Growth equations in forest research: mathematical basis and model similarities

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Abstract

Purpose of Review Growth equations have been widely used in forest research, commonly to assess ecosystem-level behaviour and forest management. Nevertheless, the large number of growth equations has obscured the growth-rate behaviour of each of these equations and several different terms for referring to common phenomena. This review presents a unified mathematical treatment of growth-rates besides several well-known growth equations by giving their mathematical basis and representing their behaviour using tree growth data as an example.

Recent Findings We highlight the mathematical differences among several growth equations that can be better understood by using their differential equations forms rather than their integrated forms. Moreover, the assumed-and-claimed biological basis of these growth-rate models has been taken too seriously in forest research. The focus should be on using a plausible equation for the organism being modelled. We point out that more attention should be drawn to parameter estimation strategies and behaviour analysis of the proposed models. Thus, it is difficult for a single model to capture all possible shapes and rates that such a complex biological process as tree growth can depict in nature.

Summary We pointed out misleading concepts attributed to some growth equations; however, the differences come from their mathematical properties rather than pure biological reasoning. Using the tree growth data, we depict those differences. Thus, comparisons of some functional forms (at least simple ones) must be carried out before selecting a function for drawing scientific findings.

Keywords Differential equations · growth-rates · von Bertalanffy · logistic · trees

Introduction

Growth is a term which everybody understands but not necessarily in the same way. Although we can track definitions of growth as far as Aristotle [1], one of the first obstacles in understanding tree growth is the lack of precision in the definition of what is meant by growth. Growth is determined by cell-division, cell-extension and cell differentiation [2]. Ergo, growth is a phenomenon that captures the interest of research in a suite of disciplines [3], especially in plant sciences [4]. The growth pattern in forest trees is divided into primary growth, i.e. the growth from a bud, root, tip or other apical meristem, and secondary growth, i.e. growth from cambium [5]. Growth implies an increase in size and the formation of new tissue. However, growth may occur when older organs, particularly leaves, are dropping off faster than new ones are being formed [6]. The term *net growth* includes also this component, whereas *gross growth* does not. In forestry, these terms are mainly

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used at the stand level, and using volume as variable of reference, as follows: net growth refers to the difference between volume at the end of the period and at the beginning; gross growth must also incorporate the growth of trees which may have died in the period [5, 7]. We refer here to the growth of variables such as height and stem diameters as the irreversible increase in leading-shoot length and stem diameter, respectively [8], or in a more physiological context, the incorporation of carbon into structural material [2]. Nevertheless, we follow [9], in the sense that the level of abstraction of our modelling framework emphasizes the physically measurable exterior tree characteristics, which we call *variables.*

Let us take a closer look at the use of the terms "growth", "increment" and "yield" in forestry. Bruce [10] stated, using height growth equations as an example, that there are *growth* and *growth-rate* equations, the first one being an expression giving the variable as a function of time, and the second as the differential of the growth equation. He also emphasized that growth-rate is determined at one point in time. In forestry, growth over a time period shorter than a year may be confusing because the growth usually occurs during summertime. Yang *et al.* [11] defined the term *increment* as the increase in size of an organism within a certain time interval i.e., as the difference in observed or predicted growth at two points in time [10]. *Current annual increment* (CAI) is the difference in the growth at the beginning and the end of the year and *periodic annual increment* (PAI) for longer time units [12]. Term *yield* has also been used in the same meaning as growth [12, 13, 14, 15, 16], but it has mainly been associated with volume. For example, Clutter [14] and Curtis [15] refer to growth-rate as the derivative form and to yield as the integral of volume. Clutter [14] defined that if integrating the growth-rate equation gives the yield equation, the models are compatible. Even though the forestry literature often recognizes the works by [12] and [14] as the first to mention the consistency between growth-rate equations and the yield equations, many researchers in plant ecology [17, 18, 19], animal growth [20], and also in forestry [21, 22, 23] have been aware of this relationship long before.

In this paper, we use the following terminology that corresponds to the mathematical explanation of derivatives and integrals in calculus [24]: If a state variable, y, is measured at times t_0 and t_1, or size at both times, we have a dynamic variable, therefore we also refer to them as growth at times t_0 and t_1 (Fig. 1). The difference between these two measurements is the *increment* of that variable, for the period of time $\Delta t = t_1 - t_0$, and is symbolized by $\Delta y = y_1 - y_0$. The ratio $\Delta y / \Delta t$, is referred to as the *average rate of change*, between t_0

and t_1, which is how fast the y variable is changing, and is the slope of a straight line connecting $f(t_0)$ to $f(t_1)$ in Figure 1. If Δt becomes infinitesimally small, then we are analyzing the derivative of y, dy/dt, in y for any particular time (i.e., the slope of the tangent line at points t_0 and t_1 in Fig. 1), which we call *(instantaneous) growth rate.* If the increment in the state variable from t_0 up to a time t_1, Δy (or dy/dt integrated), is added to y_0, then we get y_1, the growth at time t_1.
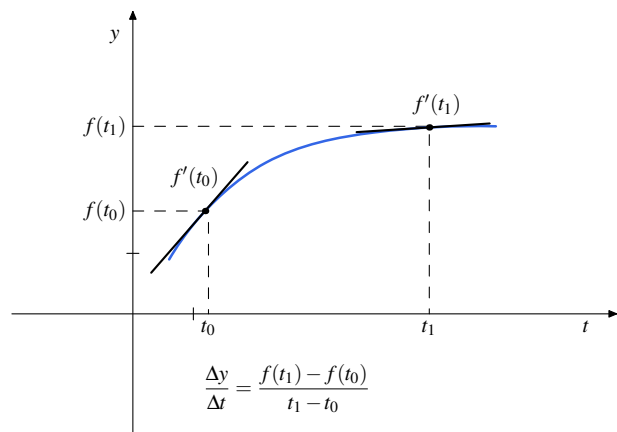

Fig. 1 Growth definitions for the state variable y obtained from function f. Growth curve (blue), state variable at time 0 ($f(t_0)$) and time 1 ($f(t_0)$), increment (Δy) between t_0 and t_1, and growth–rate or derivative (dy/dt) at t_0 ($f'(t_0)$) and t_1 ($f'(t_1)$). The derivative, or instantaneous growth-rate, is the slope of the tangent lines (black) at points t_0 and t_1.

If we were able to capture the entire lifetime of most live organisms, their empirical growth would depict a sigmoid curve. A sigmoid or S-type curve resembles trends in the life cycle of many living organisms and phenomena [25] (Figure 2a). Virtually all exterior tree dimensions develop in a sigmoid manner with respect to time [26]. A growth curve is typically separated in phases (Figure 2a). Generally three phases have been recognized [27, 28, 29], but the pattern remains the same. Baker [28] called them; acceleration, intermediate, and deceleration; [29] youth, full vigor, and old age; while [30], youth, maturity, and senescence. In phase 1, y is an exponential function of time [27]. Trees grow relatively slowly at first, increasing their growth-rate to the point of inflection of the growth curve [30]. In phase 2, y is directly proportional to time [27], and in phase 3, there is a decrease of the growth-rates [27, 30].

In addition to CAI, the forestry literature recognizes the term *mean annual increment* (MAI), which is found by dividing the growth through time t by the number of years required to produce it (red curve in
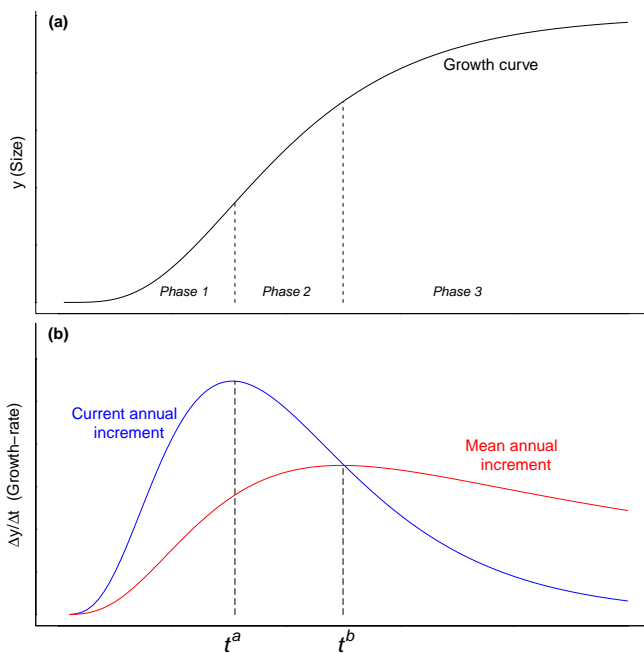
Fig. 2 Growth and growth-rates curves. (a) The trajectory of the state variable (y), generally representing an expression of size, is the growth curve. Meanwhile, (b) growth-rates curves are represented by the current (blue) and mean (red) annual increments. t^a is the time of culmination of current annual increment and t^b is the time of maximum mean annual increment.

Figure 2b), i.e. $MAI = y_t/t$. Growth and increment curves have long been used for making silvicultural decisions, using as reference the following facts. The inflection point of the CAI curve, which occurs at the time symbolized by t^a in Figure 2, is also the time of maximum CAI. It has been recognized as a good opportunity to apply thinning, since the increment of residual trees is going to reach its maximum. The point t^a is called the culmination of current annual increment [29, 30, 31]. The inflection point of the MAI curve, which occurs at the time symbolized by t^b in Figure 2, represents the point where the curves of MAI and CAI cross, and MAI is maximized. It has been recognized as a biological criterion to choose the rotation age of even-aged stands. More specifically, it is the rotation that maximizes the growth. It would be the rotation that leads to maximum carbon sequestration if the carbon of harvested biomass would never be released back to the atmosphere [32]. Otherwise, the optimal rotation for carbon sequestration would be longer. Point t^b would be an economically optimal rotation if the interest rate of the forest owner is 0%. A higher interest rate would make the optimal rotation shorter [33].

Growth equations

Many empirical and theoretical growth equations have been used in forest research. Traditionally, practitioners want to predict the value of a random variable at time t, let's say y_t, as a function of some variables that might affect the value of y_t. The usual approach is to build a mathematical model that fits the pattern of the observed data. The resulting model is called "empirical". On the other hand, growth equations have been developed from biological theory about the growth process, with parameters that have (sometimes) biological meaning. Theoretical growth equations have become preferred in research but not always in practice. Some of the so called theoretical growth equations have empirical bases. Nevertheless, we prefer to call them as such because the parameters have some biological interpretation. Empirical models serve a different purpose than do theoretical models. Thereupon, empirical models should not be viewed as poorer alternatives.

Theoretical growth equations have been developed for many biological disciplines. Several mathematical equations are based on theoretical constructs. Since many growth curves are nonlinear in terms of their parameters, growth models are an important family of nonlinear models [34]. There is an extensive number of growth equations in the literature; however, it is hard to believe that a model with three or four parameters could describe so complicated process as growth from birth to death [35, 36]. The origin of many nonlinear models in use today can be traced to scholarly efforts to discover laws of nature, to reveal scales of being, and to understand the forces of life [34]. There are several growth equations with theoretical or theoretical-empirical bases. Here, we focus on some that have been widely used in forestry research.

There are many different parameterizations of a certain growth model. Because these models start from differential equations, many trajectories can be obtained; as a result numerous models have been proposed based on the differential forms. Furthermore from different differential equations it is possible to attain the same solution or trajectory, a mathematical fact that is not fully understood, as expressed by [37, 38]. Several authors have reported different parameterization of growth models for forestry and other scientific disciplines [3, 34, 37, 39, 40, 41, 42, 43, 44]. Here, we present differential forms and solutions of selected and most widely use models in forest science. We want to stress that by selecting these mathematical functions, we are aiming to compare their mathematical differences and origins, but not providing a detailed review of all the available growth functions that can be found.

Hereafter, all the parameters are positive, as well as time (t) is positive, and the state variable y. We also provide expressions of the asymptote (i.e., the maximum level for the state variable) and the points of inflection (i.e., where the curve changes of curvature) of all models. We shall use Greek letters to refer to parameters and italics font style to refer to variables. The use of the same symbols that represent parameters in equations through the document do not represent the mathematical equivalence, unless that is clearly specified. For example, β or γ can be used in different equations, but they do not imply the same number.

Monomolecular growth model. The monomolecular model is the following differential equation

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \beta(\alpha - y), \tag{1}$$

where y is the state variable, t represent time, and β and α are parameters that represents the proportional constant and final size, respectively. For this model growth is proportional to the remaining size of the organism [34]. Therefore, the growth-rate decreases as t increases and the equation cannot describe sigmoidal growth. A solution of (1) produces the growth function

$$y_t = \alpha \left\{ 1 - \left(1 - \frac{y_0}{\alpha} \right) e^{-\beta(t-t_0)} \right\}. \tag{2}$$

If we further assume that $t_0 = 0, y_0 = 0$, then (2) becomes

$$y_t = \alpha \left\{ 1 - e^{-\beta t} \right\}, \tag{3}$$

where α is the asymptote of the state variable, but the model does not have an inflection point (Table 1). The equation form of (3) is known as the Mitscherlich law or Mitscherlich equation [34]. This function was proposed for height-diameter modelling by [45] as well and is therefore sometimes called Meyer's equation in the literature.

Logistic growth model. The logistic growth is mostly attributed to Verhulst's work in 1838 [46, 47, 48]. The logistic model imposes a restriction to the exponential growth, then representing limiting resources for population growth. There are many parametrizations of the logistic model, but we shall show the one most commonly cited in the ecological literature [46, 49],

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \theta y - \phi y^2 = y(\theta - \phi y), \tag{4}$$

where y is the state variable, θ and ϕ are parameters.

The differential logistic equation can also be parameterized as follows [48, 50], based on treating θ as β and (θ/ϕ) as α,

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \beta y - \left(\frac{\beta}{\alpha} \right) y^2 = \beta y \left(1 - \frac{y}{\alpha} \right), \tag{5}$$

where the constant α has a biological interpretation as the carrying capacity of the environment, e.g., the maximum population size for ecological studies or the maximum tree size, and β is a proportionality constant. The logistic growth equation is the simplest equation describing sigmoidal population growth in a resource-limited environment, and it forms the basis for many models in ecology [48]. A solution of the differential form of the logistic is the following growth curve,

$$y_t = \frac{\alpha}{1 + [(\alpha - y_0)/y_0] \, e^{-\beta t}}, \tag{6}$$

where y_0 is the value of the initial condition of the state variable y. From (5) we see that when $y \to \alpha$, which happen when $t \to \infty$, the growth-rate is zero, therefore the population being modelled or the size of any organism, does not grow without limit. The logistic equation is symmetric around the inflection point t_0, implying that the growth rate fulfills $f(t_0 - t) = f(t_0 + t)$ for any positive t. Also notice that, when the growth-rate of the equation (Eq. 4) is plotted as a function of the state variable y, and not time, the point of inflection $y = \alpha/2$ (Table 1) is when the growth-rate reaches its maximum. A usual parameterization found in the

Table 1 Features of the studied growth models. The differential form (i.e., growth-rate equation), a solution (i.e., growth equation), the asymptote and the inflection point are provided.

Model	Differential form	A solution	Asymptote	Point of inflection
Monomolecular	$\frac{\mathrm{d}y}{\mathrm{d}t} = \beta(\alpha - y)$	$y_t = \alpha(1 - e^{-\beta t})$	α	None
Logistic	$\frac{\mathrm{d}y}{\mathrm{d}t} = \beta y(1 - \frac{y}{\alpha})$	$y_t = \frac{\alpha}{1 + e^{\beta_0 - \beta_1 t}}$	α	$\left[\frac{\beta_0}{\beta_1}; \frac{\alpha}{2} \right]$
Gompertz	$\frac{\mathrm{d}y}{\mathrm{d}t} = \beta y(\ln \alpha - \ln y)$	$y_t = \alpha e^{-e^{-\beta(t-\gamma)}}$	α	$\left[\gamma; \frac{\alpha}{e} \right]$
Johnson-Schumacher	$\frac{\mathrm{d}y}{y} = \beta \mathrm{d}\left(\frac{1}{t^2} \right)$	$\ln y_t = \alpha - \beta \left(\frac{1}{t} \right)$	e^{α}	$\left[\frac{\beta}{2}; e^{\alpha - 2} \right]$
Bertalanffy-Richards	$\frac{\mathrm{d}y}{\mathrm{d}t} = \left(\frac{\beta}{\gamma} \right) y \left[\left(\frac{\alpha}{y} \right)^{\gamma} - 1 \right]$	$y_t = \alpha \left\{ 1 - e^{-\beta t} \right\}^{\frac{1}{\gamma}}$	α	$\left[-\frac{\ln(\gamma)}{\beta}; \alpha(1 - \gamma)^{\frac{1}{\gamma}} \right]$
Weibull	$\frac{\mathrm{d}y}{\mathrm{d}t} = \alpha \beta \gamma t^{\gamma - 1} e^{-\beta t}$	$y_t = \alpha(1 - e^{-\beta t^{\gamma}})$	α	$\left[\left(\frac{\gamma - 1}{\gamma \beta} \right)^{\frac{1}{\gamma}}; \alpha(1 - e^{\frac{\gamma - 1}{\gamma}}) \right]$
Schnute	$\frac{\mathrm{d}^2 y}{\mathrm{d}^2 t} = \frac{\mathrm{d}y}{\mathrm{d}t} \left[-\alpha + (1-\beta)\gamma \right]$	$y_t = \left\{ y_1^{\beta} + (y_2^{\beta} - y_1^{\beta}) \frac{1 - e^{-\alpha(t-t_1)}}{1 - e^{-\alpha(t_2 - t_1)}} \right\}^{\frac{1}{\beta}}$	$\alpha \left[y_1^{\beta} + \frac{y_2^{\beta} - y_1^{\beta}}{1 - e^{-\alpha(t_1 - t_1)}} \right]^{\frac{1}{\beta}}$	$\left[t_1 + t_2 - \frac{1}{\alpha} \ln\left(\frac{\beta(y_2^{\beta} e^{\alpha t_2} - y_1^{\beta} e^{\alpha t_1})}{y_2^{\beta} - y_1^{\beta}} \right); (1-\beta)\left(\frac{y_2^{\beta} e^{\alpha t_2} - y_1^{\beta} e^{\alpha t_1}}{e^{\alpha t_2} - e^{\alpha t_1}} \right) \right]$

forestry literature [31, 51] is

$$y_t = \frac{\alpha}{1 + e^{\beta_0 - \beta_1 t}} \tag{7}$$

which is equivalent to make $(\alpha - y_0)/y_0$ of Eq. (6) as equal to e^{β_0}, and β_0 and β_1 are parameters. Robertson [52] proposed the same differential equation (as in Eq. 4) to describe an autocatalytic monomolecular reaction in biochemestry. Then, the logistic equation is also known as the expression that represents the "autocatalytic law" of physiology and chemistry. When [53] commented on some recent studies on growth including the one by [52], further generalized this thought to brain (and other) growth. According to [34], Pearl and Reed promoted the autocatalytic concept not only for individual but also for population growth, in their work of 1924. In sociology, the logistic model is know as the law of Verhulst established in 1838 describing the growth of human populations with limited resources [54].

Gompertz growth model. This growth model was proposed by [55], who was concerned with modelling mortality in an arithmetical progression; however, [56] derived it as a growth model. Gompertz's differential model is

$$\frac{d\ln y}{dt} = \beta(\ln\alpha - \ln y),$$
$$\frac{1}{y}\frac{dy}{dt} = \beta(\ln\alpha - \ln y),$$
$$\frac{dy}{dt} = \beta y(\ln\alpha - \ln y), \tag{8}$$

when the relative growth-rate declines with $\ln y$ and the other terms are parameters. The most common parameterization of a solution of (8) is [3, 34]

$$y_t = \alpha e^{-e^{-\beta(t-\gamma)}}, \tag{9}$$

where α is the asymptote and γ is the time where the point of inflection occurs (Table 1). Although β is a dimensionless parameter, it affects the maximum growth-rate (i.e., $\alpha\beta/e$). As opposed to the logistic model, the Gompertz curve is asymmetric.

Johnson-Schumacher growth model. This model was independently proposed by [57] and [21], which has been also known as the "reciprocal function". [21] explained the model by saying that the growth percent varies inversely with age, which he expressed in a differential form as follows

$$\frac{dy}{y} = \beta d\left(\frac{1}{t}\right). \tag{10}$$

A solution to this differential equation is found by first, set $u = t^{-1}$ and then substitute $du = -t^{-2}dt$ for

$d(1/t) = -t^{-2}dt$ in Eq. (10)

$$\frac{dy}{y} = \beta du,$$
$$\int \frac{1}{y}dy = \int \beta du,$$
$$\ln y + \gamma_1 = \beta u + \gamma_2, \tag{11}$$

where γ_1 and γ_2 are the constants of integration. Second, by assigning $\alpha = \gamma_2 - \gamma_1$, we arrive at

$$\ln y = \alpha + \beta\left(\frac{1}{t}\right). \tag{12}$$

This model has been widely used in forestry, mainly for fitting height-age models. Eq. (12) allows parameter estimation in the context of linear modelling. However, one should notice that model fitting for $\ln y$ leads to biased predictions of y [58, 59]. Also the alternative form $y = \alpha\exp(\frac{\beta}{t})$, is used in forest sciences; however, here α has a different interpretation than in (12).

The differential equation of [21], can be represented as the growth-rate as a fraction of the state variable y, as follows

$$\left(\frac{dy}{d\left(\frac{1}{t}\right)}\right)/y = \beta. \tag{13}$$

however, as mentioned by [60], this differential equation does not represent what [21] said in words, i.e., "growth per cent varies inversely with age". Instead, that thought is represented by the following differential equation

$$\left(\frac{dy}{dt}\right)/y = \beta\left(\frac{1}{t}\right). \tag{14}$$

A solution of Eq. (14) is obtained as follows,

$$\frac{dy}{y} = \beta\left(\frac{1}{t}\right)dt,$$
$$\int \frac{1}{y}dy = \beta\int\left(\frac{1}{t}\right)dt,$$
$$\ln y + \gamma_1 = \beta\ln t + \gamma_2, \tag{15}$$

where γ_1 and γ_2 are the constants of integration, and $\alpha = \gamma_2 - \gamma_1$, as before, we get

$$\ln y = \alpha + \beta\ln t, \tag{16}$$

This function is not the growth equation proposed by [21], which is being advocated to represent growth-rate as a percentage inversely proportional to time. Using exponential transformation, we see that the equation is a linearized version of the extensively used power function $y = \phi t^\alpha$, where $\phi = e^\alpha$.

Furnival [60] also detected the error in [21], and said "the curve given by [21] is obtained if growth percentage is taken as inversely proportional to the square of age".

If we proceed as above, we arrive to

$$\ln y = \alpha + \beta \left(-\frac{1}{t} \right). \tag{17}$$

This formulation emphasizes that model (12) leads to increasing logarithmic growth only if $\beta < 0$, whereas in (17) we need to have $\beta > 0$. Therefore, we favor this expression as a correct solution of the differential equation

$$\frac{\mathrm{d}y}{y} = \beta \mathrm{d} \left(\frac{1}{t^2} \right). \tag{18}$$

Finally, we could say that the derivation of Schumacher is correct but his formulation is wrong.

Bertanlanffy growth model. This model was first published in German [61], and later the author introduced it to the English literature in a brief paper [62], and in a more developed one [20]. He originally developed it for weight growth of animals. The model is a result of a deeper developed basic idea of Pütter in 1920 [54]. That is, growth can be considered a result of a counteraction of synthesis and destruction, of the anabolism and catabolism of the building materials of the body. The differential form of the von Bertanlanffy model is

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \eta y^\theta - \kappa y^\phi, \tag{19}$$

where η and κ are constants of anabolism and catabolism respectively, and the exponents θ and ϕ indicate that both are proportional to some power of the state variable y. Leary [63] termed (19) as the Bertalanffy's anabolic-catabolic balance equation of biological growth. As explained by [20], this differential equation represents "the change of y is given by the difference between the processes of building up and breaking down". Nonetheless, this is a property that is also shared by the monomolecular (1), logistic (4) and Gompertz (8) equations, in the sense that the differential equation can be separated into different additive terms. In the Bertalanffy model, both these processes are described by the simple power models, but the form of these submodels is not justified by biological theory. [47] pointed out that von Bertalanffy did not make clear what he meant by anabolism and catabolism, and aside from all the widely quoted references to his model as a solid theoretical growth model, that is not actually true. For instance, [54] explained, when referring to his model, that the use of the exponent θ and ϕ in (19) has a pure empirical base, since it is well known that the size dependence of physiological processes can well be approximated by allometric expressions. More recently, [3] noticed that unfortunately the biological basis of these models (referring to the logistic, Gompertz, and von Bertalanffy) has been taken too seriously and had led to the use of ill-fitting growth curves. Bertalanffy [20] justified that $\phi = 1$ based on physiological experience; hence

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \eta y^\theta - \kappa y, \tag{20}$$

and he also empirically found that for a wide class of animals, the allometric power for the metabolic rate (θ) is 2/3. Thus, differential equation (19) becomes

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \eta y^{2/3} - \kappa y, \tag{21}$$

Eq. (21) is usually termed the von Bertalanffy model [3]; nonetheless, we prefer to reserve that denomination to Eq. (20).

Bertalanffy-Richards growth model. [19] doubted some theoretical considerations of the Bertalanffy model (21), and treated some of the parameters to be related to a point of inflection [3]. The Richard's differential equation is

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \left(\frac{\beta}{\gamma} \right) y \left[\left(\frac{\alpha}{y} \right)^\gamma - 1 \right], \tag{22}$$

where α, β and γ are the asymptote, a scale, and shape-related parameters [34]. Although, this equation has been termed as the Bertalanffy-Richards model by [64, 65], and also as a generalization of the Bertanlanffy model [19], it is paramount to understand that it is simply a reparametrization of (20) as shown by [38]. A solution of this differential equation is

$$y_t = \alpha \left\{ 1 - \left[1 - \left(\frac{y_0}{\alpha} \right)^\gamma \right] e^{-\beta(t-t_0)} \right\}^{\frac{1}{\gamma}}. \tag{23}$$

Notice that (23) becomes the following growth equation if $y_0 = t_0 = 0$,

$$y_t = \alpha \left\{ 1 - e^{-\beta t} \right\}^{\frac{1}{\gamma}}. \tag{24}$$

Hence, (24) is a special case of (23), being the former suitable for forestry plantations and the latter for natural forests [66]. It is key to realize, and as aforementioned, that from distinct differential equations, we can arrive at a same solution. Notice that from the following linear differential equation with a power transformation [64],

$$\frac{\mathrm{d}y^\gamma}{\mathrm{d}t} = \beta \left(\alpha^\gamma - y^\gamma \right), \tag{25}$$

we can obtain the same solution of (23), as explained in detail by [38].

Chapman [67] starting from the von Bertalanffy differential equation, in the same way as [19] did, derived a new parameterization of the model particularly suitable for fisheries population modelling. Because of that, sometimes this equation has been called "Chapman-Richards" as well [40, 68]. We can argue that the denomination for the generalized differential equation (20)

should be credited to [20], because even though he did not state it formally in his paper, he used it as the basis to obtain his proposed solution. Nevertheless, [19] made this clearer, and also gave his famous 2/3 exponent for θ in (20). Thus, the denomination "Bertalanffy-Richards" seems a better compromise. Any other denomination, e.g., Chapman-Richards, even though correct in the sense that they started from the differential equation (20), is burdensome. Similar claims had been brought by [37, 38, 39, 69]. Based on the shortcomings mentioned above, we shall focus on the Bertalanffy-Richards growth model (23).

Weibull growth model. This model is a probability density function (pdf) widely used in engineering [70] as well as in forestry for describing diameter distributions [71, 72] because of its versatility. [73] noticed that tree increment and growth curves resemble a probability density (i.e., frequency distribution) and a probability distribution (i.e., cumulative frequencies distribution), respectively. Later, [11] exploited this relationship and used it to fit growth curves of trees. Based on the review given by [74], it seems that [11] were the first to notice this. The differential form of the Weibull growth model is as follows [40]

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \alpha\beta\gamma t^{\gamma-1}e^{-\beta t^{\gamma}}. \tag{26}$$

A solution of the Weibull growth-rate model is [11, 41]

$$y_t = \alpha\left\{1 - \mathrm{e}^{-\beta t^{\gamma}}\right\}, \tag{27}$$

where α, β, and γ are parameters representing the asymptote, intrinsic rate and the shape of the curve, respectively. The last two parameters affects the point of inflection (Table 1). [40, 41, 75] found that the Weibull growth model performed as well as other common growth equations in modelling tree growth of several variables.

Schnute growth model. [76] introduced a model first tested for fisheries research. The model is capable of assuming a wide range of characteristic shapes that describe asymptotic as well as non-asymptotic growth trends [65, 77]. The Schnute's model is based upon acceleration in growth, that is the rate of a rate, hence using second derivatives as follows [76]

$$\frac{\mathrm{d}^2y}{\mathrm{d}^2t} = \frac{\mathrm{d}y}{\mathrm{d}t}[-\alpha + (1-\beta)\frac{1}{y}], \tag{28}$$

where α, β, and $\mathrm{d}y/\mathrm{d}t$ are parameters. A solution of the Schnute differential equation is [76]

$$y_t = \left\{\tau_1^{\beta} + (\tau_2^{\beta} - \tau_1^{\beta})\frac{1 - \mathrm{e}^{-\alpha(t-t_1)}}{1 - \mathrm{e}^{-\alpha(t_2-t_1)}}\right\}^{1/\beta}, \tag{29}$$

where $\alpha \neq 0$, $\beta \neq 0$, t is the time of interest, t_1 time at beginning (e.g., young), t_2 time at end of (e.g., old), τ_1 and τ_2 are parameters representing the state variable y

at time t_1 and t_2, respectively. As stated by [65], ϕ is a constant acceleration in growth-rate, and β is incremental acceleration. Unfortunately, the growth function (29) does not have a single parameter with biological interpretation (Table 1). The Schnute growth-rate model is among the very few growth investigations based upon second derivatives, with the exception of the lucid study of [78] when modelling height growth.

The use of growth equations in empirical studies

Although the logistic model has been long used in population dynamics in ecology, it has barely been used in forestry to model growth [51]. Among them, [22, 31, 51] used it for modelling growth of stand volume, stem area, and tree height growth, respectively. Unlike the logistic model, the Gompertz model is not symmetric about the point of inflection. It is a model more used in ecology than in forestry; it performed well in population models as reported by the comparison of [79] and was used with success by [80]. In forestry, it was first mentioned by [81], but was not used until the work of [82] in modelling stand volume growth. The Bertalanffy-Richards model is used more than any other function in studies at tree and stand level [41, 43]. This equation was first used in forestry by [83], but mostly popularized by [68], after which the model was termed and later known as "Chapman-Richards". The Schumacher growth equation (17) is long-established for modelling height growth of dominant trees, because it is linear in its parameters. Notwithstanding, lately the Bertalanffy-Richards model has become the preferred model. The Weibull model was first proposed by [11]. [73] earlier had mentioned the resemblance of growth and increment curves to probability density and probability distribution. The Schnute model has the property of having asymptotic as well as non-asymptotic shape depending on the parameter values combination, therefore being versatile to a wider ranges of situations. [77] were the first to introduce the model to forestry. Later on [65, 84], and [85] used this model as well.

Comparisons among growth equations are valuable both for practical and theoretical use; nonetheless, it seems that researchers tend to prefer one of the models beforehand. Researchers might conduct initial screenings, but may not report the results in detail. Considering the large number of growth functions [43], very few studies have empirically compared them. In table 2, we have summarized a comprehensive list of studies in this regard. Overall, the authors selected their models using traditional goodness-of-fit statistics. The Bertalanffy-Richards, Weibull and Schnute were the most widely selected according to these criteria.

Table 2 Empirical comparisons of growth equations in some forestry studies. The symbol ● and √ represents that the equation was assessed and selected as the best in the study, respectively.

	Model							
Source	Monomolecular	Logistic	Gompertz	Bertalanffy-Richards	Weibull	Schnute	Other	Data
[11]		●	●	●	√			Tree volume
[86]	√		●				●	Stand volume
[77]				●		√		Tree diameter
[40]		●	●	●	●		√	Tree diameter
[75]				●	√			Tree height
[87]	●	●	●		√			Plant disease
[65]				√		√		Tree diameter
[88]			●	√	√	√		Tree height
[84]				√		√		Tree height
[89]		●	●	√	√	√		Tree height
[43]	●	●	●	●	√			Tree height
[90]				√	●			Tree basal area
[91]	●	√	●	●		●	●	Weight
[85]						√	●	Tree height
[92]				√	●		√	Plant disease

Practical demonstration

To illustrate the different growth-rates, we estimated the parameters of the growth equations by using time series height data of 107 *Nothofagus dombeyi* sample trees, a native evergreen and endemic species in Chile [93], growing on secondary stands in the south of the country. The tree-level data was collected within 30 sample plots established throughout the ecological distribution of the species. Sample trees, at the time of sampling, ranged from young ages to mature (between 21 and 71 years), as well as from small trees to taller ones (between 10 to 34 meters, Table 3).

Table 3 Tree level variables summary for the 107 *Nothofagus dombeyi* trees at the time of sampling. d is diameter at breast height, h is total height, age is total age, and bha is breast-height age.

Statistic	d	h	age	bha
	(cm)	(m)	(yr)	(yr)
Minimum	5.3	9.9	21	15
Maximum	60.2	33.7	71	68
Mean	26.6	19.9	41.3	37.7
Median	26	20.8	40	37
CV(%)	19	16.6	15.8	17.3

The height growth data cover a wide variety of growing conditions (Fig. 3). Further details on the data can be found in [38].
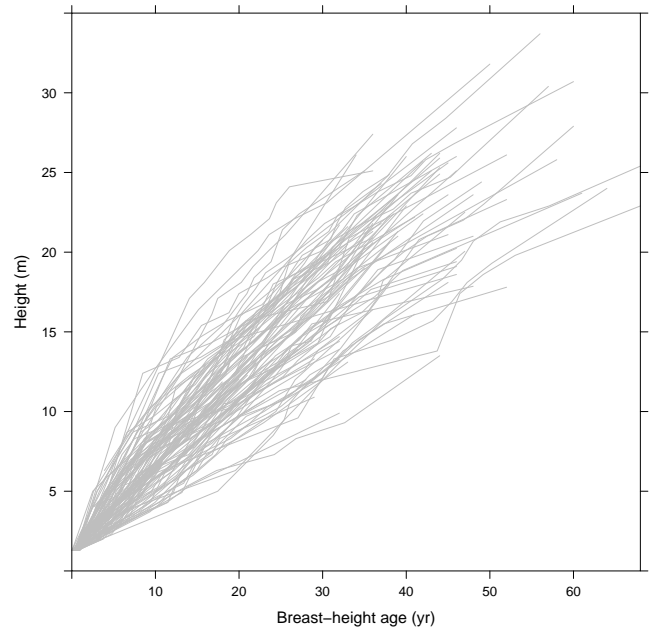

Fig. 3 Tree height growth series of dominant trees for *Nothofagus dombeyi* in southern Chile. Grey lines join successive observations of height on the same tree.

The growth equations were fitted in a mixed-effects model framework for considering the grouped structure of the data [66, 94]. A general nonlinear mixed-effects model for the kth observation on the jth tree at the ith plot is

$$y_{ijk} = f(\phi_{ij}, t_{ijk}) + \varepsilon_{ijk}, \tag{30}$$

where f is a growth equation and the parameter vector ϕ_{ij} includes the parameters of the selected growth

function. Each parameter consists of a fixed effect ($\boldsymbol{\mu}$) and two random-effects, i.e., plot ($\boldsymbol{b}_i$) and tree ($\boldsymbol{b}_{ij}$), therefore

$$\phi_{ij} = \boldsymbol{\mu} + \boldsymbol{b}_i + \boldsymbol{b}_{ij}. \tag{31}$$

We assume that the random effects among plots are independent with $\boldsymbol{b}_j \sim N(\boldsymbol{0}, \boldsymbol{D})$, as well as for the random effects among trees within plots with $\boldsymbol{b}_{ij} \sim N(\boldsymbol{0}, \boldsymbol{E})$. Also the residual errors are independent and normally distributed with $\text{Var}(\varepsilon_{ijk}) = \sigma^2$. Further details on the formulation of non-linear mixed-effects models are presented in [59, 95, 96, 97]. The models were fitted using the `nlme` package [98] of R [99]. The fixed-effects parameter estimates for each growth model are displayed in Table 4. We also computed the prediction statistics as in [100], i.e., the root mean square differences (RMSD) and the aggregated difference (AD) using the population level predicted value from the corresponding mixed-effects fitted model. These statistics provide some insight into model fit. Except for the Johnson-Schmacher equation, all models have similar precision and accuracy levels.

Using the fixed-effects estimated parameters of the non-linear mixed-effects growth models (Table 4), we represent the height growth or trajectory of the state variable h (Fig. 4a), and the instantaneous growth-rates versus time (Fig. 4b) and versus the state variable (Fig. 4c), as well. These trajectories should be interpreted as the estimates for a typical sample plot of the data set.

The number of parameters (i.e., coefficients) affects the flexibility of functions. As such, the greater number of parameters, the greater flexibility or intrinsic curvature. We used two functions (i.e., Monomolecular and Johnson-Schumacher) having 2 parameters, four (i.e., logistic, Gomperts, Bertlanffy-Richards, and Weibull) having 3 parameters, and the Schnute's function having 4 parameters. Comparing flexibility of the functions for a given number of parameters is of great interest when a generally applicable function is searched for empirical growth modelling. See [101] for such an analysis in the context of diameter distribution models. However, we leave such analysis for future studies.

Caveats

In physics, it is rare to analyze different models because they are already well established, and uncertainty is not a central feature. On the contrary, in biology-related disciplines, such as forestry, variability and uncertainty is the rule. As such, selecting a growth equation on which our findings are based is not straightforward. Most practitioners might compare a suite of equations and choose one of the merit of goodness-of-fit indices [102, 103]. On the contrary, others will start with a preferred growth equation at the very beginning of their studies [104, 105, 106]. In this vein, it is often not recognized the tremendous impact that a selected growth model will have on our inferences. For instance, let us assume that the goodness-of-fit indices are similar among the suite of growth equations examined here as a reference, a pattern that is not unrealistic. However, if we are interested in finding the maximum height for the species, a critical functional trait, the asymptote of the growth curves (Fig. 4a) varies tremendously between an unrealistic value of 15.2 m for the Johnson-Schumacher model (we used the [58] bias correction for prediction)

Table 4 Fixed-effects parameter estimates and prediction statistics for each mixed-effects growth model. All models were fitted by maximum-likelihood and using time series height data of 107 *Nothofagus dombeyi* sample trees from southern Chile. RMSD is the root mean square differences and AD the aggregated difference.

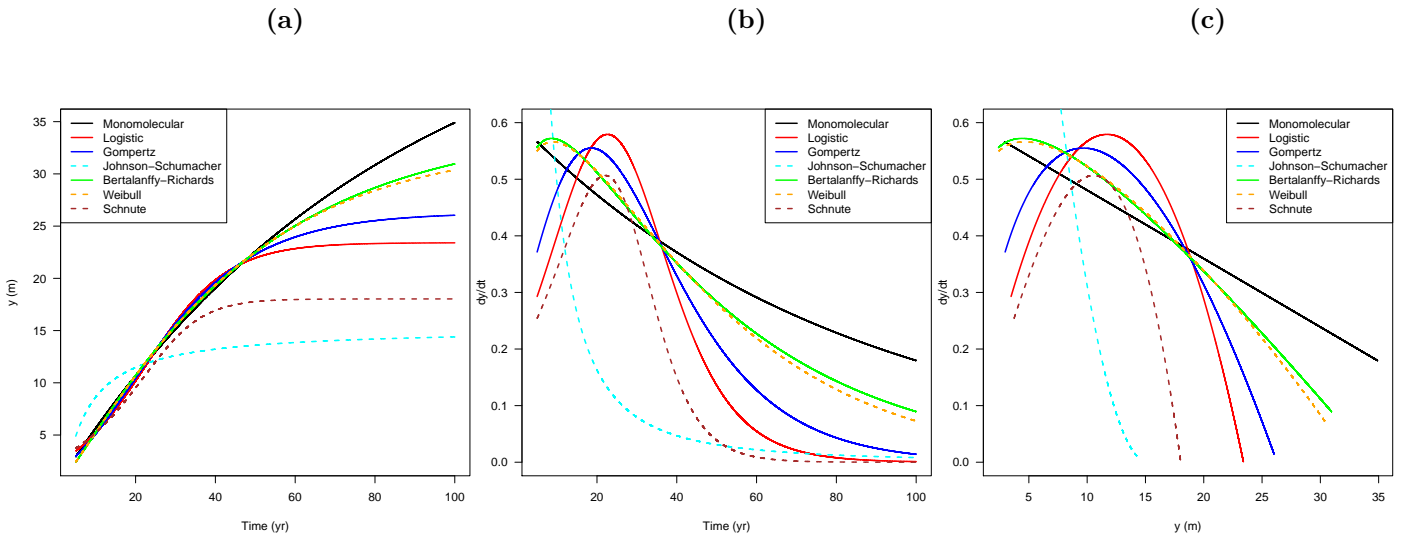| Growth model | Parameters | | | | RMSD | | AD | |
	$\widehat{\alpha}$	$\widehat{\beta}$	$\widehat{\gamma}$		(m)	%	(m)	%
Monomolecular	49.76	0.012	–		2.8249	26.2	0.0507	0.47
Logistic	23.41	2.242	0.10		2.8560	26.5	0.0689	0.63
Gompertz	26.28	0.057	18.59		2.8003	25.9	0.1082	1.00
Johnson-Schumacher	2.72	5.681	–		5.1607	47.9	1.6846	15.62
Bertalanffy-Richards	34.67	0.024	0.81		2.7876	25.9	0.1494	1.39
Weibull	32.70	0.012	1.18		2.7871	25.8	0.1487	1.38
			$\widehat{\tau_1}$	$\widehat{\tau_2}$				
Schnute	0.16	-2.13	2.84	18.02	2.9419	27.3	0.2120	1.96

Fig. 4 Growth (a) and growth-rates (b) versus time, and growth-rates versus the state variable (c) for the growth equations studied here.

and 49.8 m for the monomolecular one (Table 4). Overall, there is no theoretical reason to limit either tree or forest growth analysis by using a single equation, and claims on different reparametrizations have been proposed [107].

As previously, most growth models are non-linear. The only linear model (in the parameters) assessed here was the Johnson-Schumacher (Eq. 17). There is no closed formula to estimate non-linear models' parameters, as we have for the linear models. Nowadays, most statistical software includes tools for easing the fit of non-linear equations, such as self-starting functions that find good initial guesses for the parameters. [97]. However, a little more care and time may be needed than with linear models e.g. to run the numerical estimation routines in large data sets, to find good enough initial guesses for the parameters, and to ensure that the estimates found are the global maximum of the likelihood function, but not local [3]. Regardless, several attempts have been devoted to ecological applications to offer guidance for fitting non-linear growth models, since [108, 109] to [44], highlighting that this is still an important topic when modelling tree and forest growth. Consequently, the possibility of working with models having parameters with biological or physical interpretation is an advantage for fitting these non-linear models.

There are numerous applications for the unified mathematical treatment of growth equations presented here. The more obvious are in forest modelling, such as the ones fully described in [110, 111]. Besides, growth equations have several implications in decision support and scientific findings [112]. Nonetheless, there are a handful of other applications where growth equations are used. Among them, we can mention the studies focus on: eco-physiological aspects of sapling growth [104, 105, 106, 113]; forest-dynamics [114]; silviculture [115, 116]; and restoration ecology [117, 118, 119], where all the findings are based upon a single fitted–and–assessed growth function.

As lucidly summarized by [3], we can use x (i.e., another state variable) instead of t in the growth-rate equations, and by this simple twirl, the same mathematical models shown here, as well as their implications, can serve for representing tree allometry [120], a major scientific endeavor in biology [121, 122]. In the forestry context, growth equations have been used in modelling height-diameter [88, 123, 124], and stem taper [125, 126] allometric relationships.

Growth-rates of the tree and forest growing processes are essential in research [23, 127, 128], especially to study the partitioning of components, resources, and allocation of them to different processes. At least a basic but correct mathematical understanding of differential equations is paramount for researching these complex processes. Similar advocacy has been claimed by others in ecology [129]. It is noteworthy to realize how the forestry literature is way more focused on growth than on the growth-rates themselves; that is to say, forestry is a discipline where we seem to be trained to think in an integrated form rather than in a differential form. In contrast, we highlight the pioneer works on differential equations in forestry led by [64, 130, 131, 132, 133]. Although we might think that the reasons for focus- ing on growth, but not on growth-rates when modelling

forestry variables are a handful; the main one could be related to the fact that instantaneous growth rates are essentially unobservable, whereas realized sizes can be measured and so are amenable to exploratory data analysis. However, this can also be applied to other biological disciplines, such as wildlife ecology and landscape ecology. Regardless, the use of growth-rates, or differential equations, are just a few compared to size-time equations (i.e., a differential equation solution). Maybe the reasons are also related to a weak educational background in calculus of ecology-related scientists [129, 134]. Accordingly, we favour using growth-rates functions, such as differential equations, in forest growth modelling when justified by the research question [23, 38, 128, 133].

As a reflection of the above, the analyses of the growth rates is mandatory. The growth-rates against time for each model broadly vary (Fig. 4b). All of them implies completely different processes. For instance, the Monomolecular and the Johnson-Schumacher curves seem unrealistic. Both the Bertalanffy-Richards and the Weibull functions behave quite similar at reaching their maximum growth-rates at much earlier stages. On the contrary, the logistic, Gompertz and Bertalanffy-Richards seems to be more feasible. Finally, a graphic representing the growth-rates against time (Fig. 4b) is usually the most commonly reported; however, plotting the growth-rates against size (Fig. 4c) is also essential. These two figures describe completely different processes. For instance, the logistic growth-rate is symmetric, and the point on which this occurs is where half of the asymptote is reached, and the growth-rate is maximum. Nonetheless, no biological reasons for the symmetry have been presented. The asymmetric behaviour of the other functions seems more realistic. Both the Bertalanffy-Richards and the Weibull behave quite similarly, reaching their maximum growth-rates at much smaller sizes. Finally, the Monomolecular and the Johnson-Schumacher curves are entirely unrealistic. In general, the rules on which the growth equations are based are rather broad and motivated more by mathematical formulation than by a solid, established theory about the biological processes of growth.

Concluding remarks

We have shown that the mathematical differences among several growth equations can be more easily explained and understood using their differential equation than their integrated forms. Inter alia, the assumed-and-claimed biological basis of these growth-rate models has been taken too seriously, and the focus should be on using a plausible equation for the organism being modelled.

More attention should be put on parameter estimation strategies and behaviour analysis of the proposed models. It is difficult for a single function to capture all possible shapes and rates that such a complex biological process as tree growth can depict in nature. Therefore, comparisons of some functional forms (at least simple ones) must be carried out before selecting a function for drawing scientific findings.

Conflict of interest The authors declare that they have no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by the authors.

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