

Evaluating the Efficiency of Tree Improvement Programs¹⁾

By Richard L. PORTERFIELD, B. J. ZOBEL and F. T. LEDIG²⁾

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Introduction

Objective

The objective of this study was to develop techniques for measuring the efficiency of tree improvement programs. To accomplish this objective, the investigation provided estimates of 1) probable gain from existing improvement programs, 2) the impact of program goals on the benefits provided by tree improvement, and 3) ways in which tree improvement programs might be altered to more fully attain goals and increase benefits.

Background

Predicted increases in demand for wood products call for an intensification and expansion of forest management. However, meeting this need is complicated by the rapidly increasing demand for forest land in recreational and other non-wood producing activities which has resulted in the withdrawal of millions of acres from timber production and the serious questioning of timber production as the primary goal on many more acres. Compounding the problem is the continual loss of forest land to new power line and highway rights-of-way, reservoir construction, annual agricultural crops, and urban expansion.

Tree improvement, which emphasizes the use of better genetic stock, is one of several techniques for increasing yield per acre. In the southern United States, a 10 to 15 percent gain in volume is a conservative estimate for southern pines (BARBER, 1963). Recently, ZOBEL, et al. (1971) reported that volume from tree improvement will approximate 15 to 25 percent from one generation of selection.

The economic soundness of tree improvement work is well established even when only moderate genetic gains are achieved. Tree improvement programs had internal rates of return averaging 15.5 percent for the Alabama National Forests, based on estimated gains in both quality and quantity (SWOFFORD, 1968). After developing a framework for analysis DAVIS (1967) estimated that gains in yield of only 2.5 to 40 percent would justified current expenditures for tree improvement work. Similar conclusions were reached by BERGMAN (1968) for loblolly pine and he emphasized the influence of seed yield on profitability.

Information is now available which allows a multiple-trait analysis of tree improvement programs. Such an analysis is necessary if the total benefit from tree improvement is to be estimated. The present study formulates a model for evaluating the efficiency of tree improvement programs in terms of economic return and the attainment of stated tree-improvement goals.

A great deal of input data were required to develop the model and considerable time was taken for interviews and

data collection to obtain the most accurate information available. But, as usual with original investigations, data were incomplete in particular areas. When this was so, 'best' estimates were used. The investigation reported here is limited to loblolly pine (*Pinus taeda* L.), because the information required was most complete for this species.

Methodology

Basic Data

Five traits are included in the analysis: straightness³⁾, crown shape and size³⁾, wood specific gravity, bole volume, and resistance to fusiform rust (*Cronartium fusiforme* HEDGC. and HUNE ex CUMM.). The five characteristics chosen represent those traits most important to the two organizations serving as case studies (a large industrial concern and a state forestry division), and these traits are most important to the organizations cooperating in the TAPPI⁴⁾ survey of tree improvement programs in the southern U.S.

Each organization studied provided data on: (1) the history of their tree improvement program including age of seed orchard, initial spacing, establishment and management costs; (2) the production of the seed orchard including seed yields over time, age when rogued, cost of progeny testing; (3) the expected gains from their improvement program; and (4) the goals of their improvement program in terms of the traits they wished to improve and the minimum return they were willing to accept on the tree-improvement investment. The TAPPI survey provided information on nineteen separate loblolly pine tree-improvement programs which was combined to create a "representative" loblolly pine tree-improvement program for the South. The same type of cost-information as obtained for the case studies was available from the survey data.

Following summarization of data, a second questionnaire was made so that the traits of interest could be: (1) ranked as to absolute preference, (2) ranked relative to the other traits, and (3) assigned a minimum desired percentage improvement. For example, given the four traits W, X, Y, and Z the questionnaire might have been answered as illustrated below:

Absolute rank		Relative rank	Minimum improvement goal ⁵⁾
			(percent)
1.	W		10
2.	X	3.0	15
3.	Y	1.0	05
4.	Z	2.0	10

³⁾ Individual trees were given scores for straightness and crown from 1 to 5; best to poorest. Straightness includes the degree of lean, sweep, crook and spirality. Crown characteristics include branch angle, branch diameter, branch length, and general crown conformation. The score is for the composite effect. Each stand or plantation is graded independently and the scores should have roughly a normal distribution with a mean of 3.

⁴⁾ Technical Association of the Pulp and Paper Industry; survey is described later.

⁵⁾ The unit of measurement for calculating percent was specified in the questionnaire.

¹⁾ This article is based upon PORTERFIELD'S Ph. D. thesis completed at Yale University, New Haven, Conn. ZOBEL and LEDIG served on the doctoral committee.

²⁾ The authors are: Assistant Professor of Forestry, Department of Forestry, Mississippi State University, Mississippi State Miss.; Professor of Forest Genetics, School of Forest Resources, North Carolina State University, Raleigh, N.C., and Associate Professor of Forest Genetics, School of Forestry and Environmental Studies, Yale University, New Haven, Conn.

The absolute-rank column shows that improvement in trait W is more important than improvement in the other three traits. Improvement in trait Z is least important. The relative rank shows that improvement in trait W is three times as important as improvement in trait X, while improvement in trait Z is one-half as important as improvement in Y and only one-sixth as important as gain in trait W. The last column indicates the minimum desired percentage improvement. In addition, total per-clone selection costs were divided into expenditures related to each separate trait. Dr. B. J. ZOBEL, Director of the North Carolina State Cooperative Tree Improvement Program and Dr. J. P. VAN BUIJTENEN of the Western Gulf Forest Tree Improvement Program supplied goal estimates for their combined programs, representing over 35 tree improvement programs in the southern U.S.

Economic benefit from improvement efforts was measured in terms of volume change and specific gravity change for pulpwood, and from volume change alone for sawtimber. Because pulpwood is purchased on the basis of weight, both traits influence return but specific gravity generally does not directly affect the selling price of sawtimber. Any combination of volume change and specific

gravity change is possible and economic gain or loss will depend on the interaction between the two. The valuation of changes in specific gravity and volume is quite different however. For volume, only the marginal gain (loss) over the unimproved volume yield should be considered as a benefit (cost). An increase in specific gravity however raises the value of every cord harvested if higher specific gravity is desired.

The present value of improvement in each trait can be measured through its effect (either direct or through genetic correlations with volume and specific gravity) in the manner shown in Table 1. The cost of selecting parent trees from wild stands is the only cost which is assumed to vary according to the amount of genetic improvement.

The purpose of selection in wild stands is to choose superior individuals for inclusion in a seed orchard. For each trait, the mean value of these superior individuals will be higher than the mean value of trees in the wild population. The difference between these values measured by the selection differential which can be transferred into the familiar selection intensity or standardized selection differential(i) by dividing by the phenotypic standard deviation of the wild population:

$$i = \frac{\bar{X}_s - \bar{X}_p}{\sigma_p}$$

where \bar{X}_s is the mean of the selected population, \bar{X}_p is the mean of the wild population, and σ_p is the phenotypic standard deviation.

Since each trait is assumed to have a normal distribution, the higher the selection intensity for a particular trait the more trees that must be screened in order to find one that is suitable for orchard use. Selection costs were assumed to vary directly with the number of trees screened. The resulting relationship between selection intensity and selection cost is shown in Figure 1. To illustrate, if selection intensity is 2.6 standard deviations, selection cost is over thirty times what it would be if selection intensity were only 1.0.

A procedure for estimating the present-program selection intensities, that is the mean selection intensities of the clones used in the seed orchard, is necessary for two reasons; first, to allow an estimation of the genetic gains and economic returns from existing programs, and second, to define for each trait the relationship between selection cost and selection intensity as illustrated in Figure 1.

The general method of estimating current program selection intensity (i) was to estimate \bar{X}_s , \bar{X}_p and σ_p for each trait. This is an average for the seed orchard and it is probable that no single clone has the characteristics of the 'average' clone. A tree can be less than desired with respect to one trait if it is sufficiently better than acceptable for another trait.

The mean value of the selected population (\bar{X}_s) was computed from measurements on the select trees. For traits such as straightness, crown, and specific gravity, the estimation of wild population means (\bar{X}_p) is accurate. The wild population mean straightness and crown scores should be 3.0 by definition and regional average specific gravity estimates are available ZOBEL *et al.*, 1972; WAHLGREN and

Table 1. — Computation of present value of economic gains from tree improvement work.

$$\begin{aligned} & \text{Economic value (in present value terms per acre of seed} \\ & \text{orchard at base year } q) = \sum_{n=a}^c \left[SY_n \cdot AP \cdot \left\{ 1/(1+i)^n + j - q \cdot \right. \right. \\ & (\Delta Vol_{t,w} \cdot SP_t + \Delta SG_{t,w} \cdot VSG_t \cdot CY_t) + 1/(1+i)^n + k - q \cdot \\ & (\Delta Vol_{h,w} \cdot SP_h + \Delta SG_{h,w} \cdot VSG_h \cdot CY_h) \left. \right\} \Big] + \sum_{n=b}^c \left[SY_n \cdot AP \cdot \right. \\ & \left. \left\{ 1/(1+i)^n + j - q \cdot (\Delta Vol_{t,r} \cdot SP_t + \Delta SG_{t,r} \cdot VSG_t \cdot CY_t) + \right. \right. \\ & \left. \left. 1/(1+i)^n + j - q \cdot (\Delta Vol_{h,r} \cdot SP_h + \Delta SG_{h,r} \cdot VSG_h \cdot CY_h) \right\} \right] \end{aligned}$$

where:

- n = age of seed orchard
- a = orchard age at initial seed production
- c = orchard age when replaced by second generation orchard or age when orchard is obsolete
- b = orchard age two years after roguing
- SY = seed yield in pounds per acre
- AP = acres planted per pound of seed
- i = interest rate
- j = years until thinning age plus one year for seedling production
- k = years until harvest age plus one year for seedling production
- q = orchard age at year of analysis (base year)
- w = designates gain from wild stand selection
- r = designates gain from progeny testing and roguing
- t = designates thinning harvest
- h = designates final harvest
- ΔVol = change in volume — represents both cordwood and sawtimber ($\Delta Vol_{t,w}$ = change in volume at time of thinning resulting from wild stand selection)
- SP = stumpage price per unit of volume — represents both stumpage price per cord and stumpage price per MBF. Current stumpage prices were used in the analysis but the effect of increasing stumpage prices over time is investigated
- ΔSG = change in specific gravity ($\Delta SG_{h,r}$ = change in specific gravity at time of harvest due to additional gain from roguing)
- VSG = stumpage price per cord divided by unimproved specific gravity
- CY = cordwood yield¹⁾

¹⁾ If regional plantation-average specific gravity is 0.46, expected yield is 25 cords per acre, and the stumpage price is \$10.00 per cord, then the undiscounted value of a specific gravity increase to 0.47 is \$5.43 per acre planted with improved seed: $(.01)(21.74)(25) = (\Delta SG) \cdot (VSG) \cdot (CY) = \5.43 .

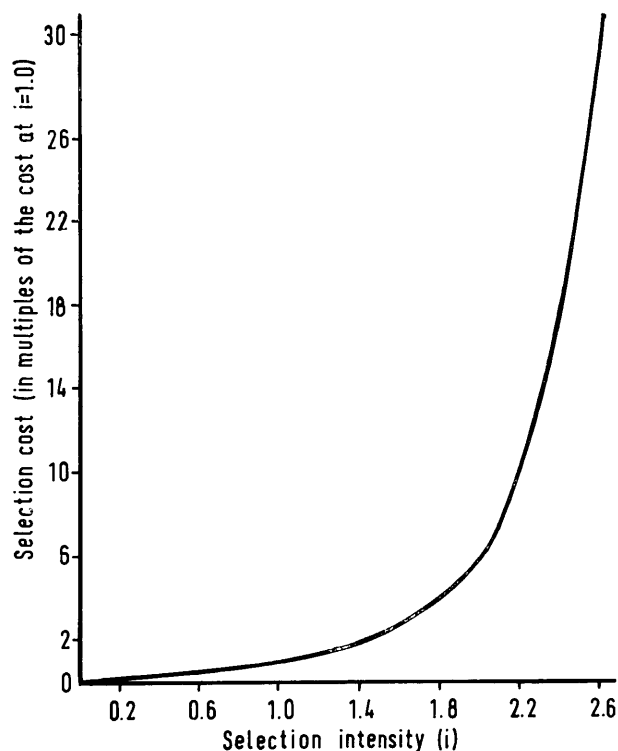


Figure 1. — Relationship between selection cost and selection intensity for each trait.

SCHUMANN, 1972). Regional mean per-tree volume, however, almost defies calculation because differences in stocking affect volume. This statistic was approximated as follows: 1) the average site index for stands from which the select trees were chosen was computed along with the average age of the select trees, 2) Table 1 of *Growth and Yield of Natural Stands of the Southern Pines* (SCHUMACHER and COILE, 1960) which provides figures for cubic foot volume and number of trees per acre for various site index-age combinations was used to estimate the average volume per tree in stands from which the select trees were chosen. Once \bar{X}_p and \bar{X}_s were estimated, σ_p was derived using coefficients of variation for each trait as obtained from a separate study in natural stands of loblolly pine.

Model Formulation

Linear programming has proven useful in several areas of forest management and analysis of mill operations and has recently been used to evaluate forest-tree improvement programs (VAN BUIJTENEN and SAIITA, 1972). The tree improvement data obtained for loblolly pine are suitable for formulation as a linear programming problem. For example, the objective might be to maximize profits (the sum of the economic value per unit of selection for each trait times each traits selection intensity) subject to meeting minimum desired gains for each trait and staying within the available budget constraint.

A major problem with such a formulation is that data are inadequate for computation of the exact economic value for each unit of selection intensity of each trait. But more importantly, because so little is known regarding genetic correlations and heritabilities (especially at the beginning of a new program), the minimum acceptable improvement levels may be set unrealistically high. If unattainable

minimum improvement levels are set, the linear programming model would reach an infeasible solution.

Fortunately the analysis of a tree-improvement program can be formulated in a more realistic manner which circumvents the major short-comings of the linear programming model. Because genetic parameters such as heritabilities and genetic correlations must be estimated, there is always uncertainty as to the exact amount of improvement that will result from a tree improvement program. Therefore, desired minimum improvements are more realistically viewed as goals rather than as constraints. For example, it is not likely that an entire program would be abandoned just because a desired 10 percent improvement in specific gravity could not be attained. The 10 percent improvement should be viewed as a goal rather than a constraint, as it is in a linear programming formulation.

If the minimum desired improvements are taken as goals, it becomes feasible to formulate a goal-programming model of a tree improvement program. Goal programming was developed in 1955 by CHARNES, COOPER and FERGUSON and later given the name 'goal programming' by CHARNES and COOPER (1961). FIELD (1973) introduced goal programming in forestry, pointing out its applicability in a multiple-use planning situation.

Basically, the goal-programming formulation seeks to minimize deviations from stated goals. The general form of the model for a tree-improvement program:

$$\text{Min. } Z = \sum (w_j^- d_j^- + w_j^+ d_j^+) \text{ (objective function)}$$

Subject to:

$$\sum a_{ji} x_i + d_j^- - d_j^+ = b_j; j = 1, 2, \dots, n \text{ (goals)}$$

$$\sum g_{ki} x_i \leq b_k; k = 1, 2, \dots, p \text{ (constraints)}$$

$$x_i, d_j^-, d_j^+ \geq 0$$

where:

$d_j^-, +$ = the number of deviation units short (—) or in excess (+) of the goal (b_j). Only one of the deviation units can be positive at any time.

$w_j^-, +$ = the weight given to a unit deviation short (—) or in excess (+) of the goal (b_j).

a_{ji} = percentage gain (loss) per unit of selection intensity for trait j when selecting for trait i .

x_i = selection intensity for trait i .

b_j = minimum desirable improvement goal for trait j (n goals).

g_{ki} = coefficient for selection intensity of trait i in constraint k (p constraints).

b_k = limiting amount of resource k available.

The formulation can be adapted for several kinds of specific problems. If overachievement of a goal is acceptable, for example, the overachievement deviation variables (d_j^+) can be dropped. If overachievement of goals is desirable, the w_j^+ weight can be made negative, which would move the solution toward overachievement since the objective function is minimized. Of course, w_j^- and w_j^+ need not have the same value. If w_1^- is higher than w_1^+ it means that it is more important to reach the goal for trait 1 than to exceed it.

The goals themselves (b_j) can be ranked absolutely, relatively, or in an absolute-relative combination. Ranking is also accomplished through the values given the weights. In the absolute case, the weights are assigned values such that a higher-ranked goal must be satisfied so far as possible before the next-lower-ranked goal can be approached. In other words, as soon as one goal cannot be met, all lower ranked goals that depend on the same limiting resource must go unsatisfied unless they were automatically met in the course of meeting higher ranked goals.

When the goals are ranked relatively, the priority scheme between them indicates the importance of movement toward each goal relative to movement toward the other goals. Ranking goals in a relative manner does not prevent the attainment of lower-ranked goals when more-important goals are not met, but it does specify explicitly the tradeoffs between goals. If w_1^- is twice as large as w_2^- , it indicates that improvement in trait 1 is twice as important as improvement in trait 2. Relative weighting of goals is used in the present study.

A method of 'linearizing' the relationship between selection intensity and selection cost is required to complete the analytical framework. The selection-intensity cost relationship (Figure 1) was approximated by a piecewise linear function divided into ten linear segments. The end points of the segments correspond to a set of "special variables" for each trait. Separable (goal) programming, an extension of linear programming, which is designed for handling certain non-linear functions was then utilized in the final model formulation. The only restrictions to the use of separable programming are: (1) that the function be separable and, (2) that the function be described in a piecewise fashion. Both conditions are met with the total-selection-cost function because the total cost of wild-stand selection is the sum of expenditures for selection of individual traits.⁹⁾

It is possible now to combine information on genetic gains, estimates of improvement-program expenditures and benefits, improvement goals, and the relation between selection intensity and selection cost in order to formulate a separable goal-programming model. This model is shown in symbolic terms in Figure 2. Only underachievement of goals is of concern in this particular formulation so the d_j^+ deviation variables are not present. The number 1.0 is given, but all other numbers are represented by x's.

Table 2. — Parent-progeny and progeny-test heritabilities (h^2) for selected traits^a.

Trait	Parent-progeny h^2	Progeny test h^2
Height	0.094	0.26 ^b
DBH	0.028	0.13 ^c
Volume	0.054	0.15 ^b
Straightness score	0.044	0.14 ^b
Crown score	0.037	0.08 ^b
Specific gravity	0.290	0.52 ^d
C. fusiforme		
— % free (transformed)	0.089	0.16 ^e
— total no. galls	0.033	0.19 ^f

^a Progeny-test heritabilities from "Inheritance Patterns of Loblolly Pine from an Unselected Natural Population" (STONECYPHER *et al.*, 1973). The following footnotes refer to tables in that publication.

^b 1966 measurements of open-pollinated study.

^c 1965 measurements of open-pollinated study.

^d Wood study of 112 six-year-old families of open-pollinated study sampled in 1967.

^e 1968 measurements of the control-pollinated study. This is an average of the heritabilities estimated for the 1963-64 plantings, on the basis of the Dempster and Lerner method for threshold traits. Percentage data were transformed to $\arcsin \sqrt{\text{percentage free}}$.

^f 1968 measurements of control-pollinated study. An average for the 1963-64 plantings.

⁹⁾ Complete details on the separable programming technique can be found in *Nonlinear and Dynamic Programming* (HADLEY, 1964). Specifics regarding the use of this estimation procedure in IBM's Mathematical Programming System (MPS), which was used for this analysis, are given in IBM's User's Manual, IBM Corporation (1968).

Estimation of Genetic Gain

The selection of superior parent trees, their propagation in a clonal seed orchard, and the later roguing of the seed orchard on the basis of progeny-test results, involves two independent opportunities for genetic improvement. Progeny testing allows an accurate estimate of the genetic value of each established clone and those that produce poor progeny are eliminated. Of course, roguing must await the proper evaluation of the progeny several years after commercial seed production begins in the orchard.

The combined gain from mass selection and roguing after progeny testing can be expressed as:

$$G_T = G_W + G_{PT}$$

or

$$G_T = i_1 \frac{\sigma_a^2}{\sigma_p} + 2 i_2 \frac{1/4 \sigma_a^2}{\sigma_{pt}} \quad (\text{NAMKOONG, et al., 1966})$$

The estimate of additive genetic variance in the parent population (σ_a^2) would be expected to be larger than the estimate of additive variance for the genetically reduced progeny-test population ($\sigma_{a'}^2$). FINNEY (1956; as reported by SHELBOURNE, 1969) has outlined a method of relating σ_a^2 to $\sigma_{a'}^2$, but for the heritabilities and selection intensities found in this study such an adjustment was minor. With one exception, explained below, it was assumed that $\sigma_a^2 = \sigma_{a'}^2$. It should be noted that the gain from selection in wild stands is linear in i_1 , the selection intensity. This important fact is the basis of a large portion of the analytical model developed previously.

Information available from the Heritability Study, a large loblolly-pine-inheritance study located at Bainbridge, Georgia was used to compute parent-progeny heritabilities (STONECYPHER, 1966). The same data were used to estimate progeny test heritabilities and genetic correlations (STONECYPHER *et al.*, 1973). Briefly, the Heritability Study is composed of over 400 progenies, produced by open-and control-pollination and replicated in each of two planting locations. The open-pollinated plantings, which supplied much of the data used in the present investigation, were established in the winter of 1960-61. Information about the control-pollinated progenies comes from plantations established in 1963 and 1964. Parent trees for the Heritability Study were randomly selected from a naturally regenerated nearby forest stand. The predominant pine species was loblolly with a mixture of shortleaf; hardwoods making up the understory.

Estimates of additive genetic variance (σ_a^2) were taken from STONECYPHER *et al.* (1973). The phenotypic variance used in the denominator of the parent-progeny heritability was derived from measurements taken on the parent trees after adjustment for age and differences in competition. This adjustment, accomplished by regression analysis, was necessary because estimates of additive variance were obtained from young progeny-test plantings of uniform age and spacing. The derived parent-progeny heritabilities and the progeny-test heritabilities on an individual tree basis, taken from STONECYPHER *et al.* (1973), are shown in Table 2. The parent-progeny heritability for volume was calculated by assuming the relationship between parent-progeny heritabilities for height, DBH, and volume was the same as the relationship among these traits for progeny-test heritabilities. The resulting 0.054 parent-progeny heritability for cubic foot volume seems reasonable in light of NAMKOONG'S (1970) comments. The heritability estimates used are very conservative compared to most published values, probably as the result of heavy fusiform rust and tipmoth attack in the Heritability Study.

	Straight. Crown	Sp. Gr. Volume	Fusiform	P.T. Str.	P.T. Crn.	P.T. S.G.	P.T. Vol.	P.T. Fus.	Str. - 1	Str. - 10	Crn. - 1	Crn. - 10	S.G. - 1	S.G. - 10	Vol. - 1	Vol. - 10	Fus. - 1	Fus. - 10	Dev. Str.	Dev. Crn.	Dev. S.G.	Dev. Vol.	Dev. Fus.	Dev. ROI	Dev. PT-Str	Dev. PT-Crn	Dev. PT-S.G.	Dev. PT-Vol	Dev. PT-Fus	Goals
Min. Dev.	A		B		C												E						F							
Str. goal	x x-x-x x		x x-x-x x														x x x x x x x x x x x						≥ x							
Crn. goal	x x -x		x x -x														1						≥ x							
S.G. goal	-x x x		-x x x														1						≥ x							
Vol. goal	-x-x x x-x		-x-x x x-x														1						≥ x							
Fus. goal	x -x x		x -x x														1						≥ x							
ROI goal	x x x x x		x x x x x		D												1						≥ x							
Sel. cost									x..x		x..x		x..x		x..x		x..x		G						≤ x					
Str. cost	-1								x..x																=0					
Crn. cost	-1								x..x																=0					
S.G. cost	-1										x..x														=0					
Vol. cost	-1												x..x												=0					
Fus. cost	-1														x..x										=0					
PT. Str.1	-x		1																				≤ 0							
PT. Str.2			1																				= 1							
PT. Crn.1	-x		1																				≤ 0							
PT. Crn.2			1																				= 1							
PT. S.G.1	-x		1																				≤ 0							
PT. S.G.2			1																				= 1							
PT. Vol.1	-x		1																				≤ 0							
PT. Vol.2			1																				= 1							
PT. Fus.1	-x		1																				≤ 0							
PT. Fus.2			1																				= 1							

Figure 2. — A separable goal programming model for computing the optimum combination of selection intensities given stated tree improvement goals.

Footnotes for Figure 2

Components of Figure 2 can be interpreted as follows:

- A— genetic response matrix for wild-stand selection. For example, genetic gain either direct or correlated, per unit of selection intensity for straightness can be obtained by reading down the straightness column. It is these wild-stand-selection intensities that are combined in the optimum manner so that (weighted) underachievement of goals is minimized while staying within the selection-cost constraint. A genetic response matrix for wild-stand selection was derived for each organization.
- B— genetic response matrix for gain from progeny testing and roguing. This gain is fixed by orchard roguing intensity and is in the solution only if the trait is selected for in wild stands. A genetic response matrix for progeny-testing gain was derived for each organization.
- C— the weights given each unit of deviation below the respective goal.
- D— present value of economic gain from selecting for the various traits. Those values under A are a function of wild-stand selection intensity (x_i) while those under B are fixed and come into the solution only if the trait is selected for in the wild stands.

- E— a diagonal matrix relating genetic gain or economic value to the weights given to each deviation unit if the respective goal is not met.
- F— the minimum desired percentage improvement goal for each trait and the total present value of tree improvement program expenditures per acre of seed orchard.
- G— the wild-stand selection cost constraint. Each trait is related to ten "special variables" so that selection cost corresponding to its current selection intensity is computed. The total expenditure for wild-stand selection over all traits must not exceed the specified level. This constraint is on a per-clone basis.
- H— these equations (two for each trait) insure: (1) progeny-test gain is not brought into the solution if the trait is not selected in wild stands and (2) when a trait is selected in the wild stand, gain from progeny testing comes into the solution at its full value. In other words, the decision variables for progeny-test gain are zero-one integer variables. Because deviations are minimized, the upper bound value of one is assured once the traits are being selected by placing small weights on deviation of progeny-test variables from unity.

The heritability estimates and gain formulas make it possible to calculate genetic gain for each trait. However, because tree improvement programs are almost always concerned with the improvement of several traits, it is important to consider the genetic correlations between characteristics. Such correlations can be used to predict how other traits will respond to selection for the trait of interest. Gain from correlated response to selection is calculated by:

$$CG_y = i_x h_x r_a \sigma_{ay} \text{ (FALCONER, 1960, p. 318)}$$

where:

CG_y = correlated gain in trait y from selecting for trait x.

i_x = selection intensity for trait x.

h_x = square root of heritability of trait x.

r_a = additive genetic correlation between traits x and

y; i.e., correlation of breeding values for traits x and y.

σ_{ay} = square root of additive variance of trait y.

The direction of the correlated response is determined by the sign of the genetic correlation. The genetic correlations used (STONECYPHER *et al.*, 1973) are shown in Table 3.

In order to correctly interpret the correlation between volume and straightness and between volume and crown, one must review how the progeny were scored. Trees received a score of 1 to 5, best to poorest, for both straightness and crown, so a positive correlation between these traits and volume is undesirable. For example, a positive relationship between crown and volume would mean that trees of greater volume tend to have poorer scoring, larger crowns. Undesirable genetic correlations make it more difficult to find a tree which is satisfactory with regard to

Table 3. — Genetic correlations (above the diagonal line) and phenotypic correlations (below the diagonal line) between individual traits of loblolly pine.¹⁾

	Volume (per tree)	Fusiform (% free)	Straightness Score	Crown Score	Specific Gravity
Volume		— .29	.09	.24	.36
Fusiform	— .25		— .06	—	—
Straightness	.08	— .04		.65	.04
Crown	.21	—	.37		—
Specific gravity	.28	—	.06	—	

¹⁾ Source: "Inheritance Patterns of Loblolly Pine from an Unselected Natural Population", (STONCYPHER *et al.*, 1973).

all traits than if traits were uncorrelated or correlated in a desirable manner.

Fusiform infection was particularly hard to assess because of the large difference in infection rate between regions of the South. A percentage improvement in the other traits, such as volume, can be assumed to apply over most loblolly pine sites. But improvement in fusiform resistance has a completely different effects in regions with different infection levels because resistance and volume are negatively correlated.

Information from the Heritability Study, other published data, and a substantial amount of data generously supplied by the Forest Service, Southeastern Area, State and Private Forestry, indicated that the relationship between the total percent infection and the percent of trees having stem galls is linear. Further, the volume loss that would occur if fusiform rust were present depends on the proportion of stem-infected trees that would die before they could be salvaged. But even this information will not give the necessary direct estimate of volume loss because questions remain as to how much potential volume of a fusiform killed tree would be captured by its surviving neighbors and how much of the volume of an infected tree is cull even when it can be harvested.

As a rough approximation, it was assumed that 40 percent of the potential volume contribution by stem-infected trees is lost. Therefore, the total percent volume loss per acre in plantations is 40 percent of the percentage with stem infections. The following are the four infection levels and corresponding volume losses as used in this analysis:

Infection level	Total infected (percent)	Stem infected (percent)	Volume loss/acre (percent)
None	0	0.0	0.0
Light	15	6.9	2.8
Medium	50	33.2	13.3
Heavy	85	59.6	23.8

Additive variance from the Heritability Study was estimated for the medium level of infection intensity. Therefore the estimated additive variance was only strictly valid at the medium infection level because additive variance would vary as infection level varied.

Adjustment to other rust infection levels was made by computing the percent gain in the medium infection level and assuming that similar percentage gains could be achieved at other infection levels. To illustrate, consider the gain from selection for fusiform resistance in natural stands at a selection intensity of one standard deviation. This calculation utilizes the estimate of heritability (h^2) for percent free from infection found in Table 2 and the estimate of phenotypic standard deviation (σ_p) for the parent trees. Gain is:

$$G_W = (i_1) (h^2) (\sigma_p) \\ = (1.0) (0.089) (45.014) \\ = 4.01 \text{ (arcsin units)}$$

The progeny in the Heritability Study had a mean of 51.4 percent free of infection which has an arcsin $\sqrt{\text{percentage}}$ value of 45.80 (STEEL and TORRIE, 1960, Table A.10, p. 448). The computed genetic gain brings percent free of infection to 58.4; an improvement of 14.4 percent on the basis of the proportion infected (gain of 7.0 as a percent of the original 48.6 percent infected). Using the 14.4 percent gain, the relationship between percent infected and percent stem infected and the assumed 40 percent volume loss of stem infected trees, the gain in the heavy infection level is calculated as follows: ($i = 1.0$)

Heavy Infection level	Percent infected	Percent stem infected	Percent Vol. loss
Unimproved	85.0	59.6	23.8
Improved	72.8	50.4	20.2
Gain	12.2(14.4% of 85.0)		3.6

One important factor must be considered in the evaluation of the genetic gain estimates. All parent trees were selected from a single large stand. Thus there is no allowance for any additional genetic gain from a heterotic effect that tree improvement programs appear to obtain when widely separated superior clones are crossed in a seed orchard.

The predicted percentage gains from selection in wild stands and from roguing based on progeny test results are presented for the industrial case study in Table 4. Gain from wild-stand selection is for a selection intensity (i_1) of 1.0 while gain from progeny testing is determined by the roguing intensity (i_2) used by the organization. Estimates of roguing intensity are explained in the next section. To illustrate the use of this table, consider selection for straightness in wild stands. Straightness improvement is 2.01 percent with the following correlated responses: crown improves 1.00 percent, specific gravity and volume decline 0.02 and 0.11 percent, respectively and volume loss to rust decreases 0.03, 0.09, and 0.16 percent in the light, medium, and heavy fusiform infection areas. Gains from wild-stand selection and progeny testing correspond to components 'A' and 'B', respectively, in the separable goal programming model (Figure 2).

The industrial case study

Only specific information regarding the industrial case study is presented in detail here. However the summary and conclusions are based on analysis of both the industrial and state forestry division case studies and the representative loblolly pine tree improvement program form from the TAPPI survey data.

Table 4. — Estimated genetic response from selection in wild stands and progeny testing for the industrial case study.¹

Cange in:	Wild-stand selection for:					Progeny test for:				
	Straight.	Crown	Sp.Gr.	Vol.	Fusif.	Straight.	Crown	Sp.Gr.	Vol.	Fusif.
Straight.	2.01	1.19	— .20	— .20	.16	2.42	1.42	— .12	— .21	.18
Crown	1.00	1.40	—	— .40	—	1.29	1.79	—	— .44	—
Sp.Gr.	— .02	—	1.96	.31	—	— .05	—	2.09	.57	—
Volume	— .11	— .27	1.15	1.38	— .51	— .71	— 1.78	3.57	7.68	— 2.86
Fusiform ²) (light)	.03	—	—	— .15	.65	.04	—	—	— .20	.90
Fusiform (medium)	.09	—	—	— .50	2.17	.14	—	—	— .67	3.00
Fusiform (heavy)	.16	—	—	— .84	3.69	.25	—	—	— 1.13	5.12

¹) Selection intensity equals 1.0 for wild-stand selection and 0.49 for progeny-test selection.²) Fusiform effects expressed in terms of volume.

The industrial concern initiated its tree improvement program in 1957 and has been actively engaged in tree improvement work since. The firm maintains 165 acres of seed orchard of several pine species which by 1976 will provide 100 percent of the seed it needs in managing over one million acres of forest land. Improved seed will be used to establish plantations which will supply both pulp-

wood and sawtimber for the organization's integrated operations. Data from thirty-one acres of older loblolly pine seed orchard were used in the industrial case study analysis. The general characteristics of the seed orchard and the costs associated with its establishment, maintenance and progeny testing are shown in Table 5.

Table 5. — Characteristics and costs associated with the industrial case study seed orchard.

General			
Program initiated	1957	Age at roguing (yrs.)	13
Orchard age (yrs.)	6 — 11	orchard size (acres)	31
Number of clones	40	Orchard fertilized	yes
Total number of grafts	3935	Orchard irrigated	no
Spacing:		Progeny test acreage	70
Initially (ft.) — 15 × 15 to 22 × 22		Approx. date of initial	
After roguing (ft.) — Approx. 20 × 30		second-generation	
		orchard establishment	1985
Costs			
1. Orchard			
Site preparation/A ¹)	\$80.00	Roguing cost/A	\$30.00
Orchard establishment/clone ²)	57.50	Land value/A	120.00
Management costs/A/Yr. ³)		Tax rate/A/Yr.	0.80
1—5 years	200.00		
6—10 years	200.00		
11+ years	175.00		
2. Progeny Test			
Controlled crosses/clone ⁴)	\$106.00	Land value/A	\$100.00
Site preparation/A ¹)	23.00	Tax rate/A/Yr.	0.80
Establishment/A ⁵)	36.00		
Measurement ⁶) Age: 1 4 8 12			
Cost/A: \$3 \$20 \$30 \$200			
3. Superior tree selection			
Total cost/clone	\$200.00		

¹) Includes land clearing, burning²) Includes grafting, planting stock trees³) Includes fertilization, mowing, insecticides, supervision⁴) Includes bagging flowers, pollen collection, pollinating⁵) Includes planting, tagging, staking, mapping⁶) Includes measurements of:

Age 1—survival; age 4—height, crown, form; age 8—height, diameter, form

Age 12—height, diameter, form, wood quality

All measurements include assessment of infection by fusiform rust.

Establishment of a second-generation seed orchard is planned around 1980. As seed production in the second-generation orchard begins to increase, the present first-generation orchard will be systemically replaced as a source of improved seed. It is estimated that replacement will be completed when the first-generation orchard is thirty years old. The base year for analysis of the industrial case study is orchard age 10 years and all costs and revenues were discounted or compounded to this point in time. Based on the costs in Table 5, the value of the tree-improvement investment at age 10 is shown below for various interest rates:

Total investment per-acre of seed orchard at age 10		
Interest rate	with progeny testing and roguing	without progeny testing and roguing
6%	\$6691	\$5779
8%	7094	6129
10%	7707	6679
12%	8553	7452

Seed production in this orchard has been exceptionally good, reaching 30 pounds of seed per acre at age 10. Roguing is planned when the orchard is approximately 13 years

old, based on 8- to 10-year-old progeny test results. Orchard thinning and roguing are expected to stabilize seed yield until the remaining tree crowns take full advantage of the increased growing space. However seed production is expected to reach approximately 50 pounds per acre by orchard age 20 and to remain steady thereafter. A piecewise linear estimation of seed yield for the industrial case study is shown in Figure 3. It is estimated that each pound of improved seed will yield approximately 9,000 plantable seedlings. At this organization's typical plantation spacing of 8×10 feet, each pound of seed is sufficient to plant 16.5 acres of improved plantation.

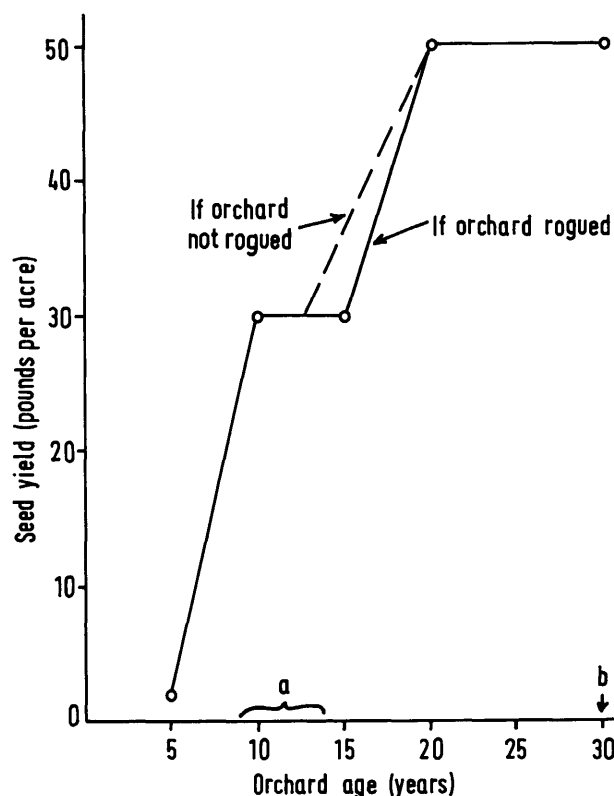


Figure 3. — Estimated seed production per acre of orchard for the industrial case study.

a — Roguing, spacing and sanitation cuts to remove fusiform infected trees.

b — Orchard replaced as a source of improved seed.

Fusiform infection varies from heavy infection to no infection depending on the location of company holdings. Increase in specific gravity is particularly emphasized in their tree improvement program because of its favorable effect on pulp yield and quality of the paper this firm produces. Selection for higher specific gravity will also reduce the specific gravity variation in the raw material input to their mills.

Characteristics of the select and wild populations, estimated selection intensities, and expenditure for selection for each trait are given in Table 6. The probability of finding a select tree which meets all the individual trait requirements is not the product of the proportions eligible for selection for each trait (0.0005) because the traits are genetically and phenotypically correlated. Conversely, the proportion of the wild population meeting requirements for all traits, even if they are perfectly correlated, can be no larger than the smallest individual trait proportion eligible, i.e., no more than 7 percent of the wild population would meet all average trait requirements. Since phenotype correlations are significantly less than 1.0, the qualified proportion of the wild population is much smaller than 7 percent.

Undesirable phenotypic correlations make it harder to find a qualified candidate. For example, the proportion of the wild population satisfying minimum requirements for only crown and volume would be $(0.27) \cdot (0.07)$ or 0.019 if the traits were independent. But, because of the undesirable correlation between these traits, the actual proportion of the wild population qualified with regard to both traits is 0.001; i.e., 1 in 1000 instead of the 2 in 100 which it would be if the traits were independent.⁷⁾

Roguing intensity was estimated from the proportion of grafts to be removed from the orchard. This organization plans to reduce orchard spacing from 15×15 feet (7.5 acres of orchard) and 22×22 feet (23.5 acres) to approximately 20×30 feet after roguing. This results in a proportion saved of 70.6 percent which corresponds to a selection intensity of 0.49 for a 40 clone population (BECKER, 1967). Thus, 28 of the clones will remain in the orchard. Of course

⁷⁾The two traits together have a bivariate normal distribution. The probability that two normally distributed random elements of known probability occur simultaneously has been tabulated for various values of correlation between the traits (National Bureau of Standards, 1959).

Table 6. — Characteristics of the selected and wild populations used in the calculation of current selection intensities and the cost of selecting for each trait for the industrial case study.

Trait	Ave. select. pop. ¹⁾	Region ave. ²⁾	Pheno. std. dev. ³⁾	Est. select. intens. ⁴⁾	Est. select. cost ⁵⁾	Prop of pop. eligible for select. ⁶⁾
Straight.	1.00	3.00	1.38	1.45	\$20	18%
Crown	1.58	3.00	1.14	1.25	10	27
Sp.Gr.	0.52	0.49	0.03	1.00	50	38
Volume	28.57	16.14	6.44	1.89	100	7
Fusiform ⁷⁾	—	—	—	0.97	20	40
Total selection cost per clone = \$200						

¹⁾ Average of selected population.

²⁾ Regional wild population average by trait.

³⁾ Phenotypic standard deviation. Product of coefficient of variation and the regional average.

⁴⁾ Estimated selection intensity. Regional population average divided by Phenotypic standard deviation.

⁵⁾ Estimated wild-stand selection costs by trait. From questionnaire data.

⁶⁾ Proportion of wild population eligible for selection. Fixed by the selection intensity.

⁷⁾ It was estimated by this organization that 40% of their natural stands of age 35 are completely free of infection. Selection intensity was computed directly from the proportion of the population eligible for selection.

this is an approximation of orchard selection intensity; the actual selection intensity for individual traits may be higher or lower than 0.49 but 0.49 was used to compute progeny testing gain for each trait (Table 4).

Although the major goal of this organization is to increase cubic/foot volume production, their minimum improvement expectations are high for all traits. Since all fusiform infection levels are of interest, the firm has two separate sets of goals. One set (ICS-A) covers the no-infection and light-infection areas and the other (ICS-B) covers the medium- and heavy-infection areas where fusiform is a serious problem (Table 7).

Table 7. — Tree improvement program goals of the industrial case study.

For the No Fusiform and Light Fusiform-Infection Areas
(ICS-A Goals)

Trait rank	Relative rank	Minimum desired improvement
1. Volume		15% ^{a)}
2. Specific gravity	6.0	10% ^{b)}
3. Fusiform resistance	2.0	5% ^{c)}
4. Straightness	1.0	15% ^{d)}
5. Crown	1.0	15% ^{d)}

For Medium and Heavy Fusiform-Infection Areas
(ICS-B Goals)

Trait rank	Relative rank	Minimum desired improvement
1. Volume		15%
2. Fusiform resistance	1.5	5%
3. Specific gravity	2.0	25%
4. Straightness	3.0	15%
5. Crown	1.0	15%

¹⁾ Desired improvement over unimproved plantation yield.

²⁾ Desired increase over regional average specific gravity.

³⁾ Desired percentage reduction in average volume loss to fusiform infection.

⁴⁾ Desired improvement over mean score of approximately 3.0 A shift to 2.0 is a 33 percent gain.

When using ICS-A goals in the goal programming model, a weight of 100 is given to each one percent of underachievement of the fusiform resistance, straightness, and crown goals while each unit deviation short of the specific gravity and volume goals would be assigned weights of 200 and 1200, respectively. Thus, as weighted deviations from goals are minimized, a one percent gain in volume reduces the objective function 12 times more than a one percent improvement in crown, straightness, or fusiform resistance. The weights assigned deviations from each goal give the same relationship between traits as the relative rank column for ICS-A goals. This organization also indicated that their minimum acceptable return on the tree improvement investment was 5 percent.

Typical per-acre yields from unimproved plantations not seriously infected with fusiform were estimated by company personnel as follows:

For Unimproved Plantations

	Thinning	Final Harvest
Age in years	15	35
Estimated yield	7 cords	17 cords
		9 MBF sawtimber
Estimated specific gravity	0.42	0.46
Current stumpage prices (1971 values)	\$12 per cord	\$12 per cord
		\$40 per MBF

Sample analysis — The industrial case study

The respondent for the industrial-case study firm estimated that on the average 60 percent of the trees in mature natural stands on their holdings are infected with fusiform rust. Therefore, the firm's present tree-improvement program is evaluated on the basis of its goals for the medium infection area. Predicted economic and genetic gains from the firm's existing tree-improvement program are shown at the left in Table 8. This portion of the table does not represent a goal-programming solution; it utilizes the genetic gain estimates (Table 4) and estimates of current selection intensities (Table 6) for the industrial case study. The goals for the medium infection level are presented only for comparative purposes.

The high goals for straightness and crown improvement cannot be attained using selection intensities and genetic gains predicted for the present seed orchard. The specific gravity goal should be attained. The 3.3 goal for fusiform resistance is 25 percent of the predicted 13.3 percent volume loss to fusiform in the medium-infection area since the goal is to reduce the volume lost to rust by 25 percent. The 8.7 percent improvement in volume represents the gain that could be obtained if the improved seed were planted in a non-infected area. An additional 3.8 percent volume gain comes from improved resistance to fusiform if the seed were planted in a medium-infection area. The total volume gain will thus be 12.5 percent in a medium-infection area. There is little doubt that the present improvement program is economically sound. The 14 percent internal rate of return is well above the minimum acceptable 5 percent rate of return for the company.

The goal programming solution for the industrial case study in the medium fusiform infection area is shown in the center of Table 8. The best combination of traits indicates there should be no selection for crown improvement *given the goals of this company*. The optimum selection intensity for fusiform resistance is quite close to 0.8 which corresponds to selection of only rust-free trees when stands are 50 percent infected. The wild-stand selection strategy derived from the goal-programming model would yield a higher volume gain and smaller improvement in straightness and crown than does the present program. The higher volume gain at a lower selection intensity is possible in the goal programming solution because crown is not selected for. Selecting for crown improvement reduces volume improvement because of their negative genetic correlation.

There appears to be some discrepancy between the selection scheme that has been used by the company and the combination of selection intensities that would move this organization closest to its goals. If crown improvement has such a low rank in the firm's goals, the selection intensity used for crown in the existing program is too high. However, overall their existing tree improvement program seems in line with their objectives. More emphasis on the quality of solid wood products would no doubt increase importance of selection for crown and straightness.

The flexibility of the model allows detailed sensitivity analysis. For example, the effect of doubling selection expenditures to \$400 per clone can be analyzed. The goal-programming solution for the medium infection level using \$400 per clone is at the right of Table 8. Total volume gain exceeds 15 percent with a \$400 per clone wild-stand selection expenditure. The selection intensity for fusiform resistance remains almost unchanged and corresponds to se-

Table 8. — The Industrial case study's existing program and sample goal programming analysis.

Trait	Present Program				Goal Programming Solution for Present Program				Goal Programming Solution if Selection Costs were \$400 per clone			
	Select. intens.	Pred. Gain (%)	Goal (%)	Diff. (%)	Select. intens.	Gain (%)	Goal (%)	Diff. (%)	Select. intens.	Gain (%)	Goal (%)	Diff. (%)
Straight.	1.45	7.7	15.0	—7.3	1.48	4.7	15.0	—10.3	1.74	5.1	15.0	—9.9
Crown	1.25	5.1	15.0	—9.9	0.0	1.6	15.0	—13.4	0.00	1.7	15.0	13.3
Sp.Gr.	1.00	5.1	5.0	+0.1	1.38	5.8	5.0	+0.8	1.74	6.6	5.0	+1.6
Volume	1.89	8.7	15.0	—6.3	1.74	11.1	15.0	—3.9	2.11	12.0	15.0	—3.0
Fusiform	0.97	3.8	3.3	+0.5	0.73	3.3	3.3	0.0	0.81	3.3	3.3	0.0
T. Volume		12.5				14.4				15.3		
		B/C @ 5% = 22.2				B/C @ 5% = 25.6				B/C @ 5% = 26.3		
		IRR = 14%				IRR = 14%				IRR = 14%		
		Cost/clone = \$200				Cost/clone = \$200				Cost/Clone = \$400		
		Infection = medium				Goals = ICS-B				Goals = ICS-B		
						Infection = medium				Infection = medium		

where: Fusiform gain and goal are expressed in volume terms.

B/C — Benefit-cost ratio for an acre of seed orchard at the specified interest rate.

IRR — Internal Rate of Return; that interest rate, to the nearest one percent, which would result in a benefit-cost ratio of one.

Cost/Clone — Expenditure per clone for wild stand selection; taken from Table 5.

Infection — Fusiform infection level.

lection of only diseasefree trees. Selection intensities for volume, specific gravity and straightness would be higher with the \$400 per clone expenditure and would bring gains closer to goals. The benefit-cost ratio for the optimum program at the medium-infection level increases from 25.6 to 26.3 with the expenditure of another \$200 per clone for wild-stand selection. This indicates that the marginal return on an additional \$200 per clone investment would be over 5 percent. Changes in infection levels, roguing intensities, goals, and other factors were also analyzed through sensitivity analysis for each organization; complete results are available upon request from the senior author.

Major findings of the study

The economic return from tree-improvement activities is high for the representative loblolly pine tree-improvement program based on TAPPI data and both case studies. Estimated internal rates of return for existing programs range from 10 to 14 percent for the three organizations. In each case, the profitability of tree-improvement was increased by the progeny-testing and roguing phase of the program. Without progeny testing and subsequent roguing of the seed orchard, internal rates of return ranged from 8 to 13 percent. When stumpage prices were assumed to increase at an annual rate of 3.2 percent, the internal rate of return for the representative improvement program was 16 percent. Based on the TAPPI data, there appear to be no significant differences in profitability between tree-improvement programs in the coastal plain and piedmont provinces. Since the genetic gains used in this study are likely under-estimates, these returns are probably conservative.

Marginal analysis of the wild-stand-selection expenditure indicates that the current level of expenditure could be substantially increased. Based on average costs for the representative improvement program, the current selection expenditure could profitably be tripled. An increase in wild-stand selection expenditure would also bring genetic gains closer to program goals.

Seed yield per-acre of orchard is sufficient to guarantee high profitability. Based on an analysis of the representative coastal plain orchard, it was found that a 4 percent volume improvement and 10 pounds of seed per acre per year between orchard age 10 to 30 years were sufficient to

return 6 percent on the tree improvement investment. The higher actual seed yields and greater volume improvement would raise the rate of return substantially above 6 percent.

The effect of varying orchard roguing intensity could only be estimated because seed yields following roguing are not well documented. However, it seemed clear from an analysis of the representative coastal plain seed orchard that economic return and genetic gains increase as roguing intensity increases. The highest roguing intensity corresponded to removal of 75 percent of the clones and increased profitability relative to less intensive roguing even though projected seed yield was significantly reduced. At 6 percent interest, the benefit-cost ratio increased from 4.2 with no roguing or progeny testing to 13.7 at the highest roguing intensity. Volume gain in a medium-rust area, increased from 5 to 25 percent as orchard roguing intensity rose from zero to the highest level.

Some minimum number of clones must be maintained in a seed orchard to insure an adequate breeding population, but if more clones were initially brought into the orchard, then a higher roguing intensity would be possible. Wild-stand selection cost and progeny-testing expenditure would undoubtedly increase with the selection of more clones, but these results suggest the value of such a strategy. By establishing grafts at a close spacing, there would still be enough trees per acre after heavy roguing to provide seed yields similar to those common with the lower roguing intensities in use today, provided data for roguing could be obtained before serious crown competition took place in the orchard.

Results also indicated that it is not necessary to select only rust-free trees in wild-stands in order to meet moderate fusiform-resistance goals. However, continuing the practice of selecting only rust-free superior trees altered genetic gains only slightly from the optimal solution and produced a higher volume gain. When selecting only rust-free trees, the optimum combination of wild-stand selection intensities differed significantly between rust-infected and non-infected areas because improved fusiform resistance is negatively related to volume gain. The difference in optimum selection intensities indicates that the criteria for judging a candidate select tree should be

different in the two infection areas. Therefore, if the practice of selecting only rust-free trees is continued, two orchards should be established for organizations with land holdings in both non-infected and infected areas. One orchard would be composed of clones from a non-infected area and the improved seed would be used in rust-free regions. Another orchard would be established with clones from infected areas and the seed produced would be used in rust-infected areas.

Tree improvement goals varied by organization and individual respondent. The industrial-case-study firm had goals which proved to be close to a profit maximizing strategy. However, the firm's current emphasis on crown improvement should be re-evaluated in light of results from the goal-programming analysis. Selection for crown improvement is not a part of the optimum goal programming solution which minimizes deviations from the firm's goals. Tree-improvement program goals given by personnel of the state forestry division were in line with their present improvement program.

Estimated total volume gain ranged from 12 to 14 percent for the existing improvement programs studied. In addition, a 5 percent improvement in specific gravity is predicted for those organizations selecting for higher specific gravity. Straightness and crown improvements for existing programs are in excess of 5 percent for each organization studied and a 10 percent reduction in volume lost to fusiform, in areas of medium infection, is easily attainable. These gain estimates are thought to be conservative.

Gains resulting from the optimum combination of traits and selection intensities for these organizations, as derived from the goal-programming model, are similar to the improvements predicted for existing improvement programs. However, it is apparent that higher gains are attainable by varying several factors in the representative tree-improvement program. Predicted total volume gain is shown below for several changes in the representative tree improvement program:

	Total Volume Gain (percent)
Existing Program (medium infection)	14.1
— Selection expenditure doubled	17.0
— Use of highest roguing intensity	25.1
— Selection of rust-free trees in heavily infected areas	20.2
— Genetic gains 25 percent higher than those used in the analysis	19.5

Of course, there would be additional gain in other traits in every case except the heavy rust-infected area. Volume gain is higher in the heavy rust-infected area because of greater improvement in resistance to rust infection.

Conclusions

In general, the organizations studied in this investigation seemed to be operating their tree-improvement programs in line with their stated tree-improvement goals. This fact strengthens the validity of the goal-programming model as a method of planning future improvement programs, including the establishment of second-generation seed orchards. The model can be used to find that combination of traits and their selection intensities that will bring genetic improvement as close as possible to program goals. A com-

plete account of tree-improvement program costs, estimates of economic and genetic gains, and a statement of tree-improvement goals by the sponsoring organization are required to utilize the model.

There is little doubt about the economic justification of tree-improvement work with loblolly pine. Even with genetic gain estimates thought to be conservative and seed yields 25 percent less than expected, the internal rate of return on the tree-improvement investment was still 12 percent for the 'representative' coastal plain tree-improvement program developed from TAPPI survey data. Progeny testing and subsequent roguing of the seed orchard increase profitability.

The results of this study indicate that first-generation loblolly pine seed orchards are providing seed which will produce a volume gain of 10 to 20 percent over unimproved plantations yields. In addition, it appears that these improved stands will have straighter stems than unimproved plantations and that there will be some decrease in crown size. The increase in specific gravity should be on the order of 5 percent.

The goal programming technique for analyzing tree improvement programs is both realistic and very effective. The model's major strength is the ease with which each component of a tree improvement program can be varied over a range of expected values. The resulting sensitivity information is useful for predicting economic and genetic gains and for formulating plans to better attain tree improvement goals.

Summary

A goal-programming model was derived to evaluate existing tree-improvement programs and find the 'optimum' selection scheme for future tree-improvement programs, including the establishment of second generation seed orchards. The model selects that combination of traits and their selection intensities which bring gains as close as possible to stated tree improvement goals. The economic return from the proposed program is also computed. The goal-programming model is quite flexible and can produce a great deal of sensitivity information when various components of a tree improvement program are varied.

Current loblolly pine improvement programs had estimated internal rates of return ranging from 10 to 14 percent with progeny testing and roguing and from 8 to 13 percent without the progeny testing and roguing phase of the program.

Estimated total volume gains over unimproved plantations range from 12 to 14 percent for the existing improvement programs studied. In addition, a 5 percent improvement in specific gravity is predicted for those organizations selecting for higher specific gravity. Straightness and crown improvement in existing programs were in excess of 5 percent for each organization studied and a 10 percent reduction in volume lost to fusiform, in areas of medium infection, appears easily attainable. The goal-programming analysis indicated that for the most part organizations were operating in line with their tree improvement goals. The analysis also indicated that volume gains of 20 percent or more were possible by varying components of the tree-improvement program such as roguing intensity and wild-stand selection expenditure. These gain estimates are thought to be conservative.

Key words: Forest Genetics, Mathematical Programming, *Pinus taeda* L., Financial Returns, Genetic Gains.

Zusammenfassung

Aus den laufenden Programmen zur züchterischen Bearbeitung der Baumart *Pinus taeda* L. wurde ein Zielmodell-Programm zur optimalen Selektion von Ausgangsbäumen für zukünftige Züchtungsprogramme entwickelt einschließlich der Erstellung von Samenplantagen der zweiten Generation. Das Modell wählt diejenigen Merkmalskombinationen aus, mit denen man den Zuchtzielen am nächsten kommt. Gleichzeitig wird der wirtschaftliche Gewinn mit kalkuliert. Das Zielmodell-Programm ist durchaus flexibel und eröffnet Möglichkeiten zur Information auch bei unterschiedlichen Komponenten eines Züchtungsprogramms.

Literature Cited

BARBER, J. C.: How much is Forest Genetics Helping the Forester by Increasing Growth, Form, and Yield? In Proceedings of the Seventh Southern Conference on Forest Tree Improvement, Gulfport, Miss., pp. 16–20 (1963). — BECKER, W. A.: Manual of Procedures in Quantitative Genetics. Second Edition, Wash. St. Univ. Press, Pullman, Wash. (1967). — BERGMAN, A.: Variation in Flowering and Its Effect on Seed Cost. N.C.S.U. — Coop. Programs Tech. Report 38, Raleigh, N.C. (1968). — BUIJTENEN, J. P. VAN and W. W. SAIITA: Linear Programming Applied to the Economic Analysis of Forest Tree Improvement. Jour. of For. 70 (3): 164–167 (1972). — CHARNES, A., W. W. COOPER, and R. D. FERGUSON: Optimal Estimation of Executive Compensation by Linear Programming, Man. Sci. 1 (2): 138–151 (1955). — CHARNES, A. and W. W. COOPER: Management Models and Industrial Applications of Linear Programming, Vol. I, John Wiley and Sons, New York, N.Y. (1961). — DAVIS, L. S.: Investment in Loblolly Pine Clonal Seed Orchards. Jour. of For. 65 (12): 882–887 (1967). — FALCONER, D. S.: Introduction to Quantitative Genetics. The Ronald Press Company, New York, N.Y. (1960). — FIELD, D. B.: Applications of Operations Research to Quantitative Decision Problems in Forestry and the Forest Products Industries — A Bibliography. School of Forestry and Environmental Studies,

Yale University Mimeo. (Revised 11/15/74) (1971). — FINNEY, D. J.: The Consequences of Selection for a Variate Subject to Errors of Measurement, Revue, Inst. Int. de Stat. 24: 1/3 (1956). — HADLEY, G.: Nonlinear and Dynamic Programming. Addison-Wesley Publishing Company, Inc., Reading, Mass. (1964). — IBM Corporation, IBM Application Program, Mathematical Programming System/360, Linear and Separable Programming — User's Manual, White Plains, N.Y. (1968). — NAMKOONG, G.: Optimum Allocation of Selection Intensity in Two Stages of Truncation Selection. Biometrics 26: 465–476 (1970). — NAMKOONG, G., E. B. SNYDER, and R. W. STONECYPHER: Heritability and Gain Concepts for Evaluating Breeding Systems Such as Seedling Orchards, Silvae Genetica 15 (3): 76–84 (1966). — National Bureau of Standards, Tables of the Bivariate Normal Distribution Function and Related Functions. U. S. Dept. of Commerce, Applied Mathematics Series, No. 50 (1959). — SCHUMACHER, F. X. and T. S. COILE: Growth and Yields and Natural Stands of the Southern Pines. T. S. Coile, Inc., Durham, N.C. (1960). — SHELBOURNE, C. J. A.: Tree Breeding Methods. Tech. Paper No. 55 Forest Research Institute, New Zealand, For. Serv., Wellington, N.Z. (1969). — STEEL, R. G. D. and J. H. TORRIE: Principles and Procedures in Statistics. McGraw-Hill Book Co. Inc., New York, N.Y. (1960). — STONECYPHER, R. W.: The Loblolly Pine Heritability Study. Tech. Bull. No. 5, Woodlands Dept., International Paper Company, South lands Experiment Forest, Bainbridge, Ga. (1966). — STONECYPHER, R. W., B. J. ZOBEL, and R. L. BLAIR: Inheritance Patterns of Loblolly Pine from an Unselected Natural Population, Tech. Bul. No. 220, N. C. Agr. Expt. Sta., Raleigh, N. C. (1973). — SWOFFORD, T. F.: An Economic Evaluation of Tree Improvement on the Alabama National Forests. U. S. For. Serv., Southern Region, Atlanta Ga. (1968). — WAHLGREN, H. E. and D. R. SCHUMANN: Properties of Major Southern Pines: Part I, Wood Density Survey, USDA, For. Serv. Res. Paper FPL 176–177 (1972). — ZOBEL, B. J., R. L. BLAIR, R. C. KELLISON, and C. H. O'GWYNN: An Operational Breeding Program — Theory and Practice. IUFRO Conference, Gainesville, Fla. (1971). — ZOBEL, B. J., R. C. KELLISON, M. F. MATHIAS, and A. V. HATCHER: Wood Density of the Southern Pines. Tech. Bull. No. 208, N. C. Agr., Expt. Sta., Raleigh, N.C. (1972).

Competition Between Selected Black Cottonwood Genotypes

By CHARLES G. TAUER¹⁾

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Information on the nature of intergenotypic competition among plants comes primarily from work with agronomic species. Studies such as those reviewed by SAKAI (1955), DONALD (1963), HARPER (1965), BRIM (1969), SCHUTZ (1969) and SAMMETA and LEVINS (1970) have shown that the pure stand performance of a genotype can be significantly different than its performance in a mixture, and that the expression and magnitude of competitive interactions increase with the diversity of the genotypes involved. Competitive interactions have been demonstrated in forest tree species by SAKAI *et al.* (1965, 1968) SNYDER and ALLEN (1971) and ADAMS *et al.* (1973). However, the potential for increasing fiber yields by exploiting intergenotypic competition and the impact of such competition on testing by tree breeders has received little consideration.

This study was initiated to investigate intergenotypic competition in black cottonwood (*Populus trichocarpa* TORR. and GRAY) grown under greenhouse conditions.

¹⁾ Research Assistant, College of Forestry, University of Minnesota, St. Paul, Minnesota, 55108. Scientific Journal Series, Article No. 8984.

Competition and Its Measurement

In plants competitive ability is genotype dependent and a heritable character (SAKAI, 1955; DONALD, 1963). The competitive relationships expressed are due to direct genetic and environmental influences and complex interactions. DONALD (1963) states that in general the effects of direct and interacting competitive factors are cumulative and, because they are integrated by plant growth, measurable.

Work by HODGSON and BLACKMAN (1956), HINSON and HANSON (1962), and SHANNON *et al.* (1971) suggests that density effects generally cause modifications of the same plant characters influenced by competition. However, competitive effects are a function of genotype while density effects are due to spacial distribution. Consequently, there is no genetic basis for differential competitive ability between propagules of the same genotype and with equal spacing density effects become constant.

SCHUTZ and BRIM (1967) presented a system for comparing a genotype's performance when grown with itself to its performance at various levels of competition with another genotype. Competition effects are quantified by the