

Growth Models for Tropical Forests: A Synthesis of Models and Methods

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ABSTRACT. Tropical forests may have many species, indeterminate ages, and a wide range of growth habits and stem sizes and thus require special modeling techniques. But technique contributes only part of model quality, and much depends on the calibration data and access to the model. Whole stand models have limited utility in these forests, as it is hard to describe the forest adequately with few stand-level variables. Stand table projection and matrix models may be useful where summarized data are available and computer resources are limited, but the many classes required detract from the method. Tree list models offer greater flexibility, enable projections under a wide range of conditions, and provide diverse information. All growth equations should ensure reliable predictions over all tree sizes, sites, and stand conditions. Mortality may be modeled with logistic functions fitted to individual tree data. Two-stage recruitment models are a practical way to predict regeneration where there are many species. Several existing models could be calibrated for tropical rainforests if suitable data were available. Sustainable use of rainforests may depend on maintaining nutrient cycles and ecosystem linkages, and new data and innovative models will be necessary to fully appraise these aspects. *FOR. SCI.* 41(1):7-42.

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IT IS 200 YR SINCE YIELD TABLES WERE PUBLISHED (Vuokila 1965), 30 yr since compatible growth and yield models were reported (Buckman 1962, Clutter 1963), and 20 yr since the first IUFRO meetings on forest growth modeling (Fries 1974). Despite this heritage, forest growth modeling remains more an art than a science. Many models are excessively empirical, relying on calibration to data rather than underlying biological theories. These problems are compounded in models that address natural forests with many species.

The tropical moist forest offers a special challenge for the growth modeler, as it may be the most complex forest ecosystem. There may be 100 tree species on a single hectare, and 1000 in a management unit, 100 of which may be of commercial importance. These may exhibit a huge range of life forms and stem sizes. In these forests, age is irrelevant as a modeling variable.

This paper reviews recent developments in forest growth modeling and highlights promising directions for further research. The emphasis is on forecasting timber yields in mixed forests, especially those in the tropics. There is no single approach optimal for modeling tropical forests; the ideal model depends on resources and applications. Accordingly, many methods are reviewed to illustrate strengths and weaknesses of various alternatives. Examples are drawn from temperate as well as tropical forests, as both may offer the challenge of many

species and sizes. The emphasis is on models with practical relevance for the management of uneven-aged mixed-species forests.

GROWTH MODELING: OPTIONS AND ALTERNATIVES

A "model" may represent some structure showing the proportions and arrangements of its component parts. It may also refer to a formal expression of a theory (Ford-Robertson 1971). Common usage of the term "growth model" encompasses the mathematical equations, the numerical values embedded in those equations, the logic necessary to link these equations in a meaningful way, and the computer code required to implement the model on a computer.

Levins (1966) suggested that biological models could not be general, realistic, and precise, but could only attain two of these goals. Prentice (1986, Prentice and Helmisaari 1991) offered a classification based on these attributes. Abstract models (Gatto and Rinaldi 1987¹) may be precise and general, but do not attempt to simulate the dynamics of specific forest types. Succession models (Shugart 1984, Botkin 1993) may be realistic and general, but may not be sufficiently precise for forest management decisions. Growth and yield models may be precise and realistic, but are limited in their scope and may require empirical data for calibration. Despite their lack of generality, growth models are of considerable importance in forest management, and it is these models with which this paper is primarily concerned.

Growth models form a continuum from normal yield tables to single tree models (Leary 1991). I emphasize the nature and detail of growth models by discussing whole stand, stand class, and single tree models. *Whole stand models* draw on stand-level parameters such as stocking (trees/ha), stand basal area, and standing volume to predict stand growth or yield. Size distributions may be inferred, but few details of individual trees are available. *Stand class models* provide more details by simulating several classes within the stand (e.g., stand table projection). The approach is a compromise between whole stand models (a single class for all trees) and single tree models (a class for each tree). The minimum input required for a single tree model is a list containing the size of every tree in the stand.

Other models draw on different foundations to help understand tree growth and stand dynamics, but have not yet been used successfully for predicting timber yields. Succession models (Shugart 1984, Botkin 1993) attempt to model species succession, but may not provide reliable information on timber yields. Process models attempt to model the processes of growth, taking as input light, temperature, and soil nutrient levels, and modeling photosynthesis and the allocation of photosynthates to roots, stems, and leaves (Sievanen et al. 1988, Bossel et al. 1991). Most process models focus on single species, but some attempts are being made to formulate such models for mixed stands (Lavigne 1992). The FORCYTE

¹ Throughout this paper, I make no attempt to cite all publications, but merely choose a few examples relevant to the tropics. Omission does not reflect on the merits of any work.

(Kimmins et al. 1990) and LINKAGES (Pastor and Post 1986) models focus on the carbon and nitrogen cycles and have been used to examine the effects of forest management on future productivity and ecosystem structure (Yarie 1990), but are ultimately driven by simple yield tables and are not intended to provide yield estimates for management. Bossel and Krieger (1991) used a process approach to build a canopy layer model for Malaysian forests. Such models currently offer limited practical relevance, in part because of difficulties in estimating the many parameters (Bossel et al. 1989), so some empirical content remains necessary for efficient models for forest management. The challenge is to provide sufficient physiological and ecological basis to ensure realistic predictions under a variety of site and stand conditions, even when empirical data for calibration are limited.

WHOLE STAND MODELS

Yields may be tabulated by age, site, and sometimes stand density (Vuokila 1965), and some yield tables have been developed for mixed stands (Duerr and Gevorkiantz 1938). Growth tables avoid the need for an age estimate by tabulating expected growth by stand density, time since logging, etc. (Spurr 1952, p. 265), but offer little utility for tropical forests.

Growth percentages have been used to predict growth in temperate and tropical forests. The percentages may be applied to individual trees, stand tables, or to estimates of standing volume. Wahlenberg (1941) warned that these methods were unreliable at best and could be very deceptive.

Mendoza and Gumpal (1987) predicted timber yields of dipterocarps in the Philippines from residual stand basal area and time since logging:

$$\text{Log}(Y_T) = 1.34 + 0.394 \text{Log}(B_0) + 0.346 \text{Log}(T) + 0.00275 S/T$$

where Y_T is timber yield (m^3/ha > 15 cm dbh) T yr after logging ($T > 0$), B_0 is residual basal area (m^2/ha) of dipterocarps (15+ cm dbh) after logging and S is the average height (m) of residual dipterocarp trees (50–80 cm dbh). While it is dangerous to extrapolate this equation, it provided useful estimates of time to and yield of the next harvest.

Yield equations assume a certain management regime throughout the projection, while growth equations allow logging and other treatments to be simulated at any time. Nelson (1963) argued that stand basal area increment (ΔB) of even-aged stands decreased asymptotically with age (A), increased with site index (S), and decreased as the stand basal area (B) diverged from the optimum:

$$\Delta B = \beta_0 + \beta_1 B/A + (\beta_2 + \beta_3/A + \beta_4 S) B^2$$

Vanclay (1988) used a similar relationship for stand basal area increment ($\text{m}^2/\text{ha}/\text{ann}$) in uneven-aged stands of *Callitris*, a subtropical conifer:

$$\text{Log}(\Delta B) = -3.071 + 1.094 \text{Log}(B) + 0.007402 B S - 0.2258 B$$

Both equations should provide sensible predictions for extremes of stand basal area (B , m^2/ha) and site quality (S , m).

Some analyses do not exploit the relationship between growth and yield, and the sum of successive growth estimates may differ from tabulated yields. Buckman (1962) and Clutter (1963) argued the need for compatibility and constructed compatible growth and yield equations which would give consistent estimates.

Clutter (1963) modified Schumacher's (1939) equation to accommodate basal area growth:

$$\text{Log}(V) = \beta_0 + \beta_1 S + \beta_2 \text{Log}(B) + \beta_3/A$$

and differentiated it to give the growth equation:

$$dV/dt = \beta_2(V/B)(dB/dt) - \beta_3 V/A^2$$

where V is standing volume at age A years. This led to five compatible equations for standing volume, basal area increment, volume growth, predicted basal area, and predicted volume yield (Clutter 1963, Sullivan and Clutter 1972), which can be estimated simultaneously (Burkhart and Sprinz 1984). The Bertalanffy (or Chapman-Richards) and several similar functions (Zeide 1989, 1990) also provide compatible growth and yield equations.

Moser and Hall (1969) predicted basal area increment of uneven-aged stands from stand basal area. By assuming an allometric relationship between stand volume and basal area, they could predict the volume increment from:

$$\Delta V = \beta_1 V(\beta_2 B^{\beta_3 - 1} - \beta_4)$$

Integrating and substituting for volume leads to compatible growth and yield equations for both basal area and volume.

Effective forest management requires more than simple estimates of standing volume, so some whole stand models predict size distributions. Many diameter distributions can be approximated by the Weibull distribution (Bailey and Dell 1973, Schreuder and Swank 1974), and since height and volume can be expressed as allometric functions of diameter, their distribution may be estimated with simple transformations of the Weibull distribution for diameter (Stacey and Mihram 1965). Hyink and Moser (1979) estimated yields by updating the three parameters describing the diameter distribution, using the stocking and sum of diameters. This approach is known as *parameter prediction*, but a better alternative is the *parameter recovery* approach (Reynolds et al. 1988). Instead of predicting the Weibull parameters directly, the stand basal area and mean diameter are predicted, and the distribution is estimated by matching the moments of the Weibull to the predicted stand attributes. The Weibull distribution can describe a great variety of shapes (Krug et al. 1984), but is always unimodal and is not suited to all stands. If the future stand basal area and stocking can be predicted, other allied methods may be used to update the existing stand table (Nepal and Somers 1992). However, all these methods are useful only where there are a limited number of species.

STAND CLASS MODELS

Stand class models simulate several classes of trees and are a compromise between whole stand models (one class) and single tree models (a class for each individual). The stand need not be partitioned into metric classes (e.g., 10 cm dbh classes); a more flexible partition may be used (e.g., "cohorts," or groups of trees with similar species, size, and other characteristics).

Stand Table Projection

Stand table projection may be the most popular way to forecast yields from tropical forests. The future stand is predicted from the present stand table using estimated diameter increments for each class. Diameter increments may be estimated from equations or directly from class mean increments observed in a database. The future stand can be forecast in three ways. One way is to increment the class boundaries so that the classes retain the same trees. An alternative which retains the original classes assumes that trees are uniformly distributed through each class, and estimate upgrowth via "movement ratios" calculated from class width and average increment (Husch et al. 1982, p. 296). The third method uses the actual movement of trees rather than movement ratios (Wahlenberg 1941).

There are important differences between these alternatives, despite the superficial similarities. For example (Husch et al. 1982, p. 299), Wahlenberg's approach may correctly predict 30, 50, and 20% of trees moving 0, 1, and 2 classes, while the movement ratio approach predicts 6, 94, and 0% respectively, underestimating growth. The second and third approaches may proliferate classes with fractional numbers of stems: this difficulty is avoided by the first approach. This proliferation can be reduced by using longer projection intervals, employing narrower classes, or by assuming a non-uniform distribution of stems within each class. Alternatively, probabilities can be accumulated until an integer number of stems can be projected. Greater flexibility can be provided by varying class widths and by estimating upgrowth using equations.

A common error in extrapolating movement ratios to longer projection cycles may introduce another significant discrepancy. If the movement ratio for a single cycle is 0.6, then the correct computation for three intervals should give 6% (0.6^3), 29%, 43%, and 22% (0.6^3) moving 0, 1, 2, and 3 classes respectively. A common mistake is to multiply the average growth rate by the interval ($0.6 \times 3 = 1.8$), and thus obtain 0%, 20%, 80%, and 0% respectively (Howard and Valerio 1992), which may overestimate the harvest.

The Ghafosim (Ghana Forest Simulation) model (Alder 1990) used 13 classes for each species group, with shaded and sunlit categories for each of the size classes (<10, 10-29, 30-49, . . . , ≥ 150 cm dbh; all trees ≥ 70 cm assumed sunlit). Movement and mortality was estimated for each class directly from the permanent plot database. Shaded and sunlit classes do not interact, but shaded trees become sunlit at 70 cm dbh, and trees may be moved to the shaded category to ensure the number of sunlit trees in any size class does not exceed a maximum consistent with natural stand structures.

Transition Matrices

Transition matrices formalize stand table projection, by assuming that a tree in one of a finite number of size classes has a known probability of moving to another class, dependent only upon its current size. During any period, a tree must either remain in its class, grow into another class, or die. The probabilities of movement can be expressed as a matrix (**M**), and used to predict change during a single time interval $V_1 = MV_0$, or over several time intervals: $V_n = M^n V_0$ where **M** represents the transition matrix and V_0 and V_n are vectors describing the initial and final states respectively. In forestry, V_0 is generally a list representing the initial numbers of trees in each diameter class (i.e., the stand table). Projections are

made in multiples of the measurement interval represented in the data, but a 1-yr matrix (\mathbf{P}) may be estimated from an n -year matrix (\mathbf{M}) such that $\mathbf{P}^n \approx \mathbf{M}$ (Harrison and Michie 1985).

Leslie (1945, 1948) pioneered the use of these matrices for animal populations using states based on age. They were adapted for stages of insect development by Lefkovich (1965), and for forestry (diameter classes) by Usher (1966). Bosch (1971) used a Leslie matrix to study redwood forests, but most forestry applications use Usher's diameter class matrix. The matrix requires fewer parameters if the time interval and class width are chosen so that no tree can grow more than one class during any period, so that growth is defined by a single probability.

Usher (1966) argued that the dominant eigenvalue of the matrix revealed the maximum exploitation, and that its eigenvector indicated the stable stand structure. These seem to be shaped more by survival than by recruitment (Enright and Watson 1991). An exponential increase in tree numbers is assumed, so the eigenvector may indicate optimal structure, but not stand density. The eigenvalue may indicate species dynamics and successional status (Enright and Ogden 1979), but it is not clear whether the eigenvalues are a characteristic of the species, an indicator of forest condition, or an artifact of the method. Enright and Watson (1991) stressed that these matrix methods cannot portray future stand conditions, but may reveal demography under current stand conditions.

Matrix probabilities depend only on the initial state and so assume that tree growth depends only on diameter. Many applications do not allow the probabilities to change over time, and so cannot account for different sites, stand structures or for temporal changes in competition. Theoretical (Hulst 1979) and empirical (Binkley 1980, Roberts and Hruska 1986) studies suggest that these assumptions are untenable for modeling forest dynamics. These assumptions may be avoided by estimating a new matrix on each iteration, either from a subset of the database or by using equations (Solomon et al. 1986), or by partitioning the stand into more fractions (e.g., based on species and crown class as well as size; Alder 1990). Despite these restrictive assumptions, matrix models remain popular.

Buongiorno and Michie's (1980) model for a hardwood forest assumed:

$$\mathbf{Y}_{i+1} = (\mathbf{M} + \mathbf{N}) \cdot (\mathbf{Y}_i - \mathbf{H}_i) + \mathbf{C}$$

where \mathbf{Y}_i is the stand table at time i , \mathbf{M} is a bidiagonal transition matrix, and \mathbf{H}_i is the harvest at time i . \mathbf{N} and \mathbf{C} were estimated from the regression equation: $R = 109 + 0.27N - 9.65B$, where R is total recruitment (stems/ha/ann), N is total stocking (stems/ha) and B is stand basal area (m^2/ha). The first row of the sparse matrix \mathbf{N} predicts recruitment as $N_i = 0.27 - 9.65B_i$, where B_i is the basal area of a tree at the midpoint of class i . The vector \mathbf{C} contains only the intercept, 109. By representing the harvest as a vector \mathbf{H} separate from the transition matrix, Buongiorno and Michie (1980) could examine harvesting options more easily. They found that undisturbed growth would tend toward an equilibrium with equal numbers in each class, and that diameter limit cutting provided the optimal harvest. In contrast, Mendoza and Setyarso's (1986) matrix model for Indonesian forests indicated that a selection harvest cutting some trees in each merchantable size class would sustain higher yields than simple diameter limit cutting. Their model also revealed that harvesting practices in Indonesia could not be sustained, as residual stockings were too low to enable the next anticipated harvest in 35 years.

Michie and Buongiorno (1984) compared four approaches for computing matrix coefficients and recommended matrices be compiled using the actual movement of trees from the initial into new classes. An alternative is to exploit the similarity in growth pattern of trees in adjacent cells by using probabilistic regression (Bonnor and Magnussen 1988). The latter approach may provide greater precision especially where data are limited.

Stand Class Distribution Models

Simple stand table projection and matrix approaches may allow some stems to move n classes in n projection intervals, and may thus overestimate yields. Two possible solutions are to use narrower classes or to smooth the stand table.

Campbell (1981) smoothed his stand table with quadratic splines, constrained to be smooth and continuous, positive through their range with the right stocking in each class, and reaching zero in the smallest and largest classes. Unlike the Weibull distribution, spline curves (Smith 1979) can fit stands which are not unimodal. Increments were estimated for each class, and a new largest class was initiated only when upgrowth exceeded a specified criterion. The smallest class was absorbed when upgrowth reduced stocking to a subcritical amount. The technique can be applied to uneven-aged stands, but becomes complex if many species groups are modeled.

Korsgaard (1989) assumed that a J-curve defined by de Liocourt's quotient described the distribution of stem size in dipterocarp forests. He found that quotients ranged from 1.3 to 1.6 and remained fairly constant. This distribution results in smaller, more realistic movement ratios. A J-distribution with quotient 1.5 could predict 20% less upgrowth than a uniform distribution (Korsgaard 1989). The model has been applied to mixed swamp forests in Sarawak (Chai and Sia 1989) and to Amazon rainforests (Silva 1989). Smith (1992) suggested that the J-distribution was transient and may not be suitable to predict upgrowth after logging.

Representative Trees Approaches

Several trees can be selected to represent cohorts of trees and form the basis of modeling. This generalization of stand table projection allows classes or cohorts to be formed on characteristics other than dbh. Cohorts need not be metric classes (e.g., 10 cm dbh classes), but may vary in scope and can be formed so that there are no empty classes. For example, Alder's (1979) model for pine plantations in Africa used deciles.

Leary's (1979) model for mixed stands allowed varying levels of resolution. At the lowest level of resolution, it used a single cohort for each species. At the intermediate level, it simulated three cohorts (based on tree size) for each species. At its highest level of resolution, each cohort represented an individual tree, and the model became a tree list model. Thus users could select a resolution suited to their requirements and budget. The potential diameter increment was predicted for mean tree of the cohort, modified for stand density and competition, and multiplied by the number of trees in the cohort. The original list of individual diameters was not discarded, but was used at the end of the simulation to update each tree with its share of the accumulated increment.

Vanclay (1989a) described a tree list model for tropical rainforests in Queensland. Species were grouped according to growth habit, size at maturity, and

tree-marking guidelines (Preston and Vanclay 1988). Each cohort was characterized by its species group code, diameter, and expansion factor (stems/ha represented by that cohort). The model maintained the number of cohorts near the maximum of 200 by doubling and merging records. Cohorts of small trees may contain many individuals; as they attained an economic size they split, reflecting increment distributions observed on permanent plots. Cohorts of overmature trees were merged as their expansion factors reduced through mortality and logging. The model was subsequently enhanced to retain individual species identities (Vanclay 1994a,b).

SINGLE TREE AND TREE LIST MODELS

As the number of trees per cohort approaches unity, the distinction between stand class approaches and single tree models becomes blurred, especially for tree list or cohort models. Single tree models simulate each individual tree (i.e., expansion factor always 1.0), whereas tree list approaches may have several trees in a cohort (expansion factor can be any real number >0). A single tree approach might model mortality stochastically to maintain expansion factors at exactly one, whereas a tree list model could deterministically reduce expansion factors to represent less than one tree per cohort.

Single Tree Spatial Models

Spatial models are of little relevance to tropical forests since suitable data are rarely available. However, these models have provided the basis for many other approaches, so an overview is appropriate. Most single tree spatial models account for two-dimensional competition, but in uneven-aged stands, competition may be three-dimensional.

Newnham's (1964, Newnham and Smith 1964) model for even-aged stands of Douglas-fir drew on three assumptions that have provided the basis for many other models, even though they have not been confirmed by independent tests (Larocque and Marshall 1988): (1) a tree free of competition has the diameter growth of an open grown tree of equal diameter, (2) a tree subject to competition has its increment reduced by an amount proportional to the level of competition, and (3) mortality occurs when diameter growth falls below a threshold level.

Models may need to accommodate some variability, since use of general trends throughout may produce untenable results (e.g., all trees identical). One solution is to model some components stochastically. Mitchell (1969) assumed that in even-aged stands: (1) annual elongation of branches depends on current height growth, so that crown radial growth can be predicted from height growth, subject to space limitations imposed by competing trees; (2) height of any tree can be predicted from dominant tree height and relative crown width compared to open-grown trees; (3) suppression and mortality can be predicted from relative crown width; (4) dbh and bole volume can be predicted from tree height and crown width. Branch length is predicted stochastically and the variation propagates to all components of the model. The approach works for even-aged white spruce (Mitchell 1969) and Douglas-fir (Mitchell 1975), but has limited utility for tropical forests where measurement difficulties make height an inferior driving variable.

Single Tree Nonspatial Models

Spatial growth models enable detailed investigations of silvicultural alternatives in intensively managed stands, but the high cost of suitable data may restrict their

use to research applications. Nonspatial methods may offer an efficient alternative for yield forecasting.

JABOWA (Botkin et al. 1972, Botkin 1993) did not predict timber yields, but was used to evaluate concepts of ecology, especially succession. It simulated annual growth on 10×10 meter plots, and modeled growth, mortality, and regeneration. Growth prediction was based on relative tree size (i.e., D/D_{\max} and H/H_{\max}) modified by environmental factors, and a simple quadratic relationship was assumed between tree height and diameter. Mortality was predicted as a probability and resolved by a random number. Random numbers were also used to decide the number and species of recruits. The approach has been adapted for many other ecosystems (Shugart 1984, Botkin 1993), including the Kiambram model (Shugart et al. 1980) for subtropical rainforest in Australia, and Doyle's (1981) model for tropical montane forest.

Tree List Models

At low resolution, tree list models (Leary 1979, Stage 1973) are stand class approaches, but with suitable resolution they may improve on the nonspatial single tree approach. A single tree model maintains a list of attributes (species, dbh, etc.) for each tree. The tree list approach does all this, but also simulates the number of trees represented by each tree record. This simplifies deterministic modeling of mortality, as the expansion factor may be a fraction. The resolution of such models can be varied, so that they can provide whole stand, stand class, or single tree predictions according to the user's requirements (Leary 1979).

Prognosis (Stage 1973, Wykoff 1986) is a tree list model for natural forests in North America. Key functions include diameter increment, height increment, crown dynamics, and mortality. Although these functions are empirical, they have been carefully formulated to provide reliable predictions over a wide range of sites and stand conditions (Wykoff 1990). The model uses a "swindle" in which tree records are incremented stochastically when there are many records, but are deterministically "tripled" when there are few records. In either case, the aggregate stand increment is assumed to be deterministic. Prognosis is now in its fifth version (Wykoff 1986), and 12 regional variants have been implemented (Farr and Johnson 1988).

Tree list models can be very flexible, allowing user control over many parameters and offering deterministic or stochastic operation. Vanclay's (1991c, 1994a) model used probabilistic functions to predict increment, mortality, and recruitment. In stochastic mode, the predicted probabilities are compared with random numbers to determine the fate of the cohort. In deterministic mode, growth predictions represent proportions to be incremented one centimeter. If the expansion factor is small, probabilities are accumulated and the whole cohort incremented when the accumulated probability reaches one. An advantage of the approach is that all subjective and control parameters in the model can be under user control, amenable to sensitivity testing (Kimmings et al. 1990).

Comparing Alternatives

Few empirical comparisons between models for mixed forests have been published. Ek and Monserud (1979) reported a comparison of a deterministic stand class model (5 cm dbh classes), and a stochastic single tree spatial model (average of 4 predictions). Both models showed close agreement with reality for short-

term predictions (5 to 26 yr) and gave comparable predictions for long-term (120 yr) forecasts.

Several estimates from a stochastic model are necessary to indicate expected growth and variability, and most information needs can be provided more efficiently with deterministic models. Variance propagation techniques (Mowrer and Frayer 1986, Gertner 1987a) may provide an efficient alternative for estimating variability. Complex models may propagate more variance than whole stand models (Mowrer 1989). This means that errors in inventory data may be magnified by methods such as single tree models but remain unaltered by less complex models such as whole stand models. The implication is that models should not be unnecessarily complex but should be designed to satisfy specific information needs.

GROWTH MODEL CONSTRUCTION

Model development involves exploring data to provide new insights into forest dynamics and reveal gaps in present knowledge. The model may be used to study forest dynamics, to explore silvicultural and management options, and to forecast future harvests and stand conditions. These applications indicate directions for model development. Modelers should critically explore available data and existing knowledge and design models to be robust in extrapolation. They should encourage both exploratory and operational use of the model.

There are several challenges to be addressed when building a growth model for tropical moist forests. There may be hundreds of species, and these may need to be grouped for analysis. Suitable equations must be formulated and estimated using appropriate analytical techniques. Finally, the components need to be assembled to form a useful model that is (Kimmins et al. 1990):

- ▶ Sufficiently general to be applicable to many stands.
- ▶ Modular with growth prediction separate from management simulators.
- ▶ Able to simulate effects of the major management options.
- ▶ As mechanistic as possible using biologically sound functions rather than empirical surrogates.
- ▶ Driven by operational inventory data rather than by data that require prolonged scientific measurement.
- ▶ Sufficiently diagnostic to permit users to identify data errors and unacceptable model performance (each component should provide a basis for rejection).
- ▶ Flexible with options to alter simulation of individual processes.
- ▶ Controlled by the user, with subjective parameters kept to a minimum and amenable to sensitivity testing by the user.
- ▶ User-friendly, with flexible "plain English" reporting to simplify interpretation of results.

PREREQUISITES

Data for Growth Models

Growth models rely on data for calibration. Too often, the model is dictated by limitations of the data rather than the needs of the application. Most models have similar data requirements, and standard procedures have been established (Alder and Synnott 1992, Campbell 1989, Vanclay 1991a). Since few tropical tree species

are amenable to stem analysis (Mariaux 1981), data must be obtained from re-measurements on permanent sample plots. Remeasurements must span a sufficient period to average anomalous weather patterns and ensure that growth is not obscured by measurement error. Limited but reliable data covering the extremes are more useful than copious data clustered about the mean. Graphical (Beetson et al. 1992) and computer algorithms (Kennard and Stone 1969, Gertner 1987b) may guide sampling schemes. Both passive monitoring and treatment response data from designed experiments are necessary. Extreme treatments need not be applied in practice but remain essential to define the response surface for growth models.

The accuracy of growth predictions depend largely on the stratification of site (Gertner and Dzialowy 1984, Smith and Burkhart 1984), but there are few techniques for site productivity assessment in tropical moist forests. The average height of dominant and codominant trees remaining after logging has been used to indicate site productivity in dipterocarp forests (Canonizado 1978, Mendoza and Gumpal 1987). Vanclay (1992a) favored a growth index based on permanent plot data, but estimated for temporary plots from presence or absence of several indicator species. Further research is necessary to develop efficient methods for site evaluation in tropical forests, and this will require comparisons with long-term permanent plot records to ensure reproducible and consistent estimates which are not unduly influenced by stand condition or management history.

Long-term studies are especially important for validation and to detect subtle trends, so "old" plots and data should not be neglected but treasured. Care should be taken in the maintenance of all existing plots and in the archiving of plot records. Collaboration between institutions and nations can expand the database, provide new extremes, and reduce duplication (Chappell et al. 1988).

Strategies for Grouping Data

Growth models must provide prediction functions for each of the many species found in tropical forests. Many species will have insufficient data for reliable parameter estimation, and the best way to provide unbiased prediction equations may be to group species that are in some sense similar. Botanical affinity may not provide a reliable basis; e.g., the genus *Eucalyptus* includes both the world's tallest hardwoods (*E. regnans*) and shrubs which barely attain 2 m maturity (e.g., *E. vernicosa*). Ecological guilds (Swaine and Whitmore 1988) may also be inadequate for growth modeling.

Meldahl et al. (1985) argued that the grouping should reflect the dynamics of growth as indicated by increment functions. They used cluster analysis on equation coefficients but obtained reasonable results only with regressions on a single explanatory variable. Diameter increment was predicted from the basal area in larger trees ($\Delta D = \beta_0 + \beta_1 BAL$), and cluster analysis led to 20 clusters from 110 equations. The number of data assigned to each cluster varied greatly, so the outcome was adjusted subjectively. The adequacy of final groups was confirmed by fitting a multiparameter linear function.

Vanclay (1991b) used pairwise comparisons between multiparameter diameter increment regressions. Initial comparisons were made between species with many data, and species with few data were only later compared with one of these major groups. There is, unfortunately, no guarantee that the outcome is optimal, and the grouping thus derived is specific to the particular data set and increment

function used. Despite these weaknesses, it provided a useful classification of 237 species into 41 groups for diameter increment prediction in Queensland rainforests.

Leech et al. (1991) grouped 27 species for volume equation estimation and their approach may work with growth data. They used a polynomial equation to predict tree volume from diameter, and created a vector of coefficients for each species: $u'_i = [\beta_{0i}, \beta_{1i}, \beta_{2i}, \dots, \beta_{ni}]$, so that Hotelling's T^2 between two species i and j could be defined as

$$d_{ij}^2 = (u_i - u_j)' S^{-1} (u_i - u_j)$$

where S^{-1} is the combined covariance matrix of regression coefficients for species i and j . By calculating all possible combinations, a symmetric matrix with a zero diagonal can be formed. Principal coordinate analysis was used to group species from this matrix. Valid results require polynomials of the same order, in which the sign of the highest term is the same.

An aggregation based on diameter increment may not be suited to modeling mortality (Vanclay 1991d), and it may be desirable to retain species identities throughout growth simulations, even though species are grouped for parameter estimation.

Choice of Equation

Empirical equations describe the behavior of the response (dependent) variable without inferring causes or explanations. This does not preclude biologically realistic predictions; empirical equations can and should be formulated to behave in a realistic way across a wide range of site and stand conditions.

Theoretical equations have an underlying hypothesis of cause or explanation. There are few such equations formulated expressly for forestry, and some from other disciplines may be rather empirical in forestry applications. Bertalanffy (1942, 1957, 1968) hypothesized that the growth of an organism could be represented as the difference between the synthesis and degradation of its building materials. He assumed that anabolism (synthesis) and catabolism (degradation) could be expressed as allometric functions of weight (W), and thus growth (dW/dt) would approximate $dW/dt = nW^m - pW^q$. In micro-organisms, catabolism is generally directly proportional to weight, so he proposed $dW/dt = nW^m - pW$.

This equation was generalized by Richards (1959) for plant growth and by Chapman (1961) for fisheries and is often known as the Chapman-Richards equation (Pienaar and Turnbull 1973). Turnbull (1963, Pienaar and Turnbull 1973) examined the use of the equation for modeling the growth of even-aged forest stands. Some forms of this and other nonlinear equations may not provide good parameter estimates, and Ratkowsky (1983, 1990) suggested suitable reparameterizations for efficient estimation.

Martin and Ek (1984) found that carefully formulated empirical equations could be more accurate than theoretical equations, but felt that theoretically based equations may provide more reliable extrapolations. Kowalski and Guire (1974) emphasized that "finding a function that makes biological sense has much more to recommend it than searching for a function that will provide only a close mathematical fit. Mere goodness of fit is no justification for adopting a given model since several functions may fit the data equally well." Any relationship that violates

accepted biological principles should be rejected, even if it results in efficient predictions for a particular data set (Hamilton 1990).

Regression Analyses

There are many techniques for fitting equations to data, and the appropriate one to use depends on the nature of the data and the model. Ultimately, however, the method of obtaining a model is irrelevant. The important thing is whether the model provides useful predictions.

Unusual data points often occur in growth data and may have an excessive effect on least squares estimates of coefficients. The best way to check data, fitted models, and statistical assumptions is to plot the data, model, and residuals (Wilson 1979). Screening of data and the removal of outliers is standard practice (Arney 1985) but should be documented so that results are reproducible. Screening forces the researcher to evaluate the data critically, a discipline not imposed by alternatives such as robust estimation (Hamilton 1979).

Two or more measurements are often taken from each tree or plot. These repeated measurements tend to be correlated and are thus not statistically independent. Ordinary least squares regression provide unbiased parameter estimates but underestimate the covariance matrix and residual variance (Davis and West 1981), precluding proper hypothesis tests. One solution is to use one observation per sampling unit to formulate the model and test for significance and to recalibrate the model using the full data set (West et al. 1984, 1986). The problem may not be serious if the number of remeasurements is small in comparison with the number of sampling units. Borders et al. (1988) found no serial correlation in data derived from nonoverlapping growth intervals and suggested the problem may be model dependent.

The coefficient of determination (R^2) is often used to measure goodness-of-fit, but has several limitations (Helland 1987) and may be misleading. The Furnival (1961) index provides a better basis for comparison by expressing the average standard error in the original untransformed units. The R^2 also gives an overoptimistic indication of the model's predictive ability, and the Prediction Sum of Squares or PRESS (Allen 1971) provides a better indication of predictive ability. Modelers should not be pre-occupied with these indices but should ensure that predictions are biologically reasonable over a wide range of possible values for the explanatory variables and that the coefficients are reasonable estimates of the effects of the individual terms (Snee 1977).

MODELING DIAMETER INCREMENT

Models can predict growth or future size of stem diameter or basal area. All four approaches are related mathematically [e.g., $d(kD^2)/dt = 2kD \cdot dD/dt$], and there should be little difference between the alternatives. Any differences in the fit may be due to the error structure and implied functional relationship, rather than the superiority of one model or another. Using basal area increment rather than diameter increment as the response variable provides higher values of R^2 (Bella 1971), but West (1980) and Shifley (1987) found no difference in the precision of diameter and basal area increment equations.

Explanatory Variables

Many variables used in plantation growth models have little relevance in tropical rainforests (e.g., age, top height, mean diameter), since growth must be pre-

dicted from accessible variables such as diameter and stand basal area. Many other variables (e.g., crown size, position, and illumination) are correlated with increment but it may be difficult to predict how these variables themselves change over time. Several models (Ek and Monserud 1974, Alder 1979) predict diameter growth from height increment, but this is not well suited to tropical forests where height measurement is difficult and inaccurate.

The basal area in larger trees (*BAL*) has been found useful in many studies (Wykoff 1990, Vanclay 1991b), and Meldahl et al. (1985) found it the most useful single variable in predicting diameter increment. It is a surrogate for "one-sided" competition for light and is complementary to stand basal area which indicates "two-sided" competition (for moisture and nutrients). Basal area in larger trees may be more suitable than relative size (e.g., BAL/B or \bar{D}/D), which may result in a counterintuitive response to thinning.

Data from plots measured once every several years are often used to predict annual growth. Biased estimates may result if a growth function is fitted to initial values of tree and stand variables, so these should be adjusted to represent the middle of the interval (e.g., use mean diameter $(D_n + D_0)/2$, not initial diameter D_0). The adjustment is not needed for the yield model.

Competition Indices and Allocation Rules

Competition indices attempt to quantify in a simple index, the effects of neighboring plants on the growth of an individual in a forest stand. They may be absolute values such as stand basal area or relative indices comparing actual with potential growth. Many competition indices have been proposed, but empirical trials suggest that basal area may be as useful as many of the other indices (Lorimer 1983, Martin and Ek 1984, Barclay and Layton 1990). However, Biging and Dobberty (1992) found some spatial indices based on crown characteristics which performed well, especially for shade-tolerant species. One robust implementation is to use the competition index to modify predicted potential increments (Ek and Monserud 1974, Leary 1979, Arney 1985). However, suitable data may not be available, and correlations for the modifier may be poor (Shifley 1987). To estimate the potential growth rate, Shifley (1987) used the 5% of trees which grew fastest between the first and last measures. Growth estimates from single consecutive remeasures may select for measurement errors rather than real growth. The potential growth equation may also be based on trees assessed as open-grown or free of competition.

Diameter increments may also be obtained by apportioning stand-level estimates among the trees in the stand. Stand increment may be predicted as basal area increment (Gibson et al. 1969, Clutter and Allison 1974) or as increment in the sum of diameters (Leary 1979, 1980). Basal area increments (ΔB_i) may be allocated according to tree size: $\Delta B_i / \sum \Delta B_i = B_i^w / \sum B_i^w$, where the weights w may vary from 0.93 (Campbell et al. 1979) to 1.25 (Opie 1972) for *Eucalyptus regnans*. In uneven-aged *Callitris* forest, the smaller trees get a greater share of the increment, so Vanclay (1988) estimated an allocation rule from the mean and standard deviation of diameters. Leary et al.'s (1979b) allocation rule for the increment in sum of diameters was estimated from six parameters, some of which depended on the species, others of which depended on stand condition. These methods may provide good results for stands with few species, but become complex if many species are present.

Diameter Increment Functions

Many increment functions have been published, and only a few which do not use age are considered here. Three broad classes (empirical, theoretical, probabilistic) allow generalizations to be made. No distinction is made between diameter and basal area increment, or between growth and yield forms.

Empirical equations describe the observed growth without hypotheses of cause or explanation. They are useful for interpolation, but may be unreliable when extrapolated (Payandeh 1983). However, empirical equations can be formulated to provide biologically realistic predictions across a wide range of values (Wykoff 1990), and may provide better predictions than theoretical equations (Martin and Ek 1984). Zeide (1990) argued that growth equations should have "an upper asymptote to express the fact that any growth is limited. Nonasymptotic growth is always temporary and can be rendered by a segment of an asymptotic model. In this sense, . . . nonasymptotic equations cannot be considered growth equations." Care is required with the quadratic $\Delta D = \beta_0 + \beta_1 D + \beta_2 D^2$, which may not provide robust results (e.g., if $\beta_2 > 0$, there is no maximum and it may overestimate growth of big trees).

Hilt (1983) used a two-stage analysis to estimate increment in even-aged oak forests. His first stage fitted $\Delta D^2 = \beta D^2$ for each plot, and the second stage fitted

$$\text{Log}(\beta) = \gamma_0 + \gamma_1 \text{Log}(S) + \gamma_2 D + \gamma_3 P$$

where D is the quadratic mean stand diameter, and P is percent stocking. The final model expressed as a diameter increment function was:

$$\Delta D = \alpha S^{\gamma_1} D e^{\gamma_2 D + \gamma_3 P}$$

Theoretical equations offer some explanation of growth but may not provide better predictions (Martin and Ek 1984). There is no particular theoretical equation specifically for tree growth (Sweda and Koide 1981), but the Bertalanffy equation may be generalized for diameter increment:

$$dD/dt = nD^m - pD = pD\{(D_{\max}/D)^{1-m} - 1\}$$

Unlike the mass of an organism, tree biomass is not zero when dbh is zero, so Leary (1980, Hahn and Leary 1979) included an intercept (β_0) to improve increment predictions for small trees:

$$dD/dt = \beta_0 + \beta_1 D^{\beta_2} + \beta_3 S.R.D^{\beta_4}$$

where D is diameter, S is site index and R is crown ratio.

Shifley (1987) adapted the Bertalanffy equation for potential growth of many species (e.g., for eastern red cedar):

$$dB/dt = (0.0124B^{0.515} - 0.0149B)(0.397 + 0.00236S + 0.0749R)$$

where B is tree basal area (m^2), S is site index (m) at age 50, and R is crown ratio ($1 \leq R \leq 9$). This was fitted in two stages. First, $dB/dt = \alpha B^{\beta} - \gamma B$ was fitted and the asymptote $A = (\gamma/\alpha)^{1/(\beta-1)}$ compared with the national register of big trees. If it seemed unreasonable, the parameter γ was revised: $\gamma = \alpha A^{\beta-1}$. The second stage estimated the effects of site and crown condition. A modifier predicted from tree size and competition further reduced the potential increments.

Several empirical functions mimic the shape of these theoretical equations, and may be easier to fit to data. By assuming that increment becomes small as trees

become very large, they may avoid the need to identify the maximum attainable diameter, which may not be a robust characteristic (since heartwood has no respiratory cost; Prentice and Helmisaari 1991). Diameter increment functions in the Prognosis model assume (Wykoff 1990):

$$\text{Log}(\Delta D^2) = \text{SITE} + \text{COMP} + \beta_1 \text{Log}(D) + \beta_2 D^2$$

where *SITE* and *COMP* reflect site and competition respectively. *SITE* is a function of slope, aspect, and elevation, and *COMP* is a function of crown ratio, competition, and relative size ($BAL/\text{Log}(D + 1)$). The equation provides sensible increment predictions for any site, tree size, and stand density. A similar equation without crown characteristics was used to predict diameter increments in Queensland rainforests (e.g., for *Flindersia pimenteliana*, Vanclay 1991b):

$$\begin{aligned} \text{Log}(\Delta D + 0.02) = & -0.2354 - 0.06056 D + 0.9673 \text{Log}(D) \\ & + 0.08851 \text{S.Log}(D) - 0.9366 \text{Log}(B) - 0.02684 BAL \end{aligned}$$

Lowell and Mitchell (1987) used a probabilistic function to predict diameter increment and mortality simultaneously in even-aged oak forest. Vanclay (1991c) used a similar probabilistic function to predict the probability that a rainforest tree would complete one centimeter of growth during a given year (i.e., that a tree less than n cm dbh would attain a size of n cm or more within a 1-yr interval, for any integer n) (e.g., for *F. pimenteliana*):

$$\begin{aligned} P = (1 + e^{-0.7378 + 0.1079 D - 1.987 \text{Log}(D) - 0.1455 \text{S.Log}(D)} \\ + 1.994 \text{Log}(B) + 0.03548 BAL - 0.4221 S})^{-1} \end{aligned}$$

where P is the predicted probability, B is stand basal area (m^2/ha), BAL is basal area in larger trees (m^2/ha), and S is a binary variable indicating preferred soils.

MORTALITY AND MERCHANTABILITY

Many growth models assume negligible mortality in well-managed stands. This may be reasonable for some plantations but is inappropriate in natural forests. Stage and Renner (1988) found that 80% of the variability in volume predictions in temperate forests was due to uncertainty in mortality estimates. Yield studies require estimates not only of natural mortality, but also of injury caused by harvesting.

Regular Mortality

Reineke (1933), Yoda et al. (1963), and others (Smith and Hann 1984, Lonsdale 1990) studied the onset of competition-induced mortality in even-aged monocultures, and many growth models draw on these theories. Competition in mixed forests is less tractable, but the need for light, nutrients, and physical space remains, and any permanent reduction below the minimum requirements will eventually lead to death. Thus it should be possible to predict limiting conditions directly from growing space, competition, or crown dynamics.

Newnham (1964) assumed that trees would die if predicted increments were less than some threshold, but observed Douglas-fir trees surviving after 25 yr with increments less than 0.3 mm/yr. Swaine et al. (1987) observed that mortality in semideciduous tropical forest in Ghana was significantly higher in trees with no measurable diameter increment: twice and four times the average rate for trees

with diameter increments of 1 and 2 mm/yr, respectively. But not all mortality can be attributed to competition; Hartshorn (1975) reported that 50% of juvenile mortality in his study could be attributed to physical causes.

Monserud (1976) and Hamilton (1980) argued that it is inappropriate to estimate relative mortality using linear functions, as these are not constrained in the interval (0,1). They suggested the logistic function, which can be expressed in several ways:

$$P = (1 + e^{-f(X)})^{-1} = 1 - (1 + e^{f(X)})^{-1} = e^{f(X)} / (1 + e^{f(X)})$$

where P is the probability of survival and $f(X)$ is a function of some explanatory variables. Mortality is given by $(1 - P)$. The advantage in predicting survival rather than mortality, is that n -year survival can be obtained from the n th power of the annual survival.

Hamilton and Edwards (1976) showed how to weight the logistic function by the remeasure interval to account for unequal intervals. Monserud (1976) suggested that remeasure interval should be used as an exponent (i.e., use $-yr$ rather than -1) rather than as a weight. While Monserud's approach is technically correct, weighting provides an efficient approximation which is reasonably accurate provided that remeasure intervals do not exceed 7–8 yr and mortality is less than about 0.7% (Hamilton, pers. comm.).

Hamilton and Edwards (1976) used the logistic function to predict mortality of several species from diameter, height, age, defect, crown class, and stand basal area. Relative size may also be a good predictor, and both relative diameter (\bar{D}/D , Hamilton 1986, 1990) and the relative position in the cumulative size distribution (BAL/B , Vanclay 1991d) have proved useful. Monserud (1976) found that many tree variables were highly correlated and provided equally good predictions when used separately but offered no further improvement when more than one variable was included (e.g., tree height and diameter).

Many models employ past diameter increment to predict probability of mortality (Buchman 1979, Hamilton 1986, Wykoff 1986). Monserud (1976) showed that mortality functions based on predicted increments have different parameter estimates and a worse fit than functions based on actual increments. His function for survival of many species in mixed northern hardwoods was:

$$P = (1 + e^{-1.45 - 0.088D - 0.62 PDI + 0.0015 CI})^{-t}$$

where P was the probability of survival over a t year period, D is diameter, PDI is predicted diameter increment, and CI is a competition index. This function correctly classified 88% of survivals and 35% of deaths, while an analog using the actual increment in the past period rather than predicted increment correctly classified 98% of survivals and 90% of deaths. Simulation studies normally rely on predicted increments which may provide inferior estimates, so it may be preferable to model mortality directly from tree and stand variables.

Several models simulate the interacting effects of pest or disease populations and stand condition. Stage (1973) predicted mortality due to mountain pine beetle using a model with tree and stand characteristics (phloem thickness, bole surface area, stand density, etc.) and beetle population. Similar models exist for many pests and diseases (e.g., for gypsy moth, Valentine and Campbell 1975). Reed (1980) considered the development of a temperate forest after elimination of one of its component species, but no such studies exist for tropical forests.

Mortality probabilities may be implemented deterministically or stochastically. A random number may be drawn to resolve the fate of a tree, or expansion factors may be reduced proportionately. These alternatives should produce compatible predictions (Weber et al. 1986), but there are computational advantages in simulating mortality deterministically unless the user is specifically interested in studies of variability.

Management-Induced Mortality

Yield studies require estimates of the number or proportion of trees harvested or retained in each class. In natural forests, the composition and stocking are variable, and the best option may be to predict probabilities. Vanclay (1989b) predicted the probability of harvesting a tree from its species, size, and the time since last harvest (e.g., *Cardwellia sublimis*):

$$P = (1 + e^{6.088 - 0.07411 D + 19.3/T - 1.696CL})^{-1}$$

where P is the probability of harvesting, T is years since last harvest, and CL is a binary variable which takes the value one if the tree exceeds the cutting limit (for this species, $D > 100$) and zero otherwise. Silvicultural treatment (liberation thinning, timber stand improvement, etc.) of stands can be modeled in the same way.

It may be necessary to simulate mortality arising from logging damage. If so, it should not be included with regular mortality, as it is dependent on the frequency of logging. Vanclay (1989b) predicted destruction in the residual stand from tree size, topographic slope, and basal area removed in logging:

$$P = (1 + e^{3.990 + 0.05958 D - 9.689 RBA - 0.05648 SL})^{-1}$$

where P is the probability that a tree of diameter D (cm) will be destroyed in a harvesting operation which removes a proportion RBA of the standing basal area, and where SL is the topographic slope in degrees. Canopy height and average log length may be other relevant variables.

Harvesting may cause mortality indirectly through changes in stand structure or through the demise of trees injured during logging. Walters et al. (1982) reported that injuries may cause a 3-fold increase in mortality for several years after logging. If these deaths can be identified, a separate model can be fitted. An alternative is combine this with regular mortality and use time since logging as an explanatory variable (Hann 1980). Vanclay (1991d) found that time since logging did not improve mortality prediction in Queensland rainforests. Hamilton (pers. comm.) also found that time since logging and type of thinning had no impact on mortality rate following thinning in temperate forests.

Merchantability

Merchantability assessment may seem unrelated to mortality prediction, but for modeling, deterioration is analogous to mortality. Trees assessed as merchantable at time of inventory may not remain so until the next harvest; some may deteriorate and become unmerchantable. Such deterioration is cumulative and may warrant inclusion in yield studies. Vanclay (1991e) predicted deterioration from stand basal area, tree size, time since logging, and soil type (e.g., for *Toona australis*):

$$P = (1 + e^{-7.450 - 0.04195 B + 22.49/D - 0.0/T + 0.4213 CG})^{-1}$$

where P is the annual probability that a merchantable tree remains merchantable, B is stand basal area (m^2/ha), T is time since last harvest (other species have nonzero parameters), and CG is a binary variable indicating coarse granite soils.

Not all trees assessed as merchantable and felled during harvesting will yield a merchantable log; some may be found after felling to be unmerchantable. The harvesting model could treat these stems as logging damage, but a more efficient alternative is to predict all stems felled and then estimate the merchantable proportion, if this is consistent with assumptions implicit in volume equations. Queensland volume equations assumed at least one merchantable log per tree, so Vanclay (1989b) corrected for trees failing to yield any logs (e.g., for *T. australis*):

$$P = (1 + e^{1.565 + 0.0129 D})^{-1}$$

where P is the proportion of apparently merchantable trees which realize at least one commercial log.

REGENERATION AND RECRUITMENT

Regeneration may be negligible in plantations and in some even-aged stands but is significant in many uneven-aged forests. Regeneration and ingrowth may be predicted at the seedling (regeneration models) or a more advanced stage. Recruitment models predict stems reaching a nominal size, often 1.3 m height, 3 m height, or 10 cm dbh. Recruitment models may predict a constant amount each year irrespective of stand condition (static approach), or may be dynamic and respond to stand condition.

Static Recruitment Approaches

Static recruitment models assume that calibration data reflect the long term average recruitment applicable to simulations. Some stand table projection models assume a constant amount of recruitment every period or that the stocking in the smallest class remains constant. These approaches may provide reasonable estimates in stands which do not differ much from the calibration data but should not be extrapolated to other stand structures. Howard and Valerio (1992) assumed a constant amount of recruitment every projection cycle, irrespective of stand condition and logging history. Many matrix models predict that recruitment will increase with the number of trees in the larger size classes (Usher 1966, Osho 1991), but some matrix models allow recruitment to vary inversely with stand density (Buongiorno and Michie 1980) or to appear only on the death of another tree (Bosch 1971).

Dynamic Recruitment Models

It is preferable to adjust recruitment estimates according to stand condition. Vanclay's (1989a) rainforest model predicted recruitment at 20 cm dbh from stand basal area and site quality, and the proportion in each of five species groups from stand density and composition (e.g., for large, fast-growing species):

$$P_1 = (1 + e^{(-2.407 - 0.005608 B + 0.01105 B_1 + 0.00464 B_1 S)})^{-1}$$

where B is total stand basal area (m^2/ha), B_1 is the basal area of group 1 species (m^2/ha), and S is binary variable indicating site (1 = good, 0 = poor). The proportions for the five groups were standardized to ensure they summed to unity: $P'_1 = P_1 / \sum P$.

JABOWA (Botkin et al. 1972) predicted recruitment at 0.5 cm dbh, randomly selecting from candidate species predicted on leaf area index, shade tolerance, growing season, and soil moisture. Mortality was simulated to ensure that only 2% of fast and 1% of slow growing seedlings reached the overstory. Shugart and West (1977) also specified substrate requirements (mineral soil or leaf litter), modeled weather and browsing stochastically, and allowed sprouting from dead trees. Reed (1980) used alternate seed-years and "off-years" and imposed a maximum stocking of 2500 stems/ha above which no recruitment could occur. These approaches provide stochastic estimates which may not be suitable for deterministic models.

Two-Stage Approaches

One difficulty in modeling recruitment is its variability. Part of this variation is because regeneration may or may not occur during any period. So it is efficient to use a two-stage system, first estimating the probability of some regeneration or recruitment, and then using a conditional function to predict the amount of recruitment, given that some is known to occur.

Ferguson et al. (1986) used a two-stage approach to predict recruitment in the Prognosis model. They used a stochastic procedure to predict the regeneration on 50 subplots, and recruited it to the main model at 10 and 20 yr after disturbance (Prognosis has a 10-yr simulation cycle). The probability of regeneration was predicted from environmental variables (habitat, slope, aspect, elevation), distance to seed source, residual basal area, and time since disturbance. Stochastic functions predicted the number of trees and the number and identity of species.

Vanclay (1992b) predicted the probability of recruitment at 10 cm dbh independently for each of 100 rainforest species. Annual probabilities were predicted from stand basal area and species composition. These could be implemented stochastically or could be summed until the cumulative probability reached 1 for deterministic predictions. The number of recruits of each species, given that some were known to occur, was predicted from stand basal area, site productivity, and the relative abundance of the species in the stand.

Regeneration Models

Regeneration models may simulate the growth of seedlings prior to recruitment into the main model. They are flexible enough to commence at any stage and use any size for recruitment into the main stand. Leak's (1968) regeneration model started from flower development, and Ek and Monserud (1974) from seed fall.

Vanclay (1988) predicted established 1-yr-old regeneration in *Callitris* forest from stand density and site productivity. Regeneration was modeled by height-based cohorts until recruited to the main model at breast height. A maximum of ten cohorts was employed. Under ideal conditions (good sites with low stocking), these cohorts represented annual flushes of regeneration. Where regeneration took more than 10 yr to reach breast height, the most similar cohorts were amalgamated to ensure that the limit of ten cohorts was not exceeded.

Ek and Monserud (1974) used cohorts based on species and age to model regeneration. Good, moderate, and poor seed years were randomly allocated according to the observed frequency for each species. Seed and sprout production were estimated for each overstory tree from its size and threshold age and were distributed according to the parent tree's position, height, and crown. Germina-

tion was predicted from microsite and canopy cover. Seedlings were recruited to the main model at breast height, and if they failed to reach it within a specified time (e.g., 25 yr for black spruce), they died. Monserud and Ek (1977) assumed that understory tree size was more relevant than age, and modeled the development of trees to 7.6 m height using five height cohorts and movement ratios. The height increment of the mean tree was predicted from the potential increment, overstory competition index, shade tolerance, and stand density. These regeneration models offer great flexibility, but demand detailed data for calibration and may add to the complexity of the model.

Inventory data frequently sample only the larger stems (e.g., ≥ 10 cm dbh), and smaller stems may remain unsampled. Thus there may be a "gap" in the data, especially where a model predicts regeneration or recruitment at a small size. To avoid this "censorship," it is necessary either for inventory to provide a count of the smaller stems, or for a model to predict the likely incidence of these stems from overstory stocking. It is preferable to augment such censored data with typical small tree distributions for the forest type than to use the unadjusted censored data (Randall et al. 1988).

VALIDATION AND USE OF GROWTH MODELS

VALIDATION

All models are imperfect; at best they are a simplification of complex processes. A model cannot be proved correct, so validation should be concerned with the inferences that may be drawn from a model rather than its "correctness." Thus the validity of a model cannot be divorced from the objectives for which it was constructed (Van Horn 1971). Accepting the null hypothesis does not mean that the model is correct or that it is the best possible model. Conversely, the decision to reject the null hypothesis need not mean that the model has no practical use. If the null hypothesis is rejected, the question is where and how the model fails and what can be done to improve it (Reynolds et al. 1981). "As long as your model output is wrong you continue to learn something" (Bunnell 1989).

Validation in its purest form requires independent data. Thus the data set may be partitioned with some for development and the rest for validation. A half and half split is common in other disciplines (Snee 1977), but fewer data are often used to validate growth models. Goulding (1979) suggested that 10–15 plots spread over a range of stand conditions could suffice if multiple silvicultural options were not being evaluated. Stands apparently with the same initial conditions may develop differently, so validation should employ sufficient data to provide a reasonable estimate of the expected actual stand condition.

The outcome of validation tests can be influenced by the selection of data: "like" data will provide a more optimistic result than validation with "unlike" data. The most convincing demonstration can be made only if the validation data are in some sense unlike the development data. Since growth models are used to forecast future forest conditions, one way to split the data is on time, and to use data collected before a certain date for development, and since then for validation. Alternatively, the DUPLEX algorithm (Snee 1977) can provide an "unlike" set by

splitting the data into two overlapping sets with similar statistical properties but covering different parts of the data space.

One way to examine model performance is to plot and compare the predicted and observed values of several tree and stand variables and see how they change over time and how they are affected by other stand variables. Such plots are interpreted visually, and appraisals of performance are necessarily subjective. Two simple criteria provide nearly all the information necessary in validation (Burk 1986): model bias $[\Sigma(\text{predicted}-\text{observed})/N]$ and mean absolute difference $(\Sigma|\text{predicted}-\text{observed}|/N)$. These formulae apply at the stand level and for size or product breakdowns. Model bias measures the expected error when several observations are to be combined by totalling or averaging, and mean absolute difference measures the average error associated with a single prediction. Estimates may be weighted $\Sigma W(P - O)$ for basal area, volume, value, etc. (Reynolds et al. 1988).

CALIBRATION

Calibration usually refers to parameter estimation, but here it is used in the more restricted sense of finding an adjustment to improve model predictions for a specific locality. The growth model may be adjusted for a new population by estimating new parameters, or by using a "fudge factor" to scale predictions. The STEMS growth model (Belcher et al. 1982) has been implemented in several other regions, and most installations retain the original equations. Some have estimated new coefficients (Shifley 1987), while others use fudge factors to scale existing equations (Holdaway 1985). These may comprise a single correction factor for each species, or may be correlated with some tree or stand variables (e.g., tree diameter or stand basal area). Calibration is not a panacea, even for existing "good" models. Attempts to calibrate STEMS to Australian forests using a single fudge factor (Swain and Turner 1988 for *Eucalyptus marginata*) or by re-estimating coefficients (Goodwin 1988 for mixed eucalypts) have been fraught with difficulty, and results to date have been poor.

Prognosis has a "self-calibration" feature to allow calibration using increment cores from temporary plots. The deviation (observed-predicted) in the logarithm of the tree basal area increment is added to the logarithmic increment function, thus adjusting the growth rate while retaining the "shape" of the function (Stage 1981). This adjustment is attenuated over time, so predictions gradually revert to the uncalibrated model. Stage (1973) argued that the approach adjusts the model to "local peculiarities of site quality, genetic character and tree vigor," but cautioned that "growth functions should be based on data derived from the area to which the model is to be applied; the self-calibration feature . . . only partially mitigates that admonition."

USING GROWTH MODELS

There is little point in developing a growth model unless it is used. Although model development may reveal some implications for forest management, the greatest benefit will accrue if forest managers use the model to investigate forest management alternatives. Involve potential users as well as researchers in the construction of the model, so that users should feel the model belongs to them

(Bunnell 1989). And make sure the model is available, adequately documented, and integrated into other information systems used by forest managers (Vanclay 1990a).

Resource Data for Simulation Studies

Growth models can only provide good predictions if the input data are also reliable. Thus users should take commensurate care in collecting the necessary input data. Sampling should be efficient and unbiased, and this requires decisions on stratification, plot size, and tree measurement. Smith and Burkhart (1984) found that stratifying by both site index and stocking improved the precision of volume estimates by two-thirds over simple random samples. Mowrer (1989, Mowrer and Frayer 1986) warned that errors in initial conditions may have a greater effect on overall precision than contributions from the growth model. Inventory plots should be approximately the same size and configuration as the plots which provided the calibration data (Hann and Zumrawi 1991). Data censorship through the failure to record small trees or noncommercial species bias model predictions and any such data should be augmented by average data for the forest type (Randall et al. 1988).

Optimization Studies

Growth models can be used to explore stand conditions which maximize revenue or other benefits, but the optimum may depend on the criterion: maximum land expectation value provides a different optimum than maximum volume growth (Bare and Opalach 1987). This reiterates the interrelationship between modeling, management objectives, and optimal silviculture. In tropical forests with many species, it may be difficult to define an optimal stand structure and may be more relevant to study the length of the harvesting cycle (Howard 1993), the minimum diameter for harvesting (Vanclay 1989a), and the number of trees harvested each cycle (Mendoza and Setyarso 1986). Many studies simplify the growth model to provide a tractable analysis, and this may influence the results. Haight and Monsrud (1990a,b) demonstrated a method for optimizing any-aged management of mixed species stands using the standard Prognosis model.

Yield Prediction

Yield prediction is an important application of growth models, but yields can also be estimated without simulation studies. Yield estimates for many tropical forests have been based on the "time of passage," the time to grow through several classes of the stand table (Alder 1992). This method may be useful where data comprise only the "leading desirables" (viz. vigorous trees assumed to form the next harvest, Dawkins 1958, p. 93) which otherwise have little utility for growth modeling, but serial correlation may bias estimates from complete enumerations (Mervart 1972). Growth models make it simple to estimate yields from single stands under various management regimes, but forest estate estimates also involve the spatial and temporal distribution of yields. Simulation studies and mathematical programming techniques (Davis and Johnson 1987, p. 592, Leuschner 1990, p. 82) can help find the best path through the sometimes contradictory requirements of maximum sustained yield and nondeclining even flow.

Yield predictions contain two sources of error (Leary et al. 1979a): error in assessing the initial state, and error in the growth prediction. The former is a problem of resource inventory, and may contribute most error associated with

predictions (Mowrer and Frayer 1986, Mowrer 1989). Hann (1980) observed that yields estimated from individual plots were more accurate than an estimate from the mean of these plots, and several studies have confirmed that precise forecasts require that plots be projected individually before averaging (Smith and Burkhart 1984, McKay 1990). Moeur and Ek (1981) compared predictions from individual plots, averages for homogeneous stands, and averages for forest types. The best predictions were obtained by averaging individual plot predictions, while projections of forest type averages resulted in overestimates.

Cutting cycle analysis has been extensively used for yield forecasting in uneven-aged forests, partly because it is simple and need not involve computers. The basic method (Davis and Johnson 1987, p. 48) is to nominate a cutting cycle length, construct a typical stand table, project this stand to the midpoint of the cutting cycle, and apply a logging rule to predict the loggable volume. Estimates can be improved by stratifying on site productivity and standing volume, and by simulating individual plots rather than stratum averages. Deficiencies include the assumption of a fixed cycle and the harvest at midcycle.

Grosenbaugh (1955) recognized these deficiencies and advocated the use of homogeneous "record-units" for all estimates and operations. He also insisted that yield forecasting should recognize the actual order of working over the resource. A trial of Grosenbaugh's "diagnostic survey technique" in an irregular eucalypt forest produced detailed yield estimates and other forest management information at a cost comparable to established forest inventory systems (Phillis 1971, p. 239). Vanclay (1994a) illustrated a similar technique for estimating yields and scheduling timber harvests in Queensland rainforests. Management units formed the basis for prediction and were stratified into homogeneous subunits for efficient sampling. User-specified constraints, including minimum yields and species mixes, ensured that the predicted harvest schedule was silviculturally and operationally relevant. Discrepancies between cutting cycle analysis and yield scheduling were also illustrated.

Sustainability

One of the important and topical issues regarding rainforest management is the question of sustainability, not only of timber harvests, but of the entire flora, fauna, and ecosystem. Growth and yield models may allow us to make some inferences about the continuity of the timber harvest and the nature of future forest stands, but tell us little about the effects of timber harvesting on other aspects of the ecosystem. Botkin (1993, p. 212) warned that simulations of 400 yr may be necessary to infer sustainability and that "reliance on three harvests can be deceptive as a way to determine whether a harvesting practice is sustainable." Models such as FORCYTE (Kimmings et al. 1990) and LINKAGES (Pastor and Post 1986) offer some insights into nutrient cycling and long-term productivity changes, but still focus on the trees. A new class of model may be required to examine the "big picture" in tropical moist forests. However, several implications of timber harvesting on rainforest sustainability can be examined with traditional growth and yield models. But models are not reality, and it is operational management that is critical to sustainability. The first step toward sustainability is not modeling, but control of harvesting to minimize damage and erosion and ensure a frequency and intensity sympathetic to the forest ecology (Vanclay 1992c).

Vanclay (1990b) examined productivity changes on 212 rainforest plots, some

of which had been established 40 yr and logged on 2 or 3 occasions. It is difficult to define a suitable measure of productivity, so Vanclay (1990b) used the residuals about a diameter increment function which accounted for site and competition (Vanclay 1991b). Regression analyses were used to look for both transient and permanent changes in productivity. Vanclay (1990b) found no long-term productivity decline, and found evidence to support the assertion that any decline did not exceed 6% per harvest ($P = 0.05$ with plot mean residuals, $P < 0.0001$ with individual tree residuals). However, this conclusion refers only to the growth rate of trees (adjusted for site and competition), and offers no insights into stand structure and composition.

Some growth models can forecast future composition of trees, if not of the whole ecosystem. Simulation studies of north Queensland rainforests suggested that timber harvesting could be sustained, but might contribute some changes in stand composition (Vanclay 1994a). Repeated harvesting would eliminate the very large merchantable trees from the areas zoned for harvesting, so that future harvests would become more uniform. Large noncommercial trees would remain throughout the forest, and large trees of all species would be retained in buffers and other areas protected from logging. Species composition may change slightly, favoring the "small gap" species which include *Flindersia* and other commercial species. Future harvests may comprise a higher proportion of high-quality cabinet-woods (up to 50%), a high proportion of a single species, often *Flindersia* (staying around 20%), and a more limited range of log sizes (90% by volume between 60 and 100 cm dbh). Comparable studies for other tropical forests are not yet available.

Few growth models are suitable for comparing uneven management versus even-aged management. The Prognosis model (Haight and Monserud 1990a,b) suggested that even-aged plantation management and uneven-aged shelterwood systems could produce identical yields indefinitely in temperate coniferous forest. However, it is unlikely that a single model could compare these alternatives satisfactorily in tropical forests. Predictions from a growth model for managed natural forest could be contrasted with plantation yield tables, but many other factors should be taken into account, and simplistic comparisons of timber yields are unlikely to lead to wise land use decisions.

CONCLUSIONS

LESSONS LEARNED

The quality of growth models and their predictions depends upon many factors, but foremost among these is the quality of calibration data. Permanent plots lay the foundations for growth modeling, yield prediction, and sustained yield management, and the reliability of these data is crucial.

While whole stand models have been useful for plantation modeling, they have less utility in tropical moist forests, where many species and multimodal size distributions make it hard to describe the forest with few stand-level variables. Stand class approaches offer several advantages and form the basis for many growth and yield models for uneven-aged forests. They are relatively simple, computationally efficient, and provide information in sufficient detail for many

applications. Classical stand table projection continues to be useful where summarized stand data are available and computer resources are limited. However, the many species and wide range of stem sizes encountered in tropical moist forests may require many classes, detracting from the method. Matrix methods are easily implemented and produce good results where stand density and silvicultural practices are maintained within a narrow range, but assumptions become untenable for long projections and diverse stand conditions. Cohort or tree list models offer greater flexibility, enable projections under a wide range of conditions, and provide diverse information for reporting.

Successful growth models require proper problem formulation, careful selection of explanatory variables and model form, good coefficient estimation procedures, and independent validation. Modelers should rely more on their knowledge of silviculture and biological principles of growth than on statistical tests when selecting models and developing algorithms. It is irrelevant whether growth or yield of basal area or diameter is modeled, but important to ensure sensible predictions over the whole range of possible tree size, site, and stand conditions. Logistic functions fitted to individual tree data may offer the best way to model mortality, deterioration, and harvesting. Although regeneration models offer several desirable features, they may be impractical in the tropics because of difficulty of species identification, absence of suitable data, and uncertainty of growth patterns. Two-stage recruitment models may be suited for yield prediction models.

A growth model must not remain a sophisticated complexity, alien to the forest manager, but must be made available for use as an everyday tool for better forest management. In short, that means that the growth model should be easy to use, well documented and readily available.

FUTURE DIRECTIONS

It is ironic that the most sophisticated models exist only for the most simple forest ecosystems (monospecific plantations), and that models for the most complex of forests, the tropical moist forest, are primitive or lacking. The technical difficulties of implementing growth models for rainforests can be overcome with sufficient time and resources, but the social and political difficulties may be less tractable (Vanclay 1993). Limited resources and facilities hamper the efforts of researchers in the tropics to gather reliable data and build robust models, and may restrict their work to the simplest approaches. Complexity does not confer utility, and simple but reliable growth models may play an important role in demonstrating to politicians and foresters the consequences of various harvesting alternatives and the need for effective forest management. However, convincing demonstrations require land-use plans and reasonable resource inventory for use in growth simulations. Sophisticated growth models are not necessary, and several existing models, if recalibrated, would be well suited to the task and could be instrumental in helping to reform tropical forest management.

Many implications of potential climate change on forest production have been examined, but results should be interpreted with caution, as it may be easier to predict the vegetation response to a specific regime than it is to predict the climate at a given time (Melillo et al. 1990). Some studies have focused on plant responses to anticipated climatic means, but it may be the less predictable extremes (e.g., infrequent frosts, fires, floods, and storms) that shape the vegeta-

tion. Climatic change may act indirectly via subtle changes in nutrient cycling and availability (Pastor and Post 1986), or via other feedback mechanisms (Myers 1991), and more sophisticated models are needed to examine these aspects. Such studies may not be a priority for the tropics, as climatic changes may be greater at higher latitudes (Mitchell et al. 1990).

Increasing sophistication in temperate forest modeling has tended toward reductionist models of nutrient cycling and partitioning, but a better understanding of the tropical forest may require a more holistic approach embracing interspecific relationships, including fauna-flora interactions (Pannell 1989, Prance 1992), and may require new concepts for old terminology. Conventionally, a spatial model would account for the placement of trees within a small plot, but a spatial model for a tropical forest might consider the distance (kilometers) to the nearest individual of the same species and the implications for pollination, pests, and disease (in tropical forests, many common species are widely scattered, with densities as low as $1/\text{km}^2$). Models such as FORCYTE and LINKAGES have commandeered the term "ecosystem model" (Pastor and Post 1986, Yarie 1990), but such a model for the tropical forest may require a much broader basis, including many fauna-flora interactions, intraspecific distances, and spatial data on intact forest fragments (what are the implications of size and distance of undisturbed refuges on pollinators, predators, pests, etc?). Nutrient cycles may assume a new importance in the moist tropics, where most of the nutrients may be held in the biomass and where cycling (especially decay) may be much more rapid. This is fertile ground for more research, and may provide important insights for conservation planning as well as for timber production.

Most forest growth modeling has been based on empirical relationships embedded in procedural models. Such models may remain the backbone for forest planning and management, but our understanding of tree growth and stand dynamics may be advanced more rapidly by research on process modeling approaches (Bossel et al. 1991) implemented with object-oriented (Kolström 1991) or declarative programming methods (Bossel 1991). The tropical forest offers ample scope for further research with these and other modeling approaches.

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