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Growth models for tropical forests:
A synthesis of models and methods.

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Growth models for tropical forests:

A synthesis of models and methods.

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 quality of calibration data. 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 may to be useful where summarized stand data are available and computer resources are limited, but the many classes required detract from the method. Matrix methods are suitable where stand density and silvicultural practices remain within a narrow range, but are untenable for general conditions. Tree list models offer greater flexibility, enable projections under a wide range of conditions and provide diverse information. Increment equations may predict growth or yield of basal area or diameter but should ensure reliable predictions over all tree sizes, sites and stand conditions. Mortality may be modelled with logistic functions fitted to individual tree data. Regeneration models are complex where there are many species, and two-stage recruitment models may be more practical. The value of a model is in the use to which it is put, so models should be easy to use, well documented and readily available.

Additional key words: Rainforest, simulation, yield prediction, forecast, sustained yield.

It is 200 years since the first yield tables were published in Germany (Vuokila 1965), 30 years since compatible forest growth and yield models were reported (Buckman 1962, Clutter 1963), and 20 years 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.

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, but some significant developments in plantation modeling are noted. There is no single approach optimal for modelling tropical forests; the ideal model depends upon resources and applications. Accordingly, many methods are reviewed to illustrate strengths and weaknesses of various alternatives.

The tropical moist forest offers a special challenge for the growth modeler, as it may be the most complex forest ecosystem. There may be over a hundred tree species on a single hectare, a thousand in a management unit, and over one hundred 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.

Growth Modeling: Options and Alternatives

My dictionary defines a "model" as the representation of some existing 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 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.

Model development involves exploring data to provide new insights into forest dynamics and reveal gaps in present knowledge. Once implemented, 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. Implementation should encourage both exploratory and operational use of the model. Although apparently obvious, these principles are not reflected in many models.

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/hectare), 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 and single tree models. If the class is infinitely large and only one class exists, it is a whole stand approach. When the class width is infinitely small and each tree is a single class, then it becomes a single tree model, in which the individual tree is the basic unit of modeling. 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 growth and stand dynamics, but have not yet successfully been used for predicting timber yields. Succession models (West et al. 1981, Shugart 1984) attempt to model species succession, but are generally unable to 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 (e.g., Landsberg 1986, Sievanen et al. 1988, McMurtrie et al. 1990). Bossel and Krieger (1991) used the process approach to build a canopy layer model for Malaysian forests. Such models currently offer limited practical relevance, and 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

Whole stand models require few details to simulate growth, but provide rather general information about the future stand. Despite this limitation, many whole stand models have been proposed and only a few innovative and recent examples pertinent to mixed forests are reviewed here.

Growth and Yield Tables

Growth models form a continuum from normal yield tables to single tree growth models (Leary 1991). Vuokila (1965) and Spurr (1952:254) reviewed yield table construction in Europe and North America. Yields were generally tabulated by age and site, but could be presented as alignment charts (Reineke 1927). The inclusion of stand density made yield tables more useful, and some were developed for mixed stands (e.g., MacKinney et al. 1937, Duerr and Gevorkiantz 1938). Yield tables usually require some estimate of stand age, and thus cannot be applied easily to uneven-aged stands. Growth tables attempt to overcome this limitation by tabulating expected growth by stand volume, density, height, average diameter and time since logging (Spurr 1952:265).

Growth percentages may be applied to individual trees, or to uniform stands by assuming that every tree grows like the mean tree. Percentages can also be applied to stand tables or to estimates of standing volume. Wahlenberg (1941) warned that these methods were unreliable at best, and could be very deceptive.

Yield estimates may be estimated from the "time of passage", the time to grow through several diameter classes. This method may be useful where data comprise only the "leading desirables" (viz. vigorous trees assumed to form the next harvest, Dawkins 1958:93) which otherwise have little utility for growth modeling. Time of passage estimates based on leading desirables may be reasonable, but serial correlation may bias estimates from complete enumerations (Mervart 1972).

Growth and Yield Equations

The distinction between tables and equations is blurred since equations can be evaluated and presented as tables, but equations do provide a concise and convenient way to express growth and yield relationships. Equations also accommodate more variables and can be estimated in a rigorous and repeatable way. Schumacher (1939) assumed that relative growth varies inversely with age ($\Delta V/V \propto 1/A^2$), so that $\text{Log}(V) = \alpha_0 + \alpha_1/A$ where the α s are simple linear functions in site index and stand density.

Mendoza and Gumpal (1987) used a similar equation to predict yield of dipterocarps in the Philippines:

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

where Y_T is timber yield (m^3/ha >15 cm dbh) T years 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 have the limitation that they assume a certain management regime throughout the projection. Growth equations have an advantage that logging and other treatments may be simulated at any time. Buell (1945) assumed that volume increment (ΔV) of a single tree could be expressed as a quadratic equation in diameter (D), $\Delta V = \alpha_0 + \alpha_1 D + \alpha_2 D^2$ and that the volume increment of the stand was the sum of the individual increments $\Delta V = \alpha_0 N + \alpha_1 \Delta D + \alpha_2 \Delta D^2$ (N is stems/hectare).

Nelson (1963) argued that stand basal area increment (BAI) 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. So he used a quadratic in basal area:

$$\Delta B = \alpha_0 + \alpha_1 B/A + (\alpha_2 + \alpha_3/A + \alpha_4 S) B^2$$

Vanclay (1988) used a similar equation for stand basal area increment ($m^2/ha/ann$) in uneven-aged conifers:

$$\text{Log}(\Delta B) = 13.071 + 1.094 \text{Log}(B) + 0.007402 B S - 0.2258 B$$

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

Early analyses did not exploit the relationship between growth and yield and so that the sum of successive growth estimates could 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. Buckman (1962) estimated basal area increment from stand basal area, age and site index, assuming that basal area remained constant in managed stands. 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. Clutter (1963, Sullivan and Clutter 1972) assumed basal area was a function of age and site index, so that basal area increment (dB/dt) could be estimated from stand basal area, age and site index. This gave five compatible equations for standing volume, basal area increment, volume growth, predicted basal area and predicted volume yield. Simultaneous estimation of parameters is also possible (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 from stand basal area using the Bertalanffy equation. By assuming an allometric relationship between stand volume and basal area, they could express volume increment:

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

Integrating and substituting for volume provides compatible growth and yield equations for both basal area and volume. The biological basis of the equation is

questionable, as it assumes that the Bertalanffy equation holds for populations as well as for individuals, and several empirical studies have reported negative coefficients (e.g., Moser and Hall 1969, Murphy and Farrar 1982) where positive coefficients should hold. However, the equation continues to provide a good empirical model for compatible growth and yield estimates.

Systems of Equations

Moser (1972) identified seven components of a mixed hardwood stand in Wisconsin: Y_1 is the number of trees (>18 cm dbh), Y_2 their basal area, Y_3 the number of trees dying during the period (t_0, t_n) , Y_4 the number of recruits, Y_5 the basal area dying, Y_6 the basal area recruited, and Y_7 the cumulative basal area growth of the surviving original trees (Y_1) during (t_0, t_n) . The intuitive relationships:

$$Y_1 = Y_1(t_0) - Y_3 + Y_4$$

$$Y_2 = Y_2(t_0) - Y_5 + Y_6 + Y_7$$

were differentiated to build up a system of equations:

$$dY_1/dt = -dY_3/dt + dY_4/dt$$

$$dY_2/dt = -dY_5/dt + dY_6/dt + dY_7/dt$$

The five variables of growth and change ($dY_3/dt - dY_7/dt$) were estimated using simple functions of stand condition Y_1 and Y_2 . Because a stochastic function was used to predict the basal area dying, the equations could not be fitted simultaneously (c.f. Furnival and Wilson 1971), and the variance-covariance matrix could not be estimated.

State Space Models

Garcia (1983, 1984, 1988) used a state space approach to model plantations, representing the stand with three state variables, stand basal area, stocking and top height. These summarize the historical events affecting stand development, and allow predictions from current state and future actions. Garcia (1984, 1988) used the multi-variate generalization of the Bertalanffy equation:

$$d\underline{X}^c/dt = \mathbf{a}\underline{X}^c + \underline{b}$$

with \underline{X}^c defined as

$$\underline{X}^c = e^{c \text{Log } \underline{X}}$$

where \underline{X} is an n-dimensional state vector and \mathbf{a} , \mathbf{c} and \underline{b} are n-dimensional matrices and vectors of parameters which can be estimated using maximum likelihood.

Although it gave excellent predictions and provided an effective framework for a series of plantation growth models, Garcia (1988) cautioned that "these methods cannot be recommended for general use by the casual growth modeler; the capacity to understand the techniques, and modify them if necessary, is essential". Adapting the approach for mixed forests would require additional variables, as it seems unrealistic that these could be described adequately with only three state variables.

Whole Stand Transition Matrices

Markov chains provide a concise way to summarize the behavior of a system, and can be used to model forest stands. Consider a system S with n distinct states S_1, S_2, \dots, S_n . If the system starts in state S_i , then in a single interval, it has

probability P_{ij} of moving to state S_j . If these P_{ij} depend only on the current state S_i , these probabilities can be expressed in a square matrix, termed the transition probability matrix or stationary Markov chain. Hool (1966) used this approach to devise optimal management regimes for even-aged mixed species forests, using a two year transition interval and 36 states based on logging history, volume and stocking. Binkley (1980) studied succession with states characterized by the dominant species on a plot. He found the assumptions inherent in the method untenable, and concluded that transition matrices were not a reliable way to predict forest stand dynamics.

Whole Stand Distribution Models

Effective forest management requires more than simple estimates of standing volume; details of sizes and species are also necessary. Some yield tables include stand or stock tables and many alignment curves predict average and minimum stem sizes (e.g., Reineke 1927). Other models may use a distribution function to infer size distributions.

Diameter distributions in even-aged forests can be quantified by the Weibull distribution (Bailey and Dell 1973, Schreuder and Swank 1974), and since height and volume can be expressed as an allometric function of diameter, their distribution may be estimated using a simple transformation of the Weibull distribution of diameter (Stacey and Mihram 1965). Hyink and Moser (1979) used these transformations to estimate top and mean heights, and total and harvested volumes,

given the total number of trees and the diameter distribution. They simulated growth by updating the three parameters describing the diameter distribution. These were predicted from stocking, sum of all diameters, and sum of diameters less than 21 cm. Lynch and Moser (1986) and Bowling et al. (1989) adapted the method to mixed stands by employing several sets of equations, one set for each species. This approach is known as the parameter prediction approach (Reynolds et al. 1988).

The alternative parameter recovery approach has been found to give better predictions (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 utility of both methods depends on the ability of the Weibull distribution to characterize the diameter distribution. The Weibull distribution can describe a great variety of shapes (Krug et al. 1984), but is always uni-modal and is not be suited to all stands.

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). They may model each class independently of others, or may account for the other classes explicitly or implicitly. The stand need not be partitioned into metric classes (e.g., 10 cm dbh classes); it may use a more flexible partition into "cohorts" or groups of trees with similar characteristics (e.g., species and size).

Stand Table Projection

Stand table projection predicts the future stand table from the present stand table using estimated diameter increments for each class. Estimates of diameter increment may be obtained from increment equations prepared using linear regression analyses, or directly by tabulating mean increments observed in each class. 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 (Gibson et al. 1969). An alternative 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. 1982:296).

The third method uses the actual movement of trees rather than movement ratios (Wahlenberg 1941). Husch et al. (1982:299) give an example where this correctly predicts that 30, 50 and 20% of trees move 0, 1 and 2 classes, but the movement ratio approach predicted 6, 94 and 0% respectively. 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 a few stems can be projected.

Greater flexibility can be provided by varying class widths and by estimating upgrowth using equations. Leak and Graber (1976) modeled an uneven-aged beech-birch-maple stand with 11 diameter classes of different widths. They estimated diameter increment from diameter and stand basal area, and used movement ratios to update the stand table. Leary (1970) used three diameter classes (10-20, 20-30, 30-40 cm), set up a system of equations and solved them simultaneously using boundary values. He assumed that growth in the largest class was dependent only upon the sum of diameters in that class, and that the growth of the smallest class was dependent upon the sum of diameters of all classes. Leary showed that simultaneous estimation leads to more precise estimates of the parameters.

Transition Matrices

Transition matrices are a formalized extension of stand table projection. They assume that a system in one of a finite number of states has a known probability of moving to another state, dependent only upon the current state. A forestry interpretation is that a tree may be in one of the diameter classes of the stand table. During the next period, it must either remain in the class, grow into another class, or die. The probabilities of movement can be expressed as a matrix (\mathbf{M}), and can be used to predict change during a single time interval $\underline{V}_1 = \mathbf{M}\underline{V}_0$, or over several time intervals: $\underline{V}_n = \mathbf{M}^n \underline{V}_0$ where \mathbf{M} represents the transition matrix and \underline{V}_0 and \underline{V}_n are vectors describing the initial and final states respectively. In forestry, \underline{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 one-year matrix (**A**) may be estimated from an n-year matrix (**P**) such that $\mathbf{A}^n \cdot \mathbf{P}$ (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 Lefkovitch (1965), and for forestry (diameter classes) by Usher (1966). Bosch (1971) used a Leslie matrix to study redwood forests, but most studies use the diameter class matrix advocated by Usher (1966). 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 the period and growth can be defined by a single probability (either a tree grows into the next class, or it does not).

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 fecundity estimates (Enright and Watson 1991). An exponential increase 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) stress 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. The probabilities do not change over time, so matrix models 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. At the start of each 5-year projection period, (Solomon et al. 1986) recomputed matrix coefficients from stand basal area, tree size and stand composition for each of the 13 species groups.

Transition matrices remain useful, despite these restrictive assumptions. Usher (1976) estimated optimum yield and rotation length for P. sylvestris plantations. Rorres (1978) showed that the optimal sustainable harvest uses a cutting limit regime which removes all the stems in one class, some stems in several smaller classes, and leaves the smallest classes untouched. Predictions may remain reliable over several intervals (Bruner and Moser 1973), provided that simulated stand conditions remain similar to those prevailing in the calibration data.

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

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

where \underline{Y}_i is the stand table at time i , \mathbf{A} is a bi-diagonal transition matrix, and \underline{H}_i is the harvest at time i . \mathbf{N} and \underline{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 \underline{C} contains only the intercept, 109. By representing the harvest as a vector \underline{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 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 thus overestimating growth. Two possible

solutions are to use narrower classes, or to smooth the stand table. Hann (1980) used 1 inch (2.5 cm) classes and predicted movement using empirical equations, but these small classes allowed recruitment in the second as well as the first class.

Campbell (1981) smoothed his stand table with quadratic splines, constrained so that the curve was smooth and continuous, enclosed the right number in each class, was positive through its range and reached zero at the lower limit of the smallest class and the upper limit of the largest class. The integral allowed numbers, basal areas and volumes to be estimated for any diameter limits. Unlike the Weibull distribution, spline curves (Smith 1979) can fit stands which are not uni-modal. Campbell (1981) predicted the increment of the mean tree in each class, and assumed a near-normal distribution of increment within each class. Upgrowth was estimated from the within-class distribution of trees and the predicted distribution of increments. A new largest class was initiated only when upgrowth exceeded a specified criterion. The smallest class was absorbed when upgrowth reduced stocking to a sub-critical amount.

Korsgaard (1989) assumed that a J-curve defined by de Liocourt's quotient described the distribution of stem size in dipterocarp forests. He found 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).

Representative Trees Approaches

Several trees can be selected to represent cohorts of trees and form the basis of modelling. 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. Cohort attributes can be updated by assuming that cohort members are identical to the representative tree. Alternatively, the distribution of stems (and increments) within any cohort may be resolved by reference to the whole stand or resolved within the class itself.

Clutter and Allison's (1974) model for P. radiata plantations used 25 cohorts, initially each with an equal number of trees (4%). The median diameter for each cohort was estimated by fitting a Weibull function and computing the diameters corresponding to the second, sixth, ..., 98th percentiles. Increment and mortality were predicted for these hypothetical median trees. Alder (1979) used deciles, and modeled the development of the ten median trees corresponding to the fifth, 15th, ..., 95th percentiles. He predicted diameter increments via height increments estimated from the height-age relationship.

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 identified size, and simulated three cohorts 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 (Hahn and Leary 1979) was predicted for mean tree of the cohort, reduced by a modifier function to account for stand density and competition, and multiplied by the number of trees in the cohort. The list of individual diameters input to the model was not discarded, but retained and after the simulation each tree was updated by its share (Leary et al. 1979b) of the accumulated increment in its cohort.

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, its 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 trees; 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 1993).

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 use in 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 model two-dimensional competition, but in uneven-aged stands, competition may be three-dimensional. Empirical studies (e.g., Opie 1968, Daniels 1976, Alemdag 1978, Martin and Ek 1984, Barclay and Layton 1990) suggest that simple measures of stand basal area may be as good as any, and that the expense of determining individual tree positions is not justified for yield forecasting.

Newnham's (1964, Newnham and Smith 1964) model for even-aged stands of Douglas-fir drew on three important assumptions which 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. Although the approach works well for both even-aged stands of white spruce (Mitchell 1969) and Douglas-fir (Mitchell 1975), it has limited utility for tropical forests where measurement difficulties make height an inferior driving variable.

Single Tree Non-spatial 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. Non-spatial methods may offer an efficient alternative for yield forecasting.

Opie's (1972) model for even-aged Eucalyptus regnans comprised two parts. The first 15 years were modeled using a whole stand distribution approach. At age 15, tree diameters were predicted from the binomial distribution, and subsequent modeling used individual trees. The annual simulation cycle included diameter increment and mortality. Key functions included height-age, basal area increment, increment allocation and a stocking guide (Reineke's line). Campbell et al. (1979) reported several enhancements to the model.

JABOWA (Botkin et al. 1972) did not predict timber yields, but was used to evaluate concepts of succession. It simulated annual growth on 10x10 meter plots, and modeled growth, death and regeneration. Growth prediction was deterministic and rather subjective, but the "birth" and death routines were stochastic. 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 (West et al. 1981, Shugart 1984), including the Kiambram model (Shugart et al. 1980) for sub-tropical rainforest in Australia, and Doyle's (1981) model for tropical montane forest.

Tree List Models

At low resolution, tree list models (e.g., Leary 1979, Stage 1973) are stand class approaches, but with suitable resolution they improve on the non-spatial single tree approach. The 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 dimensions 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. In tripling, each tree record becomes three records with 15, 60 and 25% of the original expansion factor and an increment of 1.549Φ , 0.1423Φ and 1.271Φ respectively (these are derived from the normal $N(\cdot, \Phi^2)$ distribution). Prognosis is now in its fifth version (Wykoff 1986) and twelve 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, 1993) 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 (Kimmins et al. 1990).

Comparing Alternatives

Few empirical comparisons between models 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 years) and gave comparable predictions for long term (120 year) forecasts. Daniels et al. (1979) compared two whole stand models with a single tree model. The most accurate yield estimates were provided by the whole stand distribution model, but all three provided estimates suitable for plantation management. Relative costs of the predictions were 1:25:1400 for the yield model, the whole stand distribution model and the single tree model respectively. Although the single tree approach appears

sub-optimal in both respects (accuracy and cost), it still may have a place in providing more detailed information than is available from other approaches.

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

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 (e.g., Alder and Synnot 1992, Campbell 1989, Vanclay 1991a). Since few tropical tree species are amenable to stem analysis (Mariaux 1981), data must be obtained from remeasurements 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 depends 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 co-dominant 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.

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 meters 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 single explanatory variable. Diameter increment was predicted from the basal area in larger trees ($D = \beta_0 + \beta_1 \text{BAL}$), 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 theoretical 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 non-linear 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 Techniques

There are many techniques for fitting equations to data, and the appropriate one to use depends on the nature of the data and the chosen equation. 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. Although its validity may be debated, screening of data and the removal of outliers is standard practice (e.g., Arney 1985). Robust estimators are a compromise between including all the noisy data, and using only the massaged data. One advantage of massaging data is that it forces the researcher to evaluate the data critically. Choosing parameters for robust estimation does not force the same decisions upon the researcher (Hamilton 1979). The best way to check data, fitted models and statistical assumptions is to plot the data, model and residuals (Wilson 1979).

Two or more measurements are often taken from each sampling unit. The "sampling units" may be individual trees each with several measurements, or individual plots in each of which many trees have been measured. These repeated

measurements tend to be correlated, and are thus not statistically independent. Ordinary least squares regression will provide unbiased parameter estimates, but will underestimate the covariance matrix and residual variance (Davis and West 1981), precluding proper hypothesis tests. One solution may be to use one observation per sampling unit to formulate the model and test for significance, and then 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 non-overlapping 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. For example, a yield or basal area increment function will have a higher R^2 than an equally good diameter increment function fitted to the same data. The Furnival index provides a better basis for comparison by expressing the average standard error in the original untransformed units. Furnival (1961) gave an example where the combined variable volume equation $V = \beta_0 + \beta_1 D^2 H$ had an R^2 of 0.96 and a Furnival index of 19.2, and an alternative formulation $V/(D^2 H) = \beta_1 + \beta_0/D^2 H$ gave $R^2 = 0.72$ and Furnival index 9.4. The Furnival index confirmed that the alternative formulation was preferred, as was suggested by the residuals, but this is not revealed by R^2 .

The R^2 also gives an over-optimistic indication of the model's predictive ability. The Prediction Sum of Squares or PRESS (Allen 1971) provides a better indication

of the predictive ability of an equation. Since PRESS is analogous to RSS, small values are desirable. Modelers should not be pre-occupied with these indices, but should ensure 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., $dB/dt = d(kD^2)/dt = 2kD \cdot dD/dt$) 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 over 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 tropic rainforests (e.g., age, top height, mean diameter), since growth must be predicted 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 (e.g., 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 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 D/D), which may result in a counter-intuitive 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 (e.g., dbh), 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, Modifier functions & 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 is as useful as any of the other indices (Opie 1968, Daniels 1976, Alemdag 1978, Martin and Ek 1984, Barclay and Layton 1990).

An alternative is to predict potential growth and use a "modifier function" to estimate actual 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 increment predictions among the trees in the stand. Stand increment may be predicted as basal area increment (Gibson et al. 1969, Opie 1972, 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: $\Delta B_i/3 \Delta B_i = B_i^w/3 B_i^w$, where the weights w may vary from 0.93 (Campbell et al. 1979) to 1.25 (Opie 1972) for Eucalyptus regnans. This relationship (with $w=1$) held for even-aged stands of Callitris, but in uneven-aged stands, the smaller trees got a greater share of the increment, so Vanclay (1988) predicted an allocation rule from the mean and standard deviation of diameters. Leary et al. (1979b) predicted the allocation rule for the increment in sum of diameters as:

$$\text{Log}(X_{(1)}) = \exists_0 + \exists_1 \text{Log}(X_{(2)}) + \exists_2 \text{Log}^2(X_{(2)}) + \exists_3 \text{Log}^3(X_{(2)})$$

where $Y = \sum D_i/3D_i$ and $X = D_i/3D_i$, the \exists s are constants common to species and stands, and the α s depend upon species and stand condition. These methods may provide good results for stands with few species, but become complex where 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. Non-asymptotic growth is always temporary and can be rendered by a segment of an asymptotic model. In this sense, . . . non-asymptotic equations cannot be considered growth equations".

Many studies (e.g., Leak and Graber 1976, Alemdag 1978, West 1980) use the simple quadratic $\Delta D = \exists_0 + \exists_1 D + \exists_2 D^2$, which may not provide robust results (e.g., if

$\exists_2 > 0$ 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 $\Delta D = \exists D^2$ for each plot, and the second stage fitted

$$\text{Log}(\exists) = \exists_0 + \exists_1 \text{Log}(S) + \exists_2 D + \exists_3 P$$

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

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

A similar equation was used by Wykoff (1990, with $k=2$) and Vanclay (1991b, with $k=1$):

$$\text{Log}(\Delta D^k) = \exists_0 + \exists_1 \text{Log}(D) + \exists_2 D^k$$

Theoretical equations offer some explanation of growth. There is no particular theoretical equation which relates specifically to the growth of trees (Sweda and Koide 1981), but the Bertalanffy (or Chapman-Richards) equation may be generalized for diameter growth of trees:

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

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 (\exists_0) to improve increment predictions for small trees:

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

where D is diameter, S is site index and R is crown ratio. These equations are not well suited for non-linear estimation and Ratkowsky (1990) suggested several alternatives which may offer more efficient parameter estimation.

Martin and Ek (1984) examined the Bertalanffy equation in Pinus resinosa plantations:

$$dD/dt = (0.2832 D^{2/3} - 0.04925 D) e^{-0.03922 B}$$

but found that carefully formulated empirical equations could provide more accurate predictions within the range of the data. Shifley (1987) used a similar 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 (m²), S is site index (m) at age 50, and R is crown ratio (1/R#9). This was fitted in two stages. First, dB/dt = $\lambda B^{\beta} (A - B)$ (B was fitted and the asymptote A = $(\lambda/\beta)^{1/\beta}$ compared with the national register of big trees. If it seemed unreasonable, the parameter λ was revised: $\lambda = \beta A^{\beta}$. The second stage estimated the effects of site and crown condition. The equation predicts potential increments which are reduced by a modifier predicted from tree size, basal area in larger trees and stand basal area.

Several empirical functions mimic the shape of these theoretical equations, and may be easier to fit to data. Revised diameter increment functions for Prognosis assume (Wykoff 1990):

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

where SITE and COMP reflect site and competition respectively. The final function was:

$$\text{Log}(D^2) = \beta_0 + \beta_1 \text{Log}(D) + \beta_2 D^2$$

$$\begin{aligned}
& +\beta_3 SL[\cos(\text{ASP})] + \beta_4 SL[\sin(\text{ASP})] + \beta_5 SL + \beta_6 SL^2 + \beta_7 EL + \beta_8 EL^2 \\
& + \beta_9 CR + \beta_{10} CR^2 + \beta_{11} BAL / \text{Log}(D+1) + \beta_{12} CCF
\end{aligned}$$

where D is diameter, SL is topographic slope, ASP is aspect, EL is elevation, CR is crown ratio (crown length/tree height), BAL is basal area in larger trees, and CCF is crown competition factor (Krajicek et al. 1961). The first line of this equation reflects the effect of tree size on increment, the second line is a proxy for site productivity, and the third line accounts for competition. It 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 (Vanclay 1991b):

$$\text{Log}(D+\Delta) = \beta_0 + \beta_1 D + \beta_2 \text{Log}(D) + \beta_3 S \cdot \text{Log}(D) + \beta_4 \text{Log}(B) + \beta_5 BAL$$

Lowell and Mitchell (1987) used a probabilistic function to predict diameter increment and mortality simultaneously in even-aged oak forest. Their equation for white oaks was

$$P = (1 + \exp(-8.901 + 271.1) D D^{-1.594} \text{Log}(D/3D))^{-1}$$

where P is the probability that a tree of D cm dbh will have a diameter increment exceeding ΔD cm over a five year period (3D is the sum of diameters D of all trees per hectare). The probability P₀ of a zero increment is the probability of survival, and 1-P₀ gives the predicted five year mortality. Vanclay (1991c) used a similar probabilistic function to predict the probability that a 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 one year interval, for any integer n) (e.g., for Flindersia pimenteliana):

$$P = (1 + \exp(-0.7378 + 0.1079 D - 1.987 \log(D) - 0.1455 S \cdot \log(D) + 1.994 \log(B) + 0.03548 \text{BAL} - 0.4221 S))^{-1}$$

where P is the predicted probability, B is stand basal area (m²/ha), BAL is basal area in larger trees (m²/ha), and S is a binary variable indicating preferred soils.

MORTALITY AND MERCHANTABILITY FUNCTIONS

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.

Regular Mortality

Reineke (1933), Yoda et al. (1963) and others (e.g., Drew and Flewelling 1977, 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. Mitchell (1969) modeled the crown development of trees, and assumed that when the actual crown width fell below 17% of the potential open growth crown width, there was a 50% probability of being overtopped and dying.

Newnham (1964) assumed that trees would die if predicted increments were less than an assumed threshold. The argument is supported by some empirical evidence. Spurr (1962) reported that any Pinus radiata tree attaining an annual increment less than twenty square centimeters has, on average, less than eight years to live. Swaine et al. (1987) observed that mortality in semi-deciduous 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 millimeters per year respectively. But Newnham (1964) also observed that Douglas-fir trees may attain a diameter increment less than 0.3 millimeters per year for more than 25 years and still survive. And 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:

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

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 nth 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 t yrs rather than t^{-1}) rather than as a weight. Whilst Monserud's approach is technically correct, weighting provides an efficient approximation which is reasonably accurate provided that remeasure intervals do not exceed 7–8 years 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 (D/D_0 , Hamilton 1986, 1990) and the relative position in the cumulative size distribution (BAL/B_0 , 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 (e.g., 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 analogue using actual rather than predicted diameter increment (with 50.0 D replacing 0.62 PDI) correctly classified 98% of deaths and 90% of survivals. Simulation studies normally rely on predicted increments which may provide inferior predictions, so it may be preferable to model mortality directly from tree and stand variables.

Mortality probabilities may be implemented as 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.

Catastrophic Mortality

Catastrophic mortality is often excluded from mortality functions and accommodated through an arbitrary reduction final yield estimates. Objective estimates are preferable, and Hamilton (1980) suggested that catastrophic mortality should be modeled in two stages: predict the probability of a catastrophe, and then use a conditional function to predict mortality given that a catastrophe has occurred. This two stage approach can provide a weighted estimate of annual mortality or may be implemented directly in a stochastic model.

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 forest after elimination of one of its component species.

Management Induced Mortality

Yield studies require prediction of the number or proportion of trees harvested or retained in each class. In natural forests the composition and stocking are variable so the best option may be to predict probabilities. Vanclay (1989b) predicted the probability of harvesting a tree from species, tree size and 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 death 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) modeled destruction in the residual stand using 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 rates following thinning in temperate forests.

Merchantability

Merchantability assessment may seem unrelated to mortality prediction, but for modeling they pose identical problems. 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):

$$P = (1 + e^{17.450 + 0.04195 B + 22.49/D - 0.0/T + 0.4213 CG})^{-1}$$

where P is the annual probability that a merchantable tree remains merchantable, B is stand basal area (m²/ha), T is time since last harvest (other species have non-zero 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 Toona 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 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. This approach is common in matrix models, where the number of recruits increases as the number of trees in the larger size classes increases (Usher 1966). 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).

Grimes and Pegg (1979) predicted recruitment into the smallest class (20-30 cm dbh) from the basal area of stems greater than 7.5 meters high but less than 20 cm dbh. This reserve of small stems was assumed to remain constant throughout the projection period. Many models follow this approach, assuming that stocking in the smallest class (or in the "reserve") remains constant (any upgrowth from this class is replaced by ingrowth). This may provide useful estimates of recruitment for stands which do not differ much from the calibration data.

Dynamic Recruitment Models

It is preferable to adjust recruitment estimates according to stand condition. Hann (1980) predicted recruitment from site index, stand basal area, and basal area in the smallest size class. Vanclay (1989a) 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 (m²/ha), B₁ is the basal area of group 1 species (m²/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 = P₁/3P

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 overstorey. Shugart and West (1977) followed a similar approach, but 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 per hectare, above which no recruitment could occur.

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 more efficient to use two-state 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 each 1/300 acre (about 0.001 ha), and these were aggregated into the main Prognosis model at 10 and 20 years after disturbance (Prognosis has a 10-year simulation cycle). 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 these species.

Vanclay (1992b) predicted the probability of recruitment at 10 cm dbh independently for each of 100 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 one for deterministic predictions. The number of recruits of each species, given that some was 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 one-year-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 ten years 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 in subplots within the main plot being simulated. 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 overstorey tree from tree size and threshold age, and were distributed across the subplots according to the parent tree's position, height and crown width. Germination was predicted from microsite and canopy cover. Each year, seedlings either die or survive and

grow in height (function of cover, species and age), until recruited at breast height. If not recruited within a specified time (e.g., 25 years for black spruce), trees died. Monserud and Ek (1977) assumed that understorey tree size was more relevant than age, and modeled the development of trees to 7.6 meters height using five height cohorts and movement ratios. The height increment of the mean tree was predicted from the potential increment, overstorey competition index, shade tolerance and stand density.

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 overstorey 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 AND CALIBRATION

Validation is a misnomer: a model cannot be proved correct, and can only be proved incorrect. However, the failure of several attempts to disprove an hypothesis gives more it credence. Calibration usually refers to parameter estimation, but here

is used in the more restricted sense of finding an adjustment to improve model predictions for a specific locality.

Validation

All models are imperfect; at best they are a simplification of complex processes. 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). The critical question is not whether the model is valid, but whether it is useful and whether it generates enough confidence for it to be taken as the basis for action. The decision to accept the null hypothesis does not mean that the model is correct, or that it is the best possible model. On the other hand, the decision to reject the null hypothesis does not necessarily mean that the model is not useful for practical purposes. 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).

Validation in its purest form requires independent data for validation. Thus growth modelers may have to partition their data set, 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 in validation of forest 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.

Two simple criteria provide nearly all the information necessary in validation (Snee 1977, Burk 1986): model bias ($\frac{\sum(\text{predicted} - \text{observed})}{N}$) and mean absolute difference ($\frac{\sum|\text{predicted} - \text{observed}|}{N}$). These formulae are 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 the prediction of any one observation. Estimates of model bias may also be weighted $\sum W(P/O)$ for basal area, volume, value, etc. (Reynolds et al. 1988). Reynolds (1984, Reynolds and Chung 1986) provided formulae to calculate critical errors and confidence intervals for prediction errors. Another way to examine model performance is to plot the predicted and observed values of several tree and stand variables and see how they

compare, 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.

Calibration

Calibration implies adjusting a growth model 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 "transplanted" to several other regions and most copies retain all the computer code and original equations. Some have estimated new coefficients (Shifley 1987), whilst 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 forest) or by re-estimating coefficients in component equations (Goodwin 1988 for mixed eucalypt forest) have been fraught with difficulty and results to date have been poor.

Prognosis has a "self-calibration" feature to allow calibration using increment cores on temporary plots. The deviation (observed ! predicted) in the logarithm of the tree basal area increment is added to the logarithm of the diameter increment function, thus adjusting the growth rate and 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. Thus the model should be available, adequately documented and integrated into other information systems used by forest managers.

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 2/3 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 non-commercial species bias model predictions and any such data should be augmented by average data for the forest type (Randall et al. 1988).

Vanclay (1990) described how a growth model could be integrated into an inventory reporting system so that plots can be reported as at date of measure or after simulating to any future date, and reported as individual plots or summarized into stratum or forest estate reports. Moore and Lockwood (1990) described a yield prediction system linked to a geographic information system, and Pelkki and Rose (1988) describe the integration of such a system with an expert system to enable automatic production of stand management prescriptions.

Optimization Studies

Growth models can be used to explore stand conditions which maximize revenue or other benefits. Most studies optimize the most likely outcome, but some address uncertainty (Valsta 1992). The optimum stand condition may be defined as the initial stand X_0 which gives rise to the stand X_t in t years time, such that the increase $X_t - X_0$ is maximized. Many studies rely on a "sustainable distribution" (Adams and Ek 1974): $N_{d,t+1} \leq N_{d,t}$ for all d where $N_{d,t}$ is the number of trees in a diameter class d at time t . This ensures that trees can be removed from each class to return to the original distribution. Michie (1985) used a matrix model to explore a more general case. Bare and Opalach (1987) found that the "investment efficient"

diameter distribution depends on the criterion: maximum land expectation value provides a different optimum than maximum volume growth. This reiterates the interrelationship between modeling, management objectives and optimal silviculture.

Many studies simplify the growth model to provide a tractable analysis, and this may influence the results. Haight and Monserud (1990a,b) demonstrated a method for optimizing any-aged management of mixed species stands using the standard Prognosis model. They found that even-aged plantation management and uneven-aged shelterwood systems could produce identical yields indefinitely. Sensitivity analyses are essential to ensure a global optimum and to assist the forest manager (Haight and Monserud 1990a).

Yield Prediction

Yield prediction may be the main application for many growth models. Growth models make it simple to estimate yields from single stands, but forest estate estimates also involve the spatial and temporal distribution of yields. Simulation studies can help find the best path through the sometimes contradictory requirements of maximum sustained yield and non-declining even flow.

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 1987:48) is to nominate a cutting cycle length, construct a typical stand table, project this stand to the mid-point 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 mid-cycle.

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 1971:239).

Yield scheduling by heuristic (trial and error) simulation can overcome many deficiencies of traditional cutting cycle analysis by emulating the sequence of harvesting using the appropriate cycle for each unit, rather than the nominal cycle. Heuristic simulation does not provide the maximum sustainable yield, but takes an

initial estimate by the user and provides information to enable the user to make a better estimate for a subsequent iteration (Johnson and Tedder 1983, Davis and Johnson 1987:656, Leuschner 1990:164). Vanclay (1993) illustrated heuristic simulation 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.

Linear programming (LP) and other mathematical programming techniques may also be used for estimating timber harvests (Clutter et al. 1983:272, Davis and Johnson 1987:592, Leuschner 1990:82), but have been used mainly for plantations. FORPLAN, an LP model widely used in forestry, does more than timber harvest scheduling, and assists multiple use planning and in resolving management conflicts (Mealey 1987). Whilst these techniques are useful, they do not provide an easy option, as considerable skill and resource information are necessary.

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). Reynolds (1984) gave formulae for estimating errors associated with growth projections.

Conclusions

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.

Whilst whole stand models have been useful for plantation modelling, they have less utility in tropical moist forests, where many species and multi-modal 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 modelled, 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 every-day tool for better forest management. In short, that means that the growth model should be easy to use, well documented and readily available.

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