

The potential of Weibull-type functions as flexible growth curves¹

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A new growth function, which is flexible enough in shape to accommodate most biological growth behavior, is created by adding an expanding factor to the Weibull distribution function. Many monotonically increasing biological growth phenomena can be excellently modelled by this function with various numerical values for the scale, the shape, and the upper asymptote parameters. The function is illustrated with height-age and volume-age curves for single trees and two polymorphic stand volume-age curves.

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En ajoutant un facteur à la fonction de distribution de Weibull nous obtenons une nouvelle fonction qui est suffisamment flexible pour pouvoir s'adapter à la plupart des phénomènes de croissance biologiques. Cette fonction, avec des valeurs numériques variées pour l'échelle, la forme et les paramètres asymptotiques, s'ajuste très bien aux relations croissantes et monotones de croissance biologique. Des courbes avec les variables hauteur-âge et volume-âge illustrent cette fonction.

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Introduction

In forest biology and economics, many attempts have been made to express empirical growth phenomena by elegant mathematical functions. The search for a generalized function capable of describing properly and adequately the biological growth processes of forest trees and stands has been subjected to persistent efforts by forest biometrists for the past century. Theoretical treatises on the subject are voluminous. Prodan (1968) gave a comprehensive treatment of various growth functions and growth laws that have already been studied with reference to forest growth. Grosenbaugh (1965) generalized and reparameterized functions frequently used in forest growth studies. However, as Prodan (1968) pointed out, it has not yet been possible to produce a completely satisfactory solution. A function that is flexible enough in form to accommodate all biological growth behavior and logical enough in theory to justify its applications in practice has been unavailable. This paper describes a very promising new flexible growth function, the modified Weibull.

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Characteristics of Growth and Increment Curves

Growth refers to an aspect of the changes in an organic system which can be measured as increases in length, diameter, or weight. An increment is the increase in the size of an organism within a certain time interval. A growth curve is a graphical representation of the attained sizes and an increment curve shows annual or periodic increment.

Typical growth and increment curves are schematized in Fig. 1. The growth curve, sigmoid in shape, starts at the origin or a fixed point, increases monotonically to an inflection point, and then approaches an asymptote determined by the genetic nature of the organism and its environmental constraints. The corresponding growth rate (increment) curve which shows the increment of an organism per unit of time is a derivative of the growth function with respect to time.

The increment curve as shown in Fig. 1 begins at value zero, increases slowly at first and then more steeply. After reaching a maximum, the increment diminishes and then asymptotically approaches some final value.

Peschel (1938), as quoted by Prodan (1968), prescribed the characteristics of an increment curve: (1) with $x = 0, y = 0$; (2) with $x \rightarrow \infty, y \rightarrow 0$; (3) it has two points of inflection; and (4) it has one maximum. These properties are easily visualized from the schematized increment curve in Fig. 1.

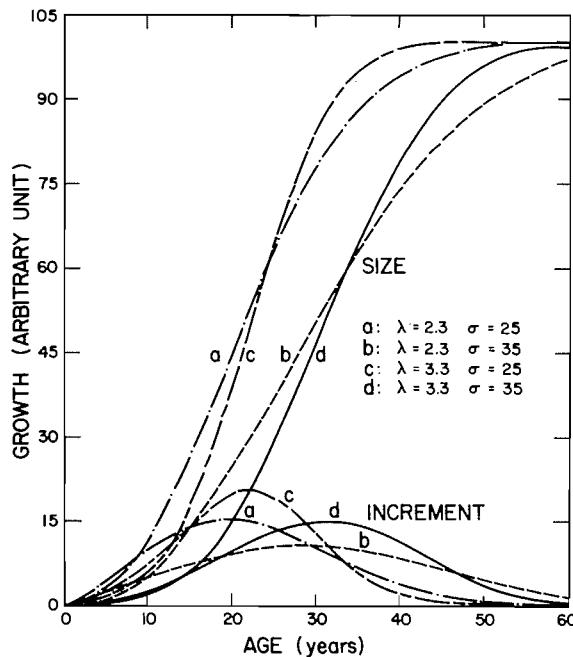


FIG. 1. Changes in shape of the modified Weibull growth and increment at various σ and λ values.

The shapes of the biological growth and its corresponding increment curves are well known to researchers in growth and yield studies. Biometricians have long sought a mathematical function capable of generating a curve system which adequately describes biological growth patterns.

Growth Function

Grosenbaugh (1965) illustrated in detail some functions of primary interest for study of forest growth and yield. Most were derived from study of population dynamics (Gompertz, Verhulst), allometry (von Bertalanffy), or chemical reactions (mono- and multi-molecular). According to Richards (1959), the von Bertalanffy growth function is a generalized form of the Gompertz, Verhulst (logistic), and monomolecular functions, provided a theoretical constraint on a parameter imposed by von Bertalanffy is discarded.

Von Bertalanffy (1941, 1957) started from the allometric relation during growth between an animal's metabolic rate and its weight, and postulated that an animal's growth rate is regulated by a general formula:

$$[1] \quad \frac{dW}{dt} = \eta W^m - \kappa W^n$$

The formula shows that the change of body weight, W , is given by the difference between the processes

of building up and breaking down: η and κ are constants of anabolism and catabolism respectively; and the exponents m and n indicate that the latter are proportional to some power of the body weight, W .

The solution of Eq. 1 when $n = 1$ is as follows:

$$[2] \quad W = \left[\frac{\eta}{\kappa} - \left(\frac{\eta}{\kappa} - W_0^{1-m} \right) e^{-(1-m)\kappa \cdot t} \right]^{1/(1-m)}$$

where W_0 is the weight at $t = 0$. Von Bertalanffy claimed that the slope, m , of the allometric line is either $\frac{2}{3}$ (for species obeying the surface rule of metabolism), unity (when oxygen consumption is proportional to animal's weight), or something intermediate between these extreme values. Richards (1959), however, argued that the imposition of restrictions on the numerical range that m should take is theoretically doubtful. By removing the limitations imposed by its theoretical background, Richards (1959) developed a generalized function that has wide application to empirical botanical studies.

The generalized von Bertalanffy function developed by Richards has been found useful in growth and yield studies in forestry. Turnbull and Pienaar (1966) and Pienaar and Turnbull (1973) by reparameterizing and imposing an initial condition at time $t = t_0$, $V_{t_0} = 0$, derived the growth function,

$$[3] \quad V_t = A [1 - e^{-k(t-t_0)}]^{1/(1-m)}$$

where V_t is volume or basal area at time t and A , k , t_0 , and m are parameters. They successfully applied this model for basal area growth and yield in even-aged stands. Rawat and Franz (1974) also used the function in the form,

$$[4] \quad W = A \times (1 - b \times e^{-kt})^{1/(1-m)}$$

to construct site index curves and concluded that the model is equally suitable for all other growth and yield studies, e.g., diameter-age, basal area - age, and total volume - age relationships.

The generalized von Bertalanffy function is by far the most sophisticated and flexible function being used in growth studies. However, it is empirical in nature as designated by Richards (1959). Also, the estimated growth curves seldom pass through the origin or a prefixed point when $x = 0$. They frequently intersect at $x = 0$ either above or below the origin and therefore are incorrect in practice.

The above arguments against the growth curves of the generalized von Bertalanffy function apply equally well to its first derivative function with respect to x , the increment curve. The increment derived from this function at $x = 0$ is often either

greater or smaller than zero. An increment unequal to zero at $x = 0$ contradicts not only the characteristics of an increment curve discussed above but also basic biological laws. Accordingly, the first derivative function is, contrary to that claimed by previous researchers, either under- or over-estimating the growth rate of an organism.

Probability Distribution Curves Versus Growth Curves

The typical growth and increment curves illustrated in Fig. 1 resemble both a probability density (frequency distribution) and a probability distribution (cumulative frequencies distribution). Fundamentally, an increment curve resembles a unimodal, asymmetric probability density. Just as a distribution function is mathematically an integration of its density function, so is the growth function of an organism, practically speaking, the accumulation of its growth rate.

The excellent analogy between a growth rate curve and a probability density curve, which was recognized by Prodán (1968), strongly suggests the possibility of adapting a suitable probability function to growth and yield study. The relationship of an increment to the growth curve is analogous to that of a probability density to a probability distribution. Because a probability function has been so scaled that the probability of a random variable lies invariably between 0 and 1, it is necessary to add an expanding factor (multiplier) to the function to suit the real growth of an organism in growth and yield studies. Usually, the expanding factor is the upper asymptote of an organism determined by its genetic nature and the environmental factors imposed on it.

It is further required that the probability density function be flexible; that is to say, it can assume a great variety of different shapes and is capable of generating a series of asymmetric curves from left to right skewness to accommodate all practical increment phenomena.

Bearing these requirements in mind, one can see that the normal and log-normal functions are of limited use in growth studies because the former generates only symmetrical curves and the latter only left skewed ones. The gamma and beta distribution functions, because their density functions are highly flexible in shape, are promising for adaption to growth study. Unfortunately, both functions involve a recursive gamma function,

$$[5] \quad \Gamma(\lambda) = \int_0^{\infty} X^{\lambda-1} \cdot e^{-X} dX$$

which makes the parameterizing procedure for these two probability functions computationally formidable.

Some of the shortcomings of other functions can be avoided by use of the Weibull probability function.

The Weibull Probability Function

The Weibull probability distribution,

$$[6] \quad F = 1 - e^{-(X/\sigma)^{\lambda}}$$

was originally developed by Weibull (1951) in a study of the probability of material failure and has since been found widely applicable in engineering. In forestry, limited studies have been made to model stand diameter distribution (Bailey 1974; Schreuder and Swank 1974). The function summarized diameter, basal area, surface area, biomass, and crown profile distribution data well for *Pinus strobus* and *Pinus taeda*.

So far the Weibull function has been primarily applied to reliability and life tests in engineering and for some distributional fitting in biology. The probability function can easily be modified to formulate a growth function which generates a wide variety of sigmoid growth curves. For growth and yield study purposes, one can take the random variate X in Eq. 6 as a time variable such as age and F as growth or yield of the organic system which increases with the increase of X . Since the F value in Eq. 6 has been scaled to yield a probability domain between 0 and 1, the growth or yield of the organic system in actual scale is obtained by multiplying an expanding factor A , the maximum attainable size of the organism, to Eq. 6, i.e.,

$$[7] \quad F = A \times (1 - e^{-(X/\sigma)^{\lambda}})$$

The Weibull function modified as in Eq. 7 is highly flexible; it is able to assume virtually all monotonically increasing sigmoid growth shapes which one will encounter in the biological universe. It also possesses some characteristics which are of particular interest in construction of theoretical growth models.

The curve system owes its flexibility to the presence of the parameters σ and λ which are scale and shape parameters, respectively. Both parameters have a numerical domain ranging from zero to positive infinity ($0 < \sigma, \lambda \leq \infty$). However, in growth and yield study, the domain for λ is usually restricted to $1 \leq \lambda < \infty$ for $1 \leq \lambda$; thus the growth curve will be a reverse J which seldom occurs in biological growth. Figures 1 and 3 illustrate a variety of growth

and increment curves generated by varying σ and λ parameter values.

In Fig. 1, *a*, *b* and *c*, *d* illustrate the change in shape in the growth and increment curves as a result of varying the numerical value of σ , the scale parameter which determines the peak of an increment curve. As shown in Fig. 1, the peak of the increment curve increases in sharpness as σ decreases in value.

The shape parameter λ , on the other hand, dominates the shape of an increment (density) curve. In Fig. 1, *a*, *c* and *b*, *d* show that the peak of a curve is shifting from left to right as λ value increases. Curves in Fig. 1 show when the increment curve changes in shape, its corresponding growth curve changes in shape as well. The reverse is also true.

Also, it can be concluded from Fig. 1 that virtually all biological growth phenomena can be modelled by the modified Weibull function with varying scale and shape parameters. This is a function with high flexibility.

Unlike most of the growth functions which are historically derived from either population dynamics or allometric relations, the modified function is derived from a morphological analogy rather than theoretical considerations. However, it possesses two very desirable characteristics: (1) it passes through the origin with $x = 0$, and (2) it approaches a maximum asymptotically when x approaches infinity. Furthermore, its growth rate curves which are derivatives of growth curves have all the properties of an increment curve prescribed by Peschel (1938, in Prodan 1968). Therefore, it can be concluded that the modified function is suitable for growth study.

Parameter Estimation

Methodology to estimate the parameters of a Weibull probability function has been detailed by many statistical studies (Bury 1976). For growth studies, it is easiest to take the modified function in Eq. 7 as a nonlinear one and to estimate the parameters by existing nonlinear regression routines such as the BMDP biomedical computer program or the IBM Share Program which are available in most large computing centers.

As a rule, nonlinear regression programs require an initial guess for each parameter to be estimated as a starting point in their parameter search routine. A good educated guess which eventually saves a great deal in both computing time and researchers' effort can be obtained by comparing the data plot from which parameters are to be estimated with some standard curves such as those above in Fig. 1. Nonlinear fitting methods are essential to estimate the parameters for the modified Weibull function.

Function Flexibility (Example 1)

Two sets of classical stem analysis data for a spruce height growth and a fir volume growth (Prodan 1968) are used here to demonstrate the flexibility and the theoretical fit of the modified Weibull function to growth phenomena. Traditional growth functions such as the Gompertz, the logistic, the generalized von Bertalanffy, the Mitscherlich together with the modified Weibull function with formula form shown below in Eqs. 8, 9, 10, 11, and 12, respectively, are fitted to the height and volume data.

$$[8] \quad Y = A \times e^{-e^{-B(X-C)}} \quad \text{Gompertz}$$

$$[9] \quad Y = A/(1 + e^{-B(X-C)}) \quad \text{logistic}$$

$$[10] \quad Y = A \times (1 - e^{-B(X-C)})^{1/(1-D)} \quad \text{von Bertalanffy}$$

$$[11] \quad Y = A \times (1 - e^{-B \cdot X})^2 \quad \text{Mitscherlich}$$

and

$$[12] \quad Y = A \times (1 - e^{-B \cdot X^C}) \quad \text{modified Weibull}$$

where $B = (1/\sigma)$ and $C = \lambda$.

The estimated parameters for these chosen functions together with the residual root mean squares (S_{y-x}) and the intercept (growth at age 0) are shown in Tables 1 and 2 for the height and volume growth of the spruce and fir tree, respectively.

In general, all the five chosen functions fit reasonably well to the spruce height growth data. The Gompertz and the modified Weibull function outperform the other three in terms of the residual root mean squares (S_{y-x}) which is a measure of how well the data fits to the function (Table 1). Since the intercept at $X = 0$ should equal zero, theoretically, the intercept at $X = 0$ can verify the model.

On the volume growth data, the performance of the five functions varies from excellent to poor. As shown in Table 2, the modified Weibull and the generalized von Bertalanffy functions are excellent by comparing the residual root mean squares while the Gompertz is satisfactory, the logistic is poor, and the Mitscherlich function failed to converge in parameterizing procedures. The failure of the Mitscherlich implies that it is not as flexible as the others. Again, the intercepts for Gompertz, logistic, and the generalized von Bertalanffy functions failed to pass through the origin when $X = 0$ (Table 2).

From the above discussions, it is clear that the best models are the Gompertz, the generalized von Bertalanffy, and the modified Weibull functions. The performance of the Gompertz and von Bertalanffy functions is excellent in one set of data but moderate

TABLE 1. Comparison of parameters, residual root mean squares, and intercepts for functions fitted to height growth data of a spruce tree

	Parameter				RRMS ^a ($S_{y \cdot z}$), m	Intercept ($X = 0$), m
	A, m	B	C	D		
Gompertz	30.6071	2.02442×10^{-2}	76.3377	—	0.220	0.281
Logistic	27.5095	3.61591×10^{-2}	89.0669	—	0.535	1.056
Von Bertalanffy	35.6441	1.21128×10^{-2}	6.5338	2.0077	0.510	—
Mitscherlich	38.7455	1.03672×10^{-2}	—	—	0.571	0.0
Weibull	29.3665	1.13886×10^{-4}	1.9284	—	0.299	0.0

^aResidual root mean squares.

TABLE 2. Comparison of parameters, residual root mean squares, and intercepts for functions fitted to volume growth data of a fir tree

	Parameter				RRMS ^a ($S_{y \cdot z}$), m ³	Intercept ($X = 0$), m ³
	A, m ³	B	C	D		
Gompertz	30.6708	8.72727×10^{-3}	228.940	—	0.067	0.190
Logistic	12.4922	2.80491×10^{-2}	174.720	—	0.138	0.092
Von Bertalanffy	99.1089	3.33791×10^{-3}	-9.007	3.5675	0.046	0.001
Mitscherlich ^b	464.3099	2.24304×10^{-4}	—	—	110.720	0.0
Weibull	38.1787	1.45928×10^{-6}	2.711	—	0.043	0.0

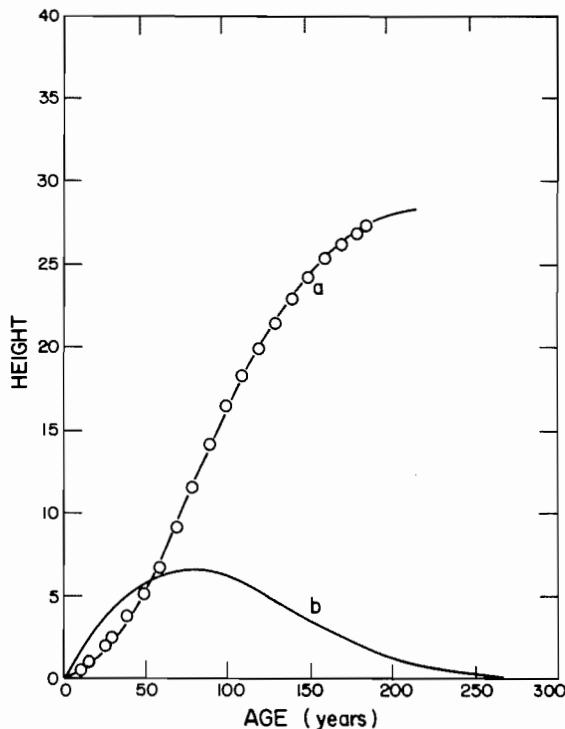
^aResidual root mean squares.^bThe function failed to converge; parameters given are a smallest RRMS from 300 iterations.

FIG. 2. A fitted height growth curve (a) and its derived increment curve (b) (four times actual size) for a spruce tree. Data from Freiburg as presented by Prodán (1968).

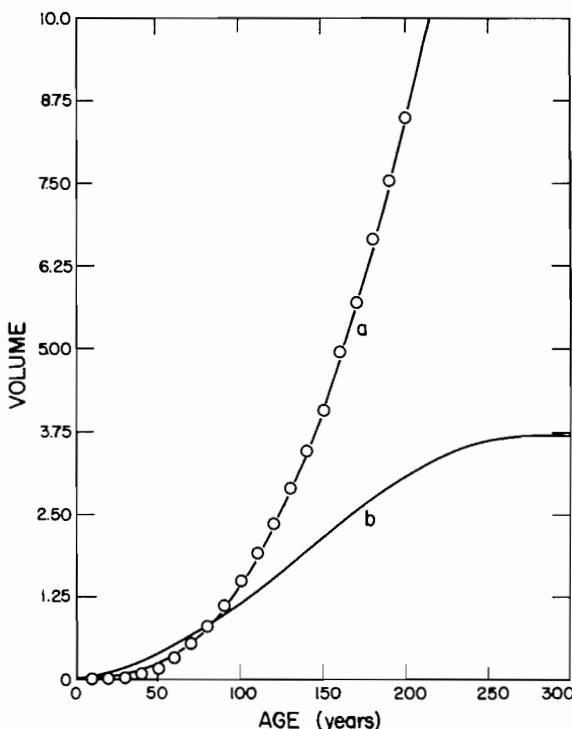
in the other. Only the modified Weibull function is good in both cases (Figs. 2 and 3). Although any function can be defeated by a particular set of data, a flexible function should be capable of assuming various parameter values to produce a satisfactory curve under most circumstances. From the above examples, and more than forty other sets of data tested (Kozak and Yang 1978), the modified Weibull function has been very flexible and, therefore, effective in modelling.

Volume-Age Curve (Example 2)

Figures 4–7 illustrate the versatility of the modified Weibull function applied to volume-age curves which are of particular interest to forest managers. The source and methods for collecting the lodgepole pine (*Pinus contorta* Dougl.) data here used were reported elsewhere (Smith 1973). The parameters for these curves are given in Table 3. Figure 4 shows the fitted volume (net mean volume per acre) and curves over age for lodgepole pine grown in the interior of British Columbia on good, medium, and poor sites. Figure 4 indicates that the function can describe growth of lodgepole pine for each site class from youth to maturity without harmonizing procedures. Figure 5 shows the mean annual increment (growth rate) curves of the three site classes. It in-

TABLE 3. Estimated parameters of the modified Weibull function for lodgepole pine volume-age data

Site class	Density class	No. plots	A			Year MMAI ^b
			ft ³ /acre ^a	m ³ /ha	B	
Good	Average	1415	6 283	439.63	2.24498×10^{-4}	1.9091
Medium	Average	664	4 241	296.75	0.78020×10^{-4}	2.1258
Poor	Average	291	3 512	245.74	0.85000×10^{-4}	1.8966
Good	Open	212	2 047	143.23	1.11421×10^{-4}	2.1589
Good	Sparse	690	3 890	272.19	1.65000×10^{-4}	1.9981
Good	Average	1415	6 283	439.64	2.24498×10^{-4}	1.9091
Good	Dense	548	8 793	615.27	1.94242×10^{-4}	1.9229
Good	Very dense	207	10 834	758.08	1.73000×10^{-4}	1.9650

^aOne acre = 0.405 ha.^bMMAI, maximum mean annual increment.FIG. 3. A fitted stem volume growth curve (*a*) and its derived increment curve (*b*) (four times actual size) for a fir tree. Data from Bamberg as presented by Prodán (1968).

dicates that the rotation of maximum increment increases with decreasing site quality and that the poor site, in addition to producing much less timber, takes longer to reach its point of maximum mean annual increment. It also appears that mean annual increment curves tend to be flat near their apex. The above observations on mean annual increments of lodgepole pine at three site qualities are in close agreement with concepts of Davis (1954).

Figure 6 demonstrates the fitted polymorphic volume-age curves for the good site lodgepole pine at

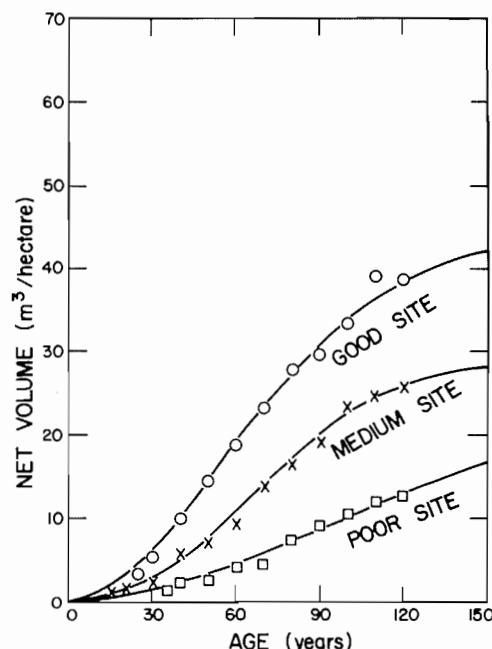


FIG. 4. Lodgepole pine net mean volume yield data (grown in the interior of British Columbia) at three site classes fitted individually by the modified Weibull function with a least square solution weighted by number of plots.

five basal area stand density levels. Curves constructed from empirical data are often inconsistent and contradicting among themselves (Meyer 1953). However, Fig. 6 exemplifies the elegance of the modified Weibull function in such polymorphic curve construction; each density is well differentiated from the others and curves are systematically consistent among themselves. Composite volume-age curves also have been based on the Gompertz function (Nokoe and Kozak 1975), but the modified Weibull function should be more appropriate for construction of such curves.

The mean annual increment (growth rate) curves

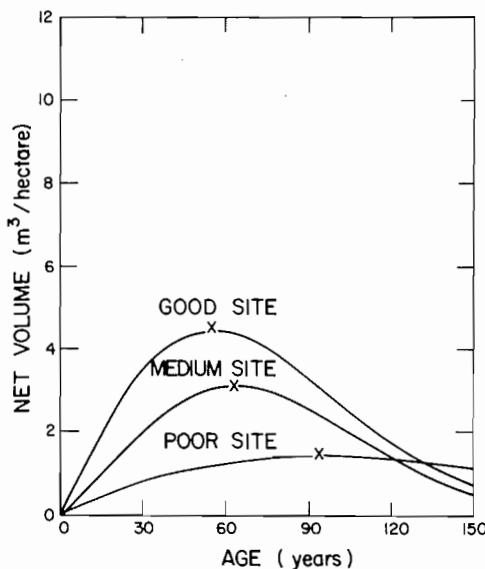


FIG. 5. Net volume increment curves of lodgepole pine at three site classes. The marked points are the locations of maximum mean annual increment.

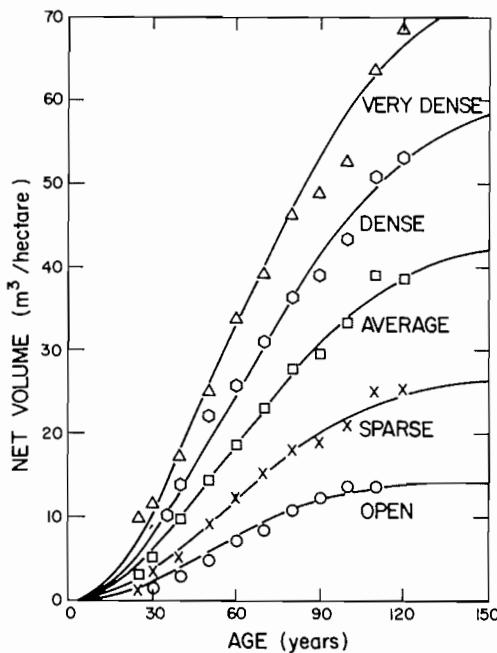


FIG. 6. Good site lodgepole pine net mean volume yield data (grown in the interior of British Columbia) at various basal area density classes fitted individually by the modified Weibull function with a least squares solution weighted by number of plots.

for the lodgepole pine are illustrated in Fig. 7. The polymorphic curves are essentially harmonious. The slight increase of rotation with increasing density

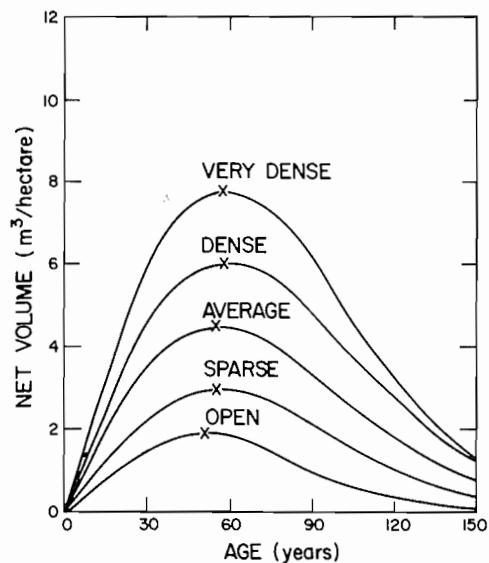


FIG. 7. Net mean volume increment curves of good site lodgepole pine at various basal area density classes. The marked points are the location of maximum mean annual increment.

may be an artifact but should be studied carefully by forest managers.

Conclusion

The modified Weibull function is rich in form and therefore suitable for many aspects of growth and yield studies. With this function many biological growth processes can be well modelled. It should help to describe and to determine the significance of genetic and environmental factors imposed during the growth of trees and stands.

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