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Selection of Traits for Growth, Form, and Wood Quality in a Population of Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) from British Columbia

by

JOHN N. KING

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

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Date 14 March 1986

Abstract

Selection of traits for growth, form, and wood quality were investigated in full-sib progeny trials of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) in British Columbia. Sources of variation for additive genetic variance were significant for 20 of 21 traits investigated. Other sources of genetic variation (dominance genetic variance and G.E.I. sources of variance) were, by and large, non-significant. High individual tree heritabilities were found for branch angle (h_i^2=0.73) and wood density (h_i^2=0.90), indicating that these traits would respond well to mass selection. Traits of form including branch number, partitioning traits (branch to stem diameter ratios and branch length to total height ratios), stem sinuosity, early height measurements, and diameters showed moderate heritabilities ($h_i^2 \geq 0.15$; $h_f^2 \geq 0.7$). Other form traits: forking and bole taper; and growth traits of later height measurements, stem volume, and direct branch growth measures were of low individual tree heritabilities ($h_i^2 \simeq 0.10$; $h_f^2 \simeq 0.50$). However all traits except for branch thickness (non-significant) indicated that they would respond well to family selection. Expected response to stem volume selections are large (≃10% per selection intensity unit) because of large phenotypic variance among family means. Moderate and favourable genetic correlations exist between traits of yield, and traits of crown form, and partitioning. Unfavourable genetic correlations exist

between traits of yield and wood density (r_A=-.53) and between traits of form and wood density. These parameter estimates are similar to results published both for Douglas-fir and other conifers.

Genetic parameters were used to establish key traits that can be effectively measured and used in Douglas-fir progeny evaluations. They were also used to point out important strategies that can be used in genetic selections. Early height can be effective for early selections for traits of growth and yield. Later selections for growth and yield are more efficiently made with diameter measurements. Partitioning traits are more effective for form selections than direct crown measurements. Genetic covariances among crown form traits and yield traits can be effectively exploited to promote a fine-branching form type. Several selection index options were investigated to deal with the strong negative correlation that exists between wood density and diameter growth. Selections that maximize the minimum expected response to both traits would offer the best strategy and would help to break down this negative correlation.

Options for incorporating these selection strategies into current breeding practices are briefly discussed.

Acknowledgments

There are many people I wish to thank for their help and interest in this study. A lot of credit must go to Chris Heaman and his predecessor Dr. Orr-Ewing who initiated this experiment and whose material I have been allowed to work with; Chris imparted a lot of his enthusiasm to this project. I would like to thank my supervisor Dr Francis Yeh for his involvement and the commitment from a busy schedule that he gave to this study. I wish to thank Ingemar Karlsson and the staff at the Cowichan Lake Forest Experimental Station for their help and hospitality. I would like to thank Dr Bruce Dancik for his editorial comments and criticisms, and Dr John Worrall for his comments on my manuscript. I wish to acknowledge the excellent financial support provided by the C.F.S. through the Department of Forest Science and N.S.E.R.C. for providing personal support. I finally wish to thank my wife Patty for all her help and support without which I could not have completed this study.

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1. INTRODUCTION

1.1 Biology and Thesis Objectives

Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominates the most productive forest lands of western North America (Silen 1978). It is valued in this region and in areas where it has been introduced as an exotic (Birot 1982) for its growth potential, good form characteristics, relative freedom from major pests, and superior wood quality. It is, therefore, a candidate for tree improvement programs in the many parts of the world where it is planted. The purpose of this thesis is to investigate the potential for genetic improvement for traits of growth, form, and wood quality in a population of coastal Douglas fir from Vancouver Island and the southern mainland of British Columbia.

1.1.1 Systematics and Distribution of Douglas-fir

Eight species of the genus *Pseudotsuga* are recognized, two in western North America and the others in Asia (Isaac and Dimock 1965). The genus *Pseudotsuga* is distinguished by its woody cones with persistent scales and protruding trident-like bracts; by conical, sharp-pointed buds; by linear, soft leaves; and by resin blisters on smooth bark that becomes furrowed and marbled with cork layers as it matures (Hosie 1973; Silen 1978). One of the species of the genus found in North America is big-cone Douglas-fir

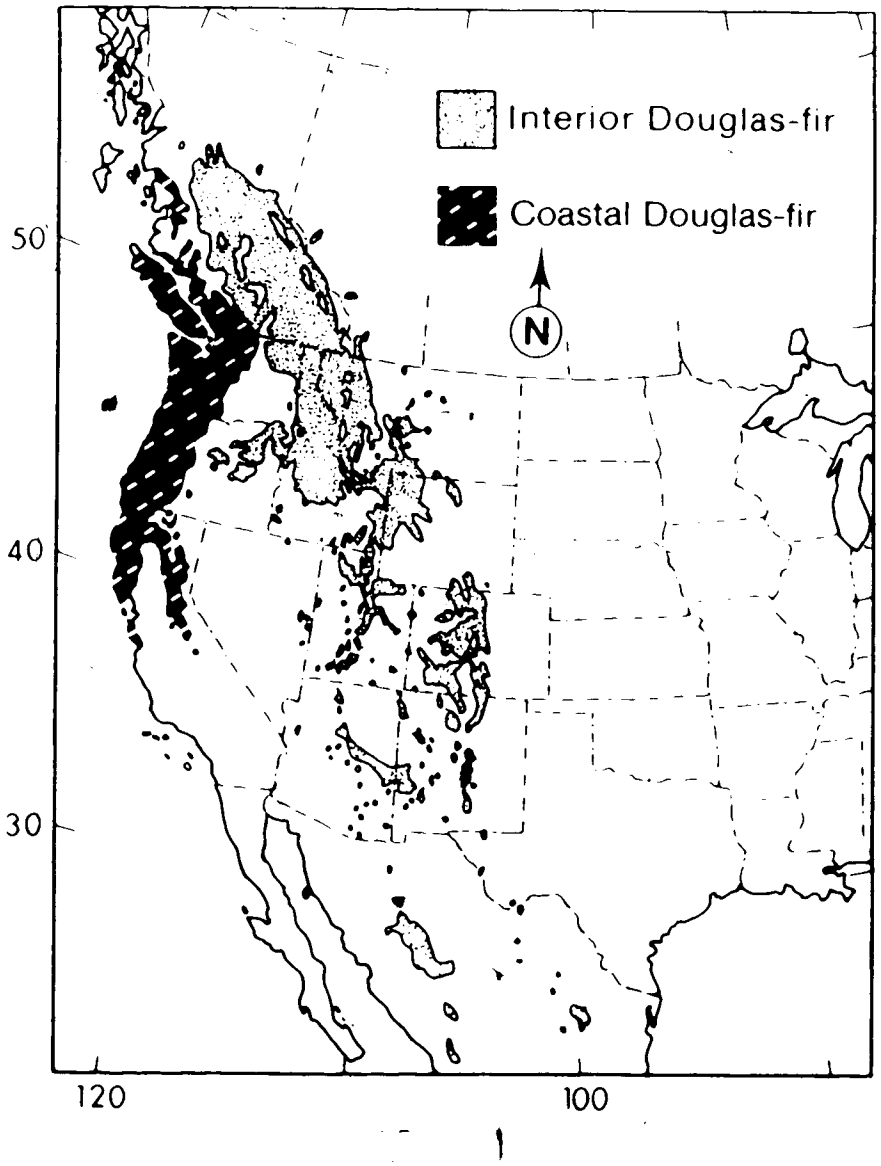
(*Pseudotsuga macrocarpa* Mayr), which has a limited range in California (Griffin and Critchfield 1972). The other species (*Pseudotsuga menziesii*) is a wide-ranging gymnosperm occurring from central British Columbia (lat. 55° N.), south along the Pacific Coast to Central California (lat. 37° N.), inland to western Alberta and down the Cordilleran chain to southern Mexico (lat. 19° N.) (Fig. 1). Elevational distribution varies with latitude ranging from over 800 m in the extreme northern part of its range, to over 3350 m for some Rocky Mountain sites (Silen 1978). Within its range rainfall varies from 450 mm to over 5000 mm per year.

The wide and varied environments together with the isolation potential of mountain topography have produced a species of extreme genetic diversity. Two main varieties are recognized: coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) and interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). The coastal variety is the more commercially valuable of the two and was the first-recognized form of the species. References in this text to Douglas-fir refer primarily to the coastal variety unless otherwise stated.

1.1.2 Ecology and Silvics of Douglas-fir

Over its wide range Douglas-fir prefers moist, well drained soils; although intolerant of wet soils and anaerobic conditions, it can be relatively tolerant of summer droughts. In the cold, wet conditions of the coastal

Figure 1. Natural range of Douglas-fir, *Pseudotsuga menziesii* (after Little 1971).



fog belt other conifers such as Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) are favoured. On poorly drained soils and on floodplains, Sitka spruce, western redcedar (*Thuja plicata* Donn.), and hardwood species such as cottonwood (*Populus trichocarpa* Torr. & Gray) are better able to survive (Krajina *et al.* 1982). The coastal variety does not tolerate frosts below -10°C for a period of more than about a week (Krajina *et al.* 1982). At high elevations it is replaced by cold-hardy species such as mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), western white pine (*Pinus monticola* Dougl.), and lodgepole pine (*Pinus contorta* Dougl.).

There are difficulties on many good sites with the establishment of Douglas-fir due to competition from shrubs (Silen 1978, Klinka *et al.* 1981). This is a particular problem on more moist soils, where it is more shade intolerant (Krajina *et al.* 1982) and shrub growth is vigourous. Compared with its commonly associated conifers, Douglas-fir ranks as a shade intolerant species (Isaac and Dimock 1965). Because of its association with shade tolerant species such as western hemlock, Sitka spruce, western redcedar, grand fir (*Abies grandis* (Dougl.) Lindl.), and amabalis fir (*Abies amabalis* (Dougl.) Forbes), Douglas-fir is recognized as a sub-climax species (Isaac and Dimock 1965). However, over much of the Pacific slopes, a region associated with summer droughts, Douglas-fir occurs in

essentially pure, even-aged stands as the major conifer species. Douglas-fir's thick fire-resistant bark, rapid growth and long life span make it a highly successful fire climax species. The noted longevity of Douglas-fir (more than 1000 years) (McArdle *et al.* 1961), and its ecological relationship with fires (Schmidt 1960) has established its dominance in the forest community.

The nutritional requirements of Douglas-fir are moderate, but it grows poorly on oligotrophic soils, where calcium, magnesium, nitrogen, phosphorus and potassium are in low supply (Krajina *et al.* 1982).

1.1.3 Breeding Methods and Goals

The growth potential and high quality timber of Douglas-fir have made it the prime species for intensive forestry practices and tree breeding in the Pacific Northwest. British Columbia's tree improvement program for Douglas-fir began in 1957 with phenotypic selection of plus-trees (Orr-Ewing 1969). Selections were made for growth and form from a broadly defined seed zone of coastal British Columbia and Northern Washington (Heaman 1967). First generation orchards currently provide much of the seed for the reforestation program (Yeh *et al.* 1981).

The breeding program in B.C. has developed; i) to establish a breed population for recurrent selections, ii) to estimate genetic variances and establish parameters as an aid to selection, and iii) to test the breeding values of

first generation selected parent trees (base population). The vehicle for this program is a disconnected six-parent half-diallel genetic test of the base population (Heaman 1981). An earlier factorial test (Yeh and Heaman 1982; EP707) of 26 trees chosen randomly from the base population is limited in its opportunity of allowing recurrent selections but provides excellent research material for objectives ii) and iii). This factorial test offers the ideal material for research because:

1. it is full-sib material from a factorial mating design, thus it permits the direct estimation of additive and dominance genetic variances (Namkoong 1979);
2. it is at an age where traits of form and quality traits can start to be evaluated;
3. it allows the opportunity of researching selection strategies that can be applied in the larger-scale breeding program.

Traits of quality refer to traits that affect the quality of the clear-wood resource. Specifically these are traits of crown form, stem form and wood quality. Traits of crown form are: branch angle, branch number, branch thickness, and branch length. Crown form traits are important, not only for their effect on the clear-wood resource - heavier and more persistent branches (knots), more compression wood, less strength in stress grading of lumber and poorer pulp and paper yield and quality; but also for management and handling - pruning and delimbing costs,

and also because of their importance to the partitioning for valuable bole wood rather than undesirable branching material. Branch thickness and branch length can also be considered as growth traits. Traits of stem form refer to straightness of stem, stem taper, and forking, and are important for their effect on the quality and uniformity of the clear-wood resource. Wood density is considered the most important clear-wood characteristic affecting wood quality for pulp, lumber, and plywood (Kellogg 1982).

1.1.4 Objectives

This thesis attempts to address the question of whether it is possible to select for traits of growth, form, and wood quality in Douglas-fir, using parameters estimated from a genetic experiment (EP707) established by the British Columbia Ministry of Forests, Research Branch. The specific objectives are:

1. to test for the significance of genetic sources of variation and estimate genetic parameters for traits of growth, form and wood quality;
2. to establish key traits of growth, form and wood quality that can be effectively measured and used in large-scale progeny test evaluations;
3. to investigate multiple trait selection strategies for the genetic improvement of Douglas-fir.

1.2 Growth of Douglas-fir

Height and growth are not only prime economic traits, but in a species such as Douglas-fir, which forms pure even-aged stands following fire (Schmidt 1960), height is an important component of fitness. Suppression and eventual mortality will occur for genotypes that cannot remain in competition with their neighbours within the dominant and co-dominant canopy classes.

Initial seedling growth (prior to six years) can be slow (Isaac and Dimock 1965) for Douglas-fir, but this probably reflects environmental constraints (Silen 1978). Once past the seedling stage annual growth can surpass 2 metres, and 60 cm annual height increments can continue for a century on best sites (Silen 1978). Volumes of over 1500 m^3/ha are not unusual in stands of coastal Douglas-fir (Silen 1978).

1.2.1 Variability Studies on the Growth of Douglas-fir

Douglas-fir achieves its greatest growth potential in Oregon and Washington west of the Cascades, southern coastal British Columbia, and Vancouver Island. In these regions, its stature and height (often exceeding 70 m) give it an imposing presence in old growth stands.

On the west coast of North America there is, in general, a cline of growth rate potential that follows a westward trend of increasing precipitation and availability of moisture in summer drought times (Silen 1978). Variation

attributable to environmental clines associated with elevation or soil moisture gradients can occur even in small-scale geographic distributions (Silen 1978, Campbell 1979).

The exploitation of seed source differences can be profitable in tree improvement programs and is a necessary first step in species introductions (Birot 1982). White and Ching (1985) found that once the poor southern Oregon provenance was removed, the differences among 13 other provenances - using 25 year field performance - was slight and often not statistically significant. One of the earliest provenance variation studies was the Douglas-fir Heredity Study (Munger and Morris 1936) established in 1912. The study was based on 120 open-pollinated (O.P.) families from 13 sources in western Oregon and Washington and was planted on five sites. Namkoong *et al.* (1972) used this study to look at time-trend results in genetic and environmental variances. Although in the end they felt they could only make general inferences from one site, they found a steady and significant increase between seed-source means as the test matured after age 15. Jarret (1978) found an increasing provenance effect with age in the French IUFRO[1] provenance trials.

Provenance research for coastal Douglas-fir in B.C. has revealed that large and real differences among seed sources can be exploited, especially by the introduction of

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[1] International Union of Forestry Research Organizations

Washington provenances into mild coastal sites (Illingworth 1978, Ying 1984). Introduction of low-elevation provenance material at high elevation sites (above 900 m) involves the risk of severe snow or frost damage (Ying 1984). If gains from seed source selections are to be realized, care must be taken that these gains are not lost to reduced hardiness and adaptability (Silen 1978).

The capture of a racial effect through wide crosses has also been investigated in Douglas-fir and may offer some promise (Orr-Ewing and Yeh 1978).

1.2.2 Genetic Variation in the Growth of Douglas-fir

Variation within populations is maintained as a method of temporal adaption for a long living species such as Douglas-fir (Hesslop-Harrison 1964). Several published accounts report that significant and important amounts of additive genetic variance are available for improvement of growth traits in Douglas-fir. Campbell (1972) found significant differences but low heritabilities (h_i^2[2] =0.10-0.16) for height increments of full-sib seedlings. Yeh and Heaman (1982) reported significant values for sources of additive genetic variance (σ_f^2) for height and diameter at age six in the same material used in this study. Heritability values were h_i^2=0.14±0.10 and 0.19±0.11 for height and diameter respectively. Estimates of non-additive

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[2] h_i^2=heritability appropriate for mass (phenotypic) selection, Appendix Table B

genetic variances were non-significant. Genetic studies of Douglas-fir in France show moderate heritabilities and expected response to selection. Jarret (1978) found, using height at eight years on 15 open-pollinated families within one of the IUFRO provenances, moderate heritability values (h_1^2=0.36±0.19). Birot and Christophe (1983) reported heritability estimates from 26 provenances of the French Douglas-fir trials that ranged from 0.0 to 0.77 for height at 12 years. Most of the provenances had levels of h_1^2=0.3; and heritabilities of tree girth were similar. Fashler *et al.* (1985) also reported significant amounts of additive genetic variances and moderate to high within-provenance heritabilities for height growth from O.P. seedlings from IUFRO collections at the U.B.C. Research Forest. Rehfeldt (1983) found high within-population heritabilities for height growth in four-year-old O.P. seedlings of interior Douglas-fir (h_1^2=0.52±0.10).

In comparison with these O.P. studies the full-sib studies of Campbell (1972) and Yeh and Heaman (1982) have reported significantly lower heritabilities. Heritability estimates derived from open-pollinated families are biased when the assumption is made that the genetic covariance between O.P. progeny is that of half-sibs (Namkoong 1966; Squillace 1974). Although Rehfeldt (1983) adjusted for an inbreeding coefficient of F=0.10 this bias may account somewhat for the differences between the O.P. studies and the full-sib studies. The testing environment and age of

material are also important factors in the determination of environmentaly sensitive traits such as height growth. Nursery and farm field trials show higher heritabilities than progeny trials that simulate production plantations and heritabilities for height growth can decline with age.

Namkoong *et al.* (1972) found later height measurents in the Douglas fir Heredity Study (Munger and Morris 1936) were non significant (P>.05) for family differences.

1.3 Form of Douglas-fir

Mature Douglas fir is characterized by a long, branch-free, cylindrical stem and a short, columnar, flat-topped crown (Hosie 1973). Young trees have narrow conical crowns that extend to the ground (Hosie 1973). In a closed stand lower limbs die rapidly with increasing overhead shade. However natural pruning of these limbs can take some time (Isaac and Dimock 1965). Branching and crown-form traits are important for the effect they have on the quality of the clear-wood resource; compression wood is increased with acute angled branching, and heavy limbedness will produce persistent knots and retard the ability to produce clear stems (von Wedel *et al.* 1968). Clear stem wood is not only desirable for clear-wood products and peeler logs. (von Wedel *et al.* 1968; Shelbourne 1970), but also in the production of uniform pulp products (Blair *et al.* 1974; Zobel and Kellison 1978).

Crown characteristics are likely to be important not only because of their effect on wood quality, but also because the biomass potential of the species is more valuable when partitioned into stem wood than into undesirable branch wood.

1.3.1 Variability Studies on the Form of Douglas-fir

Extreme phenotypic variability for limb and crown characters was found by Campbell (1958, 1961, 1963). Campbell measured crown characteristics (branch numbers, lengths, thicknesses and angles) in 15 to 35 year old Douglas-fir using 30 trees in each of 10 locations. Most of the variability of these characters could be accounted for by the variability in volume, except for that of branch angle. Relationships between branch number and volume, branch length and volume, and branch thickness and volume were strong and positive. Age of the tree had little influence, except for its influence on volume. Campbell found the following relationships between branch characters:

1. trees with acute-angled branches have thicker branches,
2. trees with fewer branches have thicker and longer branches,
3. taller trees of similar volume (less tapering) have shorter branches.

However, the association between branch characteristics was slight in comparison to the association of branch characters with volume.

Campbell (1963) used path coefficient analysis to look at the branching relationships with volume. Stem volume was most affected by variation in the number and thickness of branches. Most of the effect branch length had on volume was indirect through branch thickness. Branch number and branch thickness together were associated with 60% of the variation in stem volume. These relationships were fairly consistently expressed in the eight separate areas studied, at least when grown in open growth conditions.

Because environmental influences such as spacing, nutrients, and site quality exert a strong influence on form characters, significant differences for these characters between populations could not be verified as indicating genetic differences (Campbell 1961). Campbell also found that the phenotypic variation of branching characters was most highly expressed in areas of good height growth. Site factors exert a strong influence on the expression of form characters, and studies of their effect in Douglas-fir have been made by Walters and Soos (1961), De Champs (1978), Carter *et al.* (1985).

Jarret (1978) found a strong and significant replication effect for crown-form traits in the French IUFRO provenance-progeny trials. He also found that provenance effects were significant for crown-form traits: branch angle, branch number, knot index[3], and distribution of

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[3] knot index was a ratio of cross-sectional areas of branches to the cross-sectional area of the stem 10 cm below the whorl (Campbell 1961).

branches in the whorl, but not for branch thickness. A significant negative phenotypic correlation (r= 0.58) existed between the elevation of a provenance and its branch number. Sources from lower elevations had more branches than high elevation sources. Jarret also found that northern provenances tended to have more acute angled branching than southern provenances.

1.3.2 Genetic Variation in Crown-Form Characteristics

Heritability estimates for crown form traits vary, but tend to be larger than those of growth traits. Heritability estimates (h_i^2, appropriate for mass selection) for branching-quality traits in Finnish trials of Scots pine (*Pinus silvestris* L.) were 0.4 – 0.7, whereas growth traits were low to moderate (< 0.3) and sometimes lower than 0.1 (Poykko 1982). Merrill and Mohn (1985) found non-significant family differences in Lake States white spruce (*Picea glauca* (Moench) Voss) for total height and branch number; but significant heritabilities (h_i^2) of 0.14 for diameter, 0.16 for branch thickness, and 0.44 for branch angle.

The inheritance of branch quality traits in Douglas-fir shows similar trends (Jarret 1978; Birot and Christophe 1983). A comprehensive study of crown-form traits was conducted by Jarret (1978) using 15 O.P. families within one of the provenance's of the French IUFRO provenance. Heritabilities were reported as:

Trait	h_i^2
Branch number	non-significant
Branch angle	0.54±0.23
Branch thickness	0.34±0.18
Knot index	0.29±0.16

Non-significant results for branch numbers per whorl are similar to those reported for white spruce (Merrill and Mohn 1985) and may reflect the difficulty in assessing this trait (Campbell 1961).

Branch angle, in other studies on the French provenance-progeny material (Birot and Christophe 1983), showed a strong additive genetic effect similar to that reported by Jarret (1978). Twelve percent of the variation could be attributed to differences between families within provenances, whereas only 1.5% of the variation was attributed to provenances. Heritabilities were high (h_i^2=0.49), and large phenotypic variabilities indicated response to selection for this trait would be good (Birot and Christophe 1983). Jarret (1978) found moderate additive genetic variance for branch thickness, which contrasted to the non-significant effect he found for this trait for provenances.

1.3.3 Stem Form Traits

Although Douglas-fir stands appear relatively straight-stemmed and of good form, a surprising amount of sweep and sinuosity can occur. In stands marked for commercial pilings, where only slight deviations from straightness are permissible, seldom could 20 per cent of the trees be used (Silen 1978). Stem crookedness can increase the amount of undesirable compression wood reducing pulp yield and quality (Zobel 1971) and producing poorer quality lumber and plywood (Shelbourne 1969a). Orr-Ewing (1967) in a limited study of stem form showed that selection might be useful for stem straightness.

Sinuosity, stem crookedness confined within an interwhorl stem segment (Campbell 1965) (Fig. 2), is a conspicuous feature of young Douglas-fir. There is typically a reduction of sinuosity from the pith to the bark in young trees (Polge and Perrin 1984), and much of the minor crookedness that occurs at this stage is covered by eccentric wood growth as the tree matures. However, this dislocation from the vertical brings about the formation of compression wood (Burns 1920; Mergen 1958). A portion of compression wood may be left adjacent to the pith in what otherwise would be considered a straight tree; the amount of which may be directly related to the degree of sinuosity (Zobel and Haught 1962). In severe cases a permanent wave may be left in the stem.

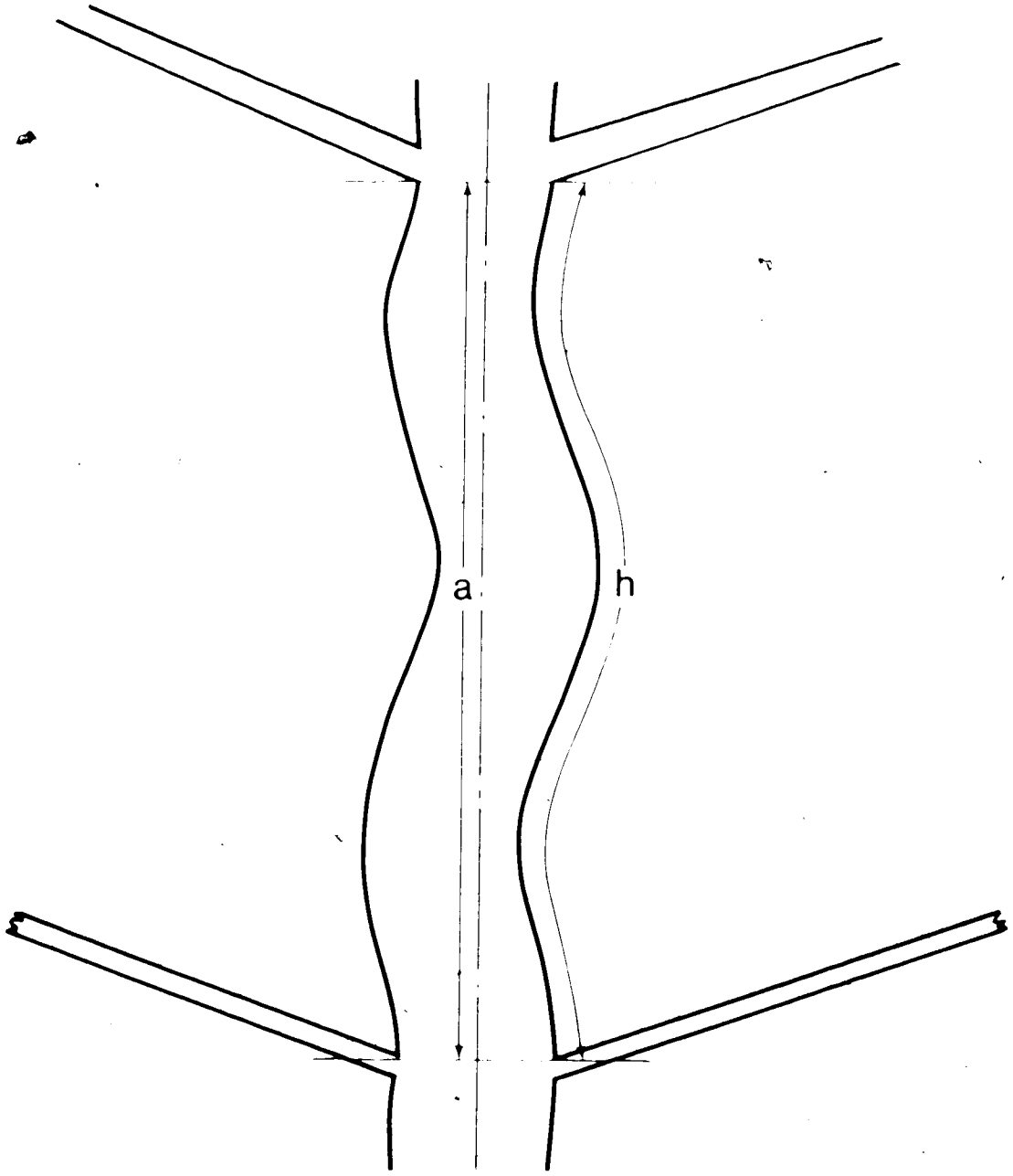

Figure 2. Sinuosity in Douglas-fir (Campbell (1965) measured sinuosity using a transformation of the ratio of *h/a*, where *a* equals the vertical length of the interwhorl and *h* equals the length along the sinuous stem).

Campbell (1965) studied sinuosity in Douglas-fir stands. He found high within-population variation (CV=42%) and significant between-stand variation for stem sinuosity. Using path analysis he showed diameter at the base of a leader was better associated with sinuosity than was length of leader. Although not working with genetic material, Campbell predicted that heritability was likely low; thus sinuosity would be a difficult character to improve through mass selection.

Forking, ramicorn branching*, and multiple leaders are other commonly occurring features of young Douglas-fir. The incidence of these growth features in young Douglas-fir is strongly associated with the occurrence of lammas shoots.

Lammas shoots or second, late-season flush is a common feature of the phenology of young Douglas-fir (Fig. 3). Lammas growth is defined as an abnormal burst of late-season shoot growth from the flushing of recently formed buds that are not expected to open until the following year (Kramer and Kozlowski 1979). Lammas shoots occur with high incidence in young plantations of Douglas-fir (Walters and Soos 1961) and are associated with favourable climatic conditions, good site quality, fertilization (Walters and Kozak 1967) and origin of provenance (Jarret 1978). However, they decline with age and are relatively uncommon in material over 12 years of age. These types of late-season shoot growth, are

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* a ramicorn branch refers to a fastigiate, large, thick branch that is associated with lammas shoots from lateral buds (Fig. 3)

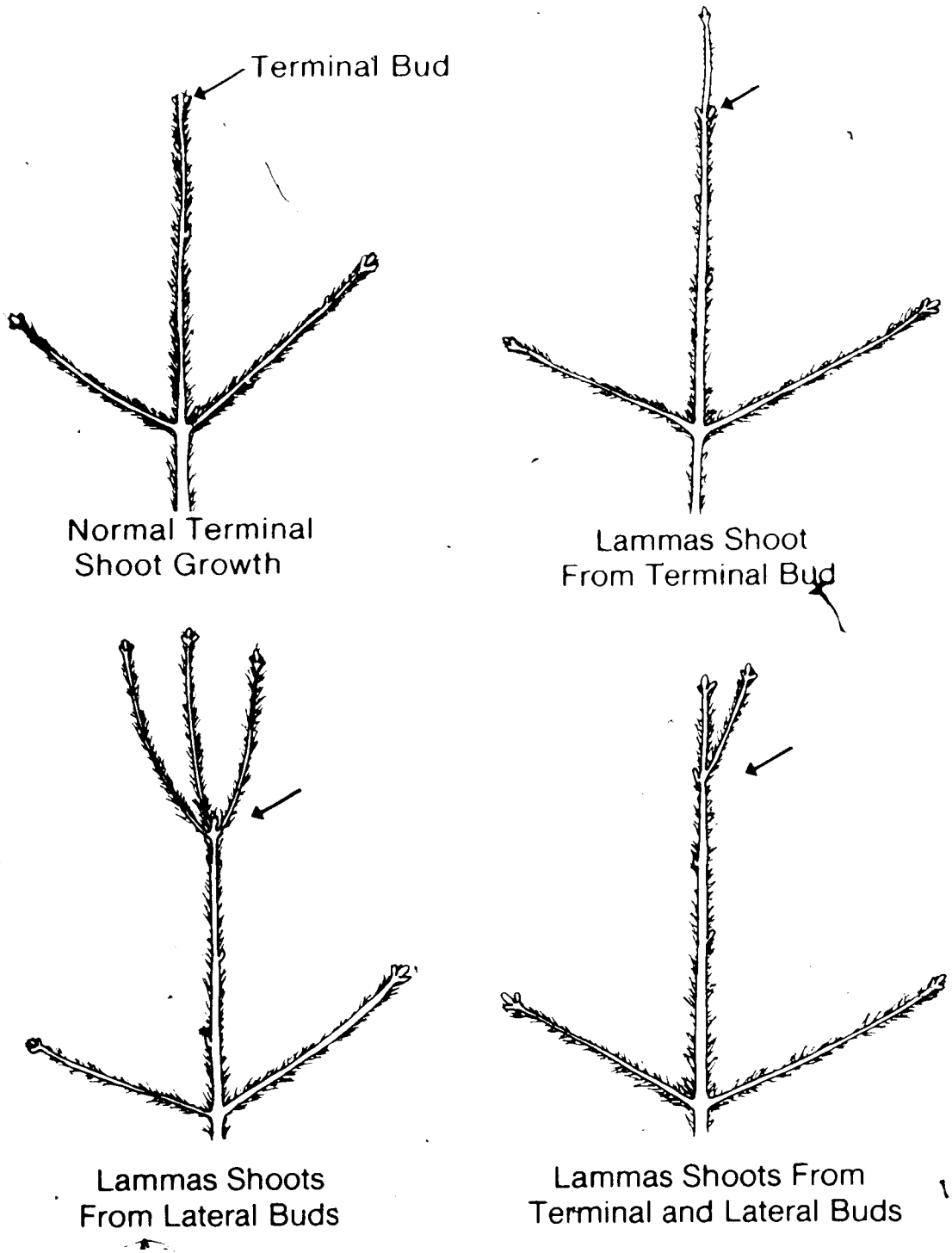

Figure 3. Abnormal late-season (lammas) shoot growth.

one of the most important juvenile growth features that promote distorted growth symptoms (Carter *et al.* 1985). They are most often manifested in young Douglas-fir plantations as multiple lateral bud lammas shoots or a combination of lammas shoots from the terminal and lateral buds (Fig. 3); the common consequences are forking, ramicorn branches, multiple leader formation, and excessive branchiness and clusters of branches (Rudolph 1964). Growth disturbances associated with secondary flushing are exasperated when early frosts occur. Although such growth deformities at a juvenile stage may be overcome, they can leave permanent detractions from a clear bole.

Stem taper is a valuable trait for its effect on yield and quality. Trees with marked taper have greater volume than trees of the same height where taper is less evident. A cylindrical stem is more profitably handled and processed for dimensional timber. Much of stem taper depends upon spacing and other silvicultural practices; genetic influences on stem taper are little understood. Jarret (1978) found a slight provenance effect for stem taper.

1.3.4 Genetic Variation of Stem Form Features

Jarret (1978) studied sinuosity and forking and found:

Trait	h_i^2
Sinuosity	0.52±0.23
Forking	non-significant

Response to selection for sinuosity was high, due to the high heritability and large phenotypic standard deviation. Moderate to high family heritabilities of sinuosity (h_f^2 >0.5) and large variation among families indicated that selection for stem straightness would be favourable in studies by the Pacific Northwest Tree Improvement Cooperative (Adams and Howe 1985). Sinuosity was reported to be of moderate heritability (h_1^2=0.39) in the study of Birot and Christophe (1983); as with Jarret (1978) forking and ramicorn branching were found to be non-significant. Birot and Christophe (1983) noted that sinuosity as well as the crown-form traits are sensitive to non-controlled environmental effect (85% residual variation), but because of large phenotypic variances among families, family selection can be very effective.

1.4 Wood Quality in Douglas-fir

The timber of Douglas-fir is highly prized and sought for structural uses, pulp and veneer. It is straight grained, moderately light to moderately heavy (wood density of 430 to 450 kg/m^3) and of intermediate durability (Cown 1976).

Wood density is not a single property, but is a complex of characteristics such as percentage of summerwood, cell-wall thickness, cell diameter, lignin content, etc. (Koch 1972); however, it is convenient to treat it as a single trait. Wood density is an important trait because of

its close relationship to the strength, quality, and yield characteristics of pulp products (Barefoot *et al.* 1970), and the strength and structural properties of clear wood products (Barrett and Kellogg 1984). In a fast-growing plantation it is important to maintain the density found in the indigenous resource (Zobel and Kellison 1978) and breed for a uniform product (Zobel *et al.* 1982).

1.4.1 Variability Studies of Wood Density of Douglas-fir

Single-tree estimates of wood density are complicated by substantial vertical within-tree variation, but much of this variation is predictable (Cown 1976), and wood density estimates from breast high increment cores can give a good indication ($r=0.91$) of weighted tree mean density (Cown 1976). Another consideration is the use of young trees to evaluate mature tree performance. Do early progeny evaluations of wood density offer reasonable guidelines for later, mature-tree wood density? Wood density increases with age and there are indications that this increase is linear and can be quite predictable. Northcott *et al.* (1964) in a study of variation patterns in a limited number (six) of Douglas-fir trees demonstrated this trend after an initial period of instability prior to the 10th year growth ring. Kellogg (pers. comm.) in a recent study of Douglas-fir demonstrated a similar trend, with under 6-years being highly unpredictable 8- to 12-year growth rings stabilizing, and after 12-15 years demonstrating an increasing

linear trend. Keller and Thoby (1977) showed significant phenotypic correlations between mean density of the first ten rings to mean density of the outer ten rings in two stands of 30- and 60-year-old Douglas-fir, but non-significant correlations for another smaller population of 60-year-old Douglas-fir. Although McKimmy (1966), working on the Douglas-fir Heredity Study (Munger and Morris 1936), recommended that predictions of stem densities not be made before 25 years, McKimmy and Campbell (1982) suggested tests on 10- to 15-year-old material could provide information applicable to older material. Other studies by Harris (1965), Thoby (1975), Keller and Thoby (1977), Reck and Sziklai (1973) and especially Cown (1976), have demonstrated that early wood material can be used to predict mature stem-wood density in Douglas-fir. These studies have indicated that wood deposited after 15 years can be acceptable for whole-tree wood-density comparisons, but wood in the 8 to 12 year range can offer, with some caution, the earliest possible evaluation of whole-tree wood density.

Although several studies have shown differences among regions and provenances (Drow 1957; USDA 1965; McKimmy 1966; Wilcox 1974; Thoby 1975) this variation is by and large minor in relation to variation among individual trees (Cown 1976, Cown and Parker 1979).

1.4.2 Genetic Variation in Wood Density

Heritability values - appropriate for mass selection - were high (h^2 most provenances > 0.8) for wood mean density from 14-year-old provenance-progeny trials in France (Bastien *et al.* 1985); genetic variability was much higher at the family level than the provenance level, confirming a similar observation made by McKimmy and Campbell (1982). Bastien *et al.* (1985) reported that potential gain for wood density would not be great because of the low phenotypic standard deviation; they also reported unfavourable correlations between wood mean density and growth traits and wood mean density and wood heterogeneity. Unfavourable genetic correlations between growth and wood density, and between form and wood density have also been reported in radiata pine (*Pinus radiata* D.Don) (Dean *et al.* 1983).

The Pilodyn wood tester has been used to assess wood density by using the wood's resistance to penetration by a spring-loaded pin (Cown 1978). Moderate-to-strong negative correlations of depth of pin penetration with wood density from a variety of conifers suggest that this may be a useful way of ranking families for wood density selections:

r = -0.86 radiata pine (Cown 1978)

r = -0.81 loblolly pine (Taylor 1981)

r = -0.71 silver fir[5] (Hoffmeyer 1978)

r = -0.83 white spruce (Micko *et al.* 1982).

Many of these studies are on larger, more mature trees,

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[5] *Abies alba*

where the bark has been removed, and may be less applicable on through-the-bark measures of juvenile-growth trees.

In order to assess this instrument for its use in making genetic selections, genetic correlations are more appropriate to look at than phenotypic correlations.

Sprague *et al.* (1983) found high genetic correlations and resulting efficiencies of indirect selection for two types of Pilodyn:

r_A = -0.89 2.0 mm needle, 6joules spring,

r_A = -0.82 3.0 mm needle, 18joules spring,

but disappointing results for a third type (r_A = 0.24; 2.5 mm 18j). Bastien *et al.* (1985) concluded that the Pilodyn was not effective for selection purposes in the French Douglas-fir provenance-progeny tests. Genetic correlations were inconsistent and too greatly influenced by environmental factors, although they suggested that the Pilodyn might be used for quick measurements not requiring great accuracy.

2. MATERIALS AND METHODS

2.1 Materials

Twenty six trees were randomly sampled from the base population of first generation selected parent trees of coastal British Columbia. (Table 1, Fig. 3). Twenty two trees (serving as seed parents) were crossed with four trees (serving as pollen parents) in April 1971 (mating design II "tester", Comstock and Robinson 1952). Seeds from all families were spot seeded in nursery beds and at the end of the first growing season, in the fall of 1972, the seedlings were transplanted into Styro 8 plugs containing a mixture of peat, sand and sterilized soil. In the spring of 1973 one group of seedlings was outplanted in the Greater Victoria Watershed (GVWS); in the following spring another group was outplanted at the Cowichan Lake Experimental Station (CLES). Progeny families were planted in a randomized complete block design with three replications of nine-tree plots at a spacing of 3 m × 3 m. Both sites were cleared and fenced prior to planting.

1. Cowichan Lake Experimental Station (elev. 165 m) was planted with 9-tree row plots. CLES is on an undulating topography. Soils are Humo-Feric Podzols and are coarse sandy loams in texture. Soil moisture regime ranges from dry to moist and soil nutrient regime from poor to rich. Rooting depth is greater than 100 cm (Klinka *et al.* 1984). Survival has been high at this site.

2. Greater Victoria Watershed (elev. 488 m) was planted with 9 tree square plots. GVWS is on a uniform slope gradient of 20-25% and a SSE exposure. It is on a Coarse Loamy Podzol with a soil moisture regime of dry to fresh and a soil nutrient regime of medium with a rooting depth of over 100 cm (Courtin 1983, Klinka *et al.* 1984). The site is presently unfenced and has had problems with browsing, first by grouse and rabbits, and later by deer. Both Armillaria root rot (*Armillaria mellea*) and laminated root rot (*Phellinus weirii*) are present. Problems have also occurred due to severe competition with broom (*Cytisus scoparius*), which mainly affects the lowest replication where there are deeper and more mesic soils. Because of the damage and lower survival at this site, the full set of measurements could be made on less than half the trees.

Measurements of height and diameter have been made at both sites at 6 years (Yeh and Heaman 1982), 10, and 12 years. Growth form measures were taken at 11 years (summer 1983), and wood density measures (taken only at CLES) were taken after the 11th growing season (winter 1984).

TABLE 1. Parent tree locations.

Tree no.†	Location	Elevation	Lat.	Long.
Seed Parents				
49	Parksville	685 m	49°17'	123°33'
57	Gold R.	150	49 52	126 06
60	Campbell R.	30	50 15	125 24
72	Koksilah	550	48 37	123 48
73	Cowichan	180	48 50	124 10
110	Powell River	290	49 52	124 19
193	Chilliwack	625	49 07	121 36
300	Howe Sound	370	49 36	123 19
303	Howe Sound	610	49 36	123 19
305	Victoria	90	48 27	122 34
310	Pitt River	300	49 42	122 43
314	Pitt River	425	49 42	122 43
315	Pitt River	225	49 42	122 42
323	Pitt River	370	49 41	122 43
408	Chilliwack	825	49 07	121 49
415	Skagit	510	49 03	121 05
418	Knight Inlet	400	51 05	125 35
422	Sechelt	435	49 26	123 52
439	West Vancouver	615	49 22	123 13
499	Kelsey Bay	150	50 26	126 14
549	Knight Inlet	150	50 50	125 50
623	Powell River	335	49 52	124 19
Pollen Parents				
28	Ladysmith	685	48 56	123 53
33	Cowichan	580	48 50	124 05
62	Sproat Lake	60	49 18	125 13
448	Garibaldi	625	49 51	123 08

†B.C. plus tree registration number

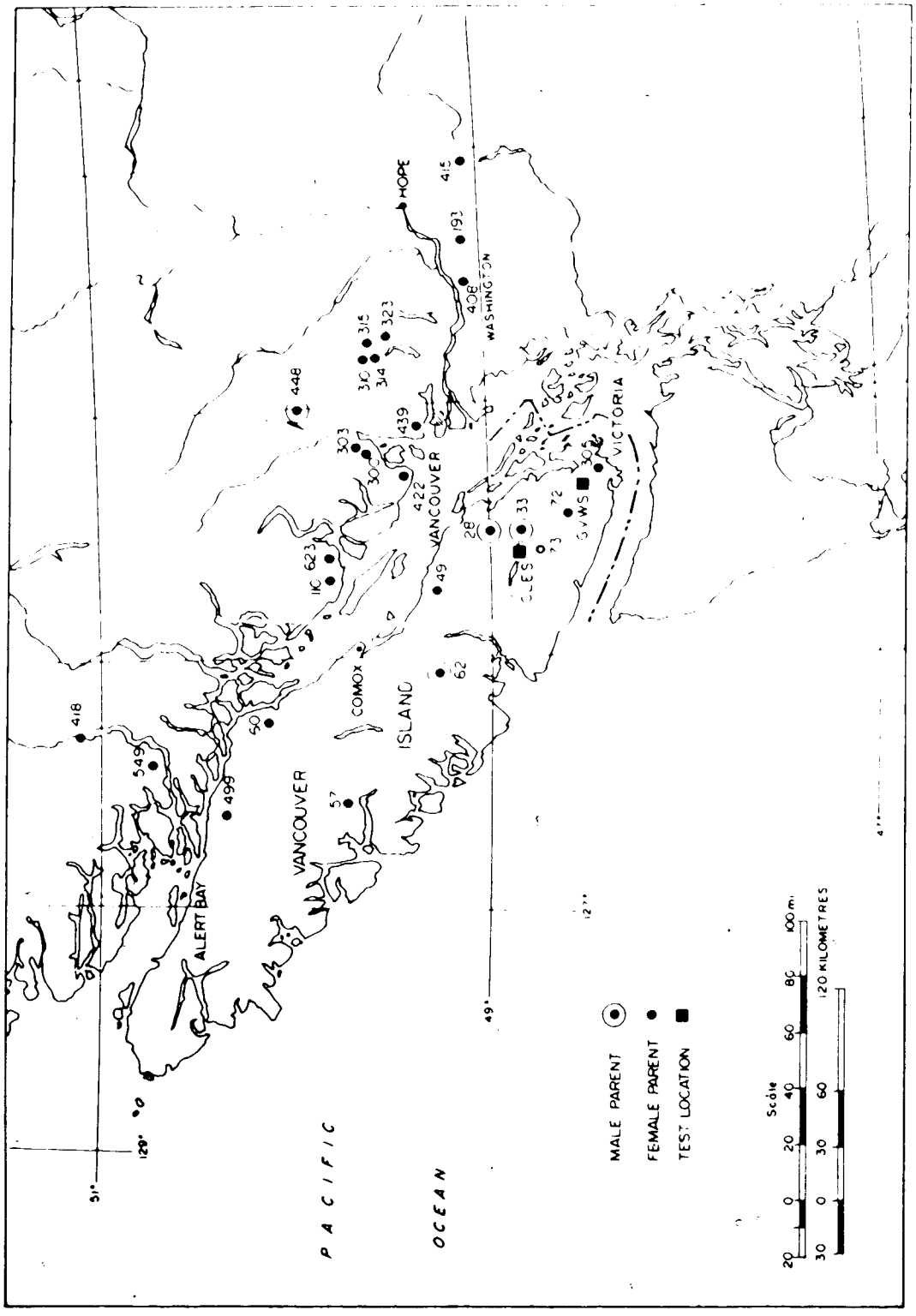

Figure 4. Geographic distribution of parent tree locations and test sites.

2.2 Statistical and Genetic Analyses

Analysis of variance was performed on the measurements for the purpose of testing hypotheses about the significance of family related effects and also for the purpose of estimating variance components for these effects. The analysis, for a random model, was conducted on individual trees using a least square analysis of variance program for unbalanced data developed by F.C.H. Yeh (Technical Advisor Genetics, British Columbia Forest Service and Department of Forest Science, University of Alberta) and UANOVA, a general purpose analysis of variance program developed by T. Taerum (Computing Services, University of Alberta).

Variance components were estimated by equating the mean square for each effect with its expectation (Tables 2-4) and solving for the component (Appendix B). Standard errors of variance components were calculated as per Becker (1975) (Appendix B). Components of covariances among traits were calculated by using the variance component models (Tables 2-4) on the sum of the values for the pair of traits in question and solving for the covariance term (Kempthorne 1957:pg 264).

Assuming no linkage, epistasis, and inbreeding, the components of variance among females (σ_f^2) and males (σ_m^2) estimates one-quarter of the additive genetic variance (σ_A^2) (Hanover and Barnes 1962). In the "tester" mating design the selection unit and the source of information for additive genetic variance is the female seed tree parent (σ_f^2).

TABLE 2. Structure of analyses of variance and covariance on individual sites.

Source of variation	Degrees of freedom	Mean squares or mean cross products	Expected mean squares or mean cross products
Replications	$r-1=2$	MS	$\sigma_e^2 + k\sigma_{\beta\gamma}^2 + k\sigma_{\alpha\gamma}^2 + k\sigma_{\alpha\beta}^2 + k\sigma_\gamma^2$
Males	$m-1=3$	MS_α	$\sigma_e^2 + k\sigma_{\beta\gamma}^2 + k\sigma_{\alpha\gamma}^2 + k\sigma_{\alpha\beta}^2 + k\sigma_\alpha^2$
Females	$f-1=21$	MS	$\sigma_e^2 + k\sigma_{\beta\gamma}^2 + k\sigma_{\alpha\gamma}^2 + k\sigma_{\alpha\beta}^2 + k\sigma_\beta^2$
Rep x males	$(r-1)(m-1)=6$	$MS_{\alpha\gamma}$	$\sigma_e^2 + k\sigma_{\beta\gamma}^2 + k\sigma_{\alpha\gamma}^2$
Rep x females	$(r-1)(f-1)=42$	$MS_{\beta\gamma}$	$\sigma_e^2 + k\sigma_{\beta\gamma}^2 + k\sigma_{\alpha\beta}^2$
Males x females	$(m-1)(f-1)=63$	$MS_{\alpha\beta}$	$\sigma_e^2 + k\sigma_{\alpha\beta}^2 + k\sigma_{\alpha\gamma}^2$
Plot	$(r-1)(m-1)(f-1)=126$	MS_γ	$\sigma_e^2 + k\sigma_{\beta\gamma}^2$
Within plot	$rmf(t-1)$	MS_e	σ_e^2

Terms and components of variance explained in Table 4.

TABLE 3. Structure of analyses of variance and covariance on combined sites.

Source of variation	Degrees of freedom	Mean squares or mean cross products	Expected mean squares or mean cross products
Sites	$s-1=1$	MS_1	
Replications/sites	$s(r-1)=4$	MS_2	
Males	$m-1=3$	MS_3	$\sigma_v^2 + k\,\sigma_{rmf}^2 + k_1\sigma_{smf}^2 + k_2\sigma_{mf}^2 + k_3\sigma_{rm}^2 + k_4\sigma_{sm}^2 + k_5\sigma_m^2$
Females	$f-1=21$	MS_4	$\sigma_v^2 + k_6\sigma_{rmf}^2 + k_7\sigma_{smf}^2 + k_8\sigma_{mf}^2 + k_9\sigma_{rf}^2 + k_{10}\sigma_{sf}^2 + k_{11}\sigma_f^2$
Site × males	$(s-1)(m-1)=3$	MS_5	$\sigma_v^2 + k_{12}\sigma_{rmf}^2 + k_{13}\sigma_{smf}^2 + k_{14}\sigma_{rm}^2 + k_{15}\sigma_{sm}^2$
Site × females	$(s-1)(f-1)=21$	MS_6	$\sigma_v^2 + k_{16}\sigma_{rmf}^2 + k_{17}\sigma_{smf}^2 + k_{18}\sigma_{rf}^2 + k_{19}\sigma_{sf}^2$
Males × females	$(m-1)(f-1)=63$	MS_7	$\sigma_v^2 + k_{20}\sigma_{rmf}^2 + k_{21}\sigma_{smf}^2 + k_{22}\sigma_{mf}^2$
Rep × males	$s(r-1)(m-1)=12$	MS_8	$\sigma_v^2 + k_{23}\sigma_{rmf}^2 + k_{24}\sigma_{rm}^2$
Rep × females	$s(r-1)(f-1)=84$	MS_9	$\sigma_v^2 + k_{25}\sigma_{rmf}^2 + k_{26}\sigma_{rf}^2$
Site × cross	$(s-1)(m-1)(f-1)=63$	MS_{10}	$\sigma_v^2 + k_{27}\sigma_{rmf}^2 + k_{28}\sigma_{smf}^2$
Plot	$s(r-1)(m-1)(f-1)=252$	MS_{11}	$\sigma_v^2 + k_{29}\sigma_{rmf}^2$
Within plot	$srmf(t-1)$	MS_{12}	σ_v^2

Terms and components of variance explained in Table 4.

TABLE 4. Components of analyses of variance models.

Term
s = number of sites
r = number of replications within sites
m = number of male pollen trees
f = number of female seed trees
t = number of trees within plots
Variance components
σ^2_w = variance among trees within plots
σ^2_{rmf} = variance among full-sib family plots within sites
σ^2_{smf} = variance among site-male-female combinations
σ^2_{mf} = variance among male-female combinations
σ^2_{rf} = variance among rep-female combinations within sites
σ^2_{rm} = variance among rep-male combinations within sites
σ^2_{sf} = variance among site-female combinations
σ^2_{sm} = variance among site-male combinations
σ^2_f = variance among female half-sib families
σ^2_m = variance among male half-sib families
σ^2_r = variance among replications within sites
σ^2_s = variance among sites
k_i = coefficient of the "i"th variance component

The component of variance among full-sibs (σ^2_{mf}) estimates one-quarter of the dominance genetic variance (σ^2_D). Because of the small number of pollen parents (four), the precision for estimating dominance genetic variance with the tester mating design is low, especially for low heritability traits (Pederson 1972).

Genotype × environment interaction (G.E.I) sources of variation can be tested by using:

σ^2_{sl} for additive × environment interaction (σ^2_{AE}),

σ^2_{sml} for dominance × environment interaction (σ^2_{DE}).

2.2.1 Heritability and Selection Concepts

One of the most important genetic parameters used in evaluating the response to selection is heritability. Heritability has value primarily as a method of quantifying the concept of whether progress through selection for a character is relatively easy or difficult to make in a breeding program (Hanson 1963). At the basic level heritability is defined as the ratio of additive genetic variance (σ^2_A) to phenotypic variance ($\sigma^2_{P_1}$) (Falconer 1982). As a utility to a breeder, heritability statements should be unified with reference to a selection concept (Hanson 1963). The concept of heritability as a regression coefficient (Falconer 1982; Hanson 1963) is:

(COV(phenotypes measured for selection, genotypes generated)

÷

phenotypic variance of the mean value of the selection unit

is useful in forestry where the relationship between the selection unit and the improved generation may have many different permutations (Namkoong *et al.* 1966; Shelbourne 1969b; Namkoong 1979).

Where individuals measured from the progeny test are the selection unit, the phenotypic variance is expressed as:

$$\sigma^2_{P_1} = \sigma^2_A + \sigma^2_D + \sigma^2_{GxE} + \sigma^2_E \qquad 1$$

in terms of the variance components from the analysis of variance (Tables 2 & 3); this becomes:

$$\sigma^2_{P_1} = \sigma^2_m + \sigma^2_f + \sigma^2_{mf} + \sigma^2_{sm} + \sigma^2_{sf} + \sigma^2_{rm} + \sigma^2_{rf} + \sigma^2_{smf} + \sigma^2_{rmf} + \sigma^2_w \qquad 2$$

The numerator of the heritability is the covariance between the genetic value produced for utilization and the phenotypes measured to estimate that value. This covariance, when genotypes are produced from selected individuals, is that of offspring-parent ($\frac{1}{2}\sigma^2_A$). In mass selection where select trees freely intermate (Shelbourne 1969b, Namkoong 1979), this covariance is σ^2_A (because both parents are selected) and the full narrow sense heritability applies:

$$h_1^2 = \frac{\sigma_A^2}{\sigma_{P_1}^2} \qquad 3$$

In a breeding program, pedigree information can be used to assess more accurately an individual's breeding value than just its own performance, as in mass selection. This is especially helpful with characters of low heritability such as growth traits (Falconer 1982). Selection can be from the parent generation where the parent's progeny are used to derive the parent's breeding value. Recurrent selections can be made on individuals within the progeny test, using the performance of an individual's half- and full-sibs to aid in the definition of its breeding value.

The phenotypic variance of half- and full-sib family means is the phenotypic variance among half- or full-sibs, divided by the number of observations making up each kind of mean. For half-sibs, the phenotypic variance from our model (Table 3) is:

$$\sigma^2_{PHS} = \sigma_t^2 + \frac{k_{23}}{k_{12}}\sigma_{mt}^2 + \frac{k_{20}}{k_{12}}\sigma_{st}^2 + \frac{k_{27}}{k_{12}}\sigma_{rt}^2 + \frac{k_{29}}{k_{12}}\sigma_{smt}^2 + \frac{k_{30}}{k_{12}}\sigma_{rmt}^2 + \frac{1}{k_{12}}\sigma_w^2 \qquad 4$$

For full-sibs, the phenotypic variance from our model is

$$\sigma^2_{PFS} = \sigma_m^2 + \sigma_t^2 + \sigma_{mt}^2 + \frac{k_{29}}{k_{23}}\sigma_{smt}^2 + \frac{k_{30}}{k_{23}}\sigma_{smt}^2 + \frac{1}{k_{23}}\sigma_w^2 \qquad 4$$

The "tester" mating design of this experiment is designed to test seed tree parents. The selection process is progeny testing, where the characteristics of progeny are used to assess the breeding value of their parents rather than the progeny themselves (Turner and Young 1969; Falconer 1982). Progeny tests can supply information about the breeding value of parents (the 22 seed tree parents) and genetic parameters for the parental population. The parameters derived from a progeny test thus refer to the parental population (the base population of select parent trees) rather than the progeny population. As pointed out by Falconer (1982) the concept of progeny-test selection can be confusing because of ambiguity about which generation is being selected, the parents or their progeny. Because this is a type of family selection, "family" and "progeny-test" selection will be used as equivalent terms in this study.

In the selection of the best parent trees based on their progeny's performance, the numerator of the heritability is the covariance between the phenotypes measured for selection (i.e., the progeny of the 22 seed tree parents) and genotypes generated for utilization (i.e., progeny of the selected trees). The relationship is thus that of half-sibs and the covariance between half-sibs is $\frac{1}{4}\sigma_A^2 = \sigma_f^2$. The heritability (family) for this selection becomes:

$$h_t^2 = \frac{\sigma_t^2}{\sigma_{PHS}^2} \qquad 6$$

Expected percentage gain from selecting the best parent trees is (Namkoong *et al.* 1966):

$$\%\Delta G_t = i \times 2 \left(h_t^2 \times \sigma_{PHS} \times 100\right) / X \qquad 7$$

where X is the population mean. This can also be stated as:

$$\%\Delta G_t = i \times 2 \left(h_t^2 \times CV_{PHS}\right) \qquad 8$$

where CV_{PHS} is the coefficient of variation of the half-sib phenotypic variance. The selection intensity "i", refers to how many standard deviations the mean of select parents are above the mean of the whole population. Response to selection can thus be expressed as percentage response per standard deviation unit of selection or per unit "i":

$$\%\Delta G_t / i = 2 \left(h_t^2 \times CV_{PHS}\right) \qquad 9$$

The "2" is because select parent trees act as both male and females (clonal seed orchard) (Namkoong *et al.* 1966).

Recurrent selections involving second generation material are limited with the present mating design (NC II)

because of the potential of inbreeding; only four unrelated second generation individuals can be selected from the entire planted stock. Thus simple recurrent selection (mass selection) or combined selection schemes are not compatible with the "tester" mating design of this study. Gain calculations from a simple recurrent selection (mass) within the progeny test are reported for comparison purposes and are calculated by:

$$\%\Delta G_i = h^2_i \times CV_{P_i} \qquad 10$$

2.2.2 Correlation of Traits

The models developed for estimating genetic and phenotypic variances also apply to covariances. Genetic and phenotypic correlations between traits were also investigated as parameters. Phenotypic correlations were assessed for individuals, r_{P_i} (based on $\sigma^2_{P_i}$ & COV_{P_i}), and for half-sib (female) families, r_{PHS} (based on σ^2_{PHS} & COV_{PHS}) (Appendix B). Genetic correlations, r_A, are the correlation of breeding values (Falconer 1982). Environmental correlations, r_E, are the correlations of environmental deviations together with the non-additive genetic deviations (Falconer 1982) (Appendix B). The standard error of r_A was calculated as per Falconer (1982) (Appendix B). Because variance estimation errors are multiplied in these parameters, they are most usefully interpreted with regard

to general magnitude and sign. Correlated response to selection was investigated for several important characters according to the formulae of Falconer (1982) (Appendix B).

Path coefficient analysis (Wright 1921, 1923) is a standardized partial regression analysis by which a model of cause and effect can be investigated (Kempthorne 1957; Li 1975). Campbell (1963) used a model of the cause and effect of the phenotypic relationships of crown characters on stem volume. Path coefficient analysis was used to emulate this model, but instead of using phenotypic relationships, additive genetic relationships between traits were used. Path analysis was also used as a graphic aid to identify key crown traits for inclusion in multiple trait selection indices for the importance of their effects (direct and indirect) on stem volume.

2.2.3 Multiple Trait Selection

Selections will seek to improve multiple economically important traits. Several methods of multiple trait selection can be used by breeders. Tandem selection (Falconer 1982) involves improving traits separately over successive generations, but is not feasable in forest tree breeding because of the long generation intervals. Independent culling establishes acceptance levels for each trait and the set of individuals failing to achieve any or all of these levels is culled. The drawbacks to independent culling are that a large population needs to be screened if

many traits are to be improved, and no account is taken of the interrelationship of traits.

Index selection, as developed by Smith (1936), and Hazel (1943), provides a linear function of an individual's phenotypic value for two or more traits (X_i), where each value is weighted by a coefficient (b_i) designed to maximize the correlation between the function and the individual's genetic worth. An individual's genetic worth is defined as an aggregate consisting of a linear function of the breeding values, g_i, of $i=(1,2,...m)$ traits, weighted by the relative economic values, a_i, of those traits:

$$H = \Sigma\, a_i g_i \qquad 11$$

The least-squares partial regression coefficient (b_i) of H on X_i provides the weighting coefficient for the index I in the form:

$$I = \Sigma\, b_i X_i \qquad 12$$

The least-squares solution for the vector of regression coefficients **b** is equal to **P**$^{-1}$**Ga**, where **P** is the matrix of variances and covariances among the X_i, **G** is the matrix of covariances between X_i and g_i, and **a** is the vector of economic weights (Appendix B). The variance of the index, σ_I^2, is calulated as **b'Pb**, and the variance of H, σ_H^2, is calulated as **a'Ga**.

The gain in genetic value of each trait in the aggregate genotype (G_I) as a result of selection on the index is:

$$\Delta G_i = i(b'G_i)\,\sigma_I \qquad 13$$

where i is the selection intensity and G_i is the i^{th} column in the G matrix or the row vector of genetic covariances between the i^{th} trait and each component trait in the index (Lin 1978). The correlation between I and H (r_{HI}) measures the ability of a given index function to model the actual value of an individual's genotype. This statistic is useful for evaluating the effectiveness of an index and is calculated by:

$$r_{HI} = \sigma_I/\sigma_H \qquad 14$$

The index used for multiple trait selections is a "progeny test index" designed to rank and select the best parents for a combination of traits. In the progeny test index, P is the phenotypic variance-covariance matrix of (female parent) half-sib family means (σ^2_{PHS} & COV_{PHS}). G is the genetic variance-covariance matrix of (female parent) family variance and covariance components (σ^2_f & COV_f) (Appendix B). Economic dollar equivalents for tree improvement traits are not known. Two approaches were made to this problem. The first was to design the index for the

improvement of one trait (volume) as per Bridgwater (1972), Robinson *et al.* (1951) and Stonecypher (1970). The second was first assume all traits going into the index have equal value ($a_i = 1$), and then change these values in relation to each other. Changes in the ranking of families that occur due to changes in different value weightings were observed. The response (both expected and that observed in the progeny test) to selections on these different rankings were empirically plotted. Sensitivity plots to different value changes were made to derive an optimum selection strategy (Arbez *et al.* 1974; Baradat 1982).

2.3 Measurement Methods

Traits of growth, form, and wood quality recorded in the progeny are given in Table 5. Metric measurements used to estimate traits of growth and form are represented schematically in Figure 5. Measurements were taken at the 3rd, 4th, 5th, and 6th whorls down from the current leader and in the associated stem segment above the branch whorl - given as whorl numbers 6 through 9 (Fig. 5).

Some of the stem and upper crown attributes recorded relied on subjective scoring methods, but most traits were derived from measurements.

TABLE 5. Traits of growth, form, and wood quality assessed.

Trait			CLBS			GVWS			COMBINED	
		units	n.obs	mean	C.V.	n.obs	mean	C.V.	mean	C.V.
Growth										
HT06	height 6th growing season	cm	23[illegible]	[illegible]3.5[illegible]	25.43	209[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
HT10	height 10th growing season	cm	2324	4[illegible]6.[illegible]	[illegible]	2034	325.20	[illegible]	[illegible]	25.4
HT12	height 12th growing season	cm	229[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
HTD	growth from 10th to 12th year	cm	229[illegible]	228.[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
DM06	diameter 6th growing season	mm	23[illegible]	[illegible]	24.88	2095	[illegible]	34.48	[illegible]	[illegible]
DM10	diameter 10th growing season	mm	2324	[illegible]	20.89	2034	82.[illegible]	[illegible]	[illegible]	[illegible]
DM12	diameter 12th growing season	mm	229[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
VOLM	volume measurement	dm³	22[illegible]	[illegible]	45.02	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Form										
BN	branch number	no	22[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
BA	branch angle	°	22[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
BT	branch thickness	mm	22[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
BTT	branch/stem diameter ratio	%	22[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
BL	branch length	cm	22[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
BLT	branch length/total height *C	%	22[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
KI	knottiness index	%	22[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
TAPER	taper measurement	mm m	22[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
SIN	stem sinuosity score	no	2285	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
FORK	forking score	no	2285	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
LAFL	lammas score	no	2285	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Wood Quality										
WD	wood density (5mm cores)	kg m	2[illegible]	[illegible]	[illegible]					
PIN	Pilodyn pin penetration	mm	2[illegible]	[illegible]	[illegible]					

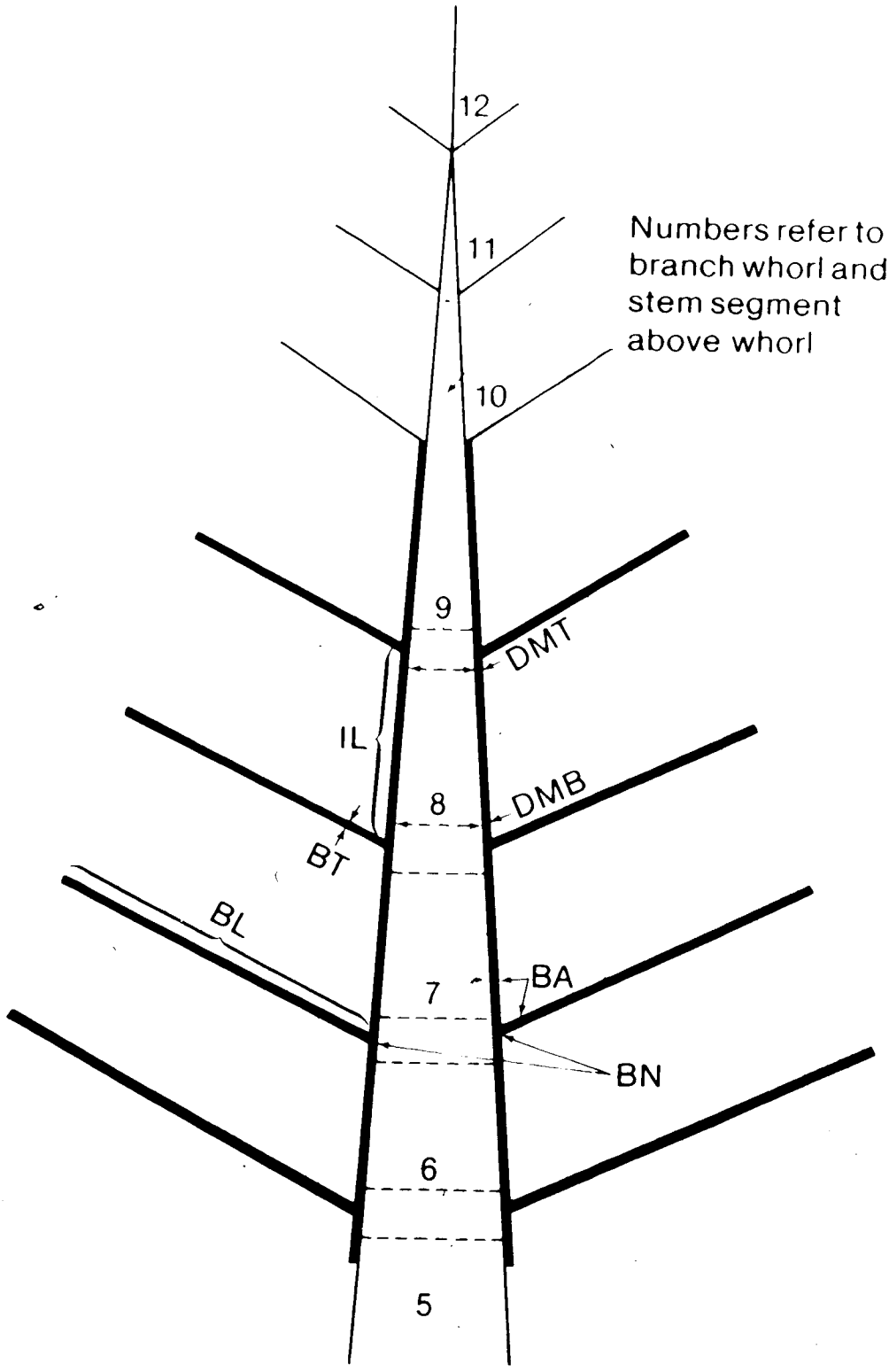

Figure 5. Schematic diagram of metric measurements made on the progeny trees.

2.3.1 Height and Growth Measures

Heights and diameters were recorded after the 6th, 10th and 12th growing season (*HT06*, *HT10*, *HT12*, *DM06*, *DM10*, *DM12*). Diameters were measured at a fixed reference height (Kovats 1977) except *DM12*, which was the mid-diameter measurement at the 7th interwhorl stem segment ((*DM71*+*DM78*)/2) (Fig. 5). *HTD* represented the growth of the trees from age 10 to age 12 (*HTD* = *HT12* − *HT10*).

Stem measurements made were (Fig. 5) of:

1. lengths of the inter branch whorl stem segment, that is the stem length between each branch whorl (Internodal length *IL*) *IL9*, *IL8*, *IL7*, and *IL6* were measured where possible, and
2. outside bark diameters at the top and bottom of each stem segment (*DMT* & *DMB*). Measurements were recorded from the bottom of the ninth segment (*DMB9*) through to the top of the fifth segment (*DMT5*) depending on the size of the tree. Diameters were measured on the stem immediately above or below the swell of the branch whorl in the first area of clear stem wood below both primary and secondary branches (≈5cm).

From these detailed stem measurements, estimates of volume and taper were made. Volume (*VOLM*) was the accumulated volume of the stem segments as tapering cylinders plus the highest diameter to the top of the tree measured as a cone volume.

2.3.2 Stem Taper

Although taper is often taken as:

$$\text{TAPER} = \frac{\text{HEIGHT}}{\text{DM 1.3}}$$

or total height over diameter at 1.3 m (Jarret 1978), an actual taper measure could be made from the diameter measures taken down the stem (Fig. 5). Taper (*TAPER*) was simply the average taper of the stem segments ($\Delta DMB/IL$).

2.3.3 Metric Branch and Crown Form Traits

Branch measures were taken at the seventh, eighth and ninth whorls or the sixth, seventh, and eighth whorls, depending on the manageability of measuring branching characters on the ninth whorl of the tree. Seventh and eighth whorls were always recorded.

Branch numbers (*BN*) were counted in the same branching whorls. Two numbers were used; the first being all of the major branches within the whorl, the second was minor branches that lay just below the branch whorl by ≃5 cm.* The sum of these two numbers counts all branches between *DMB* of the stem segment above the whorl and *DMT* of the stem segment

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* Douglas-fir does not have a definite whorl pattern, instead there often is a dominant upper portion of the whorl originating from one to five lateral buds immediately below the apical bud (major branches). A lower portion of the whorl may include branches that originate from lateral buds in the upper group of internodal buds (minor branches)(Campbell 1961). The differentiation between these types is not always clear.

below the whorl. *BN* (Table 6) represents the average number of the seventh and eighth whorls.

Branch angle (*BA*) was measured in the same branch whorls. Two randomly chosen major branches within the whorl were measured by protractor to the nearest 5°. *BA* (Table 5) represents the average angle of the seventh and eighth whorls.

Branch thickness (*BT*) was measured at two randomly chosen major branches in the whorl and measured in millimeters with calipers away from the swell where the branch joins the trunk (≥3 cm). *BT* (Table 5) represents a mean branch thickness from whorls seven and eight. *BTT* (Table 5) represents branch thickness of whorls seven and eight as a ratio of the stem diameter at the whorl:

$$BTT = \frac{BT}{DM}$$

where *DM* is the average of the diameter measured just above the whorl *DMB* and diameter measured just below the whorl *DMT*. This type of proportional branch thickness, that removes the size effect of the tree, was found to have a stronger genetic determination than direct branch thickness measures in Finnish Scots pine (Velling and Tigerstedt 1984). Campbell's (1961) measure of knottiness ratio (*KI*) - cross-sectional areas of branches at a whorl to the stem cross-sectional area - was calulated, this was derived using

the mean branch thickness and branch number and the diameter value (*DM12*) for stem cross-section areas.

Branch length (*Bl*) was measured at the same whorls. Two randomly chosen major branches within the whorl were measured to the nearest 5 cm. *Bl* (Table 5) represents the average branch length of the seventh and eighth whorls. *Bll* (Table 5) represents branch lengths of whorls seven and eight as a ratio of the total height.

2.3.4 Stem and Upper Crown Form Attributes

Stem and upper crown form attributes recorded were sinuosity, forking (including ramicorn branching), and the occurrence of lammas growth (Table 5).

Measuring sinuosity in young plantations can be difficult and time consuming. Shelbourne and Namkoong (1965) and Campbell (1965) used photographic measures. Campbell (1965) used a transfomation of *h/a* (Fig. 2) from photographs as an objective measure of sinuosity, but found that a subjective scoring system could be quite reliable ($r=.76$, $P<.01$; for a sample of 30 trees). French studies (Crisan 1977) also demonstrated good correlations ($r=.98$, $P<.01$) between measured and subjective scoring methods for assessing straightness. Adams and Howe (1985) found that subjective scoring techniques were quite effective ($r=.79$, $P<.01$) and $r_A=.96$) compared to a scoring index based on numbers and frequencies of displacements from the vertical.

Sinuosity and the other attribute traits were all recorded using a similar subjective assessment technique. They were recorded by the stem segment or growing season in which observed, the severity of the damage to form observed on a scale of 1 to 5, and a diagnostic observation. The following traits were recorded:

2.3.4.1 Sinuosity

1st no. stem segment (growing season) of occurrence.

2nd no. severity score of stem damage;

1- slight occurrence or sinuosity trend,
displacement less than ½ of internode diam.

2- noticeable sinuosity,
displacement between ½-1 of internode diam.

3- marked sinuosity of a permanent nature,
displacement between 1-1.5 of internode diam.

4- severe sinuosity,
displacement between 1.5-2.0 of internode diam.

5- extreme sinuosity.
displacement > 2.0 of internode diam.

3rd Alpha observation;

J- sinuosity or crookedness was caused by damage or loss of apical leader.

SIN (Table 5) represents a total severity score for each tree ×100.

2.3.4.2 Forking, Ramicorn Branching, and Multiple Leader Occurrence

1st no. stem segment (growing season) of occurrence.

2nd no. severity score of stem damage;

1- slight occurrence or tendancy to occurrence

2- noticeable forking occurrence,

3- marked occurrence likely to be maintained, and damage stem quality,

4 severe occurrence,

5- extreme occurrence - competes equally for apical dominance with main leader.

3rd. Alpha observation;

F- forking,

R- ramicorn branch,

M- multiple leaders.

FORK (Table 5) represents a total forking severity score per tree where the score was $\geq 2 \times 100$.

2.3.4.3 Lammas Occurrence

1st no. stem segment (growing season) of occurrence.

2nd no. severity score of stem damage:

1- slight or unnoticeable occurrence,

2- noticeable occurrence but no upper stem damage,

3- marked occurrence - some upper stem damage presence of noticeable ramicorn branch or exceptional branchiness,

4- severe upper stem damage (usually forking),

5- extreme upper stem damage.

LAFL (Table 5) represents a total number of lammas occurrences of severity score > 2 ×100.

2.3.5 Wood Density Traits

Wood density measurements were made only at CLES (Table 5). The trees in the watershed site (GVWS) were considered too small to sample for wood density. Two diametrically opposed 5 mm increment cores were taken from the first consistently clear stem segment above the base of each tree (*IL6*). Only the last four rings of each core were kept (years 8-12). Wood density (*WD*) was estimated by the maximum moisture content method (Smith 1954) with an assumed pycnometric density of 1500 kg/m^3. Samples with severe compression wood were excluded. Pilodyn estimation for wood density (*PIN*) was taken at *IL6* (approx. breast height) and consisted of two readings with a non-repeating Pilodyn of pin diameter 2.5mm and spring strength of 6 joules.

2.3.6 Transformations of Scale

There are three major reasons for making scale transformations: (1) to make the distribution normal, (2) to make the variance independent of the mean, and (3) to remove or reduce non-additive interactions (Falconer 1982). The major reasons considered with these progeny test traits were (1) and (2).

The attribute variables *SIN*, *FORK*, and *LAFL* show a markedly skewed distribution. The incidence of these

attributes in the population is low and there are large ranges between families for these traits. The low incidence of these attributes in the population causes the distribution to approach a Poisson rather than a normal distribution, therefore a square root transformation $X' = \sqrt{X + 1}$ would appear best (Montgomery 1984). The analysis was completed for transformed and untransformed data for the attribute traits.

3. RESULTS

3.1 Height and Growth and Yield Traits

Measurements reported in this chapter are total height at years 6, 10, and 12 (*HT06*, *HT10*, *HT12*); height accumulation between years 10 and 12 (*HTD*); diameters at years 6, 10, and 12 (*DM06*, *DM10*, *DM12*); and stem volume measurements (*VOLM*).

3.1.1 Height Traits

Early growth and site establishment was represented by height at six years (*HT06*). Trees at this age were slightly over 1 m (107 cm, CV=28.8%) tall with a range in family (female half-sib) means of between 92.6 cm to 118 cm (Table C1). Sources of variation for additive genetic variance (σ_A^2) were significant ($P<.05$) on the individual and combined site analyses (Table C2). The standard errors for σ_A^2 were less than half of the variances themselves.

Individual tree heritability levels were low, but for progeny test selection heritabilities were high. Heritabilities, coefficients of variation, and expected response to selection for height at age six (*HT06*) were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.14±0.06	28.00	3.86	0.73±0.31	6.10	8.87

(Table C2). Progeny test selection for early height growth should be effective in this population and nearly 9% gain per selection intensity unit is expected to be achieved.

Dominance genetic variance (σ_D^2) was non significant for the early height trait; however, lack of precision for this non-additive source of genetic variance (because of only four male parents) is shown in the large standard errors (Table C2). Sources of variation for site*female and rep*female, was non-significant, indicating that additive genetic * major environment interaction variances (σ_{AE}^2) are not important for this trait, within the limitations of these environments and experimental population.

Although σ_{st}^2 for early height growth (*HT06*) was non-significant, and significant rank changes did not occur between sites; the sites showed marked differences in their powers of genetic discrimination (Table C2). Additive genetic variance (σ_A^2) was most highly expressed at site GVWS, the slower growing site (Table C2). Coefficients of variation for phenotypic variances, $\sigma_{P_i}^2$ and σ_{PHS}^2, were higher at GVWS, and response to selection was expected to be twice the level at GVWS as at CLES (Table C2). The coefficients of variation of the experimental error (within-plot (σ_w^2) and plot-to-plot error (σ_{rmf}^2) sources of variation) were slightly higher at GVWS than CLES. However, in proportion to the CV's of family sources of variation, they are 1.5 times higher at CLES than GVWS. The higher variance component percentage of σ_w^2 at CLES (78.4% CLES, 71.4% GVWS; Table C2) indicates the

possibility that the row plots of CLES may be less precise for determining genetic differences than the square plots at GVWS.

At height 10 years (*HT10*), the overall mean was 374 cm (CV=25.1%), and families ranged from 343 cm to 397 cm (Table C3). Additive genetic variance (σ_f^2) was a significant source of variation ($P<.05$) on the combined analysis (MS_{***} = error MS), but was non-significant ($P>.10$) at CLES. At GVWS it was non-significant ($P>.05$) for the random model, but was significant ($P<.05$) using MS_{m**} as the error MS (replications as fixed effect).

Height measurement at 12 years (*HT12*) averaged nearly 6 m (587 cm, CV=20.2%) and families ranged from 546 cm to 620 cm (Table C5). The same trends of significance as with *HT10* were observed; the combined analysis was significant ($P<.05$), while CLES was non-significant ($P>.10$), and GVWS was marginal in its significance. Large standard errors of σ_A^2 ($=\sigma_A^2$) for these two later height measures (*HT10* and *HT12*) are present on individual sites, especially at site CLES, whereas on the combined analysis standard errors are less than one half of the variance components (Tables C4 & C6). Heritabilities are also more strongly expressed on the combined analysis than on the individual sites. Heritabilities and selection parameters for height at 10 years (*HT10*) and height at 12 years (*HT12*) on the combined analysis were:

h^2_i	CV_{P_i}	$\%\Delta G_i / i$	h^2_f	CV_{PHS}	$\%\Delta G_f / i$
0.12±0.04	22.36	2.68	0.64±0.23	4.85	6.19
0.14±0.05	17.12	2.40	0.66±0.23	3.96	5.18

(Table C4, C6). A decline in expected percent response to selection as trees grow (*HT06*, *HT10*, *HT12*) is not brought about by declining heritabilities, but by declining coefficients of variation (of $\sigma^2_{P_i}$ and σ^2_{PHS}). There is less relative variation between larger trees (≈6 m) than between smaller trees (≈1 m).

As with early height (*HT06*) the later height measures *HT10* and *HT12* are non-significant (P>.05) for dominance genetic variance (σ^2_{mf}) and G.E.I. sources of variation (σ^2_{sf} and σ^2_{rf}). However, they were significant (P<.05) for σ^2_{smf}.

The growth between *HT10* and *HT12* was examined in the trait *HTD* (*HTD* = *HT12* - *HT10*). There is some rationale for using this as a better trait for inherent growth rate differences than a single height measure. As height is cumulative, and the transplanting shock, growth check, and vegetative competition may effect the height of a tree for many years, the error that this is likely to introduce can be reduced by taking some multiple measure of heights or height differences as in *HTD*. An overall mean of *HTD*, of over 210 cm (CV=20.7%), shows the vigourous growth that is occurring at the plantation sites (CLES = 229 cm, GVWS = 187 cm) (Table C7). Family means over both sites range from

195 cm to 222 cm. Family differences are significant ($P<.05$) on both the combined analysis and for individual sites. *HTD* demonstrates itself as a more sensitive measure of inherent differences for growth rate than single height measures *HT10* or *HT12*, especially at CLES (Table C8). The improvement at GVWS is not as marked. However, at this site many of the trees are still in a state of growth check with the vegetative competition from broom, and with continued browsing. Heritabilities and expected response to selection for height differences (*HTD*) on the combined site analysis were:

h_i^2	CV_{g_i}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.08±0.05	18.12	1.45	0.59±0.33	3.34	3.93

(Table C8). Although significance levels are improved over straight height measures (*HT10* and *HT12*), heritabilities are lower than the *HT10* and *HT12* measures. Thus the selection parameters are not encouraging for *HTD*. Non-additive genetic variances are not significant ($P>.05$) for *HTD*.

3.1.2 Comparisons with Published Heritabilities for Height

Campbell (1972) used height increment as a measure of height growth in full-sib seedlings of Douglas-fir. Campbell (1972) found significant amounts of both additive and dominance genetic variances for this measure. Unlike the

factorial design Campbell's (1972) study study (NC I) has low reliability for differentiating these components and he suggested that the dominance effect was due to under estimation of the female effects which was part of the additive genetic variance. Campbell's (1972) report of a significant source of variation for additive genetic variance but low heritabilities (h_1^2 = 0.10-0.16) concurred with the results presented here.

In comparison with Rehfeldt's (1983) study of height in four year-old O.P. progeny of interior Douglas-fir, and published values from the French IUFRO provenance progeny values (Jarret 1978, Birot and Christophe 1983), the individual tree heritability values presented here are low:

Measurement	h_1^2	Reference
Height at 4yrs	0.52±0.10	Rehfeldt 1983
Height at 8yrs	0.36±0.19	Jarret 1978
Height at 12yrs	≃0.30	Birot and Christophe 1983
Height at 12yrs	0.14±0.05	Thesis results

Heritability estimates derived from open-pollinated families are biased when the assumption that the genetic covariance between O.P. progeny is that of half-sibs is violated (Namkoong 1966; Squillace 1974). Although Rehfeldt (1983) adjusted for an inbreeding coefficient of F=0.10 this bias may account somewhat for the differences between the O.P.

studies and the full-sib studies (Campbell 1972; Yeh and Heaman 1982). Family heritabilities between Rehfeldts (1983) study and the results presented here concur:

Measurement	h_f^2	Reference
Height at 4yrs	0.77±0.15	Rehfeldt 1983
Height at 6yrs	0.73±0.31	Thesis results

The testing environment and age of material are also important factors in the determination of environmentally sensitive traits such as height-growth. Nursery and farm field trials show higher heritabilities than progeny trials that simulate production plantations, and heritabilities for height growth can decline with age.

3.1.3 Trends in Components of Height Traits

Environmental influences and ecological conditions for growth change for a tree during its long life time. In early seedling stages it is dominated by vegetative competition from herbs and shrubs and influences of micro-climate and micro-site. Later as it dominates its immediate environment and it is influenced by only relatively large-scale climatic and site factors.

From their investigations of long-established progeny trials, Namkoong *et al*. (1972; for Douglas-fir) and Namkoong and Conkle (1976; for Ponderosa pine) recognized three broad ecological growth phases: early open growth to crown closure, a second phase after crown closure and the onset of

intraspecific competition, and a third phase of growth indicating mature tree performance under stable cohort competition. Franklin (1979) and Cannell (1982) developed models of trends in the expression of additive genetic variances through the different growth stages. Franklin (1979) suggested that initial high levels of additive genetic variance that are expressed early in the juvenile growth period will decline as trees begin competing with each other. Cannell (1982) applied the concept of "isolation", "competition", and "crop" ideotypes[1] borrowed from the crop literature to these three growth phases. Cannell suggested that genotypes that do well in open-growth conditions, "isolation" ideotypes, can be quite different than those that do well in a competitive environment.

The time trend studies of Namkoong *et al.* (1972) and Namkoong and Conkle (1976) support the concept of consistent ideotype expression during specific ecological growth phases. Early stages showed positive and reasonable correlations of family effects during the period of open-growth. In the period of crown closure, 12-15 years for Douglas-fir, and 8-15 years for ponderosa pine, disruptions of these effects took place. High positive correlations were regained between measurements made in later growth phases. Both studies showed correlation of family effects between the open-growth phase and later growth phases to be

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[1] "an ideotype is a biological model which is expected to perform or behave in a predictable manner within a defined environment" (Donald 1968)

non-existent or even negative.

Systematic and consistent trends of variance components over time have not always been observed. Lambeth *et al.* (1983) reported encouraging juvenile-mature correlations in Loblolly pine. The lack of significant family differences in the Douglas-fir study (Namkoong *et al.* 1972) and limitations in the design and objectives of these old studies, require that the interpretations made by Franklin (1979) and Cannell (1982) be approached cautiously.

Douglas-fir studies in France (Birot and Christophe 1983; Jarret 1978) indicated a sharp decline in the relative additive genetic variance after outplanting to age six and thereafter a leveling off or slight decline through the rest of the open-growth (juvenile) phase.

Trends in environmental and genetic variances as trees develop during this juvenile growth phase are shown by changes in variance component percentages and their coefficients of variation (CV). On the combined analysis the relative proportion of the variation attributable to site effects rises dramatically:

	HT06	*HT10*	*HT12*
σ_s^2	7%	36%	46%,

whereas the proportion attributable to within-plot variation declines sharply:

	HT06	*HT10*	*HT12*
σ_w^2	70%	45%	36%,

and the plot-to-plot variation declines slightly:

	HT06	*HT10*	*HT12*
σ_{rmt}^2	14%	12%	10%

(Tables C2, C4 and C6).

As trees become established on the sites during the juvenile growth phase, microsite influences are diminished and macroenvironmental influences become more important. The decline in the small-scale environmental effects as the trees grow from *HT06*≈1 m to dominating their local environment and filling the site (*HT12*≈6 m) is also shown by the decline in the coefficients of variation of the plot-to-plot (σ_{rmt}^2) and within-plot (σ_w^2) error variances, and the sources of variation of additive genetic variance (σ_t^2). This represents the fact that the scale of the overall variation within plantations declines as the trees get larger. The plantation now enters a stand growth model, where variation becomes more strongly expressed on a macro-environmental level, rather than the open-grown tree-to-tree growth model, where variation is relatively more expressed on micro-environmental level. The larger and

faster growing trees (and families) are the first to be restricted by inter-tree competition as they reach the end of the juvenile growth phase. This allows the slower growing trees (and families) to catch up. On the combined analysis there is no decline in the relative proportion of additive genetic variance (σ_A^2) during the juvenile growth phase, but the height difference (*HTD*) does show a low heritability ($h_i^2=0.08\pm0.05$). On the individual sites there is a sharp drop between *HT06* and the later height measures, and there is a decline in the heritability values between site GVWS and site CLES. Because the trees are more developed and crown closure is almost complete at CLES, the trend of declining additive genetic variances during the juvenile growth phase may be more advanced there. But the imprecision of individual sites, especially CLES, may also be caused by the insensitivity of the experiment, in addition to biological models of declining genetic variances.

The experiment at CLES was restructured to see if specific sources of experimental error could be identified as causing the insensitivity at this site. The three major sources of environmental variation are the block or environmental variance (σ_r^2; which is usually removed before inferences about the population are made), the error variance of the large-scale environmental heterogeneity within blocks (σ_{rmf}^2; which is caused by the failure of the full-sib family plots to behave the same within environmental replications), and the error variance of

small-scale environmental variation within plots (σ^2_w; which also has the remaining additive and non-additive genetic variation).

The large-scale experimental error (σ^2_{emt}), can be reduced by reblocking the experiment based on plot performance. The CLES site occupies a long, thin parcel of land on an undulating topography of porous soils. Correct blocking of the experiment (LeClerg 1966) is difficult on such a site and re-analysis was made after the site was reblocked on ranking by plot means. Although plot variation (σ^2_{emt}) declined from 19.4% to 1.1% (Table C9) of total variation, the significance levels of the female source of variation did not show an improvement in the estimate of additive genetic variatiance. In fact, estimates of heritability appropriate to mass selection had declined (h^2_i=0.05±.065; Table C9). Although this procedure restructured the blocks based on plot performance, the long, nine-tree row plots would appear to carry too much variability along with them to prove effective.

The experiment was also restructured to reduce σ^2_w by taking sub-sets of the nine-tree plots. Analysis of the five top trees of each full-sib family plot showed a substantial increase for sources of variation of additive genetic effects (h^2_i=0.18±0.12) for height. This is brought about by the reduction of the within-plot variation (σ^2_w) from 69% (Table C9) to 36% and an increase of female variation (σ^2_f) to 4% of total variation. However, σ^2_f was still

non-significant ($P>.05$) and does not become significant until the plots are reduced to four-tree plots. At this reduction σ_f^2 = 5% of total variation and h_i^2=0.22±0.13).

The lack of sensitivity of the plantation to height growth may be accounted for by both a declining amount of additive genetic variance as slower starting families catch up (following the model of Namkoong *et al.* (1972) and Franklin (1979)), and microsite heterogeneity within the nine-tree row plots. Although microsite environmental influences decline as a proportion of the total variation, the decline is not large enough to offset the similar decline in the relative amount of additive genetic variance.

3.1.4 Diameter Traits

Diameter at the six-year measure had an overall mean of 19.2 mm (CV=30.7%) and a range in values between the female half-sib families of 16.4 mm to 21.8 mm (Table C10). Additive genetic variance was strongly expressed for this trait (5.820±2.132). Selection parameters for diameter at age six (*DMO6*) were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.19±0.07	28.84	5.48	0.77±0.28	7.18	11.00

(Table C11). Heritabilities and expected response to selection were higher for *DMO6* than for *HTO6*. As with height

measures, other types of genetic variance ($\sigma^2_{m'}$, σ^2_{sf}) were non-significant.

At *DM12* the overall mean was 77.3 mm (CV=21.2%) and families range from 71.9 mm to 83.8 mm (Table C14). Selection parameters for diameters at ages 10 (*DM10*) and 12 (*DM12*) were:

h^2_i	CV_{Pi}	$\%\Delta G_i$	h^2_i	CV_{PHS}	$\%\Delta G_i$
0.16±0.06	24.72	3.96	0.75±0.26	5.73	8.55
0.16±0.06	16.94	2.79	0.73±0.25	4.03	5.85

(Tables C13 & C15). Herifability estimates for diameter measures were consistently higher than those of height measurements (Tables Appendix C). As with height measurements, heritabilities for diameter are lower than those published from the French IUFRO trials (Birot and Christophe 1983, h^2_i=0.3). A decline in percentage expected response to selection between *DM06* and *DM12* is caused by declining coefficients of variation. The trends in environmental influences that were observed for height measurement - a declining percentage of variation attributable to microsite influences (σ^2_s), and increasing influence of the macrosite (σ^2_s) - were also observed in the diameter traits.

Non-additive genetic variances were not significant (P>.05) for the two later diameter measures.

3.1.5 Volume Traits

Volume measurements were made on a reduced set of trees, only those that were not damaged by browsing or by competing vegetation. This mainly affected GVWS, where less than half of the trees had survived damage or mortality (see 2.1). The large replication (block) effect in the volume estimation (Table C17) represents a bias mainly attributable to survival and establishment at GVWS. Rep 1 is at the bottom of the slope where the soils are deeper and more moisture is available. A high incidence of broom in the replication has suppressed tree growth, and the nitrogen fixing ability of broom has likely made the trees more attractive to browsing animals. Although vigourous growth is observed in this rep, total mean height is in fact lower than in the other two reps because of these effects. The large mean for volume that was observed in this replication reflects the fact that trees were large enough to have escaped the influence of browsing and vegetative suppression and thus were measured for this trait (see also 3.2.2; Table 8).

The overall mean stem volume was 14.26 dm^3 (CV=49.2%), and families ranged from 11.24 dm^3 to 16.68 dm^3 (Table C16). Female half-sib families were a significant ($P<.05$) source of variation on the combined analysis (σ_A^2 = 3.880±2.054), and at GVWS, but not at CLES. Heritabilities and expected response to selection for stem volume (*VOLM*) on the combined analysis were:

h_i^2	CV_{Pi}	$\%\Delta G_i$ i	h_i^2	CV_{PHS}	$\%\Delta G_i$ i
0.10±0.05	44.76	4.26	0.55±0.29	9.32	10.25

(Table C17). Although the heritabilities for stem volume are lower than those for height and diameter, expected response to selection is higher because of the large half-sib phenotypic standard deviation (σ_{PHS}) of the volume measurements. Expected gains for progeny test selection are over 10% per selection intensity unit. Non-additive genetic variances were not significant (P>.05) for the volume measurement.

3.1.6 Selection of Height and Growth Traits

Genetic (r_A) and simple phenotypic correlations (r) between height and diameter measures are summarized in Table 6. All relationships are significant and positive. Detailed variances and covariances between traits *HT06*, *HT12*, *DM12*, and *VOLM* together with genetic (r_A), phenotypic (r_{Pi}, r_{PHS}) and environmental (r_ε) correlations and direct and correlated response to selections are shown in Tables C18 to C21. These correlations are shown in Table 7. The correlation values between *HT06* and *HT12* (early and late height growth) are significant, positive, and of the same strong magnitude (≃.75). Between *HT06* and *DM12* (early height and late diameter growth) the correlations are not as strong as the height correlations and r_A and r_{PHS} are somewhat lower

($\simeq$.55) to r_E and r_{P_1} ($\simeq$.65). Between *HT12* and *DM12* (late height and late diameter growth) the genetic correlation r_A=.45±.21 and half-sib phenotypic correlation r_{PHS}=.58 have declined in relation to phenotypic (individual) and environmental correlation r_{P_1}=.81 and r_E=.88. The observed phenotypic correlations between later height and diameter measures indicate a greater influence due to the sharing of a common environment than do the earlier measures (Table 6).

Figure 6 represents expected response to mass and family selection (roguing of 1st generation clonal seed orchard) and correlated response for early selection for families at *HT06*. Expected response is shown by %ΔG / 1 for the four growth traits; *HT06*, *HT12*, *DM12*, and *VOLM*. It can be seen for all growth traits that family (progeny test) selection is more effective than mass selection for expected response from these traits. %ΔG was higher for volume because the multiplicative factors of the other growth measures in its determination increase the standard deviation accordingly. Early selection for families at *HT06* (age six: mean height $\simeq$ 1 m) proved reasonably effective for a correlated response at *HT12* (age twelve: mean height $\simeq$ 6 m) with relative efficiency R.E.= 77% and for *VOLM* (R.E.= 68%), but less effective with *DM12* (R.E.= 57%) (Fig 6).

TABLE 6. Genetic and simple phenotypic correlations between height and diameter measures and individual tree heritabilities.

	HT06	*HT10*	*HT12*	*DM06*	*DM10*	*DM12*
HT06	.14	.86	.73	.78	.84	.51
HT10	.79	.12	.98	.57	.76	.65
HT12	.73	.94	.14	.45	.63	.45
DM06	.86	.77	.72	.19	.90	.62
DM10	.81	.90	.86	.83	.16	.85
DM12	.63	.83	.87	.68	.88	.16

Above diagonal records genetic correlations.

Below diagonal records simple phenotypic correlations.

Along diagonal records individual heritability.

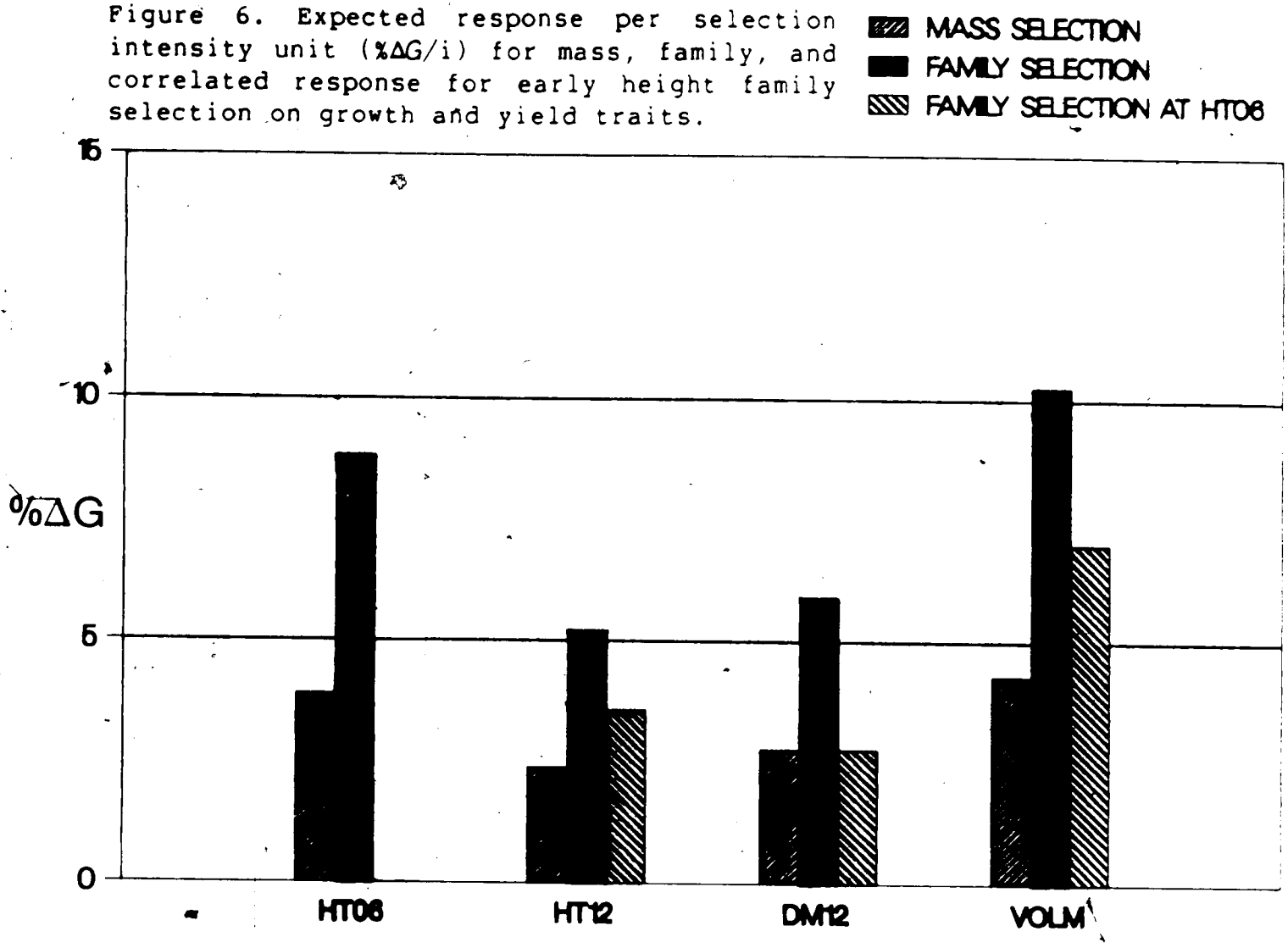
All terms significant P<.001

TABLE 7. Genetic, phenotypic, and environmental correlations between early height, later height and diameter, and volume traits.

		HT06	*HT12*	*DM12*
VOLM				
	r_A	.68±.21	.47±.28	.86±.09
	r_{P1}	.80	.80	.88
	r_{PHS}	.74	.61	.92
	r_E	.81	.84	.89
DM12				
	r_A	.51±.20	.45±.21	
	r_{P1}	.66	.81	
	r_{PHS}	.57	.58	
	r_E	.69	.88	
HT12				
	r_A	.73±.13		
	r_{P1}	.75		
	r_{PHS}	.76		
	r_E	.76		

All terms significant P<.001

Figure 6. Expected response per selection intensity unit (%ΔG/i) for mass, family, and correlated response for early height family selection on growth and yield traits.



3.1.7 Index Selection for Volume and Response to Selection

Traits of height and diameter were investigated to look at the most effective way of selecting for volume. The trait *VOLM* as an actual measure of stem segment volume was seen as the "best" measure of stem volume. Estimates of *HT12* on its own, *DM12* on its own, and a multiple trait progeny test index, *IVOL*, of *HT06*, *HT12*, and *DM12* were analysed to predict the rankings of families based on *VOLM*. The index used the phenotypic variance-covariance matrix based on the heights and diameter (*HT06*, *HT12*, and *DM12*) and the additive genetic covariance of the heights and diameter traits to predict the breeding value of *VOLM*. The b's for *IVOL* were:

HT06	*HT12*	*DM12*
0.78	0.03	3.90

The coefficient of *HT12* ($\simeq 0$) shows that it has a negligible influence in predicting volume performance when used in conjunction with diameter and early height growth in the index and thus is a poor predictor of the breeding value of parents for stem volume.

Families were ranked by their phenotypic values for *VOLM* and the response was observed for selecting the top 50% of parents based on progeny performance (R_{OBS}). Comparisons were made of progeny gains for volume using selections on rankings based on the aggregate breeding value of the index

IVOL, and by indirect selection of volume using the individual growth traits (*HT12* and *DM12*). R_{OBS} at a selection level of 1:2 in dm^1, with the percent efficiencies compared to direct selection for volume on its own; the mean of the select progeny population (X) in dm^1; and Spearman rank correlation coefficients, r_s (Steel and Torrie 1980), of the family rankings based on the different selection criteria are:

	VOLM	*IVOL*	*DM12*	*HT12*
R_{OBS}	.881(100%)	.881(100%)	.816(93%)	.381(43%)
X =	15.114	15.114	15.049	14.614
r_s	1.000	0.988	0.889	0.553

The index values provide accurate weighting coefficients for selecting stem volume; however, selecting for diameter on its own is nearly as effective as selecting for volume measures using the index *IVOL* (93%). If a single character such as diameter can accurately predict the breeding values for the desired character, the inclusion of secondary characters in an index will give no real benefit; in fact, errors of estimation will make it more unreliable (Sales and Hill 1976; Falconer 1982). *HT12* on its own is not very efficient for predicting response for biomass (*VOLM*) (43%).

Observed response to selection from selected progeny families, R_{OBS}, can be compared to expected response ΔG. For

fair comparisons the observed response was multiplied by two since expected response is calculated with the inclusion of a selected pollen source also. Values for a selection intensity of 1:2 or i=.77 were:

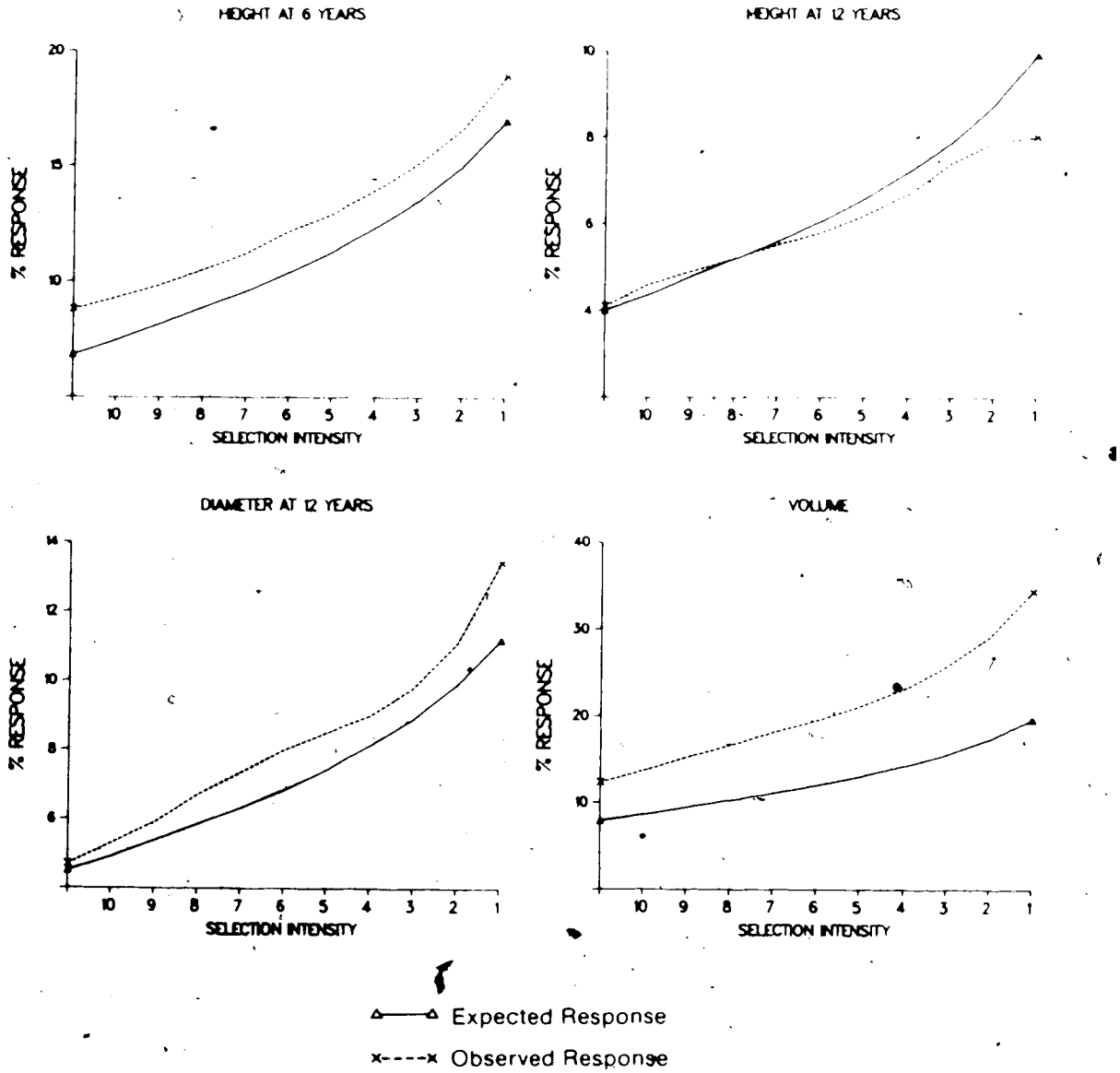
	HT06	HT12	DM12	VOLM
$\%R_{OBS}$	4.4 %	2.4 %	2.65%	6.2 %
$\%\Delta G$	3.4 %	2.0 %	2.25%	3.9 %

Values for a selection intensity of 4:22 or i=1.39 were:

	HT06	HT12	DM12	VOLM
$\%R_{OBS}$	7.0 %	4.1 %	5.75%	11.5 %
$\%\Delta G$	6.2 %	3.6 %	4.1 %	7.1 %

Observed (R_{OBS}) and expected (ΔG) response to selection for different selection intensity levels are plotted in Figure 7. Observed and expected response to selection are not independent, relying on the same progeny estimates; thus they agree quite well and gains from progeny test selection for yield trait appear quite reasonable (Figure 7). Observed response values were up to 75% higher than expected response to selection for this experimental population (Figure 7). This is in part due to the fact that the progeny were measured in family plots and shared a common environment.

Figure 7. Expected and observed response for growth and yield traits for increasing selection intensity on the 22 parent trees.



3.1.8 Height and Growth Summary

1. Sources of additive genetic variance (σ_f^2) were significant for height, diameter, and volume over combined sites. Dominance genetic variance was not significant ($P>.05$) for any of the growth traits. G.E.I. sources of variation (σ_{st}^2) were non significant for all traits. The source of variation for cross by site (σ_{smf}^2) was significant for later height measurements.

2. Individual tree heritabilites for growth and yield traits were low (0.08 ± 0.05 0.19 ± 0.07) but family heritabilities were high (0.55 ± 0.29 0.77 ± 0.28) for these traits. Individual tree heritability estimates were similar to published estimates from full-sib trials but were lower than estimates from open pollinated trials. Family heritabilities were similar to reports published from O.P. trials. Heritability estimates were higher for diameter than height growth. With large phenotypic standard deviations, expected response to selection for the better parents in a clonal seed orchard appeared quite good ≈11% for diameter and volume traits (per unit of selection intensity).

3. As trees grow and dominate the site during the juvenile open-growth phase, microsite influences decline in relation to large scale macrosite influences. Trees are influenced more by large scale environmental factors than by other factors (including additive genetic variance) that influence tree to tree variation.

4. Individual sites were less accurate for demonstrating genetic differences. Heritabilities were lower on an individual site basis than for combined sites. Site CLES was especially insensitive, and later height and volume measures were non-significant ($P>.05$) at this site. Low heritabilites and non-significant sources of additive genetic variance for height and volume appeared in part to be due to the insensitivity of individual sites caused mainly by the heterogeneous environments within the nine-tree row plots (σ^2) at CLES.

5. Correlation of growth traits was good and correlated response for family selection for later height measures (*HT12* ≈6 m), diameter, or volume could well be made from early height measure (*HT06* ≈1 m).

6. Efficiencies for volume selections would best be made by selecting for diameter.

7. Both observed and expected responses to selection indicate reasonable gains can be achieved for yield traits.

3.2 Crown and Stem-Form Traits

Crown-form traits represent an average from branches at the fourth and fifth whorls (Fig. 5). Traits recorded were branch number per whorl (*BN*), branch angle (*BA*), branch thickness (*BT*), branch thickness as a ratio of branch diameter to stem diameter (*BTT*), branch length (*BL*), and branch length as a ratio to total height (taken at height age 10) (*BLT*).

Stem traits recorded were height at age 12 (*HT12*), diameter at age 12 (recorded in the fifth stem segment) (*DM12*), stem volume (*VOLM*), bole taper (*TAPER*); and stem form attributes including sinuosity (*SIN*), forking (*FORK*), and lammas flush (*LAFL*).

3.2.1 Branching and Crown Form Traits

Total branch number per whorl averaged 5.34 (CV=22.6%), and family means ranged from 4.8 to 6.0 (Table D1). Additive genetic variance was strongly expressed with a comparatively low standard error (σ_A^2=0.255±0.093) (Table D2). Female sources of variation accounted for over 4% of the total variation. The significant source of family variation for branch number contrasts to Jarret's (1978) work; he found branch number to be non-significant ($P>.05$). Non-significant results for branch number per whorl were also reported for white spruce (Merrill and Mohn 1985). However, studies on other species and populations have recorded significant sources of additive genetic variance for this trait in Scots

pine (Peyko 1982; Velling and Tigerstedt 1984) and lodgepole pine (Cahman 1981; Rehfeldt 1985). Heritabilities, phenotypic coefficients of variation, and expected percent response to selection for branch number were:

h_i^2	CV_{p_i}	$\%\Delta G_i/i$	h_i^2	CV_{pms}	$\%\Delta G_i/i$
0.19±0.07	21.76	4.10	0.82±0.30	5.21	8.56

(Table D2). Selecting the best parent trees for a seed orchard offers gains of over 8% per selection intensity unit. Non additive genetic variances were not significant ($P<.05$) for branch number (*BN*) (Table D2).

The overall mean for branch angle (*BA*) averaged on the fourth and fifth whorls was 65.7° (CV=11.0%), and family means ranged from 59.4° to 71.2° (Table D3). Family sources of variation were highly significant ($P<.001$) for branch angle on both the combined analysis and individual sites (Table D4). On the combined site analysis 16.3% of the total variation was attributable to family differences, making branch angle (*BA*) one of the most highly heritable traits in the study. Heritability and gain estimates were:

h_i^2	CV_{p_i}	$\%\Delta G_i/i$	h_i^2	CV_{pms}	$\%\Delta G_i/i$
0.73±0.24	10.61	7.72	0.92±0.30	4.73	8.66

(Table D4). Individual tree heritability value is higher than the high values reported for coastal Douglas fir populations in France (Jarret 1978, h^2 = 0.54±0.23; Birot and Christophe 1983, h^2 = 0.49). Moderate to high individual tree heritabilities have also been expressed in other conifers for branch angle (white spruce h^2=0.44, Merrill and Mohn 1985; Scots pine h^2=0.43, Poykko 1982; Scots pine h^2 0.22±.09, Velling and Tigerstedt 1984). The high individual tree heritability values and comparatively low uncontrolled within family variation (σ^2=62%) suggest that mass selection would be effective for improving branch angle in juvenile populations of coastal Douglas-fir. Additive genetic variance is not the only genetic variance source significant for branch angle; dominance genetic variance was also significant:

σ^2_A = 35.404± 11.502 P< .001

σ^2_D = 3.983± 2.009 P< .01

(Table D4). Branch angle is one of the few traits for which this source of variation was significant; but even so this variation was only 10% of that of additive genetic variance. In a similar mating design for a similar set of traits in Scots pine, Velling and Tigerstedt (1984) reported branch angle as one of the few traits (out of thirteen) that was significant for dominance genetic variance.

Mean branch thickness (*BI*) was 19.44 mm (CV=16.8%), and family means ranged from 18.4 mm to 20.4 mm (Table D5). Branch thickness expressed as a percentage of branch diameter to stem diameter (*BII*) averaged 27.28% (CV=12.9%), with a family range of 25.6% to 29.2% (Table D7). Family differences were non-significant ($P>.05$) for direct branch thickness measures (*BI*) on both individual and combined site (significance level .065, Table D6) analyses. Velling and Tigerstedt (1984) reported a non significant heritability for branch thickness in Scots pine ($h^2<0.05$). However, significant heritability was reported by Jarret (1978; $h^2=0.34\pm0.18$) for Douglas fir in France. The characterization of branch thickness as a percentage of branch diameter to stem diameter (*BII*) was a much more sensitive indicator for family differences to branch size ($P<.001$); heritabilities were:

h^2	CV_g	$\%\Delta G_1$	h^2	CV_{gmc}	$\%\Delta G_1$
0.26 ± 0.10	11.64	3.04	0.78 ± 0.31	3.36	5.27

(Table D8). Velling and Tigerstedt (1984) showed similar results in Scots pine, where branch thickness expressed as a ratio to stem diameter, was more sensitive for genetic discrimination than direct branch measures ($h^2=0.17\pm0.14$).

Mean branch length (*BL*) was 155.8 cm (CV=17.1%), and family means ranged from 143.4 cm to 165.3 cm (Table D9).

Branch length expressed as a percentage of branch length to height at age 10 (*BLT*) averaged 39.0% (CV=12.6%), with a family range of 37.2% to 41.6% (Table D11). Although branch length on its own was significant ($P<.05$) and selection parameters were:

h^2_i	CV_{F_i}	$\%\Delta G_i/i$	h^2_i	CV_{PHS}	$\%\Delta G_i/i$
0.11±0.06	15.64	1.68	0.52±0.27	3.56	3.68

(Table D10), the ratio of branch length to total height was a more sensitive indicator of family differences ($P<.001$) and selection parameters were more favourable:

h^2_i	CV_{F_i}	$\%\Delta G_i/i$	h^2_i	CV_{PHS}	$\%\Delta G_i/i$
0.19±0.07	11.80	2.22	0.77±0.30	2.93	4.48

(Table D12). Velling and Tigerstedt (1984) found similar relationships with Scots pine for crown width (branch length); crown width h^2_i=0.26±0.18, crown width/total height h^2_i=0.31±0.20.

Branch size traits may be better characterized in terms of proportioning of biomass between stem and branches than by direct branch growth measures.

3.2.2 Stem Form Traits and Attributes

Height, diameter and volume traits were described in the chapter on growth and yield (Table C1-C17). Taper estimates averaged 19.01 mm/m (CV=25.3%) in the population, and families ranged from 16.3 mm/m to 20.6 mm/m (Table D13). Sources of variation for additive genetic variance were significant (P<.01), and selection parameters from the population were:

h^2_i	CV_{Pi}	$\%\Delta G_i$	h^2_s	CV_{PHS}	$\%\Delta G_s$
0.10±0.05	25.70	2.53	0.57±0.30	5.35	6.08

(Table D14). Stem taper is thus an effective trait for progeny test selection, and gains of 6% per selection intensity unit is expected. Dominance genetic variance was significant for taper (P<.05) but was not as strongly expressed as additive genetic variance:

$\sigma^2_A = 2.352 \pm 1.246$ P<.01

$\sigma^2_D = 1.761 \pm 0.846$ P<.05

(Table D14). Other genetic effects were non-significant.

There was a wide range in family means for stem sinuosity score, ranging from 37.04 to 180.83, with an overall mean of 83.58 (CV=175%) (Table D15). A square root

transformation was applied to the data to reduce its non-normality. For most data interpretations non-transformed data was robust because of the large data set used. Selection parameters for sinuosity on a non-transformed and transformed basis were:

h_i^2	CV_{PH}	$\%\Delta G_i/i$	h_t^2	CV_{PHS}	$\%\Delta G_t/i$
0.25±0.09	175.21	43.73	0.86±0.30	47.15	81.42
0.26±0.09	34.41	8.97	0.86±0.30	9.45	16.34

(Table D16). Although the scale effect of the distribution shows an exaggerated expected response to selection, the transformation demonstrates that family selection against this trait should be quite effective. Moderate to high heritability estimates for selections against sinuosity have been demonstrated in other studies on juvenile Douglas-fir:

h_i^2	0.52±0.23	Jarret 1978
h_i^2	0.39	Birot and Christophe 1983
h_t^2	0.5	Adams and Howe 1985.

These authors also suggest that family selection will be the most effective way of improving sinuosity. Non-additive genetic variances were non-significant for sinuosity.

Forking occurrence in the population was also highly skewed in its distribution (most trees having no forks). The trait *FORK* counts only those forks (including tammercorn branches and multiple leaders) that are noticeable and are likely to persist (score greater than or equal to 2). The overall population mean (multiplied by 100) was 26.35 (CV=204%), and families ranged from 10.26 to 45.11 (Table D17). Although the female source of variation accounted for only 1.9% of the total, it was a significant source of variation ($P<.05$). Selection parameters for forking (non-transformed and transformed) were:

h_i^2	CV_{P_i}	$\%\Delta G_i/i$	h_t^2	$CV_{P_{MS}}$	$\%\Delta G_s/i$
0.08±0.03	207.20	15.98	0.66±0.27	35.32	46.86
0.08±0.03	19.06	1.49	0.66±0.27	3.28	4.33

(Table D18). The significant source of additive genetic variance for this trait in juvenile Douglas-fir presents a different result than that of the French provenance-progeny trials (Jarret 1978; Birot and Christophe 1983) where it was found to be non-significant ($P>.05$). Although the individual tree heritability value is low, progress through progeny test selection could be expected. The high within-family variance percentage (σ^2=83%) indicates much of the variation is uncontrollable, and phenotypic selection is unlikely to be useful.

Lammas growth or late season flushing (Fig. 3) is a major cause of forking and multiple leader formation (Rudolph 1964). It is an important trait to consider under form characteristics. The trait lammas flush (*LAFL*) is a count of the occurrences of lammas growth ×100. The overall population mean was 12.93 (CV=325%), and families ranged from 2.23 to 32.07 (Table D19). Sources of variation for additive genetic variance were significant for this trait ($P<.01$). Although only 2.6% of the total sources of variation are attributable to the selection source (σ_f^2), selection parameters indicate progress through parent tree selection is possible. Parameters for non-transformed and transformed lammas score were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.11±0.05	331.84	34.73	0.62±0.28	68.38	84.28
0.10±0.05	15.47	1.60	0.61±0.28	3.19	3.38

(Table D20). *LAFL* was significant for sources of variation for dominance genetic variance (σ_{mf}^2).

3.2.3 Observations on Components of Form Characteristics

In the section on trends in components of height traits (3.1.2) it was shown that as trees grow and establish themselves on sites, microenvironmental influences (σ_e^2) decline and trees are influenced more by large scale environmental effects (σ_s^2). These large-scale environmental effects would include length of growing season, late season moisture availability, etc. - effects that are felt over a large scale and are cumulative over seasons. For many of the stem-form-attribute traits specific environmental effects appear most influential as causes of variation. Table 8 shows replication means for the juvenile stem-form-attribute traits at the Greater Victoria watershed site (GVWS). Replication 1 at GVWS shows high incidences - almost twice the site average - of juvenile growth-form features of sinuousity, forking, and lammas growth. Rep. 1 on the lower portion of the site has a high cover of broom, a nitrogen fixing species. High soil nitrogen, together with good late-season soil moisture availability on the lower part of the site, are strong causative factors of these types of growth disturbance features (De Champs 1978, Carter *et al.* 1985). Growth disturbance features appear to be affected by more specific features of the environment than are growth traits.

TABLE 8. Means and standard deviations for several growth and form traits by replication on the Greater Victoria Watershed Site.

	REPLICATION					
	1		2		3	
TRAITS	mean	S.D.	mean	S.D.	mean	S.D
HT12	507.19	115.88	509.56	98.87	525.38	109.94
VOLM	13.84	5.06	8.22	3.67	11.38	4.88
SIN	114.44	190.22	87.10	142.46	88.14	162.16
LAFL	16.26	46.43	8.60	34.46	6.75	31.00
FORK	39.36	65.87	21.51	49.91	19.93	48.56

3.2.4 Relationships Between Crown Form Characteristics

Simple correlation coefficients between crown and growth characteristics for individual sites and combined analyses are presented in Table 9. The major associations are those related to size of the tree (e.g., branch thickness and volume). Partial correlation coefficients controlling the effect of size (volume) are presented in Table 10. Consistent significant relationships similar to Campbell's (1963) study of phenotypic correlations in the branch and upper-crown attributes of Douglas fir were:

1. trees with fewer branches have more acute angles,
2. trees with fewer branches have thicker branches,
3. trees with fewer branches have proportionaly longer branches,
4. acute-angled branches are thicker,
5. acute-angled branches are longer, and
6. thicker branches are longer, even accounting for volume.

Although the correlations are not strong enough to have one or a few of the traits explain the majority of the variation in others, there is a significant association of high branch numbers, comparitively light branching (thickness and length), and high branch angle. The contrasting association in form is for few but heavy and acute-angled branches.

Detailed variances, covariances and correlations among crown traits and between crown traits and growth traits are presented in appendix tables D21 to D26. The genetic relationships are summarized in Table 11.

TABLE 9 Simple correlation coefficients between growth and crown form traits on individual and combined sites

		PEARSON CORRELATION COEFFICIENTS								
		HT12	DM12	VOLM	TAPER	BN	BA	BT	BTT	BL	BLT
HT12	CLES		79 ***	81 ***	-17 ***	07 **	-08 ***	71 ***	-05 **	79 ***	-31 ***
	GVWS		77 ***	80 ***	-19 ***	30 ***	-03	82 ***	-16 ***	73 ***	-35 ***
	BOTH		81 ***	83 ***	-18 ***	03 *	-13 ***	69 ***	-22 ***	80 ***	-22 ***
DM12	CLES			88 ***	05 **	12 ***	-04 *	78 ***	-09 ***	80 ***	-06 **
	GVWS			86 ***	07 ***	25 ***	-11 ***	79 ***	-29 ***	77 ***	-01 NS
	BOTH			88 ***	03 *	01 NS	-14 ***	77 ***	-31 ***	84 ***	-05 **
VOLM	CLES				04 *	06 ***	-07 ***	81 ***	-10 ***	82 ***	-11 ***
	GVWS				03 NS	33 ***	-10 ***	77 ***	-28 ***	75 ***	-18 ***
	BOTH				02 NS	04 *	-14 ***	80 ***	-26 ***	83 ***	-06 ***
TAPER	CLES					04 *	-09 ***	12 ***	15 ***	07 ***	26 ***
	GVWS					00 NS	-06 *	13 ***	04 NS	00 NS	26 ***
	BOTH					03 *	-01 ***	12 ***	11 ***	03 NS	31 ***
BN	CLES						08 ***	-02 NS	-10 ***	05 **	01 *
	GVWS						11 ***	-12 ***	-21 ***	19 ***	-23 ***
	BOTH						13 ***	-03 NS	-04 **	-03 NS	-15 ***
BA	CLES							-13 ***	-14 ***	-11 ***	-01 NS
	GVWS							-20 ***	01 NS	-12 ***	-11 ***
	BOTH							-19 ***	-02 NS	-17 ***	-11 ***
BT	CLES								10 ***	86 ***	03 ***
	GVWS								17 ***	78 ***	08 **
	BOTH								22 ***	83 ***	12 ***
BTT	CLES									17 ***	23 ***
	GVWS									-04 NS	05 *
	BOTH									-07 ***	09 ***
BL	CLES										22 ***
	GVWS										15 ***
	BOTH										25 ***

*, **, *** = significant at .05, .01, .001 levels of probability.

TABLE 10. Partial correlation coefficients between crown form traits controlling for volume on individual and combined sites.

		BA	BT	BTT	BL	BLT
BN	CLES	.08 ***	.12 ***	.09 ***	.00 NS	.04 *
	GVWS	.15 ***	.23 ***	.13 ***	-.10 ***	.19 ***
	BOTH	.13 ***	.10 ***	-.04 *	-.11 ***	.16 ***
BA	CLES		.12 ***	-.15 ***	-.08 ***	.01 NS
	GVWS		.19 ***	-.02 NS	-.07 **	.14 ***
	BOTH		.13 ***	.06 ***	-.11 ***	.08 ***
BT	CLES			.82 ***	.59 ***	.31 ***
	GVWS			.63 ***	.48 ***	.35 ***
	BOTH			.74 ***	.48 ***	.28 ***
BTT	CLES				.44 ***	.22 ***
	GVWS				.27 ***	.00 NS
	BOTH				.27 ***	.07 ***
BL	CLES					.56 ***
	GVWS					.44 ***
	BOTH					.54 ***

*, **, ***= significant at .05, .01, .001 levels of probability.

TABLE 1. Genetic (r_g) and phenotypic (r_{phe}) correlations between crown form traits and genetic (r_g) correlations between crown form traits and yield traits.

	BN	BA	BI	BII	BL	BLI
BN	.19	.19	.16	.59	.18	-.11
BA	.3[illegible]	.23	.05	.29	.10	.12
BI	.22	.23	.05	.38	.33	.11
BII	.46	.25	.33	.26	.04	.14
BL	.27	.16	.66	.01	.11	.61
BLI	.07	.00	.22	.06	.46	.19
HT12	.26	-.03	-.03	-.31	.38	-.59
DM12	.67	.18	-.21	-.82	.22	.21
VOLM	.71	.18	.29	-.75	.28	-.19

Between crown form traits only:

above diagonal records genetic correlations,

diagonal records individual tree heritabilities,

below diagonal records phenotypic correlations of half-sib, family means.

of the aforementioned relationships of crown character, the strongest genetic basis appears to be that between branch number (*BN*) and branch thickness as a proportion of stem thickness (*BTI*) (r_a 0.59±0.18). Thus the contrast between trees with many but light branches could be utilized effectively for selection. Branch angle shows a moderate, negative genetic relationship (r_a 0.29±0.23) with proportional branch thickness, further supporting the genetic association of these form types. Similar relationships are documented in white spruce (Merrill and Mohn 1985) and Scots pine (Pöykkö 1982; Velling and Tigerstedt 1984).

The genetic relationships between branch form associations and yield were investigated through path coefficient analysis. Path coefficient analysis is a standardized, partial regression analysis that provides a method by which direct and indirect components of an association can be segregated (Wright 1923, Li 1975). The additive genetic relationships of branch traits can thus be evaluated for their direct and indirect influences on yield. The model of cause and effect of crown characters on yield is used to emulate the model of Campbell (1963), except that additive genetic relationships are used. Path analysis is also used as a graphic aid to select key traits for multiple trait selection for form and growth characters. By this method the influences (direct and indirect) of crown traits on yield can be visualized. The analysis consists of the

simultaneous solution of the five following equations that provide all possible direct and indirect relationships among yield and crown variables (Fig. 8):

$$r_{15} = P_{15} + r_{12}P_{25} + r_{13}P_{35} + r_{14}P_{45} \quad 1$$

$$r_{25} = P_{25} + r_{12}P_{15} + r_{23}P_{35} + r_{24}P_{45} \quad 2$$

$$r_{35} = P_{35} + r_{13}P_{15} + r_{23}P_{25} + r_{34}P_{45} \quad 3$$

$$r_{45} = P_{45} + r_{14}P_{15} + r_{24}P_{25} + r_{34}P_{35} \quad 4$$

$$1 = P_{15}^2 + P_{25}^2 + P_{35}^2 + P_{45}^2 + 2r_{12}P_{15}P_{25} + 2r_{13}P_{15}P_{35} + 2r_{14}P_{15}P_{45} + 2r_{23}P_{25}P_{35} + 2r_{24}P_{25}P_{45} + 2r_{34}P_{35}P_{45} + P_{X5}^2 \quad 5$$

Results using the direct measurements for branch thickness and branch length are presented in Table 12. Stem volume is affected mainly by the number of branches (P_{15} = .416). Other effects are minor in comparison, and it can be seen that they affect volume through the indirect effect of branch number. The residual variation leaves nearly 45% of the variation unexplained by these traits.

The second analysis (Table 13) used the proportional branch measure traits (%) to predict volume. In this analysis proportional branch thickness (*BTT*) has at least as important a direct effect on volume as does branch number. These traits also have a strong indirect influence on each other. Branch number (*BN*) and proportional branch thickness (*BTT*) together account for 42% (P_{15}^2=.165, P_{25}^2=.257) of the genetic differences in stem volume by their direct influences; this is less than the 60% for phenotypic

relationships found by Campbell (1986). Branch angle and proportional branch length do not have an important effect on stem volume. The additive genetic relationships between branch angle and branch length with both branch number and proportional branch thickness mean that selecting for high branch number and light branching will also improve branch angle and branch length.

A positive association of the good form complex with growth characters is encouraging, and the promotion of more branches per whorl will be less detrimental compared to the relative reduction of branch size, flatter branch angle and increased volume. The negative phenotypic relationship of *bd* with the growth traits (Table 9) was not noted in the genetic correlations. Jarret (1978) noted a very strong positive genetic correlation between vigour (height) and branch angle (r_g=0.96). Observations of a positive relationship between volume and a similar complex of form characters was found in Scots pine by Velling and Tigerstedt (1984). They concluded that the proportional branch diameter was of great importance for wood quality, and more than offset the promotion of branch number.

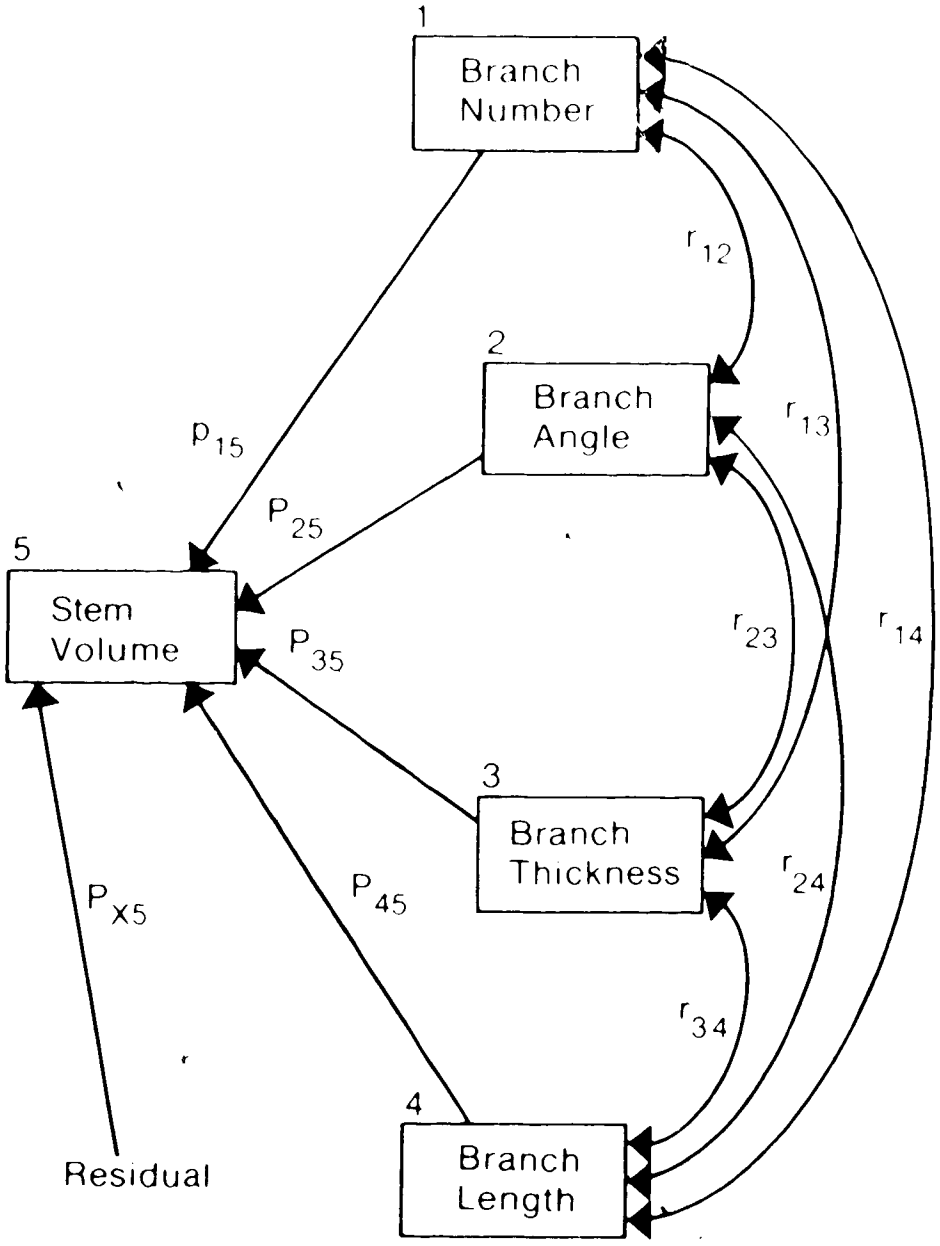


Figure 8. Model of path-coefficient analysis of the association of crown form traits with stem volume.

TABLE 12. Path-coefficient analysis of the direct and indirect genetic associations of crown variables with stem volume.

	Crown Variables				
	BN	*BA*	*BT*	*BL*	*X*
Due to direct effect:					
P_{5}	.645	.074	.140	.128	.675
Due to indirect effects:					
via branch number					
P_{15}		.123	.106	.114	
via branch angle					
P_{25}	.014		.004	.008	
via branch thickness					
P_{35}	.023	.007		.047	
via branch length					
P_{45}	.023	-.013	.044		
Totals (additive genetic correlations)	.705	.177	.286	.282	

TABLE 13. Path coefficient analysis of the direct and indirect genetic associations of crown variables with stem volume using proportional branch measures.

	Crown Variables				
	BN	*BA*	*BTT*	*BLT*	*X*
Due to direct effect:					
P_{i}	.406	-.038	-.507	-.073	.575
Due to indirect effects:					
via branch number					
P_{15}		.077	-.239	-.044	
via branch angle					
P_{25}	-.007		.011	-.004	
via branch thickness					
P_{35}	.299	.146		-.072	
via branch length					
P_{45}	.008	-.008	-.010		
Totals (additive genetic correlations)					
	.705	.177	-.746	-.193	

3.2.5 Relationships With Stem-Form Traits

Correlations between bole taper and growth and yield traits, and between bole taper and crown form traits, are summarized in Table 14. Genetic correlations, more than phenotypic correlations, reflect that taller trees are less tapering, and trees of wider girth and greater stem volume are stronger tapering. Although the estimate of r_A was weak and non significant between *DM12* and *TAPER* (r_A = 0.15±0.44), the correlation between *DM10* and *TAPER* (not shown) was strong (r_A = 0.53±0.28). Much of the volume of the stem is in the lower portion. Selection of trees for total height, without a measure of girth, will favour a less tapering bole at the expense of stem biomass. Strong, positive genetic correlations also exist between branch number and taper (r_A = 0.57±0.21), and branch thickness and taper (r_A = 0.73±0.28). These strong correlations reflect the partitioning of wood into branch material down the stem of the tree; higher-tapering trees having more and thicker branches.

Simple correlations between the stem attribute traits and growth traits are presented in Table 15. Consistent significant relationships were found that demonstrate:

1. taller trees are more sinuous,
2. trees of larger girth are more sinuous,
3. trees with a higher incidence of lammas growth are more prone to have forks and multiple leaders.

A significant negative correlation between *HT12* and *FORK* on

site GVWS demonstrates the effect of rep 1 - reduced total cumulative growth and a high incidence of growth disturbance features (Table 8).

Phenotypic (r_{P1}, r_{PHS}), genetic (r_A), and environmental (r_E) correlations between stem attributes and growth traits are presented in Table 16. With the replication effect removed, the negative relationship between forking incidence and height is removed, although the tendency of a negative but non significant genetic correlation (r_A=-0.17±0.27) is still aparent.

The major significant stem-attribute relationship with growth is that between stem sinuosity and height growth (r_A=0.41±0.21). The relationship is large enough to indicate that selection for height on its own will increase the occurrence of sinuosity in the population. These results corroborate the high genetic (r_A=0.63) and significant phenotypic correlations between height and sinuosity that were found by Jarret (1978). Results from the study population indicate that this genetic relationship is non-significant for sinuosity and stem diameter (r_A=-0.13±0.25). The phenotypic (individual) and environmental correlation between diameter and sinuosity (r_{P1}=0.23, r_E=0.33; Table 16) suggest that individual trees of larger girth are taller. In terms of selection, diameter selections are less likely to increase the occurrence of sinuosity than height selections.

TABLE 14. Phenotypic, genetic, and environmental correlations between taper and growth traits, and taper and crown form traits.

	HT12	DM12	VOLM
TAPER			
r	.18 ***	.03 *	.02 NS
r_A	.38±.31	.15±.34	.17±.36
r_{PI}	.18	.04	.04
r_{PHS}	.27	.16	.14
r_E	.16	.06	.02

	BN	BA	BI	BII
r	.03 *	-.07 ***	.10 ***	.11 ***
r_A	.57±.21	-.05±.29	.73±.19	.26±.30
r_{PI}	.08	-.08	.11	.12
r_{PHS}	.40	-.12	.52	.28
r_E	.00	-.14	.07	.10

*, **, ***= significant at .05, .01, .001 levels of probability.

TABLE 15. Simple correlation coefficients between stem attribute and growth traits on individual and combined sites.

		DM12	SIN	FORK	LAFL
HT12	CLES	.79 ***	.21 ***	.10 ***	.04 *
	GVWS	.82 ***	.30 ***	-.21 ***	.07 **
	BOTH	.87 ***	.17 ***	-.04 *	.00 NS
DM12	CLES		.18 ***	.17 ***	.08 ***
	GVWS		.29 ***	-.09 ***	.01 NS
	BOTH		.13 ***	.05 **	.05 ***
SIN	CLES			.00 NS	-.03 NS
	GVWS			-.03 NS	-.03 NS
	BOTH			-.02 NS	-.03 NS
FORK	CLES				.36 ***
	GVWS				.48 ***
	BOTH				.41 ***

*, **, ***= significant at .05, .01, .001 levels of probability.

TABLE 16. Phenotypic, genetic, and environmental correlations between stem attribute traits and growth traits on the combined analysis.

		SIN	FORK	LAI
HT12				
	r_A	.41±.21	.17±.27	.14±.31
	r_{PI}	.28	.04	.02
	r_{PHS}	.33	.04	.00
	r_E	.25	.02	.00
DM12				
	r_A	-.13±.25	-.14±.27	.10±.31
	r_{PI}	.23	.07	.06
	r_{PHS}	-.10	.02	.10
	r_E	.33	.09	.08

3.2.6 Growth and Crown Form Selections

The selection process summarized in this chapter is designed to improve traits of growth and yield, and form simultaneously. The growth trait chosen was stem diameter (*DM12*), because it is an easy trait to measure, and as has been shown, it is an accurate response variable for predicting stem volume. Crown form traits were chosen for their ease of measurement, for the likely effectiveness of their response (as demonstrated by their genetic parameters), for their value considerations, and for their genetic correlations with other traits in the fine branching form type. Three selection schemes were investigated:

1. a multiple trait index that selects for diameter and branch number (*IBN*),
2. a three trait index that selects for diameter, branch number, and against proportional branch thickness (*IBNT*),
3. selection using the composite trait of knottiness index (*KI*).

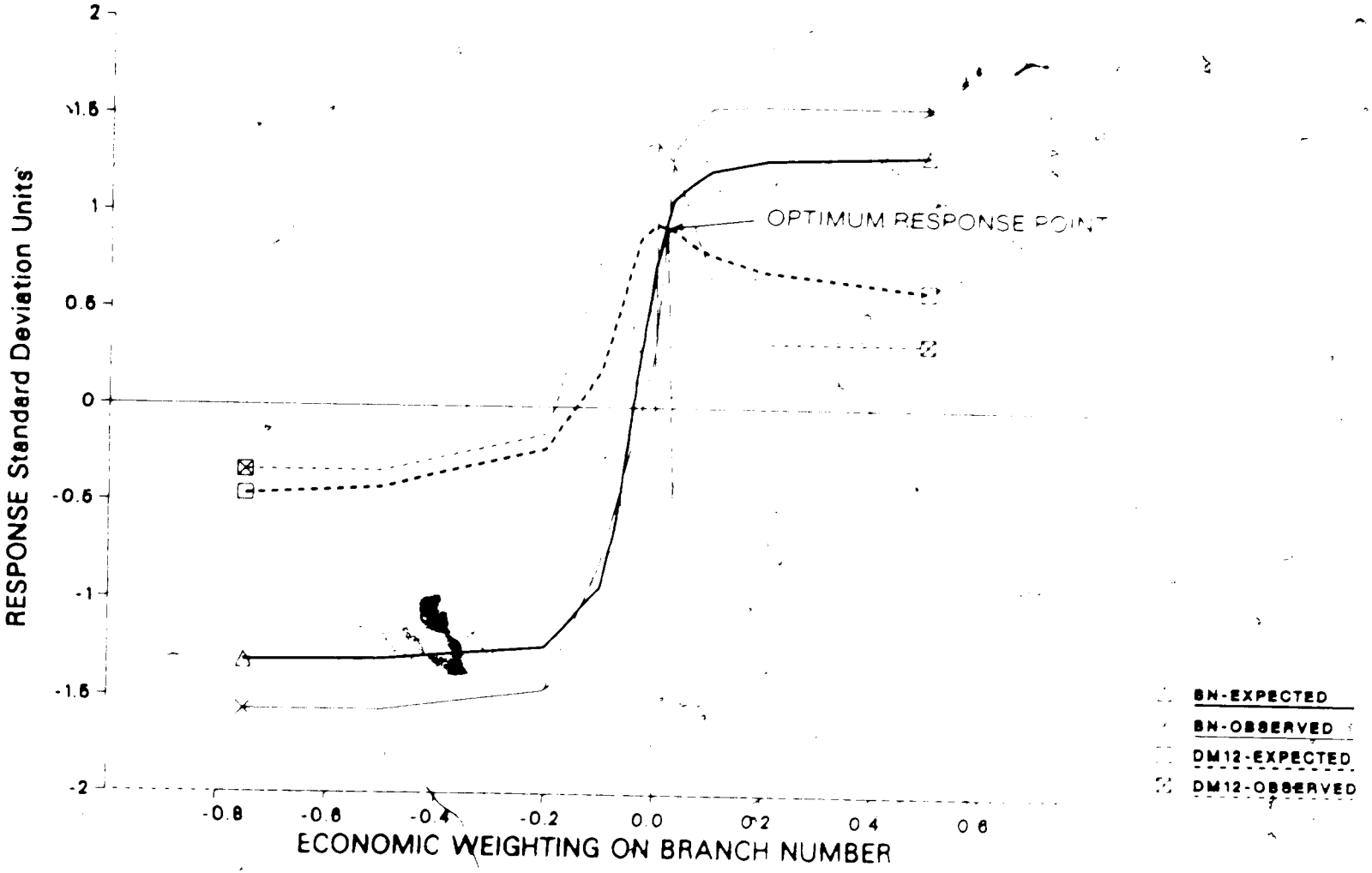
The growth and form indices developed here seek to improve the net genetic worth of the aggregate genotype (H). Correct evaluations of H requires economic weights for each trait. Since true dollar values for growth and form traits are uncertain for Douglas-fir, the economic weights of *BN* in relation to *DM12* were changed over the range of +1 to -1 (for the first index *IBN*, of *BN* and *DM12*) and the primary objective of these selection indices became one of making

empirical choices based on the estimation of genetic gains of individual traits. The response of each trait of the index for the different rankings that occur for changing economic weights is plotted in Figure 9. Both observed (R_{OBS}) and expected (ΔG) responses to selection were plotted for a selection intensity of 1:2 and were expressed in standard deviation units (R_{OBS} was multiplied by two because the pollen parent should also be selected). The optimum point for selection when economic weights are highly uncertain is where each trait is maximized for its minimum expected gain, at the curve intersection points (Namkoong 1979). The optimum response point in the *IBN* index is at a value weighting of .03 for *BN* and 1.0 for *DM12* (Fig. 9). The b values for *IBN* at the 0.03:1.0 value ratio were:

DM12	*BN*
0.49	0.03

At this optimum level the response level (R_{OBS}) for *DM12* is .628/.681=92% of the level of direct selection for *DM12* on its own, and *BN* is .661/.783=84% of its maximum response for this selection intensity. Although the maximum response of each trait is not achieved by this strategy, there is little loss from the maximum achievable response because of the strong positive genetic correlation between traits and this genetic association has been strengthened.

Figure 9. Response curves (R_{OBS} and ΔG) for branch number and diameter holding economic weight of diameter at one and changing the weight on branch number, IBN.



Because of the positive association of the fine branching form type (profuse, tight, excurrent branching) the response (R_{obs}) of the other form traits to *IBN* selections is also favorable. Branch angle is improved by .26 - .85 % of the direct selection level at the optimum level of *IBN* at the 1% selection intensity levels. Proportional branch thickness is reduced by .89 of a standard deviation unit or .89 - .95% of the level that would be achieved through direct selection against *BTI* on its own. The correlation between the index (I) and its genetic worth (H), r_{HI}, for the changing values ranged from 0.8 to 1.0 and averaged 0.9; thus indicating the relative efficiency of the index *IBN*.

The second index used *BTI* along with *BN* and *DM1_2* in a multiple trait progeny test index of crown form and yield. The sensitivity plotting of this index (*IBN1*) to changing economic weights is too complex to plot effectively, but an iterative process was used to find the maximin (Namkoong 1979) point where response of each trait in the index (R_{obs}) were approximately equal. Economic values (a_i), b values (b_i), R_{OBS} values, and comparisons with direct selection for the trait on its own (relative efficiencies), are shown for this index:

R_{IW}			
$S.E.(R_{IW})$			

The optimum strategy here is to maximize the minimum response to each trait; by losing only 10% of our efficiency in selecting for yield on its own, and 20% - 30% for the other traits, selections enforce the associations in the fine branching form type.

In both of these indices the empirically derived optimum response levels are better when crown traits are valued low (≈0) compared to the yield trait. This emphasizes the positive association of yield and crown form traits. Crown form traits are improved strongly through their genetic covariances with traits of yield.

Another way of selecting crown form is to select against the composite trait of knottiness index (*KI*) (Campbell 1961; Jarret 1978). The overall mean for (*KI*), the average of the ratio of total branching surface area to stem surface area was 31.4% (CV=32%), and family means ranged from 25.8% to 34.8% (Table D27). Family sources of variation were significant ($P<.01$) and heritability and gain estimates were:

h^2	CV_p	$\%\Delta G_{1}$	h^2_{tree}	CV_{tree}	$\%\Delta G_{1}$
0.16±0.07	22.82	3.88	0.09±0.05	5.16	1.55

(Table D28). Although not significantly different, heritability values were not as high as reported for coastal Douglas fir populations in France (Jarret 1978, h^2 0.29±0.16). Details of the analyses of covariance of *KI* with the other important form traits are presented in Appendix Tables D29-D33. The relative efficiencies (R.E.) of these form traits, to correlated response to progeny test selection against *KI* were:

	DM12	*BN*	*BI*	*BTI*	*BA*
R.E.	34%	33%	11%	9%	8%

It can be seen that selecting against the composite trait *KI* improves branch thickness and diameter but does not promote the profuse and flat branching form type.

3.2.7 Crown and Stem Form Summary

1. Sources of variation for additive genetic variance (σ^2_a) were significant ($P<.05$) for all 11 crown and stem form traits, except branch thickness, on the combined analysis. Sources of variation for dominance genetic variance (σ^2_{mt}) were significant for branch angle, bole taper, and lammas occurrences only; and even so the estimates of dominance genetic variance for these significant traits were much less than the estimates of additive genetic variance. G.E.I. sources of variation ($\sigma^2_{st}, \sigma^2_{smt}$) were not significant for any trait.

2. Branch angle should respond well to mass selection ($h^2_i=0.73\pm0.24$) as has been reported in other studies. The other form traits would respond best to family selection. Moderate heritability ($h^2_i\geq0.2$) was found for branch number, proportional branch thickness, proportional branch length, and sinuosity. Branch thickness and branch length as direct growth measures; and bole taper, forking, and lammas occurences all had low heritabilities ($h^2_i\leq0.1$).

3. Branch thickness and branch length were best measured as proportional traits - branch thickness as a proportion to stem thickness at the measuring point, and branch length as a proportion of total height.

4. There was an association among high branch number, light branch size (thickness and length), and high branch angle - in contrast to low branch number, heavy branch size (thickness and length) and acute-angled branches. Genetic

relationships were established for a fine-branching form type and were shown to be positively associated with yield.

5. Path analysis showed that branch number and proportional branch thickness were associated with 42% of family differences for stem volume.

6. Negative genetic correlations were demonstrated between height and bole taper. Strong positive genetic correlations exist between bole taper and branch number, and bole taper and branch thickness. Bole taper is thus implicated in the shifting of woody material from the bole to the branches.

7. There was a positive association between stem sinuosity and individual growth traits, especially height growth. Genetic correlations suggest that height selections will promote sinuosity whereas diameter selections will not. This corroborates the finding of Jarret (1978).

8. Multiple trait selection for the improvement of form and growth traits can accentuate the positive association of the fine-branching form type of profuse/light/excurrent branches with stem volume. Selecting key traits in the form complex (branch number and proportional branch thickness) along with stem diameter can favourably affect all traits. Selecting against a composite trait of branch/stem surface ratio can improve form but is not as effective as multi-trait selection for promoting the fine-branching form type.

3.3 Wood Quality Traits

Traits reported in this chapter were wood density, estimated using the maximum moisture content method on the outer 4 rings of two 5 mm cores (*WD*), and a wood density estimate using the resistance of wood to a non-repeating Pilodyn pin (*PIN*). Wood density measures were only made at the Cowichan Lake site (CLES).

3.3.1 Wood Quality Traits

Wood density measures averaged 363.01 kg/m^3 (CV=7.16%), and family means range from 339.5 to 382.8 kg/m^3 (Table E1). Additive genetic variance was strongly expressed, with a comparatively low standard error (σ^2_A=572.32±181.20) (Table E2). Female sources of variation were significant (P<.001) and accounted for over 20% of the total. The individual tree heritability value for wood density (*WD*) was high (h^2_i =0.90±0.28); the highest value in this study. The low comparative error of within-family variation (σ^2_w=54%) suggests this trait should respond well to mass selection. Selection parameters for wood density (*WD*) were:

h^2_i	CV_{Pi}	$\%\Delta G_i/i$	h^2_f	CV_{PHS}	$\%\Delta G_i/i$
0.90±0.28	6.97	6.23	0.93±0.30	3.41	6.37

(Table E2). The high individual tree heritability agrees with values for wood mean density from 14-year-old coastal

Douglas-fir provenance progeny trials in France (most provenances > 0.8; Bastien *et al.* 1985). In spite of the strong individual tree heritability, large percentage gains in wood density from progeny test selection cannot be expected because variation between family means was not large (CV_{FMS}=3.4). Sources of variation for dominance genetic variance (σ^2_{FM}) and G.E.I. variance (σ^2_{I}) were non significant for wood density.

Pin penetration averaged 16.7 mm (CV=12.3%), and family means ranged from 14.9 mm to 18.5 mm (Table E3). Family sources of variation were highly significant (P<.001). Heritability estimates were comparable to those found from the cores. Selection parameters for *PIN* were:

h^2_f	CV_{PF}	$\%\Delta G_{f=1}$	h^2_f	CV_{FMS}	$\%\Delta G_{f=1}$
0.81±0.26	2.06	2.71	0.90±0.29	5.72	10.23

(Table E4). The value of *PIN* for predicting genetic differences as demonstrated by the high heritability estimates is in contrast to the results of Bastien *et al.* (1985), whose heritability estimates for the Pilodyn were low. Unlike the *WD* value, dominance genetic variance for the Pilodyn measure (*PIN*) was significant (P<.01; Table E4).

The genetic correlation between the Pilodyn measure (*PIN*) and wood density (*WD*) was high (r_A=-0.95±0.02). Because of the high genetic correlation and heritability,

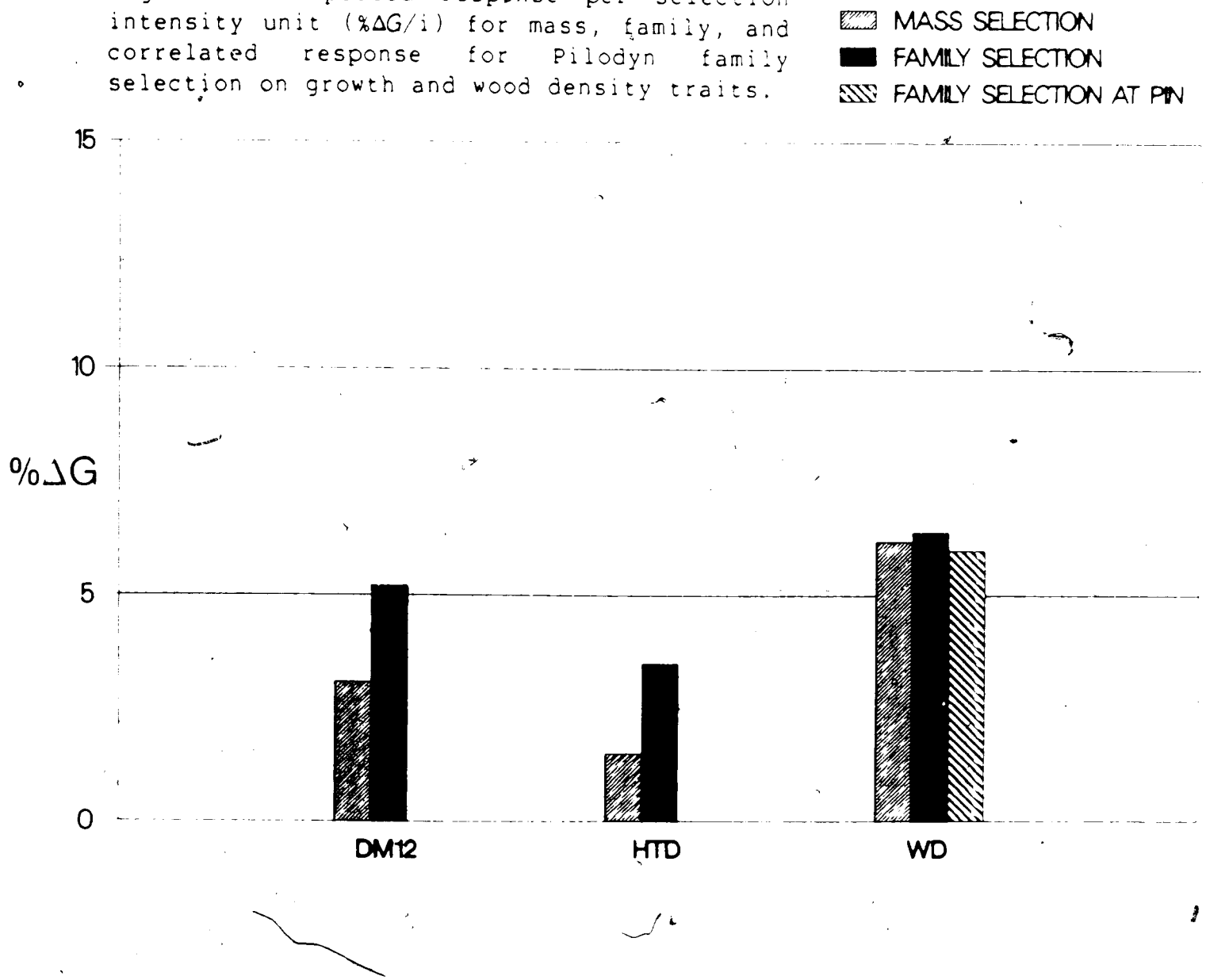
the efficiency of correlated response to family selection was 97% (Fig. 10; Table E5), and it would thus appear from this study that the Pilodyn is a valuable instrument for family selection of wood density in 12½ year old Douglas-fir. Thus family selection may be a useful application of the Pilodyn but it is likely less effective for individual selections as would be practised in the Douglas-fir provenance progeny tests in France (Bastien *et al.* 1985). It may also be, as Sprague *et al.* (1983) found, that certain types of Pilodyn configurations (e.g., different pin sizes) (and/or spring strength) are more effective than others.

3.3.2 Relationships Between Wood Density and Growth and Form

Unfortunately strong negative genetic correlations exist between wood density and growth traits Table 17. ($r_A = -0.53 \pm 0.19$). A strong negative relationship between growth and mean wood density was also reported in the French Douglas-fir provenance-progeny tests (Bastien *et al.* 1985). They also found a negative genetic correlation of wood mean density vs. wood heterogeneity, but no unfavourable correlations of wood heterogeneity and growth. Such results are discouraging for the simultaneous improvement of growth traits, wood quality, and wood density in Douglas-fir.

Relationships between wood density and form traits are also presented in Table 17. Although the simple correlations between branch number and branch angle were non-significant

Figure 10. Expected response per selection intensity unit (%ΔG/i) for mass, family, and correlated response for Pilodyn family selection on growth and wood density traits.



(P<.05), significant negative genetic correlations exist:

r_A= .32±.27 (*WD* and *BN*) and r_A=-.41±.27 (*WD* and *BA*),

and environmental correlations are positive (Table 17). Proportional branch thickness (*BTT*) was significantly correlated, r, (P<.001) to wood density and this association also shown by the genetic correlation (r_A=.26±.23; Table 17). Thus selecting for families of high wood density will produce a population of trees with fewer branches, proportionaly thicker branches and more acute-angled branching; this amounts to selecting for the heavy branching form type. Much of this association may have to do with the strong negative association of growth vs wood density, and the positive association of fine-branching vs growth. Thus a negative association of wood density vs fine-branching is not independent of other key relationships. Negative relationships between wood density and crown form traits have also been reported in Australian radiata pine (Dean *et al.* 1983).

There were significant (P<.001) negative correlations between wood density and stem attribute traits (Table 17). The strongest of these relationships on a genetic basis was that between sinuosity and wood density (r_A=-.28±.22; Table 17), which indicates that by selecting for wood density, smaller and less sinuous trees will be favoured.

TABLE 17. Phenotypic, genetic and environmental correlations between wood density and growth traits, wood density and crown form traits and wood density and stem attribute traits.

		DM12	HTD
WD			
	r	.46 ***	.21 ***
	r_A	.53±.19	.33±.27
	r_{PI}	.41	.17
	r_{PHS}	.49	.28
	r_E	.60	.24

		BN	BA	BTI	BLT
	r	.00 NS	-.01 NS	.08 ***	.02 NS
	r_A	-.32±.27	.41±.27	.26±.23	.12±.24
	r_{PI}	-.05	-.07	.02	.01
	r_{PHS}	-.23	-.37	.25	.10
	r_E	.17	2.72	-.46	.15

		SIN	FORK	LAFL
	r	-.13 ***	-.10 ***	-.06 ***
	r_A	-.28±.22	.09±.27	-.16±.24
	r_{PI}	-.14	-.10	-.07
	r_{PHS}	-.22	-.07	-.14
	r_E	.02	-.24	-.00

*, **, ***= significant at .05, .01, .001 levels of probability.

3.3.3 Growth and Wood Density Selections

Simultaneous improvement of wood density and growth characteristics is difficult in this population, because of the antagonistic genetic relationship $r_A = .53 \pm .19$ (*WD* and *DM12*). *DM12* was used as the growth characteristic because of its strong association with stem volume and because of its significance levels at site CLES, where wood density measurements were taken. Index coefficients for multiple trait selection of *WD* and *DM12* where both traits are given equal value were:

When families were ranked according to their genetic merit for an aggregate breeding value of *WD* and *DM12*, the response ($R_{OBS}I$ for a selection intensity of 1:2 was 10.04 kg/m^3 of *WD* with a concurrent decline of nearly 1 mm in *DM12*.

A plot of the response (R_{OBS}, ΔG) of the traits for a selection intensity of 1:2 in standard deviation units to changing economic weights of *WD* in relation to *DM12* is given in Figure 11. The correlation between the index (I) and its genetic worth (H), r_{HI}, for the changing economic weights ranged from 0.8 to 1.0 and averaged 0.9; thus indicating the relative efficiency of the index *IWD*. The value and efficiencies of index selection are most useful for negative

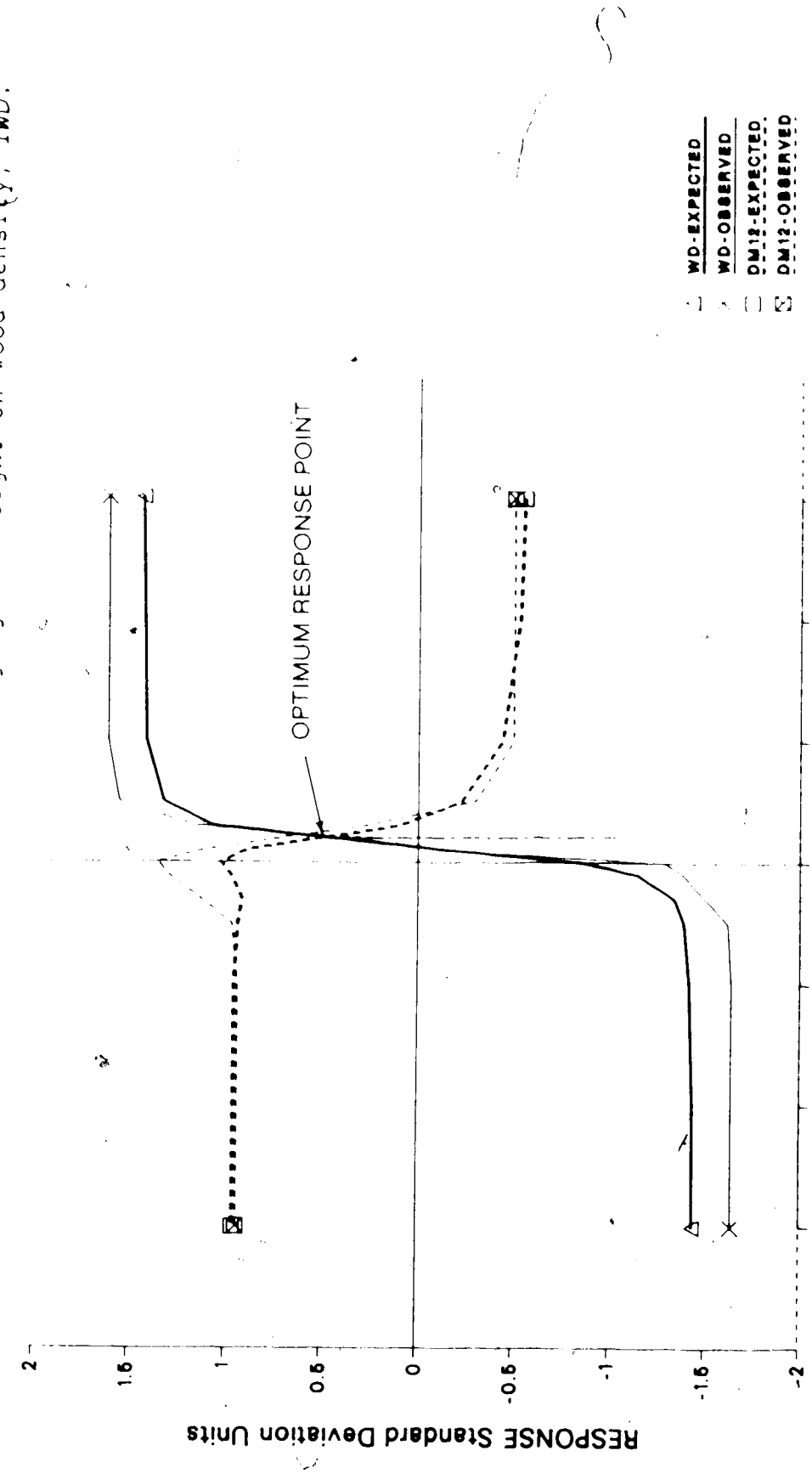
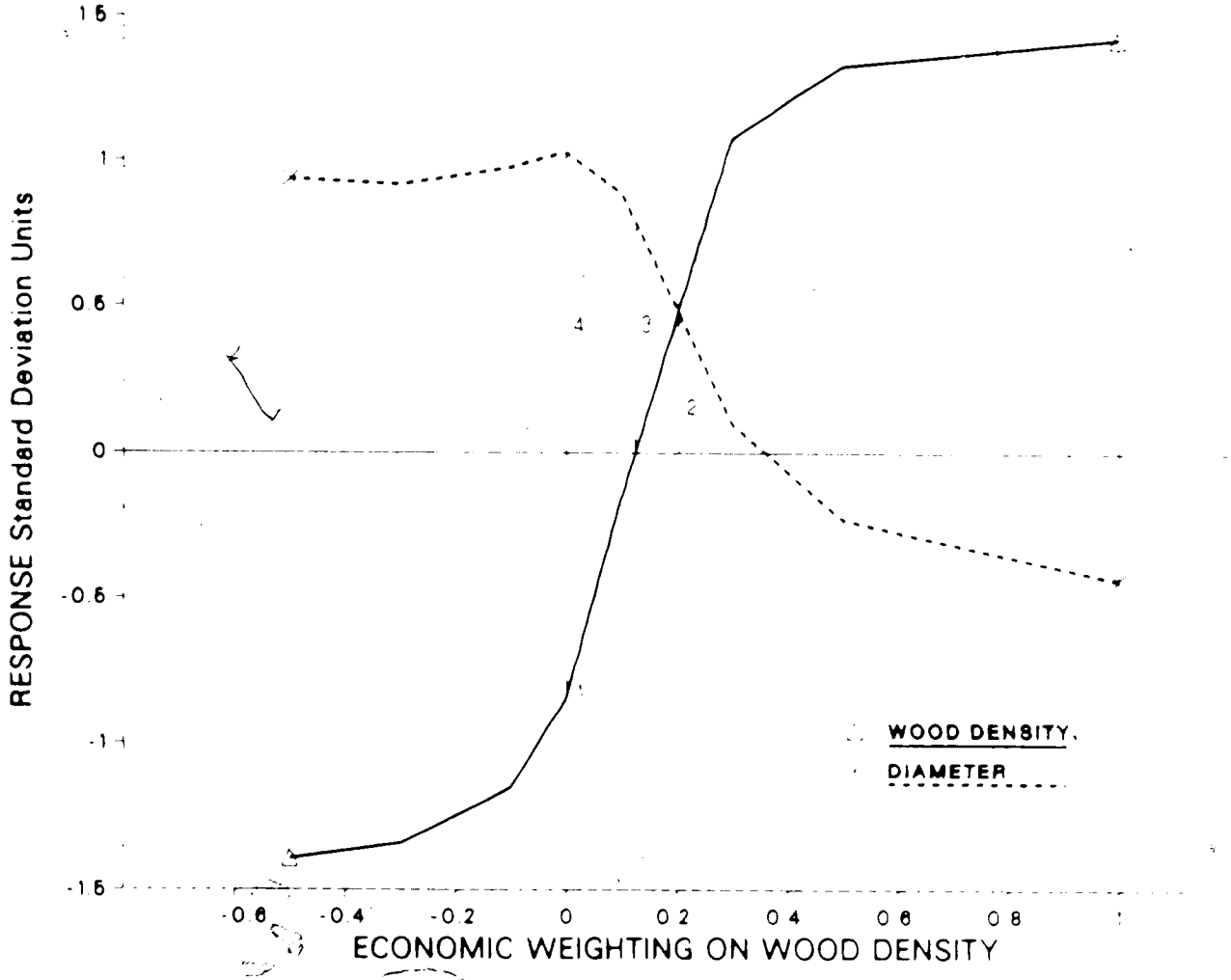


Figure 11. Response curves (R_{OBS} and ΔG) for wood density and diameter holding the economic weight of diameter at one and changing the weight on wood density, *IWD*.

Figure 12. Response curves (ΔG) for wood density and diameter for the selection index *IWD* emphasizing selection strategies.



genetic correlations (Hazel and Lush 1942), where it can elucidate important selection strategies. The appropriate selection strategy depends upon the value that each trait has in the index and the relative certainty we can apply to those values. Four such strategies that might be employed in the improvement of wood density and growth are demonstrated in Figure 12.

1. Option 1: When a unit of wood density is of equal value to a unit of diameter, the overall aggregate value would favour wood density response to diameter response. The assumption of equal values, or any other known value relationship, even if it were known to be true in present market conditions, however, could not be predicted for the future.

2. Option 2: The optimum strategy is one of maximizing the minimum response to selection when values are highly uncertain and subject to unpredictable changes (Namkoong 1979). The optimum point in this selection strategy is at the curve intersection point. Neither trait is maximized at this point; indeed because of the strong negative genetic relationships between these two traits the maximin point achieves only 42% of the maximum response (R_{OBS}) to *DM12* and 72% of the maximum response (R_{OBS}) to *WD*. However, this point is the maximum/minimum (maximin) response point for both traits and is the most appropriate if we believe both traits are economically valuable, but there is high uncertainty as to their

value functions. By selecting for positive response in both traits at this point the selection process can begin to break the negative correlation between these traits.

3. Option 3: This option constrains the change in wood density by using a restricted index as per Kempthorne and Nordskog (1959). This strategy is also a conservative strategy. It makes no assumptions as to the intrinsic value of wood density and assumes there is enough uncertainty as to its value that we should be unwilling to let it decline.

4. Option 4: This assumes that the decline in wood density by selecting for diameter is slight and economically acceptable. Although heritabilities for wood density have been reported as being high, the variability available for selection is low (Bastien *et al.* 1985). The coefficient of variation of stem volume for half-sib means is three times that for wood density. Therefore, the indirect losses in *WD* by the selection of stem volume (through *DM12* in this case) may be comparatively low compared to gains in volume even accounting for the high heritability of *WD*. At a direct selection for *DM12* on its own, with a 1:2 selection intensity, wood density declines by 0.5 (R_{OBS}) of a standard deviation (6.25 kg/m^3) or by 1.75% of its mean. This strategy would ignore wood density under the assumption that a slight decline in wood density in the population may have

little or no economic impact on the resource.

Before selection decisions and strategies are made, however, certain facts need to be known about wood density and its estimation. Information of a practical nature should address the following points regarding wood density:

1. Is juvenile core wood density of any practical consequence to the value of the mature stem wood density and clear wood product?
2. Are selections for wood density worth comparative gains for wood heterogeneity (Bastien *et al.* 1985) and losses in form?

We need to have information of this nature to ensure wood density has an intrinsic value. If it does have an intrinsic value options 3 and especially 2 are the best choices and it should have high emphasis in mass selection phases of multi-stage selection; e.g., plus tree selections and within family selections. Phenotypic selection for wood density will be highly efficient compared to growth and form selections.

3.3.4 Wood Density Summary

1. Heritabilities for wood density were high (h^2 =0.90±0.28) - wood density is a trait that can be effectively improved through mass selection.

2. Unlike the results of Bastien *et al.*, the Pilodyn proved very effective. With a genetic correlation of -0.95 the efficiency of using the correlated response to family

selection was 97%.

3. Correlations with growth traits were strongly negative.

4. Correlations with form traits reflect this negative relationship with growth and were also unfavourable.

5. An antagonistic relationship between wood density and heterogeneity of wood density (Bastien *et al.* 1985) is also of concern considering the importance of a uniform product (Zobel *et al.* 1982).

6. Index selection is highly effective for selections involving negative correlations and can be used to minimize the impact of the negative relationship between wood density and growth. Several selection strategies were examined. When the unfavourable correlations with wood heterogeneity and form are ignored, options that constrain the loss in wood density (3) or seek to maximize the minimum expected response to both traits (2) are best.

4. DISCUSSION

4.1 Expression of Genetic Differences

Twenty of the twenty one traits of growth, form, and wood quality investigated in this study had significant amounts of additive genetic variance from which to base selections. Non-additive genetic variance, σ^2_{ns}, was not significant for most of the traits, except for branch angle, bole taper, and lammas incidence; but even in these cases was much less than the additive genetic variance. G.E.I. interaction, as (determined by σ^2_{sf}) was non significant for all traits. A site×cross source of information (σ^2_{sxc}) was significant for the two later height measures (*HT10*, *HT12*), but was not significant for any other traits.

4.1.1 Selection Parameters for Individual Traits

With additive genetic variance being the major significant source of genetic variance available, selection for additive genetic effects and the creation of random mating populations within seed orchards is likely to remain the major vehicle of tree improvement for the coastal Douglas-fir program in British Columbia. In this selection process heritability is important as a method of determining the predictability of response to selection. Heritability is also important in determining the appropriate selection procedures: i) for high heritability traits where the phenotype expresses the genotype - mass selection can be

emphasized, ii) for low to moderate individual tree heritabilities progeny test selection should be emphasized. Two other parts in determining the response to selection are: i) the selection intensity applied and ii) the phenotypic variance (or standard deviation). Thus predicted response to selection will depend upon the degree of the inheritance of the trait, the amount of variability that can be selected upon, and the intensity of selection.

Heritabilities (which express the selection genetic variances over phenotypic variances), coefficients of variation (which express the amount of variation in the population in relation to their means as a percentage), and percentages expected gain per selection intensity unit are summarized for all twenty-one traits in Table 18.

Only two traits, branch angle (*BA*) and wood density (*WD*), demonstrate high individual tree heritability ($h_i^2 \geq 0.50$) values (Table 18). High individual tree heritabilities for branch angle and wood density have also been reported in other Douglas-fir studies. Phenotypic selections, therefore, can be effective for improving these traits in Douglas-fir.

Traits that demonstrate moderate genetic control ($h_i^2 \geq 0.15$; $h_t^2 \geq 0.7$) are: early height (*HT06*), diameters (*DM06*, *DM10*, *DM12*), branch number (*BN*), proportional branch thickness (*BTT*), proportional branch length (*BLT*), and sinuosity (*SIN*). For these traits, gains of 5-10% per unit of selection intensity for family selection and 2-5% per

TABLE 18. Summary of selection parameters for all traits

Trait		Mass selection			Progeny test selection		
Growth							
HT06	height 6th growing season						
HT10	height 10th growing season						
HT12	height 12th growing season						
HTD	growth from 10th to 12th year						
DM06	diameter 6th growing season						
DM10	diameter 10th growing season						
DM12	diameter 12th growing season						
VOLM	volume measurement						
Form							
BN	branch number						
BA	branch angle						
BT	branch thickness						
BTT	branch stem diameter ratio						
BL	branch length						
BLT	branch length total height						
KI	knottiness index						
TAPER	taper measurement						
SIN	stem sinuosity score						
FORM	forking score						
LAFL	lammas score						
Wood Quality							
WD	wood density 5mm cores						
PIN	Pilodyn pin penetration						

unit of selection intensity for mass selection appear achievable (Table 18).

Traits that demonstrate low genetic control ($h_i^2 \leq 0.1$; $h_f^2 \leq 0.5$) are: later height measurements (*HT10*, *HT12*), stem volume (*VOLM*), branch thickness (*BT*), branch length (*BL*), stem taper (*TAPER*), forking (*FORK*), and lammas occurrence (*LAFL*). The low individual tree (h_i^2) and moderate family (h_f^2) heritabilities for these traits indicates that family selection will more effective than mass selection. Gains of up to 5% can be expected for this type of selection. For traits where large amounts of phenotypic variability is available among families, such as volume (*VOLM*), substantial improvement can be made for progeny test selection ($\geq$10% per selection intensity unit) even though individual tree heritabilities are low (Table 18).

4.1.2 Relationships Between Traits

The important parameters between traits are genetic and phenotypic covariances and correlations; correlations among the traits of growth, form, and wood quality are summarized in Table 19. Genetic correlations were classified as negligible r_A<0.15 (0), weak r_A=0.15-0.29 (+, or -), moderate r_A=0.30-0.44 (++, or --), or strong $r_A \geq 0.45$ (+++, or ---). The direction and significance levels of phenotypic relationships are given below the diagonal (Table 19).

The major significant relationships that affect selection for improvement in areas of growth, form, and wood

TABLE 19. Summary of genetic and simple phenotypic correlations.

Traits	HT06	HT12	DM12	VOLM	BN	BA	BT	BTT	BL	BLT	TAPER	SIN	FORK	WD
HT06		***	***	***										
HT12	***		***	***	*	(	(	--	**	---	--	**	-	---
DM12	***	***		***	***	*	*	---	*	*	*	(	(	---
VOLM	***	***	***		***	*	*	---	*	-	*			--
BN		*	(	*		*	*	---	*	(	***			
BA		---	---	---	***		(	-	(	(	(			--
BT		***	***	***	(	---		**	**	(	***			
BTT		---	---	---	--	(	***		(	(	*			*
BL		***	***	***	(	---	***	---		***	(			
BLT		---	--	---	---	---	***	***	***		(			
TAPER		---	*	(	*	---	***	***	(	***				
SIN		***	***											
FORK		-	**											(
WD		---	---	---	(	(	---	***	---	(	(	---	---	

Below diagonal: simple phenotypic correlations

r=0; P>.05

r=*,-; 0.01<P<0.05

r=**,--; 0.001<P<0.01

r=***,---; P<0.001

Above diagonal: genetic correlations

r<0.15 = negligible

r=0.15-0.29 = * = weak

r=0.30-0.44 = ** = moderate

r>0.45 = *** = strong

quality are the strong negative relationship between growth traits and wood quality (wood density) and the weak to moderate, positive relationships between stem biomass and a form complex of profuse, light, and excurrent branches. (fine branching form type).

Other relationships that exist are moderate, positive correlations between height and sinuosity (r_A=0.41) a similar negative relationship was found by Jarret (1978) in French Douglas fir -, moderate negative correlations between height and taper. (r_A= 0.38), weaker but positive correlations between diameter and taper (r_A=0.15), and strong positive genetic correlations between branch number and taper (r_A=0.57), and branch thickness and taper (r_A=0.73).

Genetic relationships between wood density and crown form traits reflect the strong, negative correlation that exists between growth traits and wood density. These include a moderate, negative genetic correlation between branch number and wood density (r_A=-0.32), and between branch angle and wood density (r_A=-0.41); and a weak positive association between wood density and proportional branch thickness (r_A=0.26).

4.1.3 Selection of Traits

Early height growth can be used as an indicator of establishment and early vigour, but also where early selections are necessary it provides good strong positive

correlations with later juvenile height, diameter and volume traits (Table 19, Fig. 6). Selections for yield (stem volume) were most efficiently made by using a diameter measure rather than total height. A multiple trait index using the the genetic covariances of height at age 6, height at age 12, and diameter at age 12 to predict the ranking of progeny families for stem volume; could only marginally improved the ranking (r_s=.99) compared to ranking that occurred using indirect selection for stem diameter (r_s=.89). Height selections were not nearly as good for successful predictions of progeny families for stem volume (r_s=.55). This reflects the stronger genetic correlation between *DM12* and *VOLM*. Velling and Tigerstedt (1982) found that diameter had significant genetic covariances with harvest index (*HI*) - a ratio of stem-wood fresh weight to total tree (branches and stem) fresh weight compared to a non-significant genetic covariance between height and harvest index. Diameter measurements also maintain higher heritabilities (Table 18), therefore selections that are aimed at increasing yield and biomass in Douglas fir should use diameter rather than total height.

The growth related traits of later height measurements, branch thickness, and branch length, showed poor expression of genetic differences - especially on individual sites and at the Lake Cowichan site (CLES). This was demonstrated by a lack of significance for sources of variation for additive genetic variances (σ_a^2), high standard errors for additive

genetic variance, and low individual tree heritabilities especially on the individual site analyses. Insensitivities of the plantation sites, especially large row plots (nine trees) with relatively few replications (three reps) on an undulating site of coarse-textured soils accounted for part of this error. This was manifested by increases of σ^2_{ws}, which is the major part of the error variance for genetic sources of variation (σ^2_g).

Biological reasons can also be cited for this poor discrimination of genetic differences in growth traits. Young seedlings in their first years of growth are affected mainly by microsite influences; the major source of variation is expressed on a tree-to-tree level and inherent growth rate differences can be expressed if there is adequate replication. As trees grow into crown canopy, microsite influences decline and the accumulation of large-scale environmental effects becomes more influential; trees start to grow as a stand and the stand-to-stand level of variation is most strongly expressed. Simmonds (1978) pointed out that the potential biomass of a crop is eventually determined by the sum total of its local environment. Inherent differences in growth rate potential can be limited by this environmental ceiling. As trees enter the second growth phase with the onset of intraspecific competition, the environment becomes more limiting for the expression of inherent differences. Full utilization of inherent growth rate potential will require stand management

techniques such as thinning. Rather than attempt high gains through strong selection pressures for yield, low intensity selection for the culling of poor preformers would be better practiced.

Quality traits that are not a direct reflection of growth, such as branch angle, branch number and wood density; and growth traits when expressed in terms of partitioning of biomass (e.g. branch thickness stem diameter, branch length total height) express genetic differences more strongly (Table 18). These results reflect very closely the observations made on Scots pine by Velling and Tigerstedt (1984). Simmonds (1978) stated in relation to tree breeding that "...the first objective is simply the adapted ecotype which can realize the biomass-potential of the local environment; but in addition, the tree breeder may have some opportunity to exploit the potential of his species for improved partition (between stem and branch) and wood quality (straightness and density).".

Selection of quality and form traits can be effective and should concentrate on the promotion of the pleiotropic action for the formation of a fine-branching tree. Campbell (1963) demonstrated significant positive phenotypic correlations between thick and acute-angled branches and between fewer branch numbers per whorl and thicker branches. These relationships were found to hold for this study, especially in the partial correlations that control for the effect of stem volume. Moderate genetic associations between

branch number and stem diameter, and between branch number, proportional branch thickness and stem diameter, offer a way in which the pleiotropic action of genes might be used to not only improve stem yield but also to promote a finer branching form type over a coarse branching form type. By actively selecting for the finer branching form type, although more branches per whorl would be promoted, there would be concurrent declines in proportional branch thickness (*BTT*) and proportional crown width (*BCT*), and increases in stem diameter ($DM1.3$) and branch angle (*BA*). Some of these relationships were also apparent in Jarret's (1978) study, especially between yield (height) and branch angle (r_A=0.96), and also between branch angle and branch number (r_A=0.52). They were also shown in Scot's pine by Velling and Tigerstedt (1984), who used the same partitioning traits and came to the same conclusions regarding the promotion of the finer branching form type. Kark. (1983) has claimed that these form types in Finnish Scot's pine and Norway spruce might be controlled by single-gene action. This is not at all apparent in Douglas-fir, but the close similarity of the results in this study to those of Velling and Tigerstedt's (1978) and Merrill and Mohn's (1985) in white spruce, suggests that form and yield can be manipulated through the pleiotropic action of additive genes in conifers. Index selection of key form and yield traits can use genetic covariances to encourage the formation of this form type. Using a composite

trait such a knottiness index (a ratio of branch wood cross sectional area to stem wood area) can also improve form, but does not improve the correlation for the fine branching form type.

Selection for stem form traits of sinuosity and forking offers similar results to other studies. High within family variance component percentages for these traits (of >80%) indicates that much of the variation is uncontrollable and phenotypic selections are unlikely to be useful. Sinuosity is under moderate genetic control and should respond well to family selection (see: Jarret 1978; Birot and Christophe 1983; Adams and Howe 1985). A moderate positive genetic correlation beteen height and sinuosity was also shown by Jarret 1978. Thus selections made on the basis of height will promote sinuosity in young plantations. Diameter did not show this positive correlation. Forking and ramicorn branching had low heritabilities. Family differences were non-significant for forking in the French tests (Jarret 1978; Birot and Christophe 1983), and was also reported as having a low heritability in Australian tests of radiata pine (Cotteril and Zed 1980). Although individual tree heritabilities are low for these traits the large phenotypic variances between families and moderate family heritabilities suggest that family selection can be used for improvement for these traits.

Phenotypic selections for wood density should be very effective for both first generation mass selections or

within family selections in progeny tests. The Pilodyn proved to be a very effective way of making selections for wood density in this study. This was indicated not only by a high heritability for this method of estimating wood density but also by a strong genetic correlation between the Pilodyn values and increment core estimations. Relative efficiency for family selection of wood density using the Pilodyn was 91% (Eq. 10). Bastien *et al.* (1985) did not find the Pilodyn to be as effective, but results can vary because of pin size, spring strength (Sprague *et al.* 1983).

Although selections for growth and form can utilize positive genetic associations to benefit both traits, selections of wood density and traits of yield must contend with a strong negative correlation. A strong negative genetic correlation between wood density and yield traits has also been reported in other Douglas fir populations (Bastien *et al.* 1985). Index selection can be most valuable for the genetic improvement of negatively correlated traits (Hazel and Lush 1942). It allows an empirical choice of selection options that can be made based on expected gains of each trait in the index. Choices for the wood density and diameter index *IWD* can be made from four possible selection options:

1. The first option assumes that each trait has an equal economic weight; selections for aggregate breeding value based of this assumption will favour selection for *WD* over *DM12* because of the higher heritability of *WD*. This

assumption of equal economic weight implies that these economic weights are known and are likely to be maintained for the rotation age of Douglas fir.

2. The second option is to maximize the minimum expected gain for the simultaneous improvement of both traits (the curve intersection points). This option is most appropriate when the economic weights to the traits are highly uncertain, unpredictable, and likely to change, but both traits are valuable this is the most realistic scenario for wood density and yield in Douglas fir. This is also the most conservative strategy as no attempt is made to set explicit values. It is also the best strategy to break the negative correlation by selecting genotypes that display breeding values above the average for both traits, thus beginning the process of breaking down this negative correlation.

3. The third option places a restriction on wood density as per Kempthorne and Nordskog (1959). This option seeks to place as much emphasis as possible on yield yet restrict the losses that might occur in wood density. This is less conservative than the second option, yet seeks to maintain wood density at present levels. The assumption here is that wood density has no intrinsic value on its own and is not worth selecting for, yet there is enough uncertainty as to the value if it should decline that we are unwilling to maximize yield response.

4. Option four is based on the idea that a slight loss in

wood density is unlikely to have any serious impact on the resource. Heritability of wood density is the highest of any of the traits reported in this study yet the phenotypic variability is the lowest.

With only the information here and a knowledge that wood density has an intrinsic value (Kellog 1982), the second option is the safest and most conservative strategy to apply. However with the report of Bastien *et al.* (1985) of positive genetic correlations between wood density and wood heterogeneity and the apparent value of wood homogeneity (Zobel *et al.* 1982), large question marks still remain.

4.2 Measurement Strategies in Douglas-fir

One important objective of this study was to establish key indicator traits that can be useful for the assessment of growth, form, and wood quality in juvenile Douglas-fir progeny tests. The criteria for choosing key indicator traits were the effectiveness of selecting for the traits as determined by their selection parameters (h^2, CV, and $\%\Delta G$; Table 18), and for their relationships to other key traits as determined by their correlations (Table 19). In addition, experience derived from this study with respect to the methodology of measuring traits can be used to establish guidelines for the assessment of traits of growth, form, and wood quality in Douglas-fir progeny. Other valuable references that should be consulted are the works of Jarret (1978), DeChamps (1978) and Adams and Howe (1984) in

Douglas-fir; and some of the Finnish work with Scots Pine (e.g. Velling and Tigerstedt 1985).

4.2.1 Growth Traits

Height and diameter are the key traits of growth and yield. Although height alone is not a good trait for predicting stem biomass, it indicates establishment and survival potential especially at the early stages of growth for Douglas fir. Stem biomass is best predicted by a diameter measure. Diameters of juvenile Douglas fir can be taken, adequately and quickly with calipers, at a reference height as established by Kovats (1977). In plantations over 5 to 6 m tall, diameters can be taken from the breast high (1.3 m) stem segment at a mid point average of the stem segment. In plantations, where breast high measurements are not feasible (plantation average < 5 m) diameters can be taken at a stem segment section that is clearly expressed throughout the plantation. In this study diameter measurements were taken at stem segment seven (Fig. 5), and this was usually equivalent to a breast high measurement.

4.2.2 Form Traits

The key traits that should be emphasized for crown form are branch number, branch thickness and branch angle. Branch length need not be measured due to the strong positive correlation with branch thickness. Once a stem segment has been chosen from which to make the diameter measurements,

above and below the stem segment (Fig. 5).

Because branch number is difficult to assess, especially when trying to determine the difference between primary and secondary branching (see also Campbell 1963, Jarret 1978), a subjective measure of branching that totals all branches from the whorl to the first area of clear stem wood below the whorl (5 7cm) should be made. Small secondary branches can be added up to make equivalents of primary branches (e.g., 4×10mm secondary branches = 1×20mm primary branch).

A single measure, for each of the branch thickness and branch angle measures, should be taken at each of the whorls. In this study two randomly chosen branches were measured at each whorl. However, the experience gained from the study suggests that a single, subjectively chosen branch that reflects the average at each whorl is a more efficient measuring technique. Many form characters may best be assessed on a subjective basis, but if they are given a metric measurement based on a subjective judgement (e.g., the branch that most reflects the average at the whorl) rather than a categorical value, it is easier for data manipulation and interpretation.

Form traits can be assessed on a simple scoring method (see **2.3.4**) or through various measuring and scoring methods as reviewed by Jarret (1978), or outlined by Adams and Howe (1985). One can also treat these traits as threshold traits

scoring class 0, 1 & 2 =0; scoring class 3, 4 & 5=1) or use a polychotomous threshold distribution. Besides the advantage of overcoming problems of scale, measuring stem and upper crown traits as threshold traits is easier since only damaging incidences need to be recorded and time wasting evaluations are eliminated.

Determining lammas incidence and damage in older trees, as was done in this study, is a time consuming process. Lammas incidences should be measured in the 6 to 8 year class and not on trees any older than 10 to 12 years.

4.2.3 Wood Quality Traits

Juvenile wood quality assessments may best be made in trees older than those of this study, preferably at 15 years or older (see 1.4.1, Kellogg pers. comm.). The Pilodyn proved to be a very effective instrument for wood density selections. Although some Pilodyn configurations have proven less reliable (Sprague *et al.* 1983, Bastien *et al.* 1985) the one used here with a 2.5 mm pin diameter and a 6 joule spring appeared very useful.

4.2.4 Timing of Measurements

Measurements for the assessment of juvenile growth, form, and wood quality in Douglas-fir can be scheduled as follows:

1. Age 6-8 - height and lammas incidence plus other

measurements of survival and establishment.

2. Age 12-15 - diameter, branch number, branch thickness, branch angle, threshold measurements of stem sinuosity and forking, Pilodyn measurements (Fig. 12).

3. Age 15-20 - after a thinning operation, sub-sampling for wood heterogeneity and more details of partitioning and form types to see if they can be tied into the concept of harvest index.

4.3 Improvement Strategies for Douglas-fir

The progress of tree improvement is through both selection and breeding. This study has emphasized selection; however the two procedures cannot be treated independently, and selection strategies depend on breeding strategies.

Breeding with a high value conifer, such as Douglas-fir, grown in north-temperate latitudes, such as British Columbia, will require breeding strategies that reflect conditions of:

1. long economic rotation times (80 years minimum),
2. natural populations that are already well adapted to the local environment,
3. a large and variable land base that necessitates extensive rather than intensive silvicultural management.

The selection process should be utilized to be most efficient at different levels of selection within the breeding program. Phenotypic selections of high heritability

traits, such as branch angle and wood density, can be emphasized in selections of recombinants within families. Index selection using family information, as in the progeny testing here, will be emphasized when selecting for high levels of GCA.

4.3.1 Breeding Strategy

The breeding design used in this study, the NC II tester design, was ideal for the stated objectives of this study; and selection from this experiment has emphasized progeny test selection using the genetic relationships between a parent and its half sib progeny for the selection of parents. The selection strategies outlined here are thus easily transported to progeny test selection where GCA is estimated from open-pollinated families. However one of the major objectives of most breeding programs is to produce a population for the next generation of selection. A first generation progeny test selection scheme as outlined in this study does not achieve this objective, and recombinants of the select trees have yet to be produced for further breeding.

In fast growing species, parents can be tested, many recombinants can be generated through single-pair matings of proven parents, high selection intensities can be practised on these recombinants, and even the selected recombinants can be O.P. progeny tested (Cotterill 1984). This can be done very effectively in the short rotation of radiata pine

in Australia, for instance, where decisions on progeny tests can be made between 4, to [illegible] years (Cotterill 1984). Fast generation breeding options are less attractive to Douglas-fir improvement. There is no all around "best option" for breeding of Douglas-fir, and it as often as not depends upon the resources and commitment made by the agencies involved. Because breeding options are reduced in north temperate conifers it is most important that efficiencies in the selection process be maximized. Examples of how these efficiencies can be made for two of the most common breeding plans for Douglas-fir are given here:

1. The first generation of breeding in Douglas fir often combines the objective of testing the first generation of selection together with producing second generation material (as has been done in B.C. with a half-diallel program); second generation selections can be made, but a loss is made in the potential selection intensities that can be applied to second generation stock - the recombinants - for the cost of testing poor first generation material. Planting designs for this breeding plan must be both efficient for testing and ranking families but also for emphasizing genetic differences among individuals within families, selection in family plots will be important. Selections of this recombinant material is also reliant on the phenotype to express the genotype. The low individual-tree heritabilities for many of the traits has emphasized that genotypic

selections are more important in tree improvement of Douglas-fir than phenotypic selections. The most efficient selection strategy for a single trait or index will involve the use of a combined index that uses family and individual information to make second generation selections. Cotterill (1986) found this breeding selection strategy to be the most efficient per generation/decade of ten strategies investigated for traits of low to moderate (.05-.40) heritabilities. A multi stage family within family can be used effectively when high heritability traits are used in the second stage. An example of this multi stage selection can: 1) emphasize diameter (yield) and fine branching (*BN* and *BI*) in a low intensity family selection and 2) emphasize branch angle (*BA*) (for its correlation with fine-branching) and/or wood density (*WD*) in a within-family selection. The major difficulty with the half-diallel are the limitations on the parents that can be effectively handled, and the manpower and effort that is needed to make all the appropriate crosses.

2. A cheaper and efficient first step to screen parents for GCA are open-pollinated progeny tests. Planting design here should be efficient for family selection only, therefore should seek to minimize the error variances with corrrect blocking, and many replications of small or contiguous plots. Where parents have been cloned recurrent selection can use the methods and traits

established in the progeny test selection schemes developed in this study. Recombinants from selected parents can most effectively be regenerated from single pair matings. As selections from the next generation will rely only on within family selections; traits should be chosen that exhibit moderate to high individual tree heritabilities, and planting design should emphasize efficiencies gained by high selection intensities in large family plots. Because this will be an inefficient selection process, it may be wise to terminate this test after selection for early height growth (=*HT06*) and/or a trait such as branch angle (*BA*) and/or lammas incidence (*LAFL*) (if this trait is to be considered selection should be at this stage). This selection process is inefficient also for the use of generations but by using the appropriate selection strategies, (i.e. choosing the most effective traits) and by physically lifting the selected material for second generation breeding not that much time needs to be lost.

4.3.2 Planting Design

Inefficiencies of the experimental layout used in this study have been demonstrated by the lack of precision and inability to detect significant differences for growth traits on the individual sites. Three basic principles are used to control or minimize experimental error, these are:

replication, randomization, and local control or blocking. Although local control can be a problem on forest sites it was less of a problem as demonstrated by the error variances (σ^2_{emf}) than lack of replication and randomization that was caused by too large a plot on too few replications. The statistical efficiency of the test would increase if there was a reduction in the within plot error variance (σ^2). This is especially noticable at CLES where the plots are row plots that run up and down a rise on a coarse textured and freely draining soil. The efficiency of allocating trees to reps and plots can be derived (Yeh and Rasmussen 1985) but it depends on what level of selection is being applied.

In the progeny test function, as used in this study, efficiency is maximized by planting seedlings in many replications of small or contiguous plots. This would not be the case however if individuals within families were to be the selection unit. In this case family plots are desirable for efficient discrimination of individuals within families. A planting design that has more reps and fewer trees per plot would be more efficient however. Correct blocking of the experiment to control for environmental heterogeneity is also desirable, especially where relatively few reps are used as in this study. An effort to reduce the environmental variance within plots by having them run with the environmental gradient, rather than across, is especially necessary if within family selection is being practised.

4.3.3 Genotype by Environment Interaction and Adaptation

Sources of variation for additive genetic variance by environment interaction were non significant for all of the traits investigated in this study. Although limited by only two sites that were not extremely different, there is strong evidence that Douglas fir is relatively robust in its genotypic stability for these 21 traits of growth, form, and wood quality. For ranking and selection purposes it may only be necessary to test families across 2 to 4 sites. Further plantations on more extreme environments could be established to provide information specifically about genotype by environment interactions.

One of the current controversies in tree improvement work in Douglas-fir is that tight adaptation to narrow ecological zones has been demonstrated in seedling studies (Campbell and Sorenson 1978; Campbell 1979), and indeed one of the criticisms of the B.C. program has been that seed zones are too widely defined (Yeh *et al.* 1981). However there is little evidence from this study, from the recent provenance research in the Pacific Northwest (White and Ching 1985), and in B.C. (Ying pers. comm.) that this tight adaptation carries much beyond the seedling stage. Usually seed sources that do particularly poorly - are ill adapted - are planted on off-site locations (e.g. the southern Oregon source, White and Ching 1985; or low elevation sources planted on high elevation sites, Ying 1984).

Thus splitting the breeding region of Douglas fir from low to mid elevation sites of coastal B.C., into multiple breeding units to exploit adaptational differences for increased gain (Namkoong 1984), does not appear warranted. Although it may be considered as an option for channeling selection opportunities for traits (high W_i populations) and for gene conservation (Namkoong 1984).

4.4 Summary and Future Considerations

This study has emphasized the selection process in the improvement of the Douglas fir resource for traits of growth, form and wood quality. It has highlighted key traits, and key associations; that may be effectively measured and selected for:

1. early height can be a useful trait for early establishment and vigour as well as for its use for early selections for growth and yield traits,
2. diameter is the best indicator for yield and biomass,
3. partitioning traits are better indicators of crown quality traits and can be more effectively selected for,
4. genetic covariances among crown form traits can be utilized for selection for a fine-branching form type,
5. selection against sinuosity should be effective and selection for diameter is less likely to promote sinuosity than selections for height growth,
6. selections against forking and lammas growth will be less effective than those against sinuosity,

7. selections of wood density by either increment cores or the Pilodyn will be very effective,
8. there are strong negative correlations between wood density and growth traits and negative correlations between wood density and form,
9. these results are corroborative of similar results in Douglas fir from France (Jaret 1978, Birot and Christophe 1983), Scot's pine in Finland (Veiling and Tigerstadt 1982), white spruce in the Lake States (Merrill and Mohn 1985), and radiata pine in Australia (Dean *et al.* 1983).

The study has also high lighted key multiple trait strategies and options:

1. selections for growth traits should use family information and not be aimed at achieving high selection intensities and gains but rather the culling of poor genotypes and promotion of good vigourous growers,
2. multiple trait selection for a complex of light, flat branches, and high yield trees should be encouraged in family, combined, and even individual selection using the high heritability of branch angle.
3. several options were investigated for how to handle the negative correlation between growth and wood density; if wood density has an intrinsic value, and it is not adversely-correlated with wood heterogeneity (Bastien *et al.* 1985) then selections that maximize the minimum expected response to selection for both traits would

appear to be the best strategy (maximin option two Fig. 12). This would also go some of the way to breaking down this unfavourable correlation. The next best option under these circumstances is to constrain the loss of WP option three (Fig. 12).

4. options for incorporating these selection strategies into current breeding strategies were briefly investigated.

4.4.1 Future Considerations

This study has addressed topics related to the selection of traits of growth, form, and wood quality in Douglas fir and continues the excellent work in this subject done by Campbell and Jarret. There are many important areas of future research that should be done to extend this knowledge.

Although this study could not identify significant site * genotype interactions it is hoped another study directed at investigating the genetic stability over a more extreme range of sites will more adequately investigate questions related to this.

The experimental material used here should be maintained in order that the expression of the variances and covariances observed here can be tracked over time and clear ideas can be established as to valid ages at which these traits might be evaluated. Early progeny evaluations are essential to the effectiveness of tree-improvement

strategies for Douglas fir.

Detailed wood quality assessments need to be carried out to see if the negative correlations between mean wood density and wood heterogeneity established in France are true of most populations of Douglas fir. This information is necessary before wood density is actively incorporated as a valuable trait in the selection process and can be found when this progeny test is thinned. Traits relating to harvest index (*HI*, Velling and Tigerstedt 1982) and the detailed relationships among crown form traits may also be more fully investigated at this time.

Research will soon be needed to investigate questions related to advanced generation breeding and selection, for example the effects of mild inbreeding, subdining, and gene conservation. An active research program is necessary if we are to maintain Douglas-fir as a valued resource.

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APPENDIX A: Selection intensity expressed in standard deviations for a population of 22 parent trees

No. Selected	Percentage	Value
1	4.55	1.91
2	9.1	1.69
3	13.6	1.52
4	18.2	1.39
5	22.7	1.27
6	27.3	1.17
7	31.8	1.08
8	36.4	1.00
9	40.9	0.92
10	45.5	0.84
11	50.0	0.77

APPENDIX B: Formulae for estimation of genetic and phenotypic parameters and standard errors.

Term

s = number of sites

r = number of replications within sites

m = number of male pollen trees

f = number of female seed trees

t = number of trees within plots

Variance components

σ^2_e = variance among trees within plots

σ^2_{rsf} = variance among full-sib family plots within sites

σ^2_{smf} = variance among site-male-female combinations

σ^2_{mf} = variance among male-female combinations

σ^2_{rf} = variance among rep-female combinations within sites

σ^2_{rm} = variance among rep-male combinations within sites

σ^2_{sf} = variance among site-female combinations

σ^2_{sm} = variance among site-male combinations

σ^2_f = variance among female half-sib families

σ^2_m = variance among male half-sib families

σ^2_r = variance among replications within sites

σ^2_s = variance among sites

k_i = coefficient of the "i"th variance component

APPENDIX B. (Continued)

I. VARIANCE COMPONENTS (based on Table 3)

$$\sigma^2_{m} = (MS_{1} - k_{16}\sigma^2_{sm} - k_{20}\sigma^2_{tm} - k_{24}\sigma^2_{mf} - k_{29}\sigma^2_{smf} - k_{31}\sigma^2_{tmf} - \sigma^2_{w}) / k_{32}$$

$$\sigma^2_{t} = (MS_{2} - k_{17}\sigma^2_{st} - k_{20}\sigma^2_{tm} - k_{25}\sigma^2_{tf} - k_{29}\sigma^2_{smf} - k_{31}\sigma^2_{tmf} - \sigma^2_{w}) / k_{33}$$

$$\sigma^2_{sm} = (MS_{3} - k_{16}\sigma^2_{sm} - k_{29}\sigma^2_{smf} - k_{31}\sigma^2_{tmf} - \sigma^2_{w}) / k_{34}$$

$$\sigma^2_{st} = (MS_{4} - k_{17}\sigma^2_{st} - k_{29}\sigma^2_{smf} - k_{31}\sigma^2_{tmf} - \sigma^2_{w}) / k_{35}$$

$$\sigma^2_{mf} = (MS_{5} - k_{29}\sigma^2_{smf} - k_{31}\sigma^2_{tmf} - \sigma^2_{w}) / k_{36}$$

$$\sigma^2_{tm} = (MS_{6} - k_{31}\sigma^2_{tmf} - \sigma^2_{w}) / k_{37}$$

$$\sigma^2_{tf} = (MS_{7} - k_{31}\sigma^2_{tmf} - \sigma^2_{w}) / k_{38}$$

$$\sigma^2_{smf} = (MS_{8} - k_{30}\sigma^2_{tmf} - \sigma^2_{w}) / k_{39}$$

$$\sigma^2_{tmf} = (MS_{9} - \sigma^2_{w}) / k_{40}$$

$$\sigma^2_{w} = MS_{10}$$

APPENDIX B. (Continued)

II. GENETIC PHENOTYPIC PARAMETERS

σ_A^2 additive genetic variance = $4\sigma_t^2$

σ_I^2 dominance genetic variance = $4\sigma_{mt}^2$

$\sigma_{P_1}^2$ phenotypic variance among individuals

$$\sigma_m^2 + \sigma_t^2 + \sigma_{mt}^2 + \sigma_{sm}^2 + \sigma_{st}^2 + \sigma_{rm}^2 + \sigma_{rt}^2 + \sigma_{smt}^2 + \sigma_{rmt}^2 + \sigma_e^2$$

σ_{PHS}^2 = phenotypic variance among half-sib means

$$= \sigma_t^2 + \frac{k_{23}}{k_{12}}\sigma_{mt}^2 + \frac{k_{20}}{k_{12}}\sigma_{st}^2 + \frac{k_{22}}{k_{12}}\sigma_{rt}^2 + \frac{k_{29}}{k_{12}}\sigma_{smt}^2 + \frac{k_{26}}{k_{12}}\sigma_{rmt}^2 + \frac{1}{k_{12}}\sigma_e^2$$

h_t^2 = individual tree heritability = $\dfrac{\sigma_A^2}{\sigma_{P_1}^2}$

h_t^2 = half-sib family heritability = $\dfrac{\frac{1}{4}\sigma_A^2}{\sigma_{PHS}^2}$

APPENDIX B. (continued)

II. GENETIC / PHENOTYPIC PARAMETERS (continued)

$COV_A(X,Y)$ = additive genetic covariance between X and Y

$= 4\ COV_{(f,PHS)}$

$COV_{(f,PHS)}$ = covariance of the breeding value of a seed parent and its half-sib family mean phenotypic value

$= \frac{1}{2}\sigma^2_A$

or for different characters (X,Y)

$= \frac{1}{2}COV_A$

$COV_P(X,Y)$ = phenotypic covariance between X and Y (calculated as per either σ^2_{Pi} or σ^2_{PHS})

r_A = additive genetic correlation of X and Y

$= COV_A(X,Y) \div [\sigma_A(X) \times \sigma_A(Y)]$

r_P = phenotypic correlation of X and Y (Pi or PHS)

$= COV_P(X,Y) \div [\sigma_P(X) \times \sigma_P(Y)]$

r_E = environmental correlation

$= [r_P - h_X h_Y r_A] \div [(1-h_X)(1-h_Y)]$

APPENDIX B. (continued)

II. GENETIC / PHENOTYPIC PARAMETERS (continued)

CR_Y = correlated response of character Y is

= $i h_X h_Y r_A \sigma_P(Y)$

III. STANDARD ERRORS OF COMPONENTS/PARAMETERS

$S(\sigma_i^2)$ = the standard error of the i^{th} component

$$= \frac{2}{k_i^2} \sum_j \frac{MS_j^2}{f_j + 2}$$

where k_i is the coefficient of the variance component being estimated, MS_j is the j^{th} mean square used to estimate the variance component and f_j are the degrees of freedom of the j^{th} mean square.

$S(\sigma_A^2)$ = $4 \times S(\sigma_f^2)$

APPENDIX B. (CONTINUED)

III. STANDARD ERRORS OF COMPONENTS PARAMETERS (continued)

$$S(h_i^2) \qquad \frac{S(\sigma_i^2)}{\sigma_{P_i}^2}$$

$$S(h_i^2) \qquad \frac{S(\sigma_i^2)}{\sigma_{P_{XY}}^2}$$

$$S(r_A) \qquad = \qquad \frac{1 - r_A^2}{\sqrt{2}} \sqrt{\left[\frac{S(h_X^2)\ S(h_Y^2)}{h_X^2\ h_Y^2} \right]}$$

The formulae for standard errors of variance components and approximations of standard errors of heritabilities and genetic correlations are from Becker (1975).

APPENDIX B. (continued)

IV. FORM OF MATRIX FOR MULTIPLE TRAIT PROGENY TEST SELECTION

i. variance covariance matrix of phenotypic values P

$$\begin{matrix} \sigma^2_{PHS}X & COV_{PHS}(X,Y) \\ COV_{PHS}(X,Y) & \sigma^2_{PHS}Y \end{matrix}$$

ii. additive genetic variance/covariance matrix G

$$\begin{matrix} \tfrac{1}{2}\sigma^2_A X & \tfrac{1}{2}COV_A(X,Y) \\ \tfrac{1}{2}COV_A(X,Y) & \tfrac{1}{2}\sigma^2_A Y \end{matrix}$$

iii. b values are:

$$\mathbf{P}^{-1}\mathbf{G}\mathbf{a},$$

where **a** is a vector of economic weights

APPENDIX C: Tables of means and analyses of variance and covariance for growth and yield traits.

TABLE C1 Means and coefficients of variation for height at 6 years (HT06) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

GROUP	CLES N	CLES MEAN cm	CLES CV %	GVWS N	GVWS MEAN cm	GVWS CV %	COMBINED N	COMBINED MEAN cm	COMBINED CV %
SEED PARENTS									
415	104	98 55	24 36	92	85 79	28 28	196	92 56	26 [illegible]
300	104	109 67	25 71	91	80 89	34 66	195	96 24	32 [illegible]
49	106	106 10	31 57	92	87 41	30 [illegible]	198	97 41	32 57
72	106	107 21	24 57	91	93 08	27 8[illegible]	197	100 68	26 82
60	105	111 34	25 72	101	96 74	31 00	206	104 18	28 33
422	106	112 64	25 44	102	95 76	32 93	208	104 37	29 31
110	104	110 36	23 27	97	98 66	27 15	201	104 72	25 59
323	106	112 16	25 32	93	98 17	30 52	199	105 62	28 [illegible]
305	100	108 70	27 77	90	103 84	30 [illegible]	190	106 40	28 89
73	106	113 10	26 55	90	98 67	31 [illegible]	196	106 48	29 48
315	107	118 18	22 72	92	95 14	30 27	199	107 53	27 [illegible]
57	106	117 03	24 43	95	97 97	35 [illegible]	201	108 02	[illegible] 38
310	107	114 07	26 52	90	101 25	30 21	197	108 22	28 [illegible]
193	105	116 19	25 16	100	100 50	26 39	205	108 00	25 10
303	103	111 38	24 46	99	109 42	33 [illegible]	202	110 42	28 [illegible]
418	103	120 93	24 18	96	102 08	32 [illegible]	199	111 81	28 [illegible]
549	106	118 59	25 81	92	105 43	30 [illegible]	198	112 48	28 [illegible]
408	107	118 51	24 20	94	106 66	33 [illegible]	201	112 97	28 84
314	105	116 54	21 44	100	109 81	26 [illegible]	205	113 26	23 [illegible]
499	103	112 60	23 18	103	116 21	29 [illegible]	206	114 40	25 35
439	104	120 12	23 11	100	110 93	29 [illegible]	204	115 61	25 55
623	107	123 65	25 17	96	111 69	27 [illegible]	203	118 00	25 [illegible]
POLLEN PARENTS									
24	571	111 23	26 57	516	95 72	32 56	1087	103 88	31 12
62	579	111 15	24 05	534	98 10	31 [illegible]	1113	104 89	28 29
33	582	113 62	26 43	525	103 27	30 [illegible]	[illegible]	[illegible]	28 [illegible]
448	575	118 24	24 18	521	105 36	30 [illegible]	1096	112 11	27 93
TOTAL	2310	113 56	25 43	2096	100 61	31 [illegible]	[illegible]	[illegible]	28 [illegible]

TABLE C2 Combined sites analysis of variance for height at 6 years (HT06)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	184185 88	72 491	68 755		[illegible]		
REP/SITE	4	25485 47	32 197	20 069		[illegible]		
MALE	4	15543 07	13 287	8 983		[illegible]		
FEMALE	3	8416 44	31 202	13 225	5 201	[illegible]	3 873	[illegible]
S * F	21	2343 44	1 997	1 000		[illegible]	1 085	[illegible]
R * F	84	1900 72	0 0	10 075		[illegible]	1 [illegible]	[illegible]
M * F	63	1988 33	0 0	10 83[illegible]		[illegible]	[illegible]	[illegible]
S*M*F	63	2158 89	9 662	16 68[illegible]		[illegible]	1 [illegible]	[illegible]
R/S*M*F	252	1900 47	144 956	20 5[illegible]	11 21[illegible]	[illegible]	2 [illegible]	
WITHIN	3878	703 65	703 656	15 976	24 693	69 [illegible]		
ADDITIVE GENETIC VARIANCE			124 809	52 90[illegible]	10 402			
DOMINANCE GENETIC VARIANCE			0 0	43 324	0 0			
TOTAL PHENOTYPIC VARIANCE			904 760		28 007			
PHENOTYPIC VARIANCE HALF SIB			42 887		6 098			
PHENOTYPIC VARIANCE FULL SIB			87 271					
HERITABILITY (INDIVIDUAL)			0 138	0 058		RESPONSE [illegible]	3 864	
HERITABILITY (HALF SIB)			0 728	0 308		RESPONSE [illegible]	8 877	
HERITABILITY (FULL SIB)			0 715	0 303				

TABLE C2 (Continued) Analysis of variance for trait HT06 on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	18712 00	22 279	17 255		2 58%		
MALE	3	6474 73	7 041	7 379		0 82%		
FEMALE	42	3418 01	19 628	10 647	3 901	2 27%	2 513	0 036
R * M	6	2202 48	2 114	5 840		0 25%	1 232	0 294
R * F	42	1151 33	0 0	9 512		0 0%	0 644	0 943
M * F	63	1998 23	7 832	15 876		0 91%	1 118	0 236
R*M*F	126	1787 98	127 360	25 726	9 938	14 75%	2 643	0
WITHIN	2046	676 58	676 584	21 143	22 906	78 41%		
ADDITIVE GENETIC VARIANCE			7[illegible] 512	42 590	7 803			
DOMINANCE GENETIC VARIANCE			31 327	63 505	4 929			
TOTAL PHENOTYPIC VARIANCE			840 558		25 531			
PHENOTYPIC VARIANCE HALF-SIB			38 616		5 472			
PHENOTYPIC VARIANCE FULL-SIB			102 698					
HERITABILITY (INDIVIDUAL)			0 093	0 051		%RESPONSE		2 385
HERITABILITY (HALF-SIB)			0 508	0 276		%RESPONSE		5 563
HERITABILITY (FULL-SIB)			0 336	0 207				

TABLE C2 (Continued) Analysis of variance for trait HT06 on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	32891 90	43 992	33 320		4 28		
MALE	3	10442 10	16 810	12 723		1 63		
FEMALE	21	7246 48	46 997	23 719	6 814	4 57	2 599	
R * M	6	1538 18	0 0	4 634		0 0	1 764	
R * F	42	2663 59	19 401	19 667		1 89	1 329	
M * F	63	4137 94	4 151	19 116		0 40	1 062	
R*M*F	126	2012 97	163 323	32 218	12 702	15 88	2 743	
WITHIN	1832	733 89	733 890	24 135	26 926	71 25		
ADDITIVE GENETIC VARIANCE			187 987	94 851	13 628			
DOMINANCE GENETIC VARIANCE			16 605	76 465	4 050			
TOTAL PHENOTYPIC VARIANCE			984 572		31 188			
PHENOTYPIC VARIANCE HALF SIB			75 632		8 644			
PHENOTYPIC VARIANCE FULL SIB			153 042					
HERITABILITY (INDIVIDUAL)			0 191	0 096		RESPONSE	5 955	
HERITABILITY (HALF SIB)			0 621	0 314		RESPONSE	11 742	
HERITABILITY (FULL SIB)			0 444	0 31				

TABLE C3 Means and coefficients of variation for height at 10 years (HT10) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	%
SEED PARENTS									
415	103	393 11	15 49	90	285 03	27 84	193	342 71	25 79
72	105	388 30	19 97	84	292 41	25 10	189	345 68	25 85
306	106	410 35	18 71	89	290 00	31 25	195	355 42	28 87
305	103	400 52	21 44	95	318 05	29 02	198	360 95	27 13
422	105	415 96	17 58	101	306 30	26 91	206	362 19	26 27
310	107	398 25	17 76	88	324 95	24 38	195	365 17	22 72
49	102	417 53	19 62	90	308 02	26 12	192	366 20	26 71
323	106	413 00	17 48	93	315 52	28 52	199	367 45	25 68
303	105	396 46	19 33	87	341 88	28 09	192	371 73	24 20
60	106	415 57	15 16	96	325 17	25 85	202	372 61	23 18
73	106	423 66	19 02	94	317 91	34 02	200	373 96	28 91
193	108	416 22	18 60	95	326 21	27 50	203	374 10	25 29
57	107	423 64	15 96	95	327 16	26 05	202	378 26	23 85
315	107	429 17	14 50	89	329 63	23 85	196	379 89	23 01
110	104	423 77	15 29	89	332 33	26 78	193	381 60	23 39
418	104	431 00	16 40	91	328 76	27 48	195	383 29	24 83
549	107	426 42	17 63	94	338 33	28 10	201	385 22	24 81
439	107	423 08	19 45	90	340 61	22 24	197	385 41	23 16
499	108	409 57	19 78	98	363 00	25 68	206	387 42	23 22
408	106	440 26	15 06	94	338 44	29 72	200	392 40	25 03
623	106	439 44	18 41	98	347 77	27 10	204	395 40	24 96
314	106	430 07	15 99	94	358 98	22 68	200	396 66	20 88
POLLEN PARENTS									
62	586	411 09	16 85	511	308 86	27 63	1097	363 47	25 17
33	580	409 81	18 97	507	328 73	26 75	1087	371 99	24 33
28	582	417 57	19 08	494	318 90	28 28	1076	372 27	26 39
448	576	428 32	16 54	522	343 72	26 81	1098	388 [illegible]	23 [illegible]
TOTAL	2324	416 66	17 96	2034	325 20	27 65	4358	373 9[illegible]	26 [illegible]

TABLE C4 Combined sites analysis of variance for height at 10 years (HT10)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	9073866 00	4095 354	3415 600		36 17%		
REP/SITE	4	192391 88	232 665	153 433		2 05%		
MALE	4	125997 56	102 458	75 337		0 90%		
FEMALE	3	44047 42	209 854	74 268	3 874	1 85%	2 815	[illegible] **
S * F	21	15666 64	0 0	1 000		0 0 %	0 655	0 851
R * F	84	17965 60	60 213	93 420		0 53%	1 138	0 221
M * F	63	8738 00	0 0	87 760		0 0 %	0 412	1 000
S*M*F	63	21738 80	238 032	165 679		2 10%	1 077	0 315
R/S*M*F	252	15788 31	1315 176	171 973	9 697	11 62%	3 134	0 [illegible]
WITHIN	3830	5038 02	5038 023	115 096	18 980	44 50%		
ADDITIVE GENETIC VARIANCE			839 416	297 072	7 747			
DOMINANCE GENETIC VARIANCE			0 0	351 041	0 0			
TOTAL PHENOTYPIC VARIANCE			6993 934		22 363			
PHENOTYPIC VARIANCE HALF-SIB			329 054		4 851			
PHENOTYPIC VARIANCE FULL SIB			749 286					
HERITABILITY (INDIVIDUAL)			0 120	0 042		%RESPONSE	2 684	
HERITABILITY (HALF-SIB)			0 638	0 226		%RESPONSE	6 181	
HERITABILITY (FULL SIB)			0 560	0 198				

** MS S*F USED AS ERROR MS

TABLE C4 (Continued) Analysis of variance for trait HT10 on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	271974 00	330 285	248 523		5 76%		
MALE	3	40742 10	39 415	46 790		0 69%		
FEMALE	21	21968 30	74 318	72 034	2 069	1 30%	1 554	0 119
R * M	6	16274 10	18 432	42 814		0 32%	1 286	0 268
R * F	42	12545 30	0 0	88 379		0 0%	0 994	0 497
M * F	63	11215 80	59 264	112 219		1 03%	1 126	0 285
R*M*F	126	12654 50	956 513	180 709	7 423	16 69%	2 375	0 0
WITHIN	2060	4252 65	4252 648	132 443	15 651	74 21%		
ADDITIVE GENETIC VARIANCE			297 271	288 135	4 138			
DOMINANCE GENETIC VARIANCE			237 055	448 876	3 695			
TOTAL PHENOTYPIC VARIANCE			5400 582		17 637			
PHENOTYPIC VARIANCE HALF SIB			208 935		3 469			
PHENOTYPIC VARIANCE FULL SIB			652 690					
HERITABILITY (INDIVIDUAL)			0 055	0 053		%RESPONSE 1 =	0 97%	
HERITABILITY (HALF SIB)			0 356	0 345		%RESPONSE 1 =	2 468	
HERITABILITY (FULL SIB)			0 265	0 221				

TABLE C4 (Continued) Analysis of variance for trait HT10 on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	11129.2 69	121 775	117 682		1 46%		
MALE	3	112054 19	177 298	141 687		2 13%		
FEMALE	21	37990 39	188 939	138 584	4 227	2 27%	1 823	0 088 **
R * M	6	24749 39	31 509	74 455		0 38%	1 308	0 258
R * F	42	23289 47	128 389	179 099		1 54%	1 231	0 [illegible]
M * F	63	16468 54	0 0	162 188		0 0 %	0 870	0 728
R*M*F	126	18922 09	1713 247	313 567	12 728	20 61%	3 179	0 0
WITHIN	1770	5952 07	5952 074	199 964	23 724	71 60%		
ADDITIVE GENETIC VARIANCE			755 756	554 336	8 454			
DOMINANCE GENETIC VARIANCE			0 0	648 750	0 0			
TOTAL PHENOTYPIC VARIANCE			8191 449		27 831			
PHENOTYPIC VARIANCE HALF-SIB			436 290		6 423			
PHENOTYPIC VARIANCE FULL-SIB			1187 013					
HERITABILITY (INDIVIDUAL)			0 092	0 068		%RESPONSE 1 =	2 568	
HERITABILITY (HALF-SIB)			0 433	0 318		%RESPONSE 1 =	5 563	
HERITABILITY (FULL-SIB)			0 309	0 234				

** significant (P< 05) using M*F as error mean square

TABLE C5. Means and coefficients of variation for height at 12 years (HT12) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
72	102	612 11	14 39	77	457 27	20 13	179	545 50	21 64
415	101	618 76	12 57	87	469 23	21 13	188	549 56	21 02
422	104	641 39	13 04	94	485 00	19 66	198	567 15	20 92
300	106	645 33	14 75	83	481 45	21 66	189	573 36	22 37
305	100	632 25	15 54	89	514 21	21 08	189	576 67	20 57
49	101	653 42	14 26	84	487 98	18 54	185	578 30	21 34
303	105	616 30	15 03	85	531 65	21 96	190	578 43	19 38
323	106	639 44	15 24	88	505 97	22 72	194	578 90	21 55
310	106	629 58	13 06	78	510 59	19 27	184	579 14	18 46
418	104	646 25	12 63	87	502 47	21 36	191	580 76	20 36
193	106	617 31	14 16	87	502 89	21 92	193	582 21	21 20
60	105	654 67	11 74	93	507 67	20 34	198	585 62	19 85
57	107	646 22	12 26	91	518 13	20 19	198	587 35	19 01
73	105	653 90	14 44	89	510 06	23 18	194	587 91	21 74
439	102	653 97	13 28	90	523 17	19 93	192	592 66	19 48
110	103	659 61	13 11	83	523 07	22 03	186	598 68	20 21
315	104	665 05	10 45	83	519 10	16 27	187	600 27	17 56
499	105	641 46	14 25	90	568 00	18 07	195	607 55	17 00
549	107	665 37	14 36	88	541 76	21 13	195	609 59	19 87
408	107	671 78	12 03	90	538 11	21 47	197	610 71	19 41
623	105	674 67	13 07	91	540 05	21 61	196	612 17	19 98
314	105	676 62	12 49	89	553 93	18 94	194	620 34	18 11
POLLEN PARENTS									
62	581	644 99	12 74	487	492 67	20 94	1068	575 53	20 76
33	572	634 08	14 31	485	514 22	19 99	1057	579 09	19 59
28	573	647 73	14 37	460	507 19	21 73	1033	585 15	20 99
448	570	663 86	13 01	484	540 75	20 91	1054	607 32	19 25
TOTAL	2296	647 64	13 70	1916	513 76	21 16	4212	586 74	20 25

TABLE C6 Combined sites analysis of variance for height at 12 years (HT12)

SOURCE	D.F.	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	18720896.00	8854 547	7317 902		46 12%		
REP/SITE	4	210609 19	254 449	174 152		1 33%		
MALE	4	221620 75	170 230	138 439		0 89%		
FEMALE	3	72244 75	352 992	123 748	3 202	1 84%	3 215	0 005 **
S * F	21	22511 28	0 0	1 000		0 0 %	0 619	0 883
R * F	84	24964 95	52 919	135 578		0 28%	1 094	0 295
M * F	63	16870 17	0 0	146 173		0 0 %	0 493	0 997
S*M*F	63	34200 03	471 478	268 835		2 46%	1 499	0 016
R/S*M*F	252	22813 15	2021 027	258 700	7 662	10 53%	3 284	0 0
WITHIN	3684	6947 80	6947 801	161 839	14 206	36 19%		
ADDITIVE GENETIC VARIANCE			1411 969	494 994	6 404			
DOMINANCE GENETIC VARIANCE			0 0	584 691	0 0			
TOTAL PHENOTYPIC VARIANCE			10090 922		17 121			
PHENOTYPIC VARIANCE HALF-SIB			538 967		3 957			
PHENOTYPIC VARIANCE FULL SIB			1232 482					
HERITABILITY (INDIVIDUAL)			0 140	0 049		%RESPONSE 1 =	2 396	
HERITABILITY (HALF-SIB)			0 655	0 230		%RESPONSE 1 =	5 183	
HERITABILITY (FULL-SIB)			0 573	0 201				

** MS S*F USED AS ERROR MS

TABLE C6 (Continued) Analysis of variance for trait HT12 on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	366609 38	441 977	339 464		5 42%		
MALE	3	85079 19	83 730	98 126		1 03%		
FEMALE	21	33931 42	120 651	111 963	1 696	1 48%	1 583	0 139
R * M	6	31765 90	64 217	84 009		0 79%	1 641	0 141
R * F	42	16094 37	0 0	120 880		0 0 %	0 832	0 750
M * F	63	24689 40	200 173	190 360		2 45%	1 276	0 125
R*M*F	126	19354 04	1581 060	280 203	6 140	19 38%	3 416	0 0
WITHIN	2032	5666 47	5666 477	177 685	11 623	69 46%		

ADDITIVE GENETIC VARIANCE	482 604	447 851	3 392	
DOMINANCE GENETIC VARIANCE	800 692	761 442	4 369	
TOTAL PHENOTYPIC VARIANCE	7716 297		13 563	
PHENOTYPIC VARIANCE HALF-SIB	356 117		2 914	
PHENOTYPIC VARIANCE FULL-SIB	1146 761			
HERITABILITY (INDIVIDUAL)	0 063	0 058		%RESPONSE : 0 818
HERITABILITY (HALF-SIB)	0 339	0 314		%RESPONSE : 1 974
HERITABILITY (FULL-SIB)	0 353	0 195		

TABLE C6 (Continued) Analysis of variance for trait HT12 on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	60883 24	42 349	71 436		0 35%		
MALE	3	195062 56	350 016	259 501		2 93%		
FEMALE	21	60384 63	312 668	229 786	3 442	2 61%	1 784	0 081 **
R * M	6	27745 58	1 964	89 480		0 02%	1 056	0 393
R * F	42	33236 13	207 013	270 539		1 73%	1 265	0 161
M * F	63	26888 16	0 0	265 370		0 0 %	1 023	0 448
R*M*F	126	26272 25	2519 994	468 178	9 771	21 07%	3 082	0 0
WITHIN	1652	8523 86	8523 859	296 404	17 970	71 28%		
ADDITIVE GENETIC VARIANCE			1250 674	919 143	6 884			
DOMINANCE GENETIC VARIANCE			0 0	1061 481	0 0			
TOTAL PHENOTYPIC VARIANCE			11915 508		21 247			
PHENOTYPIC VARIANCE HALF-SIB			683 042		5 087			
PHENOTYPIC VARIANCE FULL-SIB			1874 165					
HERITABILITY (INDIVIDUAL)			0 105	0 077		%RESPONSE 1 =	2 230	
HERITABILITY (HALF-SIB)			0 458	0 336		%RESPONSE 1 =	4 657	
HERITABILITY (FULL-SIB)			0 354	0 245				

** significant (P< 05) using M*F as error mean square

TABLE C7. Means and coefficients of variation for height difference (HTD) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

GROUP	CLES N	CLES MEAN cm	CLES CV %	GVWS N	GVWS MEAN cm	GVWS CV %	COMBINED N	COMBINED MEAN cm	COMBINED CV %
SEED PARENTS									
72	102	216 70	16 13	77	166 78	19 49	179	195 23	21 48
418	104	215 25	17 55	87	178 68	21 22	191	198 59	21 11
422	104	222 75	14 11	94	175 25	19 20	198	200 20	20 08
193	106	228 34	15 05	87	176 72	22 74	193	205 07	21 98
439	102	222 14	17 53	90	185 99	30 28	192	205 20	24 88
415	101	222 65	15 11	87	185 03	20 74	188	205 24	19 71
57	107	222 58	12 40	91	187 26	17 96	198	206 35	17 05
303	105	219 39	16 20	85	190 75	23 24	190	206 57	20 38
73	105	227 49	13 67	89	182 80	20 53	194	206 99	19 69
49	101	233 49	12 27	84	177 26	21 48	185	207 96	20 90
305	100	225 03	16 27	89	189 78	21 60	189	208 43	20 38
323	106	226 44	17 40	88	188 90	21 48	194	209 41	21 02
310	106	230 31	18 82	78	182 14	24 94	184	209 89	23 90
300	106	234 58	18 20	83	187 27	23 25	189	213 80	22 91
60	105	240 02	10 90	93	184 79	22 12	198	214 08	20 39
110	103	234 88	16 74	83	189 47	21 82	186	214 62	21 47
623	105	232 21	14 08	91	194 75	20 71	196	214 82	19 04
315	104	233 68	19 34	83	194 23	14 32	187	216 17	19 91
499	105	227 34	12 61	90	203 55	19 07	195	216 36	16 49
408	107	232 34	13 86	90	201 44	16 31	197	218 23	16 50
549	107	238 95	14 84	88	199 99	19 31	195	221 37	18 81
314	105	243 94	16 95	89	195 05	22 65	194	221 51	22 15
POLLEN PARENTS									
33	572	221 59	16 65	485	183 41	20 87	1057	204 07	20 62
28	573	227 60	15 83	460	187 76	24 20	1033	209 86	21 47
62	581	232 28	14 99	487	183 54	20 07	1068	210 05	20 57
448	570	233 31	15 59	484	194 64	20 91	1054	215 56	19 93
TOTAL	2296	228 70	15 88	1916	187 32	21 68	4212	209 88	20 73

TABLE C8 Combined sites analysis of variance for height increment from years 10 to 12 (HTD)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	1788452 00	837 098	699 147		35 92%		
REP/SITE		35271 79	46 754	29 054		2 01%		
MALE	4	23355 61	15 529	14 597		0 67%		
FEMALE	3	9439 05	28 929	16 199	2 563	1 24%	2 401	0 093
S * F	21	3464 52	7 301	1 000		0 31%	1 239	0 280
R * F	84	2682 49	4 250	14 663		0 18%	1 069	0 342
M * F	63	3114 29	9 598	15 652		0 41%	1 188	0 248
S*M*F	63	2621 70	3 818	21 728		0 16%	1 045	0 397
R/S*M*F	252	2508 77	166 282	28 583	6 144	7 13%	2 085	0 0
WITHIN	3684	1203 43	1203 433	28 032	16 529	51 63%		
ADDITIVE GENETIC VARIANCE			115 717	64 798	5 125			
DOMINANCE GENETIC VARIANCE			38 391	62 610	2 952			
TOTAL PHENOTYPIC VARIANCE			1446 896		18 124			
PHENOTYPIC VARIANCE HALF-SIB			49 226		3 343			
PHENOTYPIC VARIANCE FULL-SIB			108 398					
HERITABILITY (INDIVIDUAL)			0 080	0 045		%RESPONSE 1 =	1 449	
HERITABILITY (HALF-SIB)			0 588	0 329		%RESPONSE 1 =	3 929	
HERITABILITY (FULL-SIB)			0 622	0 299				

TABLE C8 (Continued) Analysis of variance for trait HTD on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	36912 19	45 550	34 151		3 38%		
MALE	3	16468 13	23 360	18 287		1 73%		
FEMALE	21	5940 68	30 200	18 246	2 403	2 24%	2 125	0 033
R * M	6	2309 64	0 050	6 223		0 00%	1 010	0 422
R * F	42	2038 71	0 0	14 998		0 0 %	0 891	0 659
M * F	63	3044 57	28 640	23 267		2 12%	1 331	0 089
R*M*F	126	2287 45	139 250	33 260	5 160	10 32%	2 114	0 0
WITHIN	2032	1081 86	1081 860	33 924	14 382	80 20%		
ADDITIVE GENETIC VARIANCE			120 800	72 984	4 806			
DOMINANCE GENETIC VARIANCE			114 560	93 070	4 680			
TOTAL PHENOTYPIC VARIANCE			1303 360		15 786			
PHENOTYPIC VARIANCE HALF-SIB			59 274		3 366			
PHENOTYPIC VARIANCE FULL-SIB			169 919					
HERITABILITY (INDIVIDUAL)			0 093	0 056		%RESPONSE 1 =	1 463	
HERITABILITY (HALF-SIB)			0 509	0 308		%RESPONSE 1 =	3 430	
HERITABILITY (FULL-SIB)			0 484	0 215				

TABLE C8 (Continued) Analysis of variance for trait HTD on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C.V	VAR COMP %	F RATIO	PROBABILITY
REP	2	33952 14	48 550	37 674		2 89%		
MALE	3	13760 54	23 920	18 389		1 42%		
FEMALE	21	6933 30	42 560	25 741	3 483	2 53%	2 113	0 040
R * M	6	2428 28	0 0	7 920		0 0 %	0 889	0 505
R * F	42	3332 56	18 210	27 341		1 08%	1 221	0 199
M * F	63	2678 76	0 0	26 874		0 0 %	0 981	0 525
R*M*F	126	2730 09	195 530	48 933	7 465	11 63%	2 018	0 0
WITHIN	1652	1352 96	1352 960	47 047	19 636	80 45%		
ADDITIVE GENETIC VARIANCE			170 240	102 963	6 965			
DOMINANCE GENETIC VARIANCE			0 0	107 497	0 0			
TOTAL PHENOTYPIC VARIANCE			1633 179		21 574			
PHENOTYPIC VARIANCE HALF-SIB			79 944		4 773			
PHENOTYPIC VARIANCE FULL-SIB			192 379					
HERITABILITY (INDIVIDUAL)			0 104	0 063		%RESPONSE 1 =	2 249	
HERITABILITY (HALF-SIB)			0 532	0 322		%RESPONSE 1 =	5 082	
HERITABILITY (FULL-SIB)			0 346	0 268				

TABLE C9. Analysis of variance for trait HT12 on site CLES after reblocking

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	1374082 00	1792 620	1275 755		21 34%		
MALE	3	80120 44	93 810	89 313		1 12%		
FEMALE	21	34325 28	79 370	107 617	1 375	0 94%	1 318	0 202
R * M	6	7805 74	7 410	20 945		0 09%	1 222	0 299
R * F	42	7360 57	27 960	51 153		0 33%	1 153	0 271
M * F	63	25072 13	719 800	172 379		8 57%	3 926	0 000
R*M*F	126	6385 69	92 520	94 927	1 485	1 10%	1 143	0 139
WITHIN	2021	5588 74	5588 738	175 724	31 541	66 52%		
ADDITIVE GENETIC VARIANCE			317 480	430 467	2 751			
DOMINANCE GENETIC VARIANCE			2879 200	689 518	8 284			
TOTAL PHENOTYPIC VARIANCE			6609 594		12 551			
PHENOTYPIC VARIANCE HALF-SIB			330 008		2 804			
PHENOTYPIC VARIANCE FULL-SIB			1139 043					
HERITABILITY (INDIVIDUAL)			0 048	0 065		%RESPONSE 1 =	0 603	
HERITABILITY (HALF-SIB)			0 241	0 326		%RESPONSE 1 =	1 349	
HERITABILITY (FULL-SIB)			0 784	0 189				

TABLE C9 (Continued) Analysis of variance for trait HT12 of top 5 trees per full sib family, plot or site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	224594 31	476 710	361 565		10 48%		
MALE	3	43433 06	71 930	87 956		1 58%		
FEMALE	21	21294 94	179 790	118 504	1 936	3 95%	2 625	0 164
R * M	6	17915 25	57 140	82 501		1 26%	1 540	0 172
R * F	42	8718 21	0 0	118 044		0 0 %	0 751	0 858
M * F	63	13429 79	119 860	184 612		2 63%	1 155	0 246
R*M*F	126	11630 99	1998 680	291 127	6 455	43 92%	7 255	0 0
WITHIN	1055	1646 32	1646 320	71 613	5 858	36 18%		
ADDITIVE GENETIC VARIANCE			719 160	474 017	3 872			
DOMINANCE GENETIC VARIANCE			479 440	738 449	3 161			
TOTAL PHENOTYPIC VARIANCE			4073 719		9 215			
PHENOTYPIC VARIANCE HALF SIB			403 750		2 901			
PHENOTYPIC VARIANCE FULL SIB			1147 561					
HERITABILITY (INDIVIDUAL)			0 177	0 116		%RESPONSE	=	1 627
HERITABILITY (HALF-SIB)			0 445	0 294		%RESPONSE	=	2 584
HERITABILITY (FULL-SIB)			0 324	0 20[illegible]				

TABLE C9 (Continued) Analysis of variance for trait HT12 of top 4 trees per [illegible] sib fam , plot or sub [illegible]

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	1813[illegible].2 31	484 615	365 990		[illegible]		
MALE	3	33652 97	72 894	85 168		[illegible]		
FEMALE	21	17813 21	209 987	122 581	2 061	[illegible]	2 303	[illegible]
R * M	6	13833 33	47 265	79 794		[illegible]	[illegible]	[illegible]
R * F	42	7158 28	0 0	121 764		[illegible]	[illegible]	[illegible]
M * F	63	10249 52	47 961	180 640		[illegible]	[illegible]	[illegible]
R*M*F	126	9674 00	2096 177	302 745	6 513	[illegible]	[illegible]	[illegible]
WITHIN	792	1289 29	1289 291	64 708	5 108	[illegible]		

ADDITIVE GENETIC VARIANCE	839 949	490 324	4 123
DOMINANCE GENETIC VARIANCE	191 842	722 562	1 970
TOTAL PHENOTYPIC VARIANCE	3763 575		8 727
PHENOTYPIC VARIANCE HALF SIB	423 519		2 927
PHENOTYPIC VARIANCE FULL SIB	1137 008		

HERITABILITY (INDIVIDUAL)	0 223	0 130	%RESPONSE [illegible] =	[illegible] 948
HERITABILITY (HALF SIB)	0 496	0 289	%RESPONSE [illegible] =	2 303
HERITABILITY (FULL SIB)	0 291	0 216		

TABLE C10 Means and coefficients of variation for diameter at 6 years (DM06) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

GROUP	CLES N	CLES MEAN mm	CLES CV %	GVWS N	GVWS MEAN mm	GVWS CV %	COMBINED N	COMBINED MEAN mm	COMBINED CV %
SEED PARENTS									
300	104	19 12	25 29	91	10 30	34 29	195	14 40	33 59
60	105	19 61	24 11	101	14 60	36 32	206	17 16	32 61
415	104	19 18	25 72	91	15 35	31 49	195	17 33	30 11
49	106	20 08	31 08	92	14 84	33 92	198	17 64	35 01
73	106	20 32	26 47	90	15 99	36 80	196	18 33	32 16
305	100	19 28	27 40	91	17 80	33 42	191	18 59	31 31
422	106	20 86	26 05	102	16 81	38 49	208	18 88	33 31
408	107	20 64	24 76	94	17 10	37 87	201	18 98	31 81
57	106	21 58	23 06	95	16 16	33 53	201	19 02	31 11
315	107	21 58	22 82	92	16 04	32 54	199	19 02	30 28
110	104	20 64	23 60	97	17 58	35 35	201	19 16	31 03
72	106	21 23	25 06	91	16 86	29 23	197	19 21	28 12
323	106	20 82	23 59	93	17 55	31 51	199	19 29	28 31
310	107	21 09	25 61	92	17 51	33 01	199	19 46	30 13
623	107	21 00	23 91	96	17 98	29 52	203	19 57	27 41
499	103	20 84	18 84	103	18 36	31 11	206	19 60	25 72
303	103	21 05	25 04	93	18 71	35 73	202	19 90	30 48
193	105	21 60	23 81	100	18 10	29 42	205	19 91	27 68
314	105	21 06	20 76	100	19 10	29 28	205	20 01	25 85
418	103	22 79	22 20	96	18 41	34 41	199	21 67	29 51
549	106	22 97	23 32	92	19 46	30 99	198	21 31	27 8
439	104	23 67	23 26	100	19 91	32 73	204	21 83	28 88
POLLEN PARENTS									
28	574	20 55	25 00	516	16 48	34 83	1090	18 52	31 19
62	579	20 58	23 70	534	16 73	34 37	1113	18 73	31 2
448	575	21 39	24 67	520	17 51	33 49	1095	19 55	31 43
30	582	21 48	25 73	525	18 04	34 98	1107	19 85	32 31
TOTAL	2310	21 [illegible]	24 88	2095	17 19	31 38	4405	19 19	31 61

TABLE C11 Combined sites analysis of variance for diameter at 6 years (DM06)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	15952 34	6 725	5 937		12 27%		
REP/SITE	4	1260 08	1 608	0 992		4 12%		
MALE	4	396 86	0 351	0 230		0 90%		
FEMALE	3	911 42	1 455	0 533	6 287	3 74%	6 156	0 000
S * F	21	62 32	0 0	1 000		0 0 %	1 688	0 027
R * F	84	77 79	0 272	0 400		0 70%	1 146	0 211
M * F	63	74 83	0 0	0 404		0 0 %	1 927	0 018
S*M*F	63	80 71	0 489	0 619		1 26%	1 189	0 128
R/S*M*F	252	67 85	5 489	0 732	12 210	14 09%	3 009	0 0
WITHIN	3877	22 55	22 551	0 512	24 750	57 99%		
ADDITIVE GENETIC VARIANCE			5 820	2 132	12 574			
DOMINANCE GENETIC VARIANCE			0 0	1 618	0 0			
TOTAL PHENOTYPIC VARIANCE			30 616		28 838			
PHENOTYPIC VARIANCE HALF SIB			1 900		7 184			
PHENOTYPIC VARIANCE FULL SIB.			3 406					
HERITABILITY (INDIVIDUAL)			0 190	0 070		RESPONSE	5 482	
HERITABILITY (HALF SIB)			0 766	0 280		RESPONSE	11 004	
HERITABILITY (FULL SIB)			0 855	0 313				

TABLE C11 (Continued) Analysis of variance for trait DMO6 on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	1207.05	1 537	1 109		5 38%		
MALE	3	150 67	0 162	0 171		0 57%		
FEMALE	21	148 31	0 946	0 444	4 633	3 31%	3 022	0 012
R • M	6	44 48	0 0	0 121		0 0 %	0 780	0 587
R • F	42	36 56	0 0	0 303		0 0 %	0 641	0 951
M • F	63	69 56	0 471	0 540		1 65%	1 219	0 171
R•M•F	126	57 05	4 091	0 821	9 632	14 33%	2 672	0 0
WITHIN	2046	21 35	21 350	0 667	22 003	74 76%		
ADDITIVE GENETIC VARIANCE			3 786	1 776	9 266			
DOMINANCE GENETIC VARIANCE			1 885	2 159	6 537			
TOTAL PHENOTYPIC VARIANCE			27 021		24 754			
PHENOTYPIC VARIANCE HALF-SIB			1 608		6 038			
PHENOTYPIC VARIANCE FULL-SIB			3 756					
HERITABILITY (INDIVIDUAL)			0 140	0 066		%RESPONSE 1 =	3 468	
HERITABILITY (HALF-SIB)			0 589	0 276		%RESPONSE 1 =	7 115	
HERITABILITY (FULL SIB)			0 421	0 236				

TABLE C11 (Continued) Analysis of variance for trait DMO6 on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	1358 39	1 752	1 378		4 88%		
MALE	3	272 40	0 328	0 343		0 91%		
FEMALE	21	255 97	1 371	0 858	6 813	3 82%	2 022	0 037
R * M	6	95 28	0 083	0 279		0 23%	1 211	0 305
R * F	42	119 71	1 237	0 865		3 45%	1 522	0 039
M * F	63	85 57	0 211	0 756		0 59%	1 088	0 341
R*M*F	126	78 66	7 021	1 268	15 426	19 58%	3 292	0 0
WITHIN	1831	23 89	23 894	0 789	28 438	66 54%		
ADDITIVE GENETIC VARIANCE			5 485	3 432	13 625			
DOMINANCE GENETIC VARIANCE			0 844	3 025	5 345			
TOTAL PHENOTYPIC VARIANCE			34 156		34 000			
PHENOTYPIC VARIANCE HALF-SIB			2 661		9 490			
PHENOTYPIC VARIANCE FULL-SIB			5 220					
HERITABILITY (INDIVIDUAL)			0 161	0 100		%RESPONSE 1 =	5 460	
HERITABILITY (HALF-SIB)			0 515	0 322		%RESPONSE 1 =	9 782	
HERITABILITY (FULL-SIB)			0 366	0 329				

TABLE C12 Means and coefficients of variation for diameter at 10 years (DM10) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN mm	CV %	N	MEAN mm	CV %	N	MEAN mm	CV %
SEED PARENTS									
415	103	62 96	18 41	90	45 84	28 06	193	54 98	27 06
300	106	67 85	20 76	89	42 91	31 86	195	56 47	33 00
60	106	68 33	18 16	96	48 14	31 35	202	58 73	29 01
422	105	70 56	21 29	101	49 08	30 01	206	60 03	30 55
49	102	71 53	23 67	90	47 76	30 39	192	60 39	32 76
305	103	67 46	24 33	95	53 17	30 19	198	60 60	29 22
73	106	70 49	22 62	94	49 60	34 26	200	60 67	32 06
323	106	69 58	19 87	93	52 10	30 07	199	61 41	27 82
315	107	71 39	18 37	89	49 58	23 64	196	61 49	25 92
303	105	67 90	21 86	87	54 34	30 86	192	61 76	27 69
72	105	70 23	21 58	84	51 58	30 51	189	61 94	29 00
57	107	71 73	18 37	95	52 36	27 01	202	62 62	26 68
110	104	71 68	21 22	89	53 57	29 48	193	63 33	28 26
499	108	67 94	22 34	98	58 68	26 46	206	63 53	25 17
408	106	71 54	19 12	94	54 88	31 89	200	63 71	27 69
623	106	72 98	21 67	98	55 14	29 05	204	64 41	28 28
310	107	71 43	21 57	88	55 97	28 46	195	64 45	27 00
418	104	72 44	16 93	91	55 84	29 38	195	64 69	25 57
193	108	73 40	20 45	95	55 23	29 15	203	64 90	27 67
549	107	73 13	20 32	94	55 94	30 22	201	65 09	27 65
314	106	75 35	17 23	94	59 89	24 22	200	68 09	23 09
439	107	77 15	20 64	90	59 28	27 58	197	68 98	26 56
POLLEN PARENTS									
28	582	70 16	21 16	494	50 40	31 84	1076	61 09	29 93
62	586	71 36	20 25	511	51 64	30 30	1097	62 17	28 87
33	580	70 63	22 46	507	54 14	29 28	1087	62 94	28 38
448	576	71 01	19 61	522	54 89	29 15	1098	63 35	26 87
TOTAL	2324	70 79	20 89	2034	52 79	30 26	4358	62 39	28 51

TABLE C13 Combined sites analysis of variance for diameter at 10 years (DM10)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	351291 00	157 765	132 239		38 78%		
REP/SITE	4	8698 29	11 239	6 924		2 76%		
MALE	4	1318 69	0 622	0 984		0 15%		
FEMALE	3	2122 32	9 521	3 371	4 946	2 34%	3 661	0 002 **
S * F	21	579 38	0 0	1 000		0 0 %	0 962	0 528
R * F	84	533 99	0 0	2 921		0 0 %	0 926	1 656
M * F	63	306 46	0 0	2 737		0 0 %	0 475	1 998
S*M*F	63	645 52	2 625	5 071		0 65%	1 119	0 271
R/S*M*F	252	576 96	49 142	6 286	11 236	12 08%	3 292	0 0
WITHIN	3830	175 27	175 271	4 004	21 219	43 09%		
ADDITIVE GENETIC VARIANCE			38 086	13 484	9 891			
DOMINANCE GENETIC VARIANCE			0 0	10 948	0 0			
TOTAL PHENOTYPIC VARIANCE			237 800		24 716			
PHENOTYPIC VARIANCE HALF-SIB			12 758		5 725			
PHENOTYPIC VARIANCE FULL-SIB			23 098					
HERITABILITY (INDIVIDUAL)			0 160	0 057		%RESPONSE 1 =	3 958	
HERITABILITY (HALF-SIB)			0 746	0 264		%RESPONSE 1 =	8 545	
HERITABILITY (FULL-SIB)			0 824	0 292				

** MS S*F USED AS ERROR MS

TABLE C13 (Continued) Analysis of variance for trait DM10 on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	14420 80	17 830	13 172		7 82%		
MALE	3	158 03	0 0	0 643		0 0 %		
FEMALE	21	959 85	4 894	3 018	3 125	2 15%	2 163	0 056
R * M	6	684 38	0 843	1 799		0 37%	1 318	0 254
R * F	42	445 57	0 0	3 272		0 0 %	0 858	0 710
M * F	63	517 38	0 0	4 234		0 0 %	0 997	0 496
R*M*F	126	519 13	40 441	7 410	8 983	17 74%	3 167	0 0
WITHIN	2060	163 91	163 906	5 105	18 085	71 92%		

ADDITIVE GENETIC VARIANCE	19 577	12 072	6 250	
DOMINANCE GENETIC VARIANCE	0 0	16 934	0 0	
TOTAL PHENOTYPIC VARIANCE	210 084		20 475	
PHENOTYPIC VARIANCE HALF-SIB	9 810		4 424	
PHENOTYPIC VARIANCE FULL-SIB	24 573			
HERITABILITY (INDIVIDUAL)	0 093	0 057		%RESPONSE (1) = 1 908
HERITABILITY (HALF-SIB)	0 499	0 308		%RESPONSE (1) = 4 415
HERITABILITY (FULL-SIB)	0 199	0 246		

TABLE C13 (Continued) ' Analysis of variance for trait DM10 on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	2769 17	3 431	2 915		1 27%		
MALE	3	2234 98	3 866	2 828		1 44%		
FEMALE	21	1743 10	14 423	5 863	7 193	5 36%	4 123	0 010
R * M	6	477 87	0 0	1 488		0 0 %	0 753	0 608
R * F	42	615 54	0 0	4 995		0 0 %	0 970	0 532
M * F	63	442 05	0 0	4 820		0 0 %	0 636	0 944
R*M*F	126	634 79	58 952	10 515	14 543	21 90%	3 368	0 0
WITHIN	1770	188 50	188 499	6 333	26 005	70 03%		
ADDITIVE GENETIC VARIANCE			57 692	23 452	14 387			
DOMINANCE GENETIC VARIANCE			0 0	19 282	0 0			
TOTAL PHENOTYPIC VARIANCE			265 739		30 877			
PHENOTYPIC VARIANCE HALF-SIB			21 289		8 740			
PHENOTYPIC VARIANCE FULL-SIB			45 824					
HERITABILITY (INDIVIDUAL)			0 217	0 088		%RESPONSE ' =	6 703	
HERITABILITY (HALF-SIB)			0 677	0 275		%RESPONSE ' =	11 842	
HERITABILITY (FULL-SIB)			0 399	0 256				

TABLE C14. Means and coefficients of variation for diameter at 12 years (DM12) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN mm	CV %	N	MEAN mm	CV %	N	MEAN mm	CV %
SEED PARENTS									
415	101	80 58	11 53	78	60 61	22 41	179	71 88	20 95
323	106	83 04	15 40	87	62 76	20 35	193	73 90	22 02
57	107	82 97	12 74	91	63 36	19 08	198	73 96	20 19
305	100	83 75	15 08	88	63 62	22 13	188	74 33	22 44
300	106	85 22	14 78	83	61 91	22 71	189	74 98	23 46
60	105	84 30	14 53	85	65 18	17 74	190	75 75	20 11
499	105	81 65	14 97	87	69 86	17 20	192	76 31	17 62
303	105	83 31	15 73	84	67 71	20 24	189	76 37	20 21
422	104	86 11	12 49	84	64 42	16 96	188	76 42	20 00
418	104	85 17	13 59	84	66 01	19 50	188	76 61	20 16
549	107	85 80	14 95	88	66 37	21 38	195	77 03	21 49
72	102	86 55	15 15	74	64 52	17 77	176	77 29	21 38
73	105	88 52	13 86	89	64 15	24 29	194	77 34	23 85
408	107	86 22	14 00	87	66 42	20 32	194	77 34	20 79
315	104	85 88	11 45	80	66 73	14 27	184	77 55	17 50
49	101	89 09	15 46	80	65 24	17 75	181	78 55	22 24
623	105	88 65	14 26	88	66 85	22 14	193	78 71	22 16
310	106	87 26	14 47	74	68 76	19 22	180	79 66	19 77
110	103	89 04	14 40	78	68 19	20 78	181	80 06	21 14
193	106	89 38	13 12	81	68 54	21 60	187	80 35	20 79
314	105	91 79	12 03	86	71 23	18 69	191	82 53	19 20
439	102	94 55	15 71	86	71 03	15 96	188	83 79	21 20
POLLEN PARENTS									
28	573	85 62	15 03	426	69 09	21 29	999	76 87	21 77
62	581	87 17	13 83	473	64 83	19 87	1054	77 14	21 61
33	572	86 50	15 35	473	66 71	19 53	1045	77 54	21 21
448	570	85 92	14 03	470	67 53	19 55	1040	77 61	20 05
TOTAL	2296	86 31	14 58	1842	66 06	20 10	4138	77 30	21 16

TABLE C15 Combined sites analysis of variance for diameter at 12 years (DM12)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	418722 00	202 338	167 262		53 18%		
REP/SITE	4	5093 36	6 675	4 279		1 75%		
MALE	4	343 52	0 0	0 554		0 0 %		
FEMALE	3	1458 35	7 047	2 441	3 434	1 85%	4 150	0 001 **
S * F	21	351 62	0 0	1 000		0 0 %	0 873	0 621
R * F	84	342 68	0 0	2 106		0 0 %	0 764	0 926
M * F	63	298 85	0 0	2 363		0 0 %	0 587	0 992
S*M*F	63	509 05	2 266	4 252		0 60%	1 134	0 249
R/S*M*F	251	148 82	43 023	5 209	8 486	11 31%	3 199	0 0
WITHIN	3611	118 13	118 127	2 779	14 061	31 05%		
ADDITIVE GENETIC VARIANCE			28 188	9 763	6 869			
DOMINANCE GENETIC VARIANCE			0 0	9 453	0 0			
TOTAL PHENOTYPIC VARIANCE			171 460		16 941			
PHENOTYPIC VARIANCE HALF SIB			9 709		4 031			
PHENOTYPIC VARIANCE FULL SIB			17 707					
HERITABILITY (INDIVIDUAL)			0 164	0 057		%RESPONSE	= 2 785	
HERITABILITY (HALF-SIB)			0 726	0 251		%RESPONSE	= 5 852	
HERITABILITY (FULL-SIB)			0 796	0 276				

** MS S*F USED AS ERROR MS

TABLE C15 (Continued) Analysis of variance for trait DM12 on site CLES

SOURCE	D.F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	5720 34	6 587	5 317		3 93%		
MALE	3	273 44	0 0	0 827		0 0 %		
FEMALE	21	1147 21	8 210	3 445	3 320	4 90%	3 912	0 012
R * M	6	860 60	1 948	2 272		1 16%	1 776	0 109
R * F	42	306 47	0 0	2 565		0 0 %	0 633	0 955
M * F	63	471 28	0 0	3 933		0 0 %	0 973	0 540
R*M*F	126	484 47	43 561	7 012	9 647	25 98%	4 513	0 0
WITHIN	2032	107 35	107 350	3 366	12 005	64 03%		

ADDITIVE GENETIC VARIANCE	34 842	13 778	6 640	
DOMINANCE GENETIC VARIANCE	0 0	15 732	0 0	
TOTAL PHENOTYPIC VARIANCE	161 069		14 705	
PHENOTYPIC VARIANCE HALF-SIB	12 850		4 153	
PHENOTYPIC VARIANCE FULL-SIB	26 782			
HERITABILITY (INDIVIDUAL)	0 204	0 086		%RESPONSE = 2 998
HERITABILITY (HALF-SIB)	0 639	0 268		%RESPONSE = 5 308
HERITABILITY (FULL-SIB)	0 307	0 257		

TABLE C15 (Continued) Analysis of variance for trait DM12 on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	4603 30	7 071	5 311		3 79%		
MALE	3	810 46	1 237	1 183		0 66%		
FEMALE	21	648 88	4 410	2 649	3 179	2 36%	2 152	0 072
R * M	6	331 51	0 0	1 135		0 0 %	0 803	0 569
R * F	42	367 81	0 0	3 391		0 0 %	0 891	0 659
M * F	63	346 59	0 0	3 843		0 0 %	0 839	0 778
R*M*F	125	412 88	41 874	7 765	9 795	22 44%	3 128	0 0
WITHIN	1579	132 00	131 995	4 695	17 391	70 74%		

ADDITIVE GENETIC VARIANCE	17 640	10 595	6 357
DOMINANCE GENETIC VARIANCE	0 0	15 373	0 0
TOTAL PHENOTYPIC VARIANCE	179 516		20 281
PHENOTYPIC VARIANCE HALF-SIB	9 338		4 626
PHENOTYPIC VARIANCE FULL-SIB	25 462		

HERITABILITY (INDIVIDUAL)	0 098	0 059	%RESPONSE 1 =	1 993
HERITABILITY (HALF-SIB)	0 472	0 284	%RESPONSE 1 =	4 369
HERITABILITY (FULL SIB)	0 222	0 208		

TABLE C16 Means and coefficients of variation for volume (VOLM) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
415	101	12 42	42 85	42	8 40	35 35	143	11 24	48 14
57	105	15 33	40 41	66	9 79	51 14	171	13 19	48 17
305	100	15 05	48 68	62	10 22	45 49	162	13 20	51 78
72	102	15 78	47 67	53	8 52	46 38	155	13 30	55 11
60	105	15 14	43 34	59	10 04	36 69	164	13 31	45 64
300	104	15 16	45 64	43	9 39	54 69	147	13 47	51 57
323	105	15 09	43 88	48	10 52	52 17	153	13 66	48 10
499	104	14 44	47 00	65	12 70	41 72	169	13 71	45 73
422	102	15 81	39 39	53	9 87	40 93	155	13 78	45 28
303	102	14 83	50 93	60	12 08	38 08	162	13 81	48 15
315	104	16 29	38 53	51	9 77	33 97	155	14 14	41 71
418	103	16 05	41 86	57	10 81	38 98	160	14 18	45 41
310	105	15 84	42 80	54	11 08	45 61	159	14 22	48 61
73	104	16 49	42 00	55	10 85	43 72	159	14 51	45 75
549	107	16 35	46 67	61	11 69	49 38	168	14 66	50 13
110	102	16 95	43 07	52	10 99	44 15	154	14 94	47 81
408	107	16 96	49 38	62	11 70	45 03	169	15 00	51 88
49	100	16 97	49 81	39	10 62	38 58	139	15 19	52 71
193	105	17 53	44 65	61	11 44	54 22	166	15 29	51 10
314	105	18 57	37 03	78	11 57	44 35	183	15 59	45 17
623	103	18 26	43 93	63	12 08	53 23	166	15 94	51 96
439	102	19 74	40 37	68	12 08	42 10	170	16 98	47 71
POLLEN PARENTS									
33	567	16 11	47 21	343	10 74	45 72	910	14 09	51 12
28	570	15 91	48 00	271	10 62	44 36	841	14 21	51 12
62	575	16 06	42 17	284	10 63	45 90	859	14 26	47 15
448	565	16 50	42 61	353	11 28	47 35	918	14 50	47 77
TOTAL	2277	16 14	45 02	1251	10 84	46 01	3528	14 26	49 29

TABLE C17 Combined sites analysis of variance for volume (VOLM)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	22698 99	11 999	11 555		20 35%		
REP/SITE	4	3736 66	6 188	3 673		10 50%		
MALE	4	62 71	0 056	0 080		0 09%		
FEMALE	3	251 80	0 370	0 513	6 905	0 65%	2 473	0 128
S * F	21	69 60	0 127	1 000		0 22%	1 118	0 413
R * F	84	72 75	0 0	0 534		0 0%	0 781	0 928
M * F	63	111 13	0 556	0 672		0 94%	1 375	0 101
S*M*F	63	85 18	0 0	0 982		0 0%	0 894	0 711
R/S*M*F	242	95 64	10 356	1 341	22 562	17 57%	3 354	0
WITHIN	3010	28 52	28 518	0 735	37 441	48 38		
ADDITIVE GENETIC VARIANCE			3 880	2 054	13 811			
DOMINANCE GENETIC VARIANCE			2 223	2 687	10 452			
TOTAL PHENOTYPIC VARIANCE			40 764		44 764			
PHENOTYPIC VARIANCE HALF SIB			1 763		0 309			
PHENOTYPIC VARIANCE FULL SIB			3 974					
HERITABILITY (INDIVIDUAL)			0 095	0 050		%RESPONSE =	4 26%	
HERITABILITY (HALF SIB)			0 550	0 291		%RESPONSE =	10 245	
HERITABILITY (FULL SIB)			0 628	0 258				

TABLE C17 (Continued) Analysis of variance for trait VOLM on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	1898 09	6 200	4 567		12 38%		
MALE	3	41 64	0 0	0 219		0 0 %		
FEMALE	21	252 88	1 147	0 833	6 633	2 29%	1 873	0 181
R * M	6	223 23	0 445	0 623		0 89%	1 579	0 159
R * F	42	108 77	0 0	0 861		0 0	0 706	0 872
M * F	63	154 03	0 977	1 38		1 95%	1 178	0 218
R*M*F	126	117 72	13 193	2 156	22 500	26 31%	1 282	
WITHIN	2013	94 50	34 497	1 087	36 383	68 81%		
ADDITIVE GENETIC VARIANCE			4 586	3 318	13 266			
DOMINANCE GENETIC VARIANCE			3 907	5 521	12 244			
TOTAL PHENOTYPIC VARIANCE			50 258		43 915			
PHENOTYPIC VARIANCE HALF SIB			2 818		10 398			
PHENOTYPIC VARIANCE FULL SIB			7 834					
HERITABILITY (INDIVIDUAL)			0 091	0 066		%RESPONSE =	1 367	
HERITABILITY (HALF-SIB)			0 407	0 294		%RESPONSE =	8 452	
HERITABILITY (FULL-SIB)			0 271	0 212				

TABLE C17 (Continued) Analysis of variance for trait VOLM on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP *	2	2569 94	6 120	4 366		27 [illegible]%		
MALE	3	50 66	0 097	0 122		0 [illegible]%		
FEMALE	21	66 26	0 892	0 387	8 713	3 [illegible]%	2 842	[illegible]
R * M	6	37 59	0 0	0 189		0 0 %	0 962	[illegible]
R * F	42	32 09	0 0	0 466		0 0 %	0 821	[illegible]
M * F	63	30 30	0 0	0 534		0 0 %	0 775	[illegible]
R*M*F	116	39 08	5 389	1 224	21 413	18 62%	2 [illegible]	[illegible]
WITHIN	997	16 45	16 446	0 736	37 408	56 82%		
ADDITIVE GENETIC VARIANCE			3 569	1 548	17 426			
DOMINANCE GENETIC VARIANCE			0 0	2 134	0 0			
TOTAL PHENOTYPIC VARIANCE			22 824		44 069			
PHENOTYPIC VARIANCE HALF-SIB			1 580		11 596			
PHENOTYPIC VARIANCE FULL-SIB			3 809					
HERITABILITY (INDIVIDUAL)			0 156	0 068		%RESPONSE [illegible] =	6 89	
HERITABILITY (HALF-SIB)			0 565	0 245		%RESPONSE [illegible] =	10 095	
HERITABILITY (FULL-SIB)			0 260	0 202				

TABLE C18 Components of variance and covariance for traits HT06 and HT12

FOR VARIABLES	HT06			HT12			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	27 3018	S E	11 6735	303 9873	S E	113 4067	66 4441
ADDITIVE GENETIC VARIANCE	109 2072	S E	46 6941	1215 9492	S E	453 6270	265 7764
DOMINANCE GENETIC VARIANCE	0 0	S E	42 8132	0 0	S E	548 0427	0 0
PHENOTYPIC VARIANCE INDIVIDUAL	868 4045			8981 1406			2107 0273
PHENOTYPIC VARIANCE HALF-SIB	38 5958			461 6140			100 8853
PHENOTYPIC VARIANCE FULL-SIB	88 4654			1108 7012			253 0382
HERITABILTY FOR INDIVIDUAL SELECTION	0 1258	S E	0 0538	0 1354	S E	0 0505	0 1305
COEFFICIENT OF VARIATION (PI)	27 1366			15 8939			
%RESPONSE /1 (INDIVIDUAL)	3 4126			2 1519			
HERITABILTY FOR HALF-SIB SELECTION	0 7074	S E	1 2098	0 6585	S E	0 9827	0 6825
COEFFICIENT OF VARIATION (PHS)	5 7209			3 6033			
%RESPONSE /1 (HALF-SIB)	8 0937	CR_y =	5 6956	4 7458	CR_y =	3 5874	
GENETIC CORRELATIONS	0 7293	S E	0 1322				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 7545						
PHENOTYPIC CORRELATIONS H S FAMILIES	0 7558						
ENVIRONMENTAL CORRELATIONS	0 7583						

TABLE C19 Components of variance and covariance for traits HT06 and DM12

FOR VARIABLES	HT06			DM12			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	27 3018	S E	11 6735	6 5144	S E	2 3512	6 8592
ADDITIVE GENETIC VARIANCE	109 2072	S E	46 6941	26 0576	S E	9 4048	27 4366
DOMINANCE GENETIC VARIANCE	0 0	S E	42 8132	0 0	S E	8 9480	0 0
PHENOTYPIC VARIANCE INDIVIDUAL	868 4045			157 2119			245 3063
PHENOTYPIC VARIANCE HALF-SIB	38 5958			8 8543			10 5249
PHENOTYPIC VARIANCE FULL-SIB	88 4654			15 8838			22 8709
HERITABILTY FOR INDIVIDUAL SELECTION	0 1258	S E	0 0538	0 1657	S E	0 0598	0 1444
COEFFICIENT OF VARIATION (PI)	27 1366			16 0574			
%RESPONSE /1 (INDIVIDUAL)	3 4126			2 6615			
HERITABILTY FOR HALF-SIB SELECTION	0 7074	S E	1 2098	0 7357	S E	1 0622	0 7214
COEFFICIENT OF VARIATION (PHS)	5 7209			3 8107			
%RESPONSE /1 (HALF-SIB)	8.0937	CRy=	4 2454	5 6074	CRy=	2 8279	
GENETIC CORRELATIONS	0 5143	S E	0 2043				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 6639						
PHENOTYPIC CORRELATIONS H S FAMILIES	0 5693						
ENVIRONMENTAL CORRELATIONS	0 6904						

TABLE C20 Components of variance and covariance for traits HT12 and DM12

FOR VARIABLES	HT12			DM12			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	303 9873	S E	113 4067	6 5144	S E	2 3512	20 0828
ADDITIVE GENETIC VARIANCE	1215 9492	S E	453 6270	26 0576	S E	9 4048	80 3307
DOMINANCE GENETIC VARIANCE	0 0	S E	548 0427	0 0	S E	8 9483	0 0
PHENOTYPIC VARIANCE INDIVIDUAL	8981 1406			157 2119			964 9590
PHENOTYPIC VARIANCE HALF-SIB	461 6140			8 8543			37 1930
PHENOTYPIC VARIANCE FULL-SIB	1108 7012			15 8838			85 5430
HERITABILTY FOR INDIVIDUAL SELECTION	0 1354	S E	0 0505	0 1657	S E	0 0598	0 1498
COEFFICIENT OF VARIATION (PI)	15 8939			16 0574			
%RESPONSE /1 (INDIVIDUAL)	2 1519			2 6615			
HERITABILTY FOR HALF-SIB SELECTION	0 6585	S E	0 9827	0 7357	S E	1 0622	0 6961
COEFFICIENT OF VARIATION (PHS)	3 6033			3 8107			
%RESPONSE /1 (HALF-SIB)	4 7458	CRy=	2 2638	5 6074	CRx=	2 3941	
GENETIC CORRELATIONS	0 4513	S E	0 2066				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 8121						
PHENOTYPIC CORRELATIONS H S FAMILIES	0 5818						
ENVIRONMENTAL CORRELATIONS	0 8766						

TABLE C21 Components of variance and covariance for traits HTO6 and VOLM

FOR VARIABLES	HTO6			VOLM			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	17 2734	S E	8 7749	97 0063	S E	51 3499	27 9492
ADDITIVE GENETIC VARIANCE	69 0936	S E	39 0998	388 0251	S E	205 3995	111 7970
DOMINANCE GENETIC VARIANCE	43 8912	S E	40 1620	222 2556	S E	268 6882	80 8400
PHENOTYPIC VARIANCE INDIVIDUAL	778 5940			4076 4172			1425 1563
PHENOTYPIC VARIANCE HALF-SIB	31 8183			176 2940			55 5638
PHENOTYPIC VARIANCE FULL-SIB	71 1595			397 4338			129 0417
HERITABILTY FOR INDIVIDUAL SELECTION	0 0887	S E	0 0502	0 0952	S E	0 0504	0 0919
COEFFICIENT OF VARIATION (PI)	24 5405			44 7636			
%RESPONSE /1 (INDIVIDUAL)	2 1778			4 2609			
HERITABILTY FOR HALF-SIB SELECTION	0 5429	S E	1 2288	0 5503	S E	1 1651	0 5466
COEFFICIENT OF VARIATION (PHS)	4 9610			9 3090			
%RESPONSE /1 (HALF-SIB)	5 3864	CRy=	3 7026	10 2446	CRx=	6 9478	
GENETIC CORRELATIONS	0 6828	S E	0 2066				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 8000						
PHENOTYPIC CORRELATIONS H S FAMILIES	0 7419						
ENVIRONMENTAL CORRELATIONS	0 8119						

APPENDIX D: Tables of means and analyses of variance and covariance for form traits.

TABLE D1 Means and coefficients of variation for branch number (BN) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
418	103	4 68	18 61	57	5 08	20 02	160	4 82	19 52
300	104	5 04	23 41	43	4 71	26 74	147	4 94	24 45
415	101	4 85	20 41	42	5 18	23 05	143	4 94	21 44
57	105	4 83	23 28	66	5 37	25 68	171	5 04	24 87
323	105	4 96	21 68	48	5 51	21 22	153	5 13	22 03
49	100	5 01	16 03	39	5 59	21 61	139	5 17	18 69
549	107	5 05	16 92	61	5 48	16 81	168	5 21	17 31
310	105	4 98	22 35	54	5 77	22 95	159	5 25	23 69
315	104	5 08	24 26	51	5 62	21 41	155	5 26	23 58
193	105	5 06	28 44	61	5 63	21 68	166	5 27	26 32
72	102	5 10	20 70	53	5 65	19 60	155	5 29	22 84
499	104	5 05	21 67	65	5 68	20 49	169	5 29	21 93
60	105	5 08	27 30	59	5 78	23 52	164	5 33	26 51
408	107	5 20	21 71	62	5 80	19 02	169	5 42	21 28
305	100	5 07	18 54	62	6 02	18 97	162	5 43	20 58
73	104	5 21	20 84	55	5 90	38 75	159	5 45	29 96
110	102	5 31	17 98	52	5 88	19 38	154	5 50	19 11
623	103	5 53	18 86	62	5 85	15 91	165	5 65	17 89
314	105	5 27	18 29	78	6 20	19 08	183	5 66	20 10
439	102	5 35	20 12	68	6 15	19 41	170	5 67	20 97
422	102	5 61	18 67	53	5 97	20 43	155	5 74	19 53
303	102	5 58	19 69	60	6 63	16 47	162	5 97	20 19
POLLEN PARENTS									
33	567	5 00	20 81	343	5 67	19 84	910	5 25	21 32
28	570	5 10	22 08	271	5 66	28 33	841	5 28	25 19
448	565	5 08	20 87	353	5 78	22 32	918	5 35	22 48
62	575	5 34	21 52	284	5 83	19 46	859	5 50	21 20
TOTAL	2277	5 13	21 48	1251	5 73	22 51	3528	5 34	22 59

TABLE D2. Combined sites analysis of variance for branch number (BN)

SOURCE	D F	MEAN SQUARE	VAR/COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	295 12	0 164	0 150		10 47%		
REP/SITE	4	31 34	0 052	0 031		3 31%		
MALE	3	12 59	0 013	0 009		0 82%		
FEMALE	21	12 11	0 064	0 023	4 723	4 06%	5 976	0 011
S * F	21	2 64	0 0	1 000		0 0 %	0 928	0 561
R * F	84	2 26	0 002	0 015		0 11%	1 065	0 352
M * F	63	2 10	0 0	0 016		0 0 %	0 773	0 845
S*M*F	63	2 71	0 004	0 029		0 24%	1 279	0 091
R/S*M*F	242	2 12	0 155	0 030	7 367	9 89%	1 903	0 0
WITHIN	3010	1 11	1 114	0 029	19 744	71 01%		
ADDITIVE GENETIC VARIANCE			0 255	0 093	9 445			
DOMINANCE GENETIC VARIANCE			0 0	0 063	0 0			
TOTAL PHENOTYPIC VARIANCE			1 352		21 757			
PHENOTYPIC VARIANCE HALF-SIB			0 078		5 213			
PHENOTYPIC VARIANCE FULL-SIB			0 131					
HERITABILITY (INDIVIDUAL)			0 188	0 069		%RESPONSE 1 =	4 10%	
HERITABILITY (HALF-SIB)			0 821	0 299		%RESPONSE 1 =	8 557	
HERITABILITY (FULL-SIB)			0 971	0 354				

TABLE D2 (Continued) Analysis of variance for branch number on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	371706 75	480 552	346 437		3 86%		
MALE	3	124632 94	203 770	138 897		1 64%		
FEMALE	21	56334 34	338 218	172 189	3 585	2 71%	2 631	0 016
R * M	6	7909 76	0 0	25 217		0 0 %	0 370	0 897
R * F	42	20576 62	0 0	149 268		0 0 %	0 963	0 542
M * F	63	22197 26	28 275	182 985		0 23%	1 039	0 421
R*M*F	126	21361 35	1312 530	313 336	7 062	10 53%	2 116	0 0
WITHIN	2013	10097 18	10097 188	318 110	19 586	81 00%		

ADDITIVE GENETIC VARIANCE	1352 873	688 757	7 169
DOMINANCE GENETIC VARIANCE	113 099	731 940	2 073
TOTAL PHENOTYPIC VARIANCE	11979 973		21 334
PHENOTYPIC VARIANCE HALF-SIB	551 676		4 578
PHENOTYPIC VARIANCE FULL-SIB	1396 303		

HERITABILITY (INDIVIDUAL)	0 113	0 057	%RESPONSE 1 =	2 409
HERITABILITY (HALF-SIB)	0 613	0 312	%RESPONSE 1 =	5 613
HERITABILITY (FULL SIB)	0 408	0 247		

TABLE D2 (Continued) Analysis of variance for branch number on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	319322 31	744 679	542 608		4 55%		
MALE	3	16051 82	23 288	38 349		0 14%		
FEMALE	21	86033 81	1011 551	466 192	5 546	5 91%	2 871	0 004
R * M	6	6980 35	0 0	43 423		0 0 %	0 332	0 919
R * F	42	25771 42	133 086	335 895		0 78%	1 227	0 197
M * F	63	25192 54	135 298	377 328		0 79%	1 200	0 198
R*M*F	116	20995 94	1848 119	665 913	7 496	10 79%	1 587	0 000
WITHIN	997	13233 30	13233 309	592 107	20 059	77 26%		

ADDITIVE GENETIC VARIANCE	4046 205	1864 769	11 081
DOMINANCE GENETIC VARIANCE	541 191	1509 311	4 056
TOTAL PHENOTYPIC VARIANCE	16384 645		22 319
PHENOTYPIC VARIANCE HALF-SIB	1457 210		6 656
PHENOTYPIC VARIANCE FULL-SIB	2684 957		

HERITABILITY (INDIVIDUAL)	0 247	0 114	%RESPONSE =	5 512
HERITABILITY (HALF-SIB)	0 694	0 320	%RESPONSE =	9 241
HERITABILITY (FULL-SIB)	0 436	0 347		

TABLE D3 Means and coefficients of variation for branch angle (BA) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
418	103	57 61	10 63	57	62 59	11 18	160	59 38	11 55
323	105	60 63	13 26	48	64 40	12 15	153	61 81	13 15
439	102	61 70	9 74	68	62 52	9 10	170	62 03	9 48
415	101	61 25	10 48	42	64 74	9 24	143	62 27	10 39
315	104	61 87	11 25	51	65 84	10 66	155	63 17	11 41
314	105	62 02	9 48	78	65 27	10 59	183	63 41	10 29
305	100	63 23	10 99	62	65 23	10 68	162	63 99	10 95
49	100	63 48	9 79	39	66 07	11 65	139	64 21	10 49
300	104	63 86	9 37	43	65 39	11 93	147	64 31	10 23
303	102	63 06	10 42	60	67 43	9 05	162	64 68	10 42
57	105	64 03	9 49	66	68 93	10 43	171	65 92	10 52
422	102	64 61	10 43	53	69 38	6 96	155	66 24	9 88
499	104	65 96	9 30	65	67 52	7 73	169	66 56	8 76
408	107	65 44	8 94	62	68 55	8 73	169	66 58	9 12
73	104	66 45	9 84	55	68 44	9 63	159	67 14	9 84
60	105	66 17	9 36	59	69 13	8 67	164	67 24	9 32
110	102	66 91	9 68	52	68 22	10 29	154	67 35	11 06
623	103	67 20	9 79	62	68 81	7 53	165	67 80	9 05
549	107	68 71	8 63	61	68 69	8 54	168	68 70	8 57
72	102	70 65	8 23	53	70 94	9 47	155	70 75	8 65
310	105	70 28	7 96	54	72 25	7 18	159	70 95	7 78
193	105	70 50	8 22	61	72 53	8 49	166	71 24	8 41
POLLEN PARENTS									
33	567	63 43	11 96	343	66 81	10 04	910	64 71	11 53
28	570	64 68	10 93	271	66 03	11 46	841	65 12	11 11
448	565	64 64	9 99	353	67 62	10 03	918	65 79	10 24
62	575	66 49	10 61	284	69 27	9 69	859	67 41	10 48
TOTAL	2277	64 82	11 01	1251	67 43	10 41	3528	65 74	10 95

TABLE 04 Combined sites analysis of variance for branch angle (BA)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	5509 33	2 107	2 896		3 87%		
REP/SITE	4	2214 95	3 641	2 177		6 [illegible]%		
MALE	3	1306 29	1 301	0 941		2 39%		
FEMALE	21	1559 09	8 851	2 876	4 525	16 27%	11 663	[illegible]
S * F	21	90 09	0 359	1 000		0 66%	1 383	[illegible]
R * F	84	64 13	0 370	0 413		0 68%	1 218	[illegible]
M * F	63	97 24	0 996	0 502		1 83%	1 812	[illegible]
S*M*F	63	53 65	0 060	0 601		0 11%	1 019	[illegible]
R/S*M*F	242	52 65	2 942	0 747	2 609	5 41%	1 508	[illegible]
WITHIN	3010	33 58	33 583	0 865	8 815	61 75%		
ADDITIVE GENETIC VARIANCE			35 404	11 502	9 050			
DOMINANCE GENETIC VARIANCE			3 983	2 009	3 036			
TOTAL PHENOTYPIC VARIANCE			48 637		10 608			
PHENOTYPIC VARIANCE HALF-SIB			9 659		4 727			
PHENOTYPIC VARIANCE FULL SIB			12 491					
HERITABILITY (INDIVIDUAL)			0 728	0 236		%RESPONSE	1 722	
HERITABILITY (HALF-SIB)			0 916	0 298		%RESPONSE	8 664	
HERITABILITY (FULL SIB)			1 497	0 460				

TABLE D4 (Continued) Analysis of variance for branch angle on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	2238 48	2 909	2 086		5 5[illegible]		
MALE	3	919 40	1 539	1 022		2 9[illegible]		
FEMALE	21	1205 20	10 742	3 440	5 056	20 2[illegible]	12 88[illegible]	
R • M	6	19 93	0 0	0 065		0 0 [illegible]	0 34[illegible]	[illegible]
R • F	42	69 75	0 320	0 482		0 6[illegible]	1 82	1 008
M • F	63	82 28	0 910	0 627		1 7[illegible]	1 416	0 05[illegible]
R•M•F	126	58 51	2 902	0 861	2 628	5 48[illegible]	1 74[illegible]	[illegible]
WITHIN	2013	33 61	33 612	1 059	8 944	63 50[illegible]		
ADDITIVE GENETIC VARIANCE			42 968	13 762	10 113			
DOMINANCE GENETIC VARIANCE			3 640	2 50[illegible]	2 944			
TOTAL PHENOTYPIC VARIANCE			50 024		10 912			
PHENOTYPIC VARIANCE HALF SIB			11 641		5 264			
PHENOTYPIC VARIANCE FULL SIB			15 454					
HERITABILITY (INDIVIDUAL)			0 859	0 275		%RESPONSE [illegible]	9 3[illegible]	
HERITABILITY (HALF SIB)			0 923	0 296		%RESPONSE [illegible]	9 7[illegible]	
HERITABILITY (FULL SIB)			0 854	0 445				

TABLE D4 (Continued) Analysis of variance for branch angle on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	2329 69	5 294	3 960		10 26%		
MALE	3	557 17	1 365	1 147		2 64%		
FEMALE	21	421 69	6 002	2 210	3 633	11 63%	5 186	[illegible]
R * M	6	112 38	0 595	0 549		1 15%	2 428	[illegible]
R * F	42	60 53	0 567	0 780		1 10%	1 308	[illegible]
M * F	63	67 06	1 224	0 960		2 37%	1 449	[illegible]
R*M*F	116	46 28	3 039	1 478	2 585	5 88%	1 381	[illegible]
WITHIN	997	33 52	33 523	1 507	8 587	64 96%		
ADDITIVE GENETIC VARIANCE			24 006	8 851	7 266			
DOMINANCE GENETIC VARIANCE			4 896	3 839	3 281			
TOTAL PHENOTYPIC VARIANCE			46 314		10 093			
PHENOTYPIC VARIANCE HALF-SIB			7 298		4 006			
PHENOTYPIC VARIANCE FULL-SIB			11 930					
HERITABILITY (INDIVIDUAL)			0 518	0 191		%RESPONSE	5 231	
HERITABILITY (HALF-SIB)			0 822	0 303		%RESPONSE	8 589	
HERITABILITY (FULL SIB)			0 720	0 271				

TABLE D5 Means and coefficients of variation for branch thickness (BT) at the Cowichan Lake (CLES) and Gordon Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN mm	CV %	N	MEAN mm	CV %	N	MEAN mm	CV %
SEED PARENTS									
300	104	18 68	16 84	43	17 80	[illegible]	[illegible]	18 42	[illegible]
315	104	19 24	14 89	51	17 60	14 99	[illegible]	18 [illegible]	15 15
60	105	19 08	16 00	59	18 26	[illegible]	[illegible]	18 79	[illegible]
499	104	18 93	17 09	65	18 99	15 [illegible]	[illegible]	18 95	16 5[illegible]
72	102	19 87	17 52	53	17 83	15 [illegible]	[illegible]	19 [illegible]	[illegible]
415	101	19 34	13 68	42	18 45	15 [illegible]	[illegible]	19 [illegible]	[illegible]
314	105	20 05	15 34	78	17 83	15 [illegible]	[illegible]	19 [illegible]	16 28
303	102	19 58	17 79	60	18 44	14 [illegible]	[illegible]	19 16	[illegible]
305	100	19 64	16 79	62	18 67	18 25	[illegible]	19 [illegible]	[illegible]
57	105	20 15	15 15	66	18 30	12 9[illegible]	[illegible]	19 44	15 15
193	105	20 15	16 60	61	18 24	[illegible]	[illegible]	19 44	15 5[illegible]
310	105	19 88	18 73	54	18 71	14 98	[illegible]	19 48	[illegible]
408	107	20 19	15 84	62	18 38	14 [illegible]	[illegible]	19 53	16 [illegible]
422	102	20 42	14 34	53	17 95	16 [illegible]	[illegible]	19 58	15 [illegible]
73	104	20 28	14 85	55	18 35	12 54	[illegible]	19 62	[illegible]
110	102	20 21	16 07	52	18 80	15 [illegible]	[illegible]	19 73	16 [illegible]
323	105	20 14	17 10	48	19 16	[illegible]	[illegible]	19 83	[illegible]
549	107	20 53	16 89	61	18 93	20 52	[illegible]	19 95	18 5[illegible]
623	103	20 37	17 02	62	19 28	18 15	[illegible]	19 96	[illegible]
439	102	20 77	17 01	68	18 78	13 [illegible]	[illegible]	19 97	16 65
49	100	20 44	19 80	39	19 40	[illegible]	[illegible]	20 [illegible]	[illegible]
418	103	21 15	17 19	57	19 11	13 36	[illegible]	20 42	16 [illegible]
POLLEN PARENTS									
62	575	19 34	16 37	284	17 75	14 [illegible]	859	18 8[illegible]	16 [illegible]
28	570	19 92	17 14	271	18 59	16 25	841	19 49	[illegible]
448	565	20 23	16 71	353	18 85	15 95	918	19 [illegible]	16 8[illegible]
33	567	20 32	16 34	343	18 72	15 05	910	19 72	16 [illegible]
TOTAL	2277	19 95	16 75	1251	18 51	15 67	3528	19 44	16 8[illegible]

TABLE D6 Combined sites analysis of variance for branch thickness (BT)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	1679 71	0 700	0 877		5 99%		
REP/SITE	4	612 85	1 011	0 602		8 65%		
MALE	3	181 68	0 195	0 131		1 67%		
FEMALE	21	40 99	0 130	0 087	1 858	1 12%	1 991	0 055
S * F	21	13 86	0 016	1 000		0 14%	1 040	0 469
R * F	84	18 00	0 0	0 125		0 0 %	0 899	0 712
M * F	63	22 08	0 140	0 127		1 20%	1 438	0 026
S*M*F	63	15 36	0 0	0 185		0 0 %	0 767	1 000
R/S*M*F	242	20 03	1 923	0 281	7 134	16 45%	2 647	0 0
WITHIN	3010	7 57	7 567	0 195	14 152	64 75%		
ADDITIVE GENETIC VARIANCE			0 522	0 349	3 715			
DOMINANCE GENETIC VARIANCE			0 562	0 506	3 856			
TOTAL PHENOTYPIC VARIANCE			9 976		16 250			
PHENOTYPIC VARIANCE HALF-SIB			0 298		2 808			
PHENOTYPIC VARIANCE FULL-SIB			0 967					
HERITABILITY (INDIVIDUAL)			0 052	0 035		%RESPONSE) =	0 849	
HERITABILITY (HALF-SIB)			0 438	0 293		%RESPONSE =	2 458	
HERITABILITY (FULL-SIB)			0 415	0 181				

TABLE D6 (Continued) Analysis of variance for branch thickness on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	18961 08	20 836	17 861		1 81%		
MALE	3	11281 43	13 388	13 012		1 16%		
FEMALE	21	3986 85	18 481	13 522	2 155	1 60%	1 907	0 109
R * M	6	3795 84	4 934	10 182		0 43%	1 337	0 246
R * F	42	2210 16	0 0	17 133		0 0 %	0 778	0 823
M * F	63	2720 07	0 0	23 021		0 0 %	0 958	0 568
R*M*F	126	2839 88	230 130	41 486	7 604	19 97%	3 284	0 0
WITHIN	2013	864 89	864 899	27 248	14 742	75 03%		
ADDITIVE GENETIC VARIANCE			73 923	54 088	4 310			
DOMINANCE GENETIC VARIANCE			0 0	92 085	0 0			
TOTAL PHENOTYPIC VARIANCE			1131 832		16 864			
PHENOTYPIC VARIANCE HALF-SIB			45 920		3 397			
PHENOTYPIC VARIANCE FULL-SIB			141 687					
HERITABILITY (INDIVIDUAL)			0 065	0 048		%RESPONSE 1 =	1 101	
HERITABILITY (HALF-SIB)			0 402	0 294		%RESPONSE 1 =	2 734	
HERITABILITY (FULL-SIB)			0 225	0 191				

TABLE D6 (Continued) Analysis of variance for branch thickness on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	102348 25	243 421	173 853		25 70%		
MALE	3	8377 05	24 534	17 102		2 59%		
FEMALE	21	1484 87	6 470	10 015	1 374	0 68%	1 180	0 348
R * M	6	968 52	0 0	4 906		0 0 %	0 885	0 508
R * F	42	1301 76	2 238	17 045		0 24%	1 190	0 233
M * F	63	1050 75	0 0	16 894		0 0 %	0 961	0 563
R*M*F	116	1093 76	132 237	34 385	6 214	13 96%	2 032	0 0
WITHIN	997	538 33	538 333	24 087	12 537	56 83%		
ADDITIVE GENETIC VARIANCE			25 880	40 059	2 749			
DOMINANCE GENETIC VARIANCE			0 0	67 577	0 0			
TOTAL PHENOTYPIC VARIANCE			703 813		14 335			
PHENOTYPIC VARIANCE HALF-SIB			26 449		2 779			
PHENOTYPIC VARIANCE FULL-SIB			109 917					
HERITABILITY (INDIVIDUAL)			0 037	0 057		%RESPONSE 1 =	0 527	
HERITABILITY (HALF-SIB)			0 245	0 379		%RESPONSE 1 =	1 360	
HERITABILITY (FULL-SIB)			0 282	0 182				

TABLE D7 Means and coefficients of variation for proportional branch thickness (BTT) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN %	CV %	N	MEAN %	CV %	N	MEAN %	CV %
SEED PARENTS									
314	105	24 65	11 65	78	26 97	13 06	183	25 64	13 10
439	102	25 05	13 49	68	27 90	9 24	170	26 19	12 90
300	104	25 24	14 23	43	28 77	14 86	147	26 27	15 67
315	104	25 63	12 36	51	27 82	14 59	155	26 35	13 75
193	105	25 44	11 99	61	28 27	10 29	166	26 48	12 42
60	105	25 72	11 64	59	28 68	9 36	164	26 78	12 24
310	105	25 87	13 07	54	28 65	11 43	159	26 82	13 38
110	102	25 87	12 33	52	28 87	10 96	154	26 88	12 93
49	100	26 00	11 69	39	29 16	9 64	139	26 89	12 25
499	104	26 16	10 58	65	28 38	9 01	169	27 01	10 71
72	102	25 70	9 99	53	29 88	11 18	155	27 13	12 79
303	102	26 76	12 66	60	28 19	11 10	162	27 29	12 33
623	103	25 84	13 29	62	29 95	11 32	165	27 38	14 42
73	104	26 71	10 71	55	28 69	10 31	159	27 39	11 09
408	107	27 04	11 14	62	28 32	11 79	169	27 51	11 58
549	107	27 10	11 22	61	28 68	8 79	168	27 67	10 68
422	102	27 08	11 49	53	28 86	9 42	155	27 69	11 17
305	100	26 86	10 02	62	30 45	13 07	162	28 23	13 02
323	105	27 43	10 95	48	30 29	13 21	153	28 32	12 68
415	101	27 48	10 55	42	31 16	12 36	143	28 56	12 64
57	105	27 53	10 71	66	30 47	11 18	171	28 67	11 99
418	103	28 80	12 50	57	29 81	11 89	160	29 16	12 35
POLLEN PARENT									
62	575	25 27	11 74	284	28 00	12 34	859	26 17	12 95
28	570	26 43	12 76	271	28 73	12 04	841	27 17	13 12
448	565	26 82	12 72	353	29 33	11 40	918	27 78	12 95
33	567	26 95	10 78	343	29 49	11 02	910	27 91	11 75
TOTAL	2277	26 36	12 28	1251	28 94	11 80	3528	27 28	12 92

TABLE D8 Combined sites analysis of variance for branch thickness expressed as proportion (%) of stem diameter (BTT)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	5384 76	2 813	2 743		19 49%		
REP/SITE	4	929 63	1 535	0 914		10 63%		
MALE	3	470 51	0 525	0 338		3 64%		
FEMALE	21	138 14	0 659	0 261	2 976	4 56%	4 408	0 001
S * F	21	26 13	0 045	1 000		0 31%	1 115	0 362
R * F	84	22 20	0 212	0 139		1 47%	1 404	0 025
M * F	63	22 27	0 082	0 128		0 57%	1 305	0 143
S*M*F	63	17 06	0 072	0 189		0 50%	1 078	0 338
R/S*M*F	242	15 82	1 343	0 223	4 248	9 30%	2 223	0 0
WITHIN	3010	7 12	7 116	0 183	9 780	49 29%		
ADDITIVE GENETIC VARIANCE			2 636	1 046	5 952			
DOMINANCE GENETIC VARIANCE			0 328	0 513	2 100			
TOTAL PHENOTYPIC VARIANCE			15 087		11 644			
PHENOTYPIC VARIANCE HALF-SIB			0 841		3 363			
PHENOTYPIC VARIANCE FULL-SIB			1 693					
HERITABILITY (INDIVIDUAL)			0 261	0 104		RESPONSE =	3 042	
HERITABILITY (HALF-SIB)			0 783	0 311		RESPONSE =	15 267	
HERITABILITY (FULL-SIB)			0 827	0 309				

TABLE D8 (Continued) Analysis of variance for branch thickness (proportional on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	65369 38	83 482	60 919		7 62%		
MALE	3	33180 56	55 218	36 896		5 04%		
FEMALE	21	10291 68	73 989	30 018	3 263	6 75%	3 898	0 000
R * M	6	1481 50	0 0	4 088		0 0 %	0 813	0 562
R * F	42	2364 90	15 446	16 064		1 41%	1 298	0 137
M * F	63	2098 00	10 255	16 761		0 94%	1 151	0 251
R*M*F	126	1822 63	127 291	26 682	4 280	11 62%	2 496	0 0
WITHIN	2013	730 22	730 223	23 005	16 251	66 63%		
ADDITIVE GENETIC VARIANCE			295 954	120 073	6 526			
DOMINANCE GENETIC VARIANCE			41 022	67 044	2 430			
TOTAL PHENOTYPIC VARIANCE			1012 421		12 070			
PHENOTYPIC VARIANCE HALF-SIB			99 306		3 780			
PHENOTYPIC VARIANCE FULL-SIB			209 943					
HERITABILITY (INDIVIDUAL)			0 292	0 119		%RESPONSE 1 =	3 528	
HERITABILITY (HALF-SIB)			0 745	0 302		%RESPONSE 1 =	5 633	
HERITABILITY (FULL-SIB)			0 664	0 286				

TABLE D8 (Continued) Analysis of variance for branch thickness (proportional) on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	128165 75	298 515	217 737		23 36%		
MALE	3	10656 80	22 864	22 275		1 79%		
FEMALE	21	5948 59	60 861	32 488	2 695	4 76%	2 320	0 012
R * M	6	3197 89	15 877	15 616		1 24%	2 421	0 031
R * F	42	2091 50	31 409	26 089		2 46%	1 584	0 029
M * F	63	1793 23	20 144	25 955		1 58%	1 358	0 078
R*M*F	116	1320 66	153 956	41 562	4 287	12 05%	1 959	0 0
WITHIN	997	674 00	674 008	30 157	8 970	52 75%		
ADDITIVE GENETIC VARIANCE			243 446	129 953	5 391			
DOMINANCE GENETIC VARIANCE			80 578	103 822	3 101			
TOTAL PHENOTYPIC VARIANCE			979 118		10 811			
PHENOTYPIC VARIANCE HALF-SIB			99 177		3 441			
PHENOTYPIC VARIANCE FULL-SIB			199 153					
HERITABILITY (INDIVIDUAL)			0 249	0 133		%RESPONSE	= 2 688	
HERITABILITY (HALF-SIB)			0 614	0 328		%RESPONSE	= 4 223	
HERITABILITY (FULL-SIB)			0 522	0 326				

TABLE D9 Means and coefficients of variation for branch length (BL) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
72	102	152 04	15 05	53	126 88	11 98	155	143 43	16 51
303	102	157 23	16 27	60	139 33	14 96	162	150 60	16 86
300	104	157 39	15 38	43	134 37	13 93	147	150 66	16 59
110	102	158 93	14 90	52	137 23	14 42	154	151 62	16 25
323	105	158 89	17 03	48	136 65	13 97	153	151 91	17 68
415	101	159 09	13 06	42	135 81	15 26	143	152 25	15 28
57	105	162 96	14 33	66	135 77	13 37	171	152 47	16 54
499	104	156 91	17 15	65	146 02	14 43	169	152 72	16 58
315	104	162 36	13 21	51	134 43	14 24	155	153 17	15 99
305	100	165 23	15 85	62	140 42	14 08	162	155 73	17 19
549	107	163 99	15 86	61	141 74	15 11	168	155 91	17 08
314	105	169 85	14 90	78	137 73	14 43	183	156 16	17 96
193	105	167 75	15 53	61	138 09	14 49	166	156 85	17 79
422	102	168 92	12 30	53	131 23	12 93	155	157 06	16 33
439	102	171 43	15 68	68	138 04	12 62	170	158 07	18 13
623	103	168 72	15 85	62	142 33	13 77	165	158 80	17 27
60	105	167 11	14 75	59	144 40	13 96	164	158 94	16 06
310	105	167 60	16 41	54	143 77	12 94	159	159 50	17 08
73	104	170 00	14 94	55	139 88	12 22	159	159 58	16 90
408	107	171 65	15 25	62	144 50	12 71	169	161 69	16 68
418	103	173 20	13 02	57	148 25	13 58	160	164 31	15 06
49	100	171 63	18 30	39	149 00	11 71	139	165 28	18 10
POLLEN PARENTS									
33	567	161 87	15 75	343	137 42	14 12	910	152 66	17 17
28	570	162 30	15 76	271	140 53	14 33	841	155 28	16 76
448	565	167 25	15 50	353	141 76	13 69	918	157 45	16 94
62	575	167 31	15 28	284	138 54	14 14	859	157 80	17 32
TOTAL	2277	164 69	15 64	1251	139 51	14 09	3528	155 78	17 10

TABLE D10 Combined sites analysis of variance for branch length (BL)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	509219 50	306 048	257 536		33 10%		
REP/SITE	4	15388 20	24 961	15 142		2 70%		
MALE	3	4846 86	3 035	3 685		0 33%		
FEMALE	21	4185 65	15 921	8 239	2 561	1 72%	2 586	0 011
S * F	21	1000 81	6 687	1 000		0 72%	1 790	0 185
R * F	84	995 86	0 0	7 374		0 0 %	0 742	0 944
M * F	63	1522 78	13 926	8 351		1 51%	1 682	0 020
S*M*F	63	905 10	0 0	11 370		0 0 %	0 674	0 968
R/S*M*F	242	1342 00	144 096	18 815	7 706	15 58%	3 289	
WITHIN	3010	408 01	408 013	10 514	12 966	44 10%		
ADDITIVE GENETIC VARIANCE			63 683	32 956	5 123			
DOMINANCE GENETIC VARIANCE			55 704	33 406	4 791			
TOTAL PHENOTYPIC VARIANCE			593 661		15 640			
PHENOTYPIC VARIANCE HALF-SIB			30 805		3 563			
PHENOTYPIC VARIANCE FULL-SIB			66 457					
HERITABILITY (INDIVIDUAL)			0 107	0 056		%RESPONSE 1 =	1 678	
HERITABILITY (HALF-SIB)			0 517	0 267		%RESPONSE 1 =	3 683	
HERITABILITY (FULL-SIB)			0 689	0 248				

TABLE D10 (Continued) Analysis of variance for branch length on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	13222 12	15 655	12 393		2 27%		
MALE	3	5150 12	5 922	5 995		0 86%		
FEMALE	21	3752 12	23 465	11 747	2 941	3 40%	2 810	0 030
R * M	6	1868 04	0 0	5 086		0 0 %	0 970	0 448
R * F	42	1412 31	0 0	11 191		0 0 %	0 734	0 875
M * F	63	1848 53	0 0	15 626		0 0 %	0 960	0 564
R*M*F	126	1925 33	168 824	28 098	7 890	24 45%	4 041	0 0
WITHIN	2013	476 48	476 489	15 011	10 255	69 09%		
ADDITIVE GENETIC VARIANCE			93 861	46 988	5 883			
DOMINANCE GENETIC VARIANCE			0 0	62 504	0 0			
TOTAL PHENOTYPIC VARIANCE			674 700		15 772			
PHENOTYPIC VARIANCE HALF SIB			42 068		3 938			
PHENOTYPIC VARIANCE FULL SIB			103 840					
HERITABILITY (INDIVIDUAL)			0 139	0 070		%RESPONSE 1 =	2 194	
HERITABILITY (HALF SIB)			0 558	0 279		%RESPONSE 1 =	4 394	
HERITABILITY (FULL SIB)			0 283	0 226				

TABLE D10 (Continued) Analysis of variance for branch length on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	18467 32	43 637	31 380		9 93%		
MALE	3	1311 32	2 929	2 902		0 67%		
FEMALE	21	1324 88	18 720	7 564	3 100	4 26%	3 227	0 001
R * M	6	659 90	0 0	3 328		0 00%	0 932	0 475
R * F	42	516 35	0 0	7 852		0 00%	0 729	0 878
M * F	63	602 60	0 0	10 159		0 00%	0 851	0 752
R*M*F	116	708 38	104 428	22 145	7 322	23 76%	2 626	0
WITHIN	997	269 75	269 757	12 070	11 767	61 38%		
ADDITIVE GENETIC VARIANCE			74 881	30 255	6 200			
DOMINANCE GENETIC VARIANCE			0 0	40 634	0 0			
TOTAL PHENOTYPIC VARIANCE			395 833		14 254			
PHENOTYPIC VARIANCE HALF-SIB			31 191		4 001			
PHENOTYPIC VARIANCE FULL-SIB			72 757					
HERITABILITY (INDIVIDUAL)			0 189	0 076		%RESPONSE =	2 697	
HERITABILITY (HALF SIB)			0 600	0 242		%RESPONSE =	1 803	
HERITABILITY (FULL SIB)			0 298	0 208				

TABLE D11 Means and coefficients of variation for proportional branch length [illegible] at the Cowichan Lake [illegible] and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN %	CV %	N	MEAN %	CV %	N	MEAN %	CV %
SEED PARENTS									
110	102	37 76	10 89	52	36 04	12 16	154	37 18	11 18
499	104	37 94	9 49	65	36 40	13 13	169	37 35	11 11
315	104	37 97	13 50	51	36 78	13 [illegible]	155	37 58	13 12
623	103	38 58	11 90	62	36 49	9 87	165	37 [illegible]	11 [illegible]
57	105	38 41	10 14	66	36 83	11 32	[illegible]	37 81	11 [illegible]
323	105	38 78	11 18	48	37 01	12 [illegible]	153	38 23	11 83
303	102	39 52	9 47	60	36 47	15 85	162	38 33	12 55
549	107	38 83	11 42	61	37 67	13 91	168	38 11	12 11
314	105	39 51	11 75	78	37 15	12 [illegible]	183	38 51	12 18
300	104	38 81	13 79	43	37 91	9 91	[illegible]	38 57	12 83
408	107	39 32	11 50	62	37 77	12 21	169	38 75	11 52
73	104	40 19	13 33	55	36 07	11 82	159	38 76	13 81
72	102	38 76	9 99	53	39 15	12 [illegible]	155	38 89	11 [illegible]
422	102	40 40	10 54	53	37 44	11 31	155	39 39	11 35
193	105	40 38	12 07	61	37 81	13 83	166	39 11	12 [illegible]
439	102	39 99	11 88	68	39 21	29 [illegible]	[illegible]	39 68	21 36
305	100	41 06	10 62	62	38 38	11 52	162	40 03	11 24
60	105	40 52	9 61	59	39 42	12 [illegible]	164	40 12	12 52
415	101	40 44	9 87	42	39 92	10 [illegible]	143	40 29	11 [illegible]
418	103	40 54	11 75	57	40 16	9 [illegible]	160	40 40	11 5
49	100	40 87	10 54	39	40 21	9 16	139	40 69	10 25
310	105	42 38	10 60	54	40 09	10 13	159	41 61	[illegible] 15
POLLEN PARENTS									
28	570	38 90	10 30	271	38 55	12 33	841	38 79	13 21
448	565	39 08	12 33	353	37 04	12 12	918	38 29	12 52
33	567	39 58	11 51	343	37 39	11 96	910	38 75	11 98
62	575	40 77	11 45	284	38 78	12 69	859	40 [illegible]	12 [illegible]
TOTAL	2277	39 59	11 57	1251	37 86	13 81	3528	38 97	[illegible] 55

TABLE D12 Combined sites analysis of variance for branch length expressed as proportion (%) of tree height (B/T)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	2636.38	1.192	1.356		5.09%		
REP/SITE	4	694.15	1.133	0.682		4.83%		
MALE	3	512.66	0.454	0.374		1.94%		
FEMALE	21	205.33	0.995	0.387	2.561	4.24%	4.659	[illegible]
S * F	21	34.10	0.090	1.000		0.38%	1.188	0.328
R * F	84	34.72	0.119	0.227		0.51%	1.143	0.211
M * F	63	34.33	0.226	0.197		0.96%	1.415	0.088
S*M*F	63	24.35	0.0	0.290		0.00%	0.802	0.851
R/S*M*F	242	30.38	2.066	0.430	3.690	8.81%	1.788	0
WITHIN	3010	16.99	16.993	0.438	10.585	72.48%		
ADDITIVE GENETIC VARIANCE			3.980	1.550	5.123			
DOMINANCE GENETIC VARIANCE			0.905	0.790	2.443			
TOTAL PHENOTYPIC VARIANCE			21.121		11.801			
PHENOTYPIC VARIANCE HALF SIB			1.301		2.929			
PHENOTYPIC VARIANCE FULL SIB			2.436					
HERITABILITY (INDIVIDUAL)			0.188	0.173		RESPONSE =	1.224	
HERITABILITY (HALF SIB)			0.765	0.298		RESPONSE =	1.187	
HERITABILITY (FULL SIB)			0.910	0.318				

TABLE D12 (Continued) Analysis of variance for branch length (proportional to site SES)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
R L P	2	26[illegible]16 00	31 069	24 317		[illegible]		
MALE	3	40475 55	66 927	45 017		3 14%		
FEMALE	21	14545 11	104 280	42 473	2 580	4 89%	3 87[illegible]	[illegible]
R * M	6	1918 16	0 0	5 376		0 [illegible]	1 [illegible]2	1 [illegible]3
R * F	42	3289 56	15 910	22 689		0 [illegible]5	1 [illegible]1	0 [illegible]5
M * F	63	3200 09	17 738	25 503		0 83	1 [illegible]1	[illegible]2[illegible]
R*M*F	126	2732 59	110 258	40 338	2 653	5, [illegible]%	1 531	1 [illegible]
WITHIN	2013	1786 35	1786 358	56 279	10 677	83 [illegible]%		
ADDITIVE GENETIC VARIANCE			417 121	169 891	5 159			
DOMINANCE GENETIC VARIANCE			70 952	102 [illegible]	2 128			
TOTAL PHENOTYPIC VARIANCE			2101 471		11 581			
PHENOTYPIC VARIANCE HALF-SIB			140 414		2 993			
PHENOTYPIC VARIANCE FULL-SIB			294 614					
HERITABILITY (INDIVIDUAL)			0 198	0 081		%RESPONSE =	2 299	
HERITABILITY (HALF-SIB)			0 740	0 302		%RESPONSE =	4 446	
HERITABILITY (FULL-SIB)			0 641	0 288				

TABLE D12 (Continued) Analysis of variance for branch length (proportional) on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	112203 19	263 289	190 630		12 33%		
MALE	3	19833 77	57 757	40 644		2 [illegible]%		
FEMALE	21	9441 28	125 055	52 041	2 960	5 [illegible]%	3 258	[illegible]
R * M	6	3093 35	0 0	15 623		0 0 %	0 918	0 485
R * F	42	3476 84	0 0	47 076		0 0 %	1 032	0 436
M * F	63	2791 21	0 0	47 688		0 0 %	0 828	0 794
R*M*F	116	3370 13	439 609	105 719	5 550	18 25%	2 212	0 0
WITHIN	997	1523 64	1523 649	68 [illegible]	10 332	63 24%		

ADDITIVE GENETIC VARIANCE	500 221	208 163	5 920	
DOMINANCE GENETIC VARIANCE	0 0	190 754	0 0	
TOTAL PHENOTYPIC VARIANCE	2146 070		12 263	
PHENOTYPIC VARIANCE HALF-SIB	184 386		3 594	
PHENOTYPIC VARIANCE FULL-SIB	425 958			
HERITABILITY (INDIVIDUAL)	0 233	0 097		%RESPONSE [illegible] = 2 858
HERITABILITY (HALF-SIB)	0 678	0 282		%RESPONSE [illegible] = 4 876
HERITABILITY (FULL-SIB)	0 429	0 244		

TABLE D13 Means and coefficients of variation for bole taper (TAPER) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN m/m	CV %	N	MEAN m/m	CV %	N	MEAN m/m	CV %
SEED PARENTS									
300	104	16 39	25 40	43	16 16	27 58	147	16 32	25 96
315	104	17 31	23 70	51	17 94	24 38	155	17 62	23 92
57	105	18 14	25 84	66	17 90	20 07	171	18 05	23 15
60	105	17 94	24 74	59	18 78	24 27	164	18 25	24 59
49	100	18 10	24 63	39	18 84	23 90	139	18 31	24 41
193	105	17 86	24 17	61	19 32	27 66	166	18 40	25 86
408	107	18 46	24 21	62	18 77	22 98	169	18 57	23 12
499	104	18 58	19 87	65	18 80	22 18	169	18 67	20 84
623	103	18 18	31 14	62	19 51	25 85	165	18 68	29 23
73	104	18 62	25 82	55	19 21	23 09	159	18 82	24 94
310	105	18 64	26 00	54	19 67	28 81	159	18 99	27 09
303	102	19 47	21 92	60	18 24	20 86	162	19 01	21 74
415	101	18 50	24 69	42	20 36	34 32	143	19 04	28 53
549	107	18 54	19 95	61	20 38	26 23	168	19 21	23 13
314	105	19 71	27 09	78	18 64	21 12	183	19 26	24 38
323	105	20 25	27 58	48	18 41	27 11	153	19 67	27 74
110	102	20 15	27 65	52	18 91	19 29	154	19 73	25 48
418	103	19 85	23 81	57	20 86	22 81	160	20 21	23 19
422	102	20 35	28 94	53	20 10	21 49	155	20 27	26 60
439	102	20 16	23 27	68	20 46	27 31	170	20 28	24 93
305	100	20 49	24 32	62	19 96	20 63	162	20 29	23 66
72	102	19 72	22 23	53	22 27	19 45	155	20 59	21 94
POLLEN PARENTS									
448	565	18 20	23 92	353	18 74	26 91	918	18 41	25 18
28	570	18 55	26 94	271	18 81	24 54	841	18 64	26 17
33	567	19 48	27 73	343	19 08	23 51	910	19 33	26 27
62	575	19 27	22 82	284	20 58	23 02	859	19 70	23 11
TOTAL	2277	18 88	25 59	1251	19 27	24 80	3528	19 01	25 33

TABLE D14 Combined sites analysis of variance for bole taper (TAPER)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	124 1270	0 0	0 0781		0 0 %		
REP/SITE	4	81 8177	0 1003	0 0823		0 42%		
MALE	4	321 3152	0 2301	0 2394		0 96%		
FEMALE	3	160 0427	0 5880	0 3114	4 033	2 45%	2 617	0 008
S * F	21	43 9181	0 2897	0 01		1 21%	1 830	0 084
R * F	84	33 8206	0 0308	0 2248		0 13%	1 058	0 365
M * F	63	39 3816	0 4402	0 2115		1 84%	1 778	0 012
S*M*F	63	22 1455	0 0	0 2767		0 0 %	0 693	0 958
R/S*M*F	242	31 9671	1 7969	0 4538	7 050	7 49%	1 573	0 000
WITHIN	3010	20 3199	20 3199	0 5236	23 707	84 72%		
ADDITIVE GENETIC VARIANCE			2 3521	1 2457	8 066			
DOMINANCE GENETIC VARIANCE			1 7606	0 8460	6 978			
TOTAL PHENOTYPIC VARIANCE			23 8857		25 704			
PHENOTYPIC VARIANCE HALF-SIB			1 034		5 348			
PHENOTYPIC VARIANCE FULL-SIB			2 058					
HERITABILITY (INDIVIDUAL)			0 098	0 052		%RESPONSE 1 =	2 531	
HERITABILITY (HALF-SIB)			0 569	0 301		%RESPONSE 1 =	6 083	
HERITABILITY (FULL-SIB)			0 785	0 303				

TABLE D14 (Continued) Analysis of variance for trait TAPER on site CLES

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	2403 84	0 749	2 768		0 03%		
MALE	3	20471 30	32 170	22 848		1 36%		
FEMALE	21	12447 85	90 825	36 596	5 049	3 85%	4 074	0 001
R * M	6	2041 76	0 0	5 774		0 0 %	0 653	0 687
R * F	42	2928 76	0 0	21 455		0 0 %	0 937	0 585
M * F	63	3252 12	4 529	26 861		0 19%	1 040	0 418
R*M*F	126	3125 57	118 170	46 191	5 759	5 01%	1 480	0 001
WITHIN	2013	2111 43	2111 434	66 520	24 344	89 55%		
ADDITIVE GENETIC VARIANCE			363 299	146 382	10 098			
DOMINANCE GENETIC VARIANCE			18 116	107 443	2 255			
TOTAL PHENOTYPIC VARIANCE			2357 126		25 722			
PHENOTYPIC VARIANCE HALF-SIB			122 153		5 855			
PHENOTYPIC VARIANCE FULL-SIB			248 379					
HERITABILITY (INDIVIDUAL)			0 154	0 062		%RESPONSE	= 3 964	
HERITABILITY (HALF-SIB)			0 744	0 300		%RESPONSE	= 8 707	
HERITABILITY (FULL-SIB)			0 513	0 295				

TABLE D14 (Continued) Analysis of variance for trait TAPER on site GVWS

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	15565 22	32 448	26 598		1 36%		
MALE	3	21970 21	66 708	44 792		2 79%		
FEMALE	21	7579 28	78 867	43 495	4 609	3 30%	2 181	0 [illegible]
R * M	6	2003 48	0 0	10 601		0 0 %	0 612	0 [illegible]
R * F	42	3771 26	4 132	49 802		0 [illegible]%	1 152	0 [illegible]
M * F	63	2978 50	0 0	49 023		0 0 %	0 910	0 656
R*M*F	116	3273 99	333 881	103 425	9 484	13 98%	1 749	0 [illegible]
WITHIN	997	1871 59	1871 597	83 742	22 454	78 39%		
ADDITIVE GENETIC VARIANCE			315 469	173 979	9 218			
DOMINANCE GENETIC VARIANCE			0 0	196 091	0 0			
TOTAL PHENOTYPIC VARIANCE			2355 185		25 188			
PHENOTYPIC VARIANCE HALF-SIB			137 841		6 094			
PHENOTYPIC VARIANCE FULL-SIB			381 787					
HERITABILITY (INDIVIDUAL)			0 134	0 074		%RESPONSE [illegible] =	3 374	
HERITABILITY (HALF-SIB)			0 572	0 316		%RESPONSE [illegible] =	6 970	
HERITABILITY (FULL-SIB)			0 381	0 228				

TABLE D15 Means and coefficients of variation for sinuosity score (SIN) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
303	104	31 73	253 28	85	43 53	211 05	189	37 04	231 39
305	100	34 00	222 07	89	53 93	207 41	189	43 39	218 16
415	101	27 72	239 92	87	64 37	201 00	188	44 68	228 23
193	106	66 98	179 30	87	28 74	230 76	193	49 74	203 25
314	105	58 10	183 61	89	41 57	207 71	194	50 52	193 55
439	102	56 86	192 50	90	50 00	203 89	192	53 65	197 19
57	106	44 34	256 83	91	68 13	160 61	197	55 33	202 75
300	105	31 43	222 00	83	92 98	162 27	188	59 04	199 50
422	103	59 22	159 38	94	78 72	171 61	197	68 53	168 81
49	100	38 00	200 66	84	105 95	184 95	184	69 02	213 49
110	102	64 71	163 68	83	87 95	199 60	185	75 14	188 37
499	105	52 38	183 60	90	103 33	144 67	195	75 90	165 93
315	104	57 69	186 61	83	101 20	167 98	187	77 01	181 94
72	102	65 69	161 02	77	100 00	169 36	179	82 45	170 82
418	104	73 08	150 42	87	91 95	172 52	191	81 58	164 41
310	105	90 48	164 03	78	92 31	150 97	183	91 26	158 05
73	104	99 04	150 55	89	105 62	124 73	193	102 07	138 17
60	105	113 33	147 88	93	94 62	200 37	198	104 55	170 32
623	103	114 56	127 26	91	164 84	155 16	194	138 14	149 01
408	107	107 48	147 78	90	177 78	103 58	197	139 59	127 11
549	107	138 32	114 37	88	175 00	132 04	195	154 87	125 79
323	105	161 90	106 08	88	203 41	114 62	193	180 83	112 03
POLLEN PARENTS									
33	568	47 89	214 05	485	71 34	192 33	1053	58 69	204 91
28	571	58 32	185 46	460	70 87	199 44	1031	63 92	191 24
62	578	69 38	156 80	487	107 19	153 43	1065	86 67	159 58
448	568	114 44	140 61	484	136 57	150 27	1052	124 62	146 75
TOTAL	2285	72 47	172 26	1916	96 82	172 17	4201	83 58	174 59

TABLE D16 Combined sites analysis of variance for stem sinuosity (SIN)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	617589 50	241 833	243 728		1 10%		
REP/SITE	4	99167 38	119 498	82 447		0 55%		
MALE	3	940150 00	871 317	566 485		3 98%		
FEMALE	21	293517 63	1340 730	460 583	43 812	6 12%	7 804	0 000
S * F	21	38925 22	0 0	1 000		0 0 %	0 946	0 541
R * F	84	36391 14	181 016	194 650		0 83%	1 203	[redacted]
M * F	63	33691 33	0 0	187 552		0 0 %	0 962	0 560
S*M*F	63	35005 11	191 760	285 694		0 88%	1 152	0 218
R/S*M*F	252	30259 53	1660 239	347 203	48 754	7 58%	1 753	0 0
WITHIN	3673	17261 99	17261 992	402 696	157 206	78 85%		
ADDITIVE GENETIC VARIANCE			5362 918	1842 330	87 624			
DOMINANCE GENETIC VARIANCE			0 0	750 208	0 0			
TOTAL PHENOTYPIC VARIANCE			21530 723		175 571			
PHENOTYPIC VARIANCE HALF-SIB			1552 822		47 150			
PHENOTYPIC VARIANCE FULL-SIB			2940 741					
HERITABILITY (INDIVIDUAL)			0 249	0 086		%RESPONSE 1 =	43 732	
HERITABILITY (HALF-SIB)			0 863	0 297		%RESPONSE 1 =	81 421	
HERITABILITY (FULL-SIB)			0 912	0 313				

TABLE D16 (Continued) Combined sites analysis of variance for stem sinuosity (transformed)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	426 82	0 164	0 169		0 83%		
REP/SITE	4	74 64	0 082	0 062		0 42%		
MALE	3	885 60	0 823	0 534		4 18%		
FEMALE	21	275 72	1 268	0 432	8 783	6 43%	8 194	0 000
S * F	21	35 90	0 0	1 000		0 0%	0 936	0 552
R * F	84	31 72	0 183	0 169		0 93%	1 239	0 116
M * F	63	30 01	0 0	0 169		0 0%	0 930	0 612
S*M*F	63	32 26	0 275	0 260		1 40%	1 260	0 111
R/S*M*F	252	25 61	1 275	0 294	8 807	6 47%	1 679	0 0
WITHIN	3673	15 63	15 629	0 365	30 832	79 29%		
ADDITIVE GENETIC VARIANCE			5 073	1 729	17 566			
DOMINANCE GENETIC VARIANCE			0 0	0 676	0 0			
TOTAL PHENOTYPIC VARIANCE			19 465		34 40[redacted]			
PHENOTYPIC VARIANCE HALF SIB			1 467		9 445			
PHENOTYPIC VARIANCE FULL-SIB			2 764					
HERITABILITY (INDIVIDUAL)			0 261	0 089		%RESPONSE =	8 968	
HERITABILITY (HALF-SIB)			0 865	0 295		%RESPONSE =	16 335	
HERITABILITY (FULL-SIB)			0 918	0 313				

TABLE D17 Means and coefficients of variation for forking occurence (FORK) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites

GROUP	CLES N	CLES MEAN cm	CLES CV %	GVWS N	GVWS MEAN cm	GVWS CV %	COMBINED N	COMBINED MEAN cm	COMBINED CV %
SEED PARENTS									
549	107	11 22	308 08	88	9 09	359 12	195	10 26	327 95
314	105	19 10	251 63	89	10 11	334 85	194	14 43	281 94
72	102	15 69	280 04	77	16 88	278 52	179	16 20	278 75
439	102	21 57	240 85	90	20 00	239 38	192	20 83	239 79
323	105	18 10	239 68	88	25 00	203 42	193	21 24	220 92
415	101	15 84	292 46	87	27 59	189 01	188	21 28	231 81
110	102	19 61	215 77	83	25 30	212 42	185	22 16	215 35
60	105	22 86	212 41	93	21 51	236 01	198	22 22	222 64
70	104	20 00	191 06	89	20 22	237 83	193	22 80	209 91
499	105	19 05	242 51	90	28 89	195 84	195	23 59	217 67
408	107	19 63	215 03	90	28 89	209 14	197	23 86	215 15
57	106	26 42	204 38	91	24 18	241 51	197	25 38	222 35
303	104	31 73	177 11	85	18 82	238 91	189	25 93	198 51
422	103	18 45	224 51	94	35 11	175 78	197	26 40	199 36
310	105	25 71	179 09	78	34 62	185 22	183	29 51	184 71
193	106	34 91	163 23	87	22 99	206 62	193	29 53	179 84
418	104	28 85	165 04	87	32 18	198 19	191	30 37	182 55
305	100	31 00	175 76	89	35 96	183 95	189	33 30	181 43
300	105	38 10	176 02	83	32 53	186 61	188	35 64	180 22
315	104	32 69	172 84	83	42 17	161 94	187	36 96	168 08
623	103	48 54	152 27	91	38 46	188 96	194	43 81	167 75
49	100	43 00	145 04	84	47 62	132 32	184	45 11	138 63
POLLEN PARENTS									
448	568	18 84	234 71	484	15 70	252 72	1052	17 40	242 59
62	578	18 51	232 83	487	22 18	245 49	1065	20 19	240 89
33	568	26 94	199 53	485	34 64	181 74	1053	30 48	191 13
28	571	38 53	159 49	460	36 52	170 82	1031	37 60	164 74
TOTAL	2285	25 69	201 53	1916	22 14	207 08	4201	26 35	204 31

TABLE D18 Combined sites analysis of variance for forking incidence (FORK)

SOURCE	D.F	MEAN SQUARE	VAR COMP	S.E.	C.V.	VAR COMP %	F RATIO	PROBABILITY
SITE	1	2192.92	0.0	10.795		0.0%		
REP/SITE	4	37622.65	44.352	31.367		1.47%		
MALE	3	91494.50	80.512	55.351		2.66%		
FEMALE	21	14070.04	57.460	23.182	28.758	1.90%	4.501	0.012
S * F	21	3226.61	7.569	1.000		0.25%	1.259	0.341
R * F	84	3261.43	0.0	20.811		0.0%	0.672	0.983
M * F	63	4053.76	0.0	23.214		0.0%	0.976	0.539
S*M*F	63	4154.51	0.0	36.108		0.0%	0.856	0.766
R/S*M*F	252	4853.72	298.362	55.586	65.553	9.86%	1.928	0.0
WITHIN	3673	2517.93	2517.934	58.739	190.433	83.23%		
ADDITIVE GENETIC VARIANCE			229.841	92.728	57.535			
DOMINANCE GENETIC VARIANCE			0.0	92.857	0.0			
TOTAL PHENOTYPIC VARIANCE			2980.768		207.197			
PHENOTYPIC VARIANCE HALF-SIB			86.620		35.321			
PHENOTYPIC VARIANCE FULL-SIB			239.694					
HERITABILITY (INDIVIDUAL)			0.077	0.031		%RESPONSE =	15.977	
HERITABILITY (HALF SIB)			0.663	0.268		%RESPONSE =	46.861	
HERITABILITY (FULL-SIB)			0.479	0.193				

TABLE D18 (continued) Combined sites analysis of variance for forking incidence (transformed)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	1 83	0 0	0 016		0 0%		
REP/SITE	4	56 50	0 067	0 047		1 49%		
MALE	4	139 06	0 123	0 084		2 73%		
FEMALE	3	21 36	0 087	0 035	2 665	1 93%	4 101	0 [illegible]
S * F	21	4 84	0 013	1 000		0 3%	1 226	0 313
R * F	84	4 86	0 0	0 031		0 0 %	0 [illegible]	1 [illegible]
M * F	63	6 05	0 0	0 034		0 0 %	1 [illegible]	0 [illegible]
S*M*F	63	6 04	0 0	0 053		0 0 %	0 833	0 [illegible]
R/S*M*F	252	7 25	0 449	0 083	6 064	9 97%	1 914	[illegible]
WITHIN	3673	3 73	3 734	0 087	17 492	82 98%		

ADDITIVE GENETIC VARIANCE	0 347	0 140	5 331
DOMINANCE GENETIC VARIANCE	0 0	0 137	0 0
TOTAL PHENOTYPIC VARIANCE	4 433		19 059
PHENOTYPIC VARIANCE HALF SIB	0 131		3 279
PHENOTYPIC VARIANCE FULL SIB	0 362		

HERITABILITY (INDIVIDUAL)	0 078	0 032	RESPONSE	1 431
HERITABILITY (HALF-SIB)	0 661	0 268	RESPONSE	1 333
HERITABILITY (FULL-SIB)	0 480	0 194		

TABLE D19 Means and coefficients of variation for lammas flush incidence (LAF) at the Corvallis, Lewisville, and Victoria Watershed (GVWS) sites and combined over sites

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
72	102	1 96	710 59	77	2 60	616 39	179	2 23	663 [illegible]
314	105	1 90	721 06	89	3 37	538 44	194	2 58	616 11
315	104	2 88	583 04	83	3 23	360 41	187	4 81	445 32
415	101	4 95	440 36	87	6 90	484 [illegible]	188	5 85	473 55
519	107	6 54	379 74	88	5 68	409 [illegible]	195	6 15	391 52
323	105	3 81	622 45	88	9 09	359 [illegible]	193	6 22	459 33
499	105	4 76	449 36	90	8 89	400 61	195	6 61	432 56
305	100	12 00	296 82	89	5 62	491 65	189	8 99	351 [illegible]
439	102	10 78	317 13	90	10 00	425 31	192	[illegible] 42	382 [illegible]
57	106	9 43	401 40	91	13 19	323 83	197	[illegible] [illegible]	359 23
300	105	11 43	304 91	83	10 84	381 39	188	[illegible] [illegible]	337 99
422	103	16 50	282 62	94	6 38	385 [illegible]	197	[illegible] 68	325 55
408	107	14 02	316 73	90	8 89	400 61	197	[illegible] 68	341 [illegible]
310	105	9 52	399 70	78	[illegible] 95	280 28	183	[illegible] [illegible]	339 53
193	106	18 87	243 85	87	8 05	340 [illegible]	193	[illegible] 99	278 87
110	102	12 75	285 18	83	16 87	274 96	185	[illegible] 53	281 [illegible]
303	104	13 46	311 54	85	[illegible] 65	340 63	189	15 54	331 19
418	104	17 31	247 40	87	14 94	280 [illegible]	191	16 22	260 51
73	104	22 12	251 69	89	15 73	[illegible] [illegible]	193	[illegible] [illegible]	[illegible] [illegible]
623	103	34 95	186 67	91	20 88	[illegible] [illegible]	194	28 35	217 54
60	105	28 57	246 12	93	34 41	[illegible] [illegible]	198	31 31	228 21
49	100	41 00	170 17	84	21 43	251 69	184	32 [illegible]	198 17
POLLEN									
448	568	5 28	438 51	484	3 51	585 15	1052	4 47	492 58
62	578	7 61	381 44	487	4 11	575 83	1065	6 [illegible]	445 [illegible]
33	568	19 72	275 98	485	18 97	267 [illegible]	1053	19 [illegible]	[illegible] [illegible]
28	571	21 72	232 31	460	22 61	254 94	1031	22 [illegible]	[illegible] [illegible]
TOTAL	2285	13 57	309 98	1916	12 16	345 81	4201	12 94	[illegible] [illegible]

TABLE D20 Combined sites analysis of variance for Jammas flushing incidence (AFLU)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	2060 12	0 0	2 960		[illegible]		
REP/SITE	4	9491 52	6 902	8 372		[illegible]		
MALE	4	85578 50	78 666	51 583		4 26%		
FEMALE	3	13681 92	48 136	21 913	53 679	2 61%	3 051	[illegible]
S * F	21	2371 12	12 409	1 000		[illegible]	1 344	[illegible]
R * F	84	1722 73	0 0	10 800		[illegible]	[illegible]	[illegible]
M * F	63	4054 63	44 042	17 175		2 39%	2 083	[illegible]
S*M*F	63	1946 30	0 0	17 288		[illegible]	0 795	[illegible]
R/S*M*F	252	2449 21	118 561	28 160	84 244	6 42%	1 616	[illegible]
WITHIN	3673	1521 03	1521 027	35 483	301 743	82 37%		
ADDITIVE GENETIC VARIANCE			192 543	87 652	107 358			
DOMINANCE GENETIC VARIANCE			176 169	68 791	102 691			
TOTAL PHENOTYPIC VARIANCE			1839 612		331 843			
PHENOTYPIC VARIANCE HALF-SIB			78 110		68 379			
PHENOTYPIC VARIANCE FULL SIB			222 180					
HERITABILITY (INDIVIDUAL)			0 105	0 048		%RESPONSE		34 132
HERITABILITY (HALF-SIB)			0 616	0 281		RESPONSE		81 278
HERITABILITY (FULL-SIB)			0 632	0 193				

TABLE D20 (continued) Combined sites analysis of variance for lammas flushing incidence (transformed)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	4 15	0 0	0 005		0 0 %		
REP/SITE	4	14 35	0 010	0 013		0 38 %		
MALE	3	125 83	0 116	0 076		4 36 %		
FEMALE	21	19 66	0 068	0 032	2 487	2 58 %	2 980	0 000
S * F	21	3 51	0 019	1 000		0 71 %	1 961	0 115
R * F	84	2 47	0 0	0 015		0 0 %	0 704	0 973
M * F	63	5 91	0 064	0 025		2 43 %	2 488	0 000
S*M*F	63	2 83	0 0	0 025		0 0 %	0 806	0 845
R/S*M*F	252	3 51	0 171	0 040	3 936	6 45 %	1 610	0 000
WITHIN	3673	2 18	2 176	0 051	14 038	82 76 %		
ADDITIVE GENETIC VARIANCE			0 273	0 126	4 975			
DOMINANCE GENETIC VARIANCE			0 258	0 100	4 831			
TOTAL PHENOTYPIC VARIANCE			2 641		15 468			
PHENOTYPIC VARIANCE HALF SIB			0 112		3 186			
PHENOTYPIC VARIANCE FULL SIB			0 322					
HERITABILITY (INDIVIDUAL)			0 103	0 048		%RESPONSE =	1 800	
HERITABILITY (HALF SIB)			0 610	0 281		%RESPONSE =	3 884	
HERITABILITY (FULL SIB)			0 624	0 196				

TABLE D21 Components of variance and covariance for traits DM12 and BN.

FOR VARIABLES	DM12			BN			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	4 8518	S E	2 1706	637 1118	S E	232 4150	31 2220
ADDITIVE GENETIC VARIANCE	19 4072	S E	8 6824	2548 4473	S E	929 6599	148 8795
DOMINANCE GENETIC VARIANCE	6 1308	S E	8 4330	0 0	S E	631 8674	-3 0654
PHENOTYPIC VARIANCE INDIVIDUAL	138 3089			13522 1914			466 0059
PHENOTYPIC VARIANCE HALF SIB	7 9453			776 3027			60 5851
PHENOTYPIC VARIANCE FULL-SIB	14 8172			1312 1626			124 8149
HERITABILTY FOR INDIVIDUAL SELECTION	0 1403	S E	0 0628	0 1885	S E	0 0688	0 1626
COEFFICIENT OF VARIATION (PI)	14 4858			21 7566			
%RESPONSE /1 (INDIVIDUAL)	2 0326			4 1003			
HERITABILTY FOR HALF-SIB SELECTION	0 6106	S E	1 0928	0 8207	S E	1 1975	0 7229
COEFFICIENT OF VARIATION (PHS)	3 4719			5 2129			
%RESPONSE /1 (HALF-SIB)	4 2403	CRy=	3 2908	8 5565	CRy=	4 9412	
GENETIC CORRELATIONS	0 6694	S E	0 1576				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 3408						
PHENOTYPIC CORRELATIONS H S FAMILIES	0 7714						
ENVIRONMENTAL CORRELATIONS	0 2776						

TABLE D22 Components of variance and covariance for traits DM12 and BA

FOR VARIABLES	DM12			BA			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	4 8518	S E	2 1706	8 8509	S E	2 8756	1 1636
ADDITIVE GENETIC VARIANCE	19 4072	S E	8 6824	35 4036	S E	11 5024	4 6544
DOMINANCE GENETIC VARIANCE	6 1308	S E	8 4330	3 9828	S E	2 0089	-5 0568
PHENOTYPIC VARIANCE INDIVIDUAL	138 3089			48 6369			-2 8303
PHENOTYPIC VARIANCE HALF-SIB	7 9453			9 6585			0 6388
PHENOTYPIC VARIANCE FULL-SIB	14 8172			12 4912			-0 1134
HERITABILTY FOR INDIVIDUAL SELECTION	0 1403	S E	0 0628	0 7279	S E	0 2365	0 3196
COEFFICIENT OF VARIATION (PI)	14 4858			10 6078			
%RESPONSE /1 (INDIVIDUAL)	2 0326			7 7216			
HERITABILTY FOR HALF-SIB SELECTION	0 6106	S E	1 0928	0 9164	S E	1 1909	0 7481
COEFFICIENT OF VARIATION (PHS)	3 4719			4 7271			
%RESPONSE /1 (HALF-SIB)	4 2403	CRy=	0 9224	8 6638	CRx=	1 2558	
GENETIC CORRELATIONS	0 1776	S E	0 2611				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0 0345						
PHENOTYPIC CORRELATIONS H S FAMILIES	0 0729						
ENVIRONMENTAL CORRELATIONS	-0 1887						

TABLE D23. Components of variance and covariance for traits DM12 and BT

FOR VARIABLES	DM12			BT			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	4 8518	S E	2 1706	13 0385	S E	8 7298	1 6984
ADDITIVE GENETIC VARIANCE	19 4072	S E	8 6824	52 1540	S E	34 9191	6 7934
DOMINANCE GENETIC VARIANCE	6 1308	S E	8 4330	56 1908	S E	50 6246	13 5694
PHENOTYPIC VARIANCE INDIVIDUAL	138 3089			997 6316			290 2927
PHENOTYPIC VARIANCE HALF-SIB	7 9453			29 7812			7 7853
PHENOTYPIC VARIANCE FULL SIB	14 8172			96 6582			21 6033
HERITABILTY FOR INDIVIDUAL SELECTION	0 1403	S E	0 0628	0 2523	S E	0 0350	0 0850
COEFFICIENT OF VARIATION (PI)	14 4858			16 2497			
%RESPONSE /1 (INDIVIDUAL)	2 0326			0 8495			
HERITABILTY FOR HALF-SIB SELECTION	0 6106	S E	1 0928	0 4378	S E	1 1725	0 5171
COEFFICIENT OF VARIATION (PHS)	3 4719			2 8076			
%RESPONSE /1 (HALF-SIB)	4 2403	CRy=	0 7667	2 4584	CRx=	0 6200	
GENETIC CORRELATIONS	0 2135	S E	0 3694				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 7815						
PHENOTYPIC CORRELATIONS H S FAMILIES	0 5061						
ENVIRONMENTAL CORRELATIONS	0 8455						

TABLE D24 Components of variance and covariance for traits DM12 and BTT

FOR VARIABLES	DM12			BTT			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	4 8518	S E	2 1706	65 8913	S E	26 1388	-14 6056
ADDITIVE GENETIC VARIANCE	19 4072	S E	8 6824	263 5652	S E	104 5552	-58 4265
DOMINANCE GENETIC VARIANCE	6 1308	S E	8 4330	32 8068	S E	51 3189	-3 1042
PHENOTYPIC VARIANCE INDIVIDUAL	138 3089			1008 7383			-36 4907
PHENOTYPIC VARIANCE HALF-SIB	7 9453			84 1252			-16 2475
PHENOTYPIC VARIANCE FULL SIB	14 8172			169 3226			-21 2929
HERITABILTY FOR INDIVIDUAL SELECTION	0 1403	S E	0 0628	0 2613	S E	0 1036	0 1915
COEFFICIENT OF VARIATION (PI)	14 4858			11 6439			
%RESPONSE /1 (INDIVIDUAL)	2 0326			3 0423			
HERITABILTY FOR HALF-SIB SELECTION	0 6106	S E	1 0928	0 7833	S E	1 2429	0 6916
COEFFICIENT OF VARIATION (PHS)	3 4719			3 3626			
%RESPONSE /1 (HALF-SIB)	4 2403	CRy=	-3 9231	5 2075	CRx=	-3 7996	
GENETIC CORRELATIONS	-0 8169	S E	0 0991				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0 0977						
PHENOTYPIC CORRELATIONS H S FAMILIES	-0 6284						
ENVIRONMENTAL CORRELATIONS	0 0737						

TABLE D25 Components of variance and covariance for traits BN and BA

FOR VARIABLES	BN			BA			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	637 1118	S E	232 4150	8 8509	S E	2 8756	14 3451
ADDITIVE GENETIC VARIANCE	2548 4473	S E	929 6599	35 4036	S E	11 5024	57 3802
DOMINANCE GENETIC VARIANCE	0.0	S E	631 8674	3 9828	S E	2 0089	-1 9914
PHENOTYPIC VARIANCE INDIVIDUAL	13522 1914			48 6369			226 3008
PHENOTYPIC VARIANCE HALF-SIB	776 3027			9 6585			32 3118
PHENOTYPIC VARIANCE FULL-SIB	1312 1626			12 4912			99 2004
HERITABILTY FOR INDIVIDUAL SELECTION	0 1885	S E	0 0688	0 7279	S E	0 2365	0 3704
COEFFICIENT OF VARIATION (PI)	21 7566			10 6078			
%RESPONSE 1 (INDIVIDUAL)	4 1003			7 7216			
HERITABILTY FOR HALF-SIB SELECTION	0 8207	S E	1 1975	0 9164	S E	1 1909	0 8672
COEFFICIENT OF VARIATION (PHS)	5 2129			4 7271			
%RESPONSE /1 (HALF SIB)	8 5565	CRy=	1 7272	8 6638	CRx=	1 5662	
GENETIC CORRELATIONS	0 1910	S E	0 2345				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 2790						
PHENOTYPIC CORRELATIONS H S FAMILIES	0 3732						
ENVIRONMENTAL CORRELATIONS	0 4433						

TABLE D26 Components of variance and covariance for traits BN and BTT

FOR VARIABLES	BN		BTT		COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	637 1118	S E 232 4150	65 8913	S E 26 1388	-120 5745
ADDITIVE GENETIC VARIANCE	2548 4473	S E 929 6599	263 5652	S E 104 5552	-482 2981
DOMINANCE GENETIC VARIANCE	0 0	S E 631 8674	32 8068	S E 51 3189	-16 4034
PHENOTYPIC VARIANCE INDIVIDUAL	13522 1914		1008 7383		-587 4219
PHENOTYPIC VARIANCE HALF SIB	776 3027		84 1252		-118 7056
PHENOTYPIC VARIANCE FULL-SIB	1312 1626		169 3226		-199 9982
HERITABILTY FOR INDIVIDUAL SELECTION	0 1885	S E 0 0688	0 2613	S E 0 1036	0 2219
COEFFICIENT OF VARIATION (PI)	21 7566		11 6439		
%RESPONSE /1 (INDIVIDUAL)	4 1003		3 0423		
HERITABILTY FOR HALF-SIB SELECTION	0 8207	S E 0 1975	0 7833	S E 0 2429	0 8018
COEFFICIENT OF VARIATION (PHS)	5 2129		3 3626		
%RESPONSE /1 (HALF-SIB)	8 5565	CRy= -4 9192	5 2675	CRx= -3 1731	
GENETIC CORRELATIONS	-0 5885	S E 0 1758			
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0 1591				
PHENOTYPIC CORRELATIONS H S FAMILIES	-0 4645				
ENVIRONMENTAL CORRELATIONS	-0 0368				

TABLE D27 Means and standard deviations for knottiness index (KI) over both sites

GROUP	COUNT	MEAN	STANDARD DEVIATION	STANDARD ERROR	MINIMUM	MAXIMUM	95 PCT CONF INT FOR MEAN
SEED PARENTS							
300	147	25 8267	7 4739	6164	10 7311	47 1342	24 6085 TO 27 0450
193	166	28 7409	8 1277	6308	13 0243	57 0507	27 4954 TO 29 9865
315	155	28 8089	9 7207	7808	10 2643	67 4298	27 2664 TO 30 3513
49	139	29 7855	9 2425	7839	15 4108	57 6035	28 2354 TO 31 3355
314	183	30 1711	9 9930	7387	12 6259	74 9487	28 7135 TO 31 6286
73	159	30 5226	9 2288	7319	15 1229	89 8677	29 0771 TO 31 9682
310	159	30 5444	11 0273	8745	10 4307	83 6777	28 8172 TO 32 2717
60	164	30 0695	10 6735	8335	4 9164	62 8962	29 0238 TO 32 3153
72	155	30 7905	9 7992	7871	5 4127	53 6272	29 2356 TO 32 3454
415	143	31 0496	9 3946	7856	12 4129	62 0864	29 4966 TO 32 6026
439	170	31 2549	10 3964	7974	9 1114	71 2551	29 6808 TO 32 8290
110	154	31 3072	9 4954	7652	16 2091	63 6287	29 7955 TO 32 8188
499	169	31 3094	9 5930	7379	11 9886	60 0460	29 8526 TO 32 7662
418	160	31 5488	9 2661	7325	13 5790	59 2187	30 1020 TO 32 9956
408	169	31 9660	8 4776	6521	14 9646	55 5237	30 6786 TO 33 2534
549	168	32 1633	8 7404	6743	10 9531	54 7517	30 8320 TO 33 4947
57	171	32 4989	10 7578	8227	10 8522	73 3332	30 8750 TO 34 1229
323	153	33 3764	11 3164	9149	4 4183	66 2064	31 5689 TO 35 1840
623	165	33 9339	9 9908	7778	12 6121	66 2065	32 3981 TO 35 4697
305	162	33 9977	11 6097	9121	11 9714	78 4851	32 1964 TO 35 7990
422	155	34 8449	10 4914	8427	8 1963	62 1096	33 1802 TO 36 5096
303	162	35 3462	11 2436	8834	13 1678	95 3615	33 6017 TO 37 0907
POLLEN PARENTS							
62	859	29 8380	9 2682	3162	10 9531	66 4334	29 2173 TO 30 4587
24	841	31 1511	10 4379	3599	5 4127	89 8677	30 4446 TO 31 8575
33	910	31 9319	9 8152	3254	4 1183	74 9487	31 2934 TO 32 5705
448	918	32 6107	10 5160	3471	4 9164	95 3615	31 9295 TO 33 2918
TOTAL	3528	31 4126	10 0741	1696	4 4183	95 3615	31 0800 TO 31 7451

TABLE D28 Combined sites analysis of variance for knottiness index (KI) x10

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
SITE	1	9688850 00	5865 523	4899 680		43 60%		
REP/SITE	4	233768 44	366 884	229 948		2 73%		
MALE	4	75104 75	72 819	54 867		0 54%		
FEMALE	3	66856 06	279 607	129 687	4 294	2 08%	3 272	0 006
S * F	21	19256 72	96 840	1 000		0 72%	1 542	0 [illegible]
R * F	84	12663 69	82 299	81 140		0 61%	1 251	0 [illegible]
M * F	63	11126 70	11 498	69 510		0 09%	1 118	0 329
S*M*F	63	9949 73	0 0	112 296		0 0 %	0 983	0 519
R/S*M*F	242	10122 07	635 125	143 386	6 471	4 72%	1 686	0 0
WITHIN	3010	6005 36	6005 363	154 749	19 899	44 64%		
ADDITIVE GENETIC VARIANCE			1118 428	518 749	8 587			
DOMINANCE GENETIC VARIANCE			45 991	278 041	1 741			
TOTAL PHENOTYPIC VARIANCE			7219 480		21 818			
PHENOTYPIC VARIANCE HALF-SIB			403 222		5 156			
PHENOTYPIC VARIANCE FULL-SIB			617 163					
HERITABILITY (INDIVIDUAL)			0 155	0 072		%RESPONSE 1 =	3 380	
HERITABILITY (HALF-SIB)			0 693	0 322		%RESPONSE 1 =	7 151	
HERITABILITY (FULL SIB)			0 925	0 420				

TABLE D29 Components of variance and covariance for traits KI and BT

FOR VARIABLES	KI			BT			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	279 6069	S E	129 6874	13 0385	S E	8 7298	33 7012
ADDITIVE GENETIC VARIANCE	1118 4277	S E	518 7493	52 1540	S E	34 9191	134 8044
DOMINANCE GENETIC VARIANCE	45 9912	S E	278 0405	56 1908	S E	50 6246	-1 6992
PHENOTYPIC VARIANCE INDIVIDUAL	7219 4805			997 6316			1006 9375
PHENOTYPIC VARIANCE/HALF-SIB	403 2217			29 7812			40 0529
PHENOTYPIC VARIANCE FULL-SIB	617 1631			96 6582			103 1552
HERITABILTY FOR INDIVIDUAL SELECTION	0 1549	S E	0 0719	0 0523	S E	0 0350	0 0900
COEFFICIENT OF VARIATION (PI)	21 8176			16 2497			
%RESPONSE /i (INDIVIDUAL)	3 3799			0 8495			
HERITABILTY FOR HALF-SIB SELECTION	0 6934	S E	1 2865	0 4378	S E	1 1725	0 5510
COEFFICIENT OF VARIATION (PHS)	5 1562			2 8076			
%RESPONSE /i (HALF-SIB)	7 1509	CRy=	3 1714	2 4584	CRx=	1 7269	
GENETIC CORRELATIONS	0 5582	S E	0 2713				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 3752						
PHENOTYPIC CORRELATIONS H S FAMILIES	0 3655						
ENVIRONMENTAL CORRELATIONS	0 3631						

TABLE D30 Components of variance and covariance for traits KI and BN

FOR VARIABLES	KI		BN		COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	279 6069	S E 129 6874	637 1118	S E 292 4150	150 4556
ADDITIVE GENETIC VARIANCE	1118 4277	S E 518 7493	2548 4473	S E 929 6590	601 8223
DOMINANCE GENETIC VARIANCE	45 9912	S E 278 0405	0 0	S E 631 8674	-22 9956
PHENOTYPIC VARIANCE INDIVIDUAL	7219 4805		13522 1914		6540 2500
PHENOTYPIC VARIANCE HALF-SIB	403 2217		776 3027		256 9263
PHENOTYPIC VARIANCE FULL SIB	617 1631		1312 1626		399 2683
HERITABILTY FOR INDIVIDUAL SELECTION	0 1549	S E 0 0719	0 1885	S E 0 0688	0 1709
COEFFICIENT OF VARIATION (PI)	21 8176		21 7566		
%RESPONSE /1 (INDIVIDUAL)	3 3799		4 1003		
HERITABILTY FOR HALF-SIB SELECTION	0 6934	S E 1 2[illegible]	0 8207	S E [illegible] 1975	0 7544
COEFFICIENT OF VARIATION (PHS)	5 1562		5 2129		
%RESPONSE /1 (HALF-SIB)	7 1509	CRy= 2 7732	8 5565	CRx= 2 8037	
GENETIC CORRELATIONS	0 3565	S E 0 2539			
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 6619				
PHENOTYPIC CORRELATIONS H S FAMILIES	0 4592				
ENVIRONMENTAL CORRELATIONS	0 7258				

TABLE 031. Components of variance and covariance for traits KI and BTT

FOR VARIABLES	KI			BTT			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	279 6069	S E	129 6874	65 8913	S E	26 1388	71 1642
ADDITIVE GENETIC VARIANCE	1118 4277	S E	518 7493	263 5652	S E	104 5552	284 6563
DOMINANCE GENETIC VARIANCE	45 9912	S E	278 0405	32 8068	S E	51 3189	181 9109
PHENOTYPIC VARIANCE INDIVIDUAL	7219 4805			1008 7383			328 5469
PHENOTYPIC VARIANCE HALF-SIB	403 2217			84 1252			109 4626
PHENOTYPIC VARIANCE FULL-SIB	617 1631			169 3226			224 0988
HERITABILTY FOR INDIVIDUAL SELECTION	0 1549	S E	0 0719	0 2613	S E	0 1036	0 2012
COEFFICIENT OF VARIATION (PI)	21 8176			11 6439			
%RESPONSE /1 (INDIVIDUAL)	3 3790			3 0423			
HERITABILTY FOR HALF-SIB SELECTION	0 6934	S E	1 2865	0 7833	S E	1 2429	0 7975
COEFFICIENT OF VARIATION (PHS)	5 1562			3 3626			
%RESPONSE /1 (HALF SIB)	7 1509	CRy=	3 9846	5 2675	CRy=	2 5385	
GENETIC CORRELATIONS	0 5243	S E	0 2199				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 4923						
PHENOTYPIC CORRELATIONS H S FAMILIES	0 5943						
ENVIRONMENTAL CORRELATIONS	0 4896						

TABLE D32 Components of variance and covariance for traits KI and BA

FOR VARIABLES	KI			BA			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	279 6069	S E	129 6874	8 8509	S E	2 8756	-4 9000
ADDITIVE GENETIC VARIANCE	1118 4277	S E	518 7493	35 4036	S E	11 5024	-19 7335
DOMINANCE GENETIC VARIANCE	45 9912	S E	278 0405	3 9828	S E	2 0089	5 4062
PHENOTYPIC VARIANCE INDIVIDUAL	7219 4805			48 6369			-21 1211
PHENOTYPIC VARIANCE HALF-SIB	403 2217			9 6585			6 0128
PHENOTYPIC VARIANCE FULL SIB	617 1631			12 4912			-11.2558
HERITABILTY FOR INDIVIDUAL SELECTION	0 1549	S E	0 0719	0 7279	S E	0 2365	0 3258
COEFFICIENT OF VARIATION (PI)	21 8176			10 6078			
%RESPONSE /1 (INDIVIDUAL)	3 3799			7 7216			
HERITABILTY FOR HALF-SIB SELECTION	0 6934	S E	1 2865	0 9164	S E	1 1909	1 1971
COEFFICIENT OF VARIATION (PHS)	5 1562			4 7271			
%RESPONSE /1 (HALF-SIB)	7 1509	CR.=	1 8152	8 6638	CR.=	0 7414	
GENETIC CORRELATIONS	-0 0992	S E	1 2718				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0 0525						
PHENOTYPIC CORRELATIONS H S FAMILIES	-0 0963						
ENVIRONMENTAL CORRELATIONS	-0 0401						

TABLE D33 Components of variance and covariance for traits KI and DM12

FOR VARIABLES	KI			DM12			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	279 6069	S E	129 6874	4 8518	S E	2 1206	-11 8016
ADDITIVE GENETIC VARIANCE	1118 4277	S E	518 7493	19 4072	S E	8 6824	-47 3666
DOMINANCE GENETIC VARIANCE	45 9912	S E	278 0405	6 1308	S E	8 4330	-26 0610
PHENOTYPIC VARIANCE INDIVIDUAL	7219 4805			138 3089			9 5703
PHENOTYPIC VARIANCE HALF-SIB	403 2217			7 9453			-16 8112
PHENOTYPIC VARIANCE FULL SIB	617 1631			14 8172			-19 4018
HERITABILTY FOR INDIVIDUAL SELECTION	0 1549	S E	0 0719	0 1403	S E	0 0628	0 1471
COEFFICIENT OF VARIATION (PI)	21 8176			14 4858			
%RESPONSE /1 (INDIVIDUAL)	3 3799			2 0326			
HERITABILTY FOR HALF-SIB SELECTION	0 6934	S E	1 2865	0 6106	S E	1 0928	0 6557
COEFFICIENT OF VARIATION (PHS)	5 1562			3 4719			
%RESPONSE /1 (HALF-SIB)	7 1509	CRy=	2 1574	4 2403	CRy=	1 4927	
GENETIC CORRELATIONS	-0 3215	S E	0 2888				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0 0096						
PHENOTYPIC CORRELATIONS H S FAMILIES	-0 2975						
ENVIRONMENTAL CORRELATIONS	0 0669						

APPENDIX E: Tables of means and analyses of variance and covariance for wood density traits.

TABLE E1 Means and standard deviations for wood density at site CLES

GROUP	COUNT	MEAN	STANDARD DEVIATION	STANDARD ERROR	MINIMUM	MAXIMUM	95 PCT CONF INT FOR MEAN
SEED PARENTS							
110	99	339 4949	24 2558	2 4378	285 2000	404 0000	334 6572 TO 344 3327
408	103	345 6184	21 3852	2 1071	296 5000	440 9000	341 4389 TO 349 7980
193	105	345 8324	22 6667	2 2120	288 1000	410 1000	341 4458 TO 350 2189
623	94	347 7500	24 5873	2 5360	303 0000	418 2000	342 7140 TO 352 7860
314	101	351 6050	20 1674	2 0067	311 0000	401 6000	347 6236 TO 355 5863
549	102	352 6010	26 2154	2 5957	299 1000	405 1000	347 4518 TO 357 7502
418	99	357 1576	22 4651	2 2578	310 5000	412 4000	352 6770 TO 361 6382
300	97	357 4979	20 7526	2 1071	315 2000	409 7000	353 3154 TO 361 6805
310	100	357 8410	23 9978	2 3998	302 1000	442 8000	353 0793 TO 362 6027
439	96	363 2437	22 5989	2 3065	318 2000	419 5000	358 6648 TO 367 8227
422	98	364 0592	19 6184	1 9818	299 5000	423 9000	360 1259 TO 367 9924
72	96	364 6208	21 6802	2 2127	314 1000	419 6000	360 2280 TO 369 0136
73	102	368 1598	26 9444	2 6679	308 6000	429 9000	362 8674 TO 373 4522
57	99	368 5313	23 2008	2 3318	304 1000	417 2000	363 9040 TO 373 1586
303	95	370 3432	19 4941	2 0000	322 6000	413 8000	366 3720 TO 374 3143
49	95	370 5537	25 9850	2 6660	316 1000	432 8000	365 2603 TO 375 8471
315	102	371 5627	23 9418	2 3706	314 1000	431 1000	366 8601 TO 376 2654
60	102	375 6892	22 4611	2 2240	325 3000	441 6000	371 2774 TO 380 1010
415	99	377 4798	21 5213	2 1630	324 8000	431 2000	373 1875 TO 381 7721
323	97	377 4938	20 5047	2 0819	326 0000	434 7000	373 3612 TO 381 6264
499	98	379 0745	24 0179	2 4262	322 4000	439 3000	374 2592 TO 383 8898
305	94	382 8223	27 8421	2 8717	323 2000	445 6000	377 1197 TO 388 5249
POLLEN PARENTS							
448	544	354 9105	24 2572	1 0400	285 2000	432 8000	352 8675 TO 356 9534
24	540	363 9013	27 3602	1 1774	292 6000	445 6000	361 5885 TO 366 2141
33	539	364 1707	25 8854	1 1150	288 1000	440 9000	361 9805 TO 366 3609
62	550	369 0138	24 3616	1 0388	307 6000	434 7000	366 9733 TO 371 0543
TOTAL	2173	363 0113	25 9797	5573	285 2000	445 6000	361 9184 TO 364 1043

TABLE E2 Analysis of variance for wood density (WD) at the Cowichan Lake site (CLES)

SOURCE	D.F.	MEAN SQUARE	VAR COMP	S.E.	C.V.	VAR COMP %	F RATIO	PROBABILITY
REP	2	56492.28	75.454	55.166		10.55%		
MALE	3	18752.98	31.113	21.903		4.35%		
FEMALE	21	15137.61	143.079	45.300	3.295	20.01%	14.913	0.000
R * M	6	1847.86	4.614	5.151		0.65%	1.849	0.095
R * F	42	1001.74	0.0	7.535		0.0%	1.002	0.479
M * F	63	1012.69	0.0	8.819		0.0%	1.013	0.466
R*M*F	126	999.34	75.318	15.404	2.391	10.53%	2.592	0.0
WITHIN	1909	385.52	385.523	12.472	5.409	53.91%		
ADDITIVE GENETIC VARIANCE			572.316	181.198	6.590			
DOMINANCE GENETIC VARIANCE			0.0	35.276	0.0			
TOTAL PHENOTYPIC VARIANCE			639.647		6.967			
PHENOTYPIC VARIANCE HALF-SIB			153.197		3.410			
PHENOTYPIC VARIANCE FULL-SIB			214.709					
HERITABILITY (INDIVIDUAL)			0.895	0.283		%RESPONSE 1 =	6.234	
HERITABILITY (HALF-SIB)			0.934	0.296		%RESPONSE 1 =	6.369	
HERITABILITY (FULL-SIB)			0.811	0.422				

TABLE E3 Means and standard deviations for Pilodyn values at site CLES

GROUP	COUNT	MEAN	STANDARD DEVIATION	STANDARD ERROR	MINIMUM	MAXIMUM	95 PCT CONF INT FOR MEAN
SEED PARENTS							
305	94	148 9787	17 7146	1 8271	108 0000	193 0000	145 3504 TO 152 6070
323	97	153 2887	15 5382	1 5777	118 0000	195 0000	150 1570 TO 156 .203
499	98	157 0204	17 9271	1 8109	115 0000	200 0000	153 4263 TO 160 6146
415	99	157 6162	15 4621	1 5540	130 0000	203 0000	154 5323 TO 160 7000
57	99	159 5758	19 2715	1 9369	120 0000	223 0000	155 7321 TO 163 4194
315	102	160 6765	17 3006	1 7130	120 0000	200 0000	157 2783 TO 164 0746
303	95	160 7368	16 1668	1 6587	130 0000	203 0000	157 4435 TO 164 0302
49	95	162 0947	19 8928	2 0410	108 0000	208 0000	158 0424 TO 166 1471
73	102	162 1471	20 8000	2 0595	113 0000	220 0000	158 0615 TO 166 2326
72	96	163 4375	17 1113	1 7464	123 0000	198 0000	159 9704 TO 166 9046
60	102	165 4314	16 5347	1 6372	125 0000	215 0000	162 1837 TO 168 6791
314	101	168 1287	17 9998	1 7910	128 0000	218 0000	164 5753 TO 171 6821
418	99	169 9394	21 1437	2 1250	128 0000	225 0000	165 7224 TO 174 1564
422	98	170 1429	19 2354	1 9431	130 0000	220 0000	166 2864 TO 173 9993
439	96	170 6875	17 2574	1 7613	135 0000	210 0000	167 1908 TO 174 1842
300	97	172 1753	19 4519	1 9750	128 0000	230 0000	168 2548 TO 176 0957
310	100	172 7700	18 4511	1 8451	125 0000	213 0000	169 1089 TO 176 4311
408	103	173 9903	17 5015	1 7245	135 0000	235 0000	170 5698 TO 177 4108
549	102	174 6176	18 4198	1 8238	140 0000	218 0000	170 9997 TO 178 2356
623	94	180 6489	17 3526	1 7898	133 0000	225 0000	177 0948 TO 184 2031
110	99	183 9192	23 8668	2 3987	140 0000	253 0000	179 1590 TO 188 6793
193	105	184 6095	20 0890	1 9605	135 0000	230 0000	180 7218 TO 188 4972
POLLEN PARENTS							
62	550	161 4218	18 3829	7838	108 0000	215 0000	159 8821 TO 162 9615
33	539	164 7254	19 9710	8602	108 0000	230 0000	163 0356 TO 166 4152
448	544	169 9890	18 8428	8079	125 0000	225 0000	168 4020 TO 171 5759
24	540	172 0907	23 1865	9978	118 0000	253 0000	170 1307 TO 174 0508
TOTAL	2173	167 0373	20 5968	4418	108 0000	253 0000	166 1708 TO 167 9038

TABLE E4 Analysis of variance for Pilodyn measures (PIN) at the Cowichan Lake site (CLES)

SOURCE	D F	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	36459 51	48 889	35 604		10 76%		
MALE	3	12654 70	20 391	14 778		4 49%		
FEMALE	21	8871 27	81.637	26 566	5 409	17 97%	10 924	0 000
R * M	6	1198 61	3 411	3 335		0 75%	2 088	0 059
R * F	42	429 98	0 0	3 549		0 0 %	0 749	0 858
M * F	63	956 24	15 248	7 404		3 36%	1 666	0 008
R*M*F	126	574 11	40 467	8 859	3 808	8 91%	2 350	0 0
WITHIN	1909	244 32	244 320	7 904	9 358	53 77%		
ADDITIVE GENETIC VARIANCE			326 550	106 266	10 818			
DOMINANCE GENETIC VARIANCE			60 994	29 615	4 676			
TOTAL PHENOTYPIC VARIANCE			405 474		12 055			
PHENOTYPIC VARIANCE HALF-SIB			91 258		5 719			
PHENOTYPIC VARIANCE FULL-SIB			140 554					
HERITABILITY (INDIVIDUAL)			0 805	0 262		%RESPONSE 1 =	9 709	
HERITABILITY (HALF-SIB)			0 895	0 291		%RESPONSE 1 =	10 232	
HERITABILITY (FULL-SIB)			0 834	0 378				

TABLE E5. Analysis of variance for diameter at the Cowichan Lake site (CLES) (for the wood density measured trees)

SOURCE	D.F.	MEAN SQUARE	VAR COMP	S E	C V	VAR COMP %	F RATIO	PROBABILITY
REP	2	5732 55	6 803	5 635		4 83%		
MALE	3	205 72	0 0	0 907		0 0 %		
FEMALE	21	1051 05	7 851	3 309	3 225	5 57%	3 745	0 007
R * M	6	934 84	2 955	2 597		2 10%	2 376	0 033
R * F	42	269 33	0 0	2 301		0 0 %	0 685	0 920
M * F	63	404 67	0 230	3 503		0 16%	1 029	0 439
R*M*F	126	393 38	37 811	6 043	7 076	26 84%	4 616	0 0
WITHIN	1909	85 23	85 234	2 757	10 624	60 50%		
ADDITIVE GENETIC VARIANCE			31 406	13 236	6 449			
DOMINANCE GENETIC VARIANCE			0 919	14 011	1 403			
TOTAL PHENOTYPIC VARIANCE			134 081		13 325			
PHENOTYPIC VARIANCE HALF-SIB			11 892		3 968			
PHENOTYPIC VARIANCE FULL-SIB			24 031					
HERITABILITY (INDIVIDUAL)			0 234	0 099		%RESPONSE 1 =	3 121	
HERITABILITY (HALF-SIB)			0 660	0 278		%RESPONSE 1 =	5 240	
HERITABILITY (FULL-SIB)			0 336	0 275				

TABLE E6 Components of variance and covariance for traits WD and DM12

FOR VARIABLES	WD			DM12			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	143 0790	S E	45 2995	7 8514	S E	3 3091	-17 8360
ADDITIVE GENETIC VARIANCE	572 3159	S E	181 1981	31 4056	S E	13 2363	-71 3440
DOMINANCE GENETIC VARIANCE	0 0	S E	35 2759	0 9188	S E	14 0111	-0 4594
PHENOTYPIC VARIANCE INDIVIDUAL	639 6467			134 0806			-121 0718
PHENOTYPIC VARIANCE HALF-SIB	153 1971			11 8917			-20 9251
PHENOTYPIC VARIANCE FULL-SIB	214 7094			24 0306			-27 6289
HERITABILTY FOR INDIVIDUAL SELECTION	0 8947	S E	0 2833	0 2342	S E	0 0987	0 4578
COEFFICIENT OF VARIATION (PI)	6 9671			13 3252			
%RESPONSE /1 (INDIVIDUAL)	6 2337			3 1211			
HERITABILTY FOR HALF-SIB SELECTION	0 9340	S E	1 1828	0 6602	S E	1 1131	0 7853
COEFFICIENT OF VARIATION (PHS)	3 4096			3 9684			
%RESPONSE /1 (HALF-SIB)	3 1844	CR_y =	-1 4248	2 6201	CR_x =	-1 6583	
GENETIC CORRELATIONS	-0 5322	S E	0 1852				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0 4134						
PHENOTYPIC CORRELATIONS H S FAMILIES	-0 4903						
ENVIRONMENTAL CORRELATIONS	-0 5981						

TABLE E7. Components of variance and covariance for traits WD and PIN

FOR VARIABLES	WD			PIN			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	143 0790	S E	45 2995	81 6374	S E	26 5664	-102 8783
ADDITIVE GENETIC VARIANCE	572 3159	S E	181 1981	326 5496	S E	106 2656	-411 5129
DOMINANCE GENETIC VARIANCE	0 0	S E	35 2759	60 9936	S E	29 6150	-25 7648
PHENOTYPIC VARIANCE INDIVIDUAL	639 6467			405 4741			-358 5381
PHENOTYPIC VARIANCE HALF-SIB	153 1971			91 2580			-110 9650
PHENOTYPIC VARIANCE FULL-SIB	214 7094			140 5540			-146 7519
HERITABILTY FOR INDIVIDUAL SELECTION	0 8947	S E	0 2833	0 8054	S E	0 2621	0 8489
COEFFICIENT OF VARIATION (PI)	6 9671			12 0550			
%RESPONSE /1 (INDIVIDUAL)	6 2337			9 7086			
HERITABILTY FOR HALF-SIB SELECTION	0 9340	S E	1 1828	0 8946	S E	1 1645	0 9141
COEFFICIENT OF VARIATION (PHS)	3 4096			5 7190			
%RESPONSE /1 (HALF-SIB)	3 1844	CRy=	-2 9667	5 1161	CRx=	-4 9761	
GENETIC CORRELATIONS	-0 9519	S E	0 0213				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0 7040						
PHENOTYPIC CORRELATIONS H S FAMILIES	-0 9385						
ENVIRONMENTAL CORRELATIONS	0.7267						

END / FIN

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