Genetic variation in tree structure and its relation to size in Douglas-fir. I. Biomass partitioning, foliage efficiency, stem form, and wood density

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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 in size, biomass partitioning, and wood density, and genetic gains may be expected from selection and breeding of desirable genotypes. Estimates of heritability for partitioning traits, including harvest index, were particularly high. Foliage efficiency (stem increment per unit leaf area) was strongly correlated with harvest index and may represent an alternative measure of partitioning to the stem. Estimates of foliage efficiency where leaf area was estimated based on stem diameter or sapwood area were unrelated to foliage efficiency where leaf area was measured directly. Strong negative genetic correlations were found between harvest index and stem size, and between wood density and stem size. Achieving simultaneous genetic gain in stem size and either harvest index or wood density would be difficult.

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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 les caractères de dimension, de répartition de la biomasse et de densité du bois, et des gains génétiques peuvent être anticipés à partir de la sélection et du croisement des génotypes désirables. Les estimés d'héritabilité étaient particulièrement élevés pour les caractères de répartition, incluant la proportion de la biomasse de la tige relativement à la biomasse totale. L'efficacité du feuillage (l'accroissement de la tige par unité de surface foliaire) était fortement corrélée à la proportion de la biomasse de la tige relativement à la biomasse totale, pouvant ainsi représenter une mesure de remplacement de ce caractère. Les estimés de l'efficacité du feuillage où la surface foliaire était estimée à partir du diamètre de la tige ou de la surface de l'aubier ne montraient pas de relation avec l'efficacité du feuillage découlant de la mesure directe de la surface foliaire. De fortes corrélations génétiques négatives ont été observées entre la dimension de la tige et la proportion de la biomasse de la tige relativement à la biomasse totale, ainsi qu'entre la dimension de la tige et la densité du bois. L'atteinte simultanée de gain génétique au niveau de la dimension de la tige ainsi qu'au niveau de la densité du bois ou de la proportion de la biomasse de la tige relativement à la biomasse totale apparaît problématique.

[Traduit par la rédaction]

Introduction

The broad goal of many tree-improvement programs is increased wood production per unit area of land. Attaining this goal requires that traits used for selection are genetically correlated with the array of traits that lead to increased stemwood per unit area of land at rotation age. Selection of improved genotypes is most often done based on stem size of individual trees in mixtures of genotypes at a young age, often before one fourth of the rotation age, and before appreciable competition has begun. Traits associated with rapid site capture and performance of individuals in mixtures, however, may not be the same as those associated with increased yield as a community (Harper 1977; Cannell 1978). A wide crown, for example, may be advantageous to achieve a large size as an individual (both in isolation and in competition), but increased community productivity may be better achieved by a canopy of tall, narrow crowns (Jahnke and Lawrence 1965; Kellomäki et al. 1985). Inclusion of morphological and physiological traits thought to be related to community productivity, as opposed to individual-tree growth, could conceivably increase genetic gain beyond that possible from selection for stem size alone.

Forest-tree ideotypes have been proposed as a method to select for unit-area yield using individual trees (Cannell 1978; Dickmann 1985). An ideotype is defined as a biological model that is expected to perform in a predictable manner within a defined environment based on an understanding of plant morphology and physiology (Donald 1968; Dickmann 1985). The environment is most often defined in terms of its competitive nature. Three contrasting competitive environments are plants grown in isolation, plants grown in competitive mixtures of contrasting phenotypes, and plants grown in pure stands of similar phenotypes (Donald and Hamblin 1976; Cannell 1978). A model plant expected to grow well in the third competitive environment is called a crop ideotype. Crop ideotypes are expected to yield a greater quantity or quality of useful products than conventional cultivars or wild plants, mainly because they are expected to make efficient use of available resources (Donald 1968; Cannell 1978). Crop ideotypes, however, are expected to be weak competitors when in mixtures with competitive ideotypes.

Models of plant dry-matter production indicate that traits of biomass partitioning and crown structure may be among

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the most important components of stand productivity (Charles-Edwards 1982; Cannell 1989). Biomass partitioning influences crown structure and determines the proportion of fixed carbon converted to stemwood (also referred to as harvest index). Crown structure affects light interception and light-use efficiency by determining the amount and distribution of foliage. Biomass partitioning and crown structure also influence wood quality by affecting knot size and angle, stem form, and wood density, and may also have important implications for adaptation. Many traits have been proposed for a forest tree ideotype designed to maximize unit-area yield. Characteristics associated with a good crop ideotype for conifers frequently include a tall, narrow crown with less partitioning to branches and greater partitioning to the stem (i.e., high harvest index); a large needle area or dry weight per unit crown volume, crown projection area or branch weight; and a large amount of stem growth per unit leaf area (referred to as foliage efficiency) or crown projection area (Cannell 1978; Cannell et al. 1983; Axelsson et al. 1984; Velling and Tigerstedt 1984; Ford 1985; Karki and Tigerstedt 1985; Kuuluvainen 1988).

Foliage efficiency is of particular interest. Genotypes displaying large stem growth per unit leaf area may be expected to have less branch and foliage biomass (Ford 1985); thus, foliage efficiency may be hypothesized to be related to harvest index. Cross-sectional sapwood area and stem diameter are often used as indirect measures of leaf area because they are highly correlated with leaf area and are relatively easy to measure (Waring et al. 1982; Brix and Mitchell 1983). If foliage efficiency based on indirect measurement of leaf area is highly correlated with foliage efficiency based on direct measurement of leaf area, harvest index may be easily measured in an inexpensive, nondestructive manner. An efficient, nondestructive measure of harvest index is necessary if it is to be included as a selection criterion in breeding programs (Pulkkinen et al. 1989).

The objectives of this study were to explore genetic variation and covariation among traits of biomass partitioning and crown structure in trees under competition, and to examine the genetic and phenotypic relations of these traits to stemwood production. Understanding the genetic control and interrelations among these traits is important for three reasons. First, it allows evaluation of the potential to include hypothesized ideotype traits into a multiple-trait selection scheme with the objective of improving genetic gains in unit-area yield and value. Second, it allows consideration of the effects of conventional selection procedures based on stem size on correlated responses of traits that may be related to stand productivity, adaptability, or wood quality. Third, consideration of the phenotypic relations gives some insight into the morphological and physiological bases of individual-tree growth, although inferences to stand growth may be limited if performance depends on the specific mixture of genotypes (i.e., intergenotypic competition effects).

Because of the many traits considered in this study, results are presented in two papers. This first paper will consider traits of biomass partitioning, foliage efficiency, stem form (taper), and wood density, and discuss the interrelations among different traits of tree size and growth. The second paper (St.Clair 1994; this issue) considers crown structure traits including crown shape; live crown ratio; volume increment per crown projection area; branch number, size, and angle; branch weight and leaf area relative to crown size; and specific leaf area.

TABLE 1. Stand description of genetic test used in study

Character	Value	Percent of total*	Increment†
Age (years)	18		
Stand density (trees/ha)	1346		
Mean height (m)	14.5		1.1
Mean DBH (cm)	18.0		1.0
Basal area (m^2/ha)	35.2		3.4
Volume (m^3/ha)	218		30
Leaf area index	8.8		
Biomass components (Mg/ha)			
Total aboveground	128.1		17.1
Total stem	93.9	73.3	12.4
Stemwood	82.9	64.7	11.0
Stem bark	11.0	8.6	1.4
Total crown	34.2	26.7	4.6
Branches	19.5	15.2	2.9
Foliage	14.7	11.5	1.7

*Percentage is of total aboveground biomass.
†Increment is average annual increment between ages 13 and 18, where age 13 biomass is predicted from age 13 DBH using biomass equations based on the same data and given in St.Clair 1993.

Materials and methods

Materials

The study site was 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 an elevation of 100 m. The test was established in February 1974 with 1-year-old seedlings. The spacing between trees was 2.4 × 3.0 m. Stand characteristics at the time of measurement are presented in Table 1. Site productivity was high (site class I; McArdle et al. 1961), and trees had been in competition for several years before measurement; relative density was 0.40, well above the value at crown closure (0.15) but not yet where self-thinning begins (0.55) (Drew and Flewelling 1979).

Trees used in this study were a random sample of 20 open-pollinated families from a systematic thinning of half the trees in the test. The parents originated from a narrow geographic and elevational range (an area of 8.5 × 4.5 km and elevations of 225–300 m with the exception of a single family that came from approximately 30 km further south and an elevation of 75 m). The experimental design was a randomized block design with multiple-tree, noncontiguous plots. Study trees came from six blocks with two trees sampled per family per block for a total of 240 trees. Mortality was low in the genetic test, and all study trees were surrounded by competitors. Trees that were forked, had large ramicorn branches, or showed signs of past damage were not chosen for study.

Data collection

Field data were collected from January to March 1991. Only measurements concerned with stem dimensions, biomass, leaf area, and wood density are described in this paper. Before harvest, breast height (1.3 m) was marked and stem diameter at that point (DBH) was measured with a diameter tape. Diameter was also measured earlier at ages 10 and 15, and height was measured at age 5. Trees were cut at 10 cm above the ground. After felling, base of the live crown was determined, and the live crown was divided into thirds to sample branches and foliage. The base of the live crown was defined as the first whorl with live branches in at least three of four quadrants. All live branches from each crown third were removed and weighed fresh in the field. A random sample of two branches with foliage was chosen from each crown third, weighed fresh, and taken to the laboratory for determining dry weights. A random sample of needles was collected from each crown third and sealed in a plastic bag to take to the laboratory. After removing the crown, total stem height

TABLE 2. Form of the analyses of variance and covariance

Source of variation*	df	Expected mean squares†
B	5	$\sigma_w^2 + 2\sigma_e^2 + 40\sigma_b^2$
F	19	$\sigma_w^2 + 2\sigma_e^2 + 12\sigma_f^2$
B × F (plot error)	95	$\sigma_w^2 + 2\sigma_e^2$
W	120	σ_w^2

*B, block; F, family; W, within plot.

†σ_w^2, within-plot variance; σ_e^2, plot to plot variance; σ_b^2, variance among blocks; σ_f^2, variance among families. For analyses of covariance, mean cross products are used instead of mean squares.

and height to the first and fifth whorls from the top were measured to determine 1- and 5-year height increments. The entire stem was weighed fresh in two parts (above and below the base of the live crown), 8 cm thick disks were cut at 1.3 m and at the internode below the base of the live crown, and the disks were sealed in plastic bags to take to the laboratory.

Foliage and stem disk samples were stored in a cold room at 1°C until processing. A subsample of the foliage from each crown third was weighed fresh, dried to a constant weight (about 24 h), and weighed again to estimate the ratio of dry to fresh weight. The drying temperature for all samples was 80°C. The crown samples from each crown third were dried to a constant weight (about 3 days) and needles were stripped from branches and weighed. The foliage fresh weight of each sample was estimated by dividing the foliage dry weight by the foliage dry- to fresh-weight ratio. Branch fresh weight of each sample was estimated by subtracting the foliage fresh weight from the crown fresh weight. Branch dry- to fresh-weight ratio was then determined. Thus, the following variables were estimated: (*i*) total crown fresh weight for each crown third (measured in the field), (*ii*) ratios of foliage or branch fresh weight to crown fresh weight (estimated from the crown samples), and (*iii*) dry- to fresh-weight ratios for foliage or branches (estimated from the foliage and crown samples). Total foliage or branch dry weight for each crown third could then be calculated by multiplying these variables. Total foliage or branch dry weight for each tree was estimated by summation over the three crown sections.

Single-sided, projected leaf area was measured on a fresh subsample of 60 needles per crown section 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. The leaf area of each crown section 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.

Stem disks taken at 1.3 m were measured in four cardinal directions for 1- and 5-year radial increments, and the average used to estimate diameter increment. The sapwood-heartwood boundary was delineated on the disks by staining with alizarine red (Kutscha and Sachs 1962). After the boundary was marked, each disk was photocopied, and the total cross-sectional area of wood (basal area) and heartwood area of each disk were measured from the photocopy using the electronic area meter. Sapwood area was determined by subtracting heartwood area from total cross-sectional area. The bark was peeled from each of the two disks per tree, and bark and stemwood were weighed both fresh and after drying to a constant weight (about 3 days) to estimate ratios of dry to fresh weight and of bark or stemwood to total stem fresh weight. Total bark and stemwood for each stem section (above and below the base of the live crown) were estimated by multiplying total stem fresh weight by the ratio of bark or stemwood to total stem fresh weight and by the ratio of dry to fresh weight for bark or stemwood. This procedure assumed that the disk taken at 1.3 m was representative of the lower stem section and the disk taken at the base of the live crown was representative of the upper stem section. Total bark or stemwood dry weight was estimated by summation over the two stem sections.

Basal area was calculated as the area of a circle with a diameter as measured at breast height using the diameter tape. Basal area calculated in this manner was highly correlated with basal area of wood as determined from the photocopy ($r \geq 0.99$). References to basal area in the text refer to basal area as determined from DBH.

Stem volume and stem form were determined based on height and diameter using equations from Bruce and DeMars (1974). Stem form is a measure of taper; a slender tree with little taper would have a high value for stem form. Stem form was highly correlated to the ratio of height to diameter ($r_p = 0.94$).

Wood density was determined for the lower stem disk only. The density of each disk was determined as the dry weight of the disk divided by the green volume. Green volume was measured by the water displacement method (Olesen 1971).

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 (Table 2). 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., $p \leq 0.05$); probabilities greater than 0.05 are reported so that readers may make their own judgements regarding the importance of family differences. Phenotypic variance (σ_p^2) was estimated as $\sigma_p^2 = \sigma_f^2 + \sigma_e^2 + \sigma_w^2$, where σ_f^2 is the family component of variance, σ_e^2 is the error component of variance, and σ_w^2 is the within-plot component of variance. Additive genetic variance, σ_a^2, was estimated as $3\sigma_f^2$, which assumes a coefficient of relationship among wind-pollinated progenies of one third (Campbell 1979; Sorenson and White 1988). 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. Individual-tree heritabilities (h^2) and genetic gains from mass selection were estimated as given in Falconer (1981). 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 the information given by using formulas in Falconer (1981). Note that this study was done at a single site, and estimates of heritability may be inflated if genotype × environment interaction was present. Relations among traits were examined by estimating the genetic (r_a) and individual-tree phenotypic (r_p) correlations as outlined by Becker (1984). Standard errors of heritabilities and genetic correlations are not presented due to space limitations, but are easily derived from the information given using formulas in Falconer (1981). Standard errors of genetic parameters are primarily a function of the number of families. Although the number of families used in this study (20) is less than ideal, it is the most that could be measured given the practical realities of biomass studies, and is within the range of many genetic studies in the literature.

Implications of the genetic control and relations among traits of tree size, biomass partitioning, foliage efficiency, stem form, and wood density were investigated by determining the expected genetic gain (response) from direct and indirect mass selection for these traits by using equations in Falconer (1981). Relative efficiency was estimated as the ratio of indirect to direct response. Index selection procedures (Lin 1978; Baker 1986) were used to investigate the utility of using two or more stem size traits as secondary traits for improvement of stem volume and for consideration of multiple-trait selection for stem volume and partitioning. Results using stemwood biomass were similar to those using stem volume (they were highly correlated, $r_p = 0.97$), and only stem volume results are presented. Index coefficients for

TABLE 3. 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	Percent
Stem size								
Volume (dm^3)	162	31–388	131–228	0.36	0.20	0.32	19	11.5
Basal area (cm^2)	262	62–535	223–359	0.30	0.17	0.33	26	10.0
DBH (cm)	18.0	8.9–26.1	16.7–21.3	0.15	0.08	0.27	0.8	4.2
Height (m)	14.5	9.9–18.4	13.6–15.5	0.10	0.04	0.17	0.2	1.6
Biomass components (kg) and leaf area (m^2)								
Total aboveground	95.2	19.4–215.9	78.4–127.7	0.35	0.19	0.31	10.1	10.6
Total stem	69.8	14.2–158.1	57.5–92.7	0.34	0.16	0.23	5.4	7.7
Stemwood	61.6	12.5–139.5	50.7–81.6	0.34	0.16	0.21	4.4	7.2
Stem bark	8.2	1.8–18.6	6.8–11.1	0.35	0.21	0.36	1.0	12.6
Total crown	25.4	5.1–57.9	19.5–37.4	0.40	0.29	0.52	5.3	20.7
Branches	14.5	2.7–32.7	10.4–21.7	0.42	0.29	0.48	2.9	20.2
Foliage	10.9	2.4–27.7	8.6–16.1	0.41	0.29	0.50	2.3	20.6
Leaf area	65.7	16.4–145.6	50.4–94.1	0.38	0.29	0.57	14.5	22.1
Stem growth increment*								
Volume (dm^3/year)	22.0	4.5–50.3	17.6–31.5	0.36	0.22	0.38	3.0	13.5
Basal area (cm^2/year)	25.5	6.8–50.3	20.6–37.1	0.34	0.23	0.46	3.9	15.4
DBH (cm/year)	1.02	0.48–1.57	0.89–1.30	0.22	0.15	0.48	0.11	10.3
Height (m/year)	1.11	0.76–1.54	1.01–1.17	0.10	0.04	0.14	0.02	1.4
Biomass partitioning								
Total stem / total aboveground	0.74	0.63–0.83	0.70–0.77	0.05	0.04	0.60	0.02	3.1
Stemwood / total aboveground	0.65	0.54–0.73	0.61–0.68	0.05	0.04	0.55	0.02	3.0
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
Bark / total aboveground	0.09	0.06–0.14	0.08–0.10	0.13	0.09	0.42	0.00	5.6
Bark / total stem	0.12	0.08–0.18	0.10–0.13	0.12	0.07	0.33	0.00	4.0
Branch / total aboveground	0.15	0.09–0.23	0.12–0.17	0.18	0.13	0.51	0.01	9.2
Foliage / total aboveground	0.11	0.07–0.18	0.10–0.13	0.16	0.10	0.40	0.01	6.4
Foliage / total crown	0.44	0.29–0.56	0.41–0.48	0.10	0.05	0.28	0.01	2.7
Foliage efficiency ($m^3 \cdot year^{-1} \cdot m^{-2}$):								
Volume increment per leaf area	346	182–620	308–410	0.21	0.10	0.23	17	4.9
Volume increment per predicted leaf area	333	235–491	309–379	0.14	0.07	0.27	12	3.6
Stem form	0.42	0.40–0.46	0.41–0.43	0.02	0.01	0.24	0.00	0.6
Wood density	0.40	0.33–0.57	0.36–0.43	0.07	0.05	0.52	0.02	3.7

*Growth is average per year between ages 13 and 18.
†Leaf area predicted based on the equation ln(leaf area) = −1.3887 + 1.1160 ln(basal area sapwood) as derived from data of this study.

Smith–Hazel indices and expected genetic gains from index selection were calculated using the RESI program described by Cotterill and Dean (1990).

Results and discussion

Size and growth

Individual trees and families differed considerably in all size (stem dimensions and biomass) and growth increment traits, with the possible exceptions of height and height increment (Table 3). For example, stem volume ranged from 19 to 240% of the mean among individuals, and from 81 to 141% of the mean among families. Analyses of variance indicated significant variation among families for all size and growth traits (defined as $p \leq 0.05$), except height increment ($p = 0.10$); estimates of heritabilities and expected genetic gains were generally high, particularly for crown biomass components. As expected, all size and growth traits were highly intercorrelated, both phenotypically and genetically (Table 4). Height and height increment differed the most from the other stem size and biomass traits (e.g., r_p = 0.75 and r_a = 0.81 with diameter). Stem size as measured by diameter, basal area, or volume was highly correlated with biomass components, particularly with total aboveground biomass and stem biomass. Correlations between stem and crown components were somewhat weaker than within stem or within crown components.

Stem size traits showed increasing heritabilities with age (Table 5). Diameter heritabilities increased at a greater rate than height. Phenotypic coefficients of variation of both height and diameter were initially high, but decreased and leveled off after age 13. Additive genetic coefficients of variation were initially low for height but increased and leveled off after age 13. For diameter, additive genetic coefficients of variation increased steadily with age. The low estimates of heritability up to age 10 may be attributed to the high phenotypic variation, perhaps as a result of residual planting effects or high genotype × year interaction. The decrease in phenotypic variation may be a result of dimin-

TABLE 4. Phenotypic (above diagonal) and genetic (below diagonal) correlations among traits of tree size and growth increment

	VOL	BA	DBH	HT	TDW	WDDW	BKDW	BRDW	LFDW	LA	VOLYR	BAYR	DBHYR	HTYR
VOL		0.98	0.97	0.85	0.97	0.97	0.91	0.81	0.85	0.81	0.99	0.95	0.82	0.46
BA	0.99		0.99	0.74	0.96	0.96	0.90	0.82	0.85	0.82	0.96	0.95	0.81	0.33
DBH	0.99	1.00		0.75	0.95	0.95	0.90	0.83	0.85	0.82	0.96	0.95	0.82	0.34
HT	0.90	0.83	0.81		0.81	0.84	0.77	0.64	0.69	0.65	0.86	0.76	0.71	0.68
TDW	0.97	0.98	0.99	0.83		0.99	0.92	0.90	0.92	0.88	0.96	0.94	0.83	0.39
WDDW	0.99	1.01	1.01	0.77	0.99		0.92	0.83	0.86	0.82	0.96	0.93	0.82	0.40
BKDW	0.97	0.95	0.97	0.86	0.94	0.97		0.77	0.80	0.76	0.90	0.86	0.74	0.37
BRDW	0.82	0.81	0.83	0.75	0.93	0.87	0.76		0.87	0.86	0.81	0.82	0.76	0.31
LFDW	0.99	0.97	1.00	0.98	1.00	0.99	0.90	0.97		0.97	0.86	0.87	0.81	0.35
LA	0.94	0.93	0.95	0.94	1.00	0.98	0.84	1.00	0.99		0.82	0.83	0.77	0.34
VOLYR	1.00	0.99	1.00	0.91	0.98	0.99	0.97	0.82	1.00	0.95		0.97	0.88	0.52
BAYR	0.99	1.00	1.02	0.87	0.98	1.01	0.96	0.81	0.97	0.93	0.99		0.95	0.39
DBHYR	0.98	0.99	1.03	0.89	0.98	1.01	0.96	0.83	0.97	0.94	0.99	0.99		0.40
HTYR	0.83	0.77	0.74	0.90	0.80	0.70	0.71	0.76	1.08	1.02	0.85	0.83	0.85	

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)). Stem size traits include volume (VOL), basal area at 1.3 m (BA), diameter at 1.3 m (DBH), and height (HT). Biomass components and leaf area include total aboveground dry weight (TDW), stemwood dry weight (WDDW), stem bark dry weight (BKDW), branch dry weight (BRDW), foliage dry weight (LFDW), and total leaf area per tree (LA). Growth increment traits include increment per year between ages 13 and 18 for volume (VOLYR), basal area (BAYR), diameter (DBHYR), and height (HTYR).

TABLE 5. Age trends for heritability (h^2), and for phenotypic (CVP) and additive genetic (CVA) coefficients of variation for stem height and diameter at breast height (DBH)

	h^2		CVP		CVA	
Age	Height	DBH	Height	DBH	Height	DBH
5	0.003	—	0.227	—	0.012	—
10	—	0.063	—	0.191	—	0.048
13	0.127	0.107	0.123	0.153	0.044	0.050
15	—	0.185	—	0.144	—	0.062
17	0.149	0.240	0.098	0.150	0.038	0.074
18	0.165	0.274	0.097	0.154	0.039	0.081

ishing planting effects or genotype × year effects being averaged across more years. Interfamily competition may also be responsible for the higher heritabilities at later ages by its effect on magnifying genetic variation (Franklin 1979; St.Clair and Adams 1991). Competition was minimal at age 13 in this study but much stronger by age 18.

The preceding discussion suggests that height and diameter are, to some degree, distinct traits, particularly in how they react to competition. As the stand developed, larger trees appeared to allocate more stem biomass to diameter growth than to height growth, whereas smaller trees attempted to avoid suppression by allocating stem biomass to height growth at the expense of diameter. This hypothesized strategy helps explain the relatively weak correlation between stem biomass and height increment ($r_p = 0.40$) compared with that between stem biomass and diameter increment ($r_p = 0.81$), and the lower variation and heritabilities of height and height growth compared with diameter, basal area, and volume (Table 3).

The question of choice of stem size traits for improved stemwood production was investigated by determining the relative efficiencies from indirect selection of alternative stem size traits, both singly and combined into multiple-trait selection indices, as compared with direct selection for either 18-year stem volume or stem biomass (Table 6). Stem volume and stem biomass were highly correlated ($r_p = 0.97$), and results were similar; therefore, only stem volume results are presented. The single best trait for selection was basal area; the worst trait was height. The relative efficiency of selection for 18-year volume using basal area was 1.00 as compared with 0.91 for diameter and 0.64 for height. Although diameter and basal area were nearly perfectly correlated ($r_p \geq 0.99$), basal area had a different variance structure (as a consequence of the squared function), and thus, much higher estimates of heritability and genetic gain. The variance structure of basal area is much closer to that of volume (which is a cubed function with more influence from basal area than height), resulting in basal area being a better trait for selection and estimating genetic gain in stem volume than diameter. The nearly perfect correlation with diameter may be expected because basal area is simply a squared function of diameter.

TABLE 6. Genetic gain per unit selection intensity and relative efficiency of selection (RE) for 18-year stem volume given different selection criteria

Selection criterion*	Gain	% gain	RE
Traits measured at age 18			
Volume	18.63	11.48	1.00
Height	11.97	7.38	0.64
DBH	16.98	10.47	0.91
Basal area	18.63	11.48	1.00
Height, DBH	17.03	10.50	0.91
Height, basal area	18.89	11.64	1.01
Volume, height, DBH	22.84	14.08	1.23
Volume, height, basal area	21.53	13.27	1.16
Traits measured at age 13			
Volume	14.47	8.92	0.78
Height	10.08	6.22	0.54
DBH	11.41	7.03	0.61
Basal area	12.48	7.69	0.67
Height, DBH	11.73	7.23	0.63
Height, basal area	13.12	8.09	0.70
Volume, height, DBH	19.34	11.92	1.04
Volume, height, basal area	18.93	11.67	1.02

NOTE: RE is defined as indirect response as proportion of direct response for given selection criteria.

*Multiple-trait selection indices were used for selection criteria of two or more traits.

TABLE 7. Phenotypic (above diagonal) and genetic (below diagonal) correlations among traits of stem size, biomass partitioning, foliage efficiency, stem form, and wood density

	VOL	BA	HT	STTDW	WDTDW	WDSB	BKST	LFCR	VOLLA	VOLPLA	FORM	DENS
VOL	—	0.98	0.85	−0.11	−0.08	−0.05	−0.12	−0.01	0.17	0.44	−0.84	−0.41
BA	0.99	—	0.74	−0.16	−0.13	−0.10	−0.09	−0.03	0.11	0.37	−0.93	−0.42
HT	0.90	0.83	—	0.03	0.06	0.09	−0.15	0.04	0.28	0.58	−0.50	−0.30
STTDW	−0.63	−0.61	−0.72	—	0.95	0.86	0.01	0.23	0.68	0.07	0.24	0.10
WDTDW	−0.75	−0.70	−0.89	0.97	—	0.94	−0.29	0.21	0.65	0.07	0.22	0.08
WDSB	−0.65	−0.60	−0.76	0.97	0.99	—	−0.38	0.50	0.47	0.10	0.20	0.06
BKST	0.55	0.44	0.76	0.11	−0.13	−0.11	—	0.02	−0.01	0.00	0.05	0.03
LFCR	0.36	0.30	0.58	0.43	0.29	0.40	0.56	—	−0.18	0.13	0.08	−0.04
VOLLA	−0.54	−0.53	−0.64	0.99	0.87	1.00	0.51	1.17	—	0.21	0.00	−0.17
VOLPLA	0.69	0.74	0.54	−0.40	−0.49	−0.41	0.34	0.29	−0.09	—	−0.22	−0.16
FORM	−0.91	−0.96	−0.63	0.58	0.65	0.58	−0.32	−0.12	0.58	−0.81	—	0.37
DENS	−1.02	−0.99	−1.02	0.39	0.50	0.29	−0.49	−0.77	0.32	−0.70	0.88	—

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 volume (VOL), basal area at 1.3 m (BA), height (HT), stem to total aboveground dry weight (STTDW), stemwood to total aboveground dry weight (WDTDW), stemwood to stem plus branch dry weight (WDSB), bark to total stem dry weight (BKST), foliage to total crown dry weight (LFCR), volume increment per unit leaf area (VOLLA), volume increment per unit predicted leaf area (VOLPLA), stem form (FORM), and wood density (DENS).

Selection indices combining height with diameter (or basal area) did not lead to greater genetic gains than did direct selection for volume (Table 6); however, selection indices combining height, diameter (or basal area), and volume resulted in substantially larger genetic gains in volume (23% greater gains). Baker (1986, pp. 84–85), however, cautions against the use of multiple traits that are highly correlated or mathematically derived from each other, noting that expected gains may have large sampling errors and be biased upward.

Response to selection for age 18 volume based on selection of different stem size traits at age 13 was also investigated (Table 6). These two ages are of particular interest because of the increasing influence of competition at age 18 versus age 13. Results were similar to those based on selection at age 18; basal area was the single best trait for selection for stem volume at both ages, and multiple trait selection for height and diameter or basal area did not improve estimated genetic gains (Table 6). Selection based on basal area, however, was not as efficient as direct selection for volume (relative efficiency of 0.70 as compared with 0.78 for age 18 volume, or in terms of age 13 volume, relative efficiency of 0.90). Bastien and Roman-Amat (1990) found similar results; diameter squared at age 8 had a higher relative efficiency of indirect selection for 15-year volume than did height at age 8 (0.87 vs. 0.77), and was nearly as efficient as a multiple-trait index combining diameter squared and height (0.90). Adams and Joyce (1990) also considered the question of choice of traits for selection for volume and determined that height was more effective than diameter for selection for volume at ages 12 to 13 (before appreciable competition). However, they did not consider basal area as a selection criterion.

My results suggest that basal area is a better selection criterion than diameter or height and that the value of including height as well as basal area to select for volume decreases as the stand develops. These conclusions are based on the idea that height and diameter react differentially to increasing competition. This same idea could lead, however, to situations in which height is favored over diameter or basal area for selection for stem size. If large differences in competition around individual trees exist within genetic tests (e.g., many missing trees or highly variable sites), height would be less sensitive to this nongenetic source of variation and may have a higher heritability relative to diameter or basal area. Furthermore, height is used in growth models to predict stand yield because of its insensitivity to competitive influences (e.g., site index curves). Thus, selection for height could lead to more reliable gains in stand yield when competitive influences are not equal among genotypes.

Biomass partitioning

Families differed significantly in all biomass partitioning traits, including partitioning to biomass components relative to total aboveground biomass, partitioning to bark relative to total stem, and partitioning to foliage relative to total crown. Heritability estimates for partitioning were high compared with other traits (Table 3); for example, the heritability of partitioning to the stem relative to total aboveground dry weight was 0.60, whereas the heritability of stem dry weight was 0.23.

Three measures of harvest index were considered: (*i*) total stem dry weight (stemwood plus bark) relative to total aboveground dry weight, (*ii*) stemwood dry weight relative to total aboveground dry weight, and (*iii*) stemwood dry weight relative to total stem and branch dry weight. The latter measure considers partitioning only among woody components and does not include foliage. It is probably of greatest interest for breeding because foliage represents an input into net productivity through photosynthesis, and thus, breeding against investment in foliage may be undesirable. Furthermore, the numerator includes only stemwood and not bark, and stemwood is the commodity of interest. All three measures of harvest index were highly correlated ($r_p > 0.86$ and $r_a > 0.97$; Table 7), however, and breeding for total stem to total aboveground dry weight would be analogous to breeding for stemwood to total stem and branch dry weight. Harvest indices were also calculated on a fresh-weight basis, but fresh weight harvest indices were highly correlated to dry weight harvest indices and are therefore not reported (e.g., $r_p = 0.94$ and $r_a = 0.98$, respectively, for correlations between total stem dry weight relative to total aboveground dry weight and total stem fresh weight relative to total aboveground fresh weight).

The high heritabilities of biomass partitioning in this study were consistent with results from other studies. Velling and Tigerstedt (1984) found a narrow-sense heritability of 0.52

TABLE 8. Genetic gains per unit selection intensity for stem volume and biomass partitioning given various selection criteria

Selection criteria*	Genetic gain† VOL	WDSB	BKST	LFCR	Index equation
VOL alone	18.63	−0.008	0.003	0.005	—
	(11.5)	(−1.0)	(2.2)	(1.1)	
VOL, 0% WDSB	9.71	0.000	0.002	0.007	I = 0.003VOL + 3.067WDSB
	(6.0)	(0.0)	(1.7)	(1.6)	
VOL, 0% WDSB, BKST	15.10	0.000	0.006	0.012	I = 0.008VOL + 9.806WDSB + 44.976BKST
	(9.3)	(0.0)	(4.9)	(2.8)	
VOL, 0% WDSB, LFCR	14.73	0.000	0.004	0.013	I = 0.005VOL − 0.540WDSB + 12.378LFCR
	(9.1)	(0.0)	(2.9)	(2.9)	
VOL, 0% WDSB, BKST, LFCR	17.54	0.000	0.006	0.015	I = 0.010VOL + 6.697WDSB + 54.096BKST
	(10.8)	(0.0)	(4.9)	(3.4)	+ 13.136LFCR
VOL, 1% WDSB, BKST, LFCR	6.23	0.007	0.005	0.015	I = 0.006VOL + 25.862WDSB + 65.122BKST
	(3.8)	(1.0)	(4.1)	(3.4)	+ 9.521LFCR

*VOL, stem volume (dm^3); WDSB, stemwood to total stem and branch proportion; BKST, bark to stem proportion; LFCR, leaf to crown proportion. Multiple-trait selection criteria are 0 or 1% desired gain in stemwood to total stem and branch proportion with volume, bark to stem proportion, and (or) leaf to crown proportion included with equal emphasis (see Cotterill and Jackson 1985).

†Genetic gains expressed as percentage of mean of parents are given in parentheses.

for stem relative to total aboveground fresh weight in a genetic test of 30 full-sib Scots pine (*Pinus sylvestris* L.) families; heritability estimates for stem size were 0.14 for height, 0.37 for diameter, and 0.07 for stem fresh weight. Matthews et al. (1975) found large differences among 20 open-pollinated Virginia pine (*Pinus virginiana*) families in partitioning of dry matter among branches, stemwood, and bark, but families differed little in height, diameter, and biomass of components. Hook et al. (1990) found significant family differences and high heritabilities among 36 red alder (*Alnus rubra* Bong.) families in partitioning, but differences in size traits were not significant. Van Buijtenen (1978) found significant differences among nine slash pine (*Pinus elliottii* Engelm.) clones in partitioning (broad-sense heritability was 0.53 for percent stemwood) but did not find significant differences in partitioning among 15 loblolly pine (*Pinus taeda* L.) families. Taken together, these results indicate that partitioning traits are highly heritable. None of these studies considered expected genetic gain, however. Results from the study reported here indicate that only modest genetic gains may be expected from selection and breeding for partitioning (Table 3). Genetic gain is a function of both heritability and phenotypic variance, and the low genetic gain estimates are a consequence of low phenotypic variation. The high heritability simply indicates that a large proportion of the total phenotypic variance was genetic.

Despite relatively low expected genetic gains, small changes in allocation from crown to stem may be hypothesized to lead to large differences in stand productivity. Trees with higher harvest indices may be expected to have less crown biomass. Less crown biomass could lead to less competition among individual trees, and conceivably, more stems could be grown per unit area of land. Negative genetic correlations were found, however, between harvest index and different measures of stem size (Table 7). Thus, selection for stem size could lead to reduced harvest index, and conversely, selection for higher harvest index could lead to reduced individual-tree stem size. It is unknown whether a hypothesized increase in stems per unit area could offset a reduction in individual-tree stem size to lead to increased stem yield per unit area.

The unfavorable genetic correlation between stem size and harvest index was associated with a positive genetic correlation between size and partitioning to leaves relative to total dry weight (r_a = 0.92 between stem volume and leaf to total dry weight). Individuals of families that partitioned more to photosynthetic leaf area, and the branch biomass needed to support that leaf area, presumably were intercepting more light and grew better but had a reduced harvest index. Breeding for increased harvest index may be undesirable if it leads to a reduction in the amount of foliage.

Simultaneous selection for both stem volume and harvest index was evaluated using index selection procedures. Multiple-trait selection indices were determined for different combinations of stem volume, stemwood to total stem and branch dry weight (harvest index), bark to total stem dry weight, and leaf to total crown dry weight (Table 8). Assigning economic weights to partitioning traits is difficult because it is not clear what the potential increase in unit-area wood production and value would be from changes in biomass partitioning. For purposes of this study, economic weights were chosen to give equal emphasis to volume, bark to stem proportion and leaf to crown proportion, while maintaining gains in harvest index at either 0 or 1% (see Cotterill and Jackson 1985). A 1% gain in harvest index is about half that possible from direct selection for harvest index (Table 3).

Responses to selection using selection indices confirmed that tradeoffs existed between selection for stem volume versus harvest index (Table 8). A selection index that included volume and harvest index indicated that genetic gain in volume would be nearly half that of direct selection when response in harvest index was held to zero. A much greater genetic gain in volume while still maintaining response in harvest index at zero was possible, however, by also including the secondary traits of bark to stem proportion or leaf to crown proportion, or both, in selection indices. For example, including both in a selection index resulted in an estimated genetic gain in volume of 10.8%, compared with 11.5% from direct selection for volume. Including either alone resulted in nearly as much genetic gain in volume. The favorable response to including bark to stem proportion as a secondary trait resulted from a positive genetic correlation with stem volume, with only a weak negative genetic

correlation with harvest index (Table 7). The favorable response from including leaf to crown proportion resulted from positive genetic correlations with both stem volume and harvest index. Achieving even modest genetic gains in harvest index was not possible without sacrificing gains in stem volume, even when the secondary partitioning traits were included in the selection index. When a 1% increase in harvest index was specified along with selection for increased partitioning to bark and foliage, the expected genetic gain in volume was only 3.8%.

The negative genetic association between harvest index and stemwood production found in this study seemed to be much stronger than in previous studies (Matthews et al. 1975; van Buijtenen 1978; Cannell et al. 1983; Velling and Tigerstedt 1984; Hook et al. 1990). Although previous studies did not consider genetic correlations, family mean correlations between harvest index and stem size ranged from −0.34 between stemwood to total stem plus branch dry weight and stemwood dry weight in Virginia pine (based on values from Matthews et al. 1975) to 0.30 between total stem to total aboveground fresh weight and total stem fresh weight in Scots pine (Velling and Tigerstedt 1984).

Compared with the present study, most of the previous studies were done at younger ages and before appreciable stand development. Phenotypic expression of traits and estimates of genetic variation and covariation depend to some extent on the competitive environment in which traits are evaluated (Gallais 1976; Hamblin and Rosielle 1978; St.Clair and Adams 1991). Herein lies a problem with genetic studies of potential ideotype traits, including partitioning traits. If estimates of genetic variation and covariation differ depending on density, age, and the genetic composition of trees in the stand, what is the appropriate competitive environment for genetic evaluation of ideotype traits? This question is particularly relevant given that the justification for ideotype breeding is increased unit-area yield after commencement of competition based on evaluation and selection of individual trees at a young age. Another problem is that selection may be in one competitive environment, but realized genetic gains result from expression of traits in another competitive environment. Indeed, that is the basis for ideotype breeding; the concern that selection of competitive genotypes from mixed-genotype tests will result in genetic gains of less magnitude than expected when those competitive genotypes are planted together. The many open questions point to a need for further research on the effect of competitive environment (i.e., age, density, and genetic composition) on expression and inheritance of potential ideotype traits and unit-area productivity.

Foliage efficiency

Foliage efficiency (volume increment per unit leaf area) differed significantly among families and was moderately heritable (h^2 = 0.23), with an expected genetic gain of 4.9% per unit selection intensity (Table 3). As hypothesized, foliage efficiency was positively correlated with harvest index (partitioning to the stem), both phenotypically and genetically (Table 7). A strong positive correlation between foliage efficiency and harvest index has also been found among individual trees of Scots pine (Kuuluvainen and Kanninnen 1991) and among seven clones of both Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) (Cannell et al. 1983). The strong genetic correlation in this study indicated that genetic gain in both stem growth per unit leaf area and partitioning to the stem may be expected from selection and breeding for either trait, and foliage efficiency may serve as a useful surrogate for harvest index if a practical measure of leaf area is available. However, as with harvest index, foliage efficiency was unfavorably negatively correlated with tree size (Table 7). Thus, conclusions regarding correlated responses to selection for foliage efficiency and stem size are similar to those for harvest index and tree size; selection for tree size would result in a decrease in stem growth per unit leaf area, and simultaneous genetic gain in both traits would be difficult.

Estimates of foliage efficiency in which leaf area was predicted based on cross-sectional area of sapwood at breast height were uncorrelated with estimates of foliage efficiency in which leaf area was measured directly (r_p = 0.21 and r_a = −0.09; Table 7), despite a positive correlation between leaf area measured directly and predicted leaf area (r_p = 0.78 and r_a = 0.98). Thus, predicting foliage efficiency by using the easily measured and nondestructive method of sapwood area does not appear to be reliable. The lack of correlation was the same whether leaf area was predicted using cross-sectional area of sapwood at breast height or at the base of the live crown, or whether total area of wood was used instead of sapwood. The lack of correlation may be understood when foliage efficiency is considered as deviations from the regression of volume increment on leaf area. An individual or family above the regression line is considered to be of high foliage efficiency, whereas an individual or family below the regression line is considered to be of low foliage efficiency. Whether an individual or family was above or below the line when leaf area was measured directly was unrelated to whether they were above or below the line when leaf area was predicted based on sapwood area. The strong relation between volume increment and leaf area means that most points were clustered near the regression line, making it more likely that a point may change positions relative to the line when leaf area was measured indirectly versus directly, even though leaf area measured directly may be strongly, but not perfectly, related to leaf area estimated from cross-sectional sapwood area. These results lead one to question the general applicability of evaluating foliage efficiency based on an indirect measure of leaf area.

Stem form

Stem form differed significantly among families and had a moderate estimate of heritability (h^2 = 0.24; Table 3). Trees and families differed little, however, as indicated by the low estimates for phenotypic and additive genetic coefficients of variation. Consequently, little gain may be expected from breeding for stocky versus slender trees (0.6%); however, the value of small changes in stem form is unknown.

Silen and Rowe (1971) and Libby (1987) suggest that selection for stocky trees (i.e., lower values of stem form or less stem height relative to diameter) may increase the volume and value of stemwood produced. Silen and Rowe (1971) suggest breeding for both stockiness and height, whereas Libby (1987) suggests the possibility of selection for stockiness and against height. In the present study, stem form was negatively related to all size traits, both phenotypically and genetically (Table 7). Thus, large trees were more stocky and less slender than small trees, and conventional selection based on volume, diameter, basal area, or even height would result in stocky, less slender trees. Selection for increased volume while maintaining genetic gain in

height at zero (evaluated using selection index procedures) would result in substantially less genetic gain in volume (3.3% compared with 11.5% for direct selection of volume) while achieving little change in stem form (0.3% gain compared with 0.6% for direct selection).

Silen and Rowe (1971) pose the question of whether equal numbers of stocky versus slender trees can be grown on the same land area. Libby (1987) suggests that short, stocky trees may be at a competitive disadvantage in mixtures, and that selection for stockiness will lead to decreased unit-area yields unless stocky trees are grown in pure stands. My results indicated, however, that stocky trees are not necessarily short, and that they partition more to branches and less to stemwood (negative correlations between stem form and branch proportion and positive correlations between stem form and stemwood proportion). Thus, stocky trees may be more rather than less competitive, and they could potentially result in reduced stand productivity when grown together in pure stands. Silen and Rowe (1971) also thought that stockiness may be associated with increased branchiness.

Wood density

The mean wood density found in this study (0.40; Table 3) was comparable to values reported elsewhere for juvenile Douglas-fir (McKimmy and Campbell 1982; Bastien et al. 1985; King et al. 1988; Vargas-Hernandez and Adams 1991). Families differed significantly in wood density, and wood density was strongly inherited ($h^2 = 0.52$) with moderate genetic gains possible (3.7%). High individual-tree heritabilities for wood density have been reported in previous studies of Douglas-fir (Bastien et al. 1985; King et al. 1988; Vargas-Hernandez and Adams 1991).

Strong negative phenotypic and genetic correlations were found between wood density and tree size (Table 7). The estimated genetic correlation was perfect ($r_a = -1.00$). Other studies have reported strong negative genetic correlations between wood density and tree size in Douglas-fir (Bastien et al. 1985; King et al. 1988; Vargas-Hernandez and Adams 1991). Some provenances in the study of Bastien et al. (1985) had negative genetic correlations of the magnitude of those found in the present study. The consequence of a perfect negative correlation is that simultaneous improvement of both wood quality and stem size would not be possible; any genetic improvement in stem size would necessarily be accompanied by a decrease in wood density.

Conclusions

Considerable genetic variation was found for traits of stem size, biomass partitioning, and wood density, and genetic gains may be expected from selection and breeding of desirable genotypes. Biomass partitioning traits, in particular, had high heritability estimates, although genetic gain estimates were not as large as those expected for size traits. Foliage efficiency was highly correlated with harvest index and may represent an alternative measure of partitioning to the stem. Unfortunately, measuring foliage efficiency nondestructively by estimating leaf area based on cross-sectional area of sapwood did not appear feasible; foliage efficiency based on indirect measure of leaf area was unrelated to foliage efficiency where leaf area was measured directly.

High heritabilities and moderate expected genetic gains for biomass partitioning traits and wood density indicated that these traits may be successfully included in an ideotype designed to maximize unit-area productivity and value. Unfortunately, unfavorable genetic correlations with individual-tree stem size indicated that it would be difficult to achieve simultaneous genetic gain in stem size and harvest index, or in stem size and wood density. However, multiple-trait selection using selection indices that included partitioning to leaves relative to total crown and partitioning to bark relative to total stem could potentially lead to favorable gains in stem volume while preventing any unfavorable responses in harvest index. Favorable genetic correlations were found between stem size and stem form, although low variation in stem form indicated that little response to selection may be expected.

The inheritance of biomass partitioning traits is of interest because of the hypothesized relation of harvest index to increased stand productivity under competitive conditions. For this reason, the stand chosen for evaluation of genotypes was one in which trees had been in competition for several years. The competitive conditions of this study may differ though from those of another genetic test, and may differ from those in which selections will be grown and genetic gains will be realized. The effect of competitive environment on expression and inheritance of traits is unclear. Further research is needed to evaluate the effect of stand development and genetic composition on the expression and inheritance of potential ideotype traits. In particular, proposed ideotype traits are only hypothesized to be related to stand productivity, and verification of the relation between ideotype traits and stand productivity is needed. Such studies would involve evaluating alternative ideotypes in pure and mixed stands at different spacings and at different ages.

Partitioning of biomass between stem and crown and between foliage and branches is related to other traits of crown structure, including relative crown width and branch size and number. Crown structure traits may be hypothesized to be related to unit-area productivity. The second paper in this series (St.Clair 1994) will consider the inheritance and relations among crown structure traits and the relations of these traits to biomass partitioning and tree size.

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