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Genotype by environment interaction for index traits that combine growth and wood density in loblolly pine

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Abstract Genotype × environment interactions of individual traits have been assessed in numerous experiments with forest trees. However, since breeding programs rarely aim at the improvement of a single trait, the impact of G × E on index or composite traits must also be assessed. In a study with 12-year-old loblolly pine families in the southeastern U.S., G × E variance was of relatively little importance compared to genetic variance for wood density but was of greater significance for several growth traits. An index that combined stem volume and wood density to improve dry weight but maintain wood density constant (restricted selection index) resulted in substantially greater G × E variance compared to either of the component traits. The interaction variance of an index trait is shown to be a function of the index coefficients and the G × E variances and covariances for its constituent traits. As a result, for some conditions it surpasses the magnitude of G × E variance for each component trait.

Key words Gain · K-statistic · *Pinus taeda* L. · Selection index · Stability · Tree improvement

Introduction

Studies of genotype × environment interaction (G × E) in loblolly pine (*Pinus taeda* L.) have been carried out for several traits of interest to breeding programs. Generally G × E has been of little practical significance for most traits. For growth traits, Yeiser et al. (1981), Li and McKeand (1989), and McKeand et al. (1990) reported limited importance of G × E even for material originating from widely different sources and site conditions. The G × E interaction for wood specific gravity was found to be of still less importance across a broad range of sites in both the western and eastern parts of the range of loblolly pine (Byram and Lowe 1988, Jett et al. 1991).

One way to evaluate the importance of G × E is to compare its variance to the genetic variance. The ratio of the genotype × environmental variance over the genetic variance may be referred to as the K-statistic. This is a particularly meaningful measure of genotype-by-environment interaction when the environments investigated are considered to be a random sample from a larger set. For this case, the K-statistic may be interpreted as the proportional amount by which the expected genetic variance within environments is greater than the genetic variance measured over environments. Such an interpretation follows from theory developed by Yamada (1962) and Cockerham (1963) which implies that the genotype × environment interaction variance can be expressed as:

$$\sigma^2_{\mathrm{GE}} = \mathrm{E}[\sigma^2_{\mathrm{g}}] - \sigma^2_{\mathrm{G}}$$

where $\mathrm{E}[\sigma^2_{\mathrm{g}}]$ indicates expectation over environments of genetic variance within environments, and σ^2_{G} represents genetic variance determined over environments.

The K-statistic varies inversely with the intraclass correlation, t,

$$\mathrm{t} = \sigma^2_{\mathrm{G}}/(\sigma^2_{\mathrm{G}} + \sigma^2_{\mathrm{GE}})$$

described by Dickerson (1962) and Yamada (1962). This intraclass correlation is sometimes used as a lower bound for the expected genetic correlation for a trait measured on relatives in two different environments (e.g. the type-B genetic correlation of Burdon 1977).

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The functional relationship between these two measures is: $K = (1 - t)/t$.

Values for the K-statistic for the growth traits analyzed by Li and McKeand (1989) increased in the sequence: height – stem volume – breast height diameter (dbh), but were never larger than 0.35. Extremely low values for the K-statistics were observed for wood specific gravity (Byram and Lowe 1988, Jett et al 1991). Breeding, however, rarely aims at the improvement of a single trait, so it may be asked whether a composite trait or index will also have limited G × E effects. Namkoong (1985) showed that the extension of the results of G × E interaction for two individual traits to a composite trait is not simply a matter of pooling the estimates for the individual traits. For a pair of provenance test plantations of *Pinus caribaea*, he found that rank changes occurred across environments for a composite trait even though provenances did not change ranks for the individual traits. In a later paper by Namkoong and Johnson (1987), these results were extended to include variation in value functions for the component traits that were associated with the environment. Depending on the value given to each component, different provenances obtained the first rank. Besides these two papers we are not aware of any other comparisons of genotype × environment interaction for a composite trait and its components.

Since improvement of both growth and wood density is of high priority in the breeding of loblolly pine, information about performance over a series of test environments is needed for composite traits that incorporate volume and wood density. The purpose of this paper is to evaluate the magnitude of genotype × environment interaction of volume and wood density and for selection indices composed of these two traits. Analyses were carried out using data collected from a series of open-pollinated progeny test plantations in the southeastern U.S.

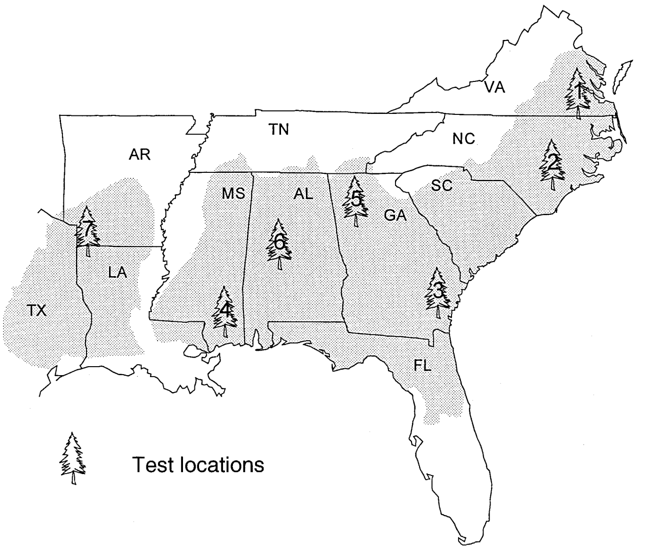

Fig. 1 Location of the seven tests used in the G × E analyses. The *shaded* area is the natural range of loblolly pine in the southeastern US. *VA* Virginia, *AR* Arkansas, *TN* Tennessee, *NC* North Carolina, *TX* Texas, *LA* Louisiana, *MS* Mississippi, *AL* Alabama, *GA* Georgia, *SC* South Carolina, *FL* Florida

Table 1 Trait means at each test location (*dbh* breast height diameters)

Test location[a]	Height (m)	dbh (cm)	Volume (m^3)	Wood Density (kg/m^3)
1-Coastal VA	10.1	17.4	0.088	409.7
2-Coastal NC	12.9	19.1	0.138	423.8
3-Coastal GA	14.3	16.9	0.118	464.3
4-Coastal MS	13.4	17.8	0.123	431.4
5-Piedmont GA	10.0	14.6	0.063	417.6
6-Piedmont AL	10.5	15.2	0.072	417.8
7-Mountain AR	12.6	17.6	0.113	417.8

[a] See Fig. 1 for observations

Materials and methods

Seven open-pollinated progeny tests with loblolly pine were established in 1975 by members of the North Carolina State University-Industry Cooperative Tree Improvement Program (see Li and McKeand 1989 and Jett et al. 1991 for details). The number of families in each test varied between 30 and 50 with 18 common to most of the seven test plantations. These 18 families were included in our analysis. They are progeny from mother trees that were used in breeding programs in the Piedmont and Coastal Plain provinces in the southeastern United States.

The seven, 12-year-old plantings utilized in this study were chosen to provide a north-south and east-west distribution (Fig. 1 and Table 1) that spanned most of the range of loblolly pine. The experimental design (randomized complete block) at each of the sites varied slightly. Either 20 or 21 trees were sampled from each family at each site (3–4 trees per family in five or seven blocks at each test site). Stem height and breast height (1.4 m) diameter (dbh) were measured at age 12 on the same trees used for wood density estimates. Volume was estimated using the formula of Goebel and Warner (1966). Breast height core samples (5 mm) were taken from bark to bark on dominant or co-dominant trees. Increment cores were divided at the pith, and wood specific gravity (unextracted) was estimated for each half core on an oven dry weight–green volume basis (Zobel and Talbert 1984). The average of the half-core pair was used to represent the wood density at breast height. Means for these traits at each location are presented in Table 1.

Genetic variance and covariance components were estimated for individual traits and pairs of traits using the VARCOMP procedure of SAS (SAS Institute 1989). Both restricted maximum likelihood (REML) and Type-1 estimation procedures were used to obtain variances, and both gave essentially equivalent results. The form of the analysis used is given in Table 2. Variance component estimates were used to compute the K-statistic for each trait as: $\hat{K} = \sigma^2_{TF}/\hat{\sigma}^2_{F}$. Individual tree heritabilities were estimated as:

$$\hat{h}_i^2 = \frac{4\hat{\sigma}_F^2}{\hat{\sigma}^2 + \hat{\sigma}^2_{BF(T)} + \hat{\sigma}^2_{TF} + \hat{\sigma}^2_F} \qquad (1)$$

See Table 2 for definition of terms.

Table 2 Form of the analysis of variance on an individual tree basis and variance components for traits. All effects were significant at $P \leqslant 0.01$

Source	*df*	Expected mean squares[a]	Variance component estimates			
			Height	dbh	Volume (var. × 10^6)	Wood density
Test	6	$\sigma^2 + 3.7\sigma^2_{BF(T)} + 19.7\sigma^2_{TF} + 62.7\sigma^2_{B(T)} + 340.0\sigma^2_T$	2.994	2.275	777.45	321.61
Block (T)	32	$\sigma^2 + 3.6\sigma^2_{BF(T)} + 60.7\sigma^2_{B(T)}$	0.084	0.106	22.10	23.62
Family	17	$\sigma^2 + 3.7\sigma^2_{BF(T)} + 19.7\sigma^2_{TF} + 131.8\sigma^2_F$	0.089	0.153	54.08	74.24
T × F	97	$\sigma^2 + 3.7\sigma^2_{BF(T)} + 19.6\sigma^2_{TF}$	0.052	0.200	51.34	9.91
B × F (T)	514	$\sigma^2 + 3.5\sigma^2_{BF(T)}$	0.165	0.673	154.19	44.11
Within plot	1713	σ^2	0.535	3.076	612.97	538.77
Total (corr)	2379					

[a] Where: σ^2 = within-plot variance; $\sigma^2_{BF(T)}$ = plot-to-plot variance within tests; σ^2_{TF} = test-by-family variance; σ^2_F = family variance; $\sigma^2_{B(T)}$ = block-within-test variance; σ^2_T = test variance

The genetic correlation between traits was estimated as:

$$\hat{r}_{G(a,b)} = \hat{\sigma}_{F(a,b)}/(\hat{\sigma}^2_{F(a)}\,\sigma^2_{F(b)})^{0.5}$$

where $\hat{\sigma}_{F(a,b)}$ represents the estimate for the family covariance between traits a and b, and $\hat{\sigma}^2_{F(a)}$ and $\hat{\sigma}^2_{F(b)}$ represent estimates of family variances for traits a and b, respectively. We used $\hat{\sigma}_{F(a,b)} = (\hat{\sigma}_{F(a+b)} - \hat{\sigma}^2_{F(a)} - \sigma^2_{F(b)})/2$, to estimate the family covariance between traits a and b. Here, $\hat{\sigma}_{F(a+b)}$ indicates the estimate for the family variance for the sum of traits a and b. Standard errors for heritability and genetic correlation estimates were computed using methods of Becker (1984) and Falconer (1989), respectively.

Stem dry weight was estimated as the product of volume (m^3) and wood density (kg/m^3) measured at breast height. No effort was made to sample wood density throughout the stem to obtain a whole-tree dry weight estimate. However, there is a very high correlation between wood density at breast height and whole-tree wood densities (Zobel and van Buijtenen 1989).

To evaluate how G × E might change depending upon the type of selection index being used, we constructed several selection indices. Two individual-tree selection indices were constructed for stem dry weight as the goal, utilizing stem volume and wood density as criteria or component traits and for stem volume using height and dbh as criteria (see Baker 1986 for details on selection indices). Using the variances and covariances of different traits, we construct the optimum index for dry weight (Index 1), and the index weights were calculated as:

$$b = p^{-1}a$$

$$= \begin{pmatrix} \hat{b}_V \\ \hat{b}_D \end{pmatrix} = \begin{pmatrix} \hat{\sigma}^2_{P(V)} & \hat{\sigma}_{P(V,D)} \\ \hat{\sigma}_{P(V,D)} & \hat{\sigma}^2_{P(D)} \end{pmatrix}^{-1} \begin{pmatrix} \hat{\sigma}_{A(V,DW)} \\ \hat{\sigma}_{A(D,DW)} \end{pmatrix}$$

where, $\hat{b}_V$ = index weight for volume
$\hat{b}_D$ = index weight for density
$\hat{\sigma}^2_{P(V)}$ = phenotypic variance for volume
$\hat{\sigma}^2_{P(D)}$ = phenotypic variance for density
$\hat{\sigma}_{P(V,D)}$ = phenotypic covariance for volume and density
$\hat{\sigma}_{A(V,DW)}$ = additive genetic covariance for volume and dry weight
$\hat{\sigma}_{A(D,DW)}$ = additive genetic covariance for density and dry weight.

The optimum index that maximized response in dry weight resulted in a negative-correlated response in wood density (due to the negative genetic correlation between dry weight and wood density). A restricted index (Baker 1986) was employed that gave weights to volume and density that resulted in an expected increased dry weight but no change in wood density (Index 2). To illustrate the impact of G × E on an index when component traits are positively correlated, we constructed an optimum index for volume as the goal using height and dbh as criteria (Index 3). Analyses of variance and covariance were conducted on these index traits and the component traits to estimate genetic and genotype-by-environmental components of variance and covariance.

To determine which families contributed to the G × E interaction sums of squares, Wricke's (1962) ecovalence ($\hat{w}_i$) and Shukla's (1972) "stability variance" ($\hat{\sigma}^2_i$) were estimated for each family. The G × E variance was partitioned into 18 components (ecovalences), 1 corresponding to each family. The stability variance of the i^th^ genotype ($\hat{\sigma}^2_i$) is the sum of the within environmental variance ($\hat{\sigma}^2_0$) and the between-environmental variance ($\hat{\sigma}'^2_i$). If a family's estimate of $\hat{\sigma}'^2_i = 0$, then that family is considered stable (Shukla 1972). The significance of each family's ecovalence was tested using Shukla's test for significance of $\hat{\sigma}^2_i$ values, since $\hat{\sigma}^2_i$ is a linear function of the $\hat{w}_i$ (Kang and Miller 1984). In these analyses, values for the five missing cells in the matrix of family and test means were calculated using the marginal effects.

The final measure used to determine the effect of G × E interaction in this population of trees was the loss of potential gain from mass selection (C_I) if the G × E is ignored (Matheson and Raymond 1984). This C_I value compares the phenotypic standard deviation ($\hat{\sigma}_P$) with and without the interaction component included:

$$\hat{C}_I = 1 - \frac{\hat{\sigma}_P \text{ without interaction}}{\hat{\sigma}_P \text{ with interaction}}$$

$$= 1 - \frac{(\hat{\sigma}^2_F + \hat{\sigma}^2_{BF(T)})^{0.5}}{(\hat{\sigma}^2_F + \hat{\sigma}^2_{BF(T)} + \hat{\sigma}^2_{TF})^{0.5}} \qquad (2)$$

Terms in Eq. 2 are defined in Table 2.

The K-statistics for a linear index may be expressed in terms of the K-statistics for its constituent traits. For pairs of traits with non-zero genetic covariances, we introduce an additional statistic of the K type, defined in terms of covariances,

$$K_{ij} = Cov_{GE}(X_iX_j)/Cov_G(X_iX_j)$$

where $Cov_{GE}(X_iX_j)$ and $Cov_G(X_iX_j)$ indicate the genotype × environment interaction and the genetic components of covariance, respectively, for the i^th^ and j^th^ traits. This joint K-statistic differs from the single-trait K-statistic in that it can take on negative as well as positive values, and its interpretation in terms of proportional differences involves covariances rather than variances.

If the value for a composite trait is represented as a linear two-trait index

$$I = b_1X_1 + b_2X_2,$$

where the X_i represents value for the individual traits and the b_i represent the index coefficients, the K-statistic for the index or component trait (K_I) may be written as

$$K_I = \frac{V_{GE}(I)}{V_G(I)}$$

$$= \frac{b_1^2 V_{GE}(X_1) + b_2^2 V_{GE}(X_2) + 2b_1 b_2 \mathrm{Cov}_{GE}(X_1 X_2)}{b_1^2 V_G(X_1) + b_2^2 V_G(X_2) + 2b_1 b_2 \mathrm{Cov}_G(X_1 X_2)} \tag{3}$$

where $V_{GE}(X_i)$ and $V_G(X_i)$ represent the genotype X environment and genetic variance components for the i^{th} trait. Letting K_i indicate the K-statistic for the i^{th} trait ($i = 1, 2$) and making substitutions based on the definition of the various K-statistics produces

$$K_I = \frac{b_1^2 V_G(X_1)}{V_G(I)} K_1 + \frac{b_2^2 V_G(X_2)}{V_G(I)} K_2 + \frac{2b_1 b_2 \mathrm{Cov}_G(X_1 X_2)}{V_G(I)} K_{12} \tag{4}$$

when $\mathrm{Cov}_G(X_1 X_2) \neq 0$. In this form, K_I is a linear combination of the joint K-statistic and the K-statistics for the component traits. For the special situation in which $\mathrm{Cov}_G(X_1 X_2)$ is exactly zero, K_{12} is not defined, and K_I cannot be written in the form shown in Eq. 4. It then must be expressed in terms of the K_i's as

$$K_I = \frac{b_1^2 V_G(X_1)}{V_G(I)} K_1 + \frac{b_2^2 V_G(X_2)}{V_G(I)} K_2 + \frac{2b_1 b_2 \mathrm{Cov}_{GE}(X_1 X_2)}{V_G(I)}$$

Estimates of joint, single-trait, and index-trait K-statistics were obtained by taking ratios of estimates of the family and test X family variance and covariance components.

To determine the sensitivity of the K_I estimate to different index weights in the restricted index for dry weight (Index 2) and the optimum index for volume (Index 3), the index weights were varied and K_I values calculated. For the restricted index for dry weight (Eq. 6), $\hat{b}_V = 2464.2$ and $\hat{b}_D = 1$, so $\hat{b}_V$ was varied from 1000 to 4000. Similarly, for the optimum index for volume (Eq. 7), $\hat{b}_H = 0.0086503$, $\hat{b}_{dbh} = 0.0008065$ so the ratio of $\hat{b}_H : \hat{b}_{dbh}$ was varied from $2\hat{b}_H : \hat{b}_{dbh}$ to $\hat{b}_H : 2\hat{b}_{dbh}$.

Results and discussion

Genetic variances and covariances

There were highly significant family effects for the individual traits (Table 2). The estimates of heritability (Table 3) for height and wood density were moderately high. While the estimate of heritability for wood density is in line with other estimates (Zobel and van Buijtenen 1989), the estimates for growth traits, especially for height and volume, are higher than commonly found. This is probably due to inflated estimates of genetic variance due to the wide geographic origin of the different families (Table 4). The large geographic variation for growth traits of loblolly pine (e.g. Kraus et al. 1984) is confounded with the family differences.

Genetic variances for all of the indices were generally large and of the same magnitude as for the component traits (i.e., similar heritabilities) (Table 3). Heritabilities for the indices ranged between 0.17 for the restricted index for dry weight and 0.41 for the optimum index for volume. Heritabilities for the component traits ranged between 0.15 for dbh to 0.45 for wood density.

Table 3 Estimates of individual tree heritabilities and the standard errors (in parenthesis) for height, breast height diameter, volume, wood density, and selection indices

Trait or index	$\hat{h}_i^2$ (SE)
Height	0.42 (0.14)
Breast height diameter	0.15 (0.06)
Stem volume	0.25 (0.09)
Wood density	0.45 (0.14)
Optimum index – dry wt.	0.36 (0.12)
Restr. index – dry wt.	0.17 (0.07)
Optimum index – volume	0.41 (0.13)

Table 4 Origin of families and ecovalences (expressed as a percentage of the G × E sums of squares) for each family for different traits. Significance of ecovalences was determined by testing the significance of Shukla's (1972) stability variance statistics ($\hat{\sigma}_i^2$) [see Kang and Miller (1984) for discussion of significance testing]

Family	Origin[a]	Ecovalence (%)		
		Volume	Wood density	Restricted index for dry weight
2-8	C, VA	3.3	16.6**	6.4$^+$
2-40	C, VA	2.7	5.5	2.0
3-7	P, NC	4.1	3.5	3.6
4-6	C, VA	10.0**	2.9	7.9*
4-18	C, VA	5.4	1.9	4.5
6-9	P, NC	5.6	5.2	5.8$^+$
6-20	P, NC	2.0	4.6	1.6
7-56	C, SC	20.2**	3.5	19.7**
8-1	C, NC	4.9	11.0*	5.9$^+$
8-59	C, NC	6.8$^+$	10.0*	7.8*
8-61	C, NC	1.8	6.0	1.7
8-68	C, NC	5.4	3.7	5.7
8-76	C, NC	2.6	1.5	2.6
9-17	P, NC	1.1	2.5	1.5
10-5	C, SC	10.0**	5.7	7.5*
11-9	C, SC	6.9$^+$	2.2	6.9*
11-16	C, SC	4.4	11.7*	6.5$^+$
17-16	C, AL	2.7	1.9	2.3
Number of families with Sig. σ_i^2		5	4	9

$^{+, *, **}$ Significant at $P \leqslant 0.10$, $P \leqslant 0.05$, and $P \leqslant 0.01$, respectively

[a] Origin: C, Coastal plain; P, Piedmont (second column), followed by state

Estimates of the genetic correlation coefficients for selected combinations of the traits investigated are presented in Table 5. The correlation estimates between wood density and the growth traits are all negative and of moderate magnitude. They differ from values near zero that have been observed in most previous investigations involving loblolly pine (Zobel and van Buijtenen 1988). As expected, the genetic correlation between dbh and height is positive and high.

Table 5 Estimates of genetic correlations and standard errors (in parenthesis) plus genotypic × environmental correlations

Trait combination	Genetic correlation	G × E correlation
Height – dbh	0.774 (0.104)	0.633
Height – wood density	– 0.316 (0.206)	0.900
dbh – wood density	– 0.408 (0.209)	0.976
Volume – wood density	– 0.475 (0.184)	0.985

Selection indices

The optimum index for dry weight that combined volume and wood density to increase dry weight had the following weights for individual trees:

$$\text{Index 1: } I_{DW} = b_V \text{ Volume} + b_D \text{ Density}$$
$$= 92.645 \text{ Volume} - 0.034 \text{ Density} \quad (5)$$

or equivalently,

$$I_{DW} = 2724.9 \text{ Volume} - \text{Density}$$

The expected response from selection of individual trees (selection intensity $i = 1.00$) using this optimum index resulted in a 6.61% gain in dry weight but gave a correlated response in wood density of – 1.74%. The restricted index resulted in a correlated response in wood density of 0% but still had a 5.20% response in dry weight (see Baker 1986 for details on selection indices). The weights for the restricted index are:

$$\text{Index 2: } I_{\text{Restr.}} = 2464.2 \text{ Volume} + \text{Density} \quad (6)$$

Note that both index weights are positive for the restricted index but that the weight for density is negative in the optimum index. Wood density and dry weight were negatively correlated ($\hat{r}_G = -0.23$), hence the negative weight for density in the optimum index and the negative expected correlated response in wood density when the optimum index is used.

For comparison purposes, an optimum index that combines height and dbh to increase volume was constructed:

$$\text{Index 3: } I_{\text{Volume}} = b_H \text{ Height} + b_{dbh} \text{ dbh}$$
$$= 0.0086503 \text{ Height} + 0.0008065 \text{ dbh} \quad (7)$$

These simple indices are used to illustrate the effect of different index weights on the expression of genotype-by-environment interaction as opposed to the effects for individual component traits. They are not appropriate for use in operational selection programs because estimates of the variance and covariance components used in determining the index weights were obtained from a collection of experiments that span a much greater geographic range than is included in typical loblolly pine breeding programs.

Genotype × environment interaction

Genotype × environment interaction effects for all traits were highly statistically significant (Table 2), and for the growth traits, were of the same magnitude as in earlier G × E studies with many of these same families (Li and McKeand 1989; McKeand et al. 1990). The interaction effects for wood density are the same as reported by Jett et al. (1991), since the same data are presented here. The high stability of the majority of these 18 families, however, is surprising considering that the sites sampled are diverse, from Virginia to Arkansas (Fig. 1), and are very different in site productivity (Table 1).

Genotype × environmental correlations were computed to provide scaled determinations of the magnitudes for the genotype × environment covariances. Correlations of this type provide a measure of the strength of the association between the genotype-by-environmental effects for two pairs of traits in terms of the maximum positive association. Estimates for these correlations (Table 5) indicate that genotype-by-environmental effects for the growth traits and wood density are highly correlated. The corresponding correlation for dbh and height is evidence that genotypic-by-environmental effects for these two traits are positively associated at an intermediate level.

The low K-statistic for wood density (Fig. 2) generally agrees with the value of 0.07 reported by Byram and Lowe (1988) for a study comprising 20 families at

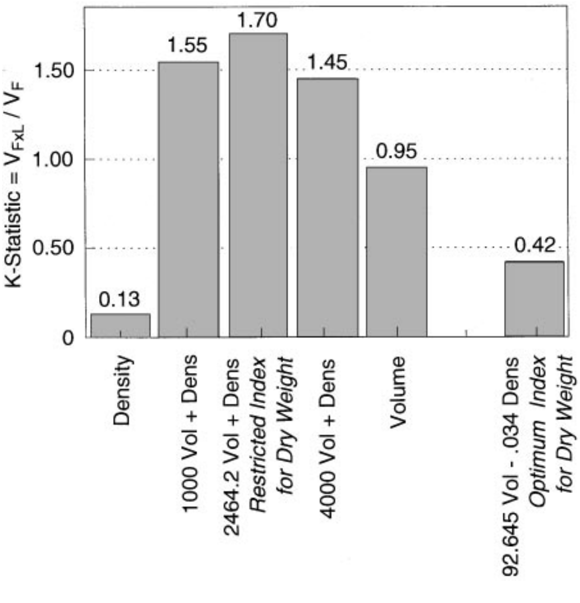

Fig. 2 K-statistic estimates for volume, wood density, and for indices that combine volume with wood density. The restricted index (Index 2 = $I_{\text{Restr.}}$ = 2464.2 Volume + Density) results in no change in wood density. The optimum index which produced the greatest dry weight response (Index 1) is I_{DW} = 2724.9 Volume – Density. Index weights for volume and density were varied as indicated

28 test sites in the western Gulf region. In Fig. 2, K-statistic estimates are illustrated for different weights for volume and density including the restricted index (Index 2) that combines the two traits to increase dry weight. For all indices with weights close to the restricted index weights, the value of K_I exceeds the K value for the trait having the greater value. The G × E for the restricted index was substantially larger than the G × E for volume (1.8 ×) and for density (13.1 ×). In contrast to these results, K-statistic estimates for the optimum indices for dry weight (Index 1) and for volume (Index 3) were intermediate to the estimates for the component traits (Figs. 2 and 3).

Variances among index values depend upon the variances of the component traits as well as their covariances, each term multiplied by a factor dependent on the weights given the individual trait. The interaction variance constitutes, in an analogous way, a sum of component interaction variances and their covariance. Furthermore, it is apparent from Eqs. 3 and 4 that the K-statistic for a two-trait linear index is a complicated function of the index coefficients and of the genetic and interaction variances and covariances. If, however, an index involves two traits with positive genetic covariance, both having positive weights (e.g., Index 3, the optimum index for volume, Eq. 7, Fig. 3), or two traits with negative genetic covariance but weights that differ in sign (e.g., Index 1, the optimum index for dry weight, Eq. 5, Fig. 2), it is evident from Eq. 4 that the K-statistic for the index is the weighted mean of the joint (K_{ij}) and single-trait (K_i) K-statistics for the traits involved. This implies that such an index will have a K value that falls in the interval bounded by the highest and lowest of the three K values associated with the constituent traits, regardless of the magnitudes of the index coefficients. Clearly then, the only way that the K value for the index (K_I) can exceed the higher single-trait K value (K_{max}) is for the value of K_{ij} to be sufficiently larger than K_{max} so that it offsets the effect of the weights associated with each of the K's. On the other hand, if K_{ij} is intermediate to the K_i's, K_I must also be intermediate to the K_i's. However, if K_{ij} falls outside of the interval bounded by K_{max} and K_{min} (value of the smaller K_i) but has a value close to either of the K_i's, values for K_I will be intermediate to the corresponding K_i over a wide range of index coefficients (b_i).

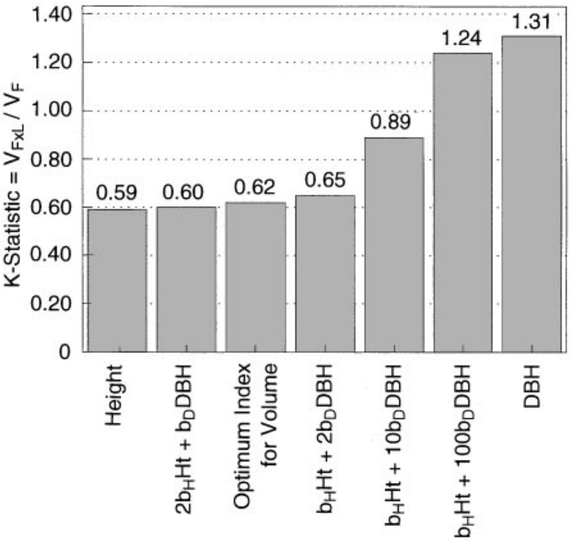

Fig. 3 K-statistic estimates for height, dbh, and for indices that combine height and dbh. The optimum index to increase volume (Index 3) has weights, $b_H = 0.0086503$ and $b_{dbh} = 0.0008065$. Index weights for height and dbh were varied as indicated

The selection indices we studied that are based on height and dbh (Index 3) fit the conditions previously described. These two traits have a positive genetic correlation, $\hat{r}_G = 0.77$ (Table 5), and an estimated K_{ij} value of $\hat{K}_{12} = 0.72$, which is between the K value estimated for height, $\hat{K}_1 = 0.59$, and the larger value obtained for dbh ($\hat{K}_2 = 1.31$) (Table 6). All five indices investigated (e.g. the weights were varied from $2\hat{b}_H : \hat{b}_{dbh}$ to $\hat{b}_H : 2\hat{b}_{dbh}$) for these two traits have positive weights and estimated K values that fall between those obtained for the traits themselves (Fig. 3). These results are consistent with the pattern described above for indices involving pairs of traits with K_{ij} values that fall between K_i values of the component traits.

Of the indices investigated involving volume and wood density to enhance dry weight, the optimum index (Index 1) has properties which ensure that the estimate for its K-statistic is the weighted mean of the estimated K values associated with these two traits. Although the trait weights in this index have differing signs, the negative estimate for the genetic covariances between volume and wood density results in a positive weight for the joint K-statistics (K_{12}). The estimate of this joint K-statistic ($\hat{K}_{12} = -0.74$) is below the interval defined by the $\hat{K}_i$ values obtained for volume and wood density (Table 6). However, the weight associated with the joint K-statistic is insufficient to move the estimated K_I value for the index out of this interval, resulting in a K_I estimate that is intermediate between the K_i values obtained for volume and wood density.

For cases in which an index has both positive and negative coefficient weights and positive $Cov_G(X_1X_2)$ or in which both coefficients are positive but

Table 6 Estimates of K-statistics for individual traits ($\hat{K}_i$) and for trait combinations ($\hat{K}_{ij}$)

Trait and trait combinations	K-statistic
Height	0.59
Breast height diameter (dbh)	1.31
Stem volume	0.95
Wood density	0.13
Height and dbh	0.72
Volume and wood density	– 0.74

$\mathrm{Cov_G}(X_1X_2)$ is negative (e.g., Index 2, the restricted index for dry weight), the relationship between K_{12} and the value of K_I relative to K_{max} and K_{min} is not straightforward. For example, Roberds and McKeand (unpublished results) have found that indices with positive b_i's but negative $\mathrm{Cov_G}(X_1X_2)$ will have a K_I greater than K_{max} only if K_{12} is less than K_{max} and

$$\frac{b_{max}}{b_{min}} > \frac{V_G(X_{min})(K_{max} - K_{min})}{2\mathrm{Cov_G}(X_1X_2)\,(K_{12} - K_{max})} \tag{8}$$

where b_{max} indicates the index coefficient for the trait with maximum K value, b_{min} indicates the coefficient for the trait with the minimum K value, and X_{min} represents the value of the trait with minimum K value.

If we can assume that the negative estimates obtained for the genetic covariances between volume and wood density (Table 7) are a reasonably accurate reflection of the parametric genetic covariances, then the conditions given in expression 4 apply for selection indices with positive coefficients. By substituting the estimates for the family components of variance and covariance (Table 7) and estimates for the K statistics (Table 6) in the expressions given in Eq. 8, we obtain $b_{max}/b_{min} > 595.8$ as the estimated interval for ratios of index coefficients that result in $K_I > K_{max}$. Estimates of K_I for the indices studied with positive coefficients that involve volume and wood density (Index 2) conform to the inequality expected from theory. Each has a coefficient ratio (b_{max}/b_{min}) substantially greater than 595.8 (i.e., for Index 2, $b_{max}/b_{min} = 2464.2$), which is the lower bound for the estimated interval that yields $K_I > K_{max}$ (Fig. 2). Correspondingly, Index 2 and the two other indices we studied with positive weights for volume and wood density all have estimated K_I values considerably greater than 0.95, the estimated K value for volume, the component trait with the greater K estimate.

The increased G × E interaction for the restricted index (Index 2) is not only reflected by its higher K-statistic (Fig. 2) but also by an increased number of families with significant stability variances ($\hat{\sigma}_i^2$) over the numbers observed for either component trait (Table 4). At $P \leqslant 0.10$, 5 families contributed significantly to the G × E variance for volume, 4 for wood density, and 9 for the restricted index. It appears that if a family is interactive for either volume or wood density, it is also interactive for the restricted index.

Table 7 Estimates of additive genetic variance ($\hat{\sigma}_G^2$, diagonal) and covariance components for different traits. Estimates for $\mathrm{COV_G}$ are above the diagonal and $\mathrm{COV_{GE}}$ are below the diagonal

	Height	dbh	Volume	Wood density
Height	0.3564	0.3610	–	–3.2470
dbh	0.2588	0.6100	–	–5.4894
Volume	–	–	0.000216	–0.1205
Density	2.5869	5.5013	0.0889	296.9538

Table 8 Values of C_I (loss of potential gain from mass selection – Matheson and Raymond 1984) for component traits and indices for dry weight

Trait or index	C_I
Height	5.9%
dbh	4.8%
Stem volume	5.5%
Wood density	2.1%
Optimum index for dry wt.	3.5%
Restricted index for dry wt.	7.2%

Additionally, the loss of potential gain in a mass selection program because of the G × E interaction (Matheson and Raymond 1984) was calculated for the traits studied and the indices for dry weight (Table 8). Estimates for C_I range from a low of 2.1% loss for wood density to a high of 7.2% loss for dry weight for the restricted index. Traits with high K-statistics have the greatest loss of potential gain from selection.

Implications

We have extended the work of Namkoong (1985) and Namkoong and Johnson (1987) on G × E interaction in index traits to multiple environments with indices having both positive and negative covariances. While the level of interaction of an index trait is a complicated function of the index coefficients and the genetic variances and covariances (Eqs. 3 and 4), the impact of combining traits that are negatively correlated becomes evident. When $\mathrm{COV_G}(X_1X_2)$ is negative, G × E for the index and hence K_I, can be large depending on the trait weights, variances, and covariances.

Fortunately, most traits that loblolly pine breeders have included in selection indices do not exhibit strong negative associations. Growth, disease resistance, form, and wood properties typically are weakly if at all correlated (Zobel and Talbert 1984; McKeand and Bridgwater 1995). The genetic correlation between volume and wood density of $\hat{r}_G = -0.475$ estimated in this study is probably a lower limit for loblolly pine. A negative genetic association is not typical for these two traits in most populations of this species (Zobel and van Buijtenen 1989; Zobel and Jett 1995) but is probably a function of the diverse origins of the families studied (Jett et al. 1991). These families varied in origin across a great N-S distance. Trees from southern provenances tend to have faster growth and lower wood density when tested together with northern provenances (Byram and Lowe 1988; Jett et al. 1991), hence the negative correlation.

There are populations of some conifers that have significant negative genetic correlations between traits (see Table 10.1 in Zobel and Jett 1995 for examples with wood density and growth traits). If breeders combine traits into indices that result in substantially more G × E interaction than expressed in the individual component traits, breeding strategies may be significantly affected. Subsets of genotypes that are not interactive over specific environments will need to be identified and utilized, thus complicating breeding programs and increasing costs. If environmental factors (e.g., rainfall patterns, length of growing season, soil type) can be identified that are responsible for the interactions, then different breeding zones can be delineated (e.g. Roberds and Namkoong 1989), also increasing costs.

Our results suggest a need for further analysis of G × E for composite traits. Different types of trait combinations, including multiplicative traits, with a broad array of genetic correlations should be studied to obtain a better biological understanding of the causes of the interactions that can occur. Additionally, how genotypes respond to specific environmental conditions must be understood for both component traits and indices before breeders can effectively manage G × E in their breeding programs.

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References

Baker RJ (1986) Selection indices in plant breeding. CRC Press, Boca Raton, Fla.

Becker WA (1984) Manual of quantitative genetics. Academic Enterprises, Pullman, Wash.

Burdon RD (1977) Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. Silvae Genet 26: 145–228

Byram TD, Lowe WJ (1988) Specific gravity variation in a loblolly pine seed source study in the western gulf region. For Sci 34:798– 803

Cockerham CC (1963) Estimation of genetic variances. In: Hanson WD, Robinson HF (eds) Statistical genetics and plant breeding. NAS, National Research Council, Washington D.C., pp 53–94

Dickerson GE (1962) Implications of genetic-environmental interaction in animal breeding. Anim Prod 4:47–63

Falconer DS (1989) Introduction to quantitative genetics. Longman Scientific & Technical, Essex, England

Goebel NB, Warner JR (1966) Volume tables for small diameter loblolly pine, shortleaf and Virginia pine in the upper South Carolina Piedmont. For Res Ser No. 7, Clemson University Clemson, S.C.

Jett JB, McKeand SE, Weir RJ (1991) Stability of juvenile wood specific gravity of loblolly pine in diverse geographic areas. Can J For Res 21:1080–1085

Kang MS, Miller JD (1984) Genotype × environment interactions for cane and sugar yield and their implications in sugarcane breeding. Crop Sci 24:435–440

Kraus JF, Wells OO, Sluder ER (1984) Review of provenance variation in loblolly pine (*Pinus taeda* L.) in the southern United States. In: Barnes RD, Gibson GL (eds) Provenance and genetic improvement strategies in tropical forest trees. Commonw For Inst, Oxford, England and For Res Cent, Harare, Zimbabwe, pp 281–317

Li B, McKeand SE (1989) Stability of loblolly pine families in the southeastern U.S. Silvae Genet 38:96–101

Matheson AC, Raymond CA (1984) The impact of genotype × environment interaction on Australian *Pinus radiata* breeding programs. Aust For Res 14:11–25

McKeand SE, Bridgwater FE (1995) Variance component and genetic gain estimates from 6-year-old diallel tests of loblolly pine. In: Proc 23rd South For Tree Impr Conf. Asheville, N.C., pp 197–203

McKeand SE, Li B, Hatcher AV, Weir RJ (1990) Stability parameter estimates for stem volume for loblolly pine families growing in different regions in the southeastern United States. For Sci 36:10–17

Namkoong G (1985) The influence of composite traits on genotype by environment relations. Theor Appl Genet 70:315–317

Namkoong G, Johnson JA (1987) Influence of value function on genotype-by-environment relations. Silvae Genet 36:92–94

Roberds J, Namkoong G (1989) Population selection to maximize value in an environmental gradient. Theor Appl Genet 77:128–134

SAS Institute (1989) SAS/STAT user's guide, version 6, 4th edn, vol. 2. SAS Institute, Cary, N.C.

Shukla GK (1972) Some statistical aspects of partitioning genotype-environment components of variability. Heredity 29: 237–245

Wricke G (1962) Uber eine methode zur erfassung der okologischen streubreite in feldversuchen. Z Pflanzenzuecht 47:92–96

Yamada Y (1962) Genotype by environment interaction and genetic correlation of the same trait under different environments. Jpn J Genet 37:498–509

Yeiser JL, van Buijtenen JP, Lowe WJ (1981) Genotype × environment interactions and seed movement for loblolly pine in the Western Gulf Region. Silvae Genet 36:196–200

Zobel BJ, Jett JB (1995) Genetics of wood production. Springer, Heidelberg New York

Zobel BJ, Talbert JT (1984) Applied forest tree improvement. John Wiley & Sons, New York

Zobel BJ, van Buijtenen JP (1989) Wood variation, its causes and control. Springer, Berlin Heidelberg New York