Genetic variation in tree structure and its relation to size in Douglas-fir. II. Crown form, branch characters, and foliage characters

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Genetic variation and covariation among traits of tree size and structure were assessed in an 18-year-old Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) genetic test in the Coast Range of Oregon. Considerable genetic variation was found for relative crown width; stem increment per crown projection area; leaf area and branch weight relative to crown size; branch diameter and length adjusted for stem size; branch stoutness; cross-sectional area of branches per crown length; and needle size. Little genetic variation was found for branch numbers per whorl, branch angle, and specific leaf area. At both the phenotypic and genetic level, large trees growing well relative to growing space had tall, narrow crowns, high leaf areas per crown projection area or branch length, greater partitioning to leaves versus branches, and stouter branches. Thus, large, efficient trees were those that invested more in the photosynthetic machinery of leaf area and the branch biomass necessary to support that leaf area, but distributed that leaf area over a greater vertical distance. Unfortunately, these traits also were associated with increased branchiness, and selection for these traits would be accompanied by reductions in harvest index and wood quality.

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La variabilité génétique et son degré de covariation parmi les caractères de dimension de l'arbre et de sa structure ont été étudiés au sein d'un test génétique âgé de 18 ans de Douglas taxifolié (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) localisé dans la chaîne côtière de l'Orégon. Une variabilité génétique importante fut observée pour la grandeur relative de la cime, l'accroissement de la tige par surface de projection de la cime, la surface foliaire et le poids des branches relativement à la grandeur de la cime, le diamètre et la longueur des branches ajustés pour la dimension de la tige, la robustesse des branches, la surface radiale des branches relativement à la grandeur de la cime, et la grandeur des aiguilles. Peu de variation génétique fut observée pour le nombre de branches par verticille, l'angle des branches et la surface foliaire spécifique. À la fois aux niveaux phénotypique et génétique, les arbres de forte dimension montrant une bonne croissance par rapport à l'espace disponible affichaient une cime grande et mince, des surfaces foliaires importantes par surface de projection de la cime ou longueur des branches, une répartition plus grande en faveur des aiguilles aux dépens des branches, et des branches plus robustes. En conséquence, les arbres de forte dimension et les plus efficaces étaient ceux investissant plus au niveau de l'appareil photosynthétique formé par la surface foliaire et au niveau de la biomasse formée par les branches nécessaires au support de la surface foliaire, tout en répartissant cette surface foliaire sur une distance verticale plus grande. Malheureusement, ces caractères étaient aussi associés à une branchaison accrue, et la sélection pour ces caractères serait accompagnée de réductions au niveau de la qualité du bois et de la proportion de la biomasse de la tige relativement à la biomasse totale.

[Traduit par la rédaction]

Introduction

The dry-matter production of a forest stand is linearly related to the amount of light intercepted by the foliage canopy (Montieth 1977; Charles-Edwards 1982; Cannell 1989). Light interception depends on the size and structure of tree crowns. A canopy of tall, narrow crowns may be expected to intercept more light and lead to increased stand productivity at higher latitudes (Jahnke and Lawrence 1965; Kellomäki et al. 1985; Kuuluvainen 1992). Stands of trees that layer leaves such that they have a higher leaf area per unit crown projection area, crown volume, or branch size may be expected to have higher leaf area indices, less photosynthate used in branch production, and higher productivities per unit area of land (Ford 1985; Kuuluvainen 1991). Crown structure also influences wood quality, particularly with respect to the size, number, and angle of knots. Inclusion of crown structure traits as selection criteria in tree-improvement programs could potentially improve unit-area forest productivity and value beyond that possible from selection for stem size alone. This approach to tree improvement has been called ideotype breeding (Cannell 1978; Dickmann 1985; St.Clair 1994).

The objectives of this study were to explore genetic variation and covariation among traits of tree structure and to examine the genetic and phenotypic relations of these traits to tree size. Because of the large number of traits considered, results are presented in two papers. The first paper (St.Clair 1994) considered traits of biomass partitioning, foliage efficiency (stem volume increment per unit leaf area), stem form (taper), and wood density and also examined traits of tree size in detail. This paper will expand on results of the first paper by considering the inheritance and relations among traits of crown structure including crown form, branch characters, and foliage characters, and relate these traits to tree size and biomass partitioning. Consideration of the inheritance and interrelations of traits of tree structure and size will allow evaluation of the potential to include these traits in a multiple-trait selection scheme designed to improve unit-area forest productivity and value. In addition, consideration of the relations between these traits and stem size

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will allow evaluation of the effects of conventional selection procedures on correlated responses of traits that may be related to stand productivity and value.

Materials and methods

Materials

Study trees were a random sample of 20 open-pollinated families from a thinning of an 18-year-old Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb) Franco) genetic test located in the Coast Range near Newport, Oreg. (44°30′N, 123°52′W) at 100 m elevation. Site and stand characteristics are described in St.Clair (1994). The spacing between trees was 2.4 × 3.0 m, and trees had been in competition for several years before measurement. The experimental design was a randomized block design with multiple-tree, noncontiguous plots. Two trees per family per block were sampled from each of six blocks for a total of 12 trees per family and 240 trees in total. Trees chosen for study were surrounded by competitor trees to eliminate any large effects of open space on one or more sides, and were free from major defects such as forks, large ramicorn branches, or signs of past damage.

Data collection

Field data were collected from January to March 1991. Stem dimensions, growth increment, wood density, and biomass of stemwood, stem bark, branches, and foliage were determined as described in St.Clair (1994). Only measurements concerned with crown dimensions, branch characters, and foliage characters are described in this paper. Crown radii were measured before felling as the distance from the center of the stem to the point directly below the longest branch in quadrants to the north and south; a clinometer was used to locate the point. Crown projection area was calculated as the area of a circle with a radius equal to the average of the crown radii in the north and south directions. After felling, the base of the live crown was determined as the whorl with live branches in three of four quadrants, and the number of live whorls was counted and crown length was measured. Relative crown width was calculated as the ratio of crown width (sum of the crown radii) to crown length. Live crown ratio was calculated as the proportion of the tree height that was live crown.

The live crown was divided into thirds, and a single sample whorl was chosen within each crown third, usually whorls two, four, and seven from the top. Campbell (1961) found considerable within-tree variation in Douglas-fir for branch number, size, and angle, and recommended three or four measurements per tree. Traits measured at each sample whorl included crown width, branch length, branch diameter, branch angle, number of branches within the whorl, number of branches between the whorl and the next lower whorl, and stem diameter. Crown width was measured as the distance across the sample whorl between the tips of the longest branches (as the tree lay on the ground). Branch length, diameter, and angle were measured on the largest measurable branch in the whorl (i.e., excluding branches underneath the stem as it lay on the ground). Branch diameter was measured at 8 cm from the stem. Branch stoutness was calculated as branch diameter relative to branch length. Branch angle was measured as degrees from the stem to a point on the branch at about one half of the branch length. Stem diameter was measured at about 20 cm below the bottom of the whorl. Interwhorl and intrawhorl branch numbers included only branches greater than 5 mm in diameter.

Crown width, branch diameter, and branch length at each sample whorl were adjusted for family differences in tree size by analysis of covariance procedures using stem diameter measured below the whorl as the covariate (Steel and Torrie 1980). Adjusted crown width, adjusted branch length and diameter, branch stoutness, and branch numbers per whorl are given as the average of the three sample whorls, unless otherwise noted. Branch number per crown length was estimated as the number of branches per whorl (both interwhorl and intrawhorl branches) multiplied by the number of whorls and divided by crown length. Branch cross-sectional area per crown length was estimated as the cross-sectional area of the largest branch at each sample whorl (calculated from branch diameter) multiplied by the number of intrawhorl branches and divided by crown length.

Crown volume was calculated as the sum of the crown volumes of each crown third, where the crown volume of each crown third was approximated by the area of a cylinder with a diameter equal to the crown width at the sample whorl and a length of one third of the total crown length. Crown surface area was calculated in a similar manner, as the sum of the surface area of three cylinders, but was highly correlated to crown volume; results are not presented. Crown volume and surface area were also calculated as the volume and surface area of a cone of length equal to the crown length and diameter equal to the crown width (as measured while the tree was standing), but results were highly correlated to the alternative measures using crown thirds and are not presented.

Leaf area and dry weight were determined from a random sample of needles taken from each crown third. Needle samples were sealed in plastic bags and stored in a cold room at 1°C until processing. Single-sided, projected leaf area was measured on a subsample of 60 needles per crown third per tree by using an electronic area meter. Oven-dried weight of the subsample was measured, and specific leaf area determined as the ratio of projected leaf area per needle to dry weight per needle. Leaf area and dry weight per 100 needles and specific leaf area are given as the average of the samples from the three crown sections, unless otherwise noted. The total leaf area of each crown third was determined by multiplying specific leaf area by the total foliage dry weight. Total projected leaf area per tree was estimated by summation over the three crown sections.

Analyses

Analyses of variance and covariance were used to estimate variance and covariance components and to test the null hypothesis of no variation among family means. Family differences were considered to be statistically significant if the probability of rejecting the null hypothesis of no family differences was 0.05 or less (i.e., $p < 0.05$); probabilities greater than 0.05 are reported so that readers may make their own judgements regarding the importance of family differences. Phenotypic and additive genetic coefficients of variation, estimated as the square root of the phenotypic or additive genetic variation divided by the mean, were used to compare levels of variation in different traits. Variance and covariance components were used to estimate genetic parameters including individual-tree heritabilities, expected genetic gains from mass selection, genetic correlations, and correlated responses to selection, as outlined in St.Clair (1994). For many applications in tree breeding, heritabilities of family means and genetic gains from family selection or combined family and within-family selection may be more appropriate; these may be derived from formulas in Falconer (1981). Note that this study was done at a single site, and estimates of heritability and genetic gain may be inflated if genotype × environment interaction was present for the traits in question.

Path analysis (Li 1975) was used to explore the direct and indirect associations of different branch traits with stem volume. Index selection procedures were used to evaluate responses to multiple-trait selection for volume combined with various potential ideotype traits (Lin 1978; Baker 1986). Index coefficients for Smith–Hazel indices and expected genetic gains from index selection were calculated by using the RESI program described by Cotterill and Dean (1990). Economic weights were chosen to give equal emphasis to all traits such that changes of one phenotypic standard deviation in each trait are of equal value (see Cotterill and Jackson 1985). Equal-emphasis economic weights were chosen because the relative values of different

TABLE 1. Overall means, ranges of individual-tree values and family means, phenotypic (CVP) and additive genetic (CVA) coefficients of variation, individual-tree heritabilities (h^2), and genetic gain per unit selection intensity from mass selection

Trait	Mean	Range of individuals	Range of families	CVP	CVA	h^2	Genetic gain	
							Absolute	%
Tree size and growth								
Stem volume (dm^3)	162	31–388	131–228	0.36	0.20	0.32	19	11.5
Total aboveground dry weight (kg)	95.2	19.4–215.9	78.4–127.7	0.35	0.19	0.31	10.1	10.6
Basal area at bh (cm^2)	262	62–535	223–359	0.30	0.17	0.33	26	10.0
Height (m)	14.5	9.9–18.4	13.6–15.5	0.10	0.04	0.17	0.2	1.6
Volume increment (dm^3/year)	22.0	4.5–50.3	17.6–31.5	0.36	0.22	0.38	3.0	13.5
Biomass partitioning								
Stemwood / total stem and branch	0.73	0.64–0.80	0.70–0.75	0.04	0.03	0.45	0.01	1.9
Foliage / total crown	0.44	0.29–0.56	0.41–0.48	0.10	0.05	0.28	0.01	2.7
Crown form								
Crown width per crown length (m/m)	0.465	0.327–0.684	0.411–0.504	0.13	0.08	0.32	0.020	4.2
Adjusted crown width (m)	2.31	1.74–2.99	2.08–2.45	0.11	0.05	0.25	0.06	2.7
Live crown ratio	0.67	0.53–0.82	0.62–0.73	0.08	0.04	0.23	0.01	1.8
Height to live crown (m)	4.8	2.6–7.3	4.1–5.5	0.17	0.05	0.07	0.1	1.2
Number of live whorls	8.6	6.0–11.0	8.1–9.3	0.10	0.03	0.09	0.1	0.9
Volume increment per CPA[1] ($m^3 \cdot year^{-1} \cdot m^{-2}$)	1384	480–2804	1086–1876	0.31	0.18	0.36	154	11.1
Foliage and branches relative to crown size								
Leaf area per CPA* (m^2/m^2)	4.11	1.41–11.31	3.27–5.46	0.33	0.22	0.45	0.60	14.6
Predicted leaf area† per CPA* (m^2/m^2)	4.16	1.79–8.37	3.52–5.08	0.27	0.14	0.29	0.32	7.7
Leaf area per branch length (m^2/m^1)	13.2	4.4–28.7	10.8–17.5	0.33	0.23	0.46	2.0	15.5
Leaf area per crown length (m^2/m)	6.64	2.12–13.43	5.24–9.01	0.31	0.22	0.51	1.06	16.0
Leaf area per crown surface area (m^2/m^2)	0.94	0.38–1.89	0.77–1.23	0.27	0.18	0.44	0.11	12.0
Leaf area per crown volume (m^2/m^3)	1.37	0.47–3.36	1.13–1.79	0.34	0.17	0.25	0.11	8.4
Branch wt per crown length (kg/m^1)	1.46	0.36–3.17	1.05–1.90	0.35	0.22	0.41	0.21	14.4
Branch wt per CPA* (kg/m^2)	0.89	0.29–1.69	0.70–1.21	0.31	0.21	0.46	0.13	14.4
Branch wt per crown volume (kg/m^3)	0.30	0.09–0.74	0.25–0.38	0.34	0.15	0.18	0.02	6.2
Branch characters								
Adjusted branch diameter (cm)	1.9	1.4–2.5	1.8–2.1	0.09	0.05	0.34	0.1	3.1
Adjusted branch length (m)	2.0	1.5–2.6	1.7–2.1	0.09	0.06	0.45	0.1	4.1
Branch stoutness (cm/m)	0.99	0.78–1.33	0.92–1.08	0.10	0.06	0.33	0.03	3.2
Total branch number per whorl	15.8	7.3–24.7	14.1–17.4	0.18	0.05	0.09	0.3	1.6
Intrawhorl branch number	7.7	4.0–12.7	6.9–8.8	0.19	0.06	0.10	0.1	1.9
Interwhorl branch number	8.2	2.3–17.3	6.6–9.6	0.31	0.02	0.01	0.0	0.2
Branch number per crown length (no/m)	14.1	8.3–21.4	12.4–15.6	0.18	0.08	0.20	0.5	3.5
Branch area per crown length (cm^2/m)	21.5	4.9–45.2	16.6–29.1	0.33	0.22	0.45	3.2	14.8
Branch angle (degrees)	55	32–78	51–59	0.13	0.03	0.06	0	0.7
Foliage characters								
Area per 100 needles (cm^2)	31.7	22.6–44.3	29.1–35.0	0.13	0.08	0.35	1.4	4.4
Dry weight per 100 needles (g)	0.529	0.313–0.810	0.473–0.605	0.16	0.09	0.33	0.00	5.4
Specific leaf area (cm^2/g)	60.9	48.8–88.9	57.2–64.7	0.10	0.03	0.08	0.5	0.8

*CPA, crown projection area.

†Leaf area predicted based on the equation ln(leaf area) = −1.3387 + 1.1160 ln(basal area sapwood) as derived from data of this study.

ideotype traits are presently unknown; no data exist on the relationship between hypothesized ideotype traits and stand productivity and value.

Results and discussion

Variation and inheritance of crown structure

Relative crown width, measured both as crown width per unit crown length and crown width adjusted for stem diameter below a sample whorl, differed significantly (defined as $p < 0.05$) among families and was highly heritable (h^2 = 0.32 and 0.25, respectively; Table 1). The two measures of crown width were not strongly correlated phenotypically (r_p = 0.28) but were strongly correlated genetically (r_a = 0.99; Table 2). Thus, selection for a narrow crown relative to crown length would be equivalent to selection for a narrow crown relative to stem diameter. Although selection for a narrow crown did appear to be promising, estimates of expected genetic gains were only moderate (4.2 and 2.7% per unit selection intensity) owing to the relatively small amount of phenotypic variation (Table 1). The value of small changes in crown width in terms of the hypothesized increase in stand productivity is unknown, however.

Evidence from crosses involving narrow-crowned parents of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) indicates that the inheritance of crown shape may sometimes be attributed to a single, dominant gene, perhaps a gene controlling apical dominance (Karki and Tigerstedt 1985). These parents were, however, extremely narrow-crowned variants. Velling and Tigerstedt (1984) evaluated crown width relative to stem height in a Scots pine progeny test of parents of more typical crown shapes and found strong polygenic inheritance with an estimate of heritability ($h^2 = 0.31$) similar to that of the present study ($h^2 = 0.32$). Although these researchers did not estimate expected genetic gains, phenotypic variation in their studies seemed to be of a similar magnitude as the present study.

Live crown ratio differed significantly among families and was heritable ($h^2 = 0.23$), but phenotypic variation and expected genetic gains were low (Table 1). Foster (1986) also found strong inheritance ($h^2 = 0.47$) of live crown ratio after crown closure in a loblolly pine (*Pinus taeda* L.) stand. Height to live crown and number of live whorls did not differ significantly among families ($p = 0.21$ and 0.16, respectively) and estimates of heritability ($h^2 = 0.07$ and 0.09, respectively) and expected genetic gains (1.2 and 0.9%, respectively) were low. In stands of closed canopies, as in this genetic test, the base of the live crown of an individual is probably strongly affected by the crowns of adjacent trees. The result is that the height to live crown, and indirectly the number of live whorls, is more a function of the stand and the canopy than of the individual and its own crown, thereby leading to low phenotypic variation and high environmental variation relative to genetic variation.

Volume increment per crown projection area differed significantly among families and was highly heritable ($h^2 = 0.36$; Table 1). Considerable phenotypic and genetic variation was found in volume increment per crown projection area, and large genetic gains (11.1%) may be expected from selection and breeding for this trait. Volume increment per crown projection may be a valuable ideotype trait. It represents the efficiency of stemwood production relative to the space occupied by an individual tree and may be expected to be related to productivity per unit area of land.

All measures of leaf area and branches relative to crown dimensions differed significantly among families and had high estimates of heritability (Table 1). Different measures of leaf area relative to crown dimensions were highly correlated, both phenotypically and genetically (Table 3); trees that had large leaf areas per crown projection area also had large leaf areas per crown lengths, crown surface areas, and crown volumes. All measures of branch weight relative to crown dimensions were highly correlated as well (Table 4). Furthermore, leaf areas per crown dimensions were highly correlated to branch weights per crown dimensions (e.g., $r_p = 0.79$ and $r_a = 1.00$ for leaf area per crown projection area correlated with branch weight per crown projection area). From this, it might be concluded that branches are required to support leaf area; however, partitioning to leaves versus branches was phenotypically and genetically variable despite a high correlation between leaf area, or biomass, and branch weight.

Leaf area per crown projection area may be considered to represent a measure of leaf area index based on individual trees, and as such, may represent an important ideotype trait for improving productivity on a unit-area basis. A drawback of including leaf area per crown projection area in selection criteria is that leaf area is difficult and expensive to measure directly and requires destructive harvest. Leaf area per crown projection area where leaf area was predicted indirectly based on sapwood area at breast height was phenotypically ($r_p = 0.72$) and genetically ($r_a = 0.76$) correlated with the same trait where leaf area was measured directly. However, the relative efficiency of selection for leaf area per crown projection based on indirect prediction of leaf area (i.e., genetic gain from indirect selection relative to direct selection) was only 0.64. An alternative indirect measure of leaf area per crown projection area is leaf area per branch length ($r_p = 0.87$ and $r_a = 1.01$). The relative efficiency of selection for leaf area per crown projection area based on leaf area per branch length was 1.03. Leaf area per branch length was estimated as the total area of leaves in a crown section relative to the longest branch sampled in the sample whorl of that crown section. A more practical measure of leaf area per branch length would be the leaf area (or biomass) of a sample branch relative to the length of a sample branch. Unfortunately, I could not evaluate this measure of leaf area per branch length because the branch sampled for branch length in this study was not the same as that sampled for branch and foliage biomass. More research is needed to explore whether leaf area per branch length given a single sample branch is highly correlated with total-tree leaf area per crown projection area.

Adjusted branch diameter and branch length differed significantly among families and was highly heritable ($h^2 = 0.34$ and 0.45, respectively; Table 1). Although genetic differences were relatively large, phenotypic differences were small, and thus, expected genetic gains were only moderate (3.1 and 4.1%, respectively). The biological and economic importance of small differences in branch size in terms of effects on wood quality or productivity is unknown, however. Adjusted branch diameter and adjusted branch length were not as strongly correlated ($r_p = 0.45$ and $r_a = 0.59$) as one might expect, given that they are both a measure of size. As a result, branch stoutness differed significantly among families and had a high estimate of heritability ($h^2 = 0.33$).

As expected, adjusted branch diameter, branch length, and crown widths decreased from the top sample whorl to the bottom sample whorl (Table 5). Heritability estimates for adjusted branch diameter and length were high for all sample whorls, although estimates of the middle whorl were slightly lower. Heritability estimates for branch stoutness and adjusted crown widths were greatest for the lower sample whorl and least for the upper sample whorl.

In contrast to branch size, families did not differ significantly in total branch number per whorl, or in intrawhorl or interwhorl branch numbers ($p = 0.15$, 0.15, and 0.44, respectively), and estimates of heritability and genetic gain were low (Table 1). Interwhorl branch number, in particular, was highly variable phenotypically, but little of the variation was heritable. The number of branches per unit crown length did differ significantly among families, however, and was moderately heritable ($h^2 = 0.20$). Furthermore, this trait was phenotypically ($r_p = 0.84$) and genetically ($r_a = 0.73$) correlated with the number of branches per whorl.

Number of branches per whorl did not differ greatly between the top, middle, and lower crown sections (Table 5). Estimates of heritability when each sample whorl is considered separately were always low, and the sample whorl in the middle crown section did not exhibit any heritable variation. Lack of or low heritability may be due to large environmental variability during the years when those whorls were being formed. The middle sample whorl was formed 4 years earlier at 14 years of age. One might speculate that at that age large differences in the amount of crown closure around each tree may have existed, thereby leading to large differences in the environment experienced by each tree.

TABLE 2. Phenotypic (above diagonal) and genetic (below diagonal)

	CWL	CWA	LCRTO	HTLC	NWRHL	VOLCPA	LACPA	LABL	BDA
CWL		0.28	−0.49	0.20	−0.39	−0.61	−0.50	−0.24	0.02
CWA	0.99		−0.14	0.13	−0.11	−0.19	−0.19	−0.10	0.23
LCRTO	−0.72	−0.06		−0.83	0.73	0.11	0.29	0.30	0.12
HTLC	0.67	−0.36	−0.93		−0.49	0.32	0.01	0.04	0.04
NWHRL	−0.66	−0.01	1.12	−1.44		0.26	0.41	0.43	0.15
VOLCPA	−0.78	−0.81	0.66	−0.44	0.46		0.73	0.61	0.11
LACPA	−0.61	−0.31	0.96	−0.73	0.97	0.86		0.87	0.16
LABL	−0.59	−0.14	0.87	−0.55	0.77	0.82	1.01		0.24
BDA	−0.18	0.20	0.66	−0.12	0.59	0.73	0.84	0.95	
BLA	0.75	1.00	0.12	−0.11	0.17	−0.26	0.16	0.26	0.59
BRST	−1.09	−0.97	0.58	−0.19	0.41	1.08	0.78	0.74	0.27
BN	0.33	0.16	−0.01	0.05	0.28	0.19	0.89	0.95	1.27
BNW	0.22	0.15	0.74	−1.26	0.74	−0.04	0.90	0.83	0.64
BNI	0.92	0.33	−1.80	3.15	−0.53	0.94	1.77	2.19	4.06
BNCL	0.62	0.45	−0.45	0.16	−0.13	−0.39	0.03	0.01	0.19
BACL	0.01	0.30	0.63	−0.53	0.73	0.48	0.86	0.86	0.95
BA	1.08	0.56	−1.04	0.46	−1.77	−1.12	−0.70	−0.46	0.28
NA	−0.16	0.04	0.47	−0.32	0.13	0.21	0.13	0.22	0.46
NDW	−0.40	−0.31	0.50	−0.37	0.17	0.39	0.15	0.18	0.59
SLA	1.03	0.97	−0.65	0.77	−0.43	−0.75	−0.22	−0.08	−0.77

NOTE: Values of $-0.12 \geq r_p \geq 0.12$ are significantly different from 0 at the 5% probability level for all phenotypic correlations presented (based on Table A 11(*i*) in Snedecor and Cochran (1980)). Traits are identified as crown width per crown length (CWL), adjusted crown width (CWA), live crown ratio (LCRTO), height to live crown (HTLC), number of live whorls (NWHRL), volume increment per crown projection area (VOLCPA), leaf area per crown projection area (LACPA), leaf area per branch length (LABL), adjusted branch diameter (BDA), adjusted branch length (BLA), branch stoutness (BRST), total branch number per whorl (BN), intra-whorl branch number (BNW), interwhorl branch number (BNI), branch number per crown length (BNCL), cross-sectional area of branches per crown length (BACL), branch angle (BA), needle area per 100 needles (NA), needle dry weight per 100 needles (NDW), and specific leaf area (SLA).

Branch cross-sectional area per unit crown length differed significantly among families and was highly heritable (h^2 = 0.45), with large genetic gains possible (14.8%). This trait is a function of both the number of intrawhorl branches and branch size, and represents the size and number of knots that may be expected. A reduction in this trait may be important for improving wood quality.

Branch angle decreased from the top sample whorl to the bottom (Table 5). When averaged over all three sample whorls, branch angle did not differ significantly among families (p = 0.25) and had a low estimate of heritability (h^2 = 0.06; Table 1). Branch angle of the lowest sample whorl, however, did differ significantly among families and was heritable (h^2 = 0.23; Table 5). One might speculate that the environmental influence was minimal in the lower crown section owing to a uniform interaction of crowns at that height. Without further knowledge of the reasons for differences in heritability estimates within the crown, one can only conclude, based on this study, that branch angle is not strongly inherited.

Heritability estimates for branch characters were compared with those of previous studies (Table 6). The low heritability of branch number per whorl was corroborated by results of Merrill and Mohn (1985) but was less than reported by King et al. (1992) and Velling and Tigerstedt (1984). The high estimate of heritability for branch diameter adjusted for stem size was greater than that of other studies. Most previous studies found a much higher estimate of heritability for branch angle.

Families differed significantly in projected leaf area per 100 needles and dry weight per 100 needles; heritability estimates (h^2 = 0.35 and 0.33, respectively) and expected genetic gains (4.4 and 5.4%, respectively) were moderate (Table 1). Needle area was highly correlated to needle dry weight, both phenotypically (r_p = 0.82) and genetically (r_a = 0.93; Table 2). Families thus did not differ significantly in specific leaf area (p = 0.17), and estimates of heritability (h^2 = 0.08) and expected genetic gain (0.8%) were low (Table 1).

The overall mean specific leaf area (60.9 cm^2/g) was somewhat lower than most estimates reported for Douglas-fir. Borghetti et al. (1986) report an overall mean specific leaf area of 65.9 cm^2/g in a detailed study of leaf area distribution in a 25-year-old Douglas-fir plantation in central Italy. Dry weight per 100 needles was much lower in their study than in this one (0.39 g compared with 0.53 g). Waring et al. (1980) use a value of 63.6 cm^2/g for the specific leaf area of Douglas-fir. Gholz et al. (1976) report values ranging from 70.8 to 82.4 cm^2/g for the specific leaf areas of old-growth stands. Del Rio and Berg (1979) report mean specific leaf areas of 72.2 cm^2/g for older needles and 85.7 cm^2/g for current needles of young understory trees, and 54.0 cm^2/g for older needles and 63.8 cm^2/g for current needles of young open-grown trees. The latter three studies report specific leaf areas in terms of total surface area of needles. For comparison with this study, total leaf area was converted to projected leaf area by correcting for the roundness of needles by dividing by 1.18, and then dividing by 2 to convert from all-sided to projected leaf area (see Del Rio and Berg 1979).

Few studies have considered the inheritance of needle size and specific leaf area. Magnussen et al. (1986) found significant differences in needle dry weight and specific leaf area among jack pine (*Pinus banksiana* Lamb.) provenances, as well as significant phenotypic differences among trees within provenances. Needle area and dry weight differed significantly among seven clones of both Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) (Cannell et al. 1983), although no mention is made of whether clones differed in specific leaf areas.

Needle size as measured by both leaf area and dry weight decreased from the top crown third to the bottom crown correlations among traits of crown structure in Douglas-fir

BLA	BRST	BN	BNW	BNI	BNCL	BACL	BA	NA	NDW	SLA
0.34	−0.29	−0.10	0.18	−0.22	0.16	0.19	0.00	0.03	−0.06	0.13
0.32	−0.12	0.07	0.07	0.03	0.06	0.14	0.27	0.05	0.02	0.03
0.07	0.04	0.06	−0.01	0.07	−0.06	0.16	−0.06	0.02	0.07	−0.08
0.00	0.07	0.18	0.06	0.17	0.05	0.01	0.17	0.10	0.16	−0.16
0.07	0.11	0.09	0.04	0.08	0.13	0.32	0.00	−0.03	0.11	−0.22
−0.22	0.38	0.31	0.07	0.31	0.00	0.21	0.11	0.10	0.27	−0.32
−0.15	0.34	0.37	0.26	0.26	0.19	0.40	0.06	0.06	0.10	−0.08
−0.08	0.35	0.39	0.33	0.25	0.20	0.54	0.13	0.12	0.17	−0.12
0.45	0.48	0.10	−0.03	0.13	−0.02	0.49	0.00	0.14	0.18	−0.14
	−0.51	0.05	0.03	0.04	0.00	0.26	−0.03	0.16	0.16	−0.07
−0.61		0.07	0.00	0.08	−0.01	0.27	0.04	0.01	0.06	−0.11
0.34	0.83		0.47	0.86	0.84	0.41	0.19	0.07	0.12	−0.13
0.55	0.14	1.15		−0.05	0.47	0.68	0.10	−0.09	−0.07	0.00
0.17	3.29	1.66	2.65		0.68	0.06	0.16	0.13	0.17	−0.15
0.19	−0.05	0.73	0.74	1.45		0.38	0.10	−0.05	−0.06	0.01
0.63	0.26	0.91	0.66	2.41	0.30		0.10	0.05	0.13	−0.17
0.30	−0.34	0.80	0.29	2.80	1.13	0.00		0.05	0.10	−0.08
0.44	−0.04	−0.59	−0.13	−2.24	−0.80	0.26	−0.38	–	0.82	−0.05
0.25	0.20	−0.54	−0.59	−0.96	−0.79	0.17	−0.47	0.93		−0.61
0.28	−0.74	0.30	1.63	−2.49	0.57	0.11	0.55	−0.40	−0.68	

TABLE 3. Phenotypic (above diagonal) and genetic (below diagonal) correlations among different measures of leaf area relative to crown dimensions

	LACPA	LACL	LACSA	LACV
LACPA		0.79	0.91	0.70
LACL	0.90		0.94	0.67
LACSA	0.94	0.99		0.74
LACV	1.01	0.74	0.83	

NOTE: Traits are identified as leaf area per crown projection area (LACPA), leaf area per crown length (LACL), leaf area per crown surface area (LACSA), and leaf area per crown volume (LACV).

TABLE 4. Phenotypic (above diagonal) and genetic (below diagonal) correlations among different measures of branch weight relative to crown dimensions

	BRCPA	BRCL	BRDEN
BRCPA		0.80	0.65
BRCL	0.94		0.70
BRDENX	1.02	0.86	

NOTE: Traits are identified as branch weight per crown projection area (BRCPA), branch weight per crown length (BRCL), and branch weight per crown volume (BRCV).

third (Table 5). Specific leaf area increased from top to bottom. Borghetti et al. (1986) found a similar effect of crown position on needle size and specific leaf area. The decrease in needle size and increase in specific leaf area may be attributed to acclimation to different light conditions within the canopy and differentiation into sun and shade leaves (Borghetti et al. 1986).

Relations among tree size, biomass partitioning, and crown structure traits

Phenotypic relations of tree size with biomass partitioning and crown structure provide some insight into the morphological and physiological bases of tree growth, whereas genetic relations are of interest for exploring correlated responses to selection. In this study, tree size refers to different measures of stem size and biomass components. Different tree size traits are highly correlated (St.Clair 1994), and stem volume is used below as a general measure of tree size.

At the phenotypic level, stem volume was strongly correlated with traits of crown form, especially with volume increment per crown projection area ($r_p = 0.82$) and with measures of leaf area and branch weight relative to crown dimensions (e.g., $r_p = 0.62$ for leaf area per crown projection area). Larger trees tended to have tall, narrow crowns as measured by crown width relative to crown length ($r_p = -0.25$). Tree size was also correlated with a greater number of live whorls ($r_p = 0.40$) and a somewhat greater live crown ratio ($r_p = 0.18$), although a positive association with increased height to live crown was also found ($r_p = 0.31$). Tree size was moderately positively correlated with needle size and negatively correlated with specific leaf area; large trees tended to have heavier, stouter needles.

Greater partitioning to the stem (increased harvest index) was phenotypically associated with a relatively small crown as indicated by correlations with a narrow crown ($r_p = -0.22$ for crown width relative to length and $r_p = -0.10$ for crown width adjusted for stem diameter), reduced live crown ratio ($r_p = -0.38$), greater height to live crown ($r_p = 0.39$), and smaller adjusted branch diameters and lengths ($r_p = -0.24$ and -0.33, respectively; Table 7). Narrow-crowned trees, as measured by crown width relative to crown length, tended to have greater volumes per crown projection areas ($r_p = -0.61$), greater live crown ratios ($r_p = -0.49$), and greater leaf areas per crown projection areas ($r_p = -0.50$) (Table 2). Thus, narrow-crowned trees appeared to have attributes that may be expected to lead to greater production per unit of land area.

Large trees tended to have both more branches per whorl ($r_p = 0.37$) and a greater adjusted branch diameter ($r_p = 0.27$). Tree size was associated with stout branches that were thick relative to their length ($r_p = 0.24$). Path analysis in which stem volume was related to branch number per whorl and adjusted branch diameters and lengths indicated that branch number and adjusted branch diameter had mod-

TABLE 5. Means and heritability (h^2) estimates of traits measured within each of three crown sections

Trait	Mean			h^2		
	Top	Middle	Bottom	Top	Middle	Bottom
Adjusted branch diameter	1.3	2.0	2.4	0.26	0.15	0.23
Adjusted branch length	1.2	2.1	2.6	0.39	0.26	0.37
Adjusted crown width	1.2	2.2	3.5	0.00	0.17	0.19
Branch stoutness	1.04	0.98	0.91	0.13	0.21	0.26
Total branch number per whorl	16.2	16.0	15.2	0.06	0.00	0.11
Intrawhorl branch number	7.3	7.6	8.0	0.11	0.00	0.08
Interwhorl branch number	8.9	8.4	7.1	0.00	0.00	0.09
Branch angle	49	55	62	0.00	0.07	0.23
Area per 100 needles (cm^2)	344	324	308	0.39	0.35	0.31
Dry weight per 100 needles (g)	0.642	0.567	0.482	0.45	0.36	0.29
Specific leaf area (cm^2/g)	54.0	57.7	64.6	0.08	0.08	0.07

TABLE 6. Selected heritability estimates from various studies

Trait	Species	h^2	Reference
Relative branch diameter	Douglas-fir	0.34	This study
	Douglas-fir	0.26	King et al. 1992
	Scots pine	0.17	Velling and Tigerstedt 1984
Branch number per whorl	Douglas-fir	0.09	This study
	Douglas-fir	0.19	King et al. 1992
	Scots pine	0.18	Velling and Tigerstedt 1984
	Norway spruce	0.01	Merrill and Mohn 1985
Branch angle	Douglas-fir	0.06	This study
	Douglas-fir	0.73	King et al. 1992
	Douglas-fir	0.49	Birot and Christophe 1983
	Scots pine	0.22	Velling and Tigerstedt 1984
	Norway spruce	0.44	Merrill and Mohn 1985

erate direct effects on stem volume, but the effect of adjusted branch length on stem volume was primarily through an indirect effect of branch diameter with no direct effect by itself (Table 8). Stout branches were related to greater partitioning to leaves versus branches ($r_p = 0.27$; Table 7) and greater leaf areas per crown projection area ($r_p = 0.34$; Table 2); a thick, short branch may be necessary to support a large leaf area.

Conclusions from genetic correlations between size and structure were similar to those from phenotypic correlations, although genetic correlations often differed in magnitude, and sometimes in sign, from phenotypic correlations, particularly when biomass partitioning was involved. Genetic correlations involving traits with low heritabilities should be judged with appropriate skepticism, however, because standard errors of genetic correlations are inversely related to heritabilities (Falconer 1981). On a genetic level, tree size was associated with a tall narrow crown ($r_a = -0.48$), greater volume per crown projection area ($r_a = 0.85$), greater leaf area and branch weight relative to crown dimensions (e.g., $r_a = 0.98$ for leaf area per crown projection area), greater live crown ratio ($r_a = 0.76$), greater number of live whorls ($r_a = 0.58$), and reduced height to live crown ($r_a = -0.52$) (Table 7).

Tree size was also genetically correlated with a reduced harvest index ($r_a = -0.65$) and increased partitioning to leaves versus branches ($r_a = 0.36$) (St.Clair 1994). Paradoxically, harvest index was strongly correlated with a decreased live crown ratio ($r_a = -1.00$) despite the negative correlation between tree size and harvest index and the positive correlation between tree size and live crown ratio. Partial correlations indicated that the genetic correlation between stem volume and harvest index became weakly positive when live crown ratio was held constant ($r_a = 0.23$), the correlation between stem volume and live crown ratio became zero when harvest index was held constant ($r_a = 0.03$), and the correlation between harvest index and live crown ratio remained strongly negative when volume was held constant ($r_a = -1.28$). Thus, the expected relationship between increased stem volume and increased harvest index (greater partitioning to the stem and reduced partitioning to the crown) might have been observed if live crown ratios had not differed among genotypes. Furthermore, a reduced harvest index was genetically correlated with a wide crown when relative crown width was measured as crown width adjusted for stem diameter below the sample whorls ($r_a = -0.44$), but was correlated with a narrow crown when relative crown width was measured as crown width per unit crown length ($r_a = 0.33$). A narrow crown as measured by crown width relative to crown length was genetically correlated with greater volume increment per crown projection area ($r_a = -0.78$), greater partitioning to leaves versus branches ($r_a = -0.81$), greater live crown ratio ($r_a = -0.72$), and greater leaf area per crown projection area ($r_a = -0.61$). These results, taken together, indicate that the greater partitioning to the crown versus stem of families of large trees was more a

Table 7. Phenotypic and genetic correlations of tree size and biomass partitioning with crown structure in Douglas-fir

	Phenotypic correlation						Genetic correlation					
	VOL	TDW	BA	HT	WDSB	LFCR	VOL	TDW	BA	HT	WDSB	LFCR
CWL	−0.25	−0.21	−0.14	−0.46	−0.22	−0.26	−0.48	−0.35	−0.38	−0.66	0.33	−0.81
CWA	−0.03	−0.02	−0.03	0.01	−0.10	−0.14	−0.27	−0.04	−0.16	−0.57	−0.44	−0.82
LCRTO	0.18	0.24	0.17	0.16	−0.38	−0.09	0.76	0.82	0.66	0.91	−1.00	−0.01
HTLC	0.31	0.23	0.25	0.41	0.39	0.10	−0.52	−0.67	−0.40	−0.69	1.02	0.50
NWHRL	0.40	0.46	0.41	0.36	−0.32	−0.09	0.58	0.70	0.50	0.51	−1.54	−0.44
VOLCPA	0.82	0.74	0.77	0.76	0.22	0.23	0.85	0.74	0.83	0.80	−0.30	0.86
LACPA	0.62	0.67	0.61	0.52	−0.12	0.34	0.98	0.98	0.94	1.01	−0.79	0.17
LABL	0.73	0.79	0.74	0.58	−0.25	0.24	0.96	0.98	0.91	1.07	−0.77	0.16
BDA	0.27	0.28	0.25	0.27	−0.24	−0.08	1.18	1.19	1.15	1.18	−0.81	−0.02
BLA	0.10	0.14	0.09	0.11	−0.33	−0.39	0.31	0.47	0.38	0.08	−0.50	−0.63
BRST	0.25	0.22	0.24	0.22	0.06	0.27	0.79	0.64	0.70	0.98	−0.19	0.80
BN	0.37	0.40	0.35	0.40	−0.05	0.09	0.26	0.35	0.36	−0.01	−0.85	0.51
BNW	0.21	0.26	0.25	0.10	−0.24	−0.03	0.10	0.37	0.19	−0.09	−0.84	−0.35
BNI	0.30	0.30	0.25	0.40	0.08	0.12	0.90	0.64	1.15	0.18	−1.73	3.02
BNCL	0.06	0.12	0.11	−0.02	−0.12	0.06	−0.39	−0.26	−0.26	−0.75	−0.33	−0.17
BACL	0.50	0.58	0.56	0.28	−0.42	−0.13	0.81	0.95	0.86	0.62	−0.82	−0.26
BA	0.16	0.15	0.14	0.20	0.06	0.10	−1.07	−1.00	−0.93	−1.47	0.02	0.33
NA	0.17	0.15	0.15	0.19	−0.07	−0.02	0.40	0.44	0.38	0.50	−0.26	−0.25
NDW	0.37	0.37	0.35	0.40	−0.04	0.08	0.39	0.28	0.35	0.48	−0.21	0.11
SLA	−0.40	−0.42	−0.38	−0.41	−0.02	−0.18	−0.23	0.19	−0.16	−0.31	0.14	−0.95

Note: Values of $-0.12 \geq r_p \geq 0.12$ are significantly different from 0 at the 5% probability level for all phenotypic correlations presented (based on Table A 11(*i*) in Snedecor and Cochran (1980)). Traits are identified as stem volume (VOL), total above-ground dry weight (TDW), basal area at 1.3 m (BA), height (HT), stemwood to stem plus branch dry weight (WDSB), leaf to crown dry weight (LFCR), and otherwise as in Table 2.

Table 8. Path coefficient analysis of direct and indirect phenotypic associations of crown variables with stem volume

	Crown variables			
	Intrawhorl branch number	Interwhorl branch number	Adjusted branch diameter	Adjusted branch length
Direct effect	0.228	0.261	0.268	−0.030
Indirect effects				
Via intrawhorl branch number	—	0.001	0.003	0.018
Via interwhorl branch number	0.001	—	0.044	0.022
Via adjusted branch diameter	0.003	0.046	—	0.130
Via adjusted branch length	−0.002	−0.003	−0.014	—
Totals	0.229	0.305	0.301	0.141

consequence of vertical crown extension rather than horizontal crown extension.

Genetic correlations of tree size with branch characters were unfavorable from the standpoint of simultaneous improvement of both stem volume and wood quality. In particular, tree size was genetically correlated with larger diameter branches (r_a = 1.18), steeper angled branches (r_a = −1.07), and more branches per whorl (r_a = 0.26) (although branch angle and branch number per whorl had low heritabilities and, thus, large standard errors for the genetic correlations). Increased size, angle, and frequency of knots results in less high-value clearwood and a reduction in structural strength in sawn lumber.

To summarize, at both the phenotypic and genetic levels, trees that were large and grew well relative to crown projection area were those that invested more into the photosynthetic machinery of leaf area and the branch biomass necessary to support that leaf area, but did not necessarily display that leaf area over a large horizontal distance, instead displaying it vertically. Thus, large trees that were efficient producers of wood relative to growing space had full, tall, narrow crowns. This crown structure is in agreement with theoretical models of the effect of crown shape on light interception and stand productivity (Jahnke and Lawrence 1965; Kellomäki et al. 1985). It also is in general agreement with the empirical results of Velling and Tigerstedt (1984) and Kuuluvainen (1988). Velling and Tigerstedt (1984) found a positive, but weak, association between stem size and a tall, narrow crown in Scots pine. Although Kuuluvainen (1988) found a weak negative association between these traits in Norway spruce, volume increment per crown projection area was positively related to a tall, narrow crown with a greater live crown ratio and greater dry weight of needles per unit crown volume. In both studies, a positive association was found between a tall, narrow crown and greater partitioning to the stem, whereas in this study, the genetic association was negative. Unfortunately, no studies, to my knowledge, report genetic correlations among traits of tree size, biomass partitioning, and crown form, although Velling and Tigerstedt (1984) did present correlations of family means.

TABLE 9. Selected estimates of correlations between tree size and branch traits from various studies

Branch trait	Tree size trait	Species	Type*	r^2	Reference
Relative branch diameter	Stem volume	Douglas-fir	P	0.27	This study
			G	1.18	
	Stem volume	Douglas-fir	P	−0.26	King et al. 1992
			G	−0.75	
	Stem fresh weight	Scots pine	P	−0.21	Velling and Tigerstedt 1984
			F	−0.58	
Branch number per whorl	Stem volume	Douglas-fir	P	0.37	This study
			G	0.26	
	Stem volume	Douglas-fir	P	0.04	King et al. 1992
			G	0.71	
	Stem volume	Douglas-fir	P	0.51	Campbell 1963
	Stem fresh weight	Scots pine	P	0.32	Velling and Tigerstedt 1984
			F	0.63	
	DBH	Norway spruce	P	0.34	Merrill and Mohn 1985
			G	0.07	
Branch angle	Stem volume	Douglas-fir	P	0.16	This study
			G	−1.07	
	Stem volume	Douglas-fir	P	−0.14	King et al. 1992
			G	0.18	
	Stem volume	Douglas-fir	P	0.05	Campbell 1963
	Stem fresh weight	Scots pine	P	−0.13	Velling and Tigerstedt 1984
			F	0.11	
	DBH	Norway spruce	P	−0.05	Merrill and Mohn 1985
			G	−0.04	

*Types of correlations are: P, phenotypic correlations of individual trees; F, phenotypic correlations of family means; G, genetic correlations

The results of this study are in disagreement with the findings of Smith and Long (1989). Working with lodgepole pine, they found that high stand growth was associated with short, compact crowns with large leaf areas per crown volume. They attributed the greater stand growth to decreased partitioning to branches and greater partitioning to stem and needles. They maintain that individual trees and stands of trees with deep, full crowns and high growth rates are not efficient in wood production relative to growing space. The present study, however, found that short, compact crowns were associated with low leaf areas per crown volume, as well as per crown projection area, and that short, compact crowns were associated with increased partitioning to branches and decreased partitioning to stem and needles. Although I did not have data on stand productivity, individual trees with deep, full crowns and high growth rates were more efficient producers of wood as measured by volume increment per crown projection area.

The relation between stem size and branch number was similar to that of previous studies (Table 9). Campbell (1963) found a strong positive phenotypic correlation between these traits in Douglas-fir ($r_p = 0.51$), and King et al. (1992), also in Douglas-fir, found a strong positive genetic correlation ($r_a = 0.71$) but a weak phenotypic correlation ($r_p = 0.04$). Genetic and phenotypic correlations in other species were either positive or near zero (Velling and Tigerstedt 1984; Merrill and Mohn 1985). Other studies differed from this study, however, by the estimates of correlations between stem size and relative branch diameter and between relative branch diameter and branch number. Other studies found negative correlations between stem size and relative branch diameter and between relative branch diameter and branch number (Table 9); correlations in this study were positive. Furthermore, Campbell (1963) and King et al. (1992) found negative partial correlations between branch number and branch diameter with constant stem volume ($r_p = -0.43$ and -0.10, respectively), whereas the partial correlation in this study was weakly positive ($r_p = 0.13$). Thus, evidence from other studies indicates that a tradeoff exists between branch number and branch diameter, whereas this study indicates that both branch number and branch diameter are associated with larger stems. The primary difference between previous studies and this study is that trees from previous studies were open grown or had minimum intertree competition. One possibility for the differences with this study is that both large branch size and large number of branches are important for supporting a large photosynthetic area under more competitive situations.

Although other studies did not consider branch length adjusted for differences in stem size, comparisons of the relative importance of branch length versus branch diameter to stem volume is possible through path analysis. Results from Campbell (1963) agree with this study in that branch diameter is more important to stem volume than is branch length. Results from King et al. (1992) also agree that branch diameter is more important (using genetic instead of phenotypic correlations), but the direct association of branch length with stem volume is nearly as strong as that of branch diameter.

Cannell et al. (1983) and Ford (1985) suggest that productive conifer genotypes are tall with sparse branching. Results from this study and others cited above suggest that productive conifer genotypes are not necessarily associated with sparse branching. In general, large trees and trees that grew well per crown projection areas were often correlated with greater branch numbers per whorl, but no clear relations existed with branch numbers per crown length or with partitioning to branches versus stemwood. Ford (1985) suggests that the ideal branching pattern is a balance between

TABLE 10. Expected correlated responses from selection for volume alone and for multiple-trait index selection (percent change from parental means per unit selection intensity)

	Traits included in selection index									
Correlated traits	VOL	VOL VOLCPA	VOL CWL	VOL LCRTO	VOL LACPA	VOL LABL	VOL BRST	VOL CWL LCRTO	VOL LABL LFCR	VOL BRST LFCR
Stem volume (dm^3)	11.5	11.6	10.7	12.4	13.8	13.4	13.1	11.7	13.2	12.5
Biomass partitioning										
Stemwood / total stem and branch	−1.0	−0.9	−1.0	−1.6	−1.5	−1.5	−0.8	−1.4	−1.0	−0.4
Foliage / total crown	1.1	1.7	2.2	0.7	0.8	0.7	2.2	1.5	1.7	3.0
Crown form										
Relative crown width (m/m)	−2.0	−2.6	−3.9	−3.0	−3.0	−2.9	−4.3	−3.9	−3.5	−4.9
Adjusted crown width (m)	−0.8	−1.5	−2.4	−0.7	−1.1	−0.6	−2.5	−1.7	−1.5	−3.1
Live crown ratio	1.6	1.7	2.0	2.2	2.3	2.2	1.8	2.3	1.9	1.5
Height to live crown (m)	−1.4	−1.4	−2.0	−2.2	−2.1	−1.7	−1.2	−2.3	−1.1	−0.4
No. live whorls	1.0	1.0	1.3	1.6	1.7	1.5	1.0	1.6	1.0	0.5
Volume incr per CPA (m^3·year^{-1}·m^{-2})	8.9	10.0	10.7	9.7	10.9	10.5	12.9	10.7	12.1	14.3
Foliage relative to crown size										
Leaf area per CPA (m^2/m^2)	12.1	12.3	12.4	14.4	15.1	15.1	13.9	13.9	13.7	12.2
Leaf area per branch length (m^2/m)	12.4	12.5	12.6	14.3	15.7	15.5	13.9	13.9	14.1	12.3
Branch characters										
Adjusted branch diameter (cm)	3.5	3.2	2.5	3.4	3.4	3.5	2.7	2.9	3.3	2.2
Adjusted branch length (m)	1.1	0.4	−0.9	0.9	0.9	1.1	−0.7	−0.3	0.3	−1.5
Branch stoutness (cm/m)	2.5	3.0	3.7	2.6	3.0	2.8	3.6	3.4	3.3	4.0
Total branch number per whorl	0.8	0.8	−0.1	0.5	2.7	3.1	2.2	0.1	2.6	2.4
Intrawhorl branch number	0.3	0.2	−0.2	1.6	2.8	2.9	0.5	0.8	1.5	−0.1
Interwhorl branch number	1.2	1.3	0.0	−0.5	2.5	3.3	3.7	−0.6	3.7	4.8
Branch number per crown length (no./m)	−1.7	−1.8	−2.8	−2.2	−0.5	−0.3	−1.2	−2.8	−1.0	−1.3
Branch area per crown length (cm^2·m^{-1})	10.2	9.3	6.4	11.1	13.0	13.0	8.5	8.5	10.2	5.6
Branch angle (degrees)	−1.9	−2.1	−2.4	−2.3	−1.8	−1.2	−1.6	−2.5	−1.1	−1.0

NOTE: Selection criteria assume equal emphasis of each trait such that changes of one phenotypic standard deviation are of equal value (economic weights equal $1/\sigma_P$). Traits included in different selection indices are 18-year stem volume (VOL), volume increment per crown projection area (VOLCPA), crown width relative to crown length (CWL), live crown ratio (LCRTO), leaf area per crown projection area (LACPA), leaf area per branch length (LABL), branch stoutness (BRST), and proportion of crown dry weight that is foliage (LFCR).

maximizing photosynthetic leaf area and minimizing the energy expenditure in the production of nonphotosynthesizing branches, with leaf area structured such that it most efficiently intercepts sunlight by avoiding self-shading and allowing light to penetrate to older needles. Although sparse branching minimizes the energy expended on branches, this study suggests that an adequate amount of branching appears to be necessary to produce a large photosynthetic leaf area. Productivity appears to be more closely associated with how photosynthetic leaf area is structured in space, rather than the relative amount of branching.

Multiple-trait selection

Results from this study indicated that potentially valuable ideotype traits include high volume increment per crown projection area, reduced crown width relative to crown length, high live crown ratio, high leaf area per crown projection area, high leaf area per branch length, greater partitioning to leaves versus branches, and stouter branches. These traits had moderate to high estimates of heritability (Table 1), were favorably genetically correlated with individual-tree stem size (Table 7), and may be hypothesized to lead to increased stemwood productivity per unit area of land. Responses to selection using different selection indices combining these potential ideotype traits with volume were compared with responses using selection for stem volume alone (Table 10). Many different combinations of traits may be considered, but only pairwise combinations of each potential ideotype trait with volume and three indices involving three-way combinations are presented.

All selection scenarios considered resulted in correlated responses of narrower crowns, lower heights to live crowns, more live whorls, greater volume increment per crown projection area, greater leaf areas per crown projection area, and greater leaf areas per branch length (Table 10). All selection scenarios had nearly the same expected genetic gains in volume, ranging from 10.7% for an index combining a narrow crown with increased volume to 13.8% for an index combining a high leaf area per crown projection area with increased volume (compared with 11.5% for selection for volume alone). Unfortunately, partitioning to the stem was lower in all selection scenarios (i.e., decreased harvest index). Results from St.Clair (1994) indicate that selection for both volume and increased harvest index would be difficult owing to the high negative genetic correlation between these traits. Although the selection index involving high leaf area per crown projection area resulted in the largest increase in volume (13.8%), it also led to a relatively large decrease in harvest index (1.5 compared with 1.0% for selection for volume alone). This selection index may also be expected to lead to decreases in wood quality as indicated by large increases in branch numbers per whorl, adjusted branch diameters, and branch cross-sectional areas per crown length. The selection index combining crown width relative to length with volume resulted in more favorable responses in these branch traits, but the estimate of genetic gain in volume was less (10.7%). The selection indices that best combined relatively large increases in volume (compared with selection for volume alone) with the most favorable responses in branchiness were the two that included branch stoutness. Interestingly, these two selection indices resulted in larger numbers of intrawhorl branches but not interwhorl branches.

Conclusions

Several crown structure traits appear to have promise as potential ideotype traits. Large trees growing well relative to their growing space had tall, narrow crowns, high leaf areas per crown projection area or branch length, and greater partitioning to leaves versus branches. Such an ideotype may be hypothesized to lead to increased productivity per unit area of land. Unfortunately, these traits were also associated with increased branchiness. Thus, selection for such an ideotype, or for stem size alone, could lead to reductions in harvest index and wood quality.

This study evaluated genetic variation and covariation in only a single competitive environment: a mixture of highly heterogeneous phenotypes in which intertree competition was high. A more appropriate competitive environment for evaluating ideotype traits would have been blocks of pure families. Pure family blocks would allow evaluation of ideotype traits in stands of homogenous phenotypes, perhaps more like the stands in which selected ideotypes would be grown. Furthermore, direct evaluation of the relation of hypothesized ideotype traits to unit-area productivity would be possible. To my knowledge, no studies have evaluated the relative importance of changes in alternative ideotype traits to stand productivity on a unit-area basis. Such a study would help address the question of the relative importance of including harvest index versus crown shape and structure in a forest tree ideotype. Combined with economic information of the relation between branchiness and wood quality, forest tree breeders would be better able to evaluate the tradeoffs between an ideotype that includes increased stem size with a full, tall, narrow crown versus one that includes reduced branchiness but at a cost of reduced stem size.

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Baker, R.J. 1986. Selection indices in plant breeding. CRC Press, Boca Raton, Fla.

Birot, Y., and Christophe, C. 1983. Genetic structures and expected genetic gains from multitrait selection in wild populations of Douglas-fir and Sitka spruce. I. Genetic variation between and within populations. Silvae Genet. **32**: 141–151.

Borghetti, M., Vendramin, G.G., and Giannini, R. 1986. Specific leaf area and leaf area index distribution in a young Douglas-fir plantation. Can. J. For. Res. **16**: 1283–1288.

Campbell, R.K. 1961. Phenotypic variation and some estimates of repeatability in branching characteristics of Douglas-fir. Silvae Genet. **10**: 109–118.

Campbell, R.K. 1963. Phenotypic correlation among branch and upper-crown stem attributes in Douglas-fir. For. Sci. **9**: 444–451.

Cannell, M.G.R. 1978. Improving per hectare forest productivity. *In* Proceedings of the 5th North American Forest Biology Workshop, March 13–15, 1978. Gainesville, Fla. *Edited by* C.A. Hollis and A.E. Squillace. pp. 120–148.

Cannell, M.G.R. 1989. Physiological basis of wood production: a review. Scand. J. For. Res. **4**: 459–490.

Cannell, M.G.R., Sheppard, L.J., Ford, E.D., and Wilson, R.H.F. 1983. Clonal differences in dry matter distribution, wood specific gravity, and foliage "efficiency" in *Picea sitchensis* and *Pinus contorta*. Silvae Genet. **32**: 195–202.

Charles-Edwards, D.A. 1982. Physiological determinants of crop growth. Academic Press, London and New York.

Cotterill, P.P., and Dean, C.A. 1990. Successful tree breeding with index selection. CSIRO Publications, Victoria, Australia.

Cotterill, P.P., and Jackson, N. 1985. On index selection. I. Methods of determining economic weight. Silvae Genet. **34**: 56–63.

Del Rio, E., and Berg, A. 1979. Specific leaf area of Douglas-fir reproduction as affected by light and needle age. For. Sci. **25**: 183–186.

Dickmann, D.I. 1985. The ideotype concept applied to forest trees. *In* Attributes of trees as crop plants. *Edited by* M.G.R. Cannell and J.E. Jackson. Institute of Terrestrial Ecology, Penicuik, Scotland. pp. 89–101.

Falconer, D.S. 1981. Introduction to quantitative genetics. 2nd ed. Longman, London and New York.

Ford, E.D. 1985. Branching, crown structure and the control of timber production. *In* Attributes of trees as crop plants. *Edited by* M.G.R. Cannell and J.E. Jackson. Institute of Terrestrial Ecology, Penicuik, Scotland. pp. 228–252.

Foster, G.S. 1986. Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. For. Sci. **32**: 944–959.

Gholz, H.L., Grier, C.C., Campbell, A.G., and Brown, A.T. 1976. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Forest Research Laboratory, Oregon State University, Corvallis. Res. Pap. 41.

Jahnke, L.S., and Lawrence, D.B. 1965. Influence of photosynthetic crown structure on potential productivity of vegetation, based primarily on mathematical models. Ecology, **46**: 319–326.

Karki, L., and Tigerstedt, P.M.A. 1985. Definition and exploitation of forest tree ideotypes in Finland. *In* Attributes of trees as crop plants. *Edited by* M.G.R. Cannell and J.E. Jackson. Institute of Terrestrial Ecology, Penicuik, Scotland. pp. 102–109.

Kellomäki, S., Oker-Blom, P., and Kuuluvainen, T. 1985. The effect of crown and canopy structure on light interception and distribution in a tree stand. *In* Crop physiology of forest trees. *Edited by* P.M.A. Tigerstedt, P. Puttonen, and V. Koski. Helsinki University Press, Helsinki, Finland. pp. 107–115.

King, J.N., Yeh, F.C., Heaman, J.C., and Dancik, B.P. 1992. Selection of crown form traits in controlled crosses of coastal Douglas-fir. Silvae Genet. **41**: 362–370.

Kuuluvainen, T. 1988. Crown architecture and stemwood production in Norway spruce (*Picea abies* (L.) Karst.). Tree Physiol. **4**: 337–346.

Kuuluvainen, T. 1991. Relationships between crown projected area and components of above-ground biomass in Norway spruce trees in even-aged stands: empirical results and their interpretation. For. Ecol. Manage. **40**: 243–260.

Kuuluvainen, T. 1992. Tree architectures adapted to efficient light utilization: is there a basis for latitudinal gradients? Oikos, **65**: 275–284.

Li, C.C. 1975. Path analysis—a primer. The Boxwood Press, Pacific Grove, Calif.

Lin, C.Y. 1978. Index selection for genetic improvement of quantitative characters. Theor. Appl. Genet. **52**: 49–56.

Magnussen, S., Smith, V.G., and Yeatman, C.W. 1986. Foliage and canopy characteristics in relation to aboveground dry matter increment in seven jack pine provenances. Can. J. For. Res. **16**: 464–470.

Merrill, R.E., and Mohn, C.A. 1985. Heritability and genetic correlations for stem diameter and branch characteristics in white spruce. Can. J. For. Res. **15**: 494–497.

Montieth, J.L. 1977. Climate and the efficiency of crop production in Britain. Philos. Trans. R. Soc. Lond. Ser. B. Biol. Sci. **281**: 277–294.

Smith, F.W., and Long, J.N. 1989. The influence of canopy architecture on stemwood production and growth efficiency of *Pinus contorta* var. *latifolia*. J. Appl. Ecol. **26**: 681–691.

Snedecor, G.W., and Cochran, W.G. 1980. Statistical methods. 7th ed. Iowa State University Press, Ames.

St.Clair, J.B. 1994. Genetic variation in tree structure and its relation to size in Douglas-fir. I. Biomass partitioning, foliage efficiency, stem form, and wood density. Can. J. For Res. **24**: 1226–1235.

Steel, R.G.D., and Torrie, J.H. 1980. Principles and procedures of statistics. McGraw-Hill, New York.

Velling, P., and Tigerstedt, P.M.A. 1984. Harvest index in a progeny test of Scots pine with reference to the model of selection. Silva Fenn. **18**: 21–32.

Waring, R.H., Thies, W.G., and Muscato, D. 1980. Stem growth per unit of leaf area: a measure of tree vigor. For. Sci. **26**: 112–117.