
Analysis of Growth Equations

BORIS ZEIDE

ABSTRACT. Growth of plants results from two opposing factors: the intrinsic tendency toward unlimited increase (biotic potential) and restraints imposed by environmental resistance and aging. The expansion tendency prevails in the beginning of a tree's life, while growth decline becomes prominent toward the end. The existing growth equations can be transformed (by differentiation, decomposition into the division components, and taking logarithms) so that the components that correspond to these two factors are exposed. This transformation reveals two basic forms intrinsic in most of the analyzed equations. Their common feature is that growth expansion is proportional to current tree size. Growth decline of individual trees appears to be more variable and can be rendered with equal accuracy by a variety of expressions. This may reflect that a greater number of factors hinder growth: scarcity of resources, competition, reproduction, diseases, herbivory, disturbances, etc. Consequently, the growth path is inherently imprecise and can be viewed as a wide valley rather than a single line. This analysis laid groundwork for the classification of known equations and made possible the discovery of a promising new equation form. *FOR. SCI.* 39(3):594-616.

ADDITIONAL KEY WORDS. Basic equation forms, classification of growth equations, components of growth, decomposition of equations, exponential increase.

GROWTH EQUATIONS DESCRIBE THE CHANGE IN SIZE OF AN ORGANISM OR a population with age. Biological growth, the outcome of numerous and enormously complex processes, appears remarkably simple, particularly for trees. As we combine more and more similar trees, the increase in their size follows an ever smoother sigmoid curve. In the beginning the curve is concave up, while in later life it becomes convex. Although growth responds to environmental trends and fluctuations, this long-term pattern remains surprisingly stable.

Many equations have been proposed to describe plant growth. Kiviste (1988) described 75 of them in a comprehensive two-volume monograph. Although only a few have proven useful, probably no biologist believes that one equation would suit all growth processes. This seems to be a belief peculiar to biology. A physicist would not use more than one equation to describe, for instance, the fall of a body in a vacuum. "If physics has its laws, biology has its variety" (Dover 1988, p. 623).

The variety of existing growth equations brings up a number of questions. Are there any relationships among the equations? Is it possible to reduce them to a small number of basic forms? How can the adequacy or inadequacy of an equation be interpreted so as to contribute to our understanding of nature?

Besides satisfying our intellectual curiosity, answering these questions may solve many practical problems. For example, an optimal rotation age extracted from a more accurate picture of forest stand growth could differ by 10 or more years from the age computed using traditional methods (such as yield tables). This means that just by doing more accurate calculations, we can utilize forest re-

sources more efficiently. Another important area of application is the detection of changes in the environment, be it negative, such as stress, or positive, such as fertilization or thinning. These changes can be revealed by comparing the actual growth in an altered environment with the growth predicted by reliable equations from the data of growth prior to the change.

Although these problems are not new, few would claim that they are solved. Therefore, given their theoretical and practical implications, I believe that further analysis of the existing equations could contribute to a better understanding of tree growth.

GROWTH EQUATIONS AND COMPUTER MODELING

Not everyone shares the belief that growth equations merit further consideration. Some view the curve-fitting approach as an ossified remnant of the precomputer past and doubt whether it is worthwhile to study these old-fashioned forms of modeling. Now we have much more comprehensive and flexible methods of computer modeling that utilize such methods as dynamic programming, difference-based equations, and neural networks. There are also conceptual objections to using growth equations. Huston et al. (1988) believe that growth equations and all models that deal with a population as a whole ("aggregated large-scale models") are based on unrealistic ecological assumptions, gloss over ecological mechanisms and individual variability, and ignore reality (in particular, feedback interactions). These authors view it as unacceptable to "combine many individuals and assume that they can be described by a single variable, such as population size. This procedure violates the biological principle that each individual is different, with behavior and physiology that result from a unique combination of genetic and environmental influences" (Huston et al. 1988, p. 682). According to these authors, the future of ecology belongs to the individual-based modeling approach, which will soon produce a mechanistic understanding of ecological systems.

This belief is not new. It has been known in philosophy for centuries under the name of nominalism. It is based on the exaggeration of differences among individuals of the same species or population and is equivalent to saying that they have nothing in common, apart from the species name. Nominalism is logically inconsistent: were there nothing common to all individuals, they could not be considered as members of the same species and combined under one name. Following the same line of reasoning a nominalist should do away with the concepts of not only population and species but of organism as well. An organism can be viewed as a population of individual cells that are different in behavior, physiology, location, and many other characteristics. Cells in their turn include many different components.

One of the reasons offered by Huston et al. (1988) in support of individual-based models is that, along with detailed information on individual interactions, they are capable of producing a general and integral picture of a system. Following this suggestion, we could determine, for example, temperature of an organism by measuring the speed and mass of each constituent particle (one mole contains $6.02 \cdot 10^{23}$ particles). It is likely, however, that even in the remote future many would prefer to use a thermometer which describes the integral behavior of many individual particles with a single variable, temperature.

Experience shows that along with differences, individuals share many common features and that it makes sense to use an average to characterize a population as a whole. Both unicellular and multicellular organisms often exhibit aggregate behavior, which is considered one of the major characteristics of complex adaptive systems (Holland 1992). Problems with the individual approach are well-known in forest ecology in which individual-based models have been applied since 1950. Substantial research has revealed that, while requiring much more effort, these models provide practically no improvement in the accuracy of growth predictions as compared with an aggregate approach (Alemdag 1978, Larocque and Marshall 1988). Interactions among individual trees are often so complicated that they preclude reliable predictions.

Even if it were possible, not all our problems could be solved by tracing the effects of numerous agents, detecting assorted disturbances, and fleeting day-to-day perturbations in growth. There is a need to describe lasting features of growth and to express long-term trends, such as aging. In studies of overall trends, a certain degree of rigidity is an asset rather than a liability. For this reason growth equations have not lost their significance even with the advent of computer modeling, although they are no longer viewed as biological versions of Newton's laws. Actually, growth equations are used more than ever before because, in addition to their independent role, the equations serve as building blocks for computer models. Of course, these two approaches do not exclude, but complement each other. Each is tuned to its own frequency: detailed computer models are designed to reflect shorter wavelengths of daily changes, while growth equations consider the entire lifespan as one wave.

Precisely because of their wide scope, growth equations, along with a description of the change, afford a glimpse at the constancy resulting from the invariance of the genetic mechanism responsible for growth. The form of an equation is a means to achieve stability of parameters. The more accurate an equation is, the less variable are its parameters. A growth equation brings together two currents, age and size, to make explicit the hidden invariance that governs their relationship.

THE PRIMARY COMPONENTS OF GROWTH

Growth results from the interaction of two opposing forces. The positive component, most vividly manifested in expansion of an organism, represents the innate tendency toward exponential multiplication. This component is associated with biotic potential, photosynthetic activity, absorption of nutrients, constructive metabolism, anabolism, etc. The opposing component represents the restraints imposed by external (competition, limited resources, respiration, and stress) and internal (self-regulatory mechanisms, and aging) factors. Those factors that adversely affect growth have been referred to as environmental resistance, destructive metabolism, catabolism, respiration, and so on.

Appropriately, laws or postulates of growth are often formulated in pairs that reflect both the multiplicative and limiting components. Hutchinson's (1978) two postulates of population growth are:

1. Every living organism has arisen from at least one parent in like kind (the postulate of parenthood);

2. In a finite space there is an upper limit to the number of finite beings that can occupy or utilize the space under consideration (the postulate of an upper limit).

In 1941 Medawar formulated five laws of biological growth. When he returned to the same problem 4 decades later, he condensed these five into two basic laws (Medawar and Medawar 1983). They are similar to Hutchinson's postulates:

1. Fundamentally, growth is multiplicative. That which results from biological growth is itself, typically, capable of growing;
2. The relative growth rate is always decreasing (Minot's law).

The conflict between infinity implicit in multiplicative reproduction and the limit imposed by finite space is the chief source of all change in living beings, including growth. This conflict is the driving force of evolution and is crucial to understanding virtually all biological and social phenomena. Growth equations provide a succinct expression of this conflict and its resolution.

ANALYZED EQUATIONS

This study analyzes existing growth equations, including popular equations such as the Chapman-Richards, the Gompertz, and the logistic models, as well as several less known, yet promising models (Table 1). The structure of any other equation can be analyzed in a similar manner. Polynominal-based equations were not considered because they are devoid of any biological interpretation.

Let's briefly review the equations starting with the oldest, the Hossfeld IV equation proposed for the description of tree growth as early as 1822 (Peschel 1938). Despite its age, this equation performs remarkably well. According to Kiviste (1988), it is the third most accurate of 31 three-parameter equations when the three main stand variables (total tree height, stem diameter, and volume) are considered together. Kiviste found it to be the best equation for volume growth. The Hossfeld IV equation is almost as accurate as the Chapman-Richard equation, which dominates growth studies in this country. The most accurate equations with three (Levakovic I and III equations) and more (Yoshida I equation) parameters are modifications of the Hossfeld equation.

The Gompertz (1825) equation was designed to describe age distribution in human populations. A century later it was applied as a growth model (Winsor 1932). The equation presents relative growth rate (the ratio of increment of size to size itself, y'/y) as an elementary exponential function of age. Therefore, this equation was called (Laird et al. 1965), the equation of *exponential decay*. Another characteristics feature of the Gompertz equation is that the position of the inflection point is controlled by only one parameter, final (asymptotic) size, a . This point occurs when current size is equal to a/e , that is, at about one-third ($1/e = 0.3679$) of the final size. Nokoe (1978, p. 41) applied the Gompertz equation to three tree species and concluded that this equation "demonstrated sufficient flexibility to warrant its use." The Gompertz equation was found by Causton and Venus (1981) and many other researchers (Laird et al. 1965, Zweifel and Lasker 1976, Zullinger et al. 1984) to be more appropriate in biological work than any other. Besides these empirical results, it was deduced theoretically by Medawar (1940) that growth should follow the Gompertz model.

TABLE 1.

Growth equations and connection of their components. y = tree or stand size (height, diameter, or volume); t = age; y' = size increment; a, b, c , and d = parameters of equations; \ln = the natural logarithmic function. Placing the parameters and variables together always indicates multiplication: $bcy^2 = b \cdot c \cdot y^2$.

Equation name and its integral form	Differential form	Subtraction components		Division components	
		Expansion	Decline	Expansion	Decline
Hossfeld IV $y = t^c/(b + f/a)$	$y' = bct^{c-1}/(b + f/a)^2$	cy/t	cy^2/at	bcy^2	t^{c+1}
Gompertz $y = ae^{-be^{-a}}$	$y' = abce^{-ay}e^{-be^{-a}}$	$\ln(a)y$	$cy\ln(y)$	$(bc)y$	e^{ct}
Logistic $y = a/(1 + ce^{-by})$	$y' = abce^{-by}/(1 + ce^{-by})^2$	by	$(b/a)y^2$	$(bc/a)y^2$	e^{bt}
Monomolecular $y = a(1 - ce^{-bt})$	$y' = abce^{-bt}$	ab	by	(abc)	e^{bt}
Bertalanffy $y = a(1 - e^{-by})^3$	$y' = 3abe^{-by}(1 - e^{-by})^2$	$3a^{1/3}by^{2/3}$	$3by$	$(3a^{1/3}b)y^{2/3}$	e^{bt}
Chapman-Richards $y = a(1 - e^{-by})^c$	$y' = abce^{-by}(1 - e^{-by})^{c-1}$	$a^{1/c}bcy^{(c-1)/c}$	bcy	$(a^{1/c}bc)y^{(c-1)/c}$	e^{bt}
Levakovic I $y = a(t^d/(b + t^d))^c$	$y' = bcdy/(b + t^d)$	cdy/t	$a^{-1/c}cdy^{(c+1)/c}/t$	$a^{-1/c}bcdy^{(c+1)/c}$	t^{d+1}
Levakovic III $y = a(t^d/(b + t^d))^c$	$y' = 2bcy/(b + t^d)$	$2cy/t$	$2a^{-1/c}cy^{(c+1)/c}/t$	$2a^{-1/c}bcy^{(c+1)/c}$	t^3
Korf $y = ae^{-bt^{-c}}$	$y' = abct^{-c-1}e^{-bt^{-c}}$	$\ln(a)y/t$	$cy\ln(y)/t$	$(bc)y$	t^{c+1}
Weibull $y = a(1 - e^{-bt^c})$	$y' = abct^c e^{-bt^c}$	$abct^{c-1}$	bcy^{c-1}	$(abc)t^{c-1}$	e^{bt^c}
Yoshida I $y = at^d/(b + t^d) + c$	$y' = abdt^d/(b + t^d)^2$	$bdy/(b + t^d)$	$bdc/t(b + t^d)$	$(bd/a)(y - c)^2$ if $d > 1$	t^{d+1}
Sloboda $y = ae^{-be^{-at^d}}$	$y' = bcdy^{d-1}e^{-at^d}$	$cdt^{d-1}\ln(a)y$	$cdt^{d-1}y\ln(y)$	$(bcd)y$ if $0 < d < 1$	e^{at^d}
					$t^{1-d}e^{at^d}$

The logistic equation (Verhulst 1838) is probably the most famous equation in ecology. An outstanding exposition of its history is given by Hutchinson (1978). The forces that counteract the exponential increase are assumed to be proportional to the square of size. No reason for this choice of the exponent is provided other than that 2 is the next integer after 1. It is doubtful that the principle of parsimony, invoked and discussed in depth on this occasion by Hutchinson (1978), is sufficient to preclude the application of numbers other than integers. The inflection point of the logistic equation corresponds to one-half of final size. The relative growth rate of the equation declines linearly with size. Several other assumptions inherent in the logistic equation appear to be questionable (Krebs 1985, p. 220). Despite its untenable assumptions and lack of accuracy—it was found (Zeide 1989) to be the least accurate among sigmoid equations for the description of diameter growth of trees—the equation is still used in research, mostly by zoologists (Ricklefs 1979, Murtaugh 1988).

The monomolecular equation, the simplest among the analyzed equations, is not inflected and therefore presents a rather unrealistic picture of growth. This equation is known as the *law of diminishing returns* in agriculture and economics and as the *law of mass action* in chemistry. Ricker (1979) attributes the first biological application of a special form of this equation to Pütter (1920), while Richards (1969) refers to it as the Mitscherlich formula, after the German agronomist who used it at the beginning of this century. I have found an even earlier use of this equation in a study of tree growth by Weber (1891).

The appeal of the Bertalanffy (1957) equation lies in the intended rigor of its theoretical foundation. Bertalanffy (1957, p. 223) claims to have succeeded in developing “a general theory of growth which establishes rational quantitative laws of growth and indicates the physiological mechanisms upon which growth is based.” This theory considers animal growth to be the result of the combined action of two opposing processes, anabolism and catabolism. Bertalanffy (1957) derived his equation from the assumptions, which he attributed to Pütter (1920), that the rate of anabolism is proportional to the surface area of an organism (or to its mass raised to the power of $\frac{2}{3}$), while catabolism is proportional to the organism’s mass. These assumptions define what he calls “the first metabolic type.” Bertalanffy also describes two other types of metabolism and their corresponding growth types. Ricker (1979, p. 707) questioned these assumptions considering them to be “fanciful speculations.” Nevertheless, to honor the presumably original author of these speculations, Ricker refers to the Bertalanffy equation as the Pütter Growth Curve No. 2.

The origin of this concept, however, goes deeper than Bertalanffy and Ricker believe. It might be one of few viable ideas from the prodigious legacy of Spencer. He was concerned with the question, “Why has individual growth a limit?” and proposed several answers that resemble structural and mechanical considerations put forth by Galileo in his “Dialogues concerning two new sciences.” In particular, Spencer (1898, p. 151) wrote, “In similar bodies, the areas vary as the squares of the dimensions, and the masses vary as the cubes; it follows that the absorbing surface has become four times as great, while the weight to be moved by the matter absorbed has become eight times as great.” As does Bertalanffy, Spencer restricts this reasoning to animals, believing that tree growth is unlimited.

The trademark of the Chapman-Richards equation is its flexibility. Although the equation was reported by Mitscherlich (1919), it became known to American

researchers from the article fittingly titled “A flexible growth curve for empirical use” by Richards (1959). This equation is valued for its accuracy and is used more than any other function in studies of tree and stand growth. The Chapman-Richards equation was derived from the Bertalanffy equation “when limitations imposed by its theoretical background are discarded” (Richards 1959, p. 291). The difference between the equations is that the parameter c , restricted to a value of three in Bertalanffy’s case, can assume any value in the Chapman-Richards equation. This modification dispensed with the biological interpretation proposed by Bertalanffy. In his review of this paper, Rolfe A. Leary remarked that compared with Bertalanffy’s equation, the one by Chapman-Richards is “a giant leap backwards from explanation to description.”

It is not clear whether flexibility is a desirable quality of growth models. When the number of parameters is equal to the number of data points, any equation will pass through each point, thus exhibiting the ultimate flexibility. I doubt that we are looking for this sort of flexibility. Our understanding of growth would benefit little from an equation that passively follows all data points. We need an equation that sets its own, and hopefully correct, path through all data points, an equation that exposes a growth trend in the maze of data and separates the essential from the accidental. The law of physics that states that the distance covered by a falling body in a vacuum is proportional to the square of the time of fall rigidly adheres to the exponent of 2. This “rigidity” is the essence of the law. An equation with a variable exponent would certainly fit empirical data better than this law. Yet, this flexible equation would be a meaningless formula rather than a cornerstone of science.

Flexibility depends on the number of parameters in an equation, and there is no reason to expect that the Chapman-Richards equation would be more flexible than any other equation with three parameters. Still, this equation is set apart from others by its computational properties. Ratkowsky (1983, pp. 83–84) showed that this equation is “the only model that has an unacceptable intrinsic nonlinearity as the solution locus departs significantly from a hyperplane.” This property leads to so much instability in parameter estimates that it makes them useless. In his personal communication (of March 23, 1992), Richard Woollons writes that parameter estimates of the Chapman-Richards equation are worthless, especially for large datasets, because convergence is achieved by “means of a *fait accompli*.”

The Levakovic I and III (1935) equations are modifications of the Hossfeld equation. They were published over half a century ago in Serbian and are little known in other countries. The Levakovic III equation may look strange because it is unclear why age should be squared. Although squaring does not contribute to the accuracy of the logistic equation, it works well for the Levakovic equation: Kiviste (1988) found it to be the most accurate among all three-parameter equations that he investigated. The Levakovic I equation is one of the best four-parameter equations.

Korf’s equation was proposed in 1939 (Kiviste 1988) in Czechoslovakia and has been rediscovered several times, in particular by Lundqvist (1957). He, as well as subsequent researchers (Stage 1963, Brewer et al. 1985), applied it to model height growth of forest stands with moderate success. Zarnovican (1979), who also used Korf’s equation in a study of height growth, was better versed in the literature and cited three papers by Korf, including his original paper of 1939. This equation is especially suitable for the description of diameter growth of a fixed

number of trees. Zeide (1972, 1975) and Zeide et al. (1972) found that the relative growth rate of diameter is a power, rather than an exponential function of age and by integration arrived at the Korf equation. Using average growth of thousands of stem analyses of different species from different locations, it was shown that the Korf equation is substantially more accurate than other growth equations (Zeide 1989). Its standard error of estimate was 2.1, 2.3, 3.4, and 4.8 times less than the errors of the Chapman-Richards, Weibull, Gompertz, and logistic equations, respectively. A special form of this equation with $c = 1$ was independently proposed by Terazaki in 1915 (cited in Peschel 1938), Johnson (1935), and Schumacher (1939).

Originally intended to describe a probability distribution, the Weibull equation has proven to be a good empirical model of tree growth. Yang et al. (1978) reported that this equation is more accurate than the Gompertz or Bertalanffy equations. No comparison with the Chapman-Richards equation was given in their work. When Dolph (1991) compared these equations in the process of construction of site index curves for red fir, he found that the Weibull equation was more accurate than the Chapman-Richards equation. Unlike all other functions, the Weibull equation presents the increase of growth as a power function of age. It occupies the fourth place in Kiviste's (1988) ranking of three-parameter equations and is particularly good for modeling diameter growth of stands. Zeide (1989) found that Weibull's equation is less accurate than the Korf and Chapman-Richards equations.

The Yoshida I equation, proposed in 1928 (Peschel 1938), is another modification of the Hossfeld equation. Kiviste (1988) found that this equation is the most accurate among 21 four-parameter equations. In addition to those of the Hossfeld equation, the Yoshida I equation contains an additive term (parameter c in Table 1) that represents initial tree size. Because this size is negligible, so is the term.

The Sloboda (1971) equation differs from the Gompertz equation by an additional parameter d . The presence of this parameter probably is responsible for the greater accuracy of the Sloboda equation. According to Kiviste (1988), it is the second best four-parameter equation.

DECOMPOSITION OF EQUATIONS

In most cases, growth equations are used in an integral form which describes the accumulated size of an organism. The form of the equations affects the perception of differences or similarities among them. Using the integral form, Kiviste (1988) divided growth equations into seven classes. He placed the logistic and Korf equations in the same class of exponential functions. The Bertalanffy, Weibull, and Chapman-Richards equations were classified as Mitscherlich functions. The Korf and Levakovic equations were located in two different classes.

It is easier to understand the process of growth and the structure of growth equations when we consider them in the differential form with the current increment, y' , as the dependent variable and tree age, t , as the independent variable (Table 1). In this form growth equations can be decomposed into two components that represent growth expansion and decline. The expansion component describes the multiplication tendency and is responsible for an increase in the in-

crement with age or keeping the increment constant. The component of growth decline causes the increment to decrease. These opposite effects on growth allow one to detect the components and decompose an equation.

The component that expresses growth decline is not just an optional “modifier” of exponential increase, as is sometimes suggested. This component is one of the two irreplaceable parts of any model of biological growth. Equations containing only one component, such as Malthus’ (1798) law of population increase (geometric progression), cannot be considered complete growth equations. This law (proposed with a balancing conjecture about the arithmetic progression of the means of subsistence) served as a progenitor and catalyst of growth equations because many scientists, including its author, felt its incompleteness. For this reason Verhulst (1838) augmented the law (in its differential form) with a subtractor that offsets the multiplicative component. The same opposition is achieved in the Gompertz equation by division.

These two example (Verhulst and Gompertz equations) are typical of all growth equations. Components with positive parameters are connected by subtraction or division but not by addition or multiplication.

SUBTRACTION

All the investigated equations can be presented in the differential form as a difference of two components. For example, using the integral form of the monomolecular equation (Table 1), we can present the term ace^{-bt} as $a - y$ (a , b , c , and d throughout this paper are constant parameters). Substituting this result in the differential form of the same equation, one would obtain:

$$y' = ab - by \quad (1)$$

The expansion component in this equation is a positive constant (ab), while the decline component (by) is proportional to the size, y . In this paper size refers to nondiminishing tree or stand variables, such as height, diameter, or volume.

As another example of decomposition, the integral form of the Weibull equation can be written as:

$$\exp(-bt^c) = 1 - y/a \quad (2)$$

Substitution in the differential form results in

$$y' = abct^{c-1} - bcy^{c-1} \quad (3)$$

Because the constants are positive, the first term causes increase of the increment (y'), while the second term contributes to its decrease.

As a form of connection of components, subtraction has received the most attention in previous accounts of equation structure. Our intimate familiarity with this simple operation (after all, we balance our checkbooks by subtraction, not by division or exponentiation) probably plays some role in this preference. Bertalanffy (1957, p. 223) considered growth as the result of “a counteraction of synthesis and destruction, of the anabolism and catabolism of the building materials of the body.” He viewed this counteraction exclusively in terms of subtraction. In a series of publications, Savageau (1979, 1980) and his students presented the most thorough and consistent development of this approach. He produced a generalized growth equation that “is not simply another empirically derived for-

mula but is based upon the nature of the elemental mechanisms in synergistic systems" (Savageau 1979, p. 5416). This equation is constructed as the difference of two terms. In order to present the Gompertz equation as a particular case of his generalized equation, Savageau admits the existence of two (and more) dominant processes of growth within the same system. The technical and linguistic difficulties (dominant, after all, means the most influential, prevailing, and, therefore, unique) with this approach can be avoided by decomposing the Gompertz equation into division components.

DIVISION

Notwithstanding the familiarity and simplicity of subtraction, it is not the only possibility for decomposition of growth equations. Division, which is the subtraction of logarithms, is an equally valid operation. Many, if not the majority of all biological phenomena are multiplicative in nature rather than additive. The components of the Gompertz equation can be presented equally well as dividend (y) and divisor (e^{ct}). For the Gompertz equation and many others, components of the division method of decomposition are simpler than those of subtraction (Table 1). For example, each of the division components of the Korf equation (obtained by substituting the right side of the integral form into the differential form) contain only one of the equation's variables, while the subtraction components contain both.

Decomposition of some equations depends not only on their form, but also on the values of parameters. In the Sloboda equation, for example, when the parameter $d > 0$, the term t^{d-1} increases the increment in the course of time and, therefore, is a part of the expansion component. When $0 < d < 1$ the same term plays the opposite role and becomes a part of the decline component.

Decomposition by division allows one to further simplify equations by taking logarithms. In many cases the equations become linear. The three steps described above (differentiation, decomposition into division components, and taking logarithms) transform equations into a form that allows one to do the following:

1. Simplify the equations and linearize most of them.
2. Homogenize their variance.
3. Apply well-developed methods for the investigation of linear equations.
4. Facilitate the design of new equations.
5. Expose basic forms or families of equations.

The last point is pursued in some detail below.

BASIC FORMS OF EQUATIONS

The described transformation reveals two basic forms behind most of the analyzed equations. To present these forms more vividly, the equations are rewritten to simplify the notation of the constant parameters. All intercepts are designated as k . Constants of size, y (or $\ln(y)$) are denoted by p , while those of age, t and $\ln(t)$, are expressed by q (Table 2). For example, for the Korf equation the parameter k in Table 2 is equal to $\ln(bc)$ in terms of the parameters of Table 1. Similarly, for the same equation $p = 1$ and $q = -(c + 1)$.

TABLE 2.

Growth equations in uniform notation. $k > 0$, $p > 0$, and $q < 0$ = parameters of equations.

Equation name	Logarithm of differential form	
Hossfeld IV	$\ln(y') = k + 2\ln(y)$	$+ q\ln(t)$
Gompertz	$\ln(y') = k + \ln(y)$	$+ qt$
Logistic	$\ln(y') = k + 2\ln(y)$	$+ qt$
Monomolecular	$\ln(y') = k$	$+ qt$
Bertalanffy	$\ln(y') = k + (\frac{2}{3})\ln(y)$	$+ qt$
Chapman-Richards	$\ln(y') = k + p\ln(y)$	$+ qt$
Levakovic I	$\ln(y') = k + p\ln(y)$	$+ q\ln(t)$
Levakovic III	$\ln(y') = k + p\ln(y)$	$- 3\ln(t)$
Korf	$\ln(y') = k + \ln(y)$	$+ q\ln(t)$
Weibull	$\ln(y') = k + p\ln(t)$	$+ qt^{p+1}$
Yoshida I	$\ln(y') = k + 2\ln(y - c)$	$+ q\ln(t)$
Sloboda if $d > 1$	$\ln(y') = k + [\ln(y) + (d - 1)\ln(t)]$	$+ qt^d$
if $0 < d < 1$	$\ln(y') = k + \ln(y) + [(d - 1)\ln(t)]$	$+ qt^d$

It becomes transparent that all the equations, except Weibull's, are particular cases of the two following forms:

$$\ln(y') = k + p\ln(y) + q\ln(t) \quad \text{or} \quad y' = k_1 y^p t^q \tag{4}$$

$$\ln(y') = k + p\ln(y) + qt \quad \text{or} \quad y' = k_1 y^p e^{qt} \tag{5}$$

where $p > 0$, $q < 0$, and $k_1 = e^k$.

In both forms the expansion component is proportional to $\ln(y)$ or, in the antilog form, is a power function of size. The forms differ in the way the decline component is presented. In Equation (4) it is proportional to the logarithm of age, t . This form will be referred to as the LT-decline or LTD form. The decline component of Equation (5) is directly proportional to age, t . Accordingly, Equation (5) can be called the TD (T-decline) form. In the integral form, the decline component is either a power function or an exponential function of age.

The LTD form includes the Hossfeld IV, Levakovic I and III, Korf, and Yoshida I equations. Each of these equations can be derived from the general equation form [Equation (4)] when its parameters assume a particular value. Thus, the Levakovic III equation is distinguished by $q = 3$ and the Korf equation by $p = 1$. The peculiarity of the Yoshida I equation (Table 2) is that its dependent variable is the difference between the current size and the initial size ($c = y(0)$). The same number of equations (Gompertz, logistic, monomolecular, Bertalanffy, and Chapman-Richards) belong to the TD form. The Sloboda equation can be viewed as a hybrid between the two forms.

Depending on the values of p and q , several distinct integral equations can be obtained from the same equation form. The Korf equation results from integration of the LTD form when $p = 1$ and $q \neq -1$. The Levakovic I follows from the same equation when $p > 1$ and $q < -1$. The selection of a particular integral equation forces its parameters into a certain range. The parameters c ($= -1/(1 - p)$) and d ($= -q - 1$) in the Levakovic I equation, for instance, must be greater than zero.

The transformed equations reveal quite different and simpler relationships than

those of Kiviste's classification. Thus, despite the difference of their integral forms, Hossfeld IV and Korf equations are varieties of the same basic form (Table 2). On the other hand, differentiation shows that the outward similarity between the Chapman-Richard and Weibull equations is misleading.

COMPARISON OF THE BASIC EQUATION FORMS

The preceding analysis brings forth a question: which of the two basic forms is more accurate? The answer provided in this paper should be considered as preliminary because it was obtained from one data set.

MATERIALS

Probably the best-known data on tree growth are the measurements of Norway spruce (*Picea abies* [L.] Karst) published by Guttenberg in 1915. This set is considered a touchstone of tree growth and has been used repeatedly by many researchers (for example, Assmann 1970, Sloboda 1971, Zeide et al. 1972, Zeide 1989). The data contain measurements of 107 average-size trees from five site classes selected from healthy, fully stocked stands growing in the Alps. Guttenberg (1915) provided actual data for each tree as well as corrected (hand-smoothed) averages from 10 to 150 yr by site classes. The number of analyzed trees and their average size at age 50 are shown in Table 3. Despite the differences in location and species, the growth pattern of these trees is similar to that of several species in the western United States (Zeide 1989).

Because stem diameter was measured at the height of 1.3 m aboveground, this variable was regressed on the age since the tree reached this height. This age can be easily calculated for each tree and site class from height growth data (Table 3). Tree height and volume were regressed on the age at stem base.

DATA SCREENING

Several trees showed an erratic pattern of growth. Unlike the majority of trees, their increment jumped up and down without apparent pattern. Sometimes outliers may provide valuable information and even lead to new discoveries. Unfor-

TABLE 3.

Average size of Norway spruce (*Picea abies* [L.] Karst) trees at 50 yr, number of trees, and age at which trees reached the height of 1.3 m by site class.

Variable	Site class				
	1	2	3	4	5
Height, m	20.0	16.4	12.2	9.4	6.1
Diameter, cm	24.4	20.0	15.1	12.6	9.3
Volume, m ³ /1000	433	245	104	56	23
Number of trees	21	37	20	21	8
Age at 1.3 m	9.5	10.0	12.0	12.4	20.0

tunately, this does not happen often. Usually, they obscure the pattern without revealing anything meaningful. In order to exclude any bias for or against analyzed equations, the outliers were detected using a completely different equation (a polynomial). Current annual increment, $i (= y')$, was used to compute statistics of the following equation for each tree:

$$i = a + bt + ct^2 \quad (6)$$

where t is age and a , b , and c are constants. The choice of the equation did not affect the detection of outliers; the same trees show a poor fit using any other three-parameter equation. Seven trees with the smallest adjusted R^2 for each variable were considered outliers and were deleted from the data set. Any measure of fit clearly showed that these trees were not typical as is seen from the distribution of R^2 for Equation (6) describing diameter growth (Table 4). The deleted trees had R^2 less than 0.32 for height, 0.60 for diameter, and 0.64 for volume. The remaining data set contained exactly 100 trees.

ENVIRONMENTAL CHANGES AND TREE GROWTH

Among other factors, tree growth is affected by long-term environmental change. This factor, however, is not reflected by the growth equations considered above that present tree growth (increment) as a function of tree size and age. To decide whether growth equations should contain a term responsible for environmental change it is necessary to investigate its effect on tree growth.

The analyzed trees were cut at ages ranging from 60 to 150 yr. This makes it possible to divide them, within each site class, into two groups containing younger and older trees. The difference between mean ages between the groups was 40–60 yr. For each group mean height, diameter, and volume were calculated at the age of 50 yr.

The results (Table 5) shows that the size of 50-yr-old trees in both groups is practically identical. The differences are neither significant nor consistent. In some classes the trees cut at an older age were slightly bigger at 50 yr, while in others they were smaller than the trees cut at a younger age. These results allow one to conclude that during the 40–60 yr prior to Guttenberg's analysis, the environment did not change enough to affect growth of the investigated trees.

TABLE 4.

Distribution of R^2 for Equation (6) describing diameter growth of trees.

Adjusted R^2	Frequency	Cumulated frequency
0.05	2	2
0.15	1	3
0.25	0	3
0.35	0	3
0.45	3	6
0.55	1	7
0.65	3	10
0.75	16	26
0.85	23	49
0.95	58	107

TABLE 5.

Height, diameter, and volume of average 50-yr-old trees in younger and older groups by site class. SD = standard deviation.

Site class	No. of trees	Group age	Height (m)		Diameter (cm)		Volume (dm ³)	
			Mean	SD	Mean	SD	Mean	SD
1	8	80.0	19.9	1.6	23.0	2.5	402.5	92.2
1	12	139.2	20.1	1.6	25.1	4.2	453.3	169.0
2	26	92.3	17.2	1.5	19.9	2.8	258.7	85.1
2	9	148.9	15.5	2.0	18.6	3.6	206.4	81.3
3	9	108.9	12.9	1.1	14.7	1.2	102.3	21.2
3	10	150.0	11.1	2.2	14.7	3.5	96.4	51.4
4	9	113.3	10.0	0.9	13.5	2.6	72.4	30.4
4	11	150.0	8.9	1.1	12.1	2.1	52.4	20.5
5	3	116.7	6.1	1.8	8.2	0.6	18.3	5.0
5	5	150.0	5.9	2.3	8.5	2.6	22.0	11.9

ACCURACY OF THE BASIC EQUATION FORMS

The two basic equation forms, LTD and TD, [Equations (4) and (5)] were compared using Guttenberg's data for three variables (total height, stem diameter at breast height, and stem volume). The equation forms were fitted to the following three types of data: (1) each tree separately, (2) all trees of the same site class (referred to in Table 6 as pooled data), and (3) smoothed average growth series provided by Guttenberg for each site class (referred to in Table 6 as average data). Comparisons were made using the standard error of estimate (Table 6). For individual trees the mean of the errors, found separately for each of the 100 trees, was calculated. Other statistics (such as R^2 or Mallows' Cp statistic) produced similar results.

The results (Table 6) show that:

1. The accuracy of the equation form depends on the data type.
2. For individual trees, both equation forms are equally accurate for any tree variable (diameter, height, volume).
3. When trees are pooled by site class, both equation forms provide an identical fit for height and volume. LTD is more accurate for diameter in all site classes.
4. LTD is more accurate than TD for average growth series data in all classes and for all tree variables. In the integral form, this difference is likely to be more substantial. Thus, the standard error of estimate of Chapman-Richards equation (an integral form of TD) is twice as large as that of Korf's equation (an integral form of LTD) for the same data (Zeide 1989).
5. The shape of growth curves depends on the data type, as is evident from the substantial differences in parameters of the same equation. For example, when LTD [Equation (4)] was applied to volume the parameter q was equal to -3.05 , -1.55 , and -2.29 for individual, pooled, and average groupings of the same data, respectively. These differences indicate that even in homogeneous tree groups (trees of average size stratified by site class) the growth of individual trees cannot be represented by the average growth of the group.
6. If we are analyzing the process of tree growth, it is safer to investigate individual trees and avoid arbitrary tree groupings, averaging, and other kinds of data manipulation.

TABLE 6.

Standard errors of estimate for the basic equation forms, LTD and TD [Equations (4) and (5)] by data type and variable (height, diameter, and volume).

Tree group	Height		Diameter		Volume	
	LTD	TD	LTD	TD	LTD	TD
	Mean results for individual trees					
Single	0.15	0.16	0.15	0.15	0.15	0.15
	Pooled data by site classes					
SC = 1	0.21	0.21	0.26	0.32	0.24	0.23
SC = 2	0.24	0.24	0.27	0.33	0.26	0.25
SC = 3	0.24	0.20	0.22	0.27	0.25	0.21
SC = 4	0.24	0.26	0.25	0.33	0.25	0.25
SC = 5	0.32	0.28	0.27	0.36	0.29	0.29
SC Mean	0.25	0.24	0.25	0.32	0.26	0.25
	Average data by site classes					
SC = 1	0.06	0.11	0.06	0.08	0.10	0.13
SC = 2	0.07	0.11	0.03	0.05	0.08	0.10
SC = 3	0.05	0.07	0.03	0.04	0.02	0.03
SC = 4	0.05	0.06	0.03	0.05	0.06	0.06
SC = 5	0.03	0.04	0.03	0.03	0.01	0.02
SC Mean	0.05	0.08	0.04	0.05	0.05	0.07

COMPARISON OF EQUATIONS WITH ALL COMBINATIONS OF TREE SIZE, AGE, AND THEIR LOGARITHMS

The LTD form clearly differs from TD. In the TD form the carrier of growth decline is age, while in the LTD form the same component is represented by the logarithm of age. Yet, it was found that the accuracy of these forms is equal when they are applied to individual trees. If these two forms cannot be distinguished by accuracy, does the choice of an equation matter? Would other combinations of variables be equally successful in growth prediction?

To answer these questions, the accuracy of growth prediction was tested for 15 differential equations in which independent variables included all possible linear combinations of tree size, age, and their logarithms. Limited degrees of freedom precluded calculation of equations with 4 variables for the 2 out of 100 trees with the shortest life span (60 yr). Calculations were performed for data pooled from all 98 remaining trees and by site class (Table 7) as well as for individual trees (Table 8).

Standard errors of estimate for analyzed equations were calculated for each tree. Their mean values are given in Table 8. Most of these means had a standard error of 0.01. Only four errors for volume increment were greater than 0.01. For equations with two or more independent variables the coefficients of determination (R^2) exceeded 0.80, 0.90, and 0.95 for height, diameter, and volume increments, respectively.

TABLE 7.

Standard errors of estimate for equations predicting increment from all combinations of tree size (x), age (t), and their logarithms ($\ln(x)$, $\ln(t)$). Size (x) designates height, diameter, and volume. The errors were calculated using pooled data for all 98 trees. Comparative accuracy of equations fitted to all trees coincided with that fitted to the data pooled by site class.

Independent variables	Height	Diameter	Volume
$\ln(x)$	0.52	0.48	0.46
x	0.50	0.50	1.00
$\ln(t)$	0.41	0.34	0.94
t	0.37	0.36	1.06
$\ln(x), x$	0.48	0.48	0.44
$\ln(x), \ln(t)$	0.26	0.26	0.27
$\ln(x), t$	0.27	0.35	0.26
$x, \ln(t)$	0.38	0.29	0.89
x, t	0.32	0.33	0.97
$\ln(t), t$	0.35	0.34	0.88
$\ln(x), x, \ln(t)$	0.23	0.26	0.25
$\ln(x), x, t$	0.26	0.32	0.26
$\ln(x), \ln(t), t$	0.24	0.26	0.25
$x, \ln(t), t$	0.31	0.28	0.73
$\ln(x), x, \ln(t), t$	0.22	0.26	0.24

These calculations showed that the basic equation forms (LTD and TD) were among the most accurate. In addition, for individual trees the equation containing tree size and its logarithm as independent variables

$$\ln(y') = k + p\ln(y) + qy \text{ or } y' = k_1 y^p e^{qy} \quad (7)$$

was equally successful (Table 8). Because the decline component is proportional to the size y , this form will be referred to as the Y-decline, or YD form.

Other results of these calculations indicate that:

1. The accuracy of equations increases drastically when the number of independent variables changes from one to two. Subsequent addition of variables had little effect. The best two-variable equations were almost as accurate as equations with three and four variables.
2. In most cases comparative accuracy of equations fitted to all trees coincided with that fitted to the data pooled by site class.
3. The effect of data type on the accuracy of a given equation, noticed for the two basic equation forms, was more pronounced when the set of 15 equations was considered (Table 7 and 8). This effect is especially clear for the YD form: it was the best form for height and diameter (Table 8) growth of individual trees and the worst form for pooled data for the same variables (Table 7).
4. The distinguishing feature of the three best two-variable equation forms (LTD, TD, and YD) is that growth expansion is proportional to the logarithm of size.

AUTOCORRELATION OF RESIDUALS

When comparing accuracy of equations, it is necessary to consider autocorrelation among residuals that often appears in time series such as tree growth data. Autocorrelation does not change parameter estimators in least square regres-

TABLE 8.

Standard errors of estimate for equations predicting increment from all combinations of tree size (x), age (t), and their logarithms ($\ln(x)$, $\ln(t)$). Size (x) designates height, diameter, and volume. The errors are averages of individual regressions of 98 trees.

Independent variables	Height	Diameter	Volume
$\ln(x)$	0.32	0.22	0.30
x	0.25	0.17	0.82
$\ln(t)$	0.28	0.18	0.41
t	0.23	0.18	0.65
$\ln(x), x$	0.15	0.14	0.15
$\ln(x), \ln(t)$	0.15	0.15	0.15
$\ln(x), t$	0.16	0.15	0.15
$x, \ln(t)$	0.18	0.15	0.18
x, t	0.21	0.14	0.26
$\ln(t), t$	0.16	0.14	0.17
$\ln(x), x, \ln(t)$	0.14	0.14	0.13
$\ln(x), x, t$	0.13	0.13	0.13
$\ln(x), \ln(t), t$	0.14	0.13	0.13
$x, \ln(t), t$	0.14	0.14	0.15
$\ln(x), x, \ln(t), t$	0.12	0.12	0.12

sions, but inflates their variance (as compared with completely uncorrelated data) and introduces bias into the standard error of estimate. This happens because autocorrelation reduces the effective number of degrees of freedom for estimating the parameters, which is equivalent to reducing the sample size. Therefore, the estimates of standard errors and the coefficient of determination (R^2) should be supplemented with an analysis of autocorrelation.

The investigation of autocorrelation among residuals of the analyzed equations showed that autocorrelation is by far the largest at the first step. This fact permitted the restriction of this investigation to first-order autocorrelation. It was calculated (using the Durbin-Watson, DW, option in the regression procedure of SAS) for pooled data, which contained 100 trees, and for each tree separately. For individual trees the results (Table 9) represented mean absolute values.

TABLE 9.

First-order autocorrelation of equations predicting tree increment.
Autocorrelations of individual trees are mean absolute values.

Tree variable	Number of observations	Pooled data			Individual trees		
		Equation			Equation		
		LTD	TD	YD	LTD	TD	YD
Height	1099	0.57	0.58	0.86	0.29	0.31	0.28
Diameter	1024	0.65	0.68	0.80	0.28	0.26	0.26
Volume	1088	0.56	0.56	0.80	0.24	0.26	0.25

These calculations demonstrated that:

1. Autocorrelation was practically identical for all equations when they were applied to individual trees.
2. When applied to pooled data, autocorrelation of the YD form was substantially greater than that of the LTD and TD forms. Autocorrelation of the latter two was statistically indistinguishable.
3. Autocorrelation for individual trees was equally likely to be positive or negative, and the mean of actual (not absolute) values was never different from zero.
4. Autocorrelation varied by data type and equation in a way that was similar to that of their standard errors (Tables 7 and 8). This fact makes the analysis of autocorrelation redundant for Guttenberg's data.
5. This analysis of autocorrelations did not change the previous conclusion based on standard errors; for individual trees all three two-variable equations, in which growth expansion was represented by the logarithm of size, were equally accurate.

SINGLE EQUATION FORMS

The preceding result brings forth the question of whether it is possible to achieve the ultimate reduction in the number of equations and obtain a single form. An easy way to do this is to combine equations (4), (5), and (7) at the expense of introducing additional parameters:

$$y' = k_1 y^{p_1} t^{q_1} + k_2 y^{p_2} e^{q_2 t} + k_3 y^{p_3} e^{q_3 y} \quad (8)$$

The LTD form corresponds to $k_2 = k_3 = 0$, and the TD form arises when $k_1 = k_3 = 0$. When all three parameters are different from zero, Equation (8) becomes a single general form that includes the discussed forms (LTD, TD, and YD) as special cases.

A similar general equation with five parameters was suggested by Dr. Insarov (personal communication, May 1, 1992):

$$y' = k_1 y^{p_1} t^q e^{k_2 t^{p_3}} \quad (9)$$

It summarizes all the equations given in Table 1.

An undeservedly ignored paper by Grosenbaugh (1965) described an equation that generalizes many nonlinear functions including several growth equations such as Bertalanffy, Gompertz, and Johnson-Schumacher equations. In this equation,

$$Y = H + A(e^{(N^2 - 1)^U} - NU)^{NM - 1} \quad (10)$$

A , H , M , and N are parameters. U is an elementary function of an independent variable and contains two additional parameters. According to the author (personal communication, March 23, 1992), no one ever made use of his equation.

An interesting attempt to arrive at a single equation form was made by Schnute (1981). Bredenkamp and Gregoire (1988) were the first to introduce this equation to forestry. While many scientists studied growth rate, y' , and relative growth rate, $z = y'/y$, Schnute went further and investigated the rate of a rate, that is, acceleration of growth. Schnute (1981, p. 1129) believed that the relative growth rate of a relative growth rate is a linear function of the relative growth rate because it is "the simplest possible assumption":

$$W = \frac{1}{Z} \frac{dZ}{dt} = -(a + bZ) \quad (11)$$

where a and b are parameters (unrelated to those of Table 1). Schnute (1981) showed that many existing equations are special cases of his Equation (9). For example, the Gompertz equation follows from Equation (9) when $a > 0$ and $b = 0$. When parameters $a > 0$ and $b = -1$, the result is the logistic equation.

The first thing that comes to the mind of an empirical researcher is to test this linear assumption (Schnute did not provide one). Perhaps this assumption is good for describing the growth of fish (the area of Schnute's research) but not that of trees. When I plotted relative acceleration, w , over relative growth rate calculated using Guttenberg's (1915) average height growth for five site classes, it became evident that the relationship is not linear (Figure 1). A power function

$$w = az^b \tag{12}$$

appeared to be more appropriate because when plotted on the log-log scale, the relationship became straight, especially if three outliers in the lower left corner are disregarded (Figure 2). This relationship is characterized by a coefficient of determination of about 0.95. Both intercepts and slopes changed little with site class.

Although a single general solution is attractive, it is not clear whether it is worth the cost of additional variables [Equations (8) and (9)]. It is probably better to rely on two or three equation forms.

DISCUSSION

This investigation revealed that many of the existing growth equations belong to one of two basic forms. The type of data used drastically affected the comparative accuracy and shape of equations. Growth curves for groups of trees belonging to the same site class and average curves differed substantially from the growth of individual trees from the same groups.

This investigation of known equations not only provided the basis for their classification but also made possible the discovery of a new promising equation

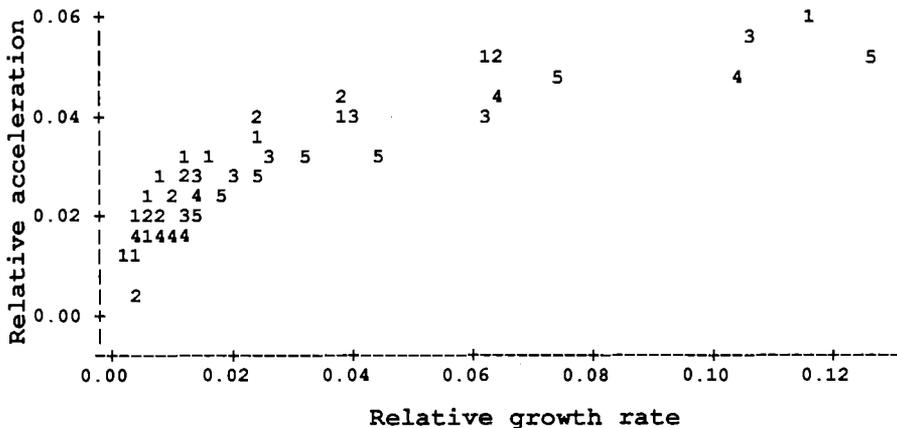


FIGURE 1. The relationship between relative growth acceleration and relative growth rate for Guttenberg's (1915) average height growth data. The plotted numbers indicate site class of investigated trees.

misleadingly precise line to a fuzzy but realistic strip brings clarity to our understanding of tree growth.

LITERATURE CITED

- ALEM DAG, I.S. 1978. Evaluation of some competition indexes for the prediction of diameter increment in planted white spruce. *Can. For. Serv. Inf. Rep. FMR-X-108*. 39 p.
- ASSMANN, E. 1970. *The principles of forest yield study*. Pergamon Press, New York. 506 p.
- BERTALANFFY, L. VON. 1957. Quantitative laws in metabolism and growth. *Quart. Rev. Biol.* 32:217–231.
- BREDENKAMP, B.V., and T.G. GREGOIRE. 1988. A forestry application of Schnute's generalized growth function. *For. Sci.* 34:790–797.
- BREWER, J.A., P.Y. BURNS, and Q.V. CAO. 1985. Short-term projection accuracy of five asymptotic height-age curves for loblolly pine. *For. Sci.* 31:414–418.
- CAUSTON, D.R., and J.C. VENUS. 1981. *The biometry of plant growth*. Edward Arnold, London. 307 p.
- DOLPH, K.L. 1991. Polymorphic site index curves for red fir in California and southern Oregon. *USDA For. Serv. Res. Pap. PSW-206*. 18 p.
- DOVER, G.A. 1988. rDNA world falling to pieces. *Nature* 336:623–624.
- GOMPERTZ, B. 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Phil. Transac. Roy. Soci. London* 115:513–585.
- GROSENBAUGH, L.R. 1965. Generalization and reparameterization of some sigmoid and other nonlinear functions. *Biometrics* 21(3):708–714.
- GUTTENBERG, A.R., VON. 1915. [Growth and yield of spruce in Hochgebirge.] Franz Deuticke, Wien. 153 p. [In German.]
- HOLLAND, J.H. 1992. Complex adaptive systems. *Daedalus* 121(1):17–30.
- HUSTON, M., D. DEANGELIS, and W. POST. 1988. New computer models unify ecological theory. *BioScience* 38:682–691.
- HUTCHINSON, G.E. 1978. *An introduction to population ecology*. Yale University Press, New Haven, CT. 260 p.
- JOHNSON, N.O. 1935. A trend line for growth series. *J. Am. Stat. Assoc.* 30:717.
- KIVISTE, A.K. 1988. Mathematical functions of forest growth. *Estonian Agricultural Academy, Tartu*. 108 p + Supplement 171 p. [In Russian.]
- KREBS, C.J. 1985. *Ecology*. Ed. 3. Harper and Row, New York. 800 p.
- LAIRD, A.K., S.A. TYLER, and A.D. BARTON. 1965. Dynamics of normal growth. *Growth* 29:233–248.
- LAROCQUE, G., and P.L. MARSHALL. 1988. Improving single-tree distance-dependent growth models. P. 94–101 in *IUFRO Forest Growth Modelling and Prediction Conference*. Ek, A.R., S.R. Shifley, and T.E. Burk (eds.) *USDA For. Serv. Gen. Tech. Rep. NC-120*. 1149 p.
- LEVAKOVIC, A. 1935. Analytical form of growth laws. *Glasnik za sumske pokuse (Zagreb)* 4:189–282. [In Serbian.]
- LUNDQVIST, B. 1957. On the height growth in cultivated stands of pine and spruce in Northern Sweden. *Medd. fran Statens Skogforsk. band 47(2)*. 64 p.
- MALTHUS, T.R. 1798. *An essay on the principle of population, as it affects the future improvement of society, with remarks on the speculations of Mr. Godwin, M. Condorcet, and other writers*. J. Johnson, London. 296 p.
- MEDAWAR, P.B. 1940. Growth, growth energy, and ageing of the chicken's heart. *Proc. Roy. Soc. B. London* 129:332–355.
- MEDAWAR, P.B. 1941. The "laws" of biological growth. *Nature* 148:772–774.

- MEDAWAR, P.B., and J.S. MEDAWAR. 1983. *Aristotle to Zoos. A philosophical dictionary of biology.* Harvard University Press, Cambridge, MA. 305 p.
- MITSCHERLICH, E.A. 1919. [Problems of plant growth.] *Landwirtschaftliche Jahrbucher* (Berlin) 53: 167–182. [In German.]
- MURTAUGH, P.A. 1988. Use of logistic regression in modelling prey selection by *Neomysis mercedis*. *Ecol. Model.* 43:225–233.
- NOKOE, S. 1978. Demonstrating the flexibility of the Gompertz function as a yield model using mature species data. *Commonw. For. Rev.* 57:35–42.
- PESCHEL W. 1938. [Mathematical methods for growth studies of trees and forest stands and the results of their application.] *Tharandter Forstliches Jahrbuch* 89:169–247. [In German.]
- PÜTTER, A. 1920. [Investigation of physiological similarities of growth processes.] *Pflüg. Arch. ges. Physiol.* 180:298–340. [In German.]
- RATKOWSKY, D.A. 1983. *Nonlinear regression modeling.* Marcel Dekker, New York. 276 p.
- RICHARDS, F.J. 1959. A flexible growth function for empirical use. *J. Exp. Bot.* 10:290–300.
- RICHARDS, F.J. 1969. The quantitative analysis of growth. P. 3–76 *in* *Plant Physiology*, Volume VA, Steward, F.C. (ed.). Academic Press, New York. 435 p.
- RICKER, W.E. 1979. Growth rates and models. *Fish Physiol.* 8:677–743.
- RICKLEFS, R.E. 1979. Patterns of growth in birds. V. A comparative study of development in the Starling, Common Tern, and Japanese Quail. *The Auk* 96:10–30.
- SAVAGEAU, M.A. 1979. Growth of complex systems can be related to the properties of their underlying determinants. *Proc. Nat. Acad. Sci. USA* 76:5413–5417.
- SAVAGEAU, M.A. 1980. Growth equations: A general equation and a survey of special cases. *Math. Biosciences* 48:267–278.
- SCHNUTE, J. 1981. A versatile growth model with statistically stable parameters. *Can. J. Fish Aquat. Sci.* 38:1128–1140.
- SCHUMACHER, F.X. 1939. A new growth curve and its application to timber-yield studies. *J. For.* 37:819–820.
- SLOBODA, B. 1971. [Investigation of growth processes using first order differential equations.] *Mitteilungen der Baden-Württembergischen Forstlichen Versuchs- und Forschungsanstalt*, Heft 32. 109 p. [In German.]
- SPENCER, H. 1898. *The principles of biology.* Vol. 1. D. Appleton, New York. 706 p.
- STAGE, A.R. 1963. A mathematical approach to polymorphic site index curves for grand fir. *For. Sci.* 9:167–180.
- VERHULST, P.F. 1838. [A note on population growth.] *Correspondence Mathematiques et Physiques* 10:113–121. [In French.]
- WEBER, R. 1891. [Textbook of forest management with emphasis on tree growth.] Springer-Verlag, Berlin. 440 p. [In German.]
- WINSOR, C.P. 1932. The Gompertz curve as a growth curve. *Proc. Nat. Acad. Sci.* 18:1–8.
- YANG, R.C., A. KOZAK, and J.H.G. SMITH. 1978. The potential of Weibull-type functions as flexible growth curves. *Can. J. For. Res.* 8:424–431.
- ZARNOVICAN, R. 1979. [Korf's growth equation]. *For. Chron.* 55:194–197. [In French.]
- ZEIDE, B. 1972. On the mathematical description of the aging process of trees. P. 169–174 *in* *Dendroclimatochronology and radiouglerod*, Kocharov, G.E., V.A. Dergachov and T.T. Bitvinskas (eds.). Institut botaniki Akademii Nauk Litovskoi SSR, Kaunas. 325 p. [In Russian.]
- ZEIDE, B. 1975. Some tree growth equations. P. 82–86 *in* *Kolichestvennie aspekti rosta organizmov*, Zotin, A.J. (ed.). Nauka, Moscow. 291 p. [In Russian.]
- ZEIDE, B. 1989. Accuracy of equations describing diameter growth. *Can. J. For. Res.* 19:1283–1286.
- ZEIDE, B., G.E. INSAROV, and F.N. SEMEVSKY. 1972. Effect of age on the current increment of the fir. P. 29–32 *in* *Tekyschii prirost drevostoev i ego primenenie v lesnom khozyaistve*, Anderson, R. (ed.). Latviiiski institut lesokhozyaistvennih problem, Riga. 237 p. [In Russian.]
- ZULLINGER, E.M., R.E. RICKLEFS, K.H. REDFORD, and G.M. MACE. 1984. Fitting sigmoidal equations to mammalian growth curves. *J. Mamm.* 65:607–636.

ZWEIFEL, J.R., and R. LASKER. 1976. Prehatch and posthatch growth of fishes—a general model. U.S. Fish Wildl. Serv., Fish. Bull. 74:609–621.

Copyright © 1993 by the Society of American Foresters
Manuscript received March 12, 1992

AUTHOR AND ACKNOWLEDGMENTS

Boris Zeide is Professor of Forestry, Department of Forest Resources, University of Arkansas at Monticello, Arkansas Agricultural Experiment Station, Monticello, AR 71656. This report is approved for publication by the Director, University of Arkansas Agricultural Experiment Station. Valuable comments by John L. Greene, Timothy G. Gregoire, Lew R. Grosenbaugh, Gregory Insarov, Rolfe A. Leary, Daniel J. Leduc, Robert A. Monserud, Lynne C. Thompson, Suzanne Wiley, Richard C. Woollons, and Voyteck T. Zakrzewski are gratefully acknowledged.