

Single- and multiple-trait index selection efficiencies in Fraser fir Christmas trees

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Selection methods for *Abies fraseri* (Pursh) Poir. for Christmas tree wholesale value were evaluated based on parameters from the species' first genetic field test. For single-trait individual selection, combined individual plus family selection at half rotation age (4 years) on total height (HT4) gave the greatest estimated full rotation (8-year) retail value (VALUE) gain of 24.3%. The best 8-year trait, crown diameter, resulted in a gain of only 22.4%. Incorporation of family mean information together with individual values in the selection process was important in maximizing gains. Only 8-year stem straightness (STR8) had unfavorable genetic and phenotypic correlations with other traits. With multitrait combined optimum index selection, use of Kempthorne restrictions to prevent adverse change in this trait seriously limited gains in other 8-year traits. Severity of this limitation increased for younger age indices, and for those with fewer traits. Unrestricted combined optimum indices offered substantial VALUE gain advantages and only small decreases in STR8. Initial selection among seed sources also increased VALUE gain, despite decreasing the effective additive genetic variation. VALUE gains through initial source selection exceeded gain reductions from the genetic variation decreases. The optimum selection strategy, with 30.5% VALUE gain, involved initial source selection followed by unrestricted combined optimum index selection on HT4, and 4-year density. Though slightly below the maximum, this strategy would provide substantial economic and technical advantage in conducting field tests.

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Les méthodes de sélection pour la valeur en gros d'arbres de Noël chez *Abies fraseri* (Pursh) Poir. ont été évaluées à partir de paramètres dérivés du premier test génétique au champ chez cette espèce. Pour la sélection à partir de caractères pris individuellement, la sélection combinée familiale et individuelle basée sur la hauteur totale (HT4) à la moitié de l'âge de révolution, c'est-à-dire 4 ans, permettait l'obtention du plus grand gain en valeur au détail (VALEUR) en fin de révolution (8 ans), ce gain étant estimé à 24,3%. Le diamètre de la cime constituait le meilleur caractère à 8 ans, mais ne permettait d'atteindre qu'un gain de 22,4%. L'utilisation combinée lors du processus de sélection des valeurs de moyennes familiales et des valeurs individuelles était importante afin de maximiser les gains. La rectitude de la tige à 8 ans (STR8) était l'unique caractère démontrant des corrélations génétiques et phénotypiques défavorables avec les autres caractères. Lors de la sélection optimale sur indices combinant des caractères multiples, l'utilisation de restrictions de Kempthorne, qui devraient empêcher des changements défavorables au niveau de la rectitude de la tige, a sérieusement limité les gains au niveau des autres caractères à 8 ans. La sévérité de cette limitation augmentait chez les indices dérivés à un plus jeune âge, ainsi que pour les indices combinant moins de caractères. Des indices combinés optimaux sans restriction ont permis d'augmenter substantiellement le gain en VALEUR, tout en entraînant que de faibles effets défavorables au niveau de la rectitude de la tige (STR8). Une sélection primaire parmi les sources de graines a aussi augmenté le gain en VALEUR, malgré une diminution de la variation génétique effective de nature additive. Les gains en VALEUR découlant de la sélection primaire de sources de graines excédaient les réductions en gain découlant des diminutions de variation génétique. La stratégie optimale de sélection, avec un gain en VALEUR de 30,5%, impliquait une sélection primaire de sources de graines, suivie d'une sélection optimale sur indices sans restriction combinant HT4 et la densité à 4 ans. Malgré qu'elle engendrait des résultats légèrement sous le maximum, cette stratégie pourrait résulter en des avantages économiques et techniques substantiels lors de la conduite des tests au champ.

[Traduit par la rédaction]

Introduction

Fraser fir (*Abies fraseri* (Pursh) Poir.) is the most valuable and highly sought after fresh cut Christmas tree species in the United States (Schultz-Hilliker 1992). It is the only species that combines the desirable attributes of pleasant aroma, dark green foliage, natural Christmas tree shape, strong branches, and excellent foliage retention.

In North Carolina, the leading producer of Fraser fir, this species accounts for over 80% of an \$85 million a year industry (Cook 1990). Unlike other high value forest plantation species, or even ornamental plant species, Fraser fir growers rely almost entirely on unimproved seed sources. The current commercial seed sources of Fraser fir are natural stands that

have been chosen solely for seed production and accessibility.

Genetic improvement of important Christmas tree species has frequently been speculated about within the industry (Gerhold and Palpant 1968; van Haverbeke 1981; Lester 1967; Madsen 1990; McCormack 1985; Nelson 1990; Proebsting 1983; Simpson 1988). To date, however, the rhetoric has rarely been matched by resources and relatively little has been achieved in any of the important species. Parental selection based on progeny performance resulted in an 18% gain in value for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) Christmas trees (Silen and Wilson 1977). Also, some unquantified value gain can reportedly be achieved with early selection and subsequent clonal multiplication of Virginia pine (*Pinus virginiana* Mill.) (Brown and Foster 1991).

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Recent Fraser fir genetic tests have revealed that substantial genetic variation exists both within and among seed sources for important traits (Li et al. 1988; Jett et al. 1993; Arnold 1993). Based on these reports, it is apparent that substantial gain is possible from genetic improvement for Fraser fir Christmas trees.

Gains achievable from tree breeding are sensitive to the procedure utilized to select genetically superior material (Cotterill and Dean 1990). Individual single trait selection, known also as mass selection (Falconer 1989), is one relatively simple approach. Estimation of gains from mass selection requires knowledge of relatively few genetic parameters for the population of interest. However, larger gains are expected from employing multiple trait index selection in tree breeding programs (Cotterill and Dean 1990; Talbert 1986). This approach enables individual phenotypic values for several traits to be combined with family mean values for the same traits into a single index value. Such index values commonly provide more accurate measures of genotypic worth than single phenotypic trait measures.

To date there has only been one reported use of an objective index in Christmas tree selection. In 3-year-old Virginia pine Belanger and Bramlett (1975) devised what they termed a Christmas tree index (CTI), which combined tree height with subjective scores of tree density, symmetry, and straightness, in a multiplicative manner. Gains for a subsequent generation from the selected trees were not reported, though family mean CTIs of the selects themselves ranged from 82.3 to 110% of the overall mean.

Genetic improvement of Christmas tree species requires quality field testing. For Fraser fir, grown under standard Christmas tree culture, such testing is very expensive. Large costs are incurred through culturing large numbers of individuals throughout a complete 8-year Fraser fir Christmas tree rotation. The latter 4 years of such rotations prove particularly costly, as each tree requires annual shearing commencing at field age 4 years. Intensive weed control, pest control, and nutritional management must also be rigorously pursued throughout the rotation. In addition to these costs, quality genetic testing sites where Fraser fir can grow in western North Carolina are scarce, and significant logistical problems can arise in conducting field tests in isolated mountain locations. Sites regarded as quality ones are those with a high uniformity, which are well drained, fertile, and have soil physical and chemical properties that can support vigorous Fraser fir growth.

Substantial benefits would accrue in Fraser fir breeding from both reduced rotation length for genetic field tests, and a reduction in the test land area required. Early selection in Fraser fir would reduce the economic burden and the logistical difficulties of culturing Fraser fir genetic tests from 4 years through to a full commercial rotation age of 8 years.

Recent maturation of the first Fraser fir seed source – progeny tests (Arnold 1993) provided breeders with the opportunity to make selections for high genetic quality individuals. The objective of this current study is to identify the best procedure for such selection in Fraser fir Christmas trees.

Materials and methods

Parameter estimation

Phenotypic and genetic parameters on Fraser fir for this study were estimated from assessments of an open-pollinated Fraser fir genetic test established in 1983. This test incorporated a total

of 82 families from nine separate seed sources planted at three different field locations in western North Carolina (Li et al. 1988; Arnold 1993). The trials were assessed at ages 0, 1, 4, and 8 years (Li et al. 1988; Jett et al. 1993, Arnold 1993). The 8-year assessment coincided with the typical full rotation age for Fraser fir Christmas trees.

Trait measurements included in this current study were as follows: (i) height at planting (HT0; centimeters), which was 3 years from seed; (ii) height at a field age of 1 year (HT1; centimeters); (iii) number of lateral buds at the terminal node at field age 1 year (BUDS1); (iv) root-collar diameter at field age 1 year (DMI; centimeters); (v) height at a field age of 4 years (HT4; centimeters); (vi) maximum crown diameter at a field age of 4 years in the field (CDM4); (vii) density factor at field age 4 years (DENS4), computed as the product of the number of lateral buds on the dominant branch of the top whorl and the number of lateral buds at the terminal node; (viii) height at a field age of 8 years (HT8; meters), measured prior to 8-year shearing; (ix) maximum crown diameter at field age 8 years (CDM8; meters), also measured prior to 8-year shearing; (x) crown density at a field age of 8 years (DN8) subjectively scored in line with USDA Christmas tree grading standards (Department of Agriculture 1989) on a 3-point scale of 1 (heavy density) to 3 (light density); (xi) straightness at field age 8 years (STR8) also subjectively scored in line with USDA grading standards on a 3-point scale of 1 (straight) to 3 (crooked).

The traits DN8 and STR8, in contrast to all others, were assessed on reverse scales with respect to improvement of economic worth. Low values for DN8 and STR8 are superior to higher values. Similarly, decreases in DN8 or STR8 values represent positive improvements.

Final assessment at a field age of 8 years also included USDA Christmas tree grade and merchandizing height class for each tree. These two parameters directly enable determination of a Christmas tree's wholesale value. However, subsequent to final assessment serious shortcomings in such measures with respect to representing true market worth as measured by retail value were revealed (Arnold 1993). USDA grade is now known to be poorly correlated with retail for Fraser fir Christmas trees within any one height class.

For the purpose of this study, Christmas tree economic worth was determined on the basis of estimated retail value. This estimated value was obtained with following multiple linear regression equation (Arnold 1993):

$$[1] \text{ VALUE} = 16.995\text{HT8} + 14.452\text{CDM8} - 2.659\text{DN8} \\ - 0.445\text{STR8} - 16.010$$

where VALUE is estimated retail value in dollars.

The data for this study incorporated a total of 5078 individuals representing 82 families. All genetic gains were estimated for selection of one superior individual of every 100, i.e., i is the standardized selection intensity = 2.665. The goal of selection in this study was always to improve VALUE. To simplify parameter interpretation, all phenotypic trait measures were standardized to have means of zero, and variances of one.

Variance and covariance components used to estimate gains from selection were calculated in two ways. First, parameters were estimated from an analysis of variance model with effects: sites; blocks (within sites); families; sites \times families; blocks \times family (within sites); and error (among trees within blocks). Gains estimated using parameters from this model are appropriate for selection within the complete set of genotypes in the study. Next, gains were estimated for selection first among seed sources, followed by selection within the best sources. Variance and covariance components appropriate for selection within the best seed sources were estimated as before, but only for the reduced population of selected seed sources.

The variance components estimates were obtained using PROC VARCOMP of the Statistical Analysis System (SAS Institute Inc.

TABLE 1. Phenotypic and genetic parameters for the Fraser fir traits estimated from analyses of all 82 families

Trait	Parameter				
	Mean	σ_a^2	σ_p^2	h_i^2	h_f^2
HT0 (cm)	25.2	0.274	0.981	0.279±0.042	0.684±0.066
HT1 (cm)	32.2	0.424	0.984	0.431±0.052	0.782±0.070
BUDS1	4.16	0.230	0.969	0.237±0.039	0.668±0.065
DM1 (cm)	0.871	0.203	0.951	0.214±0.037	0.603±0.062
HT4 (m)	1.01	0.562	0.979	0.575±0.060	0.835±0.073
CDM4 (m)	0.74	0.377	0.963	0.391±0.045	0.769±0.070
DN4	50.7	0.522	0.964	0.541±0.058	0.835±0.072
HT8 (m)	2.28	0.343	0.971	0.353±0.047	0.734±0.068
CDM8 (m)	1.18	0.454	0.910	0.499±0.056	0.814±0.072
DN8	1.91	0.290	0.944	0.308±0.044	0.716±0.067
STR8	1.60	0.188	0.938	0.201±0.036	0.634±0.063
VALUE (\$)	39.46	0.446	0.977	0.457±0.054	0.873±0.074

NOTE: Means presented are for unstandardized trait measures, while σ_a^2 and σ_p^2 are estimated additive genetic and phenotypic variances respectively for the standardized traits. h_i^2 and h_f^2 individual and family heritabilities, respectively (\pm SE); HT0, HT1, HT4, and HT8, height at field age 0, 1, 4, and 8 years, respectively; BUDS1, number of lateral buds at the terminal node at 1 year; DM1, root collar diameter at 1 year; CDM4, crown diameter at 4 years; DN4, crown density factor at 4 years; CDM8, crown diameter at 8 years; DN8 and STR8, density and straightness scores, respectively, at 8 years; VALUE, estimated retail value at 8 years.

1985a). The necessary covariance components were obtained similarly by linear combinations of traits as described by Arnold (1993).

Selection populations

The three best sources were Clingman's Dome 1500 m, Clingman's Dome 1650 m, and Richland Balsam 1650 m. These were superior to the other sources in HT8, CDM8, and Christmas tree wholesale value (Arnold 1993). Individual tree heritabilities for growth and form traits for these sources also indicated that they had the largest amounts of within source additive genetic variation (Liu 1991; Arnold 1993).

Estimated gains for combined index selection within the foregoing reduced population were compared with unrestricted combined optimum index selection within the greater population. For the reduced population, gains were obtained as the sum of those from source selection, and from index selection within the selected sources.

Single trait selection

Genetic gains for direct and indirect single trait selection were estimated for each of four different methods of selection; individual, family, within-family, and combined selection (Falconer 1989). For these computations, correlations among phenotypic values of family members, r , were estimated as

$$[2] \quad r = rh_i^2$$

where h_i^2 is the individual heritability for the trait under consideration, and r is the coefficient of coancestry. Because progeny within families were assumed to be true half-sibs with no relatedness between families, a coefficient of relatedness (r) of 0.25 was used throughout (Falconer 1989). The harmonic mean family size, which in this study equaled 60.27, was used where the parameter of number of individuals per family was required.

Index selection

Estimated genetic gains were computed for Smith-Hazel selection indices which combined individual and family mean information for each constituent trait. These indices, known as combined optimum indices (Williams 1962), were constructed following procedures described by Becker (1984) and Cotterill and Dean (1990). In each case, the genetic worth equation employed was

$$[3] \quad H = w_{HT8}A_{HT8} + w_{CDM8}A_{CDM8} + w_{DN8}A_{DN8} + w_{STR8}A_{STR8}$$

where H is an individual's genetic worth (retail value); A_{HT8} , A_{CDM8} , A_{DN8} , and A_{STR8} are the same individual's breeding values for HT8, CDM8, DN8, and STR8, respectively; w_{HT8} , w_{CDM8} , w_{DN8} , and w_{STR8} are the respective economic weights on each of the standardized traits.

For this study, these economic weights, obtained as the standardized multiple linear regression coefficients for the traits, were 0.5228, 0.3340, -0.1886, and -0.0339, respectively (Arnold 1993).

To overcome the effects of adverse phenotypic and genetic correlations between straightness and all other traits excepting density, Kempthorne restrictions (Kempthorne and Nordskog 1959) were introduced into some of the selection indices to constrain genetic change in straightness to zero. Restricted selection indices were developed by retaining the equations of constraint explicitly in the system following the methodology given by Cunningham et al. (1970).

Gains from selection on combined optimum indices were obtained as

$$[4] \quad \Delta G = \frac{iCb}{(bPb)^{1/2}}$$

where: ΔG is the vector of predicted genetic gain for the traits defining H ; i is the standardized selection intensity; C is the genetic covariance matrix between the selection traits and the traits defining H ; b is the vector of estimated index weights; and P is the phenotypic covariance matrix of the selection traits.

All matrix computations for development of combined optimum indices were done with in the SAS Interactive Matrix Language (SAS/IML; SAS Institute Inc. 1985b).

Results and discussion

Single trait selection

The additive genetic variances and heritabilities, appropriate for estimating genetic selection gains from this Fraser fir study, were generally large (Table 1) owing to the high quality of the field tests, and the diverse genetic basis of the families tested. Strong and generally favorable correlations also existed among the important traits (Table 2). Early reports on this field test had also revealed favorable correlations among important traits, even at young ages (Li et al. 1988; Jett et al. 1993; Arnold 1993).

TABLE 2. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) among Fraser fir traits measured for 82 families

	HT0	HT1	BUDS1	DM1	HT4	CDM4	DENS4	HT8	CDM8	DN8	STR8	VALUE
HT0		0.871	0.322	0.616	0.857	0.741	0.284	0.813	0.794	-0.345	0.285	0.799
HT1	0.936		0.454	0.665	0.899	0.768	0.383	0.836	0.790	-0.385	0.309	0.816
BUDS1	0.050	0.175		0.607	0.566	0.483	0.532	0.549	0.456	-0.476	0.214	0.548
DM1	0.546	0.607	0.192		0.752	0.791	0.567	0.628	0.587	-0.566	0.395	0.650
HT4	0.538	0.635	0.529	0.251		0.864	0.591	0.980	0.916	-0.592	0.353	0.975
CDM4	0.566	0.630	0.561	0.199	0.766		0.541	0.854	0.894	-0.483	0.535	0.869
DN4	0.150	0.198	0.209	0.201	0.499	0.365		0.533	0.446	-0.660	0.191	0.567
HT8	0.417	0.495	0.409	0.225	0.751	0.600	0.403		0.903	-0.561	0.377	0.976
CDM8	0.452	0.518	0.408	0.187	0.712	0.667	0.376	0.665		-0.538	0.462	0.949
DN8	-0.155	-0.184	-0.206	-0.086	-0.298	-0.292	-0.247	-0.211	-0.295		0.024	-0.683
STR8	0.096	0.107	0.069	0.226	0.113	0.139	0.056	0.085	0.151	0.051		0.339
VALUE	0.461	0.540	0.230	0.451	0.800	0.684	0.445	0.927	0.847	-0.453	0.040	

NOTE: HT0, HT1, HT4, and HT8, height at field age 0, 1, 4, and 8 years, respectively; BUDS1, number of lateral buds at the terminal node at 1 year; DM1, root collar diameter at 1 year; CDM4, crown diameter at 4 years; DN4, crown density factor at 4 years; CDM8, crown diameter at 8 years; DN8 and STR8, density and straightness scores, respectively, at 8 years; VALUE, estimated retail value at 8 years. All phenotypic correlations were significant at $P \leq 0.05$.

TABLE 3. Genetic gains in 8-year Fraser fir Christmas tree value estimated value, total height, crown diameter, density, and straightness resulting from individual selection on various single trait

Selection trait	Estimated gains				
	HT8 (m)	CDM8 (m)	STR8	DN8	VALUE (\$)
HT0	0.63 (14.1)	0.56 (7.4)	0.13 (32.0)	-0.19 (32.0)	5.88 (32.0)
HT1	0.81 (14.4)	0.69 (7.6)	0.17 (23.5)	-0.27 (23.5)	6.76 (23.5)
DM1	0.43 (12.1)	0.36 (7.7)	0.16 (22.1)	-0.28 (22.1)	3.50 (22.1)
BUDS1	0.39 (8.4)	0.30 (4.6)	0.09 (30.3)	-0.25 (30.3)	3.18 (30.3)
HT4	1.10 (12.3)	0.93 (4.8)	0.23 (39.8)	-0.48 (39.8)	9.20 (39.8)
CDM4	0.79 (3.3)	0.75 (3.2)	0.29 (12.9)	-0.32 (12.9)	6.67 (12.9)
DN4	0.58 (10.4)	0.44 (6.8)	0.12 (18.3)	-0.52 (18.3)	4.80 (18.3)
HT8	0.88 (16.2)	0.72 (11.1)	0.19 (-26.4)	-0.35 (48.6)	7.22 (-1002.8)
CDM8	0.94 (13.2)	0.95 (4.4)	0.28 (25.8)	-0.40 (25.8)	8.33 (25.8)
DN8	0.46 (9.5)	0.40 (5.8)	-0.01 (3.6)	-0.59 (3.6)	4.37 (3.6)
STR8	-0.25 (8.8)	-0.28 (-4.3)	-0.36 (49.7)	-0.01 (1.4)	-1.57 (218.1)
HT8	0.85 (15.1)	0.86 (13.2)	0.20 (-27.8)	-0.49 (68.1)	8.37 (-1162.5)

NOTE: HT0, HT1, HT4, and HT8, height at field age 0, 1, 4, and 8 years, respectively; BUDS1, number of lateral buds at the terminal node at 1 year; DM1, root collar diameter at 1 year; CDM4, crown diameter at 4 years; DN4, crown density factor at 4 years; CDM8, crown diameter at 8 years; DN8 and STR8, density and straightness scores, respectively, at 8 years; VALUE, estimated retail value at 8 years. Gains are presented as the absolute gain with the percentage gain given in parentheses. All gains are estimated for selection at an intensity of one tree in every 100.

Large genetic gains² in the important 8-year Fraser fir Christmas tree traits were estimated for single trait selection strategies (Table 3). Negative absolute gains estimated in some cases for the traits STR8 and DN8 are desirable since lower scores on these traits represent higher Christmas tree quality. The highest expected gain in 8-year VALUE, \$9.20 per tree (23.3%), was obtained by selection on the 4-year trait HT4. In comparison, the best selection gain for VALUE from a single trait at full rotation was achieved by direct selection on VALUE (i.e., selection on VALUE). The expected VALUE gain was nearly \$1.00 less at \$8.37 per tree (21.2%). However, this gain virtually equaled that for direct selection on VALUE at age 8 (21.2%).

Direct selection at 8 years for VALUE gave no real gain advantage over indirect selection at the same age on CDM8 for VALUE improvement; \$8.37 (21.2%) versus \$8.33 (21.1%). However, the direct selection would have substantial disadvantages. Determination of tree VALUE first requires

measurement of four traits including HT8, CDM8, STR8, and DN8. Consequently, direct selection would incur greater expense and be prone to greater error than the indirect selection.

The greatest expected gains in HT8 of 0.33 m (14.7%) and CDM8 of 0.24 m (12.4%) were also achieved by selection at half rotation age on the trait HT4. For improvement of DN8, the contrived 4-year parameter DN4 was very effective as a measure of final genetic potential for DN8. The gain it provided, -0.52 (27.2%), was only -0.07 (2.6%) less than that of direct selection on DN8.

These results show final age traits were poorer than earlier measures of genetic potential in Fraser fir Christmas trees. This occurred because annual Christmas tree shaping and shearing treatments, which commenced after 4-year measurement of the study trees, partially masked phenotypic expression of genetic potential at later ages (Arnold 1993).

Very early age selection on HT0 or HT1 was very effective in improving rotation-age traits. These traits provided VALUE gains of \$5.88 (14.9%) and \$6.76 (17.1%) respectively, and HT8 gains of 0.19 m (8.4%) and 0.25 m (10.8%) respec-

²All gains hereafter refer to predicted gain at rotation age in the subsequent generation unless otherwise specified.

TABLE 4. Estimated genetic gains in 8-year Fraser fir Christmas tree VALUE from alternative methods of single trait selection, based on various traits

Selection method	Estimated gain in VALUE (\$) by selection on			
	HT1	HT4	HT8	CDM8
Individual	6.76 (17.1)	9.20 (23.3)	7.22 (18.3)	8.33(21.1)
Within family	5.33 (13.5)	7.40 (18.7)	5.62 (14.3)	6.63(16.8)
Family	5.07 (12.9)	6.08 (15.4)	5.89 (14.9)	5.86(14.9)
Combined (family + within family)	7.35 (18.6)	9.57 (24.3)	8.14 (20.6)	8.84(22.4)

NOTE: HT1, HT4, and HT8, height at field age 1, 4, and 8 years, respectively; CDM8, crown diameter at 8 years. Gains are presented as the absolute gain with the percentage gain given in parentheses. All gains are estimated for selection at an intensity of one tree in every 100.

tively. Such early age selections also provided substantial improvement in the other 8-year traits excepting for STR8 (Table 3).

Adverse genetic and phenotypic correlations between STR8 and all other traits except DN8, resulted in marked deterioration in STR8 with indirect selection. The greatest expected deterioration of 0.29 (-18.1%) resulted from positive selection on CDM4. In comparison, direct selection for improvement of STR8 provided a gain of -0.36 (22.4%) in STR8, but this is expected to result in small deteriorations in HT8 (-0.08 m, -0.6%) and CDM8 (-0.07 m, -3.7%). However, of the four traits used in the determination of VALUE, STR8 is the one of least importance. In the economic worth equation developed for standardized traits, its weighting coefficient of -0.0339 is approximately one 15th the magnitude of that on HT8, the trait of greatest influence on VALUE (Arnold 1993).

The potential for very early age selections of Fraser fir is revealed by the preceding gain estimates. At such a stage, a more intensive individual selection than that for the forgoing estimates, could be used. Selecting on HT0 for one superior individual per 1000 would provide a VALUE gain of \$7.43 (19.0%); a substantially larger gain than that given for HT0 in Table 3. This gain becomes even more significant when we consider that it could have been achieved with none of the substantial expenses associated with field testing. Such early selection would enable selected individuals to be established directly in, or readily transplanted to, either breeding or seed orchards.

Fraser fir Christmas tree breeding will benefit substantially from the effectiveness of individual single trait selection at half rotation or younger, relative to 8-year full rotation selection. Future genetic field tests could be terminated after selection at only 4 years, without sacrificing gain. Cost-saving potentials of such midrotation selections would be substantial.

Comparisons of VALUE gains from alternative methods of single trait selection on HT1, HT4, HT8, and on CDM8 are presented in Table 4. Within-family single-trait selection on any one of these traits provided \$1.43 (3.6%) to \$1.80 (4.6%) less gain in VALUE than individual selection. With selection on HT4, for example, VALUE gain decreased from \$9.20 (23.3%) for individual selection to \$7.40 (18.7%) for within-family selection. These results demonstrate the importance of the among-family component of Fraser fir variation for important traits in selection. The significance of family differences in this species was revealed in earlier studies (Li et al. 1988; Jett et al. 1993; Arnold 1993). If selec-

tion was restricted to within families, as would be an alternative for selection of a breeding population with minimum relatedness, breeders must understand that VALUE gains stand to be substantially compromised.

Family selection, ignoring variation of individuals within, offers variable gain responses relative to within-family and to individual selection. Selection on HT1 or on HT8 gave very similar VALUE gains for family (\$5.07 and \$5.89, respectively), and for within-family (\$5.33 and \$5.62, respectively) single-trait selection. However, family selection was inferior to within-family selection for VALUE improvement when selection was on the traits HT4 or CDM8 that had relatively high individual heritabilities (0.58 and 0.50, respectively).

Combined family plus within-family single-trait selection in Fraser fir provided a small but clear superiority in gain over any one of the three other single-trait selection alternatives (Table 4). Gains for VALUE with the former ranged from \$0.37 (1.0%) to \$0.92 (2.3%) of mean VALUE higher than those with individual selection. Combined selection on HT8 provided a \$8.14 (20.6%) VALUE gain compared to a \$7.22 (18.3%) gain by individual selection on the same trait. In the course of assessment and analyses for Fraser fir Christmas tree selection, incorporation of family information would involve negligible additional cost. This factor, combined with the small but distinct gain advantage, reveals that ignoring family information in Fraser fir selection, where available, would compromise gain readily obtainable in the species.

Index selection

Gains obtainable for a range of Fraser fir combined optimum indices are presented in Table 5. The index gains presented are select representative examples of a more comprehensive set spanning the range of practical selection trait combinations examined in the course of this study. The Kempthorne restriction was initially employed to prevent deterioration in STR8. The target of zero gain in this trait is quite acceptable in a comprehensive Fraser fir Christmas tree improvement program in North Carolina. The test mean for STR8 of 1.60, though amenable to improvement, represents a relatively high quality for straightness.

For the restricted indices, No. 1, containing all 11 traits drawn from the four different age assessments, provided the highest expected gains in VALUE, \$10.05 (25.5%); HT8, 0.32m (42.5%); CDM8, 0.26m (6.6%); and DN8, -0.59 (30.8%). However, these gains may tend to be slightly inflated due to the large, favorable correlations between the traits it contains. Removing traits to simplify this index

TABLE 5. Estimated genetic gains in the 8-year Fraser fir Christmas tree traits, HT8, CDM8, STR8, DN8, and VALUE obtained with restricted combined optimum indices and with equivalent unrestricted indices

Index	Component traits	Age at selection (years)	<i>r</i>	Gains				
				HT8	CDM8	STR8	DN8	VALUE (\$)
Indices with restriction								
1	HT0, HT1, DM1, BUDS1, HT4, CDM4, DN4, HT8, CDM8, DN8, STR8	8	0.73	0.32 (42.5)	0.26 (6.6)	0.00 (0.0)	-0.59(30.8)	10.05 (25.5)
2	HT0, HT1, HT4, HT8	8	0.71	0.28 (37.3)	0.21 (5.3)	0.00 (0.0)	-0.40 (20.9)	6.90 (17.5)
3	HT8, CDM8, STR8, DN8	8	0.64	0.27 (35.6)	0.22 (5.7)	0.00 (0.0)	-0.57 (29.8)	6.94 (17.6)
4	HT4, DN4	4	0.58	0.21 (27.9)	0.14 (3.7)	0.00 (0.0)	-0.35 (18.3)	4.76 (12.1)
5	HT1, HT4	4	0.04	0.01 (1.2)	0.01 (0.2)	0.00 (0.0)	-0.15 (7.8)	0.23 (0.6)
6	HT0, HT1	1	0.07	0.15 (19.8)	0.04 (1.0)	0.00 (0.0)	0.02 (-1.0)	0.79 (2.0)
Indices without restriction								
7	HT0, HT1, DM1, BUDS1, HT4, CDM4, DN4, HT8, CDM8, DN8, STR8	8	0.84	0.36 (48.6)	0.31 (8.0)	0.17 (-10.6)	0.56 (-29.3)	11.40 (28.9)
8	HT0, HT1, HT4, HT8	8	0.78	0.35 (46.6)	0.29 (7.3)	0.17 (-10.6)	-0.48 (25.1)	10.67 (27.0)
9	HT8, CDM8, STR8, DN8	8	0.75	0.32 (42.5)	0.29 (7.4)	0.19 (-11.9)	-0.52 (27.2)	10.30 (26.1)
10	HT4, DN4	4	0.77	0.34 (45.4)	0.28 (7.2)	0.16 (-10.0)	-0.50 (26.1)	10.50 (26.6)
11	HT1, HT4	4	0.77	0.34 (45.8)	0.28 (7.3)	0.17 (-10.6)	-0.48 (25.1)	10.52 (26.7)
12	HT0, HT1	1	0.62	0.28 (37.3)	0.23 (5.8)	0.14 (- 8.8)	-0.32 (16.7)	8.42 (21.3)

NOTE: *r*, correlation of the specific index with genetic worth (i.e., VALUE) on an individual basis; HT0, HT1, HT4, and HT8, height at field ages 0, 1, 4, and 8 years, respectively; BUDS1, number of lateral buds at the terminal node at 1 year; DM1, root collar diameter at 1 year; CDM4, crown diameter at 4 years; DN4, crown density factor at 4 years; CDM8, crown diameter at 8 years; DN8 and STR8, density and straightness scores, respectively, at 8 years. Restricted indices were developed using a Kempthorne restriction to hold gain in STR8 at zero. Gains are presented as the absolute gain with the percentage gain given in parentheses. All gains are estimated for selection of one tree in every 100.

resulted in a deterioration of gain estimates. Index 2, containing only height growth traits, provided only \$6.90 (17.5%) gain in VALUE and index 3, containing only 8-year traits, provided only a \$6.94 (17.6%) gain. Indices 5 and 6 provided almost no gain in VALUE or any of the of the 8-year traits. Their poor performance arises from the restriction of holding change in STR8 under index selection to zero, and the adverse genetic and phenotypic correlations between this trait and all others excepting DN8.

The inherent restriction of zero change in STR8 in the foregoing indices comes at a high "price." This price is reduced gains in VALUE, in HT8, and in some cases even in DN8. The magnitude of the price is revealed by comparisons of gain responses for the restricted to equivalent unrestricted indices (Table 5). The VALUE gain reduction gets larger for early age indices, and for those with fewer selection traits. Removing the restriction from index 1, resulted in only a \$1.35 (3.42%) increase in VALUE gain, i.e., index 7, while doing the same to index 5 resulted in a substantial \$10.29 (26.1%) increase in VALUE gain, i.e., index 11.

Despite the high price incurred for preventing deterioration in STR8 under combined optimum index selection of Fraser fir Christmas trees, unrestricted selection actually resulted in minor STR8 deteriorations. The worst case encountered, index 9 containing all four 8-year traits, gave a deterioration of mean STR8 score of only 0.19 (-11.9%). The same index though yielded a DN8 improvement of -0.52 (27.2%) and VALUE gain of \$10.30 (26.1%), which was \$3.40 (9.5%) above that for the equivalent but restricted index.

The STR8 deteriorations obtained in this study with unrestricted combined optimum index selection in Fraser fir are not expected to move STR8 outside of acceptable limits. In addition, the magnitude of the deteriorations, taken alone, would have small impact on VALUE. Due to the relatively low economic weight on STR8 ($w_{STR8} = -0.0339$), each

deterioration of 0.1 in mean score for this trait, when taken in isolation, decreases VALUE by only \$0.06 (0.2%). Consequently, even the magnitude of STR8 deterioration in the worst case, 0.19 (-11.9%), would be a minor concern in this first generation of improvement.

For the unrestricted indices, the largest gains in all 8-year traits, excepting STR8, were obtained with index 7. This index, however, is very complex in composition. Relatively small gain in VALUE and other traits would be foregone by opting for a less complex four-trait, or even only the two-trait, combined optimum index containing traits from a single assessment age. Index 10 is particularly attractive in this respect, offering a \$10.50 (26.6%) VALUE gain from a single midrotation assessment. In comparison, index 9, containing four 8-year traits, which involve greater assessment costs commensurate with larger tree size, would yield a slightly lower VALUE gain of \$10.30 (26.1%). Though the other four-trait index, number 8, provided a slight VALUE gain superiority (\$10.67, 27.1%) to these two preceding ones, its formulation required assessment of the test at four separate ages, an even more costly and logistically difficult requirement.

Most of the aforementioned unrestricted combined indices provided definite VALUE gain advantages over the best single trait selection option; i.e., combined selection on HT4. These advantages in terms of VALUE ranged from \$0.63 (2.0%) to \$1.83 (5.0%). Combining information on two or more traits can clearly provide superior measures of 8-year Fraser fir genotypic potential over that provided by any single phenotypic trait. Such gain superiorities of the multi-trait combined optimum indices over single-trait selection in this species are largely manifestations of favorable genetic and phenotypic correlations between the traits concerned.

Early unrestricted combined index selection also offers great potential in Fraser fir Christmas tree improvement. Index 12 with only the two component traits HT0 and HT1

TABLE 6. Comparison of estimated genetic gains in 8-year Fraser fir Christmas tree VALUE obtained from different selection populations with unrestricted, combined optimum indices

Traits included in index	Age at final selection (years)	Selection gains in VALUE for all 9 seed sources			Selection gains in VALUE for the best 3 seed sources		
		Gain by source selection	Gain by index	Total	Gain by source selection	Gain by index	Total
HT8, CDM8, STR8, DN8	8	0.00	10.67	10.67 (27.0)	1.84	10.53	12.37 (31.4)
HT4, DN4	4	0.00	10.50	10.50 (26.6)	1.84	10.18	12.02 (30.5)
HT0, HT1	1	0.00	8.42	8.42 (21.3)	1.84	6.98	8.82 (22.3)

NOTE: HT0, HT1, HT4, and HT8, height at field ages 0, 1, 4, and 8 years, respectively; DN4, crown density factor at 4 years; CDM8, crown diameter at 8 years; DN8 and STR8, density and straightness scores, respectively, at 8 years. Individual and family mean information was incorporated in each index for all component traits. Gains are presented as the absolute gain over the study mean (i.e., all nine sources) with the percentage gain given in parentheses. All gains are estimated for selection of one tree in every 100.

would produce a VALUE gain of \$8.32 (21.3%), compared with only \$7.35 (18.6%) by combined selection on HT1. Factors contributing to this situation, and the substantial economic and logistical advantages arising through it, have already been highlighted.

Indices with few traits, such as Nos. 10–12, also have advantages of lower expected error and therefore greater precision. The accuracy of estimates for the index weights, and consequently the index itself, depend on how accurately the **C** and the **P** matrices can be estimated. Even small errors in estimates of genetic and phenotypic variances and covariances on each parameter or parameter pair can compound into large errors where many traits are combined into the one index (Namkoong et al. 1988). Also, in index application, there is measurement error on each selection trait and these can also compound to produce erroneous or inappropriate index values. Consequently for indices such as Nos. 1 and 7 with numerous traits, index weight estimates can be poor and selection based on derived index values may, in practice, result in poor realized gains (Namkoong et al. 1988).

The correlations obtained between combined optimum index scores and VALUE on an individual tree basis; r in Table 5, were closely aligned to VALUE gains. Development of an optimum index involves determining index weights which optimize the correlation between the index and H , the genetic worth. In this study, genetic worth was simply defined as VALUE. Truncation selection on the index constitutes an indirect selection for this breeding objective (Cotterill and Jackson 1985). Accordingly, the indexes of higher correlation with genetic worth produced the higher gains in VALUE.

Prior seed source selection

Preceding reports have revealed significant genetic variation between Fraser fir seed sources in at least Christmas tree growth, quality, and wholesale value (Li et al. 1988; Jett et al. 1993; Arnold 1993). Consequently, breeders could wisely precede any family or individual selection with a seed source selection. Incorporation of such an initial source selection into the selection process for Fraser fir increased the expected total genetic VALUE gain (Table 6). For combined index selection cases, this gain increase ranged from \$0.40 (1.0%) to \$1.70 (4.4%). Unrestricted combined optimum index selection on HT4 and DN4 within the best three sources produced a total VALUE gain of \$12.02 (30.5%), compared with \$10.50 (26.6%) for that within all nine sources.

Examination of each of the stages of gain obtained with ini-

tial source selection and subsequent index selection reveals the initial stage provided a relatively small but important contribution (Table 6). When followed by combined optimum index selection on HT4 and DN4, the contribution of the source selection of \$1.84 (4.7%) to total VALUE gain accounted for 15.3% of the total gain. Gains estimated for selection indices within the best three sources were lower than the gains by equivalent indices within the greater group. However, the combination of source selection gain and index selection gain within the selected sources yielded superior VALUE gains in each case. Apparent poorer gains within the reduced group arose primarily through a reduction in estimated additive genetic variance that occurred with the source selection. The overall variance among families within the study was greater than that among families within the reduced group of families from just the best three sources. Consequently, any genetic selection exploiting additive genetic variance could be expected to yield higher within-group gain in the nine source groups. Initial seed source selection is clearly very important to maximize genetic gain in this first generation of Fraser fir genetic improvement.

This study incorporated a collective total of only 28 families from these best three sources. While this may be adequate for assembling a good seed production population, it is critically small for assembling a genetically broad breeding population with minimal relatedness. However, the best three natural sources actually represent the two largest of the disjunct subpopulations of Fraser fir. Consequently, only a very small sample of the extant genetic variation within them was represented in this study. Additional sampling from these natural sources would be prudent for breeders assembling a longer term breeding population.

Gains in perspective

The unrestricted combined optimum indices selection gains in Fraser fir height growth estimated in this study are comparable to similar type selections in forest grown trees of the closely related species balsam fir (*Abies balsamea* (L.) Mill.). Combined optimum indices in the later species gave estimated gains of 34% in height at both 5 and 10 years (Beaulieu et al. 1990). These were based on combined optimum index selection of one in every 200 individual progeny from one seed source. The index used contained the three favorably correlated traits of height, diameter, and a subjective bole straightness score.

It must be emphasized that all Fraser fir VALUE gains estimated in this study have been presented on a per tree

basis. Their magnitudes can better be understood from the perspective of Christmas tree growers. Typically, 800 Fraser fir Christmas trees are grown per acre. Increased average VALUE of only \$1.00 per tree would therefore generate \$800/acre in additional revenue from the 8-year harvest. Similarly, if gains from some of the best combined optimum index strategies of this study were realized in production plantations, the gain to a grower's harvest revenue would be up to \$8400/acre or more. In the state of North Carolina as a whole, if 50% of the maximum gain could be realized from all commercial plantings, the annual returns for the Fraser fir Christmas tree industry could increase by \$10 million or more.

Increased height growth alone can be beneficial to growers. Where Christmas trees can be harvested 1 or more years sooner, growers would gain through increased rates of return on their investments. Also, such faster growth and earlier harvest would increase the number of trees available for harvest each year.

Conclusions

This study shows large genetic improvement of VALUE can be achieved with selection among Fraser fir Christmas trees. The strength of these gains is supported by the magnitude and generally favorable nature of genetic and phenotypic correlations between important traits. The only unfavorable correlations all involved STR8, a trait which has a relatively small though significant influence on VALUE. By accepting small deteriorations in STR8, VALUE gains are increased substantially.

Of the selection strategies examined, the best involved two distinct stages; an initial selection of the best sources followed by within-source selection. Each of these stages was vital to establish the superiority of this approach over selection among all nine sources involved in the study.

Overall, the best within-group selection strategy was unrestricted combined optimum index selection on the traits HT4 and DN4. Though this provided slightly lower VALUE gain than more complex multitrait unrestricted combined optimum indices, it has big advantages over the latter. These advantages include economic and technical efficiency in testing and genetic assessment.

Of all the traits examined, HT4 was the best single trait for improvement of VALUE. Such superior discrimination of Fraser fir genetic potential at 4 years, in comparison with 8 years, resulted from a decline in additive genetic variability for many traits over the same period.

As the potential gains identified in this study are transferred into production populations, Christmas tree growers stand to reap substantial benefits. Gains to the North Carolina state Fraser fir industry should result in increased financial revenue that is several orders of magnitude greater than the costs incurred in achieving those genetic gains.

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