

## **EVALUATING REALIZED GENETIC GAINS FROM TREE IMPROVEMENT**

**J.B. St.Clair**

**Research Geneticist, USDA Forest Service  
PNW Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331**

### **ABSTRACT**

Tree improvement has become an essential part of the management of forest lands for wood production, and predicting yields and realized gains from forests planted with genetically-improved trees will become increasingly important. This paper discusses concepts of tree improvement and genetic gain important to growth and yield modelling, and reviews previous studies of the growth and yield of genetically-improved stands. Three types of studies that have been done include: (1) simulations in which assumptions have been made about key inputs into the models, (2) studies of genetic variation in stand productivity at the level of seed sources or families, and (3) actual comparisons of improved versus unimproved stands. Simulation studies indicate that genetic gains are highly likely, but how much gain is realized will depend on height-age trajectories after crown closure. Studies of genetic variation in stand productivity are ambiguous with respect to genetic variation in parameters of the height-age curve. Few studies have been published of actual comparisons of improved versus unimproved stands, although many such studies have recently been established. The design of a study to evaluate realized genetic gains from Douglas-fir tree improvement programs is presented.

### **INTRODUCTION**

Tree improvement efforts began in earnest in the 1950's and 1960's in many regions of the world, and have become an essential part of the management of forest lands for wood production. Presently many forestry organizations are embarking on second and third generations of improvement. In the Douglas-fir region of the Pacific Northwest, tree improvement programs have been initiated over the last 30 years to provide improved trees for over 6.5 million hectares (Silen and Wheat 1979; Adams et al. 1990). These programs represent a cumulative effort of approximately 42,000 parent trees evaluated at over 1,350 progeny test plantations with an investment of approximately a quarter-billion dollars (Adams et al. 1990). Seed orchards are now beginning to produce large amounts of improved seed and landowners are now utilizing improved planting stock in their reforestation programs.

Despite large investments in tree improvement programs like those in the Pacific Northwest, fundamental questions about the interaction of genetics and silviculture and the use of genetically-improved stock remain unanswered. Specifically, it has not yet been demonstrated that expected genetic gains, which are based on growth

differences measured on individual trees in young progeny tests, are achievable as per-unit-area gains at rotation. Although forest geneticists are confident in the efficacy of tree improvement, they are less confident in their ability to predict with any certainty the level of achievable gains in stand productivity. Developing the techniques needed to predict the growth and yield of improved stands will require the integrated knowledge of geneticists, biometricians, silviculturists, economists, and land managers.

Several reasons exist for wanting to predict the final yield of improved stands (Flewelling and Talbert 1990). Besides providing justification for the large investment in tree improvement programs, knowledge of the productivity of genetically-improved forests will facilitate better-informed land management and economic decisions. These include establishing the allowable cut for sustained wood production, making decisions on establishing new mills and new markets, altering silvicultural treatments to best utilize the growth behavior of the improved stock, making decisions on how best to allocate improved stock to different sites, and making decisions on how much to invest in tree improvement versus other activities. In addition, understanding the biology of increased stand growth and yield may lead to changes in the selection process, including decisions concerning the competitive regimes of genetic tests (i.e., stand density and mixed versus pure family blocks) and the inclusion of physiological or morphological traits in selection criteria (Ford 1976; Cannell 1978).

The goal of this paper is bring together concepts of forest genetics and stand modelling important to the prediction of yield and realized genetic gains from genetically-improved forest stands. I will first review some concepts of tree improvement and genetic gain, and consider some of the factors important in determining expected and realized gains. I will then discuss growth and yield modelling of improved stands, including a review of past studies. In the final section, I will present the outline of a study recently initiated by the USDA Forest Service Pacific Northwest Research Station and members of the Northwest Tree Improvement Cooperative designed to evaluate realized genetic gains from Douglas-fir tree improvement programs.

## **EXPECTED VERSUS REALIZED GAINS FROM TREE IMPROVEMENT**

The primary objective of most tree improvement programs is increased value production per unit area of land at rotation. Unfortunately, this trait is not easily measured. To get around this, tree breeders do several things. First, they measure and select multiple traits thought to be related to value, in particular, stem size, but also traits related to wood quality (e.g., wood density, stem straightness, branch characters) and adaptability (e.g., cold and drought tolerance, disease and insect resistance). The different traits are then combined by a variety of techniques, including index selection, independent culling levels, tandem selection and multiple population breeding, to select genotypes in one or more generations. Second, they

measure and select genotypes at a much younger age than rotation length. Although no studies exist relating early performance to performance at typical rotation ages, several studies suggest that correlations are sufficiently high to make early selection worthwhile (Lambeth 1980; Lambeth et al. 1983). Third, selection is done based on performance of individual trees rather than yield per unit area. At younger ages before appreciable competition, individual-tree yield and stand yield should be highly correlated after correcting for differences in survival. At older ages, however, relative family performance and estimates of genetic parameters may be influenced by differential responses to density and intergenotypic competition (Foster 1989; St.Clair and Adams 1991).

Realized genetic gains refer to those gains actually obtained from tree improvement. Realized gains in value or volume production per unit area at rotation are rarely tested due to the considerable expense and time commitment involved in establishing trials. Instead, expected genetic gains are predicted based on estimates of heritabilities and genetic values of parents from genetic tests. The primary objective of most genetic tests is to evaluate the relative performance of genotypes for purposes of selection. Estimating components of variance and covariance for purposes of estimating heritabilities, genetic correlations and expected genetic gains are usually only secondary objectives.

Genetic tests are usually established using a randomized block design with row or non-contiguous plots of a few trees (e.g., one to five trees). Several studies indicate that a test design using small, non-contiguous plots is the most efficient design for estimating family means, and designs using large, pure-genotype plots are the least efficient (Lambeth et al. 1983; Loo-Dinkins and Tauer 1987). Although family ranking for selection appears to be stable among different plot configurations, variance component estimates may differ greatly between large block plots, row plots and non-contiguous plots (Foster 1989). Intergenotypic competition among families may lead to much larger estimates of genetic variance, heritability, and expected genetic gain. In a seedling study of Douglas-fir, I found that the expected genetic gain for selection for biomass when families were evaluated in mixtures was 26%, whereas the same families tested in pure family plots resulted in estimates of genetic gain of only 8% (St.Clair and Adams 1991). Which estimate of gain is most appropriate is a question that is not easily answered. If genotypes are evaluated in pure stands (for example, to obtain estimates of yield per unit area), the gains calculated may not be appropriate if the improved material is to be deployed in mixtures in production forests. However, if genotypes are evaluated in mixtures, the mixture used in the genetic test will necessarily differ from the mixture of selected genotypes deployed in production forests. This may lead to reductions in realized genetic gains if selection in mixtures leads to selection of trees that are more competitive. This concern is the basis for ideotype breeding which attempts to select tree types that are less competitive and may lead to larger yields per unit area (Cannell 1978; Dickmann 1985).

Expected genetic gains predicted from genetic tests may differ from realized gains for

the reasons given above, that is, the trait of interest is not directly selected, juvenile-mature correlations may be less than perfect, and competitive interactions may affect relative performance and variances. Other factors that may be important include poor design and siting of genetic tests, pollen contamination in seed orchards, unequal contributions of parents to the improved population, and interactions between genotypes and silvicultural practices. Much research in forest genetics is aimed at addressing these concerns. However, establishing genetic gain trials and applying techniques of growth and yield modelling to existing genetic tests and improved plantations will be required if we are to be able to confidently predict yields and realized genetic gains from improved plantations.

## **GROWTH AND YIELD OF GENETICALLY-IMPROVED FOREST STANDS**

### **Growth and Yield Modelling**

Many different models have been developed to predict the growth and yield of forest stands. Growth and yield models are commonly classified as either stand-level models or tree-level models, dependent upon whether the stand or the individual-tree is the basic prediction unit (Clutter et al. 1983). Stand-level models use stand statistics as input variables, whereas tree-level models include at least some individual-tree statistics. Diameter distribution models are a type of stand-level model that produce some individual-tree outputs in the form of frequencies and average heights by diameter classes. Tree-level models include distance-independent models and distance-dependent models, which are distinguished by whether or not information on the positions and distances between trees are included. Data needed for input into models include height, diameter, and stand density at different ages. Given this data, modelers attempt to mathematically describe and interpret several important relationships. These include (Buford and Burkhart 1987; Foster 1992): (1) the development of height over time (the height-age relationship or site index), (2) the frequency distributions of height and diameter, (3) the relationship between height and diameter, (4) mortality trends over time, and (5) the relationship between individual-tree size and stand density (the self-thinning line). Some models may include other types of data such as information on wood quality, crown structure, or physiological variables.

Current genetic tests are ideal for initial development of models for predicting yields from improved stands. Information on height, diameter, and stand density at different ages is readily available in many genetic tests. Both stand-level and tree-level models may be used for predicting yields using genetic test data, since data is collected on an individual-tree basis. Inferences from current genetic tests, however, will be limited due to the unknown effects of intergenotypic competition.

Evaluating genetic effects on growth and yield involves several steps. First, the mathematical model that best describes the relationships of interest must be selected. Two mathematical functions commonly used to describe relationships of interest are

the Schumacher function and the Chapman-Richards function (Clutter et al. 1983). The Schumacher function includes an asymptote, or level, parameter, and a slope parameter, which defines curve shape. The Chapman-Richards function also includes an asymptote parameter, but curve shape is defined by two parameters, commonly referred to as shape and rate. The choice of mathematical model may be important to conclusions from the analysis (Knowe and Foster 1989; Sprinz et al. 1989). In the next step, genetic treatments are compared for differences in the parameters of the mathematical model. Ideally, comparison of genetic treatments should be between improved and unimproved populations. Alternatively, comparisons may be among different pure stands of genetic entities (clones, families, or provenances), but if pure stands are not used in operational plantings, extrapolation to mixing of selections involves assumptions of no effects of intergenotypic competition. Finally, growth and yield models are modified to accommodate differences between improved and unimproved stands. Once growth and yield models are developed for improved stands, they should be validated using independent data sets.

Past studies of genetic effects on growth and yield have been of three types: (1) simulations in which assumptions are made about key inputs into the models, (2) studies of genetic variation in stand productivity at the level of seed sources or families, and (3) actual comparisons of improved versus unimproved stands. These three types of studies are reviewed in the following sections.

### **Simulations of Improved Versus Unimproved Forest Stands**

Studies involving simulations indicate that assumptions made about key inputs into the model are important to predictions of growth and yield from genetically-improved stands. For example, assumptions about the trajectories of genetic gains in height and diameter after crown closure may result in large differences in stand volume gains (Nance and Bey 1979; Du and Fins 1990; Rehfeldt et al. 1991). Rehfeldt et al. (1991) predicted genetic gains in stand volume for western white pine grown to two rotation ages and at two planting densities given three possible scenarios for the trends in levels of gains after crown closure. Initial genetic gains at 25 years were 5.6% for height and 6.1% for diameter, as estimated from three genetic tests planted at two sites in northern Idaho. After 25 years, genetic gains were either: (1) truncated and no further gains allowed to accumulate, (2) continuously accumulated throughout the rotation at annual rates equal to those observed during the first 25 years, or (3) augmented to a value of twice the annualized rate and allowed to accumulate continuously. Genetic gains at age 55 for stands planted at a high density were 5.0% assuming gains are truncated, 10.3% assuming gains are continuous, and 14.9% assuming gains are augmented. Genetic gains were also affected by choice of initial planting density and rotation age. Thinning may also be important for capturing gains.

Assumptions concerning phenotypic variances (frequency distributions of size) may also be important to predictions of stand yield from improved populations. Simulations by Mitchell (1975) and Nance and Bey (1979) indicate that reduced

phenotypic variance may result in reduced stand volume, presumably because large, vigorous trees must compete with each other to a greater degree. Phenotypic variance may be reduced by planting single family or single clone blocks, or, theoretically, as a consequence of genetic selection. Reductions in phenotypic variance from genetic selection, however, are likely to be small since environmental variation within a typical forest stand is large and considerable genetic variation still exists even within a single family. Buford and Burkhart (1985) found no significant differences in variances of height and diameter among eleven open-pollinated families and a woodsrun checklot of loblolly pine.

Simulation studies demonstrate the likelihood of achieving genetic gains from tree improvement. However, these studies require estimates of initial genetic gains before crown closure and assumptions about the trajectories of genetic gains after crown closure. Information from the second and third types of studies is needed in order to test those assumptions.

### **Studies of Genetic Variation in Stand Productivity**

Studies of genetic variation in stand productivity require genetic tests with large, pure-genotype block plots, and of sufficient age to account for competitive effects. These types of genetic tests are rare. Provenance tests often involve large block plots, and, consequently, most studies combining genetics and growth and yield modelling have been at the seed source level. Most have involved one or more sites of the loblolly pine portion of the Southwide Pine Seed Source Study. Few genetic tests involve large block plots of families. This is the level of genetic variation of greatest interest to evaluating genetic gain from tree improvement programs.

Site index and the related height-age curves are among the most important input parameters of growth and yield models. Most studies of genetic effects on growth and yield consider genetic variation in parameters of the height-age curve. Conclusions from these studies are ambiguous. Nance and Wells (1981) and Buford and Burkhart (1987) found significant differences among seed sources and families in the asymptote of the height-age curve, but not in the shape. Thus, a simple adjustment in the level of site index may be sufficient to account for genetic differences in stand productivity for purposes of growth and yield modelling. However, results using the same set of seed sources, but considering only a single site in Arkansas, indicate that sources differ in the shape of the dominant height-age relationship, but not in the asymptote (Sprinz 1987; Talbert and Strub 1987; Sprinz et al. 1989). East Coast sources were tallest and yielded more than western and interior sources at the Arkansas site, but trends were beginning to converge at older ages. Knowe and Foster (1989) considered family variation in the same set of study material as Buford and Burkhart, but used the three-parameter Chapman-Richards function. Families differed significantly in the asymptote and rate parameters, but not in shape. Their results, along with those from Arkansas, indicate that different genotypes have different growth patterns relative to one another, and that simply adjusting the level of site index may not be sufficient for predicting growth and yield.

The study of Knowe and Foster (1989) illustrates how genetic differences in height-age curves may be used to study genetic variation in stand productivity. They incorporated family differences in height-age curves into a growth and yield model to predict stand yield for each family in their test. Expected genetic gain from selection of the top three families was then calculated based on the predicted stand yields. This estimate of expected genetic gain was highly correlated to the expected genetic gain estimated from observed family differences. Although these results do not tell us anything about the relationship between expected genetic gains and realized genetic gains, their technique does represent a unique method to estimate the genetic value of different families and the expected genetic gains from selection. For example, height-age curves could be determined for families in genetic tests involving row or non-contiguous plots and used to estimate expected genetic gain in volume per hectare at different rotation ages (assuming no intergenotypic competition effects on height growth).

Seed source variation in the size-density relationship was explored in two studies using material from the loblolly pine Southwide Seed Source Study. Results from both Schmidting (1988) and Buford (1989) indicate that seed sources vary in the intercept of the self-thinning line, but not in the slope. Furthermore, strong positive correlations were found between the intercepts and the site indices of seed sources. These results indicate that loblolly pine seed sources differ in their carrying capacities at a given site. It would be of great interest to consider the morphological and physiological variables associated with these differences in carrying capacity.

The height-diameter relationship in loblolly pine was considered by Buford and Burkhart (1987) and Schmidting and Clark (1989). Height-diameter relationships are used in growth and yield modelling to predict mean heights for a given diameter or diameter class, which in turn are used to predict stand volume and value. Buford and Burkhart found that the shape of the height-diameter relationship does not differ among families or seed sources, but the level does. Schmidting and Clark found seed source differences in both shape and level. These results indicate that prediction equations for height and volume differ among seed sources and families due to differences in stem form. Although these differences may be important for predicting stand volume from different families or seed sources, they may not be large enough to be of practical importance to the relative ranking of families or seed sources for purposes of selection.

### **Comparisons of Improved Versus Unimproved Forest Stands**

Few organizations have established designed studies to compare stand productivity of improved versus unimproved stands. Although studies have been initiated for Douglas-fir, western hemlock, radiata pine and loblolly pine, few studies have been published. Janssen and Sprinz (1987) compared improved and unimproved families of loblolly pine grown in pure family blocks. They found that improved families were

superior in individual-tree diameter and volume per hectare at 30 years of age. However, no estimates of the overall level of superiority are given, and no mention is made of what the criteria were for choosing improved and unimproved families. Eldridge (1982) reported on an Australian trial in which a radiata pine seedlot from an early seed orchard was compared with a control seedlot representative of the population from which the trees in the orchard were selected and typical of much of the early commercial seed. At 10 to 12 years of age, the realized genetic gain in volume per hectare at three sites was 9, 16, and 22%. Growth and yield parameters were not determined in this study, and no mention is made of trends in the results. Interestingly, genetic gains were smallest at the most productive site, possibly indicating decreasing genetic gains with increasing stand development and competition.

When designing studies to evaluate realized gains in improved versus unimproved forest stands, one must address the question of what is improved and what is unimproved. An improved population may be considered to be the seedlot from a typical seed orchard. However, the genetic composition of that seedlot may differ dependent upon orchard design and management, location of the orchard relative to potential sources of contamination, age of the orchard, and the particular year of seed collection. The genetic composition of the improved population may be controlled, however, by using controlled pollinations among the parents for which gain is to be estimated. Another problem with designating an improved population is that the level of improvement in a tree improvement program is a moving target. By the time data is collected to evaluate realized gains from an improved population, another round of selection has been completed. The realized gains and growth and yield models developed for the earlier improved population will not be appropriate for later populations. One solution to this problem is to develop a general relationship between realized genetic gains and the expected genetic gains as determined from genetic tests used for selection. The unimproved population is used as a standard for determining realized gains, but what is the appropriate standard to use? If your goal is to estimate response to selection, the appropriate unimproved population is the population from which the original selections were made. But if your goal is to estimate gains from tree improvement relative to alternatives, the appropriate unimproved population would be that which would be used if improved stock were not available.

### **EVALUATING REALIZED GENETIC GAINS IN DOUGLAS-FIR**

Forestry organizations in the Pacific Northwest have recently become more concerned about their ability to predict realized genetic gains and productivity from the large number of stands planted with genetically-improved Douglas-fir. As a result, members of the Northwest Tree Improvement Cooperative asked the Genetics Team of the Pacific Northwest Research Station to help design and coordinate a region-wide study to look at the growth and yield of improved Douglas-fir stands. The two primary objectives of this study are: (1) to compare estimates of growth and yield



parameters among genetic populations having different expected growth potential, and (2) to develop a predictable relationship between expected genetic gain based on individual-tree growth characteristics and realized genetic gain in stand productivity.

Three different genetic quality types will be tested at six sites within the breeding zones of each of three different tree improvement programs. The large number of sites and inclusion of three different programs will allow us to test the generality of relationships across sites and across programs. The three genetic quality types include an unimproved control and two improved populations representing two levels of expected genetic gain. We chose to test two levels of genetic gain for each of three breeding zones in order to have a range of expected gains for developing the model to predict realized gains. Expected genetic gains are determined based on estimates of heritabilities and selection differentials from extensive progeny tests within each breeding zone.

The improved genetic quality types will be produced by controlled pollinations among 20 clones of the original parent trees. In one of the three programs, the mating design is single-pair matings among the 20 parents, while in the other two programs, the mating design is a polycross in which each selected parent is pollinated with a common mix of pollen from the other 19 selected parents. The "elite" genetic quality type aims for the highest level of genetic gain. It will include crosses among the best 20 parents in each breeding zone. The "intermediate" genetic quality type will include crosses among 20 parents targeted at a level of genetic gain of about half that of the elite genetic quality type. The unimproved genetic quality type will be a random selection of 50 to 100 "wild" trees that are well distributed throughout the breeding zone. The unimproved type is assumed to represent both the average genetic quality of seed that would be used for reforestation in the absence of tree improvement and the original base population from which selections were made. The genetic growth potentials of these two populations are probably equal since the average parent tree in progeny tests was essentially randomly selected from natural stands within each breeding zone.

Each test site will also include two different planting densities and an optional thinning treatment in order to test the effect of stand density. The low density treatment (772 trees per hectare) was chosen to represent operational conditions assuming no thinnings. The high density treatment (1250 trees per acre), besides allowing consideration of density effects, will provide early results by promoting stand competition effects at a relatively young age. Later, data from the low density plots can be used to verify the accuracy of information from earlier ages in the high density plots. The high density plots may be particularly valuable in providing timely information on genetic effects on self-thinning. The objective of the thinning treatment is to evaluate the role of intermediate cuttings in capturing potential gains in yield from genetically-improved stands. The hypothesis to be tested is that the magnitude of realized genetic gains will be larger in thinned versus unthinned stands due to the avoidance of competition effects (Talbert 1981; Switzer and Shelton 1981).

The experimental design at each site will be a split-plot design with density treatments occupying the whole-plots and the genetic quality types occupying the split-plots. Plot size will be 100 trees planted in a 10 tree x 10 tree square plot for the low and high density treatments. The thinning treatment will initially have 162 trees to be thinned to a final number of 81 trees per plot (9 tree x 9 tree). The number of trees per plot in this study are more than that used in previous studies of the genetics of growth and yield, and within the range of numbers recommended in a review by Curtis (1983).

This study represents a considerable effort by members of tree improvement cooperatives in the Pacific Northwest. However, we feel that the benefits from this study will greatly outweigh any costs. It is hoped that the results from this study will be generally applicable to a Douglas-fir tree improvement programs throughout the region, and will allow us to confidently predict the yield and realized genetic gains from genetically-improved Douglas-fir stands. Furthermore, we feel that results from this study will go a long way to establishing the value of tree improvement programs in the Pacific Northwest.

## CONCLUSIONS

Tree improvement has become an important part of forest management throughout the world. Predicting the yields and realized gains from forests planted with genetically-improved trees will become increasingly important. Developing the techniques needed to do so will require the integrated knowledge of geneticists, biometricians, silviculturists, economists, and land managers. We can begin the task by applying techniques of growth and yield modelling to the analysis of data from genetic tests already in the ground. Much of the information needed for growth and yield modelling is available for many of these tests, although assumptions about the influences of intergenotypic competition may be required. Studies are needed to evaluate the effects and importance of density and intergenotypic competition, including comparisons of families or clones in pure plots versus in mixtures. Finally, we must establish new trials to compare realized gains and yield in improved versus unimproved forest stands. Such trials are now being established for Douglas-fir in the Pacific Northwest.

## LITERATURE CITED

- ADAMS, W. T., G. JOHNSON, D. L. COPES, J. DANIELS, R.G. QUAM, J. C. HEAMAN, and J. WEBER. 1990. Is research keeping up with the needs of Douglas-fir tree improvement programs? *West. J. Appl. For.* 5: 135-137.
- BUFORD, M. A. 1989. Mean stem size and total volume development of various loblolly pine seed sources planted at one location. *Can. J. For. Res.* 19: 396-400.
- BUFORD, M. A., and H. E. BURKHART. 1985. Dynamics of improved loblolly

pine plantations and the implications for modeling growth of improved stands. P. 170-177 in Proc. 18th So. For. Tree Improv. Conf., Long Beach, MS.

BUFORD, M. A., and H. E. BURKHART. 1987. Genetic improvement effects on growth and yield of loblolly pine plantations. *For. Sci.* 33: 707-724.

CANNELL, M. G. R. 1978. Improving per hectare forest productivity. P. 120-148 in Proc. 5th No. Amer. For. Bio. Workshop, Gainesville, FL.

CLUTTER, J. L., J. C. FORTSON, L. V. PIENAAR, G. H. BRISTER, and R. L. BAILEY. 1983. *Timber Management: A Quantitative Approach*. John Wiley & Sons, New York.

CURTIS, R. O. 1983. Procedures for establishing and maintaining permanent plots for silvicultural and yield research. USDA For. Serv. Gen. Tech. Rep. PNW-155.

DICKMANN, D. I. 1985. The ideotype concept applied to forest trees. P. 98-109 in M. G. R. Cannell, and J. E. Jackson. *Attributes of Trees as Crop Plants*. Institute of Terrestrial Ecology, Pinicuik, Scotland.

DU, W., and L. FINS. 1990. Using growth models to predict genetic gains in forestry. P. 3.12-3.22 in Proc. Joint Meet. of West. For. Gen. Assoc. and IUFRO Working Parties S2.02-05, 06, 12, and 14, Olympia, WA.

ELDRIDGE, K. G. 1982. Genetic improvements from a radiata pine seed orchard. *New Zeal. J. For. Sci.* 12: 404-411.

FLEWELLING, J. W., and C. B. TALBERT. 1990. Should growth models be used in predicting gain at harvest? P. 3.12-3.22 in Proc. Joint Meet. of West. For. Gen. Assoc. and IUFRO Working Parties S2.02-05, 06, 12, and 14, Olympia, WA.

FORD, E. D. 1976. Competition, genetic systems and improvement of forest yield. P. 463-472 in M. G. R. Cannell, and F. T. Last. *Tree Physiology and Yield Improvement*. Academic Press, New York.

FOSTER, G. S. 1989. Inter-genotypic competition in forest trees and its impact on realized gain from family selection. P. 21-35 in Proc. 20th So. For. Tree Improv. Conf., Charleston, SC.

FOSTER, G. S. 1992. Estimating yield: beyond breeding values. P. 229-269 in L. Fins, S. T. Friedman, and J. V. Brotschol. *Handbook of Quantitative Forest Genetics*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

JANSSEN, J. E., and P. T. SPRINZ. 1987. Modeling distributions of stem characteristics of genetically improved loblolly pine. P. 367-375 in Proc. 19th So. For. Tree Improv. Conf., College Station, TX.

- KNOWE, S. A., and G. S. FOSTER. 1989. Application of growth models for simulating genetic gain of loblolly pine. *For. Sci.* 35: 211-228.
- LAMBETH, C. C. 1980. Juvenile-mature correlations in Pinaceae and implications for early selection. *For. Sci.* 26: 571-580.
- LAMBETH, C. C., J. P. VAN BUIJTENEN, S. D. DUKE, AND R. B. MCCULLOUGH. 1983. Early selection is effective in 20-year-old genetic tests of loblolly pine. *Silv. Genet.* 32: 210-215.
- LOO-DINKENS, J. A., and C. G. TAUER. 1987. Statistical efficiency of six progeny test field designs on three loblolly pine (*Pinus taeda* L.) site types. *Can. J. For. Res.* 17: 1066-1070.
- MITCHELL, K. J. 1975. Dynamics and simulated yield of Douglas-fir. *For. Sci. Mono.* 17, 39 p.
- NANCE, W. L., and BEY, C. F. 1979. Incorporating genetic information in growth and yield models. P. 140-148 in 15th Proc. So. For. Tree Improv. Conf., Mississippi State, MS.
- NANCE, W. L., and O. O. WELLS. 1981. Site index models for height growth of planted loblolly pine (*Pinus taeda* L.) seed sources. P. 86-96 in Proc. 16th So. For. Tree Improv. Conf., Blacksburg, VI.
- REHFELDT, G. E., W. R. WYKOFF, R. J. HOFF, R. J. STEINHOFF. 1991. Genetic gains in growth and simulated yield of *Pinus monticola*. *For. Sci.* 37: 326-342.
- ST. CLAIR, J. B., and W. T. ADAMS. 1991. Relative family performance and variance structure of open-pollinated Douglas-fir seedlings grown in three competitive environments. *Theor. Appl. Genet.* 81: 541-550.
- SCHMIDTLING, R. C. 1988. Racial variation in self-thinning trajectories in loblolly pine. P. 611-618 in A. R. Ek, S. R. Shifley, and T. E. Burk (eds.). *Forest Growth Modelling and Prediction*. USDA For. Serv. Gen. Tech. Rep. NC-120.
- SCHMIDTLING, R. C., and A. CLARK, III. 1989. Loblolly pine seed sources differ in stem form. P. 421-425 in Proc. 5th Biennial So. Silv. Res. Conf., New Orleans, LA.
- SILEN, R. R., and J. G. WHEAT. 1979. Progressive tree improvement program in coastal Douglas-fir. *J. For.* 77: 78-83.
- SPRINZ, P. T. 1987. Effects of genetically improved stands on growth and yield principles. P. 338-348 in Proc. 19th So. For. Tree Improv. Conf., College Station, TX.

SPRINZ, P. T., C. B. TALBERT, and M. R. STRUB. 1989. Height-age trends from an Arkansas seed source study. *For. Sci.* 35: 677-691.

SWITZER, G. L., and M. G. SHELTON. 1981. Stand productivity: some considerations in evaluating genetic improvement. P. 18-31 *in Proc. 16th So. For. Tree Improv. Conf., Blacksburg, VI.*

TALBERT, C. B., and M. R. STRUB. 1987. Dynamics of stand growth and yield over 29 years in a loblolly pine source trial in Arkansas. P. 30-38 *in Proc. 19th So. For. Tree Improv. Conf., College Station, TX.*

TALBERT, J. T. 1981. One generation of loblolly pine tree improvement: results and challenges. P. 106-120 *in Proc. 18th Can. Tree Improv. Assoc. Mtg., Duncan, B.C.*

# **Modelling Stand Response To Silvicultural Practices**

**Proceedings of the IUFRO S4.01 Conference**

**September 27 - October 1, 1993  
Blacksburg, Virginia, U. S. A.**

**Edited by**

**Harold E. Burkhart  
Timothy G. Gregoire  
James L. Smith**

**Endorsed by**

**A3 Biometrics and D2 Silviculture Working Groups  
Society of American Foresters**

**Department of Forestry  
Virginia Polytechnic Institute and State University**

---

**Publication FWS-1-93  
College of Forestry and Wildlife Resources  
Virginia Polytechnic Institute and State University  
Blacksburg, Virginia 24061-0324 U. S. A.**

**Printed on recycled paper**