth rate.

B Some of the models have an inflection point. The plant mass W^* and time t^* at the inflection point are obtained by solving $d^2W/dt^2 = 0$ for W and t, respectively.
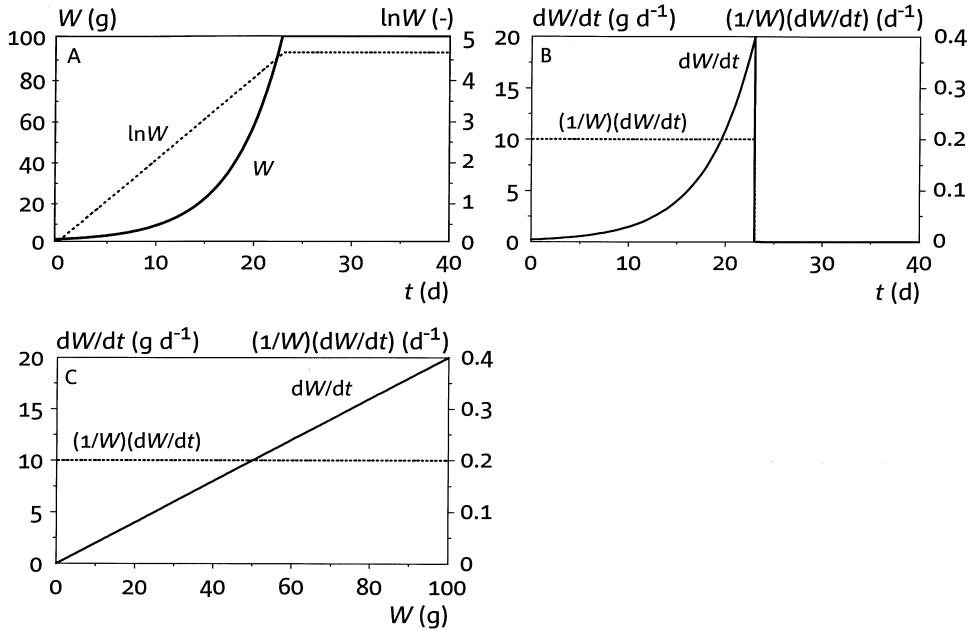
Figure 1. Exponential growth: (A) W_e and $\ln W_e$ as a function of t, (B) dW_e/dt and $(1/W_e)(dW_e/dt)$ as a function of t, and (C) as function of W_e; with $W_{e0} = 1$ g, $W_{ef} = 100$ g, $k_e = 0.2$ d^{-1}.

Substituting W^* into the expressions for growth rate and relative growth rate yields values for these rates at the inflection point, $(dW/dt)^*$ and $((1/W)(dW/dt))^*$, respectively.

C One expects the growth rate for $W \rightarrow 0$ to be finite. To check this, the limit for $W \rightarrow 0$ of dW/dt is determined, and for comparison also the limit for $W \rightarrow 0$ of $(1/W)(dW/dt)$ is given.

The aspects of A are described in the forthcoming sections. The six models considered are: *exponential*, *monomolecular or Mitscherlich*, *logistic or autocatalytic*, *Gompertz*, *Richards or general logistic*, and *second order exponential polynomial* growth. The common parameters appearing in all models will be distinguished by the subscripts e, m, l, g, r, and p, respectively. For convenience, all main symbols with their dimensions are described in Table 1 and not in the text, and the expressions for $W(t)$ are summarized in Table 2. The properties mentioned in B and C are listed in Table 3, and will not be discussed in the text. Finally, for all models graphical representations are given of W, $\ln W$, dW/dt and $(1/W)(dW/dt)$ as a function of t, and of dW/dt and $(1/W)(dW/dt)$ as a function of W. In all models the lower asymptote is absent.

Exponential growth

The growth rate is proportional to the amount of plant mass already formed. Growth is irreversible and stops at a certain time, t_f (T), e.g. when one of the growth factors

Table 1. Description of symbols used in text including their dimensions (M: mass, T: time, 1: dimensionless).

Symbol	Description	Dimension
A	Dummy parameter (Eq. (63), and Appendix A)	1
B	Dummy parameter (Appendix A)	M^{n-1}
W	Plant mass	M
Y	Plant mass	M
a,b,c,d	Constants in exponential polynomial (non-subscripted)	$1, T^{-1}, T^{-2}, T^{-3}$
a,b,c	Parameters in section 'Equivalent expressions for growth models' (subscripted); a represents the lower asymptote, $(a+c)$ represents the upper asymptote, and b is a measure for the slope	M, T^{-1}, M
k	Proportionality constant	T^{-1}
k_l'	Proportionality constant (for logistic growth only)	$M^{-1}T^{-1}$
k_g	Non-constant proportionality constant (for Gompertz growth only)	T^{-1}
m	Time of inflection	T
n	Dimensionless constant	1
p	Dimensionless constant	1
r	Dimensionless parameter	1
t	Time	T
t_f	Time when growth stops (for exponential growth only)	T
t_{mi}	Last time of measurement interval	T
t_s	The second order exponential polynomial is symmetrical at time $t = t_s$	T
y	Expected value of Y	M
α, β, γ	Parameters in universal growth equation (Eq. (61)); dimensions depend on choice of growth function (see, e.g., Table 6)	
ε	Constant (used in ln-transformation of exponential polynomial growth)	1
μ, ν	Curve shape parameters	$1, T^{-1}$
σ	A stochastic deviation	M

Sub- and superscripts

*	Property at inflection point	
0	Property at $t = 0$	
1	Referring to some time at start of growth period	
2	Referring to some time at end of growth period	
e	Reference to the exponential growth function	
f	Property for $t \to \infty$; for exponential growth: $t = t_f$	
g	Reference to the Gompertz growth function	
l	Reference to the logistic or autocatalytic growth function	
m	Reference to the monomolecular or Mitscherlich growth function (not in t_m)	
p	Reference to the exponential polynomial growth function	
r	Reference to the Richards growth function	
t	ln-transformed data (exponential polynomial growth)	

Mathematical operators

d	Derivative operator	
e, exp	Natural base	
lim	Limit operator	
$f()$	Any functional relationship	
ln	Natural logarithm	
$\int$	Integral operator	

Table 2. Names, expressions for $W(t)$, and reference to equation number in text for the growth equation used in this paper.

Model	Expression for $W(t)$	Eq.
Exponential	$W_e(t) = \begin{cases} W_{e0}e^{k_e t} & 0 \leq t < t_f \\ W_{ef} & t_f \leq t \end{cases}$	(4)
Monomolecular or Mitscherlich	$W_m(t) = W_{mf} - (W_{mf} - W_{m0})e^{-k_m t}.$	(7)
Logistic or autocatalytic	$W_l(t) = \dfrac{W_{l0}W_{lf}}{W_{l0} + (W_{lf} - W_{l0})e^{-k_l t}}$	(10)
Gompertz	$W_g(t) = W_{g0}e^{\frac{k_{g0}}{k_g}\left(1-e^{-k_g t}\right)} = W_{gf}e^{-\frac{k_{g0}}{k_g} e^{-k_g t}}$	(15, 17)
Richards or general logistic	$W_r(t) = \dfrac{W_{r0}W_{rf}}{(W_{r0}^n + (W_{rf}^n - W_{r0}^n)e^{-k_r t})^{\frac{1}{n}}}, \; n \geq -1$	(23)
Second order exponential polynomial	$W_p(t) = W_{p0}e^{k_p^2 t(t_s - 0.5t)} = W_{pf}e^{-0.5k_p^2 t(t_s - t)^2}$	(43)

becomes depleted (c.f. Liebig's law of the minimum) (Figure 1). The growth rate is given by

$$\frac{\mathrm{d}W_e}{\mathrm{d}t} = \begin{cases} k_e W_e & 0 \leq t < t_f \\ 0 & t_f \leq t \end{cases}, \tag{2}$$

and the relative growth rate is given by

$$\frac{1}{W_e} \frac{\mathrm{d}W_e}{\mathrm{d}t} = \begin{cases} k_e & 0 \leq t < t_f \\ 0 & t_f \leq t \end{cases}. \tag{3}$$

Integrating Eq. (2) yields (Figure 1)

$$W_e(t) = \begin{cases} W_{e0}e^{k_e t} & 0 \leq t < t_f \\ W_{ef} & t_f \leq t \end{cases}. \tag{4}$$

From Eq. (4) expressions for t_f or k_e can be derived.

Monomolecular or Mitscherlich growth

The mathematical representation of monomolecular growth is borrowed from physical-chemistry, where it describes a first order irreversible chemical reaction. In plant nutrition and soil fertility it is also known as the Mitscherlich growth (Mitscherlich,

Table 3. Some characteristic properties at the inflection point (if existing), i.e. weight W^*, time t^*, growth rate $(dW/dt)^*$ and relative growth rate $((1/W)(dW/dt))^*$, and the growth rate and relative growth rate in the limit $W \to 0$ for the exponential (Eq. (4)), the monomolecular (Eq. (7)), the logistic (Eq. (10)), the Gompertz (Eqs. (15) + (17)), the Richards (Eq. (23)), and the second order exponential polynomial (Eq. (43)) growth models.

Model	W^*	t^*	$\left(\dfrac{dW}{dt}\right)^*$	$\left(\dfrac{1}{W}\dfrac{dW}{dt}\right)^*$	$\lim\limits_{W\to 0}\left(\dfrac{dW}{dt}\right)$	$\lim\limits_{W\to 0}\left(\dfrac{1}{W}\dfrac{dW}{dt}\right)$
Exponential					0	k_e
Monomolecular					$k_m W_{mf}$	∞
Logistic	$\dfrac{W_{lf}}{2}$	$\dfrac{1}{k_l}\ln\left(\dfrac{W_{lf}-W_{l0}}{W_{l0}}\right)$	$k_l\,\dfrac{W_{lf}}{4}$	$\dfrac{k_l}{2}$	0	k_l
Gompertz	$\dfrac{W_{gf}}{e}$	$\dfrac{1}{k_g}\ln\left(\ln\left(\dfrac{W_{gf}}{W_{g0}}\right)\right)$	$k_g\,\dfrac{W_{gf}}{e}$	k_g	0	∞
Richards	$\dfrac{W_{rf}}{(n+1)^{\frac{1}{n}}}$	$\dfrac{1}{k_r}\ln\left(\dfrac{W_{rf}^{n}-W_{r0}^{n}}{W_{r0}^{n}}\right)$	$k_r\,\dfrac{W_{rf}}{(n+1)^{1+\frac{1}{n}}}$	$\dfrac{k_r}{n+1}$	$\begin{cases}0 & n>-1\\ k_r W_{rf} & n=-1\end{cases}$	$\begin{cases}0 & n\le 0\\ \dfrac{k_r}{n} & n>0\end{cases}$
Second order exponential polynomial	$\dfrac{W_{pf}}{\sqrt{e}}$	$\dfrac{1}{k_p}\left(\sqrt{2\ln\left(\dfrac{W_{pf}}{W_{p0}}\right)}-1\right)$	$k_p\,\dfrac{W_{pf}}{\sqrt{e}}$	$k_p \equiv \dfrac{1}{t_s}=\sqrt{2\ln\left(\dfrac{W_{pf}}{W_{p0}}\right)}$ $=\sqrt{\dfrac{b}{t_s}}=\sqrt{-2c}$	0	∞

1928). Growth is irreversible, and the growth rate is proportional to the difference between the asymptotic maximum plant mass W_{mf} and the plant mass already formed W_m according to (Figure 2)

$$\frac{dW_m}{dt} = k_m(W_{mf} - W_m), \tag{5}$$

and the relative growth rate is given by

$$\frac{1}{W_m}\frac{dW_m}{dt} = k_m\left(\frac{W_{mf}}{W_m} - 1\right). \tag{6}$$

Integrating Eq. (5) yields (Figure 2)

$$W_m(t) = W_{mf} - (W_{mf} - W_{m0})e^{-k_m t}. \tag{7}$$

The proportionality constant k_m can be expressed in terms of the parameter W_{mf} (Table 3).

Logistic or autocatalytic growth

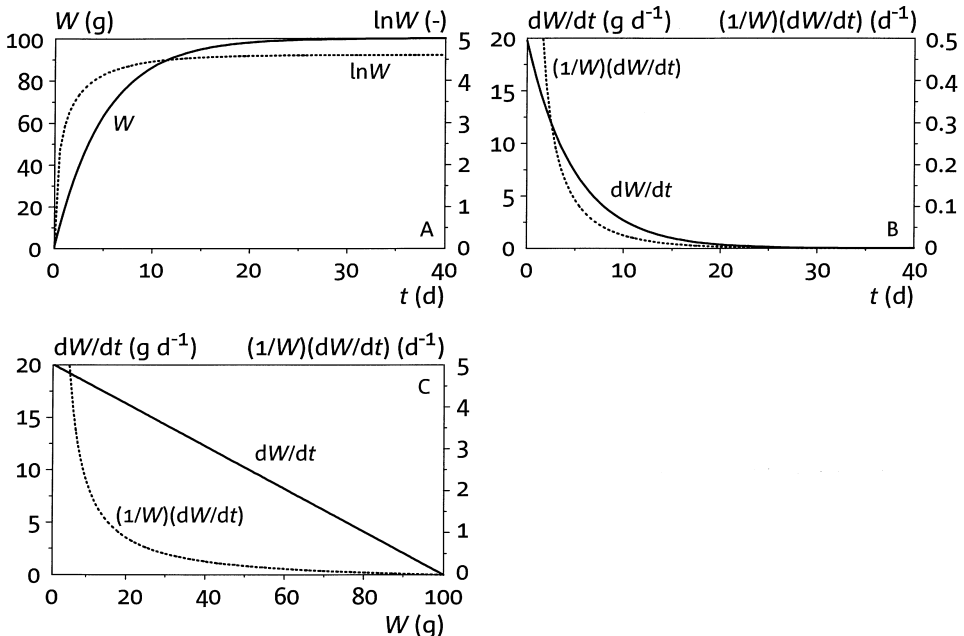The growth rate of the logistic growth model is a combination of the growth rates of

Figure 2. Monomolecular or Mitscherlich growth: (A) W_m and ln W_m as a function of t, (B) dW_m/dt and $(1/W_m)(dW_m/dt)$ as a function of t, and (C) as a function of W_m; with $W_{m0} = 1$ g, $W_{mf} = 100$ g, $k_m = 0.2$ d^{-1}.

the exponential and the monomolecular growth models. The growth rate is irreversible and it is proportional to W_l and the difference between the asymptotic maximum W_{lf} and W_l (Figure 3):

$$\frac{dW_l}{dt} = k_l' W_l (W_{lf} - W_l) = k_l W_l \left(1 - \frac{W_l}{W_{lf}}\right). \tag{8}$$

The relative growth rate is given by

$$\frac{1}{W_l} \frac{dW_l}{dt} = k_l'(W_{lf} - W_l) = k_l \left(1 - \frac{W_l}{W_{lf}}\right), \tag{9}$$

where $k_l = k_l'/W_{lf}$. Integrating Eq. (8) (see Appendix A) yields (Figure 3)

$$W_l(t) = \frac{W_{l0} W_{lf}}{W_{l0} + (W_{lf} - W_{l0}) e^{-k_l t}}. \tag{10}$$

Logistic growth has an inflection point (Table 3). From Eqs. (8) or (9) with $W_l = W_l^*$ it follows that k_l is a measure for the (relative) growth rate at the point of inflection (Table 3).
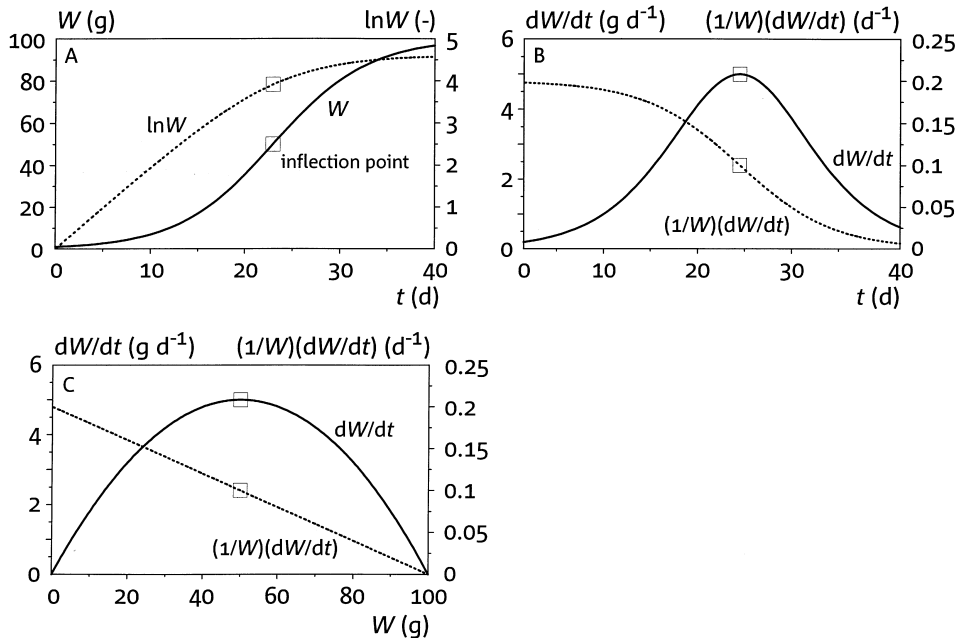

Figure 3. Logistic growth: (A) W_l and ln W_l as a function of t, (B) dW_l/dt and $(1/W_l)(dW_l/dt)$ as a function of t, and (C) as a function of W_l; with $W_{l0} = 1$ g, $W_{lf} = 100$ g, $k_l = 0.2$ d^{-1}.

Gompertz growth

B. Gompertz introduced in 1825 (as mentioned by Hunt, 1982) a growth model, in which the growth factors are non-limiting. The growth rate is proportional to W_g and the relative growth rate decreases with time according to first-order kinetics (exponential decrease)

$$\frac{\mathrm{d}W_g}{\mathrm{d}t} = k_g'W_g, \tag{11}$$

where k_g' decreases exponentially in time (e.g., due to aging or differentiation) according to

$$\frac{\mathrm{d}k_g'}{\mathrm{d}t} = -k_g k_g', \tag{12}$$

where k_g is a proportionality constant (T^{-1}). The result of integrating Eq. (12) between the limits $t = 0$, $k_g' = k_{g0}$ and $t = t$, $k_g' = k_g'$ introduced in Eq. (11) yields (Figure 4)

$$\frac{\mathrm{d}W_g}{\mathrm{d}t} = k_{g0}W_g\mathrm{e}^{-k_g t}, \tag{13}$$

and the relative growth rate is given by
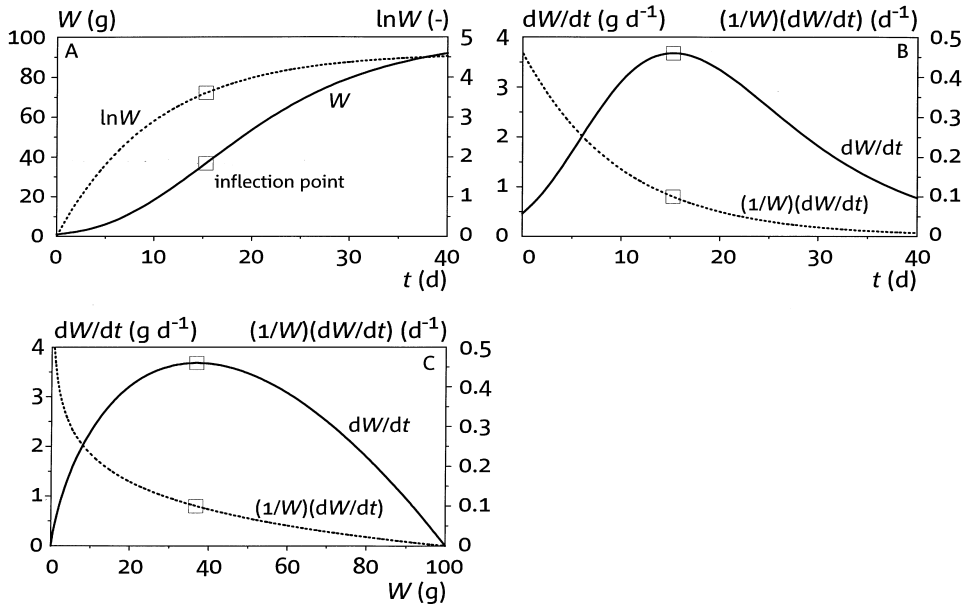
Figure 4. Gompertz growth: (A) W_g and ln W_g as a function of t, (B) $\mathrm{d}W_g/\mathrm{d}t$ and $(1/W_g)(\mathrm{d}W_g/\mathrm{d}t)$ as a function of t, and (C) as a function of W_g; with $W_{g0} = 1$ g, $W_{gf} = 100$ g, $k_g = 0.1$ d^{-1}.

$$\frac{1}{W_g}\ \frac{\mathrm{d}W_g}{\mathrm{d}t}\ = k_{g0}\mathrm{e}^{-k_g t}. \tag{14}$$

Integrating Eq. (13) yields (Figure 4)

$$W_g(t) = W_{g0}\mathrm{e}^{\frac{k_{g0}}{k_g}\left(1-\mathrm{e}^{-k_g t}\right)}. \tag{15}$$

Since for $t \rightarrow \infty$, $W_g = W_{gf}$ it follows that

$$W_{gf} = W_{g0}\mathrm{e}^{\frac{k_{g0}}{k_g}}. \tag{16}$$

Introducing Eq. (16) into Eq. (15) yields (Figure 4)

$$W_g(t) = W_{gf}\mathrm{e}^{-\frac{k_{g0}}{k_g}\ \mathrm{e}^{-k_g t}}. \tag{17}$$

Equation (17) can also be obtained directly by integrating Eq. (13) between the limits $t = t$, $W_g = W_g$ and $t = t_f \rightarrow \infty$, $W_g = W_{gf}$. From Eq. (16) it follows that

$$k_{g0} = k_g\ln\left(\frac{W_{gf}}{W_{g0}}\right). \tag{18}$$

Equation (13) is still not of the form of Eq. (1), i.e. a function of W_g only, because time t is still included. This can be obtained by extracting an expression for $\exp(-k_g t)$ from Eq. (15) and substituting this result into Eq. (13) yielding (without or with using Eq. (16); Figure 4)

$$\frac{\mathrm{d}W_g}{\mathrm{d}t} = W_g\left(k_{g0} - k_g\ln\left(\frac{W_g}{W_{g0}}\right)\right) = k_g W_g\ln\left(\frac{W_{gf}}{W_g}\right), \tag{19}$$

and the relative growth rate is given by

$$\frac{1}{W_g}\ \frac{\mathrm{d}W_g}{\mathrm{d}t}\ = k_{g0} - k_g\ln\left(\frac{W_g}{W_{g0}}\right) = k_g\ln\left(\frac{W_{gf}}{W_g}\right). \tag{20}$$

Gompertz growth has an inflection point (Table 3). From Eqs. (19) or (20) with $W_g = W_g^*$ it follows that k_g is a measure for the (relative) growth rate at the inflection point (Table 3).

Richards or general logistic growth

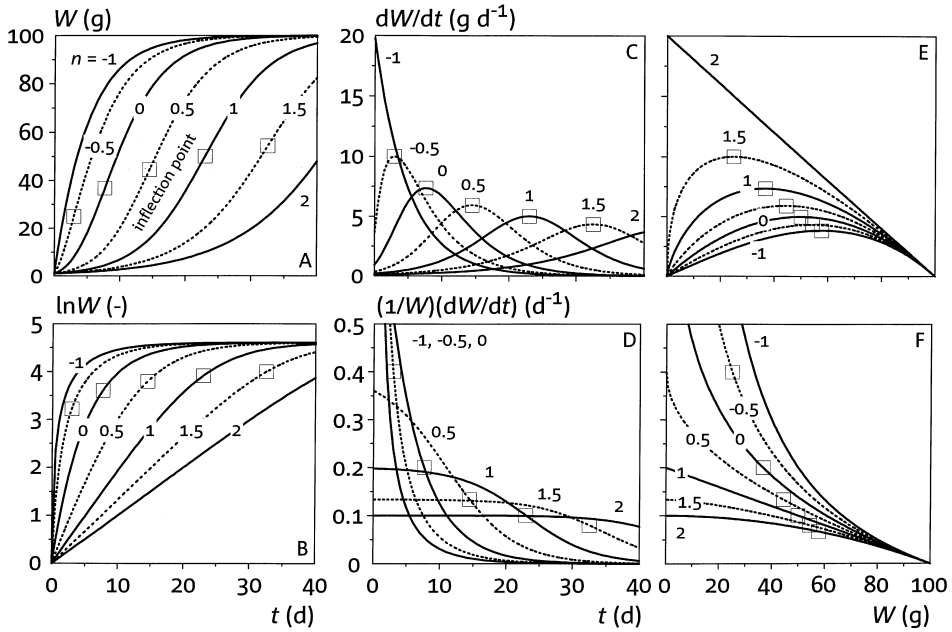Richards (1959) introduced a generalization of the above mentioned logistic model (Figure 5)

Figure 5. Richards or general logistic growth: (A) W_r, (B) $\ln W_r$, (C) dW_r/dt, and (D) $(1/W_r)(dW_r/dt)$ as a function of t, and (E) dW_r/dt and (F) $(1/W_r)(dW_r/dt)$ as a function of W_r; with $W_{r0} = 1$ g, $W_{rf} = 100$ g, $k_r = 0.2$ d^{-1} for several values of the dimensionless n parameter: $n = -1, -0.5, 0, 0.5, 1, 1.5, 2$.

$$\frac{dW_r}{dt} = k_r W_r \frac{W_{rf}^n - W_r^n}{n W_{rf}^n} = \frac{k_r}{n} W_r \left(1 - \left(\frac{W_r}{W_{rf}}\right)^n\right), \tag{21}$$

and the relative growth rate is given by

$$\frac{1}{W_r} \frac{dW_r}{dt} = k_r \frac{W_{rf}^n - W_r^n}{n W_{rf}^n} = \frac{k_r}{n} \left(1 - \left(\frac{W_r}{W_{rf}}\right)^n\right), \tag{22}$$

where the dimensionless constant n must be larger than -1, since then the growth rate in the limit $W_r \to 0$ is finite (see below). Integrating Eq. (21) (see Appendix A) (Figure 5) yields

$$W_r(t) = \frac{W_{r0} W_{rf}}{(W_{r0}^n + (W_{rf}^n - W_{r0}^n)e^{-k_r t})^{\frac{1}{n}}}, \quad n \geq -1. \tag{23}$$

The Richards growth equation includes some special cases. For $n = 1$ Eq. (23) reduces to the logistic model (Eq. (10)). Substituting $n = -1$ in Eq. (23) and using simple algebra one obtains the monomolecular or Mitscherlich growth curve (Eq. (7)). For $n = 0$ it represents the Gompertz model, as is shown next. By taking the limit $n \to 0$ of dW_r/dt and by using the expansion series for x^n (with $x = W_r/W_{rf}$), it can be shown that this limit corresponds to Eq. (19):

$$\lim_{n\to 0} \frac{\mathrm{d}W_r}{\mathrm{d}t} = \lim_{n\to 0} k_r W_r \left(\frac{1}{n} - \frac{1}{n}\left(\frac{W_r}{W_{rf}}\right)^n \right). \tag{24}$$

The expansion for x^n is

$$x^n = e^{n\ln x} = 1 + \frac{n\ln x}{1!} + \frac{(n\ln x)^2}{2!} + \frac{(n\ln x)^3}{3!} + \dots, \tag{25}$$

so that Eq. (24) can be written analogous to Eq. (19), i.e.,

$$\lim_{n\to 0} \frac{\mathrm{d}W_r}{\mathrm{d}t} = -k_r W_r \left(\ln\left(\frac{W_r}{W_{rf}}\right) + \frac{n}{2!}\left(\ln\left(\frac{W_r}{W_{rf}}\right)\right)^2 + \frac{n}{3!}\left(\ln\left(\frac{W_r}{W_{rf}}\right)\right)^3 + \dots \right) = k_r W_r \ln\left(\frac{W_{rf}}{W_r}\right). \tag{26}$$

The Richards model has an inflection point (Table 3; Figure 6; $n > -1$). For $n = 1$ and $n = 0$ the inflection points of the logistic and the Gompertz model are obtained. For $n > -1$, the limit $W_r \to 0$ of $\mathrm{d}W_r/\mathrm{d}t$ equals

$$\lim_{W_r\to 0} \frac{\mathrm{d}W_r}{\mathrm{d}t} = -\frac{k_r}{nW_{rf}^n} \lim_{W_r\to 0} W_r^{n+1} = 0, \quad n > -1. \tag{27}$$
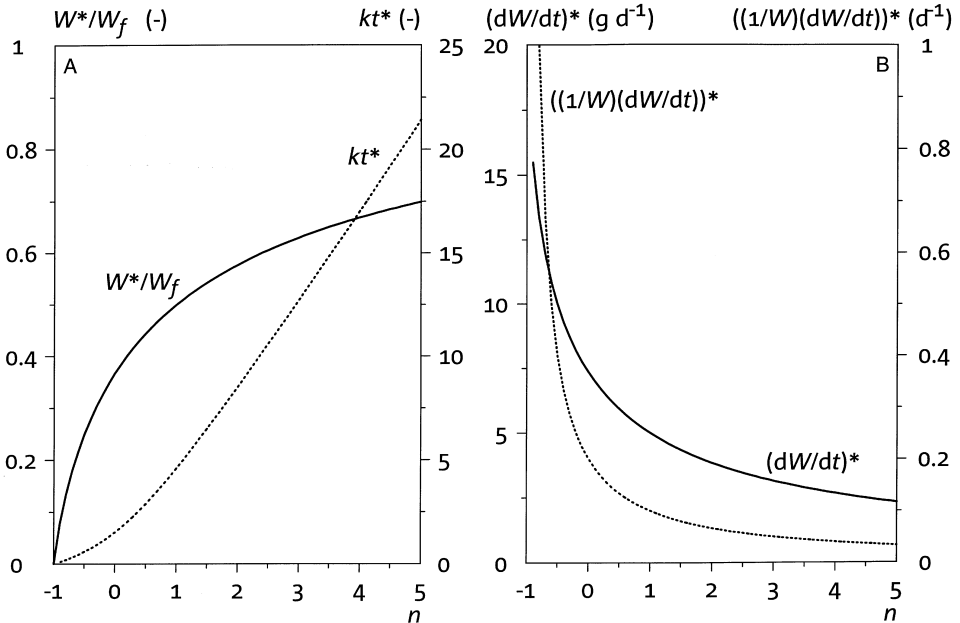

Figure 6. (A) The normalized plant mass at inflection point, W_r^*/W_{rf}, and the normalized time of inflection, $k_r t_r^*$, as a function of n, and (B) the growth rate, $(\mathrm{d}W_r/\mathrm{d}t)^*$, and the relative growth rate, $((1/W_r)(\mathrm{d}W_r/\mathrm{d}t))^*$, at inflection point as a function of the dimensionless n parameter in the Richards growth model.

For $n < -1$ this limit is undefined, and for $n = -1$ this limit yields $k_r W_{rf}$ (monomolecular growth).

From Eqs. (21) or (22) with $W_r = W_r^*$ it follows that k_r is a measure for the (relative) growth rate at the inflection point (Table 3).

Exponential polynomial growth

Exponential polynomials do not have any physiological meaning from which they can be derived. Only afterwards the parameters of these polynomials can be given a physiological meaning. The general form of exponential polynomials equals

$$W_p(t) = e^{a + bt + ct^2 + dt^3 + \dots}. \tag{28}$$

The first order exponential polynomial reads

$$W_p(t) = e^{a + bt} = a' e^{bt}, \tag{29}$$

where $a' = e^a$. Equation (29) is analogous to exponential growth (cf. Eq. (4)).

The second order exponential polynomial reads (Figure 7)

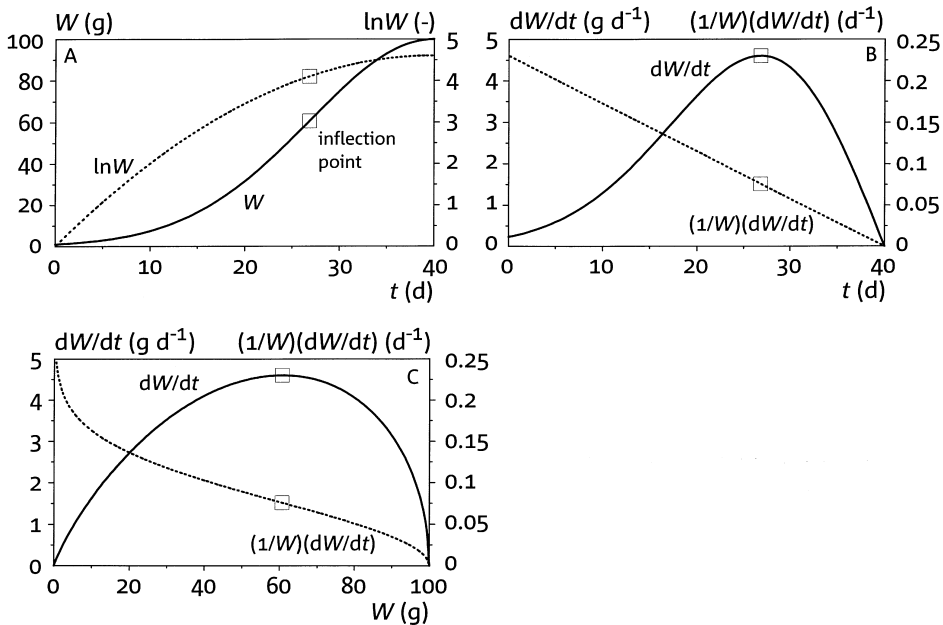$$W_p(t) = e^{a + bt + ct^2}. \tag{30}$$

Figure 7. Second order exponential polynomial growth: (A) W_p and ln W_p as a function of t, (B) dW_p/dt and $(1/W_p)(dW_p/dt)$ as a function of t, and (C) as a function of W_p; with $W_{p0} = 1$ g, $W_{pf} = 100$ g, $t_s = 40$ d, $k_p = 0.075871$ d^{-1}.

For $t = 0$ the parameter a is a measure for W_{p0}:

$$a = \ln W_{p0}. \tag{31}$$

The form of the second order exponential polynomial depends on the values of b and c. For our purposes $b > 0$ and $c < 0$ is the most interesting case. Equation (30) is symmetrical around $t = t_s$, with a positive growth rate between $t = 0$ and $t = t_s$. This is the time interval which is considered, and we require t_s to be the time at the end of the growth period at which $W_p = W_{pf}$. The growth rate is obtained by differentiating Eq. (30) with respect to t yielding (Figure 7)

$$\frac{dW_p}{dt} = (b + 2ct)e^{a + bt + ct^2} = (b + 2ct)W_p, \tag{32}$$

and the relative growth rate is given by

$$\frac{1}{W_p} \frac{dW_p}{dt} = (b + 2ct). \tag{33}$$

From Eq. (33) it can be seen that b equals the relative growth rate at $t = 0$. The maximum of the curve is obtained by solving $dW_p/dt = 0$ for t yielding t_s:

$$t_s = -\frac{b}{2c}. \tag{34}$$

At t_s $W_p = W_{pf}$, and an expression for W_{pf} follows from Eq. (30) using Eq. (34):

$$W_{pf} = e^{a - \frac{b^2}{4c}} = W_{p0}e^{-\frac{b^2}{4c}}. \tag{35}$$

From Eqs. (34) and (35) expressions for the two unknown parameters b and c in terms of the quantities W_{p0}, W_{pf} and t_s can be derived as

$$b = \frac{2}{t_s} \ln\left(\frac{W_{pf}}{W_{p0}}\right), \text{ and } c = -\frac{1}{t_s^2} \ln\left(\frac{W_{pf}}{W_{p0}}\right). \tag{36}$$

The inflection point inside the time interval $[0, t_s]$ occurs at (Table 3)

$$t_p^* = t_s - \sqrt{-\frac{1}{2c}} = t_s\left(1 - \sqrt{\frac{1}{2\ln\left(\frac{W_{pf}}{W_{p0}}\right)}}\right). \tag{37}$$

Evaluating Eqs. (30), (31), (36), and (37) at the point of inflection results in an expression for W_p^* (Table 3). From Eqs. (34) and (37) it follows that b and c are measures for the difference between t_s and t_p^*:

$$b = \frac{t_s}{(t_s - t_p^*)^2}, \text{ and } c = -\frac{1}{2(t_s - t_p^*)^2}.$$ (38)

Parameters b and c can not be expressed in terms of W_{pf} and W_p^*, since one can imagine that at different $(t_s - t_p^*)$ the same difference in W_{pf} and W_p^* can be obtained.

In Eq. (32) dW_p/dt is not explicitly given as a function of W_p only, because t is included. From Eq. (30) an expression for t, within the interval $[0,t_s]$, can be obtained yielding (using Eq. (36))

$$t = t_s \left(1 - \sqrt{\frac{\ln\left(\frac{W_{pf}}{W_p}\right)}{\ln\left(\frac{W_{pf}}{W_{p0}}\right)}} \right).$$ (39)

Substituting Eq. (39) into Eq. (32), using Eq. (36), yields (Figure 7)

$$\frac{dW_p}{dt} = 2 \frac{W_p}{t_s} \sqrt{\ln\left(\frac{W_{pf}}{W_p}\right)\ln\left(\frac{W_{pf}}{W_{p0}}\right)},$$ (40)

and the relative growth rate is given by

$$\frac{1}{W_p} \frac{dW_p}{dt} = \frac{2}{t_s} \sqrt{\ln\left(\frac{W_{pf}}{W_p}\right)\ln\left(\frac{W_{pf}}{W_{p0}}\right)}.$$ (41)

Since the logistic, Gompertz and Richards growth models have a proportionality constant k which is a measure for the relative growth rate at the point of inflection, it is interesting to see if we can define a similar parameter k_p. We define k_p as the relative growth rate at the inflection point. Evaluating Eq. (41) at the inflection point using the expression of W^* (Table 3) yields

$$k_p = \frac{1}{t_s} \sqrt{2\ln\left(\frac{W_{pf}}{W_{p0}}\right)} = \sqrt{\frac{b}{t_s}} = \sqrt{-2c}.$$ (42)

Now we can write expressions for $W_p(t)$, dW_p/dt and $(1/W_p)(dW_p/dt)$ in terms of the parameters W_{p0}, W_{pf} and k_p. Substituting Eqs. (31), (36), and (42) in Eq. (30) yields

$$W_p(t) = W_{p0}e^{k_p^2 t(t_s - 0.5t)} = W_{pf}e^{-0.5k_p^2(t_s-t)^2}.$$ (43)

Differentiating Eq. (43) to t, or substituting Eq. (42) in Eq. (40), yields

$$\frac{dW_p}{dt} = W_p k_p^2(t_s - t) = k_p W_p \sqrt{2\ln\left(\frac{W_{pf}}{W_p}\right)}.$$ (44)

The relative growth rate follows from Eq. (44) as

$$\frac{1}{W_p} \frac{\mathrm{d}W_p}{\mathrm{d}t} = k_p^2(t_s - t) = k_p \sqrt{2\ln\left(\frac{W_{pf}}{W_p}\right)}. \tag{45}$$

France and Thornley (1984) advise not to use higher order exponential polynomials, because of possible "overfitting" of the measured data.

Equivalent expressions for the growth models

The statistical processing program Genstat (Anon., 1993) uses equivalent expressions for the non-linear – in terms of the unknown parameters – growth equations presented above (as listed in Table 2). The *exponential and monomolecular* growth equations are both described by

$$Y_{em}(t) = a_{em} + b_{em}r^t. \tag{46}$$

The *logistic* growth equation is described by

$$Y_l(t) = a_l + \frac{c_l}{1 + e^{-b_l(t-m_l)}}, \tag{47}$$

the *Gompertz* equation by

$$Y_g(t) = a_g + c_g e^{-e^{-b_g(t-m_g)}}. \tag{48}$$

and the *Richards* equation by

$$Y_l(t) = a_r + \frac{c_r}{1 + pe^{-br(t-mr)\frac{1}{p}}}, \tag{49}$$

The variable Y represents the plant mass W. The parameters a and $(a+c)$ in Eqs. (46) to (49) represent the lower and upper asymptotes, respectively. As in the previous section, a will be absent in Eqs. (47)-(49). The parameters b are measures of the slopes of the curves, the parameters m represent the time of inflection, i.e. $m = t^*$, and p and r are dimensionless parameters. It is clear that for the Richards model $p = n$. In Genstat's directive FITCURVE the choice of the model can be given as an option. Genstat determines estimators for the parameters a, b, c, m, p and r for given measured data. The relation between the unknown parameters in Eqs. (4), (7), (10), (15)+(17) and (23) and the Genstat parameters will be given below. For convenience, the relationships are listed in Table 4.

The second order exponential polynomial, i.e. Eq. (30) or Eq. (43), can be fitted via linear regression after ln-transformation.

Table 4. The relation between the parameters k, W_f, W_0 k_{g0} and n of the exponential (Eq. (4)), monomolecular (Eq. (7)), logistic (Eq. (10)), Gompertz (Eqs. (15) + (17)), Richards (Eq. (23)), and second order exponential polynomial (Eq. (43)) growth models, and the estimated parameters a, b, c, m, r, and p of equivalent expressions by Genstat.

Model	k	W_f	W_0	k_{g0}	n
Exponential	$\ln r$		b_{em}		
Monomolecular	$\ln \dfrac{1}{r}$	a_{em}	$a_{em} + b_{em}$		
Logistic	b_l	c_l	$\dfrac{c_l}{1 + e^{b_l m_l}}$		
Gompertz	b_g	c_g	$c_g e^{-e^{b_g m_g}}$	$b_g e^{b_g m_g}$	
Richards	b_r	c_r	$\dfrac{c_r}{(1 + p e^{b_r m_r})^{\frac{1}{p}}}$		p
Second order exponential polynomial	$\sqrt{\dfrac{b}{t_s}}$, or $\sqrt{-2c}$	$e^{a - \frac{b^2}{4c}}$	e^a		

Exponential growth
With the substitution $r = \exp(k_e)$ and the assumption $a_{em} = 0$, Eq. (46) becomes

$$Y_{em}(t) = b_{em} e^{\, k_e t}. \tag{50}$$

Equation (50) is equivalent to Eq. (4) for $b_{em} = W_{e0}$ and $\ln r = k_e$.

Monomolecular or Mitscherlich growth
With the substitution $r = \exp(-k_m)$ Eq. (46) becomes

$$Y_{em}(t) = a_{em} + b_{em} e^{\, -k_m t}. \tag{51}$$

Equation (51) is equivalent to Eq. (7) for $a_{em} = W_{mf}$, $a_{em} + b_{em} = W_{m0}$ and $\ln(1/r) = k_m$. In Genstat it is possible that the program uses the restriction $r > 1$. This yields a negative value for a_{em}, and this means that W_{mf} becomes negative, which is impossible. In that case Genstat assumes exponential growth.

Logistic or autocatalytic growth
In Eq. (10) W_{lf} is the asymptotic maximum for W_l, which is represented by c_l in Eq. (47), i.e. $c_l = W_{lf}$. With $b_l = k_l$ and $m_l = t_l{}^*$, and using the definition of $t_l{}^*$ (Table 3) Eq. (47) becomes

$$Y_l(t) = \frac{W_{lf}}{1 + e^{k_l \, t_l^*} e^{\, -k_l t}} = \frac{W_{l0} W_{lf}}{W_{l0} + (W_{lf} - W_{l0}) e^{\, -k_l t}}. \tag{52}$$

Under the given conditions, Eq. (47) is equivalent to Eq. (10) (= Eq. (52)). W_{l0} follows from the definition of $t_l{}^*$ (Table 3) and the given conditions:

$$W_{l0} = \frac{c_l}{1 + e^{b_l\,m_l}}. \tag{53}$$

Gompertz growth
In Eq. (17) W_{gf} is the asymptotic maximum for W_g, which is represented by c_g in Eq. (48), i.e. $c_g = W_{gf}$. With $b_g = k_g$ and $m_g = t_g{}^*$, and using the definition of $t_g{}^*$ (Table 3) Eq. (48) becomes

$$Y_g(t) = W_{gf}{}^{-e^{k_g t_g^* e^{-k_g t}}} = W_{gf}\,e^{-\frac{k_{go}}{k_g}\,e^{-k_g t}}. \tag{54}$$

Under the given conditions, Eq. (48) is equivalent to Eq. (17) (= Eq. (54)). k_{g0} follows from the definition of $t_g{}^*$ (Table 3) and the given conditions:

$$k_{g0} = b_g e^{\,b_g m_g}. \tag{55}$$

W_{g0} follows from Eq. (16) and Eq. (55) under the given conditions:

$$W_{g0} = c_g e^{\,-e^{b_g m_g}}. \tag{56}$$

Richards or general logistic growth
In Eq. (23) W_{rf} is the asymptotic maximum for W_r, which is represented by c_r in Eq. (49), i.e. $c_r = W_{rf}$. With $p = n$, $b_r = k_r$ and $m_r = t_r{}^*$, and using the definition of $t_r{}^*$ (Table 3) Eq. (49) becomes

$$Y_r(t) = \frac{W_{rf}}{\left(1 + n e^{k_r t_r^*}e^{\,-k_r t}\right)^{\frac{1}{n}}} = \frac{W_{r0}W_{rf}}{\left(W_{r0}^n + (W_{rf}^n - W_{r0}^n)e^{-k_r t}\right)^{\frac{1}{n}}}. \tag{57}$$

Under the given conditions, Eq. (49) is equivalent to Eq. (23) (= Eq. (57)). W_{r0} follows from the definition of $t_r{}^*$ (Table 3) and the given conditions:

$$W_{r0} = \frac{c_r}{\left(1 + e^{b_r m_r}\right)^{\frac{1}{n}}}. \tag{58}$$

Exponential polynomial growth
The parameters of the second order exponential polynomial cannot be estimated directly using standard fit-procedures in Genstat (Anon., 1993). After ln-transforming Eq. (30) a linear equation – in terms of the parameters – is obtained

$$\ln W_p = a + bt + ct^2. \tag{59}$$

Equation (59) can be solved directly using linear regression giving estimates of a, b and c. A disadvantage of the ln-transformation method is that the fitted curve may show its optimum within the measurement interval $[0, t_{mi}]$ (the lower W_p values "pull stronger" at the curve to be fitted), with t_{mi} the last time of the measurement interval. For the exponential polynomial (as described above) we assumed that the maximum occurs at the end of the growth period, i.e. at $t = t_s = t_{mi}$. The method of transformation determines the place of this optimum. Therefore, it is advised to transform the data as follows

$$W_{p,t} = \ln(W_p(t) + \varepsilon), \ \varepsilon > 0. \tag{60}$$

In that case the optimum is a function of the constant ε. It is proposed that in case the data show a S-shape-like distribution, ε is chosen such that the optimum occurs at $t = t_s = t_{mi}$. That means that the parameters b and c are restricted according to Eq. (34).

Example

To demonstrate the use of the models described above, the dry weight data of lettuce heads of Heinen *et al*. (1991) were fitted to the logistic, Gompertz, Richards, and second order polynomial growth equations (Figure 8A). It goes beyond the scope of this report to discuss the observations, since similar discussions are given in Heinen *et al*. (1991). The estimated parameters of the logistic, Eq. (47), Gompertz, Eq. (48), Richards, Eq. (49), and second order exponential polynomial, Eq. (60), models were used to calculate the parameters in Eqs. (10), (15) + (17), (23), and (43) respectively, according to Table 4 (Table 5). The value of ε in Eq. (60) was iteratively estimated as 0.05823, in which case the optimum of the exponential curve occurs at the last time of the measurement interval. Similarly, the cumulative uptake by the lettuce heads of N, P and K were fitted to the logistic model (Table 5). These fitted data were scaled by dividing them by the fitted maximum value W_f (Figure 8B).

The question remains which of the functions is the best. The answer will depend on the researcher and his/hers interests and ideas about the growth of the crop. Judgement of a good fit is mostly done based on high correlation coefficient r^2 combined with a visually good fit, and the choice of the function with the least number of parameters or the function that comes closest to the concept of growth used by the researcher. Here, one could say that the logistic function is preferred: highest r^2 and the least number of parameters. It is recognized that the fit is biased by measurement errors. For the data used in this example no measurement errors are known, since data refer to a single sample obtained from several plants. Moreover, if the crop has distinct growth stages, such as vegetative growth and flowering, for each growth stage a growth function may be used. For example, Hammond and Kirkham (1949) used exponential growth functions for three growth periods of soybeans and four growth periods of corn.
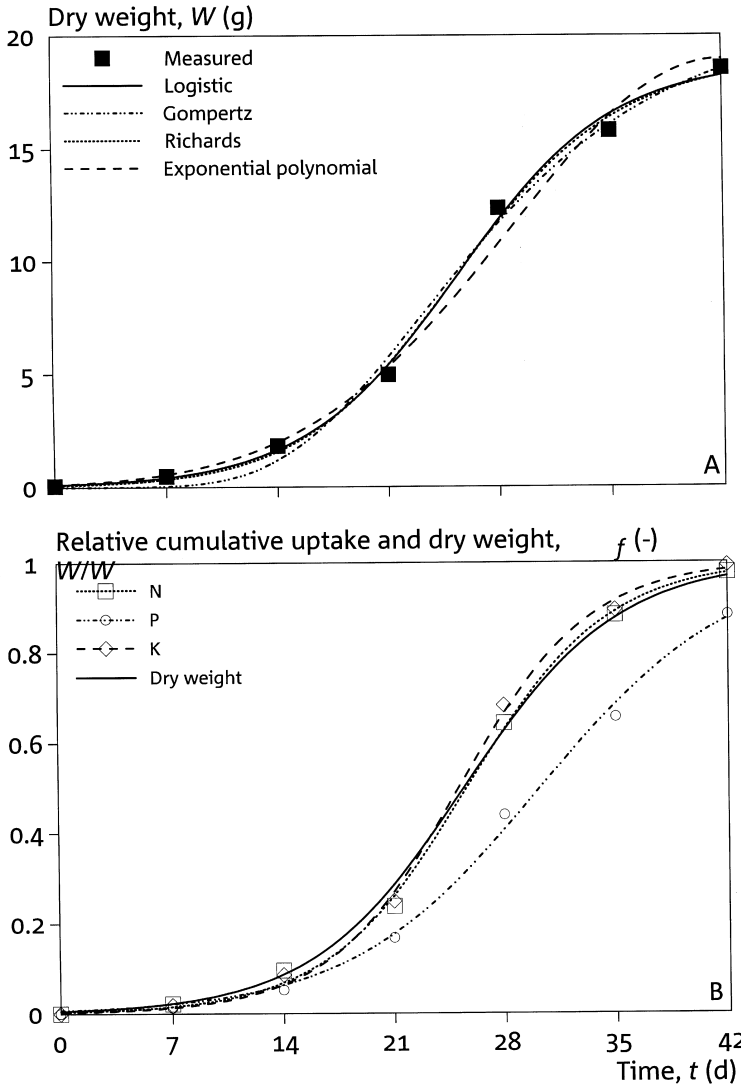
Figure 8. (A) Dry weight data of lettuce head from Heinen *et al*. (1991) fitted to the logistic, Gompertz, Richards and second order exponential polynomial models. (B) Cumulative uptake data of N, P and K by lettuce head from Heinen *et al*. (1991) fitted to the logistic model.

One model fits all

As was mentioned before, the Richards growth model includes the logistic, the monomolecular or Mitscherlich, and the Gompertz growth equations. In fact, these four models and the exponential growth equation can be represented by the following family of equations, which is analogous to Eq. (46) (Hunt, 1982)

Table 5. The estimated and calculated parameters (PM) of the logistic (L, Eq. (10)), Gompertz (G, Eqs. (15) + (17)), Richards (R, Eq. (23)) and second order exponential polynomial (EP, Eq. (30) or (43)) models for the dry weight data (g per lettuce head), and the estimated and calculated parameters for the cumulative uptake data (mmol per lettuce head) of nitrogen (N), phosphorus (P) and potassium (K) for the logistic model. The correlation coefficient is given as by r^2. For the estimated parameters the standard errors, as given by Genstat, are listed between brackets.

PM	L				G	R	EP
	dry	N	P	K	dry	dry	dry
W_0 (g or mmol)	0.100	0.218	0.044	0.111	0.0	0.067	0.115
W_f (g or mmol)	18.78	68.97	6.65	47.46	20.81	19.04	18.94
	(0.669)	(1.60)	(0.422)	(1.05)	(1.55)	(1.25)	
k (d^{-1})	0.2054	0.2244	0.1660	0.2409	0.1145	0.1854	0.0761
	(0.0208)	(0.0160)	(0.0178)	(0.0178)	(0.0189)	(0.0716)	
t^* (d)	25.47	25.63	30.16	25.14	23.24	25.12	28.86
	(0.646)	(0.407)	(1.10)	(0.387)	(0.972)	(1.65)	
n						0.785	
						(0.761)	
k_{g0} (d^{-1})					1.6396		
a							-2.1661
							(0.0742)
b (d^{-1})							0.24319
							(0.00827)
c (d^{-2})							−0.002895
							(0.000189)
ε							0.05823
r^2	99.9	99.9	99.8	99.9	99.9	99.8	99.9

$$Y = \alpha + \beta\gamma^t, \tag{61}$$

where Y is a function of W, and the parameters α, β and γ depend on the kind of growth model under consideration (Table 6).

For completeness, it is mentioned here that in Genstat a procedure is available called FITSCHNUTE. It can be used to fit data according to the growth model of Schnute (1981). It is available in the CBW-DLO Genstat-procedures-library which can be downloaded from the Internet (visit www.cpro.dlo.nl/cbw; CBW stands for Centre for Biometry Wageningen and DLO stands for the Dutch Agricultural Research Organization). The procedure is described in detail by Keen (1988). The model reads

$$Y = y + \sigma, \tag{62}$$

where y is a function of t according to

$$Y(t) = \left(y_1^\mu + (y_2^\mu - y_1^\mu) \frac{1 - e^{-\nu(t-t_1)}}{1 - e^{-\nu(t_2-t_1)}} \right)^{\frac{1}{\mu}}. \tag{63}$$

Table 6. Expressions for the parameters y, α, β and γ of Eq. (61) to obtain the exponential, the monomolecular, the logistic, the Gompertz and the Richards growth models.

Model	y	α	β	γ
Exponential	W_e	0	W_{e0}	e^{k_e}
Monomolecular	W_m	W_{mf}	$W_{m0} - W_{mf}$	e^{-k_m}
Logistic	W_l^{-1}	W_{lf}^{-1}	$W_{l0}^{-1} - W_{lf}^{-1}$	e^{-k_l}
Gompertz	$\ln W_g$	$\ln W_{gf}$	$\ln \dfrac{W_{gf}}{W_{g0}} = -\dfrac{k_{g0}}{k_g}$	e^{-k_g}
Richards	W_r^{-n}	W_{rf}^{-n}	$W_{r0}^{-n} - W_{rf}^{-n}$	e^{-k_r}

The y_1 and y_2 parameters are the values of y at t_1 and t_2, respectively. S-shaped curves are obtained for $v > 0$ and $\mu > 1$ (Keen, 1988). At given μ, parameter v determines the measure of curvation of the upper and lower curves. Parameter μ regulates the curvature of the upper curve in relation to the lower curve. The Schnute model encompasses eleven submodels, including the exponential ($v < 0$, $\mu = 1$), monomolecular ($v > 0$, $\mu = 1$), logistic ($v > 0$, $\mu = -1$), Gompertz ($v > 0$, $\mu = 0$), and Richards ($v > 0$, $\mu < 0$) growth models.

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Appendix A

The partial fractioning method is demonstrated by integrating the Richards growth equation Eq. (21) (leaving out the subscript r for convenience)

$$\frac{dW}{dt} = kW\frac{W_f^n - W^n}{nW_f^n}. \tag{A-1}$$

Integrating Eq. (A-1) over $t = 0$, $W = W_0$ and $t = t$, $W = W$ yields

$$\int_{W_0}^{W} \frac{nW_f^n}{W_f^n - W^n} dW = \int_{O}^{t} k\, dt = kt. \tag{A-2}$$

The left integral of Eq. (A-2) can be written as follows (partial fractioning)

$$\int_{W_0}^{W} \frac{nW_f^n}{W_f^n - W^n}\, dW = n\int_{W_0}^{W}\left(\frac{A}{W} + \frac{B}{W_f^n - W^n}\right) dW. \tag{A-3}$$

Values for A and B can be obtained from

$$A(W_f^n - W^n) + BW = W_f^n, \tag{A-4}$$

yielding $A = 1$ and $B = W^{n-1}$. The left integral of Eq. (A-2) can now be written as

$$\int_{W_0}^{W} \frac{nW_f^n}{W_f^n - W^n}\, dW = n\int_{W_0}^{W}\left(\frac{1}{W} + \frac{W^{n-1}}{W_f^n - W^n}\right) dW = n.\int_{W_0}^{W}\frac{1}{W}\, dW + n\int_{W_0}^{W}\frac{W^{n-1}}{W_f^n - W^n}\, dW. \tag{A-5}$$

With $dW^n = nW^{n-1}dW$ the left integral of Eq. (A-2) now becomes

$$\int_{W_0}^{W} \frac{nW_f^n}{W_f^n - W^n}\, dW = n\int_{W_0}^{W}\frac{1}{W}\, dW - \int_{W_0}^{W}\frac{1}{W^n - W_f^n}\, dW^n. \tag{A-6}$$

The solution of the left integral of Eq. (A-2) follows easily from Eq. (A-6)

$$\int_{W_0}^{W} \frac{nW_f^n}{W_f^n - W^n}\, dW = n\ln\frac{W}{W_0} - \ln\left(\frac{W^n - W_f^n}{W_0^n - W_f^n}\right) = \ln\left(\frac{W^n\, W_0^n - W_f^n}{W_0^n\, W^n - W_f^n}\right). \tag{A-7}$$

From Eq. (A-2) and Eq. (A-7) it follows that

$$\frac{W^n}{W_0^n}\frac{W_0^n - W_f^n}{W^n - W_f^n} = e^{kt}. \tag{A-8}$$

Equation (A-8) can be solved simply for W yielding Eq. (23).