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A Flexible Growth Function for Empirical Use

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SUMMARY

The application of an extended form of von Bertalanffy's growth function to plant data is considered; the equation has considerable flexibility, but is used only to supply an empirical fit. In order to aid the biological analysis of such growth data as are capable of representation by the function, general rate parameters are deduced which are related in a simple manner to its constants.

THE many attempts which have been made to simulate curves of limited growth by mathematical formulations either aim at accounting for their form through certain fundamental postulates about the growth process, or else are severely practical in scope and inspired by the desire to obtain any relatively simple equation which contains the essence of the numerical data. In the empirical approach the magnitudes of the constants in the fitted equations may be used to assess the importance in growth of experimentally controllable factors, but the constants themselves are not regarded as having any absolute significance for the theory of growth. Obviously the usefulness of any empirical equation is enhanced if its constants yield easily information of direct biological interest.

The three best-known 'growth functions' are as follows:

	<i>Monomolecular</i>	<i>Autocatalytic</i>	<i>Gompertz</i>
Equation	$W = A(1 - be^{-kt})$	$W = A/(1 + be^{-kt})$	$W = Ae^{-be^{-kt}}$
Growth-rate	$k(A - W)$	$kW(A - W)/A$	$kW \log_e(A/W)$

Here W represents the size at time t and A its ultimate limiting value; k is the 'rate constant' which determines the spread of the curve along the time axis. The magnitude of b is usually unimportant biologically, since it reflects only the choice of the zero of time. The monomolecular function has no point of inflexion, its growth-rate declining linearly with increasing W ; it is used sometimes (cf. Gregory, 1928) to represent the later portions of life history. The autocatalytic or 'logistic' curve is symmetrical round its point of inflexion; its *relative* growth-rate declines linearly with increasing W . It has been used widely both from a theoretical standpoint (e.g. Robertson, 1923) and as a convenient empirical curve. The Gompertz curve resembles the autocatalytic in many features, but is asymmetrical, inflecting at $W = A/e$, or 0.368 A ; linear relations exist both between its relative growth-rate and $\log W$, and between the logarithm of its relative rate and time. This curve has been used more extensively in population studies and to represent the course of animal growth than it has by botanists; it was deduced as a theoretical curve

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for the growth of chicken's heart in an interesting paper by Medawar (1940), and on the botanical side has recently been applied to the growth of *Pelargonium* leaves by Amer and Williams (1957).

Each of these functions represents but a single curve, whose only changes of form are such as may be realized by rescaling the co-ordinate axes. Not unnaturally many growth curves fail to conform satisfactorily with any of the three. Sometimes (cf. Pearl and Reed, 1923) a fit is then obtained by substituting a cubic function of time for kt in the formula given above for the autocatalytic; a quadratic function is unsuitable. By thus increasing the fitted constants from 3 to 5 considerable flexibility is introduced into the shape of the curve, but this 'generalized logistic' function does not supply its information in an easily comprehensible manner and it has been used but little.

The present purpose is to examine a growth function developed for animals, from theoretical considerations, by von Bertalanffy (1941, 1957; the second paper especially contains references to relevant earlier work), and to show how, when limitations imposed by its theoretical background are discarded, it may have wide applications in empirical botanical studies, facilitating comparisons between sigmoid growth curves of quite different shapes. In its general form it includes all the three functions mentioned above, although with von Bertalanffy's restrictions the autocatalytic and the Gompertz are excluded as impossible types. While the function may not have all the flexibility of the generalized logistic, its information is conveyed much more conveniently and it contains only four constants.

Von Bertalanffy's function and its extension. Von Bertalanffy starts from the allometric relation during growth between an animal's metabolic rate and its weight, claiming that the slope (m) of the allometric line is either $2/3$ (for species obeying the *surface rule* of metabolism), unity (where oxygen consumption is proportional to the animal's weight instead of its surface area), or something intermediate between these extreme values; he thus recognizes among animals three 'metabolic types'. Following Pütter (1920), he argues further that the rate of anabolism is proportional to the m th power of weight, but the rate of catabolism to weight itself. Hence the growth-rate in weight, the difference between these two, becomes: $\eta W^m - \kappa W$, where η and κ are constants of anabolism and catabolism respectively. When $m = 1$,

$$dW/dt = (\eta - \kappa)W$$

and growth is exponential. For lower values of m integration leads to the growth equation: $W = \{\eta/\kappa - [\eta/\kappa - W_0^{1-m}]e^{-(1-m)\kappa t}\}^{1/(1-m)}$, where W_0 is the weight at $t = 0$. The graph of this function is sigmoid, approaching asymptotically the value $(\eta/\kappa)^{1/(1-m)}$, which in present usage is the constant A .

While it is interesting, the derivation of the growth-rate contains assumptions and approximations which *in toto* cast grave doubt on its theoretical validity; moreover values of m above unity are rejected, not apparently because they are shown never to occur, but presumably from the theoretical need to confine η and κ within a numerical range compatible with their

interpretation as proportionality constants of anabolism and catabolism. It is easy to show that with limited growth and $m > 1$, η and κ must be negative, which falsifies this interpretation. Yet if used empirically, m being assessed from the growth data themselves instead of from dubiously relevant metabolic studies, von Bertalanffy's function will find its chief application with values over 1.

The growth equation may be abbreviated to: $W^{1-m} = A^{1-m} - \beta e^{-kt}$, where A^{1-m} , β , and k are constants: $A^{1-m} = \eta/\kappa$, $\beta = \eta/\kappa - W_0^{1-m}$, and $k = (1-m)\kappa$. As defined here, β is negative when $m > 1$, since it equals $A^{1-m} - W_0^{1-m}$. Since negative values may cause confusion in the linear form of the function, the equation is better written as: $W^{1-m} = A^{1-m}(1 - be^{-kt})$ when $m < 1$, and as: $W^{1-m} = A^{1-m}(1 + be^{-kt})$ when $m > 1$; here $b = \pm\beta A^{m-1}$. By putting $m = 0$ the first of these reduces immediately to the formula for the monomolecular curve, while if $m = 2$ the second equation becomes:

$$W = A(1 + be^{-kt})^{-1},$$

the autocatalytic function. Hence values of m much exceeding unity are necessary if the general function is to have wide empirical applications.

Neither is an exponential curve the only possibility when $m = 1$; a solution for limited growth also exists, which is in fact the Gompertz (see below). By taking logarithms the usual formula for this curve becomes:

$$\log_e W = \log_e A - be^{-kt},$$

in which form it may be fitted to data (Stevens, 1951). Such a fitting corresponds to a value of 1 precisely for m in von Bertalanffy's equation. Although the equation: $W^{1-m} = A^{1-m} - \beta e^{-kt}$ becomes insoluble when $m = 1$, nevertheless a Gompertz curve can still be fitted with considerable accuracy (again by Stevens's method) if a value of, say, 0.999 or 1.001 be chosen for m . It may be shown that, with limited growth, when m becomes unity the η and κ of von Bertalanffy become equal and infinitely great. Hence his interpretation of these constants again breaks down and he accepts only the exponential solution. Yet values of m ranging between 1 and 2 represent curve types grading from the Gompertz to the autocatalytic; moreover with $m > 2$ the point of inflexion may be carried as far as desired beyond $W = A/2$. On the other hand, when m lies between 0 and 1 the curves are transitional in form between the monomolecular and the Gompertz. Representative types are shown in Fig. 1.

The absolute growth-rate ($\eta W^m - \kappa W$) in any one of these curves now becomes: $kW[(A/W)^{1-m} - 1]/(1-m)$, and the relative rate:

$$k[(A/W)^{1-m} - 1]/(1-m).$$

Substitution of 0 and 2 for m in the former leads to the expressions given earlier for the rates in the monomolecular and autocatalytic functions respectively. These formulae break down when $m = 1$ exactly; but since as $x \rightarrow 0$ the limiting value of $(a^x - 1)/x$ is $\log_e a$, the growth-rate then becomes:

$kW \log_e(A/W)$, which is the rate appropriate to the Gompertz function. This derivation demonstrates that the limiting form of the general function when $m \rightarrow 1$ is indeed the Gompertz.

Interpretation of the constants. Apart from their degree of compression the differing shapes of these growth curves are due solely to differences in m . For example, this constant determines the proportion of the final size at which the inflexion point occurs, viz. at $W/A = m^{1/(1-m)}$; as $m \rightarrow 1$ (Gompertz) this becomes $1/e$. The constant A is the final size of the plant or organ,

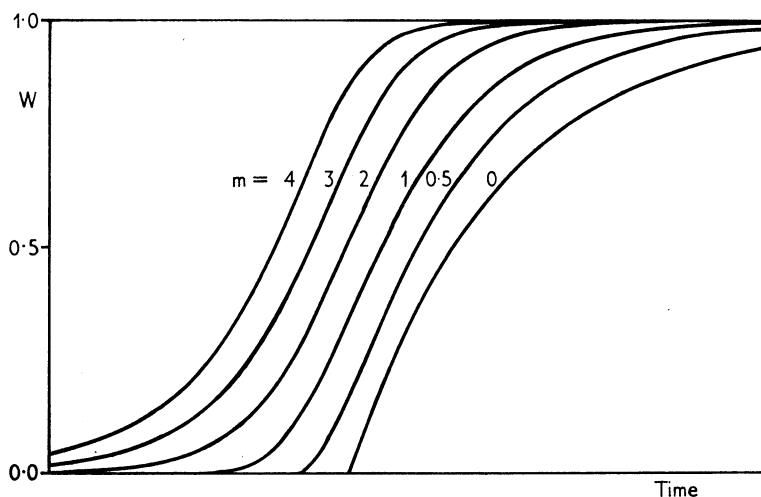


FIG. 1. Asymptotic curves from the family described, for the values of m indicated. In all cases $A = 1$ and $k/(2m+2)$ is uniform throughout.

while b , which equals $(W_0/A)^{1-m} \sim 1$, usually has no biological implication and can be eliminated from the equation by adjustment of the time scale. For this purpose the time when $W^{1-m} = 2A^{1-m}$ must be taken as $t = 0$, provided $m > 1$; for the autocatalytic this gives $W = 0.5 A$, its point of inflexion. Where $m < 1$, b is unity if $t = 0$ when $W = 0$. Over this lower range of m the growth curve is tangential here to the time axis; mathematically it continues beyond the point, as either a real or an imaginary extension. In the Gompertz curve b has a unique significance; as with the autocatalytic it becomes unity when time is measured from the point of inflexion—in this case when $W = A/e$.

The remaining constant k needs a little consideration. It expresses the rate at which the value of some function of W changes, e.g. $\log_e[(A-W)/A]$ in the monomolecular, $\log_e[(A-W)/W]$ in the autocatalytic, and $\log_e \log_e(A/W)$ in the Gompertz. The general linear equation for the family is:

$$\log_e[1 \sim (W/A)^{1-m}] = \log_e b - kt.$$

Since the function of W which is involved is specific for each curve type, depending on m , it is difficult to interpret usefully differences between k 's derived from curves of differing forms, although such comparisons have been

attempted; thus Amer and Williams (1957) tentatively compared the rate constants of Gompertz and autocatalytic curves fitted to growth data from leaves of different species. Use of the comprehensive function would often lead to the need for some more practical alternative procedure.

It may be asked just what information of biological interest is supplied by the k 's from curves of a single type, e.g. the autocatalytic. The function of W which happens to change linearly with time assumes importance only in relation to theories about growth which attribute to the constant A (final size) a quantitative *causative* significance throughout development. From the empirical standpoint its interest is limited, mathematical rather than biological, so that the lack of easy correspondence in meaning between the k 's from curves having different m 's is no great loss from this point of view. Parameters which allow comparisons between general rates of change of W itself in the various curves would be of more immediate interest.

Among these curves, however, the relation between growth rate and time is affected in a complex manner by k , viz.

$$\frac{dW}{dt} = \frac{\mp kAbe^{-kt}}{1-m} (1 \pm be^{-kt})^{m/(1-m)}$$

and
$$\frac{1}{W} \cdot \frac{dW}{dt} = \mp kbe^{-kt} / [(1-m)(1 \pm be^{-kt})]$$

—the upper signs apply when $m > 1$ and the lower when $m < 1$. Since the growth curves approach $W = A$ asymptotically their mean rates are uniformly zero. It is easier to obtain suitable parameters from the relation between growth-rate and W , graphs of which are shown in Fig. 2 for selected values of m . The *form* of any such rate curve is determined exclusively by m , but its *height* depends on A and k as well. The area under the curve is:

$$\int_{W=0}^{W=A} \frac{kW}{1-m} \left[\left(\frac{A}{W} \right)^{1-m} - 1 \right] dW,$$

which equals $A^2k/(2m+2)$. Hence the mean height is $Ak/(2m+2)$. If now for every growth curve the unit in which W is measured is its own final size A , and the rate be plotted against W (in other size units, $dW/A \cdot dt$ against W/A), the diagram will represent the rate of change in 'proportional size' over the whole size range 0–1. The area beneath the curve is now $k/(2m+2)$, and the mean height is numerically the same. Among a group of such curves all having the same m , the relative average heights depend only on the various k values; $k/(2m+2)$, however, is more definite in that it states the mean height, so that in its terms all 'proportional rate' curves become directly comparable, e.g. $k/4$ in a Gompertz function is equivalent in this sense to $k/6$ in an autocatalytic. Curves conforming to the general function, and for each of which k is proportional to $m+1$, are therefore equal as regards this parameter. In Figs. 1 and 2 this condition is fulfilled; since also A is kept uniform throughout, the areas under the several curves of Fig. 2 are equal.

The allied parameter $Ak/(2m+2)$ measures the average height of the plot of absolute rate against W . Hence it represents the mean growth-rate within a hypothetical population in which all *size* classes are equally abundant, i.e.

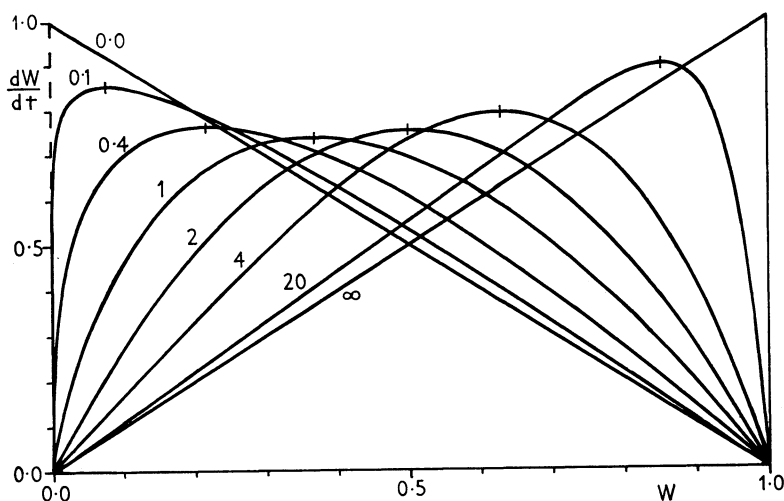


FIG. 2. Relation between growth-rate and size (W) for curves having the m values indicated. In all cases $A = 1$ and $k/(2m+2)$ is uniform throughout. The position of the maximum on each curve is shown.

a population having a rectangular distribution with respect to size. I am indebted to Mr. B. M. Church for an interesting alternative interpretation of the parameter, as a weighted mean growth-rate throughout the whole period of growth. If the weighting applied to the rate is itself a function of time, the weighted mean will be:

$$\int_{t=-\infty}^{t=+\infty} \frac{dW}{dt} \cdot f(t) dt \bigg/ \int_{t=-\infty}^{t=+\infty} f(t) dt$$

(for reasons given on p. 293, where $m < 1$ integration should start from the time when $W = 0$ instead of from $t = -\infty$). Greatest weight should evidently be given to the period of active growth, when the rate will be estimated most accurately, and little weight to the ends of the time scale. Beyond this the choice is arbitrary, but the simplest procedure is to weight proportionally to the actual rate, i.e. to make $f(t)$ equal to dW/dt itself. With this convention the weighted mean becomes:

$$\int_{t=-\infty}^{t=+\infty} \left(\frac{dW}{dt} \right)^2 dt \bigg/ \int_{t=-\infty}^{t=+\infty} \frac{dW}{dt} dt,$$

which equals:

$$\frac{1}{A} \int_{W=0}^{W=A} \frac{dW}{dt} dW$$

again. This parameter will therefore be referred to as the *weighted mean growth-rate*. The parameter $k/(2m+2)$ has a similar interpretation in relation to 'proportional growth' rates.

Over the most useful range of m (say 1–3) the maxima on the curves of Fig. 2 are not very variable. As stated earlier any such maximum occurs at $W = Am^{1/(1-m)}$ and its magnitude is $Akm^{m/(1-m)}$; even if this latter were regarded as a more easily comprehended parameter than the weighted mean growth-rate, its mathematical expression is more complex and its evaluation more time-consuming. The ratio of the two preceding expressions, k/m , is the relative growth-rate at the point of inflexion of the growth curve, and is a more interesting parameter, as will appear shortly.

As $m \rightarrow 1$ (Gompertz) the maximal growth-rate approaches kA/e , this being the lowest maximum in the family of curves represented in Fig. 2. The autocatalytic derivative ($m = 2$) is the only symmetrical curve among them, a parabola. The monomolecular ($m = 0$) provides a straight line, while at the other extreme as m becomes large the growth-rate is virtually proportional to W until the maximum size A is neared, when it quickly falls to zero. This type of rate curve represents exponential increase which is nevertheless limited and ends abruptly.

Where $m < 1$ the corresponding relative growth-rate curves are convex to the axis of W and are infinite initially, indicating that this range of m can usefully be employed only if the data do not include early stages of growth (nevertheless von Bertalanffy's hypotheses permit only such values). Where $m > 1$ the initial relative rates are finite; the curves flatten until $m = 2$, at which value the fall with increasing W becomes linear. Above $m = 2$ the direction of curvature reverses, the early portions of the curves becoming more and more nearly horizontal with increasing m . Where $m = 3$, for example, the initial relative rate does not fall by as much as 10 per cent. until more than 30 per cent. of the total growth is realized, while if m should be as high as 20 nearly 80 per cent. of growth would be over before the fall reached 1 per cent. Since close approximations to exponential increase frequently occur in the early stages of plant growth, curves with $m > 2$ offer new possibilities for the more accurate reproduction of many growth histories without undue complication in the mathematical function employed.

A *weighted mean relative growth-rate* may be determined exactly as was the corresponding absolute rate, i.e.

$$\frac{1}{A} \int_{W=0}^{W=A} \left(\frac{1}{W} \cdot \frac{dW}{dt} \right) dW = \frac{1}{A} \int_{W=0}^{W=A} \frac{k}{1-m} \left[\left(\frac{A}{W} \right)^{1-m} - 1 \right] dW = k/m.$$

This integral may also be written as:

$$\int_{t=-\infty}^{t=+\infty} \left(\frac{1}{W} \cdot \frac{dW}{dt} \cdot \frac{dW}{dt} \right) dt \bigg/ \int_{t=-\infty}^{t=+\infty} \frac{dW}{dt} \cdot dt$$

(when $m < 1$ the lower limit of integration should again be the time at which $W = 0$). The parameter k/m is therefore the mean relative growth-rate of a population wherein all size classes are represented equally, and is also a weighted mean relative rate throughout the growth period, the weighting at any time again being proportional to the absolute rate at that time. It was indicated earlier that k/m is, moreover, the actual relative growth-rate at the point of inflexion on the growth curve, where the absolute rate is maximal. This parameter therefore has three distinct interpretations. It provides a further means of generalizing part of the information conveyed by k alone when curves of a single form are compared.

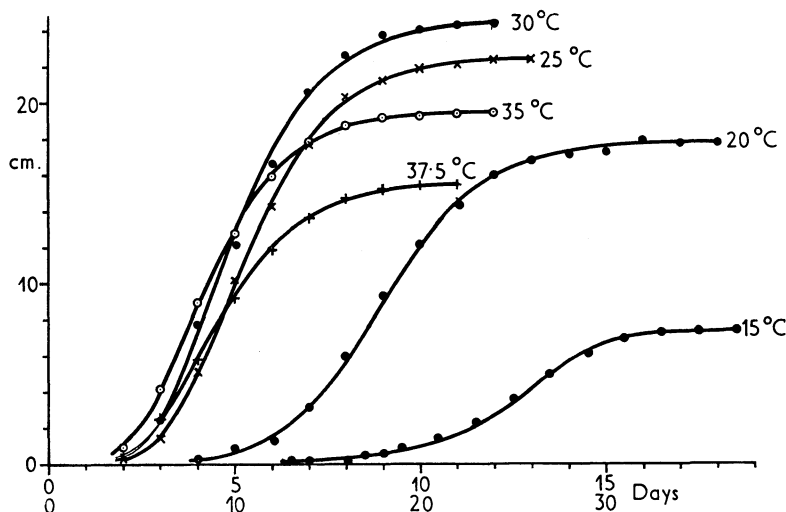


FIG. 3. Curves fitted to data of Pearl *et al.* (1934) concerning the growth in length of the hypocotyl of *Cucumis melo* at different temperatures; the points shown represent the actual data. The origin represents the time of planting, and the time scale for the data at 15° C. (lower scale) is contracted to half that for the others.

The four parameters b , m , k/m , and $Ak/(2m+2)$ define the growth curves completely, and in a way that enables useful treatment comparisons to be made immediately of 'average' rates of growth (both absolute and relative) and of the manner in which these rates vary with increasing W . For this last purpose it might be preferred to replace m by $m^{1/(1-m)}$, since this states explicitly the proportion of the final size at which the growth rate is maximal.

A practical example. In order to illustrate the versatility and convenience of the present function, curves from the family have been fitted to some data of Pearl *et al.* (1934) concerning the increase in length of the hypocotyl of *Cucumis melo* when grown in darkness at constant temperatures ranging from 15–37.5° C. (Fig. 3). The method of fitting will be indicated after the results have been presented. The four curves within the range 25–37.5° C. are close to the Gompertz in form, m varying only between 1.0 and 1.2 (see Table I). As temperature decreases below 25° C. the maximal rate of growth is delayed progressively in developmental history until at 15° C. m reaches 3.0. The

changes in m with temperature summarize sufficiently the associated changes in general form of the growth and rate curves. The estimated final length (A) is also sensitive to temperature, being maximal at about 30° C. The weighted mean elongation rate, $Ak/(2m+2)$, is maximal at about the same temperature, its value there being over seven times as great as at 15°. Expressed as 'proportional growth' the weighted mean rate, $k/(2m+2)$, is much less variable; at 25° it is only two and a quarter times the rate at 15°, and above 25° is virtually constant. The reciprocal (T) of this parameter is also stated in the table; it may loosely be considered to measure the time required for the major

TABLE I
Growth parameters calculated from data of Pearl et al. (1934)

° C.	15	20	25	30	35	37.5	30
b^*	395.0741	259.457	5.46848	15.4148	3.37595	1.52248	5.13941
A (mm.)	73.6	178.2	225.0	246.0	195.2	156.0	245.0
m	3.0	1.7	1.2	1.0	1.2	1.1	1.2
k (per day)	0.5538	0.6707	0.6813	0.6302	0.7391	0.6718	0.7207
$m^{1/(1-m)}$	0.58	0.47	0.40	0.37	0.40	0.39	0.40
$\frac{Ak}{2m+2}$ (mm. per day)	5.1	22.1	34.8	38.8	32.8	25.0	40.1
$\frac{k}{2m+2}$ (per day)	0.069	0.124	0.155	0.158	0.168	0.160	0.164
$\frac{k}{m}$ (per day)	0.185	0.395	0.568	0.630	0.616	0.611	0.601
T (days)	14.44	8.05	6.46	6.35	5.95	6.25	6.11

* These values apply when age is measured from the day of planting. The constant from the Gompertz fitting at 30° C. is not comparable with the others.

part of growth, and for comparative purposes probably represents the period of development as well as any other figure derivable from an asymptotic function. Consideration of these times in relation to the curves of Fig. 3 to which they apply shows that in each instance T indicates to a very close approximation the period during which 90 per cent. of the growth was made, provided the period it represents is chosen so as always to embrace the largest possible increment in W . Finally, the weighted mean relative rate, k/m , trebles between 15 and 25° C., but above this range alters little.

All these characteristics thus change markedly between 15 and 25° C. Some of them, e.g. m , $k/(2m+2)$, k/m , are insensitive to temperature increase beyond 25°, while others, e.g. A , $Ak/(2m+2)$, have a distinct maximum at about 30° C. The reduction in A at low temperatures was associated with a considerable alteration to m , indicating large differential effects of temperature on the growth-rate during development. On the other hand the results suggest strongly that whatever the causes leading to the reduction in final length at high temperatures, they must have been operative uniformly throughout the whole period of the measurements, for m was unaffected. This conclusion modifies considerably some of those drawn in the original paper, but it is beyond the present purpose to discuss this and other questions raised.

Fitting the curves. The estimates of m in Table I are probably within 0.1 of their optimal magnitudes, the only likely exception being the 1.0 at 30° C., where the data are somewhat irregular. Since these are fitted almost as well by m values as high as 1.2, constants appropriate to this value also are presented, in the last column of the table. The estimate of k is increased 14.4 per cent. by this change, a result which indicates the sensitivity of the constant to errors in m . The suggested substitutes for k are considerably less affected; in the present instance the use of $m = 1.2$ lowers the estimate of k/m from 0.6302 to 0.6006 (by 4.7 per cent.) and raises that of $k/(2m+2)$ from 0.1576 to 0.1638, i.e. 3.9 per cent. Thus wherever m can be assessed only approximately these parameters have the advantage of greater precision than k .

Unfortunately, sound statistical methods cannot be suggested at present either for determining the best value for m or for estimating the probability that any difference between the m 's selected for two growth curves is statistically real. Hence more empirical means must be adopted. A provisional m might be assigned by comparing a freehand curve through a plot of the data with a set like those in Fig. 1, but more complete. A better alternative is to assume some reasonable value for A and to assess the magnitude (I) of W at the point of inflexion, from the position of the maximum in a graph of the observed increments in W , per unit time, plotted against W . The value of m which satisfies $m^{1/(1-m)} = I/A$ should be close to the best possible; it might be read from a graph of $m^{1/(1-m)}$ against m .

The approximations to m and A may be improved by making use of the linear form of the growth function, i.e. by plotting $\log [1 \sim (W/A)^{1-m}]$ against t . Any departure from a straight line may then be corrected as far as possible by small changes in the magnitudes of m and A first used. Alteration of A modifies considerably the end where $W \rightarrow A$, but has little effect elsewhere, while a change in m alters the whole course of the line, its greatest effect being where W is small. With care and good data the best value of m may be found thus with an error not much, if at all, exceeding 0.1; with irregular data the uncertainty rapidly increases.

Having determined m to one's satisfaction, the other constants might be estimated from the equation: $W^{1-m} = A^{1-m} - \beta e^{-kt}$ (see p. 292), by the method of Stevens (1951) or, if the number of observations along the curve does not exceed seven, by the less laborious method of Patterson (1956). For many purposes it will be good enough to accept the value of A already used for the linear plot, and simply to estimate k and b from the graph itself, or from a linear regression through its points. This easier procedure was adopted for the data examined here.

Concluding remark. If justification be required for using this curve family to represent growth data it may perhaps be sought in the allometric relationship ($Y = pW^q$) so frequently found between two correlated growth characteristics, e.g. leaf length and leaf width, throughout their development. It is easily seen that if W is a growth characteristic conforming with one of the present curves, any other characteristic Y increasing allometrically with it

must have a different member of the same family as its growth curve: for allometry $b_Y = b_W$ and $k_Y = k_W$; then $q = (1 - m_W)/(1 - m_Y)$ and

$$p = A_Y/A_W^q.$$

Hence if, as is commonly admitted, the autocatalytic curve fits many data and its use is legitimate, then other such curves also having $m > 1$ must be equally legitimate; similarly, if the monomolecular is sometimes justified, so also will be other curves of the family wherein $m < 1$. The Gompertz is again unique; it is allometric only with other Gompertz curves, and then only in a rather trivial sense (Lumer, 1937), for k_W and k_Y must be equal and q becomes b_Y/b_W , i.e. a ratio of constants which have little biological significance.

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