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Scaling from trees to forests: tractable macroscopic equations for forest dynamics.

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Appendix C: Self-Thinning in the simplest case. Derivation of the Law of Constant Final Yield and Yoda's Law

Here we model the effects of variation in sapling size at the time of planting, but it is also possible to use the same methods to model variation in high-light growth rate. We derive the Law of Constant Final Yield and the Yoda's Law under the simplest assumptions. Please note that the model also predicts a variety of self-thinning asymptotes, different from the -3/2 slope, under more sophisticated conditions (see. Fig. 14c).

Firstly we assume for simplicity that trees die immediately if they fall into the shade. This assumption is not too restrictive in the context of data on self thinning because most plantations involve fast-growing shade intolerant species.

Let $N(s_0, 0)$ be the density of saplings of size s_0 at planting ($t = 0$). We define the integral of this function over all initial sizes as N_0 (i.e. the total density of saplings planted), the mean initial size as $\bar{s}_0$, and the variance in initial size as σ^2. Before any individual is shaded, the total area of all crowns is:

$$\text{(C-1)} \quad \int_0^\infty N(s_0,t)e^{-\mu_L t}\alpha(s_0+G_L t)^2 ds_0 = e^{-\mu_L t}\alpha N_0\left(\bar{s}_0^2+\sigma^2+2G_L\bar{s}_0 t+G_L^2t^2\right).$$

The canopy closes when this total area equals one. A simple expression for the time of canopy closure, t^*, can be obtained in the reasonable case of negligible μ_L, $\bar{s}_0$, and σ^2:

$$\text{(C-2)} \qquad t^* \approx \frac{1}{G_L\sqrt{\alpha N_0}}.$$

Now let the biomass of a tree be $\varphi D^2 h$, or using the height allometry in the simulator (equation 3):

$$\text{(C-3)} \quad \textit{Tree Biomass} = \varphi D^2 H_2(1-e^{-\frac{H_1}{H_2}D}) = \varphi(s_0+G_L t)^2 H_2(1-e^{-\frac{H_1}{H_2}(s_0+G_L t)}).$$

Total yield before t^* is simply surviving tree density, $N_0 e^{-\mu_L t}$, times tree biomass from (C-3) or:

$$\text{(C-4)} \quad \textit{Total Yield} = N_0 e^{-\mu_L t}\varphi(s_0+G_L t)^2 H_2(1-e^{-\frac{H_1}{H_2}(s_0+G_L t)}),\ \textit{if}\ \ t<t^*.$$

The canopy is closed for $t > t^*$, and so:

$$\text{(C-5)} \qquad 1 = \int_{s_0^*}^\infty N(s_0,t)e^{-\mu_L t}\alpha(s_0+G_L t)^2 ds_0,$$

where s_0^* is the size that the smallest canopy trees at time t were at the time of planting. At time t, all trees that started taller than s_0^* are in the canopy and have overtopped and killed all trees that started smaller than s_0^*. After canopy closure, trees are generally large enough that the overwhelming majority of their crown area, $\alpha(s_0 + G_L t)^2$, is due to diameter growth since planting ($G_L t$) rather than their initial diameter (s_0). We thus approximate diameter as $G_L t$ in the integrand of (C-5), again assuming negligible μ_L, and solve yielding:

$$\text{(C-6)} \qquad 1 = N(t)\alpha G_L^2 t^2 \ \ \textit{or:}\ \ N(t) = \frac{1}{\alpha G_L^2 t^2},$$

where $N(t)$ is the density of surviving trees. Total yield after t^* is simply $N(t)$ from (C-6) times tree biomass from (C-3):

$$\text{(C-7)} \quad \textit{Total Yield} = \frac{1}{\alpha G_L^2 t^2}\varphi(s_0+G_L t)^2 H_2(1-e^{-\frac{H_1}{H_2}(s_0+G_L t)}),\ \textit{if}\ \ t>t^*.$$

To obtain the Law of Constant Final Yield from (C-2), (C-4) and (C-7) we need only invert equation (C-2):

$$\text{(C-8)} \qquad N_0^*(t) = \frac{1}{\alpha G_L^2 t^2},$$

where $N_0^*(t)$ is the critical density for which time t is the time of canopy closure. Thus, at any time t, a plot of planting density vs. total yield is given by (C-4) for initial densities less than $N_0^*(t)$, and so total yield will increase linearly with initial density up to the critical density $N_0^*(t)$ (Fig. 13). In contrast total yield is given by equation (C-7) for densities greater than $N_0^*(t)$. Because initial density appears nowhere in (C-7), yield is constant across all initial densities greater than $N_0^*(t)$ (Fig. 13). Moreover, the critical density (C-8) itself decreases as time increases. This is precisely the Law of Constant Final Yield.

To obtain Yoda's Law, in Figure 14 we plot the log of tree biomass (C-3) against the log of surviving tree density ($N_0 e^{-\mu_L t}$ if $t < t^*$ and equation (C-6) if $t > t^*$). Each series of dots in the figure represents a time trajectory for a monoculture starting at a different planting density. Note that each trajectory follows the line with slope -3/2 after the kink which corresponds to the time of canopy closure. Why does this occur? Again, taking initial size s_0 to be a negligible fraction of total diameter after canopy closure, we can substitute (C-6) into (C-3):

$$\text{(C-9)} \qquad \textit{Tree Biomass} = \varphi \frac{1}{\alpha N(t)} H_2 (1 - e^{-\frac{H_1}{H_2} \frac{1}{\sqrt{\alpha N(t)}}}).$$

Although this is not the three-halves thinning law, we note that the tree height is approximately proportional to tree diameter while trees are still young, i.e., the allometry (3) is approximately: $h = H_1 D$, for small diameters. Using this approximation, (C-9) becomes:

$$\text{(C-10)} \qquad \textit{Tree Biomass} \approx \varphi \frac{1}{\alpha N(t)} H_1 \frac{1}{\sqrt{\alpha N(t)}} = \varphi H_1 \alpha^{-\frac{3}{2}} N(t)^{-\frac{3}{2}},$$

which is exactly the three-halves thinning law. In contrast, note that if trees are large then the right-hand side of (C-9) approaches $\varphi / \alpha N(t)$ and so the thinning exponent is negative one. Finally, please note that runs of the individual-based simulator started with a single age cohort in plantation also produce the Law of Constant Final Yield and Yoda's Law (Figures 13a and 14a).