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A COMPARISON OF TREE GROWTH MODELS

V.H. DALE, T.W. DOYLE and H.H. SHUGART

Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831 (U.S.A.)

ABSTRACT

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Tree growth models project the growth and development of forest ecosystems by increasing the size of each simulated tree in the forest on an annual or greater periodic basis. These models are often referred to as 'tree models' because they are based on the birth, growth and death of individual trees, and the characteristics of individual trees are aggregated to describe the stand. This paper distinguishes between two types of models based upon their major purpose for development and data requirements. Forest growth models are defined as those used to assess the yield of a managed forest under prescribed conditions and usually require large calibration data sets. Community dynamics models are defined as those applied to ecological questions about the feedback of environment and species characteristics on growth and yield, and have species-specific rather than site-specific data requirements. The structure and data requirements for each model type affects their regional and temporal applicability as well as their predictive value. A combination approach using the two types of models may be the most general model of tree growth and stand development.

INTRODUCTION

Several hundred digital computer models project changes in forest stands by simulating the growth (and sometimes the birth and death) of individual trees. These models have been reviewed recently from both a forestry and an ecological perspective (Munro, 1974; Shugart and West, 1980; Shugart, 1984) and are often referred to as 'individual tree-based models' or simply 'tree models'. Whereas stand models project the growth and development of entire forests, individual tree-based models present a unique challenge and broader applicability. Much insight is gained by considering the forests from a tree perspective rather than as a collective unit. With tree-based models, variability within and between forest systems can be projected. Age structure, spacing, and diversity as well as individual tree attributes can be examined.

Although general modeling approaches of many tree-based models are similar, the details of the functional forms vary. Most models use tree diameter as the basic unit of measured growth; others use tree height, bole diameter at different heights, and crown size. Individual tree characteristics are aggregated to describe the stand. The equations that increment the state variables to simulate tree growth are almost always at annual or greater time scales.

We assign tree models to one of two groups based upon their primary purpose for development and data requirements. We define 'forest growth' models as those tree models which are generally applied to managed forests and are closely tied to site-specific data required for model calibration. We define 'community dynamics' models as tree models which have been used mainly to ascertain the impact of the feedbacks between the tree species and their environment on forest development. Although community dynamics models are initialized by site-specific data, model parameters are species-specific rather than site-specific. Both types of models have been used to project stand production. Forest growth models can be derived from community dynamics models, but not vice versa. For example, multiple regression equations for growth (e.g., Solomon, 1981) can be derived from data generated by community dynamics models (e.g., FORET — Shugart and West, 1977), but the functional relationship between light and tree growth necessary for a community dynamics model are not available from forest growth models.

In this paper, we first review the functional approaches of a spectrum of tree models that simulate the growth of individual trees. We also consider the implicit assumptions and tradeoffs involved in the various models. We discuss the expression for competition which is a component of both types of models. In the second part of the paper we present a comparison of the growth equations based on the user's intent and available data. Structural design of the models resulting from the goals of the modeling effort revolves around species diversity, age structure, and spatial relations. The structure of the data determines the regional and temporal applicability, the predictive value, and the manner in which the model can be tested. We discuss the future of tree growth models which may involve a combination of forest growth and community dynamics models.

GROWTH EQUATIONS

Tree models vary with respect to several fundamental assumptions used to develop tree growth equations. A general feature of current tree models first implemented by Newnham (1964) is that some optimal open-grown tree attribute (e.g., growth or crown size) is reduced by competition.

Forest growth models

Forest growth models are generally derived from extensive growth records using regression analysis. Table 1 lists examples of forest growth equations illustrating different levels of complexity and data requirements. Regression models describe the predictive relationship between a dependent variable and one or more independent variables. These equations may replicate the data and be statistically significant yet not have any biological basis. Such growth functions usually predict the expected tree diameter increment under given site and stand conditions. In some models, change in bole volume (e.g., Solomon, 1981) or basal area are substituted for radial growth estimates.

In most forest growth models, realized growth is calculated as potential growth (a function of tree size, age, and site quality) modified by the effect of competition. More elaborate designs predict a larger set of tree and stand characteristics such as tree form and merchantability. Some detailed regression models estimate stem diameter along the bole as related to height and age at a given point of measurement (Arney, 1971). STEMS, one of the more extensive forest growth models, uses species-specific growth functions derived from nonlinear regressions to predict potential annual diameter growth (Belcher et al., 1982). A site quality function reduces potential growth to approximate actual growth. Coefficients for this model were developed from over 6000 permanent remeasured plots and 51 000 trees in the Lake State Region.

Perhaps the most complex model of forest dynamics is the FOREST model (Ek and Monserud, 1974). Local species parameters are derived by regression procedures for seven major relationships, including a height–diameter curve, dominant tree-height–age curve, and open-grown crown–width and diameter–height relationships. The model explicitly considers the spatial and horizontal distribution of each tree and computes competition as a function of crown overlap. Since portions of the equation (Table 1) are raised to the power $\mathrm{Bl}(J, M)$. which is the height–age equation, this age relationship has a predominant influence on the resultant growth.

Fitted regression models are subject to sample variation and sampling error because they represent a sample-based estimate. Linear models are often good approximations of curvilinear relationships, though polynomial expression and log transformations often yield better estimates. With the forest approach, growth is generally treated in a deterministic manner. Some authors (e.g., Ek and Monserud, 1974), however, include stochastic elements to simulate residual or unexplained variation for their regression-based growth equation. Some regression models have a large number of parameters (see Table 1). However, increasing the number of regression variables

TABLE 1

Examples of forest growth equations

Equation	Reference
$\text{DIN} = 7.3833 + 0.0176\ \text{DBH} - 0.0215\ \text{DBH}^2/1000 - 0.2881\ \text{BA} + 0.0024\ \text{BA}^2$	Leak and Graber (1976)
$V_i = \delta_0 + \delta_1 h_i + \delta_2 h_i^2$	Solomon (1981)
$\ln(\text{DG}+1) = b_0 + b_1 SA^{-2} + b_2/\text{DBH} + b_3 C$	Beck (1974)
$\text{DIB}_i = 1.01237 + 0.15761\ L_i - 0.00941\ A_i$	Hegyi (1974) as follows Arney (1971)
$\text{DIN} = [d_1 + d_2\ \text{DBH}^{d_3} + d_4 S\ \text{CR}\ \text{DBH}^{d_5}][Y_{\text{int}}(1 - e^{-B_0((\text{BA}_{\max} - \text{BA})/\text{BA})^{0.5}})]$	Belcher et al. (1982)
$\log Y = g_{10} + g_{20} S + g_{30} B_D + g_{40} B_1 + g_{50} \log(\text{DH}) + (g_{11} + g_{21} S - g_{31} B_D + g_{41} \log(\text{DH}))(1/A) + (g_{13} + g_{23} S + g_{33} B_D + g_{43} \log(\text{DH}))(1/A)^2$	Lemmon and Schumacher (1962)
$\text{DIN} = \text{B7}(1, M)\,[1 - \exp(-\text{B7}(2, M)/(1 + \text{CIA})^{\text{B7}(3, M)})][(H(\text{I}) - \text{Bole(I)})/H(\text{I})]^{\text{B8}(5, M)} \times (\text{POTD} - \text{DINV})(1 + \text{WNOISE}(2))$	Ek and Monserud (1974)

where

$$\text{POTD} = \begin{cases} \text{B2}(1, M) + \text{B2}(2, M)\ (\text{POTH} - \text{HDMEAS})^{\text{B2}(3, M)}; & \text{if POTH} \geq \text{HDMEAS} \\ 0; & \text{if POTH} < \text{HDMEAS} \end{cases}$$

$$\text{POTH} = \text{B1}(1, M)\ \text{SITE}(M) \exp[\text{B1}(2, M)\,(1 - \exp(-\text{B1}(3, M)\ \text{AGEPOT}))\ \exp[\text{B1}(4, M)\ \text{SITE}(M)]^{\text{B1}(5, M)}]$$

$$\text{DINV} = \begin{cases} \text{B2}(1, M) + \text{B2}(2, M)\ (\text{TEMPH} - \text{HDMEAS})^{\text{B2}(3, M)}; & \text{if TEMPH} \geq \text{HDMEAS} \\ 0; & \text{if TEMPH} < \text{HDMEAS} \end{cases}$$

$$\text{TEMPH} = \begin{cases} 0.999\ B1(1, M)\ \text{SITE}(M)^{\text{B1}(2, M)}; & \text{if } H(i) \geq \text{B1}(1, M)\ \text{SITE}(M)^{\text{B1}(2, M)} \\ H(i); & \text{otherwise} \end{cases}$$

$$\text{AGEPOT} = \log\left(\frac{1.0 - (\text{TEMPH}/[\text{B1}(1, M)\ \text{SITE}(M)])\ \exp\left[[\text{B1}(2, M)]\ \exp\left[(1/(\text{B1}(2, M))\ \text{SITE}(M))^{\text{B1}(5, M)}\right]\right]}{-\text{B1}(3, M)}\right)$$

Symbols for forest growth models (some values were specified in Anglo-Saxon units by the original authors)

DIN = diameter increment

DBH = diameter at breast height

BA = basal area

V_i = cumulative bole volume growth of ith height

h_i = ith height above ground

δ_0, δ_1, δ_2 = growth coefficients predicted from regressions

DG = 5-year diameter growth
S = site index
A = initial age
C = competition index
b_0, b_1, b_2, b_3 = coefficients to be calculated by regression procedures
DIB_i = diameter (in) at L_i distance from tip of tree
L_i = length in feet from tip of tree to DIB measurement
A_i = age in years at DIB measurement point
CR = tree crown ratio code
d_1, d_2, d_3, d_4, d_5 = species-specific regression coefficients
Y_{int} = y intercept; used as a correction factor for errors in growth potential
$\text{BA}_{\max}$ = maximum basal area per acre which can be expected for the species
B_0 = a function which relates actual tree diameter to average stand diameter as derived from two regression equations using a total of six regression coefficients (b_1, b_2, b_3, b_4, C_1, C_2): $B_0 = \text{f}(R)\ \text{g}(\text{AD})$, where $\text{f}(R) = b_1[1 - \exp(b_2 R)]b_3 + b_4$ and $\text{g}(\text{AD}) = C_1(\text{AD} + 1)\exp(C_2)$ for R = relative dbh of tree (ratio of the tree's dbh to average stand diameter) and AD = average stand diameter
Y has been used for 5- and 10-year periodic annual growth of a tree in (ft^3), periodic 5-year radial growth of sample trees during last 5 years, and number of rings per last radial inch of diameter increment of sampled trees
D = present diameter at breast height of a tree (in)
H = present total height of tree (ft)
A = present age of tree (years)
B_D = basal area of the surrounding dominant stand (ft^2/acre)
HDMEAS = the height at which diameter is measured
BOLE(I) = clean bole length
H(I) = initial height
CIA = competition index adjusted by tolerance
WNOISE(2) = correlated random variables
SITE(M) = average dominant height at index age
B1(J, M) = height–age equation
B2(J, M) = parameters for open-grown diameter–height equation
B7(J, M) = parameters for adjusting diameter increment by competition
B8(J, M) = parameters for adjusting height increment by competition

artificially improves the probability of statistical significance while making any biological interpretation more difficult.

Community dynamics models

The community dynamics approach to modeling individual tree growth includes for major considerations: (a) approximation of the potential production as a function of the tree's morphology; (b) approximation of the respiratory and tissue maintenance costs of the tree; (c) the allocation of net production to tree growth with some restraints on tree morphology; and (d) feedbacks between these factors. Clearly there is some latitude in the exact formulation used, but most models attempt to include the gain, loss, and allocation of fixed carbon to produce a single tree's growth response that resembles a logistic curve. Three types of community dynamics models are presented in Table 2.

Pienaar and Turnbull (1973) show how the Richards–Chapman generalization of the Von Bertalanffy growth equation is appropriate for tree growth. Von Bertalanffy (1951) hypothesized that the growth rate of an organism can be calculated as the difference between anabolic rate (constructive metabolism) and catabolic rate (destructive metabolism). The anabolic rate is thought to be proportional to surface area, while the catabolic rate is proportional to volume. These rates are related by the allometric relation between surface and total volume (Von Bertalanffy, 1951). Assuming an allometric relation between living biomass and photosynthetic area, this equation applies to individual trees in even-aged stands (Pienaar and Turnbull, 1973).

Phipps (1979) presents one example of a community dynamics model that has nonmultiplicative limitations on growth. In the absence of climate or competition, volume growth is assumed to be paraboloid following the natural radial growth pattern of wide rings at the center of the tree and narrow rings toward the outside. The complete growth equation explicitly treats climatic variation, soil moisture, and shade tolerance. Ring widths vary between years and increase when a competitor dies.

The most widely published community dynamics model of tree growth was first developed by Botkin et al. (1972). The change in an individual tree's diameter is obtained by assuming that the volume of wood added to a tree over the course of one year increases as a linear function of leaf area. Leaf area, in turn, is a function of the tree's diameter raised to a power. The model contains the further assumption that the volume change is decremented by the increasing repiration cost of maintaining more living tissue on larger stems. This increased respiratory load is functionally related to area of the tree or diameter times height of the tree. A species-specific optimal

growth equation is based on maximum diameter and age for the species. Under particular environmental conditions, optimal growth is reduced by the multiplicative effects of light, crowding, and temperature effects on growth. This formulation assumes that there is no overlap in the expressions for limiting factors and that each factor is independent. If many factors are incorporated in a multiplicative function, growth tends to be underestimated (Swartzman and Bentley, 1979). Pastor and Post (1985) demonstrate that when light, nutrients, soil moisture, and the prevailing temperature regime are explicitly considered, Liebig's Law of the Minimum gives a better projection of stand dynamics than does the multiplicative function. The simulations can be run by using either stochastic or user-specified climatic conditions. Death of individual trees is a probabilistic function of tree age and suppression.

Competition functions

Competition is a key component of both forest growth and community dynamics type models. Competition is generally a function of actual growth compared with that expected under open-grown condition. Many forest studies evaluate competition from growth performance in relation to mean spacing and density (Harper, 1977). This approach works favorably in homogenous stands of evenly spaced individuals, as in monocultures. In unmanaged stands, however, the proximity, size, and species of competing individuals may vary greatly from the mean stand condition and composition. This shortfall has warranted the development of spatially explicit and size-weighted expressions known as competition indices. Turnbull (1978) notes that 'crowding' rather than 'competition' is actually being assessed by these indices (particularly when distance measures are used) since competition involves the processes of uptake and assimilation of light, nutrients and water, which are difficult to measure.

Competition indices attempt to incorporate the factors that best describe a tree's ability to exploit the available resources relative to its neighbors. In general, they consider the size, number, and distance of neighboring trees, but they vary in mathematical design and detail, ranging from simple competitor density values to elaborate crown geometry estimates. Table 3 outlines four major types: (a) stand density measures; (b) influence-zone overlap indices; (c) distance-weighted size ratios; and (d) growing-space polygons.

Stand density measures assume that the greater the stem number and/or living biomass the more intense the competition. Many forest growth models simply account for crowding by incorporating state variables that define a stand estimate of total stem density or basal area. Botkin et al. (1972)

TABLE 2

Examples of community dynamics growth equations

Effect	Equation	Source
(1) *Growth rate results from anabolic and catabolic rates*		
Potential rate of growth	$B_t = A\{1-\exp[-K(t-t_0)]\}^{1/(1-M)}$	Pienaar and Turnbull (1973) based on Von Bertalanffy (1951)
(2) *Growth has nonmultiplicative limitations*		
Diameter increment	$i_n = A_n\left[\frac{r_{n-1}}{p}\left(\left(r_{n-1}^2 + GH\right)^{0.5} - r_n\right)\right]$	Phipps (1979)
Crowding, shading and shade tolerance	$G = tM(r_n^2 - r_1^2)/n$	
Soil moisture	$H = 1-0.05511(T-W)^2$	
(3) *Growth has multiplicative limitations*		
Optimal growth equation	$\mathrm{DGRO}_1 = \frac{G\ \mathrm{DBH}[(1-\mathrm{DBH\ HT})/(D_{\max}H_{\max})]}{274+3b_2\ \mathrm{DBH}-4b_3\ \mathrm{DBH}^2}$	Botkin et al. (1972)
	$\mathrm{DGRO}_2 = \frac{b_1\ \mathrm{FBIO}^{b_4}[(1-\mathrm{DBH\ HT})/(D_{\max}H_{\max})]}{274+3b_2\ \mathrm{DBH}-4b_3\ \mathrm{DBH}^2}$	Dale and Hemstrom (1984)

Light effect on diameter growth	$\mathrm{DLIT} = 1 - \exp[t_1(A_1 - t_2)]$	Botkin et al. (1972)
Temperature effect on diameter growth	$\mathrm{DTEMP} = \dfrac{4(\mathrm{DEGD} - \mathrm{DMIN})(\mathrm{DMAX} - \mathrm{DEGD})}{(\mathrm{DMAX} - \mathrm{DMIN})^2}$	Botkin et al. (1972)
Moisture stress on diameter growth	$\mathrm{DWAT}_1 = 1 - \mathrm{FJ}/(\mathrm{TGS}\ D3(i))$	Solomon and Shugart (1984)
	$\mathrm{DWAT}_2 = \begin{cases} \sqrt{1-\mathrm{FJ}}/(\mathrm{TGS\ D3}(i)); & \text{if TGS D3}(i) > \mathrm{FJ} \\ 0; & \text{otherwise} \end{cases}$	Pastor and Post (personal communication)
	$\mathrm{DWAT}_3 = \begin{cases} \dfrac{(\mathrm{PMS} - a_w)(\mathrm{WMIN} - \mathrm{PMS})}{(\mathrm{OPT} - a_w)(\mathrm{WMIN} - \mathrm{OPT})} \exp\left(\dfrac{\mathrm{WMIN} - \mathrm{OPT}}{\mathrm{OPT} - a_w}\right); \\ \quad a_w \leqslant \mathrm{PMS} \leqslant \mathrm{WMIN} \\ 0; \quad \text{otherwise} \end{cases}$	Reed and Clark (1979)
Nutrient stress and diameter growth	$\mathrm{DNUT}_1 = a_N + b_N(C_N(1 - 10\exp(-d_N(\mathrm{N} + f_N))))$	Aber et al. (1979) based on Mitchell and Chandler (1939)
	$\mathrm{DNUT}_2 = g_N + (h_N + \mathrm{RNA}) + (K_N\ \mathrm{RNA}^2)$	Weinstein (1982) based on Mitchell and Chandler (1939)

(To be continued)

TABLE 2 (continued)

Definition of terms

(1) Growth rate results from anabolic and catabolic rates
B_t has been used for tree basal area, height, or volume
A = asymptote value of B_t
K, t_0, M = parameters fit to data by iterative procedures

(2) Growth has nonmultiplicative limitations
i_n = width of the nth ring increment
r_{n-1} = radius length to the outside of the previous (or n-1) ring
P = radius length at the inflection point where ring shape changes from conical to paraboloid ($= r_{n-1}$ if $r_{n-1} \leqslant P$)
H = growth multiplier for moisture effects
G = crowding multiplier
n = number of measured rings
M = parameter accounting for stocking density
t = shade tolerance parameter
T = water table depth of sample plot
W = optimum water table depth by species
A_n = "climatic noise" multiplier generated from comparing ratios of actual ring width for a 100 year series to theoretical ring width

(3) Growth has multiplicative limitations: depending on the model used, the optimal diameter growth equation (DGRO) is multiplied by equations representing the effects of light (DLIT), temperature (DTEMP), soil moisture (DWAT), nutrients (DNUT), or competition (as given in Table 3)
(a) *Optimal growth*
DBH = diameter at breast height (137 cm)
HT = height of tree
D_{max} = maximum diameter for species
H_{max} = maximum height for species
G = growth parameter of a species
$b_2 = 2(H_{max} - 137)/D_{max}$
$b_3 = H_{max} - 137)/(D_{max})^2$
FBIO = foliage biomass of tree
b_1, b_2, species-specific parameters based on those in Reed and Clark (1979)

(b) *Light effect*
A_1 = available light a tree receives
t_1, t_2, species-specific or species group light effect parameters
(c) *Temperature effect*
DEGD = degree days
DMIN = minimum number of degree days a species can withstand
DMAX = maximum number of degree days a species can withstand
(d) *Soil moisture effect*
FJ = drought days per growing season
TGS = length of growing season (days)
D3 = proportion of growing season a species can withstand soil moisture below wilting point
PMS = negative xylem potential
WMIN = minimum value of water stress for a species
OPT = optimum xylem potential for growth
a_w = negative x intercept
(e) *Nutrient effect*
N = relative nitrogen availability
a_N, b_N, C_N, d_N, f_N, parameters of species groups from Aber et al. (1979)
g_N, h_N, k_N, parameters of species groups from Weinstein (1982)
RNA = proportion by which the exchangeable nutrient pool would be reduced if the trees grew without nutrient limitation

TABLE 3

Type, mathematical expression, and authorship of competition indices

Index type	Expression [a]	Authorship
Stand density measures	$\sum_{j=1}^{n} BA_j$	Beck (1974)
	$1.0 - SBIO/SOILQ$	Botkin et al. (1972)
Influence-zone overlap	$1/A_i * \sum_{j=1}^{n} O_{ij}$	Gerrard (1969)
	$\sum_{j=1}^{n} O_{ij}/A_i * (D_j/D_i)^{EX}$	Bella (1971)
Distance-weighted size ratios	$\sum_{j=1}^{n} D_j/D_i * I/DST_{ij}$	Hegyi (1974)
	$\sum_{j=1}^{n} (D_j/D_i)^2 * 1/DST_{ij}$	Daniels (1976)
	$\sum_{j=1}^{n} D_j/D_i * e^{-\phi * DST_{ij}/(CR_i + CR_j)}$	Monserud and Ek (1977)
Growing-space polygons	$\sum_{j=1}^{n} \frac{\theta_{ij}}{360} * (\frac{D_i}{D_i + D_j} * DST_{ij}\ CR_i)^2$	Doyle (1983)

[a] SBIO = total stand basal area, SOILQ = maximum recorded forest basal area (61 m^2/ha), BA = basal area, j = competitor, i = subject tree, n = total number of competitors, A = influence-zone area, O = overlap area, D = dbh, EX = exponential factor (= 2), DST = distance between trees, ϕ = parameter estimate for competitive rate (= 2), CR = open-grown crown radius, θ = subtended angle of crown influence of competitors on subject tree.
Source: modified from Doyle (1983).

introduced a relative measure of stand density wherein the competitive effect is modeled as a function of total stand basal area and the maximum expected basal area. This function supposes a linear relationship between growth and competition and, because it is calculated on a plot basis, assumes that the competitive effect is the same for all trees regardless of size, species, vigor, and/or distribution. Other relative size density indices (Spurr, 1962; Curtis, 1967; Glover and Hool, 1979) assume that the distribution of resources and growth is proportional to the individual tree's diameter at breast height (dbh) or basal area relative to its competitors.

The influence-zone concept is based on an assumed circular zone about every tree, roughly equivalent to the crown area of an open-grown tree,

wherein direct competition occurs (Staebler, 1951). This zone is thought to be related to the expected growing space given full crown and root development (Opie, 1968). The extent to which this area overlaps the influence zones of neighboring trees represents a measure of encoachment and crowding of the subject tree's optimum functional environment. Zonal overlap indices (Staebler, 1951; Newham, 1966; Opie, 1968; Gerrard, 1969; Bella, 1971; Keister, 1971) vary with the type of overlap expression (i.e., linear, angular, areal) and relative tree sizes.

Distance-weighted size ratios specify the competitive effect as the sum of size ratios multiplied by distance of selected competitors from the study tree. Hegyi's (1974) index, the first and most noted index of this design, is a function of the sum of the competitor-study tree size ratios and the inverse distance between them. A modified Hegyi index tested by Daniels (1976) differs from the above only in that the size measures are squared and treated as areal estimates. Monserud and Ek (1977) introduced a hybrid of Hegyi's model and the influence-zone overlap concept by adding an exponential term onto the distance measure that accounts for linear overlap of maximum crown widths of subject tree and competitor.

Another class of competition model approximates actual or available growing space using elaborate geometrical constructions, appropriately termed polygons (Brown, 1965; Moore et al., 1973; Adlard, 1974; Alemdag, 1978; Pelz, 1978; Doyle, 1983). Growing area is a polygon shaped by nonoverlapping crown boundaries defined by the proximity and size of neighboring trees. This assumes that only one competitor is eligible to affect the limits on crown growth in any one direction. The degree to which any one competitor confines crown development is determined by the dbh ratio of the subject tree and competitor or the maximum expected crown size, whichever is least.

Determining which neighbors are actual competitors and to what degree is an unresolved problem (Liu, 1981). Stand density and relative size measures generally assume that all competitors lie within a fixed radius regardless of tree size (Hegyi, 1974). Zone overlap indices specify competing neighbors as those whose influence zones intersect that of the subject tree, based on crown spread of open-grown trees of the same diameter. In this approach, large trees are potential competitors even though they may stand more than a fixed distance from the study tree. Designation of competitors that limit individual crown area, as in the polygon models, depends on the subjective interpretation by the researcher. Other less noted selection methods include angular dispersion criteria (Newnham, 1966), quadrant searches (Lin, 1974), or nearest neighbors (Thompson, 1956; Prodan, 1968; Liu, 1981).

Competition may be unequal for trees of different age, size, or species, or for the resources they demand. Light, for example, is essentially a vertically

distributed resource, the interception of which is related to individual crown area and forest canopy structure. However, competition indices and competitor selection are almost exclusively based on horizontal stem spacing and size. While crown architecture dictates the quantity and quality of light absorption, root development influences water and nutrient uptake. Root development, turnover, and overlap are difficult to observe or measure directly. Competition models assume that the above-ground condition also adequately describes the below-ground processes and conditions. Interspecific and intraspecific distinctions are not explicit in these models, so the competitive effect is treated equally. Resolving analytical techniques and modeling efforts to specify competitive interactions among individuals and species will provide a major contribution to forest research.

Comparison of forest growth and community dynamics models

Forest growth and community dynamics growth equations can be compared on the basis of the objectives of the research and the data needed to parameterize each type. The following comparison illustrates how characteristics of the modeling approaches are derived from the research objectives and data structure as outlined in Table 4. Forest growth and community

TABLE 4

A general comparison of tree growth models

Major factors that dictate model type	Implications of the major factors	Type of model	
		Forest growth	Community dynamics
User intent		Management	Ecological research
	Species diversity	One or few species	Multispecies
	Age diversity	One or few ages	Multi-aged
	Spatial distribution	Plantations or evenly spaced stands	Natural forests
Data structure		Multiple measurements of many trees	Ecological characteristics of species
	Regional applicability	Local area	Large region
	Temporal applicability	Short term	Long term
	Predictive value	Interpolative	Extrapolative
	Model testing	Easily verified by comparison with data	Verified by realism of processes and comparison with data
		Difficult to validate	Validated by applying model to new forest system

dynamics models are contrasted on the basis of the ramifications of the user's objectives and the data structure. The basic data structure influence the regional and temporal applicability as well as the predictive values of the models.

User intent

The objectives of each model dictate the type of tree growth equation used. One way to assess the objectives is to consider the research needs of the user. We have depicted researchers as being from either a purely commercial forestry or an ecological background, although we realize that those two extremes bound a continuum. The implications of the user's purpose include the way species diversity, age structure, and plant spacing are modeled.

Foresters are commonly interested in an assessment of merchantable timber production at one or a few sites under specified environmental and silvicultural conditions. Forest growth equations are more specifically oriented toward forest production under prescribed site and management conditions than community dynamics. They are most useful in determining optimum rotation and thinning schedules and plant spacing designs for maximum wood production under specific silvicultural treatments. Applications of ecological interest include testing hypotheses on growth relationships and growth-influencing factors, particularly competition.

Ecologists, on the other hand, are generally more interested in large-scale, long-term, successional processes of natural forests. They examine species composition and dynamics as the forest changes over time under a variety of geographical regions and climatic regimes. Forest structure is one area of interest in which these two approaches meet. Structure of the forest includes factors such as the species composition, density, and size distribution of trees. Foresters are greatly concerned with the quantity and quality (which includes size and growth patterns) of the trees. Structural aspects influence the compositional and functional features of the forest such as species diversity or nutrient cycling (Franklin et al., 1981) and thus have implications for forest succession.

Species diversity. Models have been used to simulate either mixed or single species stands. The degree of detail and functional complexity of the growth equations influence modeled species diversity. Foresters commonly use mono-species approaches for plantations and for commercially important species. Because there is a considerable amount of growth rate data for such species, there is also a tendency to incorporate rather elaborate statistical models that capitalize on these large data sets. Ecologists generally employ mixed-species models because natural forests contain a variety of species

whose interactions influence succession. Including a mix of species in a community dynamics model incorporates species differences in growth rates, shade tolerance, response to moisture stress, and response to nutrient conditions.

Age diversity. There are many even-aged stand models which are generally used to simulate plantations of commercially important species. There are also several species that naturally regenerate in a single cohort, and those species are frequently simulated with models that assume an even-aged structure. Models of mixed-age structure are generally used by ecologists to simulate dynamics of natural forests. The principal purpose of using a mixed-age structure is to consider explicity the simulation of the births and deaths of trees. As a result of the mixed-age approach, the shading component of the growth equation becomes more complex due to vertical stratification from canopy layering of trees at different ages and stages of development.

Spatial distribution. Because trees in plantations are regularly placed, spatial effects are disregarded in most plantation models. Instead, density is used as a state variable describing spatial distribution (Clutter, 1963; Moser and Hall, 1969; Dress, 1970; Curtis, 1967). These models obtain an estimate of wood volume per unit area over time and a simultaneous estimate of the stand basal area as functions of the number of trees in the stand and their geometry. Sullivan and Clutter (1972) developed a set of regression equations that accounted for approximately 99% of the variation in mean volume after a 5-year period as a function of site index, stand age, and basal area for 102 study plots from Georgia, Virginia, and South Carolina.

Highly detailed, spatially explicit models of individual tree growth were developed by Newnham (1964), Lee (1967), Mitchell (1969), Lin (1970), Bella (1970), Arney (1971) and Hatch (1971). Spatially explicit models reflect both the irregular spacing in natural stands and the tendency of conifers to branch-prune adjacent tree canopies. Crown-overlap indices (in two and sometimes three dimensions) are used to account for branch pruning of adjacent trees. The spatially explicit nature of these models requires a detailed representation of the architecture of individual trees under different environmental and silvicultural conditions. Since these architectural representations are usually calibrated by regression equations, the range of this calibration data influences the range of application. The models often compute both the height and the diameter increment of the trees, and some models provide considerable detail about the shapes of the trees. For example, Hegyi's (1974) model of jack pine (*Pinus banksiana*) computes the diameter of each tree at regular 25.4-cm (10-inch) intervals along the stem as a function of competition, age and size of the tree, and site factor.

In contrast, the community dynamics models project forest dynamics without specifying horizontal placement of the trees. A stand measure of competition is used (Table 3), so tree spacing does not affect competitive interactions. The model developed by Botkin et al. (1972) simulates trees as disks of leaves at different levels above the forest floor and spread continuously over the plot. The stem location is not specified.

Basic data structures

Forest growth models are usually parameterized by using large data sets obtained by remeasuring trees. Community dynamics models have parameters derived from ecological characteristics of each species and use site-specific driving variables. Detailed and sophisticated measurement techniques have been used to obtain the data necessary for forest growth models. Regional forest inventories provide a systematic means to remeasure plots over time (e.g., Nilson, 1978). These efforts are usually labor-intensive, field-oriented, and time-limited. However, low-level stereo photographs have provided data for a forest growth model of Douglas fir (Mitchell, 1975).

Regional applicability. Forest growth models are so closely tied to the calibration data that it requires a major research effort to gain the necessary data to transfer the models to a new site. As the number of parameters increases, generally the difficulty of obtaining the data increases. Even so, enough data has been collected from the lake states region of the United States for the STEMS model to be applied to the area (Belcher et al., 1982). Community dynamics models are more easily transferred as is illustrated by the numerous versions of the FORET model which have been applied (Botkin et al., 1972; Shugart and West, 1977; Doyle, 1981; Shugart and Noble, 1981; Dale et al., 1984; etc.). The species parameters for these models can usually be obtained from standard silvicultural studies.

Temporal applicability. The calibration data required for forest growth models restrict the model in time as well as space. Usually foresters consider one or two rotations in their uses of these models. Community dynamics models, on the other hand, have been used for short- as well as long-term studies. Aber et al. (1982) examined productivity and species composition of northern hardwood forests during 90 years of stand management. Emanuel et al. (1978) hypothesized cycles of 200 years or more in biomass using long-term simulations of the FORET model. Solomon et al. (1980) compared simulated tree biomass for the past 16,000 years with the fossil record of pollen. Forest projections of community dynamics models are also used to test hypotheses concerning long-term future forest composition and structure (Dale et al., 1984).

Interpolative versus extrapolative. Forest growth models reliably estimate forest yield within the range of the data set and thus are useful tools for foresters. A prime assumption of these models is that the range of the data are not exceeded. Because forest growth models are calibrated under a particular set of conditions, they are restricted to that scenario and are most useful for plantations where the tree sizes and species are limited. However, even in managed forests, the limitations of forest growth models are exceeded when new genetic stock or silvicultural practices are introduced. Since much of plantation silviculture is founded upon experimental plantings, it may take decades to obtain data. As a result, the plantation forester has to work outside the calibration range of the yield tables that are the mainstay of evaluating plantation yield.

Most community dynamics models have parameters developed from standard silvicultural information for such characteristics as the maximum age, diameter, and height of a species. The ease of obtaining the parameter values for community dynamics models greatly enhances the portability and value of those models to ecologists. Community dynamics models are more robust than forest growth models because they can project forest development under changing conditions. On the other hand, the models may not have the ability to describe a single stand as well as empirically derived models for that site. Community dynamics models can include the feedbacks of environmental changes and species variation by reformulating certain process equations, changing parameter values, or introducing new parameters, e.g., for pollution effect on tree growth (West et al., 1980).

Model testing. It is necessary to consider how data structure influences the ability of a model to be tested. One gains an appreciation for the usefulness of the model by comparing model results with field data. Performance is evaluated by verification (how well the model describes the forest system used to develop the model) and validation (how well the model predicts characteristics of an independent forest system) (Shugart et al., 1981). Forest growth model results can usually be compared with a subset of the data used to develop them. The regression least squares procedure gives some measure of the ability of the forest growth model to predict patterns in the calibration data set (e.g., Ek and Monserud, 1979). Community dynamics models are routinely verified by comparison of model projections to forest attributes, e.g., species composition and density diameter distribution (Doyle, 1981). Validation may be a problem with forest growth models that require large calibration data sets because it is difficult to parameterize the computer code for a new site. Community dynamics models, on the other hand, are more readily validated due to the relative ease with which the codes can be calibrated for a new site. Shugart (1984) reviews seven forest systems where

versions of the FORET model independently predict some known feature of a forest (including species composition and abundance, density-diameter classes, basal area, mean dbh, and stocking density). The general applicability of any model can be evaluated only if the data for the model initialization are available for a variety of forest systems.

All comparisons between model output and field data involve some question as to which forest attributes should be examined. Model testing can be based on tree, species, stand, or ecosystem characteristics. Turnbull (1978) points out that in validating tree models one must compare tree as well as stand attributes and that such comparisons could provide a link with physiological processes. For example, the change in diameter of a tree could be related to a model of the mechanisms by which trees increase their diameter increment on a cell-by-cell basis. At the present time there is no direct link between a photosynthetic model and one that predicts stand response.

FUTURE MODEL DEVELOPMENT

Development of tree models of forest dynamics has been rapid over the past two decades. Starting in the mid-1960s, a decade of model formulation and exploration of different approaches resulted in the eventual development of a diverse array of individual tree-based simulators. Beginning in the mid-1970s these models were applied to a wide variety of forests to address an equally wide range of theoretical and practical problems. Over this 20-year period, there has been a sharp decrease in the per-operation cost of computation with an associated increase in computer speed and size. These technological advances have created a research environment of accelerated application of forest simulation models, but there has been considerably less model development over this period. Indeed, most of the tree-based simulation models in use today have been in use for more than 10 years. Changes in the models have tended to be of the nature of fine tuning or incorporating additional environmental processes — e.g., nutrients (Aber et al., 1982; Weinstein, 1982) – as opposed to model reformulation.

In the present forum, it seems appropriate to speculate on possible considerations that may influence the application and development of these models over the coming decade. First, there is the need to include an increased level of mechanism in the community dynamics models if the models are to be used to project the longer term consequences of finer-scale changes. The applications of forest growth models are restricted to cases within the calibration data sets. However, the community dynamics-based approach to simulating individual tree growth is based on extremely simplified representations of the actual physiological processes that operate in

trees. A reasonable question is, "How can one best determine the annual growth of trees from a detailed understanding of tree physiology?" Given appropriate functions for tree growth under longer than annual time scales, several forest dynamic models can project growth into forest structural and compositional dynamics over centuries. There seem to have been many studies of the physiology of leaf surfaces under different conditions, but the whole-plant metabolism of trees seems much less characterized. An area needing additional study is the allocation of photosynthate to tissue growth and the dynamics of these allocations under different environmental constraints.

Considering the sorts of equations used in the models, it may be difficult to add additional physiological detail without greatly increasing the computational costs of calculating a tree's annual increment. Changes in modeling the pattern of tree growth can increase the computational time at least one order of magnitude. An example might be a model algorithm that allocated height and diameter growth to optimize photosynthetic geometry and mechanical strength. Even such simple additions would push the cost of computation beyond that typically used in model development. For example, the FOREST model (Ek and Monserud, 1974) projects 100 simulated plots for 1000 years using about 30 CPU minutes on IBM mainframes. Such computer costs are not acceptable for production runs to assess specific problems. Brute force parameter exploration or data filling under such constraints could very well call for a dedicated mainframe computer. Improvement of the mechanistic detail in tree models will require clever simplifications of the underlying formulations rather than model tuning. Some of the developments used in modeling crop plant canopies and some of the results that have been presented in this volume seem to fall into this category.

Second, we would like to point out the need for information on many aspects of large tree morphology and physiology. The models simulating the more natural mixed-aged, mixed-species stands are particularly dependent on considerations arising from mechanisms limiting the growth of larger trees.

Finally, no model will ever predict all of the forest attributes precisely due to the complexity and variability of ecological factors affecting tree growth. The best models will explain the model variation from the data and be appropriate for the questions at hand whether they relate to forest management or ecological succession. It might be that the most generally useful modeling approach would be a combination of the forest growth and community dynamics models. If the projections of a forest growth and community dynamic model compare well for one forest system, then one could use the community dynamic model to simulate forest development on a regional basis. This joint use of two models would be less costly than

obtaining a new set of parameter values for the forest growth model. Of course this approach would depend upon adequate independent testing of both models. Such a combination of approaches would take advantage of the best features of each of the modeling schemes and would meet the needs of both the forester and ecologist.

CONCLUSIONS

Tree models examine tree growth and forest development from a variety of perspectives. Almost all are based on the diameter changes of single trees. The complexities and applications of the models depend on the user's intent and on the data structure.

Research and management practices in the past few years provide a prediction of the future of tree models. These models have reached their current peak of development along with widespread use of computers. Most models mentioned in this paper are relatively inexpensive and easy to run. They represent an advance in the tools to understand forest dynamics in that individual tree characteristics as well as stand attributes can be examined. The future of forestry involves more intense management and management on a larger scale than occurs today. DeBell et al. (1984) predict that a wider range of silvicultural practices will be used in future forest management due to the changing age structure of forests, the increase in timber value, and a better understanding of growth responses. Forest growth models provide the greater detailed understanding on a site-specific basis that may be useful locally for exploring the ramifications of various management options. Community dynamics models can provide a regional view and interpretation of future forest development in the face of various environmental impacts and changing genetic stock. Both types of models will undoubtably continue to be useful in their own right.

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REFERENCES

Aber, J.D., Botkin, D.B. and Melillo, J.M., 1979. Predicting the effects of different harvesting regimes on productivity and yield in northern hardwoods. Can. J. For. Res., 9: 10–14.

Aber, J.D., Melillo, J.M. and Federer, G.A., 1982. Predicting the effects of rotation length, harvest intensity, and fertilization on timber yield from northern hardwood forests in New England. For Sci., 28: 31–45.

Adlard, P.G., 1974. Development of an empirical competition model for individual trees within a stand. In: J. Fries (Editor), Growth Models for Tree and Stand Simulation. Res. Note 30, Department of Forest Yield Research, Royal College of Forestry, Stockholm, pp. 22–37.

Alemdag, I.S., 1978. Evaluation of some competition indices for the prediction of diameter increment in planted white spruce. Can. Dep. Environ. For. Man. Inst. Inf. Rep. FMR-X-108, Forest Management Institute, Ottawa, Ont., 39 pp.

Arney, J.D., 1971. Computer simulation of Douglas-fir tree and stand growth. Ph. D. Thesis, School of Forestry, Oregon State University, Corvallis, OR, 79 pp.

Beck, D.E., 1974. Predicting growth of individual trees in thinned stands of yellow poplar. In: J. Fries (Editor), Growth Models for Tree and Stand Simulation. Res. Note 30, Department of Forest Yield Research, Royal College of Forestry, Stockholm, pp. 47–55.

Belcher, D.M., Holdaway, M.R. and Brand, G.J., 1982. A description of STEMS—the stand and tree evaluation and modeling system. USDA For. Serv. Gen. Tech. Rep. NC-79, 18 pp.

Bella, I.E., 1970. Simulation of growth, yield and management of aspen. Ph. D. Thesis, Faculty of Forestry, University of British Columbia, Vancouver, B.C., 190 pp.

Bella, I.E., 1971. A new competition model for individual trees. For. Sci., 17: 364–372.

Botkin, D.B., Janak, J.F. and Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. J. Ecol., 60: 849–872.

Brown, G.S., 1965. Point density in stems per acre. For. Res. Inst. N.Z. For. Serv. For. Res. Note 38, Forest Research Institute, Rotorura, New Zealand, 11 pp.

Clutter, J.L., 1963. Compatible growth and yield models for loblolly pine. For. Sci., 9: 354–371.

Curtis, R.O., 1967. A method for estimation of gross yield of Douglas-fir. For. Sci. Monogr., 13: 1–24.

Dale, V.H. and Hemstrom, M.A., 1984. CLIMACS: a computer model of forest stand development for western Oregon and Washington. USDA For. Serv. Res. Pap. PNW-327, 60 pp.

Dale, V.H., Hemstrom, M.A. and Franklin, J.F., 1984. The effect of disturbance frequency of forest succession in the Pacific Northwest. In: New Forests for a Changing World. Proc. Convention of the Society of American Foresters, 16–20 October 1983, Portland, OR, pp. 47–51.

Daniels, R.F., 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. For. Sci., 22: 454–456.

DeBell, D.S., Harms, W.R., Marquis, D.A. and Curtis, R.O., 1984. Trends in stand management practices for U.S. foresters. In: New Forests for a Changing World. Proc. Convention of the Society of American Foresters, 16–20 October 1983, Portland, OR, pp. 47–51.

Doyle, T.W., 1981. The role of disturbance in the gap dynamics of a montane rain forest: an application of a tropical forest succession model, In: D.C. West, H.H. Shugart and D.B. Botkin (Editors), Forest Succession: Concepts and Application. Springer, New York, NY, pp. 56–73.

Doyle, T.W., 1983. Competition and growth relationships in a mixed-aged, mixed-species forest community. Ph.D. Thesis, University of Tennessee, Knoxville, TN, 85 pp.

Dress, P.E., 1970. A system for the stochastic simulation of even-aged forest stands of pure species composition. Ph. D. Thesis, Purdue University, West Lafayette, IN, 267 pp.

Ek, A.R. and Monserud, R.A., 1974. FOREST: a computer model for the growth and reproduction of mixed species forest stands. Res. Rep. A2635, College of Agricultural and Life Sciences, University of Wisconsin, Madison, WI, 90 pp.

Ek, A.R. and Monserud, R.A., 1979. Performance and comparison of stand growth models based on individual tree and diameter-class growth. Can. J. For. Res., 9: 231–244.

Emanuel, W.R., West, D.C. and Shugart Jr. H.H., 1978. Spectral analysis of forest model time series. Ecol. Modelling, 4: 313–326.

Franklin, J.F., Cromack, K., Jr., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F. and Juday, G., 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-118, 48 pp.

Gerrard, D.J., 1969. Competition quotient: a new measure of the competition affecting individual forest trees. Mich. State Univ. Agric. Exp. Stn. Res. Bull. 20, 32 pp.

Glover, G.R. and Hool, J.N., 1979. A basal area ratio predictor of loblolly pine plantation mortality. For. Sci., 25: 275–282.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, New York, NY, 892 pp.

Hatch, C.R., 1971. Simulation of an even-aged red-pine stand in northern Minnesota. Ph.D. Thesis, University of Minnesota, St. Paul, MN, 182 pp.

Hegyi, F., 1974. A simulation model for managing jack-pine stands. In: J. Fries (Editor), Growth Models for Tree and Stand Simulation. Res. Note 30, Department of Forest Yield Research, Royal College of Forestry, Stockholm, pp. 74–87.

Keister, T.D., 1971. A measure of the intraspecific competition experienced by and individual tree in a planted stand. La. State Univ. Agr. Exp. Stn. Bull. 652, 30 pp.

Leak, W.B. and Graber, R.E., 1976. Seedling input, death and growth in uneven-aged northern hardwoods. Can J. For. Res., 6: 368–374.

Lee, Y., 1967. Stand models for lodgepole pine and limits to their application. Ph.D. Thesis, Faculty of Forestry, University of British Columbia, Vancouver, B.C., 333 pp.

Lemmon, P.E. and Schumacher, F.X., 1962. Volume and diameter growth of ponderosa pine trees as influenced by site index, density age, and size. For. Sci., 8: 236–249.

Lin, J.Y., 1970. Growing space index and stand simulation of young western hemlock in Oregon. Ph. D. Thesis, School of Forestry, Duke University, Durham, N.C., 182 pp.

Lin, J.Y., 1974. Stand growth simulation model for Douglas-fir and western hemlock in the Northwestern United States. In: J. Fries (Editor), Growth Models for Tree and Stand Simulation. Res. Note 30, Department of Forest Yield Research, Royal College of Forestry, Stockholm, pp. 102–118.

Liu, J.Y., 1981. Competition index and its relationship to individual tree growth. In: XVII IUFRO World Congress, Kyoto, Japan, pp. 135–148.

Mitchell, H.L. and Chandler, R.F., 1939. The nitrogen nutrition and growth of certain deciduous trees of northern United States. Black Rock For. Bull. 11, 94 pp.

Mitchell, K.J., 1969. Simulation of the growth of even-aged stands white spruce. Sch. For. Yale Univ Bull. 75, 48 pp.

Mitchell, K.J., 1975. Stand description and growth simulation from low-level stereophotos of tree crowns. J. For., 73: 12–16, 45.

Monserud, R.A. and Ek, A.R., 1977. Prediction of understory tree height growth in northern hardwood stands. For. Sci., 23: 391–400.

Moore, J.A., Budelsky, C.A. and Schlesinger, R.C., 1973. A new index representing individual tree competitive status. Can J. For. Res., 3: 495–500.

Moser, J.W. and Hall, O.F., 1969. Deriving growth and yield functions for uneven-aged forest stands. For. Sci., 15: 183–188.

Munro, D.D., 1974. Forest growth models. A prognosis. In: J. Fries (Editor), Growth Models for Tree and Stand Simulation. Res. Note 30, Department of Forest Yield Research, Royal College of Forestry Stockholm, pp. 7–21.

Newnham, R.M., 1964. The development of a stand model for douglas-fir. Ph. D. Thesis, Faculty of Forestry, University of British Columbia, Vancouver, B.C., 201 pp.

Newnham, R.M., 1966. Stand structure and diameter growth of individual trees in a young red-pine stand. Can. Dep. For. Rural Dev. Int. Rep. FMR-1, Forest Management Institute, Ottawa, Ont., 19 pp.

Nilson, N., 1978. Long range forest development models. In: J. Fries, H.E. Burkhart and T.A. Max (Editors), Growth Models for Long Term Forecasting of Timber Yields. FWS-1-78, School of Forestry and Wildlife Resources, Virginia Polytechnic Institute and State University, Blacksburg, VA, pp. 159–171.

Opie, J.E., 1968. Predictability of individual tree growth using various definitions of competing basal area. For. Sci., 14: 314–323.

Pastor, J. and Post, W.M., 1985. Development of a linked forest productivity-soil process model. ORNL/TM-9519, Oak Ridge National Laboratory, Oak Ridge, TN, 162 pp.

Pelz, D.R., 1978. Estimating individual tree growth with tree polygons. In: J. Fries, H.E. Burkhart and T.A. Max (Editors), Growth Models for Long Term Forecasting of Timber Yields. FWS-1-78, School of Forestry and Wildlife Resources, Virginia Polytechnic Institute and State University, Blacksburg, VA, pp. 172–178.

Phipps, R.L., 1979. Simulation of wetlands forest vegetation dynamics. Ecol. Modelling, 7: 257–288.

Pienaar, L.V. and Turnbull, K.J., 1973. The Chapman–Richards generalization of Von Bertalanffy's growth model for basal area growth and yield in even-aged stands. For. Sci., 19: 2–22.

Prodan, M., 1968. The spatial distribution of trees in an area. Allg. Forst Jagdztg., 139: 214–217.

Reed, K.L. and Clark, S.G., 1979. SUCcession SIMulator: a coniferous forest simulator model description. Coniferous Forest Biome, Ecosystem Analysis Studies, U.S./International Biological Program, Bull. 11, University of Washington, Seattle, WA, 96 pp.

Shugart, H.H, 1984. A Theory of Forest Dynamics: An Investigation of the Ecological Implications of Several Computer Models of Forest Succession. Springer, New York, NY, 278 pp.

Shugart, H.H. and Noble, I.R., 1981. A computer model of succession and fire response of the high-altitude eucalyptus forest of the Brindebella Range, Australian Capital Territory. Aust. J. Ecol., 6: 149–164.

Shugart, H.H. and West, D.C., 1977. Development and application of an Appalachian deciduous forest succession model. J. Environ. Manage., 5: 161–179.

Shugart, H.H. and West, D.C., 1980. Forest succession models. BioScience, 30: 308–313.

Shugart, H.H., West, D.C. and Doyle, T.W., 1981. Verification, validation, and application of detailed forest succession models. In: M.A. Hemstrom and J.F. Franklin (Editors), Successional Research and Environmental Pollutant Monitoring Associated with Biosphere Reserves. Proc. 2nd US-USSR Symposium on Biosphere Reserves, 10–15 March 1980, Everglades National Park, FL. U.S. National Committee for Man and the Biosphere in cooperation with Forest Service, U.S. Department of Agriculture, and U.S. Department of the Interior. Denver Service Center, National Park Service, Denver, CO, pp. 103–121.

Solomon, D.S., 1981. Individual tree growth of red spruce as related to tree characteristics and environmental influences. In: XVII IUFRO World Congress, Kyoto, Japan. Japanese IUFRO Congress Council, Ibaraki, pp. 72–83.

Solomon, A.M. and Shugart, H.H., 1984. Integrating forest-stand simulations with paleoecological records to examine long-term forest dynamic. In: G.I. Ågren (Editor), State and Change of Forest Ecosystems—Indicators in Current Research. Rep. 13, Department of Ecology and Environmental Research, pp. 333–356.

Solomon, A.M., Delcourt, H.R., West, D.C. and Blasing, T.J., 1980. Testing a simulation model for reconstruction of prehistoric forest stand dynamics. Q. Res., 14: 275–293.

Spurr, S.H., 1962. A measure of point density. For. Sci., 8: 85–96.

Staebler, G.R., 1951. Growth and spacing in even-aged stand of Douglas-fir. M.S. Thesis, University of Michigan, MI, 46 pp.

Sullivan, A.D. and Clutter, J.L., 1972. A simultaneous growth and yield model for loblolly pine. For. Sci., 18: 76–86.

Swartzman, G.L. and Bentley, R., 1979. A review and comparison of plankton simulation models. ISEM J., 1: 30–81.

Thompson, H.R., 1956. Distribution of distance to nth neighbor in a population of randomly distributed individuals. Ecology, 37: 391–394.

Turnbull, K.J., 1978. Long-term yield forecasting models; Validation and iterative estimation. In: J. Fries, H.E. Burkhart and T.A. Max (Editors), Growth Models for Long Term Forecasting of Timber Yields. School of Forestry and Wildlife Resources, Virginia Polytechnic Institute and State University, Blacksburg, VA, pp. 224–229.

Von Bertalanffy, L., 1951. Theoretische Biologie, Band II. Franke, Bern, 403 pp.

Weinstein, D.A., 1982. The long-term nutrient retention properties of forest ecosystems: a simulation investigation. Ph. D. Thesis, University of Tennessee, Knoxville, TN, 142 pp.

West, D.C., McLaughlin, S.B. and Shugart, H.H., 1980. Simulated forest response to chronic air pollution stress. J. Environ. Qual., 9: 43–49.