

SELECTION INDICES FOR WOOD QUALITY
IN LOBLOLLY PINE

M. D. Wilcox and H. D. Smith^{1/}

Abstract.--Classical Smith-Hazel linear selection indices were developed to aid in selecting groups of loblolly pine clones with desired combinations of wood characteristics. Mean specific gravity is increased and mean lignin content decreased in an index designed to identify clones with improved kraft pulping properties. Another index, for improving the yield and brightness of mechanical pulps, identifies clones which combine high specific gravity and high brightness. Improvement in the strength and brightness of mechanical pulps is the objective of the third index, favoring clones combining low specific gravity and high brightness. No matter what combination of characteristics is desired, aggregate expected gains from index selection are always greater than from single trait selection.

Within-clone variances for specific gravity, lignin content and brightness are highly heterogeneous. A further index is described which chooses clones such that the total variability (among clones and within clones) of a wood property is minimized. Much better wood uniformity can be achieved by this method than by selecting on means alone.

For multiple trait selection, the two kinds of indices can, in effect, be combined, resulting in an index that not only changes the mean of each wood property in the desired direction but also increases the uniformity of the wood as a raw material for pulping.

Additional keywords: Pinus taeda, clonal selection, selection indices, wood brightness, specific gravity, lignin content, specific light absorption coefficient, improved wood uniformity, improved pulping properties.

^{1/} Graduate students, School of Forest Resources, North Carolina State University, Raleigh, N. C. 27607. (Dr. B. J. Zobel is thanked for making the clones available for this study and for his help with the paper.)

INTRODUCTION

Multiple trait selection is most efficiently handled by some form of selection index which gives optimum weight to each trait. Empirical selection indices have been embodied in numerous tree scoring or grading methods for selecting superior trees (van Buijtenen, 1969). A disadvantage of these arbitrary point systems is that they do not always recognize and properly take into account the genetic characteristics and economic importance of the traits involved, and thus have no optimum properties--in fact, no properties at all other than that they seem "reasonable." Analytical indices derived from measures of variability and covariability and economic importance of traits have the advantage of optimizing the aggregate gain in a number of traits, thus allowing maximum economic returns from the tree breeding program.

The purpose of this paper is to describe the development and application of two kinds of selection indices in clonal selection: one for optimizing the aggregate gain in several wood properties, the other for minimizing the variability of the wood properties. Further, it will be shown that the two types of indices may be combined to select groups of clones having all-round better and more uniform properties. When the proper economic weights are assigned to each trait, and to unit reductions in variability versus unit increases in the means, these selection methods should optimize the economic gain per unit volume of wood from clonal selection.

SMITH-HAZEL LINEAR SELECTION INDICES

Theory

Information pertaining to n traits can be combined in a linear clonal selection index of the form

$$I_i = \sum_j^n b_j P_j \quad (\text{Equation 1})$$

where P_i is the index value for the i^{th} clone. For two traits, as in the examples to be described,

$$I_i = b_1 P_1 + b_2 P_2 \quad (\text{Equation 2})$$

The b_j 's are least squares solutions to a set of equations and are estimated from

$$\underline{\hat{b}} = P^{-1} A S^{-1} \underline{a} \quad (\text{Equation 3})$$

where P is the phenotypic variance-covariance matrix, A is the clonal variance-covariance matrix, S is a diagonal matrix of the phenotypic standard deviations, and \underline{a} is a vector of economic weights. The S matrix is included to weight the economic values by the inverse of the phenotypic standard deviations, freeing the index values of scaling effects due to different units of measurement. If phenotypic and clonal covariances are zero, the matrix $P^{-1}A$ simplifies to a diagonal matrix, H , of the clonal repeatabilities.

The index coefficients (b_j 's) define an optimum index theoretically allowing maximum aggregate gain for the n traits. This is a unique property of the classical Smith-Hazel index. As pointed out by Namkoong (1969), in practice there are two serious problems limiting the usefulness of this kind of selection index. One is that the economic value functions of many traits are unlikely to be linear. The other is that poorly estimated index coefficients, resulting from poorly estimated variance-covariance matrices, are far from optimum and may result in selection indices that do no better (or may even do worse) than arbitrary "common-sense" point systems.

Indices to select clones with improved pulping qualities

Indices were derived from variances and covariances estimated in a study of variation in wood brightness and specific gravity in 37 grafted clones of loblolly pine (*Pinus taeda* L.). The three traits considered were specific gravity, wood brightness and specific light absorption coefficient, which is a good indirect measure of lignin content (Wilcox, 1973).

Index 1 is designed to select clones with improved kraft pulping properties by favoring those which combine high specific gravity and low absorption coefficient (= low lignin content). High juvenile wood specific gravity is the breeding objective emphasized for this trait because of the need to increase the generally poor pulp yields from young wood (Kirk, et al., 1972). Expected benefits are increases in pulp yield per unit volume and per unit dry weight of wood, increases in tear strength (Barefoot, et al., 1970), and possibly reductions in cooking times and chemical consumption in pulping to a given Kappa number.

Index 2 is designed to select clones with a high specific gravity and high brightness. This combination of characteristics is expected to reduce the cost of production of stone-groundwood and refiner mechanical pulp by increasing the yield of pulp per unit volume of wood, by reducing the energy requirement per ton of pulp produced, and by increasing the production rate per stone or per refiner day (Bryant, 1970). Brightness increases may be sufficient to eliminate the need for or reduce the cost of chemical brightening, and to improve the bleachability of high-yield pulps to high brightnesses (Wilcox, 1973).

Index 3 selects clones with improved high-yield pulp (e. g. chemi-groundwood, disk refiner mechanical pulp) qualities by favoring clones combining high brightness and low specific gravity. Pulps from clones having wood with these characteristics will have improved brightness and superior fiber-to-fiber bonding (Smith and Byrd, 1972), giving papers with good printing qualities (improved smoothness, brightness, and perhaps scattering coefficient and opacity) as well as improved burst and tensile strengths. The index could also be used to select clones with improved qualities for the manufacture of printing papers and tissue papers from pine kraft pulp (Fahey, et al., 1968).

The indices are:

Index 1 = $(36.043 \times \text{specific gravity}) - (.1543 \times \text{absorption coefficient})$

Index 2 = $(32.786 \times \text{specific gravity}) + (.464 \times \text{brightness})$

Index 3 = $(-36.598 \times \text{specific gravity}) + (.4223 \times \text{brightness})$

Gains from index selection

In the analyses made here, specific gravity, brightness and absorption coefficient were assigned equal economic weights. This means that equal economic values have been attached to changes of one standard deviation in specific gravity (0.023), brightness (1.36 points) and absorption coefficient ($-4.7 \text{ cm}^2/\text{g}$ --equivalent to a reduction of 0.5% in Klason lignin content of wood). Different selection procedures can therefore be evaluated from comparisons of aggregate realized gains expressed in standard deviation units (Table 1).

Index 1, favoring high specific gravity and low absorption coefficient, gives worthwhile improvement in both wood properties (Table 1). There is effectively no linear correlation between the two traits--in fact, both low and high specific gravities may be associated with high absorption coefficients. Selection solely for low absorption coefficient does not change the specific gravity, and maximum gain in absorption coefficient can be made without an effect on specific gravity. Gains from Index 1 were an increase of 0.027 in specific gravity and a reduction in absorption coefficient of $4.5 \text{ cm}^2/\text{g}$, this latter being approximately equivalent to a reduction in lignin content of 0.5%, from 28.95% to 28.45% (Wilcox, 1973).

The negative correlation between specific gravity and brightness makes it difficult to select clones combining both high specific gravity and high brightness. Selection for either characteristic alone results in a loss in the other. However, selection Index 2 more than doubles the aggregate gain possible from single trait selection (Table 1), showing that it is effective in working against and breaking the unfavorable specific gravity-brightness correlation. Index 1 and Index 2 both select the same group of clones since high brightness is associated with low absorption coefficient.

The negative correlation between specific gravity and brightness is highly advantageous when clones combining low specific gravity and high brightness are desired (Index 3). Selection for either characteristic alone guarantees some improvement in the other; but even here, index selection is worthwhile, resulting in 13% more aggregate gain than from single trait selection (Tables 1 and 2). However, the advantage of this kind of selection index over other methods of multiple trait selection is greatest when the characteristics desired tend to be unfavorably correlated.

If improvement in wood brightness is to be the major thrust in a breeding program for loblolly pine, the realized gain from selecting the best 3 clones out of 37 solely for brightness is 2.3 points, based on the data from 12-year-old grafts (Wilcox, 1973). The best alternative is Index 3 (Table 2) with a gain of 1.9 points. Selection only for low specific gravity produces a correlated gain in brightness of 1.0 point. A gain of one point in wood brightness translates into a saving in groundwood bleaching cost of approximately \$1 per ton of pulp, or \$1 per cord of pulpwood processed. Put another way, a one point gain in wood brightness represents about a \$40-per acre saving to the mill.

Table 1.--Effectiveness of alternative methods of selecting
3 best loblolly pine clones from a total of 37 clones

A. Combining high specific gravity and low lignin content

Selection method	Clones selected	Aggregate gain ^{a/}
Select only for high specific gravity	8-61, 8-49, 8-26	1.101
Select only for low absorption coefficient	8-24, 8-107, 8-83	1.568
Selection Index 1	8-24, 8-49, 8-67	2.137 (36%)

B. Combining high specific gravity and high brightness

Selection method	Clones selected	Aggregate gain
Select only for high specific gravity	8-61, 8-49, 8-26	0.525
Select only for high brightness	8-27, 8-107, 8-44	0.765
Selection Index 2	8-49, 8-67, 8-24	1.632 (113%)

C. Combining low specific gravity and high brightness

Selection method	Clones selected	Aggregate gain
Select only for low specific gravity	8-126, 1-9, 8-27	2.434
Select only for high brightness	8-27, 8-107, 8-44	2.575
Selection Index 3	8-126, 8-27, 8-107	2.968 (13%)

^{a/}Standard deviations. (%) is superiority of index over next best method.

Table 2.--Use of Index 3 to select clones giving maximum aggregate gain in brightness and specific gravity^{a/}

Clone ^{b/}	Rank			Mean		
	Index 3 ^{c/}	SG	Brightness	Index	SG	Brightness (%)
8-126	1	1	13	9.9930	.305	50.11
8-27	2	3	1	9.9869	.329	52.18
8-107	3	4	2	9.7643	.333	52.03
1-77	4	10	5	8.9558	.342	50.84
1-9	5	2	23	8.9539	.322	49.16
8-44	6	14	3	8.8133	.349	51.14
1-60	7	7	15	8.7465	.338	50.03
8-46	8	9	16	8.6598	.340	49.98
8-73	9	5	19	8.5723	.337	49.54
8-134	10	15	9	8.4331	.351	50.44
8-114	11	21	4	8.3776	.359	50.93
8-128	12	18	11	8.3447	.353	50.38
8-50	13	16	14	8.2416	.352	50.05
8-129	14	6	26	8.2299	.337	48.73
8-120	15	8	25	8.2209	.340	48.92
4-19	16	13	21	8.1743	.347	49.41
8-130	17	22	10	8.1439	.359	50.44
8-144	18	12	24	8.0590	.347	49.13
1-25	19	20	17	7.9758	.358	49.92
1-23	20	17	20	7.9534	.353	49.45
8-123	21	27	8	7.8632	.367	50.46
8-37	22	11	31	7.7956	.345	48.37
8-13	23	24	18	7.7662	.364	49.92
8-83	24	30	12	7.5775	.373	50.28
8-67	25	32	6	7.5413	.378	50.65
8-24	26	31	7	7.4872	.378	50.49
8-29	27	19	30	7.4617	.357	48.62
1-68	28	25	29	7.2324	.364	48.65
8-10	29	26	28	7.1845	.365	48.67
8-7	30	23	32	7.1029	.362	48.21
8-5	31	29	27	6.9122	.373	48.68
8-49	32	36	22	6.2560	.398	49.33
8-80	33	34	33	5.8335	.394	47.98
1-16	34	33	36	5.3692	.386	46.19
1-22	35	28	37	5.3187	.370	44.66
8-26	36	35	35	5.2977	.394	46.68
8-61	37	37	34	4.8289	.412	47.14

a/

Low specific gravity and high brightness are the desired wood characteristics in this example.

^{b/}Clones with the prefix 1- belong to Hiwassee Lnd Company (Bowaters Southern Paper Corporation), the clone with prefix 4- to Chesapeake Corporation, and the clones with 8- to Weyerhaeuser Company.

^{c/}Index 3 = (-36.598 x specific gravity) (.4223 x brightness).

An empirical index for maximizing aggregate selection differentials

In the indices previously discussed, clonal and phenotypic covariances were small, clonal repeatabilities were approximately equal, and economic weights of the traits were assumed to be equal. Under these special circumstances, a simple method of approximating the expected Smith-Hazel index rankings is to compute and rank the actual aggregate selection differentials in standard deviations for each clone. Indices of this form are:

$$I_i = \sum_j^m \frac{c_{i(j)}}{\frac{1}{a_j} \sigma_{P_j}} \quad \text{(Equation 4)}$$

where I_i is the aggregate selection differential in standard deviations from selecting the i^{th} clone based on its performance for m traits; $c_{i(j)}$ is the effect (i.e., $\mu - \mu^{\wedge}$) of the i^{th} clone for the j^{th} trait; a_j is the economic weight of the j^{th} trait; and σ_{P_j} is the phenotypic standard deviation of the j^{th} trait.

The I 's for each clone can therefore be calculated from the clone means, the grand means of all the clones, and the phenotypic standard deviations appropriate to the proposed method of selection. Selection involves only ranking the I 's and picking the winners.

An example of this kind of selection index, using the data from the wood brightness study (Wilcox, 1973) is

$$\text{Index 4} = [(SG-.358)/.0232] + [(15.9-SUMM)/4.212] + [(52.956-ABSORP)/4.6656] + [(BRIGHT -49.52)/1.3565] + [(3.438-COMPR)/2.211]$$

Characteristics favored are high specific gravity, low summerwood percent, low absorption coefficient (= low lignin content), high brightness and low percent compression wood. All characteristics have been assigned the same economic weight. Clone 8-67, a loblolly pine from the Coastal Plain of North Carolina, has an unusually favorable combination of characteristics and a high index value (Table 3). It is exceptional in that it has a combination of the lowest summerwood percent of all clones, with the sixth highest specific gravity.

Equation 4 (see above) can be used to compute the approximate expected Smith-Hazel index rankings, against which the rankings based on the corresponding analytical indices can be compared. Very good agreement between expected (i. e., the actual aggregate clone values) rankings and those from the analytical indices were obtained. Ranks for the best 10 clones for each of three combinations of desired characteristics are shown in Table 4. The analytical indices clearly come very close to giving the the expected maximum aggregate gain, showing that the index coefficients are reasonable estimates of the parameters. At the same time, the good agreement between observed and expected ranks (Table 4) indicates that simple empirical indices based on Equation 4 are generally useful for ranking clones when no information is available on the heritabilities and correlations of the traits in question.

Table 3.--Use of Index 4 to identify clones having an optimum combination of wood quality characteristics

Clone ^{a/}	Index 4 ^{b/}	Rank					
		INDEX	SG	SUMM	ABSORP	BRIGHT	COMPR
8-67	4.7112	1	6	1	7	6	8
8-107	4.4669	2	34	5	2	2	2
8-83	4.1313	3	8	12	3	12	3
8-27	3.4515	4	35	4	8	1	6
8-134	3.3892	5	23	11	4	9	1
8-130	3.0453	6	16	15	9	10	5
8-123	2.7213	7	11	14	5	8	18
8-24	2.4614	8	7	32	1	7	20
8-44	1.6358	9	24	19	17	3	12
8-13	1.6344	10	14	25	14	18	11
8-50	1.5030	11	22	28	10	14	7
8-128	1.0437	12	20	26	13	11	16
8-114	0.8812	13	17	35	6	4	19
8-5	0.8663	14	9	30	11	27	10
1-68	0.6654	15	13	13	19	29	9
8-25	0.4095	16	18	6	26	17	22
8-46	0.1237	17	29	21	12	16	23
8-10	0.0965	18	12	29	23	28	4
8-49	-0.1721	19	2	36	16	22	28
1-60	-0.2372	20	31	2	31	15	21
1-23	-0.6550	21	21	18	18	20	29
8-120	-0.7727	22	30	10	21	25	17
8-37	-0.8143	23	27	8	29	31	13
8-29	-0.9373	24	19	16	32	30	15
4-19	-0.9844	25	25	9	25	21	27
8-144	-1.1475	26	26	20	20	24	25
1-77	-1.3137	27	28	24	15	5	36
8-129	-1.5454	28	32	7	27	26	24
8-80	-1.8230	29	4	37	22	33	26
8-126	-2.0677	30	37	23	28	13	14
8-61	-2.1793	31	1	22	35	34	32
8-73	-2.2248	32	33	3	30	19	35
8-7	-3.0280	33	15	34	24	32	30
1-9	-3.6750	34	36	17	33	23	31
8-26	-3.8883	35	3	31	34	35	33
1-16	-4.8966	36	5	28	36	36	34
1-22	-11.4537	37	10	33	37	37	37

^{a/}Clones with the prefix 1- belong to Hiwassee Land Company (Bowaters Southern Paper Corporation), the clone with prefix 4- to Chesapeake Corporation, and the clones with 8- to Weyerhaeuser Company.

^{b/}Aggregate selection differential in standard deviations

Table 4.--Comparison of rankings for clones which actually give maximum aggregate selection differentials with rankings derived from Smith-Hazel analytical selection indices.^{a/}

Clone	Actual Rank	Index 1 Rank	Clone	Actual Rank	Index 2 Rank	Clone	Actual Rank	Index 3 Rank
8-24	1	1	8-67	1	2	8-27	1	2
8-49	2	2	8-49	2	1	8-107	2	3
8-83	3	4	8-24	3	3	8-126	3	1
8-67	4	3	8-83	4	4	1-77	4	4
8-123	5	5	8-123	5	5	8-44	5	6
8-5	6	7	8-114	6	6	1-9	6	5
8-80	7	6	8-44	7	10	1-60	7	7
8-114	8	9	8-107	8	12	8-46	8	8
8-13	9	10	8-130	9	9	8-114	9	11
8-130	10	11	8-27	10	13	8-134	10	10

a/

High specific gravity--low absorption coefficient

Actual aggregate

$$\text{selection differential} = [(SG-.358)/.0232]+[(52.956 - ABSORP)/4.6656]$$

$$\text{Index 1} = (36.043 \times SG)-(.1543 \times ABSORP)$$

High specific gravity--high brightness

Actual aggregate

$$\text{selection differential} = [(SG -.358)/.0232] + [(BRIGHTNESS -49.52)/1.3565]$$

$$\text{Index 2} = (32.786 \times SG) + (.464 \times ABSORP)$$

Low specific gravity--high brightness

Actual aggregate

$$\text{selection differential} = [(.358 - SG)/.0232] + [(BRIGHTNESS - 49.52)/1.3565]$$

$$\text{Index 3} = (-36.598 \times SG) + (.4223 \times BRIGHTNESS)$$

UNIFORMITY INDICES

Variation in uniformity

Heterogeneous within-treatment variances are usually regarded in the context of their role in violating the assumptions underlying the analysis of variance. Thus, rather than accept the fact that some treatments are inherently more uniform than others, experimenters frequently attempt one or more mathematical transformations in an attempt to rescale the data and homogenize the variances. When the objective of an experiment is to rank and compare treatment means, there is naturally some reluctance to loudly advertise the existence of heterogeneous variances since this will cast doubt upon the validity of the numbers in the ANOVA table and on the significance of treatment differences.

The objective in assessing a clonal or progeny test is selection--not to do an analysis of variance. Since variances are as much a property of individual families or clones as are means, their separate calculation and recognition as important family traits are essential to determining the best families. Clonal variation in the uniformity of lignin content in loblolly pine wood is illustrated in Figure 1. Although the means of the two clones are the same, the variances are not, and clone 8-134 is preferred to clone 8-123 because of its greater uniformity.

An F-test is the usual way of establishing whether or not there are important differences among family means. The best known and most powerful of the many available tests that could be used to demonstrate variation among family variances is Bartlett's test (Gartside, 1972),

In our examples, clonal variances comprise two components: within-ramet, and among ramets at one site. The within-ramet variance contributed over 90% of the within-clone variation in wood characters. Within-clone variance can be regarded as a measure of the phenotypic plasticity (as opposed to genotypic stability) of a character (Bradshaw, 1965; Hanson, 1970). A uniform or stable clone produces similar wood year after year, regardless of varying annual environments; in a given season it also produces similar wood in different parts of the bole. Such morphological homeostasis is a desirable clonal characteristic and could be an important selection criterion for certain wood characters such as specific gravity. Another reason for recognizing clonal differences in wood uniformity is that clones with the smallest variances also have the most precise means and therefore the most predictable performances.

Application

Pulp manufacturers usually express a desire for more uniform wood. Reduced variability may be just as economically important as changes in the mean for certain wood properties such as lignin content and latewood percent. In kraft pulping, wide variation in lignin content (see Figure 1) of the raw material results in inefficient pulping: some of the wood is undercooked and some overcooked. Under given cooking conditions, variation in wood lignin content results in variation in pulp Kappa number. Thus, it becomes difficult to produce high-yield or "hard" pulp since that proportion of the wood with the highest lignin content will be undercooked, resulting in skives. Likewise the bleachability of "soft" or low Kappa kraft pulps will be reduced because some of the wood will have been cooked to a higher Kappa number than desired. Variation in latewood percent and specific gravity may have similar detrimental effects due to the variability in the accessibility of the pulping chemicals to the lignin. Therefore, improved wood uniformity will increase pulp yields, reduce pulping costs, and improve the uniformity of the product, thus improving economic returns.

Theory

In the application of the concept of variation in phenotypic uniformity to clonal selection it must be recognized that the total variability of a wood trait stems from two sources: variation among the clones in the select group, and the average within-clone variation. Equal importance is attached to both sources of variation in the following index procedure proposed as an aid to selection for uniformity.

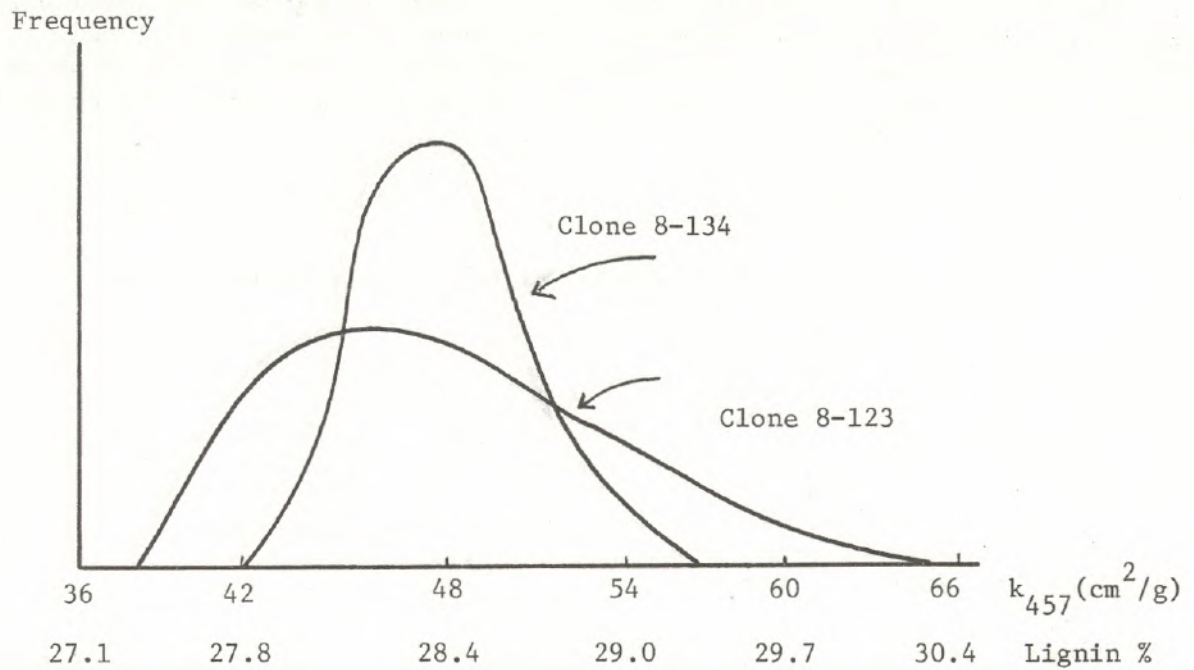


Figure 1.--Variation in the uniformity of lignin content in two loblolly pine clones (12-year-old grafts)^{a/}

a/ Statistics of the two clones

A. Absorption coefficient (cm²/g)

Clone	Mean	Variance	Range
8-134	47.7	13.0	43.3 - 55.2
8-123	47.8	63.9	37.7 - 66.2

B. Lignin content (% of wood dry weight)

Clone	Mean	Range
8-134	28.4	27.9 - 29.2
8-123	28.4	27.3 - 30.4

The objective is to select a group of n clones such that the total variability of a given trait is minimized. Individual clone means ($\hat{\mu}_i$) and within-clone variances ($\hat{\sigma}_w^2$) must first be estimated. The uniformity index, J , of a select group of i clones from the array is the quantity to be minimized. It is the total variance,

$$J = \sigma_A^2 + \sigma_W^2 \quad (\text{Equation 5})$$

where σ_A^2 = the among-clone variance of the select group

$$\begin{aligned} &= \frac{\sum_i^n (\hat{\mu} - \hat{\mu}_i)^2}{n - 1} \\ &= \frac{\sum_i^n c_i^2}{n - 1} \end{aligned} \quad (\text{Equation 6})$$

and σ_W^2 = the average with-clone variance of the select group

$$\begin{aligned} &= \frac{\sum_i^n \hat{\sigma}_{wi}^2}{n} \end{aligned} \quad (\text{Equation 7})$$

$$\text{with } df_W = \sum_i^n df_i$$

[$\hat{\mu}_i$ = the mean of the i^{th} clone, c_i = the effect of the i^{th} clone ($i = 1, 2, \dots, N$), $\hat{\sigma}_{wi}^2$ = variance of the i^{th} clone, $\hat{\mu}$ = the mean of the select group]

Since J is the sum of two mean squares, i. e.,

$$J = \text{MSA} + \text{MSW},$$

its degrees of freedom can be calculated using Satterthwaite's procedure:

$$df(J) = \frac{[\text{MSA} + \text{MSW}]^2}{\left[\frac{\text{MSA}^2}{df_A} + \frac{\text{MSW}^2}{df_W} \right]} \quad (\text{Equation 8})$$

A computer program (see Appendix) was written to compute and rank J for all possible groups of n clones from an array of N clones. In our examples, $n=3$ and $N=37$ or 10 , with $df(J)$ averaging 60. The total number of combinations of size n from an array of size N is

$$C = \frac{N(N-1)\dots(N-n+1)}{n!} \quad (\text{Equation 9})$$

For example, for groups of size 3 from an array of 37 clones, there are

$$C = \frac{37 \times 36 \times 35}{6} = 7770 \text{ combinations.}$$

To test whether one clone group is more variable than another, an F statistic can be calculated from the ratio of the larger J over the smaller J and compared to F_{1-a} . In addition, the ranked variances can be ordered into distinct groups using a multiple range test based on the maximum F-ratio test (Tietjen and Beckman, 1972).

Examples

(1) Unrestricted uniformity index--absorption coefficient

In this example the sole objective is to minimize J, the variability of absorption coefficient, as a measure of wood lignin content; no account is taken of average performance. Any gain in the mean will therefore result only from a favorable correlation between absorption coefficient means and variances.

From the array of 37 clones the group of 3 having the minimum J was

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Clone   :      8-107      8-134      8-83
Variance:    14-65      13.01      24.80
Mean:     46.12      47.66      47.43
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Index J = 18.1761
Group mean, absorption coefficient = 47.07 cm² /g
Group mean, lignin content = 28.31%
Range of J for all 7770 combinations of 3 clones
= 18.1761 to 516.4746 (this represents a 28-fold
difference in wood uniformity between the most
uniform and least uniform groups).

The above group of clones is significantly more uniform than the group (8-24, 8-107, 8-83) selected only to maximize mean performance (F = 3.027**).

(2) Unrestricted uniformity index--specific gravity

With the objective of again only minimizing J, the most uniform group of clones is

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Clone:      8-134      8-128      8-44
Variance:   .000194   .000171   .000267
Mean:       .351      .353      .349

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Index J = .000215
Group mean = .351
Range of J for all 7770 combination of 3 clones
= .000215 to .018798 (this represents an 87-fold
difference in wood uniformity between the most
uniform and least uniform groups).

The above group of clones is significantly more uniform than the group (8-61, 8-49, 8-26) with the highest mean specific gravity ($F = 20.379^{**}$), or the group (8-126, 1-9, 8-27) with the lowest specific gravity ($F = 2.338^{**}$).

If there is doubt as to whether high or low specific gravity is the desired pulpwood characteristic, then a strategy which will always result in some improvement in wood quality is to select only to maximize uniformity. Especially for wood lignin content it is felt that this strategy will pay greater economic dividends than the maximin approach suggested by Namkoong (1969).

Although the examples used to illustrate the technique involved wood properties only, the uniformity index procedure should also have application wherever differences in "within-family" or "within-seed source" variability are apparent. For example, one has only to walk through an open-pollinated progeny test to be aware of sometimes striking family differences in diameter variability.

JOINT SELECTION FOR HIGH MEANS AND LOW VARIANCES

In many situations, reducing the variability of performance and increasing the average performance of a quantitative character should be dual objectives of selection. One way of insuring simultaneous improvement in mean and reduction in variance is to restrict the application of the uniformity index (J) to the clones with the best average performances. The top group of clones can be determined arbitrarily (e. the top 10) or from a multiple comparison procedure such as Duncan's range test.

From the 10 clones having the lowest absorption coefficients, the same group of clones (8-107, 8-83, 8-134) is selected by this procedure as was selected by the unrestricted uniformity index (Table 5). This correspondence results from the clonal absorption coefficients means and variances being strongly and positively correlated ($r = 0.70^{**}$) and is not a general outcome of this selection procedure. Since the correlation between means and variances for specific gravity is weak ($r = 0.34^*$), a completely different set of clones (8-5, 8-24 and 8-67) is selected for uniformity from among the top 10 as was selected from among all 37 clones (8-134, 8-128 and 8-44).

A joint index of aggregate gain

An alternative method of jointly selecting for means and variances is to use an index combining measures of both variability and mean performance. If it is assumed that a unit reduction in the phenotypic standard deviation is as valuable as a unit increase (or decrease) in the mean, the aggregate gain in value of a trait j from selecting the kth clone group can be expressed as

$$\Delta G_j(k) = \sqrt{J_o - J_k} + (|\hat{\mu}_o - \hat{\mu}_k|) \quad (\text{Equation 10})$$

where J is the uniformity index of the unselected array of clones; J_k is the uniformity index of the k^{th} selected group of clones; and $\hat{\mu}_o$ is an estimate of the grand mean of the unselected array of clones; and $\hat{\mu}_k$ is the mean of the k^{th} selected group. Finding the group of clones giving the maximum change in G

thus becomes the logical objective of single trait selection. Examples in Table 5 show that AG for absorption coefficient is maximized by selecting clones 8-107, 8-83 and 8-134--the same group selected previously. However, the group selected for specific gravity contains clones not previously selected by any other method.

Table 5.--Aggregate gains from four different methods of jointly selecting for means and variances

Combining low and uniform lignin content (as estimated from light absorption coefficient)

Selection method	Clones selected	μ_k	J_k	$\Delta G^{a/}$
Select only for lowest means	8-24, 8-107, 8-83	46.20	55.02	16.38
Select only for the lowest variances(J)	8-107, 8-134, 8-83	47.07	18.18	17.27
Select only for the lowest variances(J) among the top 10 clones	8-107, 8-134, 8-83	47.07	18.18	17.27
Select to maximize ΔG	8-107, 8-83, 8-134	47.07	18.18	17.27

$\frac{a/}{\mu_k}$ = select group mean ($\mu_o = 52.96 \text{ cm}^2/\text{g}$); J_k = select group variance ($J_o = 147.59$); ΔG = gain (cm^2/g)

B. Combining high and uniform specific gravity

Selection method	Clones selected	μ_k	J_k	$\Delta G^{b/}$
Select only for highest means	8-61, 8-49, 8-26	.401	.00438	-.0144
Select only for the lowest variances(J)	8-134, 8-128, 8-44	.351	.00021	.0225
Select only for the lowest variances(J) among the top 10 clones	8-5, 8-24, 8-67	.376	.00044	.0433
Select to maximize ΔG	1-16, 8-80, 8-26	.391	.00050	.0570

$\frac{b/}{\mu_k}$ = select group mean ($\mu_o = .358$); J_k = select group variance ($J_o = .00108$); ΔG = gain.

Joint multiple trait selection for means and variances

There now remains the extension of the multiple trait index concept to include selection for uniformity as well as for aggregate gain in means. The ultimate index is one which gives the maximum aggregate gain in total merit for several traits, jointly with dual selection for means and variances.

By direct amalgamation of Equations 4 and 10, the aggregate selection differential in uniformity and average performance of several traits can be found from:

$$\begin{aligned} \Delta g_k &= \sum_j^m \left\{ \frac{\sqrt{J_o - J_k} + (|\hat{\mu}_o - \hat{\mu}_k|)}{\frac{1}{a_j} \sigma_{P_j}} \right\} \\ &= \sum_j^m \left(\frac{\Delta G_{j(k)}}{\sigma_{P_j}} \right) \\ &= \sum_j^m \Delta g_{j(k)} \end{aligned} \quad \text{(Equation 11)}$$

where

- Δg_k = aggregate gain in value for the k^{th} clone group, based on m traits.
- J_o = the uniformity index of the unselected array of clones for the j^{th} trait.
- J_k = the uniformity index of the k^{th} selected group of clones for the j^{th} trait.
- μ_o = the grand mean of the unselected array of clones for the j^{th} trait.
- $\hat{\mu}_k$ = the mean of the k^{th} selected group of clones for the j^{th} trait.
- σ_{P_j} = the phenotypic standard deviation of the j^{th} trait.
- a_j = the economic weight of the j^{th} trait.

For the combined desired characteristics of high specific gravity and low lignin content, and maximum uniformity in each of these wood properties, the clone group giving the maximum Δg was 8-5, 8-83 and 8-67 (Table 6) with a gain of 5.131 standard deviations. Another possible way of finding the group of clones which maximize the gain is to compute and rank J for the top 10 clones for Index 1. The gain, Δg , by this method is 4.8402 standard

Table 6.--Three alternative methods of selecting the group of clones giving maximum aggregate gain in average performance and uniformity of several traits

A. Combining high and uniform specific gravity with low and uniform lignin content

Selection method	Clones selected	Index 1		change in $g^{b/}$	
		Mean	J_k		
Select the top 3 clones using Index 1	8-24, 8-49, 8-67	6.3988	4.6551	1.0873	3.1626
Select only for the lowest variance (J) from among the top 10 clones, using Index 1.	8-5, 8-123, 8-67	5.9435	1.7829	2.8039	4.8402
Select to maximize change in G	8-5, 8-83, 8-67	6.0290	1.9593	2.8330	5.1310

B. Combining high and uniform specific gravity with high and uniform brightness

Selection method	Clones selected	Index 2		AG	Ag
		Mean	J_k		
Select the top 3 clones using Index 2	8-49, 8-67, 8-24	35.8881	3.0044	0.5205	2.3454
Select only for the lowest variance (J) from among the top 10 clones, using Index 2	8-44, 8-130, 8-67	35.4248	1.2444	1.8909	4.1039
Select to maximize change in G	8-130, 8-83, 8-67	35.5509	1.2570	2.0113	4.44907

C. Combining low and uniform specific gravity with high and uniform brightness

Selection method	Clones selected	Index 3		AG	Ag
		Mean	J_k		
Select the top 3 clones using Index 3	8-126, 8-27, 8-107	9.9147	1.6012	4.0266	6.5184
Select only for the lowest variance (J) from among the top 10 clones using Index 3	8-126, 8-27, 8-107	9.9147	1.6012	4.0266	6.5184
Select to maximize AG	8-126, 8-27, 8-107	9.9147	1.6012	4.0266	6.5194

^{a/} change in G = aggregate gain in value of Index based on Equation 10, and expressed in Index units

^{b/} change in g = aggregate selection differential based on Equation 11, and expressed in standard deviation units

deviations, which is short of maximum possible gain from Equation 11. Equation 11 is also better than ranking J for the top 10 clones based on Index 2 when high specific gravity and high brightness, and maximum uniformity, are desired (Table 6). In contrast to these two cases, selection combining low and uniform specific gravity with high and uniform brightness is equally effective by any of three methods (Table 6).

A separate program was not found necessary for finding the clone groups which maximize Ag. The best clone groups for Ag ranked fifth out of 120 for Index 1, second out of 120 for Index 2, and first out of 120 for Index 3, and it was therefore easy to detect the best groups by inspection or with the aid of some simple hand calculations.

SUMMARY AND CONCLUSIONS

Three main ideas regarding multiple trait selection have been discussed in this paper.

(1) Maximum aggregate gain in economic value of pulpwood from selecting simultaneously for several characteristics can be accomplished using linear selection indices. In the traditional Smith-Hazel linear index, superiority in one trait can compensate for mediocrity in another. This type of index is particularly valuable in identifying the best aggregate genotypes when selection is for pairs of desired characteristics not often associated with each other--such as high specific gravity and low wood brightness, or high specific gravity and low summerwood percent.

(2) Increased morphological and chemical uniformity. Greater uniformity in wood specific gravity, for example, might be preferable to either very high or very low genotypic values on account of the yield-quality conflicts in pulping. In selection for better wood uniformity from a group of clones, the means and variances of the numerous possible combinations of different clones, as well as the means and variances of individual clones, have to be reckoned with. Group selection rather than individual clone selection is necessary to obtain maximum aggregate improvement in phenotypic uniformity and mean value. For illustration, in the examples considered, a reduction of one standard deviation in the total phenotypic variability was considered equally valuable as a gain of one standard deviation unit in the mean. A restricted uniformity selection index is illustrated which identifies the most uniform group of clones from candidates whose means exceed some specified value.

(3) Joint multiple trait selection for maximum aggregate gain in genotypic value and improved uniformity can be accomplished using an index procedure which gives appropriate weights to each trait for mean value and uniformity.

