

# **Growth Curve Modeling**

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# 3

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## PARAMETRIC GROWTH CURVE MODELING

### 3.1 INTRODUCTION

The preceding chapter considered the computation of a variety of growth rates for a generic variable measured over time, with time either expressed in terms of discrete units or treated as a continuous variable. Also included was a very special type of parametric growth model that exhibited a constant relative rate of growth, namely, the exponential growth model. In this chapter we shall explore a whole host of alternative growth models that have been employed to study growth behavior in diverse fields such as forestry, agriculture, biology, engineering, and economics, to name but a few.

While linear or exponential growth may at times be appropriate, we shall, for the most part, concentrate on sigmoidal (S-shaped) growth curves. In this regard, some of the more common parametric growth models covered herein are:

|                        |                              |
|------------------------|------------------------------|
| Linear                 | Janoschek                    |
| Logarithmic reciprocal | Lundqvist–Korf               |
| Logistic               | Hossfeld                     |
| Gompertz               | Stannard                     |
| Weibull                | Schnute                      |
| Negative exponential   | Morgan–Mercer–Flodin (M–M–F) |
| von Bertalanffy        | McDill–Amateis               |

Chapman–Richards (C–R)  
Log logistic  
Brody

Levakovic (I, III)  
Yoshida (I)  
Sloboda

Although this list is by no means exhaustive, it gives a very good account of the mainstream types of growth models, which have become popular over the recent past.

We have referred to the aforementioned growth models as being “parametric” in nature. This is because these functions (and their properties) have been defined in terms of a set of parameters, which describe (either separately or in combination) their fundamental characteristics. Such parameters represent or relate to an *asymptote*, an *intercept on the Y-axis*, the *rate at which the response variable Y changes* from some starting or initial value to its terminal or final value, and additional parameters as required for suitable *flexibility in modeling*.

### 3.2 THE LINEAR GROWTH MODEL

Let us assume that the series of  $Y$  values is generated by the *linear model*

$$Y_t = Y_0 + \beta t, t = 1, 2, \dots, n, \quad (3.1)$$

where  $Y_0$  is the value of  $Y$  at the beginning of period 1 and  $\beta$ (=constant) is the slope (Fig. 3.1). Then the sequence of  $Y_t$  values and the relative rates of change in  $Y$  between periods  $t - 1$  and  $t$  (the  $R_t$ 's) are provided in Table 3.1.

Note that for  $Y_0$  positive and for increasing  $t$ , if  $\beta > 0$ , then the  $R_t$ 's steadily decrease in value; and if  $\beta < 0$ , then the  $R_t$ 's steadily increase. So even if the slope of Equation 3.1 is constant, the period-to-period relative growth rates determined from this expression are monotonic increasing or decreasing, depending on the sign of the slope.

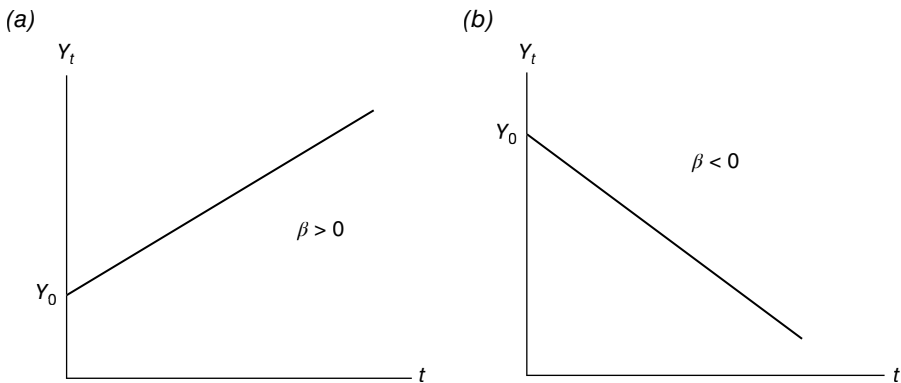


FIGURE 3.1 Linear models: (a) Positive slope; (b) Negative slope.

**TABLE 3.1** Relative Growth Rates in  $Y$ 

| Period $t$ | $Y_t$                | $R_t$  |
|------------|----------------------|--|
| 1          | $Y_1 = Y_0 + \beta$  | $R_1 = \frac{Y_1 - Y_0}{Y_0} = \frac{\beta}{Y_0}$                      |
| 2          | $Y_2 = Y_0 + 2\beta$ | $R_2 = \frac{Y_2 - Y_1}{Y_1} = \frac{\beta}{Y_0 + \beta}$              |
| 3          | $Y_3 = Y_0 + 3\beta$ | $R_3 = \frac{Y_3 - Y_2}{Y_2} = \frac{\beta}{Y_0 + 2\beta}$             |
| .          | .                    | .  |
| .          | .                    | .  |
| .          | .                    | .  |
| $n$        | $Y_n = Y_0 + n\beta$ | $R_n = \frac{Y_n - Y_{n-1}}{Y_{n-1}} = \frac{\beta}{Y_0 + (n-1)\beta}$ |

### 3.3 THE LOGARITHMIC RECIPROCAL MODEL

Suppose that the series of values of a variable  $Y$  is generated by the *logarithmic reciprocal model*

$$Y_t = e^{\alpha - \beta/t}, \quad t \neq 0, \quad (3.2)$$

or, upon transforming to logarithms,

$$\ln Y_t = \alpha - \frac{\beta}{t}, \quad t \neq 0, \quad (3.2.1)$$

where  $Y_t \rightarrow 0$  as  $t \rightarrow +0$  (i.e., this expression is right-continuous at the origin) so that this function is defined as zero for  $t=0$ .

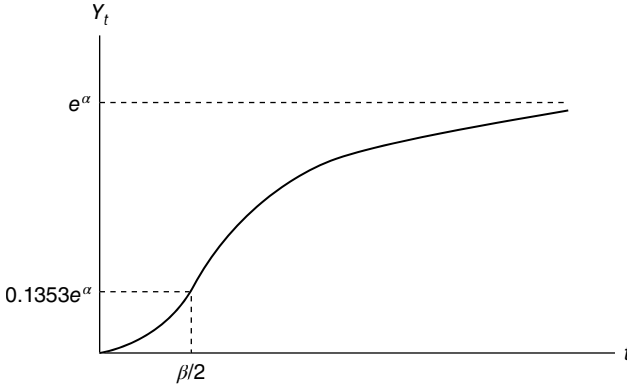
What about the general shape of the logarithmic reciprocal function? Given Equation 3.2, it is readily demonstrated that

$$\frac{dY_t}{dt} = \left( \frac{\beta}{t^2} \right) Y_t, \quad (3.3a)$$

$$\frac{d^2 Y_t}{dt^2} = \frac{\beta}{t^3} \left( \frac{\beta}{t} - 2 \right) Y_t. \quad (3.3b)$$

Since  $d^2 Y_t / dt^2 = 0$  for  $t = \beta/2$ , it follows that Equation 3.2 has a point of inflection<sup>1</sup> at  $t_{\text{inf}} = \beta/2$ . Substituting  $t = \beta/2$  into Equation 3.2 yields  $Y_{t_{\text{inf}}} = e^{\alpha - 2} = e^{\alpha} e^{-2} = 0.1353 e^{\alpha}$  (Fig. 3.2). Moreover, for  $t < \beta/2$ ,  $d^2 Y_t / dt^2 < 0$  (the slope increases with  $t$  so that the

<sup>1</sup> A *point of inflection* is a point where a curve crosses over its tangent line and changes the direction of its concavity from upwards to downwards, or vice versa. In this regard, for  $Y = f(t)$ , if  $f''(t_0) = 0$  and  $f'''(t_0) \neq 0$ , then  $f$  has a point of inflection at  $t = t_0$  (a sufficient condition).



**FIGURE 3.2** Logarithmic reciprocal model.

curve is concave upwards); and for  $t > \beta/2$ ,  $d^2Y_t/dt^2 > 0$  (the slope decreases as  $t$  increases so that the curve is concave downwards). Hence, Equation 3.2 provides an S-shaped pattern to growth. Additionally,

$$\lim_{t \rightarrow \infty} e^{\alpha - \beta/t} = e^\alpha = Y_\infty$$

so that  $e^\alpha$  is a horizontal (upper) asymptote for  $Y_t$  and represents a *saturation point* for growth in  $Y$ .

Next, the instantaneous rate of growth of  $Y_t$  at time  $t$  is

$$\frac{dY_t/dt}{Y_t} = \frac{\beta}{t^2}, \quad (3.4)$$

while the relative rate of change in  $Y$  between periods  $t-1$  and  $t$  is

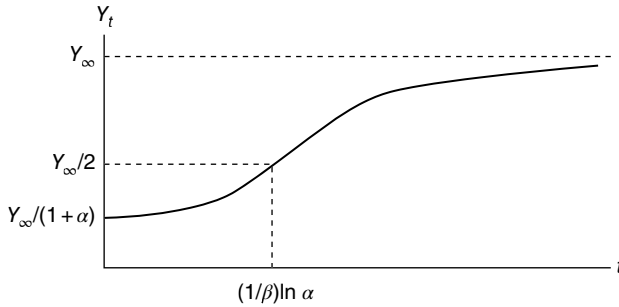
$$R_t = \frac{Y_t}{Y_{t-1}} - 1 = e^{\beta/t(t-1)} - 1 \quad (3.5)$$

( $\beta$  is thus a rate of growth parameter). Note that neither of these growth rates is constant and both decrease as  $t$  increases. In fact, each rate of growth drops abruptly beyond very small values of  $t$ .

### 3.4 THE LOGISTIC MODEL

Let the series of values of a variable  $Y$  over time be determined by the *logistic model* (Verhulst, 1838)

$$Y_t = \frac{Y_\infty}{1 + \alpha e^{-\beta t}}, \quad t \geq 0, \quad (3.6)$$

**FIGURE 3.3** Logistic model.

where the parameters  $\alpha, \beta$  (a growth rate parameter) and  $Y_\infty$  are all positive. At  $t=0$ , this curve starts out at  $Y_0 = Y_\infty / (1 + \alpha)$ , and as  $t \rightarrow \infty$ ,  $Y_t \rightarrow Y_\infty$  ( $Y_\infty$  is the (upper) horizontal asymptote of the logistic function—it is termed the *saturation* or *limit to growth parameter*).

To examine the shape of the logistic function, let us first find

$$\frac{dY_t}{dt} = \frac{\beta}{Y_\infty} Y_t (Y_\infty - Y_t), \quad (3.7a)$$

$$\frac{d^2 Y_t}{dt^2} = \frac{\beta}{Y_\infty} (Y_\infty - 2Y_t) \frac{dY_t}{dt}. \quad (3.7b)$$

From Equation 3.7 it is easily seen that  $d^2 Y_t / dt^2 = 0$  for  $Y_t = Y_\infty / 2$  (half the saturation level). Then a substitution of this  $Y$  value into Equation 3.6 yields  $t = \ln \alpha / \beta$ , where it is assumed that  $\alpha > 1$  so that  $\ln \alpha > 0$ . Hence, the logistic function has a point of inflection at  $(t_{\text{inf}}, Y_{t_{\text{inf}}}) = (\ln \alpha / \beta, Y_\infty / 2)$  and is symmetric about this point (Fig. 3.3). Also, for  $t < \ln \alpha / \beta$ ,  $d^2 Y_t / dt^2 > 0$  (the curve is concave upwards); and for  $t > \ln \alpha / \beta$ ,  $d^2 Y_t / dt^2 < 0$  (the curve is concave downwards). Here too Equation 3.6 exhibits an S-shaped pattern to growth.

Next, from Equations 3.7a and 3.7b,

$$\frac{dY_t / dt}{Y_t} = \frac{\beta}{Y_\infty} (Y_\infty - Y_t), \quad (3.8)$$

so that the instantaneous rate of growth of  $Y_t$  at time  $t$  is proportional to the amount by which  $Y_t$  falls short of the saturation parameter ceiling to  $Y$  growth ( $Y_\infty - Y_t$ ). Also, the relative rate of change in  $Y$  between periods  $t-1$  and  $t$  is

$$R_t = \frac{Y_t}{Y_{t-1}} - 1 = \frac{e^{\beta-1}}{Y_\infty} (Y_\infty - Y_t). \quad (3.9)$$

Here also this growth rate is proportional to  $Y_\infty - Y_t$ .

A more detailed discussion of the logistic function (its derivation and comparison with the exponential or semilogarithmic function) is offered in Appendix 3.A.

### 3.5 THE GOMPERTZ MODEL

Suppose the time profile of a variable  $Y$  is specified by the *Gompertz (1825) model*

$$Y_t = Y_\infty e^{-\alpha e^{-\beta t}}, \quad t \geq 0, \quad (3.10)$$

where the parameters  $\alpha$ ,  $\beta$  (the rate of growth parameter) and  $Y_\infty$  are all positive. (A derivation of this expression is provided by Appendix 3.B.) For  $t=0$ , the initial value of  $Y$  is  $Y_0 = Y_\infty e^{-\alpha}$ , and as  $t \rightarrow +\infty$ ,  $Y_t \rightarrow Y_\infty$  (the upper limit (a horizontal asymptote) to growth). As was the case for the logistic function,  $Y_\infty$  is termed the *limit to growth parameter*.

To help ascertain the shape of the Gompertz function, we first look to

$$\frac{dY_t}{dt} = \alpha \beta e^{-\beta t} Y_t, \quad (3.11a)$$

$$\frac{d^2 Y_t}{dt^2} = \alpha \beta^2 e^{-\beta t} (\alpha e^{-\beta t} - 1) Y_t. \quad (3.11b)$$

From Equation 3.11b, it is readily seen that  $d^2 Y_t / dt^2 = 0$  at  $t = \ln \alpha / \beta$ . Then a substitution of this  $t$  value into Equation 3.10 gives  $Y_t = 0.36788 Y_\infty$ . Thus, the Gompertz function has a point of inflection at  $(t_{\text{inf}}, Y_{t_{\text{inf}}}) = (\ln \alpha / \beta, 0.36788 Y_\infty)$  (see Fig. 3.4) and thus is S-shaped or sigmoidal.

Next, from Equation 3.11a, it follows that

$$\frac{dY_t / dt}{Y_t} = \alpha \beta e^{-\beta t}. \quad (3.12)$$

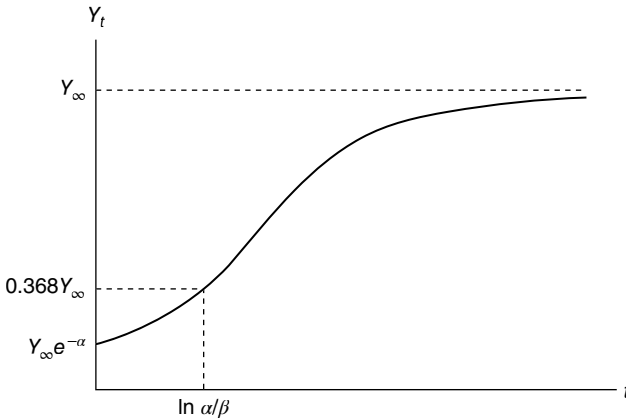


FIGURE 3.4 Gompertz model.

Thus, the instantaneous rate of growth of  $Y_t$  at time  $t$  is an exponentially decreasing function of time. Given Equation 3.12, it is easily demonstrated, via Equation 3.10, that

$$\frac{dY_t / dt}{Y_t} = \beta(\ln Y_\infty - \ln Y_t) \quad (3.13)$$

(we have a linear relationship between the instantaneous growth rate and  $\ln Y_t$ , with the said growth rate proportional to the amount by which  $\ln Y_t$  falls short of  $\ln Y_\infty$ ), while (again using Eq. 3.12)

$$\ln \left( \frac{dY_t / dt}{Y_t} \right) = \ln(\alpha\beta) - \beta t \quad (3.14)$$

(we have a linear relationship between the logarithm of the instantaneous growth rate and  $t$ ). Also, the relative rate of change in  $Y$  between periods  $t$  and  $t-1$  is

$$R_t = \frac{Y_t}{Y_{t-1}} - 1 = \left( \frac{Y_t}{Y_\infty} \right)^{e^\beta - 1} - 1. \quad (3.15)$$

### 3.6 THE WEIBULL MODEL

Let us assume that the series of values of a variable  $Y$  over time are generated by the *Weibull (1951) model*

$$Y_t = Y_\infty - \alpha e^{-\beta t^\gamma}, \quad t \geq 0, \quad (3.16)$$

where the parameters  $Y_\infty$ ,  $\alpha$ ,  $\beta$  (the growth rate parameter for a fixed  $\gamma$ ) and  $\gamma$  (a shape parameter) are all positive. The source of this expression is a generalization (extension) of the Weibull cumulative distribution function

$$F(t; \alpha, \theta) = 1 - e^{-(t/\alpha)^\theta},$$

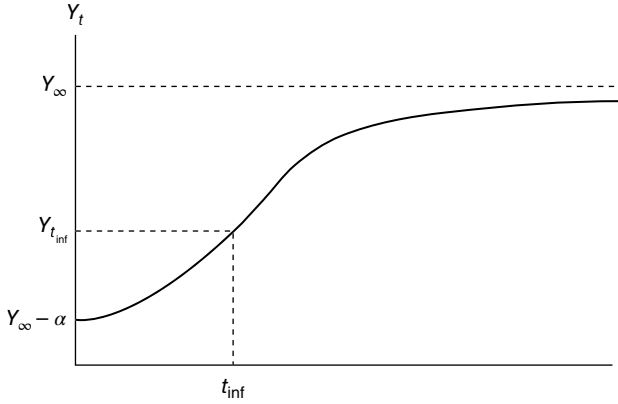
$\alpha$  and  $\theta$  being parameters. Along with the introduction of additional parameters, “1” is replaced by  $Y_\infty$  as a less restrictive upper limit to growth; that is,  $\lim_{t \rightarrow \infty} Y_t = Y_\infty$ . Hence,  $Y_\infty$  is termed the *limit to growth parameter*. For  $t=0$ , the initial value of  $Y$  is  $Y_0 = Y_\infty - \alpha$ .

Looking to the first and second derivatives of Equation 3.16, we have, respectively,

$$\frac{dY_t}{dt} = \beta \gamma t^{\gamma-1} (Y_\infty - Y_t), \quad (3.17a)$$

$$\frac{d^2 Y_t}{dt^2} = \beta \gamma t^{\gamma-1} \left[ (\gamma-1) t^{-1} (Y_\infty - Y_t) - \frac{dY_t}{dt} \right]. \quad (3.17b)$$





**FIGURE 3.5** Weibull model.

Using Equation 3.17b, we can readily determine that  $d^2Y_t/dt^2=0$  for  $t=t_{inf}=[(\gamma-1)/\beta\gamma]^{1/\gamma}$ . Substituting this  $t$  value into Equation 3.16 gives  $Y_t=Y_{t_{inf}}=Y_{\infty}-\alpha\exp[-(\gamma-1)/\gamma]$ . Thus, the Weibull growth equation has a point of inflection at  $(t_{inf}, Y_{t_{inf}})$  and thus is S-shaped (Fig. 3.5).

From (3.17a) it follows that

$$\frac{dY_t/dt}{Y_t} = \beta\gamma t^{\gamma-1} \left\{ \frac{Y_{\infty}}{Y_t} - 1 \right\}. \quad (3.18)$$

Hence, the instantaneous rate of growth in  $Y_t$  at time  $t$  approaches zero as  $t \rightarrow +\infty$  (or as  $Y_t \rightarrow Y_{\infty}$ ). And from Equation 3.18, we can write

$$\ln \left( \frac{dY_t/dt}{Y_t} \right) - \ln \left( \frac{Y_{\infty}}{Y_t} - 1 \right) = \ln(\beta\gamma) + (\gamma-1)t \quad (3.19)$$

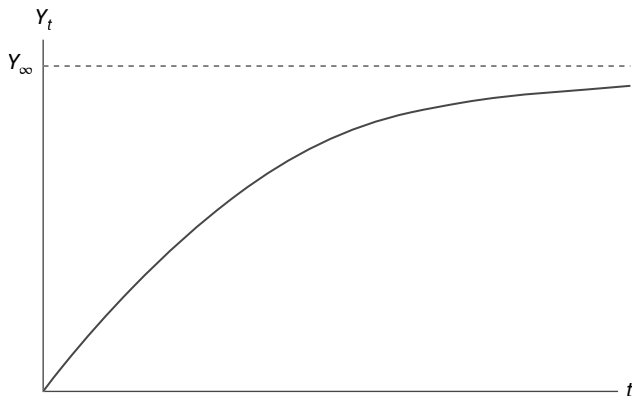
(we have a linear relationship between the logarithm of the instantaneous growth rate less the logarithm of a type of “feedback term”  $\ln((Y_{\infty}/Y_t)-1)$  and  $t$ ). (To gain some insight into the role of a feedback term, see Equation 3.A.4).

### 3.7 THE NEGATIVE EXPONENTIAL MODEL

Suppose that the time profile of the values of a variable  $Y$  reflects the operation of the *negative exponential model*

$$Y_t = Y_{\infty} (1 - e^{-\beta t}), \quad t \geq 0, \quad (3.20)$$

where the parameters  $Y_{\infty}$  and  $\beta$  are both positive. (The derivation of Eq. 3.20 is provided in Appendix 3.C.) Here  $Y_{\infty}$  is the *limit to growth parameter*  $(\lim_{t \rightarrow \infty} Y_t = Y_{\infty})$ , while  $\beta$  is the growth rate parameter. For  $t=0$ , the initial value of  $Y$  is  $Y_0=0$ .



**FIGURE 3.6** Negative exponential model.

Calculating the first and second derivatives of (3.20) yields

$$\frac{dY_t}{dt} = \beta(Y_\infty - Y_t); \quad (3.21a)$$

$$\frac{d^2Y_t}{dt^2} = -\beta \frac{dY_t}{dt} = -\beta^2(Y_\infty - Y_t). \quad (3.21b)$$

As Equation 3.21a and 3.21b reveals, as  $t \rightarrow \infty$ , the slope of the negative exponential function is positive and decreasing as  $Y_t \rightarrow Y_\infty$  (Fig. 3.6).

Using Equation 3.21a, we can easily see that

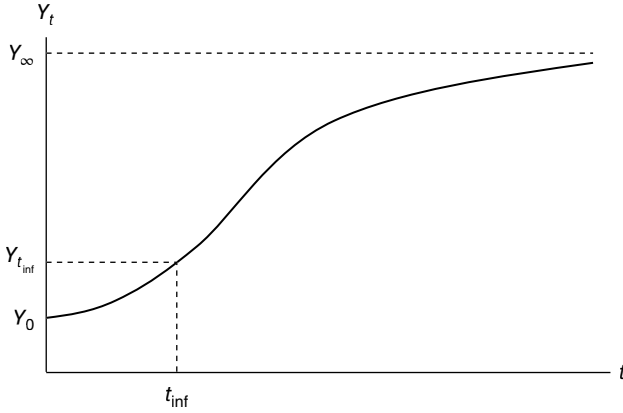
$$\frac{dY_t / dt}{Y_t} = \beta \left( \frac{Y_\infty}{Y_t} - 1 \right). \quad (3.22)$$

Thus, the instantaneous rate of growth in  $Y_t$  at time  $t$  approaches zero as  $t \rightarrow \infty$  (or as  $Y_t \rightarrow Y_\infty$ ). Note that this rate of growth is proportional to the “feedback term”  $\frac{Y_\infty}{Y_t} - 1$ .

### 3.8 THE VON BERTALANFFY MODEL

To describe a positive *net growth process* (pertaining to either length, weight, or size), von Bertalanffy (1957) asserted that the anabolic rate had to exceed the catabolic rate.<sup>2</sup> If the anabolic rate is a multiple of the  $k$ th power of  $Y_t$  and the catabolic

<sup>2</sup>We may view *anabolism* as constructive metabolism (requiring energy derived mainly from oxidation of organic compounds), while *catabolism* reflects destructive metabolism (living tissue is broken down into waste matter).



**FIGURE 3.7** von Bertalanffy model.

rate is simply proportional to  $Y_t$ , then the *von Bertalanffy* (1957) *growth law* can be written as

$$\frac{dY_t}{dt} = \eta Y_t^k - \lambda Y_t, \quad (3.23)$$

where  $\eta$  and  $\lambda$  are constants. Once this expression is integrated (see Appendix 3.D), the *von Bertalanffy growth model* is of the form

$$Y_t = Y_\infty \left[ 1 - \beta e^{-\lambda(1-k)t} \right]^{1/(1-k)}, \quad (3.24)$$

where

$$Y_\infty = \lim_{t \rightarrow \infty} Y_t = (\eta / \lambda)^{1/(1-k)}$$

is the *limit to growth parameter*,  $\beta = \alpha / \eta$  ( $\alpha$  a constant of integration),  $\lambda$  is a growth rate parameter,  $1 - k$  is a shape parameter, and the initial value of  $Y$  is

$$Y_0 = \left( \frac{\eta}{\lambda} - \frac{\alpha}{\lambda} \right)^{1/(1-k)}.$$

If  $k > 1$  and both  $\eta$  and  $\lambda$  are negative, Equation 3.24 is sigmoidal with lower asymptote  $Y_0$ , upper asymptote  $Y_\infty$ , and a point of inflection where  $d^2Y_t/dt^2 = 0$  (Fig. 3.7). If  $k < 1$  and both  $\eta$  and  $\lambda$  are positive, there is no lower asymptote. (An important variation of Eq. 3.24 is the *Chapman–Richards* (C–R) *growth model*, which is also considered in Appendix 3.D.)

von Bertalanffy determined empirically that  $k = 2/3$  for a wide variety of animals (e.g., fisheries research tends to support this result). In general, to accommodate the possibility of exponential growth, von Bertalanffy allowed for  $k \in [2/3, 1]$ .

Given Equation 3.24, we can readily find

$$\frac{dY_t}{dt} = \beta \lambda Y_\infty^{1-k} e^{-\lambda(1-k)t} = \lambda Y_t \left[ \left( \frac{Y_\infty}{Y_t} \right)^{1-k} - 1 \right]; \quad (3.25a)$$

$$\begin{aligned} \frac{d^2 Y_t}{dt^2} &= \beta \lambda Y_\infty^{1-k} e^{-\lambda(1-k)t} Y_t^k \left[ \lambda(k-1) + k Y_t^{-1} \frac{dY_t}{dt} \right] \\ &= \lambda \frac{dY_t}{dt} \left[ k \left( \frac{Y_\infty}{Y_t} \right)^{1-k} - 1 \right]. \end{aligned} \quad (3.25b)$$

If we set  $d^2 Y_t / dt^2 = 0$ , then it can be demonstrated that the point of inflection occurs at

$$(t_{\text{inf}}, Y_{t_{\text{inf}}}) = \left( \frac{1}{\lambda(k-1)} \ln \left( \frac{1-k}{\beta} \right), Y_\infty k^{1/(1-k)} \right).$$

Next, from Equation 3.25a, the instantaneous rate of growth in  $Y_t$  at time  $t$  is

$$\begin{aligned} \frac{dY_t / dt}{Y_t} &= \beta \lambda Y_\infty^{1-k} e^{-\lambda(1-k)t} Y_t^{k-1} \\ &= \lambda (Y_t^{k-1} Y_\infty^{1-k} - 1) = \lambda \left[ \left( \frac{Y_\infty}{Y_t} \right)^{1-k} - 1 \right]; \end{aligned} \quad (3.26)$$

that is, this growth rate is proportional to the “feedback term”  $(Y_\infty / Y_t)^{1-k} - 1$ . It is interesting to note that the instantaneous rate of growth in  $Y_t$  is maximal at the point of inflection and, at this point, equals

$$\frac{dY_t / dt}{Y_t} = \frac{\lambda(1-k)}{k}.$$

### 3.9 THE LOG-LOGISTIC MODEL

If in the logistic function Equation 3.6 we replace  $t$  by  $\ln t$ , then we obtain the *log-logistic model*

$$Y_t = Y_\infty / (1 + \beta e^{-k \ln(t)}), \quad t > 0. \quad (3.27)$$

From Equation 3.27,

$$\frac{dY_t}{dt} = \frac{\beta k Y_t^2}{Y_\infty t e^{k \ln(t)}} \quad (3.28)$$

so that the instantaneous growth rate at time  $t$  can be written as

$$\frac{dY_t / dt}{Y_t} = \frac{\beta k}{t(\beta + e^{k \ln(t)})} \quad (3.29)$$

( $k$  is thus a rate of growth parameter for a fixed  $\beta$ ) with

$$\lim_{t \rightarrow \infty} \frac{dY_t / dt}{Y_t} = 0.$$

Setting  $d^2Y_t/dt^2=0$  enables us to obtain the coordinates of the point of inflection as

$$(t_{\text{inf}}, Y_{t_{\text{inf}}}) = \left\{ \left[ \frac{1+k}{\beta(k-1)} \right]^{-1/k}, Y_{\infty} \left( \frac{k-1}{2k} \right) \right\}.$$

A popular application of the log-logistic function is in the fitting of dose–response curves. Specifically, one can determine the efficacy of a new “agonist” (a drug that causes a response) or the impact of some toxin (e.g., a weed-control agent). To this end, one should not simply apply small doses in small increments. It is typically the case that when researchers want to assess the impact of, say, some toxin, they increase doses logarithmically since, in this instance, the dose concentrations are equally spaced on the log scale.

For example, if dose concentration (in mg/kg) increments are displayed as

$$X: 1, 3.1623, 10, 31.623, 100, 316.228, 1000, 3162.28, 10,000, \dots,$$

then the log (dose) values are

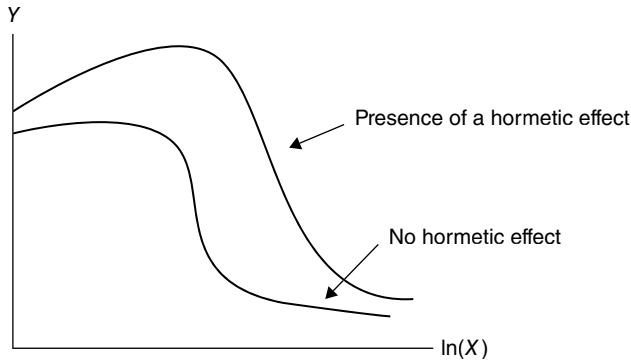
$$\log_{10}(X): 0, 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, \dots$$

(Note that there is no dose of  $X=0$ ; the actual dose is 1 mg/kg since  $10^0=1$ .) Hence, the log(dose)–response function serves to highlight the region of greatest interest wherein the percent of response increases at the highest rate. In fact, the dose response will reach the 50% level when  $\log(\text{dose})=\log(\text{ED}_{50})$ , where  $\text{ED}_{50}$  is the “effective dose” at which 50% of the total response is achieved or  $Y_{\infty}/2$ .

If a lower asymptote or baseline response level ( $Y_L$ ) is warranted, then Equation 3.27 can be reparameterized as

$$Y = Y_L + \frac{Y_{\infty} - Y_L}{1 + \beta e^{-k \ln(X)}}, \quad X > 0, \quad (3.30)$$

where now the effective dosage at which 50% of the total effect is attained is  $(Y_{\infty} - Y_L)/2$ .



**FIGURE 3.8** Presence of a hormetic effect.

Equation 3.30 may be modified further (Brain and Cousens, 1989) to capture “hormetic effects” (Fig. 3.8)<sup>3</sup> associated with low dosages as

$$Y = Y_L + \frac{Y_\infty - Y_L + \gamma X}{1 + \beta e^{-k \ln(X)}}, \quad X > 0, \quad (3.31)$$

where the parameter  $\gamma$  serves to measure the initial rate of increase at low dosages.

### 3.10 THE BRODY GROWTH MODEL

Brody (1945) partitions the sigmoidal process into two distinct phases:

Phase I. An expansionary phase that applies to a temporarily limited period of growth. For this phase  $Y_t$  is exponentially increasing or

$$Y_t = \alpha e^{kt}. \quad (3.32)$$

This phase I growth equation clearly has an infinite asymptote. Next follows:

Phase II. A declining phase in which  $Y_t$  is exponentially decreasing beyond the point where exponential growth ends. For this phase

$$Y_t = Y_\infty (1 - \beta e^{-kt}). \quad (3.33)$$

Since  $Y_t$  is either exponentially increasing via Equation 3.32 or exponentially decreasing (from Eq. 3.33), the Brody model lacks any point of inflection.

<sup>3</sup> Southman and Ehrlich (1943) (see also Schultz (1988) and Thimann (1956)) observed that subinhibitory levels of a toxin can produce stimulatory effects in organisms (e.g., increased growth in weeds can occur for subinhibitory doses of a herbicide). The presence of “hormesis” can raise the average response for low dosages above some control value.

### 3.11 THE JANOSCHEK GROWTH MODEL

A growth equation that is almost as flexible as the Richards growth function (Appendix 3.D) is the *Janoschek sigmoidal function* (Janoschek, 1957)

$$Y_t = Y_\infty \left(1 - \beta e^{-bt^c}\right), \quad c > 1, \quad (3.34)$$

where  $b$  is a growth parameter for a fixed  $c$  and  $c$  is a shape parameter. Given this expression,

$$\frac{dY_t}{dt} = -bct^{c-1} e^{-bt^c} \quad (3.35)$$

and thus, the instantaneous rate of growth at time  $t$  is

$$\frac{dY_t / dt}{Y_t} = bct^{c-1} \left( \frac{Y_\infty - 1}{Y_t} - 1 \right), \quad (3.36)$$

where  $[(Y_\infty - 1)/Y_t - 1]$  serves as a type of “feedback term.” Setting  $d^2Y_t/dt^2 = 0$  enables us to find the coordinates of the point of inflection

$$(t_{\text{inf}}, Y_{t_{\text{inf}}}) = \left( \left( \frac{c-1}{cb} \right)^{1/c}, Y_\infty - (1 - e^{-(c-1)/c}) \right), \quad c > 1.$$

A modification of Equation 3.34 (Sager, 1984), for an initial value  $Y_0$  greater than zero, can be written as

$$Y_t = Y_\infty - (Y_\infty - Y_0) e^{-kt^p}. \quad (3.37)$$

For  $p < 1$ , this function exhibits simple exponential growth; and for  $p > 1$ , sigmoidal growth occurs. Given Equation 3.37,

$$\frac{dY_t}{dt} = kp(Y_\infty - Y_0) t^{p-1} e^{-kt^p} \quad (3.38)$$

with the instantaneous growth rate at time  $t$  appearing as

$$\frac{dY_t / dt}{Y_t} = kpt^{p-1} \left( \frac{Y_\infty}{Y_t} - 1 \right). \quad (3.39)$$

Here too  $(Y_\infty/Y_t - 1)$  represents a “feedback term.” This modified Janoschek growth model has a point of inflection (which is optional) at

$$(t_{\text{inf}}, Y_{t_{\text{inf}}}) = \left( \left( \frac{p-1}{kp} \right)^{1/p}, Y_\infty - (Y_\infty - Y_0) e^{-\left( \frac{p-1}{p} \right)} \right), \quad p > 1.$$

### 3.12 THE LUNDQVIST-KORF GROWTH MODEL

Let us consider the *Lundqvist-Korf equation* (Korf, 1939; Lundqvist, 1957)

$$Y_t = Y_\infty e^{-kt^{-d}}, \quad (3.40)$$

where  $d$  denotes the shape parameter and  $k$  is a scale parameter. Then it is readily demonstrated that

$$\frac{dY_t}{dt} = kdt^{-d-1}Y_t \quad (3.41)$$

so that the instantaneous growth rate time  $t$  is

$$\frac{dY_t / dt}{Y_t} = kdt^{-d-1}. \quad (3.42)$$

And when  $d^2Y_t/dt^2=0$ , we can solve for the coordinates of the point of inflection as

$$(t_{\inf}, Y_{t_{\inf}}) = \left( \left( \frac{d+1}{kd} \right)^{-1/d}, Y_\infty e^{-(d+1)/d} \right).$$

Equation 3.40 is actually a generalization of the *Schumacher* (1939) *growth model*

$$Y_t = Y_\infty e^{bt^{-c}}. \quad (3.43)$$

### 3.13 THE HOSSFELD GROWTH MODEL

The *Hossfeld growth function* (Hossfeld, 1822) has the form

$$Y_t = Y_\infty \left( 1 + b_1 t^{-b_2} \right)^{-1}, \quad b_1 > 1, \quad (3.44)$$

where

$$\frac{dY_t}{dt} = b_1 b_2 Y_t t^{-b_2-1} \left( 1 + b_1 t^{-b_2} \right)^{-1}. \quad (3.45)$$

Given this latter expression, the instantaneous rate of growth at time  $t$  is

$$\frac{dY_t / dt}{Y_t} = b_1 b_2 \left( \frac{Y_t}{Y_\infty} \right) t^{-b_2-1}, \quad (3.46)$$

where  $b_2$  serves as a growth rate parameter for a fixed  $b_1$ .



Additionally, setting  $d^2Y_t/dt^2=0$  enables us to ultimately determine that Equation 3.44 has a point of inflection at

$$(t_{\text{inf}}, Y_{\text{inf}}) = \left\{ \left( \frac{1+b_2}{b_1(b_2-1)} \right)^{-1/b_2}, Y_{\infty} \left( \frac{b_2-1}{2b_2} \right) \right\}.$$

### 3.14 THE STANNARD GROWTH MODEL

The *Stannard growth function* (Stannard et al., 1985) has the form

$$Y_t = Y_{\infty} \left\{ 1 + e^{-[(\alpha+kt)/p]} \right\}^{-p}. \quad (3.47)$$

Given that

$$\frac{dY_t}{dt} = kY_t \left\{ 1 + e^{-[(\alpha+kt)/p]} \right\} e^{-[(\alpha+kt)/p]}, \quad (3.48)$$

we may easily express the instantaneous rate of growth at time  $t$  as

$$\frac{dY_t/dt}{Y_t} = k \left[ 1 - \left( \frac{Y_t}{Y_{\infty}} \right)^{\frac{1}{p}} \right], \quad (3.49)$$

where  $k$  serves as a rate of growth parameter given  $p$  and  $[1 - (Y_t/Y_{\infty})^{1/p}]$  constitutes a “feedback term.” And setting  $d^2Y_t/dt^2=0$  enables us to determine the coordinates of the point of inflection as

$$(t_{\text{inf}}, Y_{\text{inf}}) = \left\{ \frac{p \ln p - \alpha}{k}, Y_{\infty} \left( \frac{p}{p+1} \right)^p \right\}.$$

### 3.15 THE SCHNUTE GROWTH MODEL

The Schnute (1981) study models the accelerated growth of a (fish) population by considering the relative growth rate of the relative growth rate. To this end, Schnute starts from the postulates:

1. The relative growth rate of a population  $Y_t$  is

$$k = \frac{d \ln Y_t}{dt} = \frac{dY_t/dt}{Y_t}. \quad (3.50)$$

2. The relative growth rate varies linearly with  $k$  and appears as

$$\frac{d \ln k}{dt} = \frac{dk/dt}{k} = -(a + bk). \quad (3.51)$$

Here  $a$  is a fixed growth rate and  $b$  is a shape parameter, which determines the point at which the initial acceleration of growth transitions to a slower growth pace.

Two forms of *Schnute's growth equation* now follow.

First,

$$Y_t = Y_\infty \left(1 - \delta e^{-at}\right)^{1/b}, \quad (3.52)$$

with  $a$  representing a growth rate parameter and  $b$  serving as shape parameters. Then

$$\frac{dY_t}{dt} = \left(\frac{a\delta}{b}\right) Y_t e^{-at} \left(1 - \delta e^{-at}\right)^{-1} \quad (3.53)$$

and thus, the instantaneous rate of growth at time  $t$  is

$$\frac{dY_t/dt}{Y_t} = \left(\frac{a\delta}{b}\right) \left(e^{at} - \delta\right)^{-1}. \quad (3.54)$$

Also, setting  $d^2Y_t/dt^2=0$  enables us to solve for the coordinates of the point of inflection as

$$(t_{\text{inf}}, Y_{t_{\text{inf}}}) = \left(\frac{1}{a} \ln(\delta/b), Y_\infty (1-b)^{1/b}\right).$$

An alternative to Equation 3.52, which is useful for evolutionary computations, is obtained by coupling Equations 3.50 and 3.51 with the initial and terminal conditions

$$Y_1 = Y(t_1) \quad \text{and} \quad Y_2 = Y(t_2),$$

where  $t_1$  and  $t_2$  are the initial and final times and  $Y_1$  and  $Y_2$  are the initial and final population densities, respectively. Then it can be demonstrated that the system

$$\frac{dY_t}{dt} = kY_t, \quad \frac{dk}{dt} = -k(a + bk),$$

$$Y_1 = Y(t_1), \quad Y_2 = Y(t_2)$$

has solution

$$Y_t = \left[ Y_1^b + (Y_2^b - Y_1^b) \frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2-t_1)}} \right]^{1/b}. \quad (3.55)$$

As  $t \rightarrow +\infty$ , Equation 3.55 approaches an upper asymptote when  $a > 0$ . (For details on the derivation of Equations 3.52 and 3.55, see Appendix 3.E.)

For Equation 3.55, the instantaneous rate of growth at time  $t$  is

$$\frac{dY_t / dt}{Y_t} = \frac{a}{b} \left[ 1 - \left( \frac{Y_1}{Y_2} \right)^b \right] (e^{a(t-t_1)} - 1)^{-1}, \quad (3.56)$$

and upon setting  $d^2Y_t/dt^2=0$ , we can determine that a point of inflection occurs at

$$(t_{\text{inf}}, Y_{t_{\text{inf}}}) = \left\{ t_1 - \frac{1}{a} \ln \left[ b \left( \frac{Y_2^b - Y_1^b e^{-a(t_2-t_1)}}{Y_2^b - Y_1^b} \right) \right], (1-b)^{1/b} \left( \frac{Y_2^b - Y_1^b e^{-a(t_2-t_1)}}{1 - e^{-a(t_2-t_1)}} \right)^{1/b} \right\},$$

save for the combination  $a > 0, b > 1$ .

Equations 3.52 and 3.55 are quite general and have some other well-known growth models subsumed within their structure. For instance, the following special cases emerge for selected values of the parameters  $a$  and  $b$ :

von Bertalanffy ( $a > 0, b = 1$ )

Richards ( $a > 0, b < 0$ )

Logistic ( $a > 0, b = -1$ )

Gompertz ( $a > 0, b = 0$ )

Exponential ( $a < 0, b = 1$ )

Note that the first four of these subcases are sigmoidal since  $a > 0$ .

### 3.16 THE MORGAN-MERCER-FLODIN (M-M-F) GROWTH MODEL

Two early models pertaining to biological kinetics were developed by Michaelis and Menten (1913) and Hill (1910, 1913). The *Michaelis-Menten equation*, which relates reaction velocity ( $Y$ ) to substrate concentration ( $X$ ) in an enzyme-catalyzed chemical reaction, is of the form

$$Y = -\frac{dX}{dt} = \frac{Y_\infty X}{k + X}, k > 0. \quad (3.57)$$

Here Equation 3.57 describes a law that governs the rate at which the body processes a drug and structurally represents a *hyperbolic saturation curve* since

$$\frac{dY}{dX} = \frac{kY_\infty}{(k + X)^2} > 0$$

and

$$\frac{d^2Y}{dX^2} = \frac{-2kY_\infty}{(k+X)^3} < 0.$$

(A generalization of the Michaelis–Menten equation is offered in Appendix 3.H.)

The *Hill equation*, which was used to describe the kinetics of the binding of oxygen to hemoglobin in respiratory physiology, appears as

$$Y = \frac{Y_\infty X^n}{k + X^n}, k > 0, \quad (3.58)$$

and depicts a *sigmoidal saturation function*, where  $k$  is a constant with the property that  $Y = Y_\infty/2$  when  $X = k^{1/n}$  and  $n$  (the *Hill coefficient*) is the kinetic order of the saturation function that describes its shape.

While Equations 3.57 and 3.58 were not originally applied in a growth context, several studies (Mercer et al., 1978; Morgan et al., 1975) used these equations as the basis for deriving a general saturation equation useful for modeling biological efficiency or for describing the ability of a nutrient to produce a response in humans or animals. An important feature of Equations 3.57 and 3.58 is that they pass through the origin. However, since most estimated nutrient–response curves have not been found to display this characteristic (such curves tend to an upper asymptote at high nutrient intake levels as well as exhibit a curvature as the asymptote is approached, which reflects either hyperbolic or sigmoidal behavior), M–M–F adopted two criteria that are to be satisfied by a general saturation function for modeling nutrient responses: (i) the equation must be able to display both hyperbolic and sigmoidal behavior, and (ii) the equation must be free to intersect the ordinate axis at any point dictated by the data. (Clearly the sigmoidal Hill equation (3.58) satisfies the first requirement since, for  $n=1$ , it reduces to the Michaelis–Menten hyperbolic equation (3.57). However, the second criterion is not met.)

Morgan–Mercer–Flodin thus modify Equation 3.58 by a simple translation of the ordinate axis, to wit, their general saturation function (which now satisfies both of the aforementioned criteria) takes the form

$$Y = \frac{ab + Y_\infty X^n}{b + X^n}, \quad (3.59)$$

where  $a$  is the ordinate intercept when  $X=0$ ,  $n$  is a shape parameter (for  $n=1$ , Equation 3.59 is a rectangular hyperbola; when  $a=0$ , we get the Hill equation (3.58); and for  $a=0$  and  $n=1$ , the Michaelis–Menten equation (3.57) obtains), and  $b = (X_{0.50})^n$ , with  $X_{0.50}$  the value of  $X$  when  $Y$  is halfway to the maximum response, that is, a nutrient response level equal to  $(Y_\infty + a)/2$ .

For purposes of growth process modeling, a convenient alternative form of Equation 3.59 is

$$Y_t = Y_\infty - \frac{Y_\infty - \beta}{[1 + (kt)^\delta]},^4 \quad (3.60)$$

where  $\beta$  depicts size or yield at  $t=0$ ,  $k$  is the rate of growth, and  $\delta$  is a parameter that controls the point of inflection. Given Equation 3.60,

$$\frac{dY_t}{dt} = (Y_\infty - Y_t) \frac{\delta k^\delta t^{\delta-1}}{[1 + (kt)^\delta]} \quad (3.61)$$

with the instantaneous rate of growth at time  $t$  determined as

$$\frac{dY_t / dt}{Y_t} = \left( \frac{Y_\infty}{Y_t} - 1 \right) \frac{\delta k^\delta t^{\delta-1}}{[1 + (kt)^\delta]}, \quad (3.62)$$

where  $(Y_\infty/Y_t - 1)$  constitutes a “feedback term.” Setting  $d^2Y_t/dt^2=0$  enables us to solve for the point of inflection

$$(t_{\text{inf}}, Y_{t_{\text{inf}}}) = \left( k^{-1} \left( \frac{\delta + 1}{\delta - 1} \right)^{1/\delta}, \frac{(\delta - 1)Y_\infty + (\delta + 1)\beta}{2\delta} \right).$$

### 3.17 THE MCDILL–AMATEIS GROWTH MODEL

McDill and Amateis (1992) develop a growth model of (pine) forest site quality that utilizes, as a measure of site quality, the values of site-specific parameters of a stand-height-growth equation, where observed “highest growth” refers to the height growth of a particular stand component chosen to assess “site quality.” Ostensibly height growth is a good indicator of site quality, with site quality in turn reflecting the potential for a site to yield wood fiber/products.

The *McDill–Amateis height-growth function* contains two biologically meaningful parameters—a rate parameter and a maximum height parameter. Moreover, this expression also includes initial conditions (i.e., initial height at some predetermined initial age) that can either be treated as an additional (third) parameter to be estimated or specified from the data. The essential variables appearing in a height-growth equation are height ( $H$ ), age ( $A$ ), height growth ( $dH/dA$ ), and asymptotic

<sup>4</sup> Let us rewrite Equation 3.60 as

$$Y_t = \frac{Y_\infty [1 + (kt)^\delta] - (Y_\infty - \beta)}{[1 + (kt)^\delta]} = \frac{\beta k^{-\delta} + Y_\infty t^\delta}{k^{-\delta} + t^\delta} = \frac{\alpha \beta + Y_\infty t^\delta}{\alpha + t^\delta},$$

where  $\alpha = k^{-\delta}$ . Clearly this expression coincides with Equation 3.59.

maximum height ( $H_\infty$ ) that trees on a given site can attain. In this regard, the McDill–Amateis stand-height-growth function has the form

$$H = \frac{H_\infty}{1 - \left(1 - \frac{H_\infty}{H_0}\right) \left(\frac{A_0}{A}\right)^a}, \quad (3.63)$$

where  $H_0$  and  $A_0$  serve as initial conditions. (Details on the derivation of this expression appear in Appendix 3.F.) For tree growth estimation, we require that  $H_\infty > H_0 > 0$  and  $a > 0$ . Here height  $H \rightarrow 0$  as age  $A \rightarrow 0$ , while  $H \rightarrow H_\infty$  as  $A \rightarrow +\infty$ .

From Equation 3.63,

$$\frac{dH}{dA} = a \left(\frac{H}{A}\right) \left(1 - \frac{H}{H_\infty}\right), \quad (3.64)$$

while the instantaneous rate of growth at age  $A$  is

$$\frac{dH / dA}{H} = \frac{a}{A} \left(1 - \frac{H}{H_\infty}\right) \quad (3.65)$$

with  $1 - H/H_\infty$  serving as a “feedback term.” Next, setting  $d^2H/dA^2 = 0$  enables us to obtain the coordinates of the point of inflection

$$(A_{\text{inf}}, H_{A_{\text{inf}}}) = \left( A_0 \left(1 - \frac{H_\infty}{H_0}\right)^{1/a} \left(\frac{1-a}{a+1}\right)^{1/a}, \frac{H_\infty}{2} \left(1 - \frac{1}{a}\right) \right), \quad a > 1.$$

For  $a \leq 1$ , the growth equation is concave.

McDill and Amateis stipulate that their model works well for remeasurement data from permanent plots or for data that, in general, span a fairly long time period. As far as the initial conditions are concerned, the authors recommend using the data to set the initial conditions and treat measurement intervals as observations (i.e., each observation consists of an initial measurement ( $A_0, H_0$ ) and a terminal measurement ( $A, H$ )). Hence, all measurements, save for the first and last, belong to two observations—as the initial measurement in one observation and as the ending measurement in another.

### 3.18 AN ASSORTMENT OF ADDITIONAL GROWTH MODELS

The following three growth functions (all modifications of the Hossfeld equation 3.44) have been found to be quite accurate in practice:

1. *The Levakovic I growth model:* Levakovic’s *I* growth equation (1935) takes the form

$$Y_t = Y_\infty (1 + bt^{-d})^{-c}. \quad (3.66)$$

Then

$$\frac{dY_t}{dt} = cbdY_\infty (1 + bt^{-d})^{-c-1} t^{-d-1} \quad (3.67)$$

and thus, the instantaneous rate of change in  $Y_t$  at time  $t$  is

$$\frac{dY_t / dt}{Y_t} = cbd t^{-d-1} (Y_t / Y_\infty)^{1/c}. \quad (3.68)$$

Setting  $d^2 Y_t / dt^2 = 0$  enables us to solve for the point of inflection

$$(t_{\text{inf}}, Y_{t_{\text{inf}}}) = \left( \left( \frac{b(cd-1)}{d+1} \right)^{1/d}, Y_\infty \left( \frac{cd-1}{d(c+1)} \right)^c \right).$$

2. *The Levakovic III growth model:* The *Levakovic III growth equation* (1935) is a special case of Equation 3.66 and appears as

$$Y_t = Y_\infty (1 + bt^{-2})^{-c}. \quad (3.69)$$

Then expressions for  $dY_t/dt$ ,  $(dY_t/dt)/Y_t$ , and the point of inflection can be obtained by setting  $d=2$  in Equation 3.66, in Equation 3.67, and in  $(t_{\text{inf}}, Y_{t_{\text{inf}}})$ , respectively.

3. *The Yoshida I growth model:* *Yoshida's I growth equation* (1981) is structured as

$$Y_t = Y_\infty (1 + bt^{-c})^{-1} + c, \quad (3.70)$$

where  $c$  is a parameter indicating initial size. Here

$$\begin{aligned} \frac{dY_t}{dt} &= bdY_\infty (1 + bt^{-d})^{-2} t^{-d-1} \\ &= \frac{bd(Y_t - c)}{(1 + bt^{-d})} t^{-d-1}, \end{aligned} \quad (3.71)$$

with the instantaneous rate of growth at time  $t$  given by

$$\frac{dY_t / dt}{Y_t} = bd \left\{ 1 - \frac{c}{Y_t} \right\} (1 + bt^{-d}) t^{-d-1}. \quad (3.72)$$

Equation 3.70 has a point of inflection at

$$(t_{\text{inf}}, Y_{t_{\text{inf}}}) = \left( \left( \frac{b(d-1)}{d+1} \right)^{\frac{1}{d}}, Y_\infty \left( \frac{2d}{d-1} \right) + c \right).$$

### 3.18.1 The Sloboda Growth Model

A growth function similar to the Gompertz equation (3.10) is the *Sloboda growth function* (1971a, b)

$$Y_t = Y_\infty e^{-\alpha e^{-\beta t^\gamma}}, \quad t \geq 0 \quad (3.73)$$

(note that this expression differs from the Gompertz equation by the presence of the additional parameter  $\gamma$ ). Then

$$\frac{dY_t}{dt} = \alpha \beta \gamma Y_t^{\gamma-1} e^{-\beta t^\gamma} \quad (3.74)$$

and thus, the instantaneous rate of change in  $Y_t$  at time  $t$  is

$$\frac{dY_t / dt}{Y_t} = \alpha \beta \gamma t^{\gamma-1} e^{-\beta t^\gamma}. \quad (3.75)$$

## APPENDIX 3.A THE LOGISTIC MODEL DERIVED

For the simple exponential growth model, it is assumed that the instantaneous growth rate of a variable  $Y$  is a constant  $\beta$ ,

$$\frac{dY_t / dt}{Y_t} = \beta, \quad \text{or} \quad \frac{dY_t}{dt} = \beta Y_t; \quad (3.A.1)$$

that is, the rate of change in  $Y$  is proportional to the current size of  $Y$  at time  $t$ ,  $Y_t$ . Then

$$\int \frac{dY_t}{Y_t} = \int \beta dt$$

or

$$\ln Y_t = \beta t + \ln C \quad (\ln C \text{ a constant})$$

and thus

$$Y_t = C e^{\beta t}. \quad (3.A.2)$$

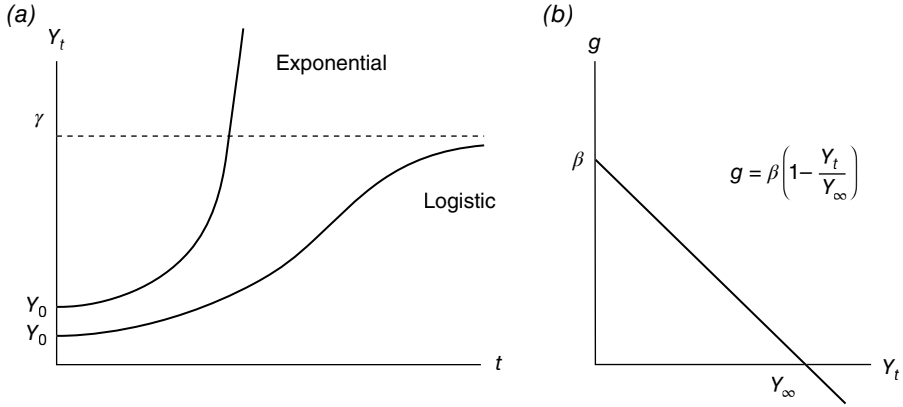
For  $t=0$ ,  $Y_0=C$  so that Equation 3.A.2 can be rewritten as

$$Y_t = Y_0 e^{\beta t}. \quad (3.A.3)$$

As Equation 3.A.3 reveals, there is no limit to growth; as  $t \rightarrow +\infty$ , it follows that  $Y_t \rightarrow +\infty$  (Fig. 3.A.1a).

The so-called logistic law of growth states that, essentially, the rate of growth in a system or population  $Y$  may be limited. More specifically,  $Y$  grows exponentially at,





**FIGURE 3.A.1** (a) Exponential versus logistic growth; (b) Feedback dependency.

say, rate  $g$  until an upper limit (the saturation parameter  $Y_\infty$ ) to the capacity of the system to grow is approached, at which point the growth rate slows, and the characteristic S-shaped or sigmoidal curve emerges. In this regard, let us assume that the growth rate  $g$  is dependent upon the *density of  $Y$  at time  $t$*  ( $Y_t/Y_\infty$ ) or

$$g = \beta \left\{ 1 - \frac{Y_t}{Y_\infty} \right\}, \quad (3.A.4)$$

where  $1 - (Y_t/Y_\infty)$  is called a *feedback term*, the role of which is to account for the growth rate declining to zero as  $Y_t \rightarrow Y_\infty$ . That is, at low densities ( $Y_t$  is much smaller than  $Y_\infty$ ),  $g$  is maximal and close to  $\beta$  (Fig. 3.A.1b), and thus, the behavior of the logistic curve resembles that of an exponential growth curve; but at high densities ( $Y_t$  is near  $Y_\infty$ ), the feedback term slows growth until saturation is attained (when  $Y_t = Y_\infty$ ), at which point the growth rate  $g = 0$ . (If  $Y_t > Y_\infty$ , then the growth rate in  $Y$  turns negative.)

This said, we can now derive the logistic function as follows. Let us start with an exponential growth equation:

$$\frac{dY_t}{dt} = gY_t.$$

Then from Equation 3.A.4, the dynamics of  $Y$  growth is now characterized by the *logistic differential equation*

$$\frac{dY_t}{dt} = \beta Y_t \left\{ 1 - \frac{Y_t}{Y_\infty} \right\}. \quad (3.A.5)$$

Let us set  $x = Y_t/Y_\infty$ . Then

$$\frac{dx}{dt} = \frac{1}{Y_\infty} \frac{dY_t}{dt}$$

and thus, Equation 3.A.5 can be rewritten as

$$\frac{dY_t / dt}{Y_\infty} = \beta \frac{Y_t}{Y_\infty} \left( 1 - \frac{Y_t}{Y_\infty} \right)$$

or

$$\frac{dx}{dt} = \beta x(1-x). \quad (3.A.6)$$

Then the sequence of steps for solving Equation 3.A.6 is

$$\begin{aligned} \int \frac{dx}{x(1-x)} &= \int \beta dt, \\ -\ln \frac{1-x}{x} &= \beta t + \ln C, \quad (\ln C \text{ a constant}) \\ \ln \frac{1-x}{x} &= -\beta t - \ln C, \\ \frac{1-x}{x} &= \alpha e^{-\beta t}, \quad (\alpha = C^{-1}). \end{aligned}$$

Then solving for  $x$  gives

$$x = \frac{1}{1 + \alpha e^{-\beta t}}.$$

And since  $x = Y_t/Y_\infty$ , we ultimately obtain

$$Y_t = \frac{Y_\infty}{1 + \alpha e^{-\beta t}}, \quad t \geq 0 \quad (3.A.7)$$

(or Eq. 3.6). For  $t=0$ ,  $Y_0 = Y_\infty/(1+\alpha)$  so that  $\alpha = (Y_\infty/Y_0) - 1$ . (Note that a discrete version of Equation 3.A.7 is

$$Y_t = \frac{Y_\infty}{1 + \alpha \beta^t}.) \quad (3.A.8)$$

Let us define the *growth time* (denoted  $\Delta t$ ) as the length of the time interval during which  $Y$  progresses from 10% to 90% of the capacity limit  $Y_\infty$ . To find  $\Delta t$ , let us first set

$$(Y_t =) 0.90 Y_\infty = \frac{Y_\infty}{1 + \alpha e^{-\beta t}}.$$

Then solving for  $t$  yields

$$(t =) t_{0.90} = \frac{2.19723}{\beta} + \frac{\ln \alpha}{\beta}.$$

Next, from

$$0.10Y_{\infty} = \frac{Y_{\infty}}{1 + \alpha e^{-\beta t}},$$

we find

$$t_{0.10} = -\frac{2.19722}{\beta} + \frac{\ln \alpha}{\beta}.$$

Hence,

$$\Delta t = t_{0.90} - t_{0.10} = \frac{4.39445}{\beta} + \frac{\ln(81)}{\beta}.$$

Additionally, the *midpoint* is the time  $t_m$  where  $Y_{t_m} = Y_{\infty}/2$ —it is the time of most rapid increase in  $Y$  and occurs at the point of inflection so that  $t_m = \ln \alpha / \beta$  (see Fig. 3.3).

The logistic model can be linearized by a change of variable. To this end, again set  $x = Y_t / Y_{\infty}$ . Then from Equation 3.A.7,

$$x = \frac{1}{1 + \alpha e^{-\beta t}}, \quad 1 - x = \frac{\alpha e^{-\beta t}}{1 + \alpha e^{-\beta t}},$$

and thus

$$\frac{x}{1 - x} = \alpha^{-1} e^{\beta t}.$$

Hence,

$$\begin{aligned} \ln \frac{x}{1 - x} &= \ln(\alpha^{-1}) + \beta t \\ &= a + \beta t. \end{aligned} \tag{3.A.9}$$

### APPENDIX 3.B THE GOMPERTZ MODEL DERIVED

Let us write what is called the *Gompertz differential equation* as

$$\frac{dY_t}{dt} = \beta Y_t \ln \left( \frac{Y_{\infty}}{Y_t} \right) \tag{3.B.1}$$

(see Equation 3.13 and its interpretation). Here the instantaneous rate of growth in  $Y$  is proportional to  $\ln Y_{\infty} - \ln Y_t$ . If we set  $x = Y_t / Y_{\infty}$ , then

$$\frac{dx}{dt} = \frac{1}{Y_{\infty}} \frac{dY_t}{dt}$$

and thus, Equation 3.B.1 can be rewritten as

$$\frac{dY_t/dt}{Y_\infty} = \beta \frac{Y_t}{Y_\infty} \ln \left( \frac{Y_\infty}{Y_t} \right)$$

or

$$\frac{dx}{dt} = \beta x \ln \left( \frac{1}{x} \right). \quad (3.B.2)$$

Then the solution of Equation (3.B.2) proceeds as follows:

$$\begin{aligned} \int \frac{dx}{x \ln(1/x)} &= \int \beta dt, \\ -\ln \left( \ln \frac{1}{x} \right) &= \beta t + \ln C, \quad (\ln C \text{ a constant}) \\ \ln \left( \ln \frac{1}{x} \right) &= -\beta t - \ln C, \\ \ln \left( \frac{1}{x} \right) &= \alpha e^{-\beta t}, \quad (\alpha = C^{-1}) \\ \ln x &= -\alpha e^{-\beta t}. \end{aligned}$$

Solving for  $x$  gives

$$x = e^{-\alpha e^{-\beta t}}.$$

But since  $x = Y/Y_\infty$ , we ultimately obtain

$$Y_t = Y_\infty e^{-\alpha e^{-\beta t}}, \quad t \geq 0 \quad (3.B.3)$$

(or Eq. 3.10). For  $t=0$ ,  $Y_0 = Y_\infty e^{-\alpha}$  so that  $\alpha = \ln(Y_\infty/Y_0)$ . (The discrete version of Eq. 3.B.3 is

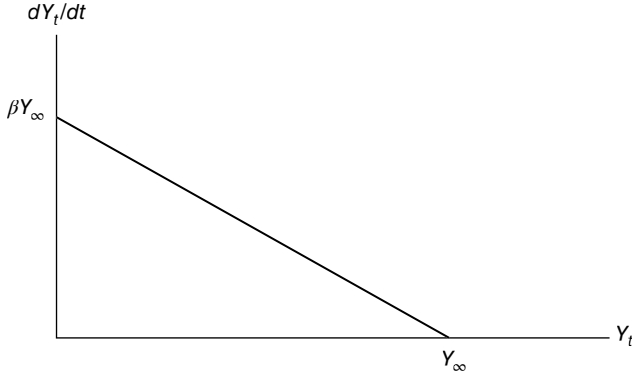
$$Y_t = Y_\infty \alpha^{\beta^t}). \quad (3.B.4)$$

### APPENDIX 3.C THE NEGATIVE EXPONENTIAL MODEL DERIVED

Suppose we posit that  $dY_t/dt$  is a linear function of  $Y_t$  or

$$\frac{dY_t}{dt} = \beta(Y_\infty - Y_t), \quad (3.C.1)$$

where  $\beta$  is constant and  $Y_\infty$  is the value of  $Y_t$  for which  $dY_t/dt=0$ , that is, as  $t \rightarrow \infty$ ,  $Y_t \rightarrow Y_\infty$ , and  $dY_t/dt \rightarrow 0$ . So if, for instance, we plot  $dY_t/dt$  against  $Y_t$ , then, as Equation 3.C.1



**FIGURE 3.C.1**  $dY_t/dt$  is a linear function of  $Y_t$ .

reveals, we have a linear function with slope  $-\beta$ , which cuts the  $Y_t$ -axis at a point  $Y_\infty$  beyond which  $Y$  will not grow. Hence,  $Y_\infty$  is the asymptote of  $Y_t$  as  $t \rightarrow \infty$  (Fig. 3.C.1).

Let us rewrite Equation 3.C.1 as

$$\frac{dY_t}{Y_\infty - Y_t} = \beta dt$$

so that

$$\int \frac{dY_t}{Y_\infty - Y_t} = \int \beta dt,$$

$$-\ln(Y_\infty - Y_t) = \beta t + \ln C, \text{ (} \ln C \text{ a constant)}$$

$$\ln(Y_\infty - Y_t) = -\beta t - \ln C,$$

$$Y_\infty - Y_t = \alpha e^{-\beta t}, (\alpha = C^{-1})$$

and thus

$$Y_t = Y_\infty - \alpha e^{-\beta t}. \quad (3.C.2)$$

For  $t=0$ ,  $Y_0 = Y_\infty - \alpha = 0$  or  $\alpha = Y_\infty$ . Hence, Equation 3.C.2 becomes

$$Y_t = Y_\infty (1 - e^{-\beta t}). \quad (3.C.3)$$

Note that if we set  $Y_0 = Y_\infty - \alpha$ , then  $\alpha = Y_\infty - Y_0$ . Substituting this value for  $\alpha$  into Equation 3.C.2 gives

$$Y_t = Y_\infty - (Y_t - Y_0)e^{-\beta t} = Y_\infty \left[ 1 - \left( 1 - \frac{Y_0}{Y_\infty} \right) e^{-\beta t} \right] = Y_\infty (1 - \theta e^{-\beta t}), \quad t \geq 0, \quad (3.C.4)$$

the *monomolecular growth function*. For this growth equation,

$$\frac{dY_t}{dt} = Y_\infty \beta \theta e^{-\beta t} = \frac{Y_\infty \beta \theta}{e^{\beta t}}.$$

Since  $\lim_{t \rightarrow \infty} dY_t / dt = 0$ , the monomolecular function is continually decreasing; it has no point of inflection since  $d^2 Y_t / dt^2 = -Y_\infty \theta \beta^2 e^{-\beta t} < 0$  for all  $t$ . Additionally, the instantaneous growth rate is

$$\frac{dY_t / dt}{Y_t} = \frac{\beta \theta}{e^{\beta t} - \theta}$$

with

$$\lim_{t \rightarrow \infty} \frac{dY_t / dt}{Y_t} = 0.$$

### APPENDIX 3.D THE VON BERTALANFFY AND RICHARDS MODELS DERIVED

Given the von Bertalanffy growth law

$$\frac{dY_t}{dt} + \lambda Y_t = \eta Y_t^k \quad (3.D.1)$$

(see Eq. 3.23),<sup>5</sup> set  $x = Y_t^{1-k}$  so that

$$\frac{dx}{dt} = (1-k) Y_t^{-k} \frac{dY_t}{dt}$$

or

$$\frac{1}{1-k} Y_t^k \frac{dx}{dt} = \frac{dY_t}{dt}. \quad (3.D.2)$$

A substitution of Equation 3.D.1 into Equation 3.D.2 gives

$$\begin{aligned} \frac{1}{1-k} \frac{dx}{dt} &= \eta - \lambda x, \\ \int \frac{dx}{\eta - \lambda x} &= \int (1-k) dt, \end{aligned}$$

<sup>5</sup> Equation 3.D.1 is a special case of the (Jakob) *Bernoulli differential equation*  $y' + p(t)y = q(t)y^n$ ,  $n$  a constant (not necessarily an integer), with  $p$  and  $q$  given functions of  $t$ . If  $n \neq 0$  or  $1$ , the substitution  $x = y^{1-n}$  (due to Leibnitz in 1696) linearizes the Bernoulli equation.

$$-\lambda^{-1} \ln(\eta - \lambda x) = (1 - k)t + \ln C, \text{ (}\ln C \text{ a constant)}$$

$$\ln(\eta - \lambda x) = -\lambda(1 - k)t - \lambda \ln C,$$

$$\eta - \lambda x = \alpha e^{-\lambda(1-k)t}, (\alpha = C^{-\lambda})$$

$$x = \frac{\eta}{\lambda} - \frac{\alpha}{\lambda} e^{-\lambda(1-k)t}. \quad (3.D.3)$$

Then substituting  $Y_t^{1-k}$  for  $x$  in Equation 3.D.3 enables us to write

$$Y_t = \left[ \frac{\eta}{\lambda} - \frac{\alpha}{\lambda} e^{-\lambda(1-k)t} \right]^{1/(1-k)}. \quad (3.D.4)$$

For  $t=0$ ,

$$Y_0 = \left[ \frac{\eta}{\lambda} - \frac{\alpha}{\lambda} \right]^{1/(1-k)}$$

so that

$$\frac{\alpha}{\lambda} = \frac{\eta}{\lambda} - Y_0^{1-k}.$$

Hence, Equation 3.D.4 becomes

$$Y_t = \left[ \frac{\eta}{\lambda} - \left( \frac{\eta}{\lambda} - Y_0^{1-k} \right) e^{-\lambda(1-k)t} \right]^{1/(1-k)}. \quad (3.D.5)$$

And since

$$\lim_{t \rightarrow \infty} Y_t = Y_\infty = \left( \frac{\eta}{\lambda} \right)^{1/(1-k)},$$

Equation 3.D.5 can be rewritten as

$$\begin{aligned} Y_t &= \left[ Y_\infty^{1-k} - (Y_\infty^{1-k} - Y_0^{1-k}) e^{-\lambda(1-k)t} \right]^{1/(1-k)} \\ &= Y_\infty \left[ 1 - \beta e^{-\lambda(1-k)t} \right]^{\frac{1}{1-k}}, \end{aligned} \quad (3.D.6)$$

the *von Bertalanffy growth equation*.

A modification of this function has been offered by Chapman (1961) and Richards (1959) (C-R). Specifically, C-R rewrite Equation 3.D.6 as

$$Y_t = Y_\infty \left[ 1 - a e^{-\lambda t} \right]^m, \quad t \geq 0, \quad (3.D.7)$$

the so-called four-parameter C–R function. Here:

$Y_\infty$  is an upper asymptote (the saturation level when  $t \rightarrow \infty$ ).

$a$  is essentially a position parameter (it locates the curve on the  $t$ -axis).

$\lambda$  regulates the growth rate for a fixed value of  $m$ . It serves as a *maturity index*—a smaller (larger)  $\lambda$  indicates late (early) maturing.

$m$  relates to curve shape—it allows a variable or optional point of inflection that is not a “fixed” proportion of  $Y_\infty$ . For  $m > 0$ , the growth curve is S-shaped and

the point of inflection is located at  $\left(t_{\text{inf}}, Y_{t_{\text{inf}}}\right) = \left(\lambda^{-1} \ln(am), Y_\infty \left(\frac{m-1}{m}\right)^m\right)$ .

If  $m > 1$ , the initial growth phase is exponential.

In addition, from (3.D.7), it can be shown that

$$\frac{dY_t}{dt} = m\lambda Y_t \left[ \left( \frac{Y_\infty}{Y_t} \right)^{1/m} - 1 \right]; \quad (3.D.8a)$$

$$\frac{dY_t / dt}{Y_t} = m\lambda \left[ \left( \frac{Y_\infty}{Y_t} \right)^{1/m} - 1 \right]. \quad (3.D.8b)$$

As Equation 3.D.8b reveals, the instantaneous rate of growth in  $Y_t$  at time  $t$  is proportional to the “feedback term”  $(Y_\infty/Y_t)^{1/m} - 1$ .

It is interesting to note that the C–R growth function is actually a generalization of some well-known growth curves, for example, for  $m = -1$ , we get the logistic function; for  $m$  near  $\pm \infty$ , the Gompertz function emerges; for  $m = 3$ , the von Bertalanffy equation results (see von Bertalanffy (1957)); and for  $m = 1$ , the (second) Brody function obtains.

It is important to mention that the original Richards (1959) growth equation represents a generalization of the logistic growth function (Eq. 3.A.7). That is, Richards generalized the logistic growth law (Eq. 3.A.5) by considering the modified growth equation (law)

$$\frac{dY_t}{dt} = \beta Y_t \left[ 1 - \left( \frac{Y_t}{Y_\infty} \right)^r \right] \quad (3.D.9)$$

(the growth rate is proportional to  $Y_t$  times a “feedback term”) or

$$\frac{dY_t}{dt} = \beta Y_t + \eta Y_t^{r+1}. \quad (3.D.10)$$

Since Equation 3.D.10 is a Bernoulli differential equation (see footnote 5), it integrates to the *Richards growth function* (or *generalized logistic equation*)

$$Y_t = \frac{Y_\infty}{(1 + \alpha e^{-\beta r t})^{1/r}}, \quad t \geq 0, \quad (3.D.11)$$

where  $\alpha = (Y_\infty/Y_0)^r - 1$  and both  $\beta, r > 0$ .



Note that relative to the logistic equation 3.A.7, Equation 3.D.11 has an additional *shape parameter*  $r$ , which allows the shape of the sigmoid to be varied. In fact, varying  $r$  allows the point of inflection of the curve to be located at any value between the lower and upper asymptotes. Here too other growth curves are subsumed under Equation 3.D.11 for specific values of  $r$ , for example, when  $r = 1$ , we get the standard logistic model; as  $r \rightarrow 0$ , the Richards curve tends towards the Gompertz curve; for  $r = -1$ , the monomolecular (or second Brody) case emerges; and for  $r = -1/3$ , the von Bertalanffy function obtains.

The preceding derivation of the von Bertalanffy growth equation was carried out in a purely mechanistic fashion. As an alternative to this approach, it is instructive to offer a derivation of this growth model based on physiological concepts (Beverton and Holt, 1957; von Bertalanffy, 1957). To this end, von Bertalanffy considers an individual organism as analogous to a reacting chemical system that obeys the *law of mass action*<sup>6</sup> and, consequently, classifies the physiological processes responsible for the mass of an organism at time  $t$  into those of anabolism (or synthesis) and catabolism (breakdown); that is, the rate of change in the body weight ( $w$ ) of an organism can be written as

$$\frac{dw}{dt} = hw^n - kw^m, \quad (3.D.12)$$

where  $h$  and  $k$  are the coefficients of anabolism and catabolism, respectively, and the exponents  $n$  and  $m$  have a physiological basis. In this regard, how should these parameters be chosen? Suppose the rate of anabolism is taken as proportional to the resorption rate (the rate at which a “structure” is remodeled) of nutrients or to the magnitude of the resorbing surfaces, and suppose the rate of catabolism is specified as proportional to the total mass being broken down, with a constant percentage of body material being transformed to waste matter per unit time.

Given these considerations, Equation 3.D.12 can be rewritten as

$$\frac{dw}{dt} = hs - kw, \quad (3.D.13)$$

where:

$h$  = rate of synthesis of mass per unit of resorbing surface

$s$  = effective resorbing surface of the organism

$k$  = rate of breakdown of mass per unit mass

If the organism is assumed to be growing isometrically and has a constant specific gravity, then we can express  $s$  and  $w$  in terms of the linear dimension  $l$  of the organism as  $s = pl^2$  and  $w = ql^3$  ( $p$  and  $q$  are constants). Hence, it follows that

$$\frac{dw}{dt} = \frac{d}{dt}(ql^3) = 3ql^2 \frac{dl}{dt}$$

<sup>6</sup> This law (an assertion about “kinetics”) states that the rate of a given chemical reaction is proportional to the product of the activities (or molecular concentration) of the reactants (Guldberg and Waage, 1879).

and thus, from Equation 3.D.12,

$$\frac{dl}{dt} = \frac{hpl^2}{3ql^2} - \frac{kql^3}{3ql^2} = \frac{hp}{3q} - \frac{kl}{3}. \quad (3.D.14)$$

Setting  $hp/3q = E$  and  $k/3 = K$ , Equation 3.D.14 becomes

$$\frac{dl}{dt} = E - Kl$$

or

$$\frac{dl}{E - Kl} = dt$$

with solution

$$l_t = \frac{E}{K} - \left( \frac{E}{K} l_0 \right) e^{-Kt}, \quad (3.D.15)$$

where  $l_0$  is the length of the organism at time  $t=0$ . Note that as  $t \rightarrow +\infty$ ,  $l_t \rightarrow E/K = L_\infty$ —the maximum possible length of the organism (under normal conditions). So as the organism ages, its length increases asymptotically to  $L_\infty$ . Under this discussion, Equation 3.D.15 becomes

$$l_t = L_\infty - (L_\infty - L_0) e^{-Kt}. \quad (3.D.16)$$

Given Equation 3.D.16, the associated equation for weight ( $w$ ) becomes, from  $w = ql^3$ ,

$$w_t = \left\{ W_\infty^{1/3} - \left( W_\infty^{1/3} - W_0^{1/3} \right) e^{-Kt} \right\}^3, \quad (3.D.17)$$

where  $W_\infty$  and  $W_0$  are the weights corresponding to  $L_\infty$  and  $L_0$ , respectively. If we now set  $W_t = 0$  and let  $t = t_0$  in Equation (3.D.17), it follows that

$$W_0 = W_\infty (1 - e^{Kt_0})^3.$$

Then a substitution of this expression into Equation 3.110 renders

$$w_t = W_\infty \left( 1 - e^{-K(t-t_0)} \right)^3.$$

### APPENDIX 3.E THE SCHNUTE MODEL DERIVED

Given Equations 3.50 and 3.51 or

$$k = \frac{1}{Y_t} \frac{dY_t}{dt} \quad \text{and} \quad \frac{1}{k} \frac{dk}{dt} = -(a + bk),$$

respectively, let us differentiate  $dY_t/dt = kY_t$  with respect to  $t$  so as to obtain

$$\begin{aligned}
 \frac{d^2 Y_t}{dt^2} &= Y_t \frac{dk}{dt} + k \frac{dY_t}{dt} \\
 &= Y_t [-k(a + bk)] + \frac{1}{Y_t} \left( \frac{dY_t}{dt} \right)^2 \\
 &= Y_t \left[ -\frac{1}{Y_t} \frac{dY_t}{dt} \left( a + b \frac{1}{Y_t} \frac{dY_t}{dt} \right) \right] + \frac{1}{Y_t} \left( \frac{dY_t}{dt} \right)^2 \\
 &= -\frac{dY_t}{dt} \left( a + b \frac{1}{Y_t} \frac{dY_t}{dt} \right) + \frac{1}{Y_t} \left( \frac{dY_t}{dt} \right)^2 \\
 &= \left[ -a + (1 - b) \frac{1}{Y_t} \frac{dY_t}{dt} \right] \frac{dY_t}{dt}. \tag{3.E.1}
 \end{aligned}$$

Let us rewrite Equation 3.E.1 as

$$\frac{1}{dY_t / dt} \frac{d^2 Y_t}{dt^2} = \left[ -a + (1 - b) \frac{1}{Y_t} \frac{dY_t}{dt} \right]. \tag{3.E.2}$$

Then integrating this expression yields

$$\begin{aligned}
 \ln \left( \frac{dY_t}{dt} \right) &= -at + (1 - b) \ln Y_t + \ln C_0, \quad (\ln C_0 \text{ a constant}) \\
 \frac{dY_t}{dt} &= C_0 e^{-at} Y_t^{1-b}, \\
 Y_t^{b-1} dY_t &= C_0 e^{-at} dt, \\
 \frac{1}{b} Y_t^b &= C_0 \left( -\frac{1}{a} e^{-at} \right) + C_1 \quad (C_1 \text{ a constant})
 \end{aligned}$$

or

$$\begin{aligned}
 Y_t^b &= -\frac{a}{b} C_0 e^{-at} + bC_1 \\
 &= bC_1 \left( 1 - \frac{C_0}{aC_1} e^{-at} \right). \tag{3.E.3}
 \end{aligned}$$

Then

$$Y_t = (bC_1)^{\frac{1}{b}} \left( 1 - \frac{C_0}{aC_1} e^{-at} \right)^{1/b}. \tag{3.E.4}$$

Since

$$\lim_{t \rightarrow \infty} Y_t = (bC_1)^{1/b} = Y_\infty,$$

Equation 3.E.4 can be rewritten as

$$Y_t = Y_\infty (1 - \delta e^{-at})^{1/b}, \quad (3.E.5)$$

where  $\delta = C_0/aC_1$ .

To derive Schnute (Eq. 3.55), let us employ Equation 3.E.3 to obtain

$$Y_1^b = bC_1 - \frac{b}{a}C_0e^{-at_1},$$

$$Y_2^b = bC_1 - \frac{b}{a}C_0e^{-at_2}$$

so that

$$Y_2^b - Y_1^b = -\frac{b}{a}C_0(e^{-at_2} - e^{-at_1}).$$

Then

$$(Y_2^b - Y_1^b)e^{at_1} = \frac{b}{a}C_0(1 - e^{-a(t_2 - t_1)})$$

and, via Equation 3.E.3,

$$(Y_t^b - Y_1^b)e^{at_1} = \frac{b}{a}C_0(1 - e^{-a(t - t_1)}).$$

Eliminating  $\frac{b}{a}C_0$  from the latter two equations enables us to obtain

$$Y_t^b - Y_1^b + (Y_2^b - Y_1^b) \frac{1 - e^{-a(t - t_1)}}{1 - e^{-a(t_2 - t_1)}}$$

or

$$Y_t = \left[ Y_1^b + (Y_2^b - Y_1^b) \frac{1 - e^{-a(t - t_1)}}{1 - e^{-a(t_2 - t_1)}} \right]^{1/b}. \quad (3.E.6)$$

### APPENDIX 3.F THE MCDILL-AMATEIS MODEL DERIVED

McDill and Amateis derive their growth equation using *dimension analysis*, which ensures that the dimensions associated with the arguments on each side of a dimensionally compatible equation cancel. The process first identifies the relevant variables

**TABLE 3.F.1 Variables and Dimensions**

| Variable  | $H$ | $A$ | $dH/dA$ | $H_\infty$ |
|-----------|-----|-----|---------|------------|
| Dimension | $l$ | $t$ | $l/t$   | $l$        |

to be included in the model. Next, these variables are grouped into dimensionless products  $\Pi_1, \Pi_2, \dots, \Pi_k$ , and the implicit function  $f(\Pi_1, \Pi_2, \dots, \Pi_k) = 0$  depicts all the dimensionally compatible equations involving the set of relevant variables.

The set of relevant variables and their associated dimensions appear in Table 3.F.1, where  $l$ =length and  $t$ =time. Then step two earlier has us form two dimensionless products:

$$\Pi_1 = \frac{dH}{dA} \frac{A}{H}, \Pi_2 = \frac{H}{H_\infty};$$

and the general function of these two dimensionless products is

$$f(\Pi_1, \Pi_2) = f\left(\frac{dH}{dA} \frac{A}{H}, \frac{H}{H_\infty}\right) = 0.$$

By virtue of the conditions underlying the implicit function theorem, there exists a function  $\phi$  such that

$$\frac{dH}{dA} \frac{A}{H} = \phi\left(\frac{H}{H_\infty}\right). \quad (3.F.1)$$

How should  $\phi$  be specified? The inclusion of the variable  $H_\infty$  in the growth equation mandates that the projected height growth of trees approaches zero as tree height  $H$  reaches  $H_\infty$ . The simplest functional form of  $\phi$  that exhibits this property is

$$\phi\left(\frac{H}{H_\infty}\right) = \left(1 - \frac{H}{H_\infty}\right); \quad (3.F.2)$$

that is,  $\phi \rightarrow 0$  as  $H/H_\infty \rightarrow 1$ . Substituting Equation 3.F.2 into Equation 3.F.1 enables us to obtain

$$\frac{dH}{dA} = a \left(\frac{H}{A}\right) \left(1 - \frac{H}{H_\infty}\right). \quad (3.F.3)$$

Clearly height growth goes to zero as  $H \rightarrow H_\infty$ .

Let us rewrite Equation 3.F.3 as

$$\frac{dH}{H(H_\infty - H)} = \left(\frac{a}{H_\infty}\right) \frac{dA}{A}.$$

Then

$$\begin{aligned}
 -\frac{1}{H_\infty} \ln \left( \frac{H_\infty - H}{H} \right) &= \left( \frac{a}{H_\infty} \right) \ln A + \ln C, \text{ (} \ln C \text{ a constant)} \\
 \left( \frac{H_\infty - H}{H} \right) &= C^{-H_\infty} A^{-a}, \\
 H &= \frac{H_\infty}{1 + C^{-H_\infty} A^{-a}}.
 \end{aligned} \tag{3.F.4}$$

Evaluating Equation 3.F.4 at  $(A_0, H_0)$  yields

$$H_0 = \frac{H_\infty}{1 + C^{-H_\infty} A_0^{-a}},$$

from which we may obtain

$$C^{-H_\infty} = \left( \frac{H_\infty}{H} - 1 \right) A_0^a.$$

Then a substitution of this expression into Equation 3.F.4 gives the final form of the McDill–Amateis height-growth equation or

$$H = \frac{H_\infty}{1 - \left( 1 - \frac{H_\infty}{H_0} \right) \left( \frac{A_0}{A} \right)^a}.$$

### APPENDIX 3.G THE SLOBODA MODEL DERIVED

Starting from the differential equation

$$\frac{dY_t}{dt} = \ln \left( \frac{Y_\infty}{Y_t} \right) b_1 Y_t t^{-b_2}, \tag{3.G.1}$$

let us rewrite Equation 3.G.1 as

$$\frac{dY_t}{\ln(Y_t/Y_\infty) Y_t} = -b_1 t^{-b_2} dt. \tag{3.G.2}$$

Then

$$\ln \left( \ln \left( \frac{Y_t}{Y_\infty} \right) \right) = \frac{-b_1}{-b_2 + 1} t^{-b_2 + 1} + \ln C, \text{ (} \ln C \text{ a constant)}$$

and thus,

$$\ln\left(\frac{Y_t}{Y_\infty}\right) = Ce^{(b_1/(b_2-1))t^{-b_2+1}},$$

$$\frac{Y_t}{Y_\infty} = e^{Ce^{(b_1/(b_2-1))t^{-b_2+1}}},$$

or

$$Y_t = Y_\infty e^{Ce^{(b_1/(b_2-1))t^{-b_2+1}}}$$

$$= Y_\infty e^{-\alpha e^{-\beta t^\gamma}}, \quad (3.G.3)$$

where  $-\alpha = C$ ,  $-\beta = b_1/(b_2 - 1)$ , and  $\gamma = -b_2 + 1$ .

### APPENDIX 3.H A GENERALIZED MICHAELIS-MENTEN GROWTH EQUATION

In this section we consider a generalized Michaelis-Menten-type equation that exhibits a flexible functional form for describing (animal) growth and can produce sigmoidal and diminishing returns behavior in that it has a variable inflection point (Lopez et al., 2000). Assuming a closed system (no inputs or outputs), the increase in biomass ( $Y$ , kg) per unit of time (say, in weeks) is proportional to the substrate level  $S$  (kg) with proportionality factor  $\mu$  (week<sup>-1</sup>) or

$$\frac{dY}{dt} = \mu S. \quad (3.H.1)$$

Suppose  $\mu$  changes with time according to

$$\mu = \frac{ct^{c-1}}{k^c + t^c}, \quad (3.H.2)$$

with  $c$  (dimensionless) and  $k$  (wk) being positive constants. (The conditions  $c > 0$  and  $k > 0$  ensure that  $\mu > 0$ , with  $k$  serving as the time when half-maximal growth is attained.) In Equation 3.H.2,  $\mu$  can decrease continually for  $c \leq 1$ ; it can increase to reach a maximum and then decrease again when  $c > 1$ .

A substitution of Equation 3.H.2 into Equation 3.H.1 gives

$$\frac{dY}{dt} = \mu S = \left( \frac{ct^{c-1}}{k^c + t^c} \right) (Y_\infty - Y),$$

where  $S = Y_\infty - Y$ . Then from this expression,

$$\int_{Y_0}^Y \frac{dY}{Y_\infty - Y} = \int_0^t \left( \frac{ct^{c-1}}{k^c + t^c} \right) dt$$

and, upon integrating,

$$\begin{aligned}
 -\ln(Y_\infty - Y) \Big|_{Y_o}^Y &= \ln(k^c + t^c) \Big|_o^t, \\
 -\ln(Y_\infty - Y) + \ln(Y_\infty - Y_o) &= \ln(k^c + t^c) - \ln k^c, \\
 \frac{Y_\infty - Y_o}{Y_\infty - Y} &= \frac{k^c + t^c}{k^c}, \\
 Y &= \frac{Y_o k^c + Y_\infty t^c}{k^c + t^c},
 \end{aligned} \tag{3.H.3}$$

the *generalized Michaelis–Menten growth function*.

This function has a point of inflection  $(t^*, Y^*)$ , which occurs where  $d^2Y/dt^2=0$  (provided  $d^3Y/dt^3 \neq 0$ ), with

$$t^* = k \left( \frac{c-1}{c+1} \right)^{1/c}, \quad c > 1, \tag{3.H.4}$$

and

$$Y^* = \left[ \left( 1 + \frac{1}{c} \right) \right] Y_o + \left( 1 - \frac{1}{c} \right) Y_\infty / 2. \tag{3.H.5}$$

Additionally:

1. When  $c=1$ , we have  $\mu = 1/(t + k)$ , where  $k$  is the inverse of  $\mu_{\max}$ . Then

$$Y = \frac{Y_o k + Y_\infty t}{k + t}. \tag{3.H.6}$$

Here Equation 3.H.6 is a rectangular hyperbola. And if  $Y_o=0$  in Equation 3.H.6, we obtain an expression of the form Equation 3.57, the Michaelis–Menten equation, with time replacing substrate concentration. The growth rate decreases continually and there is no point of inflection.

2. If  $\mu = \text{constant}$ , then Equation (3.H.1) (with  $S = Y_\infty - Y$ ) integrates to

$$Y = Y_\infty - (Y_\infty - Y_o) e^{-\mu t},$$

the *monomolecular growth function* (which decreases continually and has no point of inflection).