

Summary

- Empirical *versus* biologically based growth functions
- Theoretical growth functions:
 - Lundqvist-Korf type
 - ✓ Richards type
 - ✓ Hossfeld IV type
 - Other growth functions
- (Zeide decomposition of growth functions)
- Formulating growth functions without age explicit
- Simultaneous modeling of several individuals (Families of growth functions)
 - Growth functions formulated as difference equations ADA, (GADA and mixed models)

 The selection of functions - growth functions - appropriate to model tree and stand growth is an essencial stage in the development of growth models

✓ Differencial form

$$\frac{dy}{dt} = f(t)$$

✓ Integral form

$$y = \int f(t) dt$$

- Growth functions must have a shape that is in accordance with the principles of biological growth:
 - ✓ The curve is limited by yield 0 at the start (t=0 ou $t=t_0$) and by a maximum yield at an advanced age (<u>existence of assymptote</u>)
 - ✓ the <u>relative growth rate</u> (variation of the x variable per unit of time and unit of x) presents a maximum at a very early stage, <u>decreasing afterwards</u>; in most cases, the maximum occurs very early so that we can use decreasing functions to model relative growth rate
 - ✓ The slope of the curve increases in the initial stage and decreases after a certain point in time (existence of an <u>inflexion point</u>)

Two types of functions have been used to model growth:

Empirical growth functions

 Relationship between the dependent variable - the one we want to model - and the regressors according to some mathematical function - e.g. linear, parabolic, without trying to identify the causes or explaining the phenomenon

Analitical or functional growth functions

- Conceived in terms of the mechanism of the system, usually having an underlying hypothesis associated with the cause or function of the phenomenon described by the response variable
- The distinction between the two is not sharp and most modeling applications contain both empiricism and mechanism in varying mixtures

Theoretical growth functions

- Theoretical growth functions have commonly been developed in their growth form - either absolute or relative growth - and the respective yield form has been obtained by integration
- Generally this approach allows interpretation of the function parameters and helps to impose restrictions on the values that the parameters can take to be biologically consistent
- Theoretical growth functions are grouped according to their functional form in:
 - ✓ Lundqvist-Korf type
 - ✓ Richards type
 - ✓ Hossfeld IV type
 - ✓ Other growth functions

Theoretical growth functions

Lundqvist-Korf type

Differential form:

✓ The model proposed by Schumacher is based on the hypothesis that the relative growth rate has a linear relationship with the inverse of time² (which means that it decreases nonlinearly with time):

$$\frac{1}{Y}\frac{dY}{dt} = k\frac{1}{t^2} \qquad \Leftrightarrow \qquad$$

where:

- Y is the quantity of interest,
- t is time,
- k is a constant.

Rearranging the equation to separate variables:

$$\frac{dY}{Y} = k \cdot \frac{1}{t^2} \, dt$$

Integrating both sides:

$$\int \frac{dY}{Y} = k \int \frac{1}{t^2} \, dt$$

The left side gives:

$$\ln |Y| = k \int t^{-2} \, dt$$

For the right side, the integral of t^{-2} is:

$$\int t^{-2}\,dt = -rac{1}{t}+C$$

where C is the integration constant. Therefore, the equation becomes:

$$\ln |Y| = \frac{k}{1 + C}$$

Exponentiate both sides to isolate Y:

$$Y(t)=e^{-rac{k}{t}+C}=e^C\cdot e^{-rac{k}{t}}$$

Let $A = e^C$, a positive constant. Then, the solution is:

$$Y(t) = A \cdot e^{-rac{k}{t}}$$

Integral form:

$$y = A \quad e^{-k\frac{1}{t}} \qquad A = Y_0 e^{k/t_0}$$

- ✓ where the A parameter is the assymptote and (t_0, Y_0) is the initial value
- \checkmark the *k* parameter is inversely related with the growth rate

Differential form:

 Lundqvist-Korf is a generalization of Schumacher function with the following differential forms:

$$\frac{1}{Y}\frac{dY}{dt} = k\frac{m}{t^{(m+1)}}$$

where:

- Y is the quantity of interest,
- t is time,
- k and m are constants.

Step 1: Separate Variables

Rewriting the equation to separate the variables:

$$rac{dY}{Y} = k \cdot rac{m}{t^{m+1}} \, dt$$

Step 2: Integrate Both Sides

Integrate both sides to solve for Y:

$$\int rac{dY}{Y} = k \cdot m \int t^{-(m+1)} \, dt$$

The left side becomes:

$$\ln |Y| = k \cdot m \int t^{-(m+1)} \, dt$$

The right side is integrated as follows:

$$\int t^{-(m+1)}\,dt = \int t^{-(m+1)}\,dt = rac{t^{-(m+1)+1}}{-(m+1)+1} + C = -rac{1}{m}\cdot t^{-m} + C$$

where C is the integration constant. Thus, the equation becomes:

$$\ln |Y| = k \cdot m \left(-rac{1}{m} \cdot t^{-m}
ight) + C$$

Simplify:

$$\ln |Y| = -k \cdot t^{-m} + C$$

Step 3: Solve for Y

Exponentiate both sides to isolate Y:

$$Y(t)=e^{-k\cdot t^{-m}+C}=e^C\cdot e^{-k\cdot t^{-m}}$$

Let $A = e^C$, a positive constant, to obtain the integral form:

$$Y(t) = A \cdot e^{-k \cdot t^{-m}}$$

Integral form:

$$Y = A e^{-k\frac{1}{t^m}}$$

- ✓ The *A* parameter is the assymptote
- ✓ The k and m parameters are growth rate and shape parameters:
 - k is inversely related with the growth rate
 - *m* influences the age at which the inflexion point occurs



Location of the inflection point



Relationship between the functions of the Lundqvist-Korf type

Lundqvist function

✓ Schumacher's function is a specific case of Lundqvist function for m=1

Theoretical growth functions

Richards type

Differential form

 $\frac{dY}{dt} = k(A - Y)$

 \checkmark Assumes that the absolute growth rate is proportional to the difference between the maximum yield (asymptote) and the current yield:

Step 2: Integrate Both Sides

Integrating both sides, we have:

$$\int rac{dY}{A-Y} = \int k \, dt$$

The left side is integrated using the rule:

$$\int rac{dY}{A-Y} = -\ln |A-Y| + C_1$$

where C_1 is the integration constant. Thus,

$$-\ln |A-Y| = kt + C_1$$

Multiplying by -1:

 $\ln|A-Y| = -kt - C_1$

Differential form

✓ Assumes that the absolute growth rate is proportional to the difference between the maximum yield (asymptote) and the current yield:

$$\ln |A - Y| = -kt - C_1$$

 $\frac{dY}{dt} = k(A - Y)$

Exponentiating both sides to isolate A - Y:

$$|A-Y| = e^{-kt-C_1} = e^{-kt} \cdot e^{-C_1}$$

Let $e^{-C_1} = C$, a positive constant, so we have:

$$A-Y=Ce^{-kt}$$
 or $Y-A=Ce^{-kt}$

Since the absolute value can yield both positive and negative solutions, we consider the general solution:

$$Y(t) = A - Ce^{-kt}$$

where C is determined by initial conditions.

Differential form

✓ Assumes that the absolute growth rate is proportional to the difference between the maximum yield (asymptote) and the current yield:

 $\frac{dY}{dt} = k(A - Y)$ Step 3: Determine *C* with Initial Condition
If $Y(0) = Y_0$ (initial value), then:

$$Y_0 = A - Ce^{-k \cdot 0} = A - C$$

$$C = A - Y_0$$

Thus, the final integral form of the solution is:

$$Y(t) = A - (A - Y_0)e^{-kt}$$

Integral form:

$$Y = A \left(1 - c e^{-k t} \right)$$

$$\boldsymbol{c} = \boldsymbol{e}^{k t_0} \left(1 - \frac{Y_0}{A} \right)$$

A- assymptote;*k* - shape parameter, expressing growth intensity

Logistic function

Differential form:

✓ The logistic function is based on the hypothesis that the relative growth rate is the result of the biotic potential k reduced by the current yield or size mY (environmental resistence):

$$\frac{1}{Y}\frac{dY}{dt} = (k - mY)$$

 Relative growth rate is therefore a decreasing linear function of the current yield

Logistic function

Integral form:

$$Y = \frac{A}{\left(1 + c \ e^{-kt}\right)}$$

$$c = \frac{Y_0/m}{k - mY_0} e^{kY_0}$$
$$A = \frac{k}{m}$$

The inflection point occurs at t=log(c)/k and Y=A/2, which implies that the curve is symmetric around the inflection point

Generalized logistic functions

Grosenbaugh (1965):

$$Y = \frac{A}{\left(1 + c \ e^{-\left(k_{1}t + k_{2}t^{2} + k_{3}t^{3}\right)\right)}\right)}$$

Monserud (1984)

$$Y = \frac{A}{\left(1 + c \ e^{-f(\boldsymbol{X},t)}\right)}$$

 \checkmark where X is a vector of several variables

Gompertz function

Differential form:

✓ This function assumes that the relative growth rate is proportional to the difference between the logarithms of the maximum yield and current yield

$$\frac{1}{Y}\frac{dY}{dt} = k(\log A - \log Y)$$

✓ Which is equivalent to being inversely proportional to the logarithm of the proportion of current yield to the maximum yield

$$\frac{1}{Y}\frac{dY}{dt} = -k\log\left(\frac{Y}{A}\right)$$

Gompertz function

Integral form:

$$Y = A e^{-c e^{-kt}}$$

$$\boldsymbol{c} = (\log \boldsymbol{A} - \log \boldsymbol{Y}_0) \boldsymbol{e}^{-k t_0} = \log \left(\frac{\boldsymbol{A}}{\boldsymbol{Y}_0}\right) \boldsymbol{e}^{k t_0}$$

Differential form

The absolute growth rate of biomass (or volume) is modeled as:

- the *anabolic rate* (construction metabolism), proportional to the photossintethicaly active area (expressed as an allometric relationship with biomass)
- the *catabolic rate* (destruction metabolism), proportional to biomass

Anabolic rate $c_1 S = c_1 (c_0 Y^m) = c_2 Y^m$ Catabolic rate $c_3 Y$ Potential growth rate $c_2 Y^m - c_3 Y$ Growth rate $c_4 (c_2 Y^m - c_3 Y)$

S - photossintethically active biomass ; Y - biomass; m - alometric coefficient; c0,c1,c2,c3 - proportionality coefficients; c4 - eficacy coefficient

The differential form of the Richards function follows:

$$\frac{d\mathbf{Y}}{dt} = \eta \mathbf{Y}^m - \gamma \mathbf{Y}$$

Integral form:

✓ By integration and using the initial condition $y(t_0)=0$, the integral form of the Richards function is obtained:

$$Y = A \left(1 - c e^{-kt} \right)^{\frac{1}{1-m}}$$

with parameters *m*, *c*, *k* and *A* where: $c = e^{-(1-m)\gamma t_0} = e^{-kt_0}$

$$\boldsymbol{k} = (1 - m)\boldsymbol{\gamma}$$

$$\mathbf{A} = \left(\frac{\eta}{\gamma}\right)^{\frac{1}{1-m}}$$





Location of the inflection point



Relationship between the functions of the Richards type

<u>Richards function</u>

✓ Monomolecular, logistic and Gompertz are specific cases of Richards function dor the m parameter equal to 0, 2, \rightarrow 1

Theoretical growth functions

Hossfeld IV type

Hossfeld IV function

The Hossfeld IV function is a sigmoid function, originally proposed in 1822 (Zeide 1993), for the description of tree growth:

$$Y = \frac{t^{k}}{c + t^{k}/A} = A \frac{t^{k}}{Ac + t^{k}} = A \frac{t^{k}}{c + t^{k}}$$

The function can also be obtained from the generalized logistic by using f(X,t)=-klog(t). Consequently some authors designate it as the log-logistic growth function

McDill-Amateis / Hossfeld IV function

Differential form:

✓ The variables considered in the development of the growth function and the respective dimensions were:

Variable	dY/dt	t	Y	Α
Dimension	L T ⁻¹	Т	L	L

where L indicates length, T is time and A is the asymptote

✓ Applying differential analysis to these variables, the following differential form is obtained:

$$\frac{dY}{dt} = k \frac{Y}{t} \left(1 - \frac{Y}{A} \right)$$

where k is a parameter related to the growth rate

McDill-Amateis / Hossfeld IV function

Integral form:

$$Y = \frac{A}{1 - \left(1 - \frac{A}{Y_0}\right) \left(\frac{t_0}{t}\right)^k}$$

where (t_0, Y_0) is the initial condition and k expresses the growth rate

✓ By making

$$\boldsymbol{c} = \left(\frac{1}{Y_0} - \frac{1}{A}\right) \boldsymbol{t}_0^K$$

the integral form of the McDill-Amateis function coincides with the Hossfeld IV function

Hossfeld IV function



Hossfeld IV function

Location of the inflection point



(Zeide decomposition of growth functions)

Zeide decomposition of growth functions

- Zeide found out that all the growth functions can be decomposed into two components:
 - ✓ Growth expansion represents the innate tendency towards exponential multiplication and is associated with biotic potential, photosynthetic activity, absorption of nutrients, constructive metabolism, anabolism
 - ✓ Growth decline represents the constraints imposed by external (competition, limited resources, respiration, and stress) and internal (self-regulatory mechanisms and aging) factors

Zeide decomposition of growth functions

- The decomposition can be achieved either by a subtraction or a division (subtraction of logarithms) of the two effects
- All the equations analyzed by Zeide, except Weibull's, are particular cases of the two following forms:

• LTD
$$\ln y' = k + p \ln y + q \ln t \leftrightarrow y' = k_1 y^p t^q$$

◆ TD
$$ln y' = k + p ln y + q t \leftrightarrow y' = k_1 y^p e^{q t}$$

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

- In both forms the expansion component is proportional to ln(y) or, in the antilog form, is a power of size
- In LTD the decline component is proportional to the ln of age while in TD it is proportional to age

Zeide decomposition of growth functions

 Zeide proposed a third form in which the declining component is expressed as a function of size instead of age:

 $ln y' = k + p ln y + q y \leftrightarrow y' = k_1 y^p e^{q y}$

The three forms are very useful for the direct modeling of tree and/or stand growth - these forms provide some assurance that the resulting model will display appropriate behavior form a biological stand point

Formulating growth functions without age explicit

Formulating growth functions without age explicit

- In many applications age is not known, e.g. in trees that do not exhibit easy to measure growth rings or in uneven aged stands
- For these cases it is useful to derive formulations of growth functions in which age is not explicit
- The derivation of these formulations is obtained by expressing t as a function of the variable and the parameters and substituting it in the growth function writen for t+a (Tomé et al. 2006)

Formulating growth functions without age explicit

Example with the Lundqvist function



Simultaneous modeling of several individuals (Families of growth functions)

Families of growth functions

 The fitting of a growth function to data from a permanent plot is starightforward

Example:

✓ Fitting the Lundqvist function to basal area and doiminant height growth data from a permanent plot

$$\boldsymbol{Y} = \boldsymbol{A} \boldsymbol{e}^{-\boldsymbol{k} \left(\frac{1}{t^{n}}\right)}$$

A - asymptotek, n - shape parameters

Basal area

A = 58.46, k = 5.13, n = 0.81 Modelling efficiency = 0.995

<u>Dominant height</u> A = 48.75, k = 4.30, n = 0.75

Modelling efficiency = 0.960



But how to model the growth of a series of plots? This is our objective when developing FG&Y models...



Those plots represent "families" of curves

Using growth functions formulated as difference equations - ADA

- Algebraic difference approach (ADA)
 - ✓ When formulating a growth function as a difference equation, it is assumed that the curves belonging to the same "family" differ just by one parameter - the free parameter
 - ✓ A growth function with 3 parameters allows for 3 different formulations, usually denoted by the free parameter
 - For example for the Richards function: Richards-A (model with site specific asymptote) Richards-k (model with common asymptote) Ricjards-m (model with common asymptote)

Using growth functions formulated as difference equations - ADA

Example with the Lundqvist function, formulation with common asymptote and common n parameter, A as free parameter (Kundqvist-A):

$$Y = A e^{-k\frac{1}{t^m}} \Rightarrow A = \frac{Y}{e^{-k\frac{1}{t^m}}} \longrightarrow \frac{Y_2}{e^{-k\frac{1}{t^m}}} = \frac{Y_1}{e^{-k\frac{1}{t^m}}}$$
$$\xrightarrow{P_2} e^{-k\frac{1}{t^m}} e^{-k\frac{1}{t^m}$$

A specific curve of the family is defined by the value of the free parameter In practice, the free parameter is a function of an initial condition (Y_0, t_0)

Using growth functions formulated as difference equations - GADA

- Generalized algebraic difference approach (GADA)
 - ✓ One of the problems with ADA is the fact that it originates formulations that differ just by one parameter
 - ✓ With GADA it is possible to obtain formulations that have more than one site-specific parameter
 - ✓ In GADA parameters are assumed to be function of an unobservable set of variables (denoted by X) that expresse site differences
 - ✓ The equations is then solved by X, which, for a particular site, is substituted in the original equation (X_0)

Using growth functions formulated as difference equations - GADA

• Example with the Schumacher function $ln(Y) = \alpha + \frac{\beta}{t}$

Suppose that $\alpha = X$ and $\beta = \gamma X$, then

$$\ln(Y) = X + \frac{\gamma X}{t} \qquad \longrightarrow \qquad X = \frac{\ln(Y)}{1 + \gamma/t} \qquad \longrightarrow \qquad X_0 = \frac{\ln(Y_0)}{1 + \gamma/t_0}$$

By substituting X0 into the previous expression, we get

$$ln(Y) = ln(Y_0) \frac{t_0(t-\gamma)}{t(t_0-\gamma)}$$

Using growth functions formulated as difference equations - GADA

• Another example with the Schumacher function Suppose now that $\alpha = X$ and $\beta = X$, then $\ln(Y) = X - \frac{\beta}{t}$ and $\ln(Y) = \alpha - \frac{X}{t}$ \longrightarrow $2 \ln(Y) = \left(X - \frac{\beta}{t}\right) + \left(\alpha - \frac{X}{t}\right)$

Solving for X:

$$X = \frac{t[ln(Y) - \alpha] + \beta}{t - 1} \qquad \longrightarrow \qquad X_0 = \frac{t_0[ln(Y_0) - \alpha] + \beta}{t_0 - 1}$$

• Finnally, substituting X0 in the previous expression $\ln(Y) = \alpha - \frac{\beta}{t} + \frac{(t-1)t_0}{(t_0-1)t} \left[\ln(Y_0) - \alpha + \frac{\beta}{t_0} \right]$

Expressing parameters as a function of tree/stand variables

 Example with the Lundqvist function fit to basal area growth of eucalyptus (GLOBULUS 2.1 model) :

$$G = A_g e^{-k_g \left(\frac{1}{t}\right)^{m_g}}$$

$$A_g = A_{gQ}S^2$$

$$k_{g} = k_{g0} + k_{gQ}S + k_{gNp}\frac{Npl}{1000} + k_{gf}fe \quad with \ fe = \frac{100}{S\sqrt{Npl}}$$
$$m_{g} = m_{g0} + m_{gQ}\ln(S) + m_{gNp}\frac{N}{1000}$$

Using mixed-models

- Mixed-models (linear and non-linear) "split" the model error according to different sources of variation, such as:
 - ✓ Region
 - ✓ Stand
 - ✓ Plots

✓ ...

- When using a model fitted with mixed-models theory it is possible to calibrate the parameters with random components by measuring a small sample of individuals
- This means that it is possible to use specific parameters for a particular tree/stand

Which is the best method to model "families" of growth functions?

- There is no best method to model "families" of growth functions
- If appropriate the three methods can be combined in order to obtain more flexible growth models

The end !!!