- **Basic equations and allometric relations individual-based models**

Individual trees of each species can grow (i.e., change tree volume with time) competing for light, soil water and nutrients and are affected by temperature. Each species have response to restrictions of these resources or values of the environmental conditions.

The volume *V* of each tree is calculated approximately as

$$V = D^2 H \qquad (1.1)$$

where *D* is diameter at breast height (dbh) and *H* is height. The height *Ho* at which dbh is measured 1.37 m.

This volume calculation assumes a cylinder and ignores tapering and irregularities. The dynamics of volume are given by the rate of change of volume dV/dt= volume growth rate (m^3/yr) which is expressed by a logistic or sigmoid type of equation, in such a manner that rate of change is proportional to difference with respect to maximum dimensions

$$\frac{dV}{dt} = GL\left[1 - \frac{DH}{D_{\max} H_{\max}}\right] \qquad (1.2)$$

where *G* = growth rate [m^3 wood per m^2 of leaf area/ yr] or [m/yr] and *L* = total leaf area [m^2] and *Hmax* and *Dmax* are maximum height and diameter for a tree of this particular species.

Growth rate depends on diameter: increases for small trees, reaches a maximum and then declines to zero when the maximum diameter is reached. The rate of increase in volume $d(D^2H)/dt$ is directly proportional to leaf area *L* but decreases linearly due to maintenance costs (1- DH/DmaxHmax). When the tree reaches maximum size, DH=DmaxHmax, the growth in volume is zero; all productivity goes into maintenance.

These models assume that *H* is related to *D* by an allometric relationship. JABOWA and FORET used a parabolic form, $H = Ho + b_1 D - b_2 D^2$,

But ZELIG and FACET use an exponential form

$$H(D) = H_{\max}(1 - \exp(b_3 D))^{b4} \qquad (1.3)$$

and b_3,b_4 are coefficients for the exponential form. These coefficients are species-specific. Actually the exponential form should be

$$H(D) = Ho + (H_{\max} - Ho)(1 - \exp(b_3 D))^{b4} \qquad (1.4)$$

so that *H*= *Ho* when *D*= 0 as in the parabolic form.

Hmax and Dmax are estimated from maximum values attained by the species. It is assumed that *H*=Hmax when *D*=Dmax. Using a data set for pairs *H*,*D* for each species the parameters b3,b4 can be calculated by regression.

An allometric relationship is also used to calculate *L* from diameter. For example assuming that *L* is proportional to basal area

$$L = cD^2 \tag{1.5}$$

Both L and D^2 are in m^2 and therefore *c* is unitless. A value of c=0.16 is used in JABOWA. A slightly more refined expression to account for the height to the base of the crown Hc is

$$L = c' D^2 \left(\frac{H - Hc}{H} \right) \tag{1.6}$$

which reduces to the previous one if foliage goes all the way to the ground. ZELIG uses a more complicated LA allometric relations that takes into account sapwood and more complicated geometrical considerations. A simple assumption is to make *Hc*=*uH* where *u* is a fraction of 1 and constant for the species

$$L = c' D^2 \left(\frac{H - uH}{H} \right) = c'(1-u)D^2 = cD^2 \tag{1.7}$$

In the following we will use equation (1.5) where we assume that parameter c includes the effect of Hc as in the previous equation (1.7).

• Growth equation in terms of diameter

To convert the growth equation (1.2) into an ordinary differential equation (ODE) where D is the state variable. Expand derivative $d(D^2H)/dt$

$$\begin{aligned} \frac{d(D^2H)}{dt} &= \frac{d\left(D^2 H(D)\right)}{dt} = \\ &= 2D(dD/dt)H(D) + D^2(dH(D)/dt)(dD/dt) = \\ &= dD/dt\left(2DH(D) + D^2(dH(D)/dt)\right) \end{aligned} \tag{1.8}$$

and solve for dD/dt

$$dD/dt = (dV/dt)\left(2DH(D) + D^2(dH(D)/dt)\right)^{-1} \tag{1.9}$$

substitute the sigmoid equation (1.2) for dV/dt and the allometric L vs D (eqn (1.5))

$$\frac{dD}{dt} = GcD^2 \frac{\left(1 - \frac{DH(D)}{D\max H\max}\right)}{2DH(D) + D^2(d(H(D)/dt)} \tag{1.10}$$

so that the rate dD/dt is given purely in terms of D. For brevity in algebraic results denote the denominator as

$$h(D) = 2DH(D) + D^2(d(H(D)/dt) \tag{1.11}$$

Now substitute the exponential model for the allometric relation H vs D (eqn (1.3)) and after algebraic manipulation we would obtain

$$h(D) = 2DH_{\max}(1-\exp(b_3 D))^{b_4} - H_{\max} D^2 b_3 b_4 \exp\left(b_3 D\right)\left(1-\exp\left(b_3 D\right)\right)^{b_4 - 1} \quad (1.12)$$

This equation can be developed using the H vs D that takes into account Ho given in equation (1.4)

$$\begin{aligned} h(D) = 2D\left(H0 + (H_{\max} - Ho)(1-\exp(b_3 D))^{b_4}\right) - \\ (H_{\max} - H0) D^2 b_3 b_4 \exp\left(b_3 D\right)\left(1-\exp\left(b_3 D\right)\right)^{b_4 - 1} \end{aligned} \quad (1.13)$$

Note that equation (1.10) is a nonlinear expression and can be re-written as

$$\frac{dD}{dt} = Gf(D) \quad (1.14)$$

of two terms G, and f(D), where

$$f(D) = cD^2 \frac{\left(1 - \frac{DH(D)}{D\max H\max}\right)}{h(D)} \quad (1.15)$$

There are five coefficients to parameterize f(D): c, Hmax, Dmax and b3,b4. The form of f(D) shows a maximum. So if we know these five coefficients by regression, the only unknown in (1.14) is the growth rate G.

Now, recall that *G*, growth rate is a function of environmental limiting factors. *G* is calculated from multipliers affecting a hypothetical optimum rate (when conditions are optimum). Gap models use multipliers with values between 0 and 1 to reduce the growth rate due to environmental conditions. Multipliers are independent: light (exponential), soil moisture (parabolic), soil fertility (parabolic), air temperature (parabolic).

$$G = G_{\max} g(E) = G_{\max} F(Q) F(Sw) F(T) F(N) \quad (1.16)$$

F(X) = limiting factor (between 0 and 1), due to environmental variable X, where X can be Q=solar radiation (light), Sw= soil moisture, T=temperature, N= nutrients. The functions F(X) have parameters which depend on species type: shade-tolerance, drought-tolerance, cold-tolerance. Community dynamics feedbacks on environmental factors: as the trees grow: total basal area increases and crowding effects reduce growth: less light, more light attenuation by canopy (Beer's law), less nutrients, less water.

We can combine equation (1.16) and (1.14) to get

$$\frac{dD}{dt} = G_{\max} g(E) f(D) \quad (1.17)$$

which we will use to estimate G_{max} as the only unknown in the expression.

• Estimation of Gmax

So, now assume that the data we have available to estimate G_{max} is a collection of values of D for each year. We assume that we can calculate dD/dt for each year from the D values. So the data set is a set of paired values D, dD/dt. This set can be converted to pairs of dD/dt, f(D) using (1.15). We will assume that there is an environmental condition in the data set that lead to maximum growth, i.e, g(E)~1. In other words, there is a pair of values f(Dopt) and (dD/dt)max that corresponds to g(E)~1.

$$\left(\frac{dD}{dt}\right)_{\max} = G_{\max} f(D_{opt}) \tag{1.18}$$

note that we can solve for G_{max}

$$G_{\max} = \frac{\left(\frac{dD}{dt}\right)_{\max}}{f(D_{opt})} \tag{1.19}$$

The estimation process consists then of four steps:

1) Calculate the maximum of dD/dt, in the series, that is $(dD/dt)_{max}$
2) Determine the corresponding Dopt at which this occurs, Dopt,
3) Calculate *f*(Dopt) using equation (1.15) and
4) Calculate Gmax using equation (1.19)

• Sensitivity of Gmax

It is important to understand how the uncertainty in the allometric parameters affects the uncertainty of Gmax estimation. Therefore we need to characterize the sensitivity of Gmax to parameters c, Hmax, Dmax,b3, b4. Note that this is basically the sensitivity of 1/*f*(*D*) to these parameters.

$$1/\ f(D) = \frac{h(D)}{cD^2\left(1 - \frac{DH(D)}{D\max H\max}\right)} \tag{1.20}$$

To be continued. This section needs developing. MFA 01/02/05.