

derosa and red pine. Genetics (in press) (1982). — ALLENDORF, F. W., MITCHELL, N., RYMAN, N. and STAHL, G.: Isozyme loci in brown trout (*Salmo trutta* L.): detection and interpretation from population data. Hereditas 86: 179—190 (1977). — ALLENDORF, F. W. and PHELPS, S. R.: Use of allelic frequencies to describe population structure. Can. J. Fisheries and Aquatic Sci. 38: 1507—1514 (1981). ALLENDORF, F. W. and UTTER, F. M.: Population genetics. In: Fish Physiology, Vol. 8. (Ed. HOAR, W. S., RANDALL, D. J., and BRETT, R.): 407—454. Academic Press, New York. (1979). — BROWN, A. H. D. and MORAN, G. F.: Isozymes and the genetic resources of forest trees. Proc. of the Symposium on Isozymes of North American Forest Trees and Forest Insects. USDA Forest Serv. Gen. Tech. Rep. PSW-48: 1—10 (1981). — CHAKRABORTY, R.: A note on NEI's measure of gene diversity in a substructured population. Human-genetik 21: 85—88 (1974). — CLAYTON, J. W. and D. N. TRETIAK: Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Can. 29: 1169—1172 (1972). — CONKLE, M. T.: Isozyme variation and linkage in six conifer species. Proc. of the Symposium on Isozymes of North American Forest Trees and Forest Insects. USDA Forest Serv. Gen. Tech. Rep. PSW-48: 11—17 (1981). — COOPER, D. W.: The significance level in multiple tests made simultaneously. Heredity 23: 614—617 (1968). — DAHMS, W. G. and BARRET, J. W.: Seed production of central Oregon ponderosa and lodgepole pines. USDA Forest Serv. Res. Pap. PNW-191 (1975). — FERET, P. P.: Genetic differences among three small stands of *Pinus pungens*. Theor. Appl. Genet. 44: 173—177 (1974). — GURIES, R. P. and LEDIG, F. T.: Genetic structure of populations and differentiation in forest trees. Proc. of the Symposium on Isozymes of North American Forest Trees and Forest Insects. USDA Forest Serv. Gen. Tech. Rep. PSW-48: 42—47 (1981). — HAMRICK, J. L., MITTON, J. B. and LINHART, Y. B.: Levels of genetic variation in trees: influence of life history characteristics. Proc. of the Symposium on Isozymes of North American Forest Trees and Forest Insects. USDA Forest Serv. Gen. Tech. Rep. PSW-48: 35—41 (1981). — KIMURA, M. and CROW, J. F.: The number of alleles that can be maintained in a finite population. Genetics 49: 725—738 (1964). — LEVENE, H.: On a matching problem arising in genetics. Ann. Math. Stat. 20: 91—94 (1949). — LI, W. H.: Maintenance of genetic variability under the joint effect of mutation, selection and random drift. Genetics 90: 349—382 (1978). — LIBBY, W. J., STETTLER, R. F. and SEITZ, F. W.: Forest genetics and forest tree breeding. Ann. Rev. Genet. 3: 469—494 (1969). — LINHART, Y. B., MITTON, J. B., STURGEON, K. B. and DAVIS, M. L.: An analysis of genetic architecture in populations of ponderosa pine. Proc. of the Symposium on Isozymes of North American Forest Trees and Forest Insects. USDA Forest Serv. Gen. Tech. Rep. PSW-48: 53—59 (1981). — LUNDKVIST, K.: Allozyme frequency distributions in four Swedish populations of Norway spruce (*Picea abies* KARST.). I. Estimates of genetic variation within and among populations, genetic linkage and a mating system parameter. Hereditas 90: 127—143 (1979). — LUNDKVIST, K. and RUDIN, D.: Genetic variation in eleven populations

of *Picea abies* as determined by isozyme analysis. Hereditas 85: 67—74 (1977). — MADSEN, J. L. and BLAKE, G. M.: Ecological genetics of ponderosa pine in the northern Rocky Mountains. Silvae Genet. 26: 1—8 (1977). — MITTON, J. B., LINHART, Y. B., HAMRICK, J. L. and BECKMAN, J. S.: Observations on the genetic structure and mating system of ponderosa pine in the Colorado Front Range. Theor. and Appl. Genet. 51: 5—13 (1977). — NEI, M.: Genetic distance between populations. Amer. Nat. 106: 283—292 (1972). — NEI, M.: Analysis of gene diversity in subdivided populations. Proc. Natl. Acad. Sci. 70: 3321—3323 (1973). — NEI, M.: Molecular population genetics and evolution. Amer. Elsevier Publ., N. Y. (1975). — NEI, M., FUERST, P. A. and CHAKRABORTY, R.: Testing the neutral mutation hypothesis by distribution of single locus heterozygosity. Nature 262: 491—493 (1976). — NEI, M. and ROYCHOUDHURY, A. K.: Sampling variances of heterozygosity and genetic distance. Genetics 76: 379—390 (1974). — O'MALLEY, D. M., ALLENDORF, F. W. and BLAKE, G. M.: Inheritance of isozyme variation and heterozygosity in *Pinus ponderosa*. Biochem. Genet. 17: 233—250 (1979). — RICHARDSON, N. E.: Stand structure and patterns of conifer regeneration near Colstrip, Montana. M. S. Thesis, Univ. of Montana, Missoula. 122 p. (1981). — RIDGWAY, G. J., SHERBURNE, S. W. and LEWIS, R. D.: Polymorphisms in the esterases of Atlantic herring. Trans. Am. Fisheries Soc. 99: 147—151 (1970). — SAKAI, K. I. and PARK, Y. G.: Genetic studies in natural populations of forest trees III. Genetic differentiation within a forest of *Cryptomeria japonica*. Theor. and Appl. Genet. 41: 13—17 (1971). — SCHAAL, B.: Isolation by distance in *Liatris cylindracea*. Nature 252: 703 (1974). — SHAW, D. V. and ALLARD, R. W.: Analysis of mating system parameters and population structure in Douglas-fir using single-locus and multilocus methods. Proc. of the Symposium on Isozymes of North American Forest Trees and Forest Insects. USDA Forest Serv. Gen. Tech. Rep. PSW-48: 18—22 (1981). — STEWART, F. M.: Variability in the amount of heterozygosity maintained by neutral mutations. Theor. Popul. Biol. 9: 188—201 (1976). — WOODS, J. H., BLAKE, G. M.: Effects of stratification on *Pinus ponderosa* (var. *scopulorum* ENGELM.) seed from Colstrip, Montana. Montana Forest and Conservation Exp. Sta. Missoula, Montana. Res. Note 18 (1981). — WOODS, J. H., ALLENDORF, F. W., BLAKE, G. M. and KNUDSEN, K. L.: Inbreeding in natural stands of ponderosa pine. Isozyme Bull. (in press) (1982). — WRIGHT, S.: Evolution and the genetics of populations. Vol. II. The theory of gene frequencies. Univ. of Chicago Press, Chicago, IL. (1969). — YEH, F. C.: Analyses of gene diversity in some species of conifers. Proc. of the Symposium on Isozymes of North American Forest Trees and Forest Insects. USDA Forest Serv. Gen. Tech. Rep. PSW-48: 48—52 (1981). — YEH, F. C. and O'MALLEY, D.: Enzyme variations in natural populations of Douglas-fir, *Pseudotsuga menziesii* (MIRB.) FRANCO, from British Columbia. I. Genetic variation patterns in coastal populations. Silvae Genet. 29: 83—92 (1980). — YANG, J. CH., CHING, T. M. and CHING, K. K.: Isoenzyme variation of coastal Douglas-fir. I. A study of geographic variation in three enzyme systems. Silvae Genet. 26: 10—18 (1977).

## Index Selection For Increased Dry Weight in a Young Loblolly Pine Population

By F. E. BRIDGWATER, J. T. TALBERT and S. JAHROMI  
North Carolina State University, Raleigh,

North Carolina, USA

(Received 12th October 1982)

### Summary

Several selection models incorporating different traits into combined family-plus-individual multiple trait indexes were compared for their expected efficiency in increasing dry weight of individual trees. In our population, combined selection for volume with increased dry weight as the desired goal resulted in 10% less expected gain than combined selection based directly on dry weight. The most efficient single trait combined family-plus-individual selection model for dry weight used height as the selection

criterion. Expected gain for this model was 8% greater than for combined selection with dry weight as the criterion because of the high genetic correlation of height and dry weight yield and the higher heritability of height.

Combining family and individual values for height, d.b.h. and volume in an index whose goal was dry weight increased expected gain over combined selection for dry weight by 17%. Extending the index to include specific gravity and dry weight increased expected efficiency to 120%. This small improvement in expected gain over the

best model which did not require specific gravity determinations (120% vs. 117%) is probably insufficient to warrant the expense of determining wood specific gravity of individual trees in the population if improved dry weight yield of wood is the single goal of selection.

*Key words:* Combined selection, multiple-trait selection index, wood dry weight, and wood specific gravity.

### Zusammenfassung

Es wurden mehrere Selektionsmodelle, die verschiedene Merkmale und Familien- und Individualinformation für die Konstruktion von Selektionsindizes verwenden, miteinander verglichen. Untersucht wurde dabei deren erwartete Effizienz im Hinblick auf eine Erhöhung des Trockengewichtes des Holzes individueller Bäume. In der untersuchten Population erbrachte die kombinierte Selektion für Volumen mit erhöhtem Trockengewicht als erwünschtem Züchtungsziel 10% weniger Züchtungsfortschritt als eine kombinierte Selektion, die direkt auf dem Trockengewicht basiert. Das effizienteste auf einem Merkmal basierende Selektionsmodell, das Familien- und Individualleistung kombiniert, benutzt die Höhe als Selektionskriterium. Der erwartete Züchtungsfortschritt war für dieses Modell 8% höher als für die kombinierte Selektion mit dem Trockengewicht als Selektionskriterium, weil zwischen der Höhe und dem Trockengewicht eine hohe genetische Korrelation besteht und die Höhe eine größere Heritabilität besitzt.

Wenn Familien- und Individualwerte für Höhe, Brusthöhendurchmesser und Volumen in einem Index für Trockengewicht kombiniert werden, erhöht sich der erwartete Gewinn gegenüber kombinierter Selektion für Trockengewicht um 17%. Erweitert man den Index, um die Merkmale spezifisches Gewicht und Trockengewicht einzuschließen, erhöht sich die erwartete Effizienz auf 120%. Diese kleine Verbesserung des erwarteten Gewinns gegenüber dem besten Modell (120% gegenüber 117%), ist wahrscheinlich zu gering, um die Kosten zu rechtfertigen, die die Bestimmung des spezifischen Gewichtes des Holzes einzelner Bäume verursachen würde.

### Introduction

Selection in southern pine tree improvement programs most often emphasizes stem volume production. Other characteristics like disease resistance, form, and wood specific gravity are often included as selection criteria, but for a variety of reasons are given unspecified emphasis in the selection procedure. The most important reason is that relative economic values of traits are poorly quantified.

Loblolly pine (*Pinus taeda* L.) tree improvement programs are generally well advanced, and information on relatives is available to increase the accuracy of selection and the genetic gains from selection. Family information is often used subjectively when evaluating individual candidate trees. Hence, the weights given the information on relatives and the information on individual candidates are not quantified. The failure to use the information available on multiple traits and on relatives in such a way that gain can be accurately quantified makes evaluating different selection alternatives difficult, at best.

Selection indexes can be constructed by a form of multiple regression to include information on several traits and on relatives of candidate trees. Selection indexes are more efficient than other commonly considered means of selection if they are based on good estimates of genetic parameters and relative economic weights. Formulating a selection index is also one of the best ways to organize and interpret genetic information on a population.

In the study described here, we compared several indexes with different selection criteria but with the same goal of selection, total dry weight of wood in loblolly pine. Total dry weight of wood is governed by tree volume and wood specific gravity and is a major determinant of pulp yields from stands of loblolly pine.

### Materials and Methods

The population studied is a portion of the control-pollinated loblolly pine heritability study established jointly by North Carolina State University and International Paper Company in the Company's Southlands Experiment Forest in southwestern Georgia. The study was designed to determine the inheritance of important characteristics of loblolly pine from a nonselected natural population. The mating scheme, genetic test design, and results of the study through age 7 years were reported in detail by STONECYPHER *et al.* (1973); a summary of information pertinent to the present investigation will be given here.

#### Test Design and Sampling Procedures

A nested or hierarchical mating scheme was used to create the progeny population. Sixty-five randomly chosen trees were designated as male parents and each was mated to a different sample of 4 or 5 female parents. The study was established in the field during the winters of 1963, 1964, and 1965. Since each male group was planted in only one year, male groups are confounded with planting years. Each full-sib family was planted in 12-tree row plots within each of 3 blocks at each of 2 locations in the Experiment Forest. To reduce unaccountable environmental variation due to large block size, sets of 5, 6, or 7 male groups were planted as a unit in every block.

After 10 growing seasons in the field, each family plot was thinned. Trees to be thinned were chosen randomly within each 12-tree plot with only the restriction that spacing was to be as uniform as possible for remaining trees. This approach ensured that estimates of parameters would be unbiased for both the thinned and remaining portions of the study. Tree height and diameter at breast height were recorded for each felled tree.

A total of 36 male groups was sampled for wood specific gravity. Specific gravity was determined from oven-dry weight and green volume on sectors of wood discs taken from the top of the first and second 5-foot (2.13 m) bolts above the stump. Specific gravity for each tree was estimated by weighting the specific gravity at 5 feet (2.13 m) by the volume of the first 5-foot (2.13 m) bolt and the specific gravity of the sectors taken at 10 feet (4.27 m) by the volume of the second bolt. Weighted specific gravities are reported here. Only the data from thinned trees were used in this study.

#### Index Selection

Selection indexes were first developed for the selection of plant lines in 1936 (SMITH 1936). Since then, the method has been modified and extended many times (See LIN 1978 for a review). Selection indexes combine economic and genetic information in a multiple regression equation to predict the total worth of a genotype. Multiple-trait indexes combine information from several traits into a single value and are theoretically more efficient than tandem selection to improve one trait at a time or independent culling, a selection method whereby only those individuals that exceed culling levels for each trait are saved (HAZEL and LUSH 1942). Information from relatives and for mul-

multiple traits can be incorporated into a combined family and multiple trait index for use in applied tree breeding programs (ARBEZ, *et al.* 1974). The methodology for combining phenotypic and genotypic variances and covariances and relative economic values into a single index is directly analogous to the procedure described by BURDON (1979).

The general form of the selection index used in this investigation can be written as:

$I = b_{11}P_{i1} + b_{12}P_{i2} + \dots + b_{in}P_{in} + b_{j1}\bar{P}_{j1} + b_{j2}\bar{P}_{j2} + \dots + b_{jn}\bar{P}_{jn}$ , where  $b_{11}, b_{12}, \dots, b_{in}$  and  $b_{j1}, b_{j2}, \dots, b_{jn}$  are regression coefficients,  $P_{i1}, P_{i2}, \dots, P_{in}$  are individual phenotypic values for the measured traits (1 to n), and  $\bar{P}_{j1}, \bar{P}_{j2}, \dots, \bar{P}_{jn}$  are half-sib family averages for the same traits. In matrix notation, regression coefficients are determined through least squares analysis by the method

$$\hat{b} = \hat{P}^{-1}r \hat{A} \hat{a},$$

where:

$\hat{b}$  = vector of the 2n regression coefficients (i.e. index weights)

$\hat{P}^{-1}$  = inverse of the 2n x 2n phenotypic variance-covariance matrix (with respect to family means and individual tree values)

$r$  = diagonal matrix of rank 2n, of relationship values (CROW and KIMURA, 1970)

$\hat{A}$  = additive genetic 2n x 2n variance-covariance matrix (with respect to family means and individual tree values), and

$\hat{a}$  = vector (2n) of relative economic weights, one or more being non-zero.

Genetic gains for each trait from selection on each index were calculated from

$$G_i = \frac{(i) \hat{b} r \hat{A} i}{\sqrt{\hat{b}' \hat{P} \hat{b}}}$$

where: (i) = the selection intensity; ((i) = 2.66 for 1/100 saved),

$\hat{A}_i$  = the  $i^{\text{th}}$  column (1 x n) of the additive genetic variance-covariance matrix,

$\hat{b}$ ,  $\hat{P}$ , and  $r$  are as above.

#### Statistical Analyses

Analyses of variance and covariance were done for total tree height, breast height diameter (d.b.h.), total tree volume, weighted whole-tree specific gravity, and dry weight of trees. Age 10 data were pooled from all three planting years to gain precision in the estimates of variance components. In the analyses of variance and covariance, we pooled the interactions of families with blocks and locations and the within-plot variance (Table 1). Analyses showed that location x half-sib family (male group) interactions were not significant, which implies that one index could be used for selecting at both locations. Block x family interactions were significant for some traits, which means that individual and family values should be adjusted for block effects before calculating index values, or that the indexes should be applied within each block of the study. The pooling should not have materially affected estimates of parameters for the comparisons described in this paper.

Variance components were estimated from individual-tree values by Procedure VARCOMP in the Statistical Analysis System (SAS®) (SAS Institute Inc., 1979). Components of covariance were estimated by Procedure GLM in SAS®. Components of variance and genetic parameters calculated from them are presented in Table 2. Components of covariance among male groups and genetic correlation coefficients are presented in Table 3.

Table 1. — Form of analysis of variance for combined planting years and locations. The appropriate analysis of covariance is analogous except that mean cross-products and covariance components are involved in place of mean squares and variance components.

Source of Variation	d.f.	Expected Mean Squares
YEAR PLANTED	2	
LOCATION (YRP)	3	
REPS (YRP LOC)	12	
SET (YRP)	7	
LOC x SET (YRP)	7	
REP x SET (YRP LOC)	28	
MALE (YRP SET)	26	$\sigma^2_E + 19.84 \sigma^2_{F(YSM)} + 52.81 \sigma^2_{M(Ys)}$
FEMALE (YRP SET MALE)	63	$\sigma^2_E + 19.13 \sigma^2_{F(YSM)}$
POOLED ERROR	1803	$\sigma^2_E$

where:  $\sigma^2_{M(Ys)}$  = the component of variance (or covariance) attributable to differences among male groups (half-sib families), within year/set subclasses.

$\sigma^2_{F(YSM)}$  = the component of variance (or covariance) attributable to differences among female groups (full-sib families), within year/set/male subclasses.

$\sigma^2_E$  = the component of variance (or covariance) attributable to pooled error.

Table 2. — Estimates of components of variance, phenotypic variance, phenotypic variances on an individual ( $\sigma^2_P$ ) and family mean basis ( $\sigma^2_D$ ) and heritabilities on an individual basis.

Source 1/	Height	D.b.h.	Volume	Specific Gravity	Dry Weight
$\sigma^2_{M(Ys)}$	0.74118	0.02124	0.05132	0.00017	36.33736
$\sigma^2_{F(YSM)}$	1.22210	0.08954	0.11822	0.00010	83.27022
$\sigma^2_E$	8.71484	0.71646	0.97226	0.00053	641.23461
$\sigma^2_P$ 2/	10.67812	0.82724	1.1418	0.0008	760.84219
$\sigma^2_D$ 3/	1.36544	0.06845	0.11415	0.00022	79.77042
$h^2$ 4/	0.28	0.10	0.18	0.85	0.19

1/ See footnote Table (1) for description of sources.

$$2/ \sigma^2_P = \sigma^2_{M(Ys)} + \sigma^2_{F(YSM)} + \sigma^2_E$$

$$3/ \sigma^2_D = \sigma^2_{M(Ys)} + \frac{19.84}{52.81} \sigma^2_{F(YSM)} + \frac{1}{52.81} \sigma^2_E$$

$$4/ h^2 = 4 \cdot \frac{\sigma^2_{M(Ys)}}{\sigma^2_P}$$

Table 3. — Genetic correlation coefficients (above diagonal) and estimates of components of covariance (below diagonal) among male groups.

	Height	D.b.h.	Volume	Specific Gravity	Dry Weight
Height		0.779	0.862	0.290	0.943
D.b.h.	0.09771		1.00	-0.084	0.906
Volume	0.1682	0.03315		-0.068	0.920
Specific Gravity	0.00326	-0.00016	-0.0002		0.333
Dry Weight	4.89503	0.79568	1.25612	0.02615	

#### Results and Discussion

Estimated narrow-sense heritabilities on an individual tree basis (Table 2) and genetic correlations (Table 3) agree closely with those published elsewhere (STONECYPHER, *et al.* 1973). The single exception is the negative, although

Table 4. — Expected response and efficiency of family selection indexes with five traits as criteria for selection compared to combined selection for dry weight yield.

Economic Relative Weights <sup>1/</sup> For Traits					Expected Response						
Ht.	D.b.h.	Vol.	Sp. Gr.	Dry Wt.	Height (ft)	D.b.h. (in)	Volume (ft <sup>3</sup> )	Specific Gravity	Dry Weight (lb per tree)	% Dry Weight	Efficiency <sup>2/</sup> (%)
1	1	1	1	1	2.8	.36	.61	.02	19.8	26	120
1	0	0	0	0	2.8	.35	.60	.02	19.6	25	118
0	1	0	0	0	2.2	.45	.73	-.02	15.5	20	094
0	0	1	0	0	2.4	.45	.73	-.01	16.1	21	097
0	0	0	1	0	1.0	-.11	-.15	.06	8.1	11	049
0	0	0	0	1	2.8	.35	.59	.03	19.9	26	120
1	1	0	0	0	2.8	.38	.64	.02	19.5	25	118
1	1	1	0	0	2.8	.40	.67	.01	19.2	25	116
1	1	0	1	0	2.8	.37	.63	.02	19.6	25	118
-	-	-	-	1	-	-	-	-	16.5	22	100

<sup>1/</sup> Relative economic weights are for individual values of height, d.b.h., volume, specific gravity, and dry weight, respectively. No economic weight was assigned to family values included in the indexes.

<sup>2/</sup> Efficiency is the correlated response in dry weight as a % of gain for combined selection using dry weight as the criterion.

weak, genetic correlation found between d.b.h. and specific gravity (-0.08) and consequently between volume and specific gravity (-0.07). Negative correlations among growth traits and specific gravity have been reported previously for this loblolly pine population (STONECYPHER and ZOBEL 1965). This negative relationship (-0.08) is very small and certainly not demonstrably different from zero considering the imprecision of estimates of components of variance and covariance based on only 36 half-sib families. We note it here because the effect of even this small negative value will be apparent in the index models presented later.

Several selection indexes were considered. All had increased dry weight yield as the goal of selection. The bases for evaluating each index were gain in dry weight and efficiency compared to combined family-plus-individual selection (FALCONER 1960, p. 227) made directly for dry weight yield. The proportion saved was 1 in 100 ( $i = 2.66$ ) for all indexes considered. The expected gain from combined selection for dry weight was 16.5 lb (7.48 kg) per tree which represents a 22% increase over the mean per tree dry weight of 76.8 lb (34.84 kg) (Table 4). This value was assumed to represent an efficiency of 100%.

Expected gain (and efficiency) generally increase as more information is included in a selection index provided the information is of good quality. Thus, tree breeders with information on height, d.b.h., volume, specific gravity, and dry weight could combine all of these into a single index to increase gain in dry weight yield. Constructing multiple-trait indexes requires appropriate weighting for each of the traits that determine genetic worth. This means that relative weights had to be assigned to height, d.b.h., volume, and specific gravity, as well as dry weight. These weights reflect the relative importance of each trait in changing dry weight yield. The relative importance of each trait in the index also depends on its heritability and on its genetic correlation with dry weight yield.

It is apparent from Table 4 that efficiencies of selection for dry weight yield can be increased by including information on all traits into a selection index for dry weight yield, as long as dry weight and/or height are given substantial weight in the index. Greatest efficiency was obtained when weight was given to dry weight or when all traits were weighted equally. The least efficient index (49%) resulted when all economic weight was placed on specific gravity because of the relatively low genetic cor-

Table 5. — Gain in dry weight from combined selection on other single traits.

Selection Criterion	↑		Gain in Dry Weight (lb per tree)	Gain in Dry Weight (%)	Efficiency <sup>1/</sup> (%)
	Individual	Family			
Height	0.24677	0.40885	17.9	23	108
D.b.h.	0.09497	0.28079	11.8	15	71
Volume	0.16175	0.37683	14.9	19	90
Specific Gravity	0.80666	0.15652	9.8	13	59
Dry Weight	0.17185	0.37723	16.5	22	100

<sup>1/</sup> Efficiency is the correlated response in dry weight as a % of gain from combined selection using dry weight as the criterion.

Table 6. — Expected gain in dry weight from reduced family selection indexes with different criteria for selection.

Relative Economic Weights <sup>1/</sup> For Traits			Individual			Family			Gain in Dry Weight (lb per tree)	Gain in Dry Weight (%)	Efficiency (%)
Height	D.b.h.	Volume	Height	D.b.h.	Volume	Height	D.b.h.	Volume			
1	1	1	.24954	-1.94743	1.78944	.36605	.65626	.87680	19.4	25	117
1	0	0	.21766	-1.36329	1.12897	.29736	.32179	.50947	19.2	25	116
0	1	0	.00688	-.24863	.28786	.02188	.13331	.15208	18.4	24	111
0	0	1	.02501	-.33552	.37262	.04681	.20117	.21524	19.0	25	115
1	1	0	.22454	-1.61191	1.41683	.31924	.45510	.66155	19.3	25	117

1/ Relative economic weights are for individual values of height, d.b.h., and volume, respectively. No economic weight was assigned to family values included in the indexes.

2/ Efficiency is the correlated response in dry weight as a % of gain from combined selection using dry weight as the criterion.

relation of wood specific gravity and total dry weight of trees (Table 3).

Selection in loblolly pine tree improvement programs often ignores potential gains to be had in dry weight yield by using specific gravity information because of difficulty in deciding on the proper selection criteria, and because determining specific gravity is expensive (JETT and TALBERT 1981). Therefore, selection sometimes has been to increase tree volume even when the desired goal was to increase the dry weight yield of wood. Combined selection just for increased volume in this population would result in a 10% reduction in selection efficiency if dry weight yield was the goal of selection (Table 5). The best method of combined selection based on a single trait would have been to select for increased height. Combined selection for height resulted in a greater expected gain for dry weight than combined selection for dry weight (Table 4). This result arises from the strong genetic correlation between height and dry weight ( $r_g = 0.943$ , Table 3) and the greater heritability for height than for dry weight (0.28 - 0.19). Similar results were reported from the open-pollinated portion of the heritability study (STONECYPHER, *et al.* 1973).

The most cost-efficient form of selection in this situation would be a reduced selection index, where information on the covariance of dry weight with measured traits are included in the genetic ( $\hat{A}$ ) matrix, but only information on measured traits are included in the phenotypic ( $\hat{P}$ ) matrix. (Information on genetic covariance may be known from special studies or from previous generations.)

Efficiencies of reduced selection indexes in improving dry weight yield when different relative economic weights are given to height, d.b.h., and volume are shown in Table 6. The expected response in dry weight is not sensitive to changes in the relative weights given to each trait unless both height and volume are given no weight. The only index with substantially reduced efficiency from the others is the one that assigns all weight to d.b.h.. The most efficient indexes give substantial weight to height. Again, this result reflects the relatively high heritability for height and its high genetic correlation with dry weight. An important result is that selection for dry weight yield with the reduced selection index giving equal weights to height, and d.b.h. is nearly as efficient (117%) as the best index

which includes individual measurements of all characteristics (Efficiency = 120%, Table 4). If dry weight yield is the goal of selection, these analyses indicate that the small gains in efficiency (120% vs. 117%) do not justify measuring specific gravity and estimating dry weight yield.

We are not suggesting that dry weight should be the goal of selection, or that the sole impact of wood specific gravity on product quantity or value is on dry weight yield. Wood specific gravity *per se* has important influences on quality of pulp (BLAIR *et al.* 1976, VAN BUIJTENEN *et al.* 1974) and on the major strength properties of wood (PEARSON and GILMORE 1980). The appropriate weight to give wood specific gravity relative to other traits in an advanced generation loblolly pine tree improvement program can only be determined by knowing the relative impact on product yield of a unit improvement in each trait.

#### Literature Cited

- ARBEZ, M., P. BARADAT, J. P. MAUGE, C. MILLIER, and J. BADIA: Some problems related to use of selection indices in forest tree breeding. Proc. Joint IUFRO Meeting, S.02.04.01-3, Stockholm, pp. 97-116 (1974). — BLAIR, R., B. ZOBEL, R. C. HITCHINGS, and J. B. JETT: Pulp yield and physical properties of young loblolly pine with high density juvenile wood. Applied Polymer Symposium No. 28, p. 435-444 (1976). — BURDON, R. D.: Generalization of multi-trait selection indices using progeny test information from several sites. N. J. For. Sci., vol. 9, No. 2, pp. 145-152 (1979). — CROW, J. F. and MOTOO KIMURA: An Introduction to Genetic Statistics. Harper and Row, New York, N. Y. 591 p. (1970). — FALCONER, D. S.: Introduction To Quantitative Genetics. The Roland Press Co., N. Y., 365 pp. (1960). — HAZEL, L. N. and J. L. LUSH: The efficiency of three methods of selection. J. Hered. (33), pp. 393-399 (1942). — JETT, J. B. and J. T. TALBERT: The place of wood specific gravity in the development of advanced generation seed orchards and breeding programs. S. J. A. F. (In press) (1981). — LIN, C. Y.: Index selection for genetic improvement of quantitative characters. T. A. G., Vol. 52, No. 2, pp. 49-56 (1978). — PEARSON, R. G. and R. C. GILMORE: Effect of fast growth rate on mechanical properties of loblolly pine. Forest Products Journal 30: 47-54 (1980). — SAS Institute, Inc. SAS Users Guide, 1979 Edition, SAS Institute Inc., Cary, N. C. 494 p. (1979). — SMITH, H. F.: A discriminant function for plant selection. Ann. Eugen. (7), pp. 240-250 (1936). — STONECYPHER, R. W., B. J. ZOBEL, and R. BLAIR: Inheritance patterns of loblolly pines from a nonselected natural population. N. Carolina Ag. Exp. Sta., Tech. Bul. No. 220, August, 1973, 60 pp. (1973). — VAN BUIJTENEN, J. P., J. D. ALEXANDER, D. W. EINSFAHR, A. FERRIE, T. HART, R. M. KELLOGG, and B. Z. ZOBEL: Quality control in the forest and in the mill. TAPPI, CA Report No. 54, 96 pp. (1974).