GROWTH AND YIELD MODELING -- A PLACE FOR GENETIC IMPROVEMENT EFFECTS

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Abstract.--A wide array of growth and yield models, ranging from whole stand models to individual tree models, has been developed for southern species. These models for "woods run" stock can potentially be modified to provide preliminary estimates of growth and yield in stands established from genetically improved stock. The approach necessary and the likelihood of success in incorporating genetic improvement effects in growth and yield models depends on the components of the model, the predictor variables used, the interdependence of the components, and, of course, the extent and nature of the data base on genetic effects.

Additional keywords: Yield tables, stand models, simulation

INTRODUCTION

For over two decades considerable effort has been devoted to the selection and propagation of forest trees for seed orchard establishment in the South. Seed collected from these orchards is now providing genetically improved stock for stand establishment. During the 1979-80 planting season, the forest products industry in the Southern U. S. planted 787,743,422 pine and hardwood seedlings. Of the more than three-quarters of a billion seedlings planted, a record 327,341,410 were from seed orchard-produced stock (information provided by Southern Forest Institute). At present, information concerning the effect of genetic variation on yield is limited. Yield tables that are currently available apply only to natural stands or plantations established from "woods run" stock. It is essential that yield estimates be developed for the increasing acreage of genetically improved stands if prudent forest management decisions and realistic wood supply projections are to be made.

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The purpose of our paper is two fold: (1) to present an overview of growth and yield modeling approaches that have been commonly employed in the past, and (2) to suggest how the effects of genetic gain might be incorporated into the various types of models.

OVERVIEW OF GROWTH AND YIELD MODELING APPROACHES

Modern quantitative analysis of forest growth and yield dates to MacKinney and Chaiken's (1939) application of multiple regression techniques to the problem of variable-density yield estimation in natural stands of loblolly pine. Since that time, a wide variety of approaches has been taken to growth and yield estimation. Throughout this discussion emphasis will be placed on techniques and approaches taken to growth and yield modeling for even-aged stands of southern species. The current modeling approaches may be considered to lie on a continuum with respect to structural complexity and output detail. This continuum may be broken into three broad categories: (1) whole stand models, (2) size class distribution models, and (3) individual tree models.

Whole Stand Models

Many investigators have used multiple regression techniques to predict growth and/or yield for the total stand or for some merchantable portion of the stand (such as Beck and Della-Bianca 1972, Bennett 1970, Bennett *et al.* 1959, Brender and Clutter 1970, Burkhart *et al.* 1972a, b, Clutter 1963, Coile and Schumacher 1964, Dale 1972, Farrar 1979, Goebel and Warner 1969, Murphy and Sternitzke 1979, Schumacher and Coile 1960, Smith et *al.* 1975, Sullivan and Clutter 1972, Sullivan and Williston 1977). Stand level variables such as age, site index, basal area or number of trees per unit area are utilized in the whole stand approach to predict some specified aggregate stand volume. Volume distribution by size class is not provided. A commonly used multiple linear regression model for natural stands is:

$$\log(Y) = b_0 + b_1 (1/A) + b_2 (SI) + b_3 \log(BA)$$

where

Y = net yield per unit area
A = stand age
SI = site index
BA = basal area per unit area
1 = parameters to be estimated from the data

Whole stand models for plantations generally involve number of trees rather than basal area per unit area as the expression for stand density.

Net growth is estimated by differencing predicted yield at two points in time. When obtaining growth estimates by differencing a yield equation, it is necessary to have a function that describes the change in stand density over time. For natural stands this has generally involved an equation to project basal area as a function of site index, initial basal area and age, and the length of the projection period. Numbers of trees per unit area must be projected for typical models of planted stands. These "survival curves" commonly express the number of live trees at any given time as a function of the number planted, site index and age.

Many of the published multiple regression models are highly empirical "best fits to the data," although some work has been reported on biologically-based model forms (for example, Pienaar and Turnbull 1973). A major improvement in model specification methodology was suggested by Clutter (1963) when he derived compatible growth and yield models for loblolly pine. Clutter's (1963) definition of compatibility was that the yield model should be obtainable through mathematical integration of the growth model.

Size Class Distribution Models

A number of models have been developed which consider the stand in terms of the distribution of the number of trees per unit area by size-class. In most cases dbh classes have been used. The most common stand models for southern species in this general category are based on a diameter distribution analysis procedure (for example, Beck and Della-Bianca 1970, Bennett and Clutter 1968, Burkhart and Strub 1974, Clutter and Belcher 1978, Dell *et al.* 1979, Feduccia et al. 1979, Lenhart 1972, Lenhart and Clutter 1971, Schreuder *et* al. 1979, Smalley and Bailey 1974a, b). In this approach, the number of trees per unit area in each diameter class is estimated through the use of a probability density function (pdf) which provides the relative frequency of trees by diameters. Mean total tree heights are predicted for trees of given diameters growing under given stand conditions. Volume per diameter class is calculated by substituting the predicted mean tree heights and the diameter class midpoints into tree volume equations. Yield estimates are obtained by summing the diameter classes of interest. Although only overall stand values (such as age, site index, and number of trees per acre) are needed as input, detailed stand distributional information is obtainable as output.

The various diameter distribution models differ chiefly in the function used to describe the diameter distribution. Initial applications of this technique (Beck and Della-Bianca 1970, Bennett and Clutter 1968, Burkhart and Strub 1974, Lenhart 1972, and Lenhart and Clutter 1971) used the beta probability density function, whereas more recent applications have utilized the Weibull function (Clutter and Belcher 1978, Dell et al. 1979, Feduccia et al. 1979, Schreuder et al. 1979, and Smalley and Bailey 1974a, b).

Regardless of the probability density function used, the procedure involves estimating the pdf parameters for each plot in the data set (usually by the method of moments or maximum likelihood) and then developing regression equations to relate these parameter estimates to stand characteristics such as age, site index and number of trees per unit area. Unfortunately, functions for relating the pdf parameters to stand characteristics have not been fully satisfactory. Currently, there is much interest in an alternative to the conventional methods for estimating diameter distribution. This alternative, sometimes called a "parameter recovery method," consists of forecasting overall stand attributes (such as total cubic volume, total basal area) and solving for the parameters of a theoretical diameter distribution model (such as the beta or Weibull) that will give rise to the overall stand attributes. Although there is little published on this technique, it does have potential for producing more consistent diameter distributions and it provides a direct mathematical link between the overall stand volume and the distribution of that volume. Additional information on parameter recovery methods can be found in the recent papers by Hyink **(in** press) and Matney and Sullivan (in press).

Individual Tree Models

Approaches to predicting stand yields which use individual trees as the basic unit will be referred to as "individual tree models". The components of tree growth in these models are commonly linked together through a computer program which simulates the growth of each tree and then aggregates these to provide estimates of stand growth and yield. This approach, while receiving extensive attention and application in the Western and Lake States regions of the U. S. as well as in Canada, has not been applied widely in the South.

Individual tree models are generally divided into two classes, distance dependent and distance independent depending on whether or not individual tree locations are required tree attributes. Distance independent models project tree growth either individually or by size classes, usually as a function of present size and stand level variables such as site index and basal area per unit area. These models vary widely in structure; examples of distance independent models are Dale (1975) and Stage (1973).

Distance dependent models that have been developed vary in detail but are quite similar in overall concept and structure. Initial data of a stand are input or generated and each tree is assigned a coordinate location. The growth of each tree is simulated as a function of its attributes, the site quality, and a measure of competition from neighbors. The competition index varies from model to model but in general is a function of the size of the subject tree and the size of and distance to competitors. Tree growth is commonly adjusted by a random component representing genetic and/or microsite variability, and survival is controlled either stochastically or deterministically as a function of competition and/or individual tree attributes. Yield estimates are obtained by summing the individual tree volumes (computed from tree volume equations) and multiplying by appropriate expansion factors. Models of this type have been developed by Arney (1974), Daniels and Burkhart (1975), Ek and Monserud (1974), Hegyi (1974), Newnham and Smith (1964), and others. The loblolly pine stand simulator published by Daniels and Burkhart (1975) is presently the only fully operational distance-dependent stand model for a southern species.

INCORPORATING GENETIC IMPROVEMENT EFFECTS IN GROWTH AND YIELD MODELS

Preliminary estimates of growth and yield are needed for stands established from genetically improved stock prior to large acreages reaching merchantable size. Modification of existing growth and yield models for "woods run" stock will likely be the most feasible means of developing these preliminary estimates.

Past Studies

Relatively little work has been done on modeling genetic improvement effects on growth and yield. Tisdale (1973) evaluated a whole stand model and a diameter distribution model for loblolly pine plantations to determine which could best predict dry weight yield after constant growth increases in diameter and height and increases in specific gravity were incorporated. He found the diameter distribution model was more readily modified to include assumed changes in growth characteristics and that the predicted yields from the modified diameter distribution model conformed more closely to expected values than did those from the whole stand model.

Mitchell (1975) modified the mean and variance in height growth in his Douglas-fir stand simulator to depict the effects of hypothetical selection programs on yields. His results indicated that a simultaneous increase in the mean and decrease in the variance of height growth may result in little or no increase in total volume and will probably decrease the volume in the larger "crop trees".

Nance and Bey (1979) modified four relationships in Daniels and Burkhart's (1975) individual tree model to reflect genetic differences. Predicted yields from the modified version were then compared to yields with the original model. These comparisons indicated that early height growth gains must be maintained throughout the rotation to materially affect final yield, that mixing of seed could be more desirable than separate plantings of woods run and improved seed, and that reducing phenotypic variance may reduce total volume production.

Genetic improvement effects on "optimal" rotation age of loblolly pine plantations were studied by Thurmes (1980). Using Daniels and Burkhart's (1975) stand model, he found that arbitrarily increasing height growth decreased optimal rotation age in the same manner as experienced by increasing site index. Thurmes also decreased the stochastic variability in the model in an attempt to simulate genetic selection. This decreased variability (without any shift in the mean) resulted in fewer peeler-sized trees and decreased the stand value.

Some Possible Approaches for Future Studies

In the ensuing discussion of possible approaches for future studies aimed at incorporating the effects of genetic improvement in growth and yield models, we assume that an existing model for "woods run" stock is to be modified. When modifying an extant model, it will be necessary to develop biological paradigms of how genetically improved stock might grow, specify mathematical models of these paradigms, and evaluate the resultant predictions against conventional wisdom and experimental data. As additional data from genetically improved stands become available, this information can be used to evaluate the appropriateness of the original models and to estimate coefficients in growth and yield models.

The approach to incorporating genetic improvement effects in growth and yield models will be determined by the type of model(s) and the extent and nature of data on realized genetic gain that are available. Genetic improvement may affect many different aspects of tree growth and stand development. First we will examine some of the individual components and suggest how modifications may be made to reflect the effects of genetic selection.

Specific gravity modification can be modeled by simply changing the constant for converting cubic volume to dry weight.

Form changes can be incorporated by modifying the tree volume or taper equations that are used to convert dbh and height values to tree volumes.

Disease resistance, for example resistance to fusiform rust, can be partially incorporated by modifying the survival curve. If selection for disease resistance affects the distribution as well as the total amount of mortality, this shift must also be incorporated to provide realistic estimates of surviving volume by size class.

Diameter growth changes can be incorporated into the diameter growth function, or, depending on the type of models, perhaps into the basal area projection equation.

Height growth modification may be reflected through a height growth function or through a shift in the site index value.

Selection for any one factor is not necessarily independent of the other factors, of course. Thus, it would not be realistic to assume a simple change in diameter or height growth with no corresponding change in factors such as tree form and mortality rates. In many instances, models are structured such that a change in one factor will affect many other factors. For example, if height growth is increased without any increase in diameter growth and both dbh and height are used to estimate tree volume, an improvement in form is implied even if the coefficients in the tree volume or taper equation are not modified.

As a further example, consider how mortality might be affected by genetic selection. In growth and yield models where mortality is expressed as a function of initial number of trees planted and stand age, increased (or decreased) diameter or height growth would not influence survival. If, however, surviving number of trees is modeled as a function of stand age, basal area, average height of the dominant stand, and initial number of trees planted, then an increase in diameter or height growth (or both) would affect survival. In cases where the components are interrelated, a change in only one component may affect all other components. When the components are not interrelated it may be necessary to modify several functions to appropriately reflect a change in a single factor. The approach necessary and the likelihood of success in incorporating genetic improvement effects in growth and yield models depends on the components of the model, the predictor variables used, and the interdependence of the components.

Decreased variability is often a result of selective breeding. In deterministic models, decreased variability can be modeled by adjusting growth equations so that trees are more uniform in size. This decreased variability is commonly expressed in stochastic models by the adjustment of the variance of selected random components in the model. An appropriate variance reduction for random components is difficult to determine, however, because these components reflect both microsite and genetic variability. In general, stochastic models provide some advantages over deterministic models when attempting to model many genetic gain effects because either growth functions or random components (or both) can be modified.

SUMMARY AND CONCLUSION

In summary, a wide array of growth and yield models -- ranging from whole stand models to size class distribution models, to individual tree models -- have been developed for southern species. With the increasing acreage of stands established from genetically improved stock, it is essential that growth and yield estimates be developed for these conditions as quickly as feasible. Preliminary estimates can be derived through the modification of existing growth and yield models for "woods run" stock. The approach to this modification will depend on the type of model(s) available and the extent and nature of data on genetic gain. Incorporation of genetic improvement effects into growth and yield models must proceed in light of components of the model, the predictor variables used, and the interdependence of the components. Until adequate validation data are available, these tentative estimates of the effects of genetic selection should be used cautiously.

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