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Noble fir (Abies procera Rehd.), an important conifer in the Pacific Northwest, is valuable for timber, Christmas trees, and greenery products. A number of tree improvement programs emphasizing genetic improvement of bole volume growth are underway in this species. The purpose of this study was to estimate genetic control of stem volume, stem form, and branching traits and the genetic interrelationships among these traits in sapling Noble fir eleven years old. Trees from sixty families growing on three progeny test sites in southwest Washington were utilized.

Large family x site interactions were evident when all 3 sites were analyzed together, consequently sites were grouped into low (two sites) and high (one site) planting environments for genetic parameter estimation. Significant amounts of family variation were present in at least one environment for ten of the thirteen traits examined. Mean estimates of individual narrow-sense heritabilities were low to moderate for all traits: volume (.22), height (.31), stem diameter (.21), taper (.09), stem sinuosity (.33), branch diameter ratio (.15), branch length ratio (.49), branch angle (.23), branch number (.10), and knot index (.13). Family heritabilities for size traits were often twice as large as individual heritabilities. Genetic correlations were strong and positive among stem growth traits (≥.73), between branch length ratio and branch diameter ratio (.75), and between sinuosity and stem growth traits (.49-.54). With the exception of branch number, genetic correlations between branch traits and stem growth were weak or favorable, such that selection for stem volume should little or no negative impact on branching characteristics. Amounts of genetic and phenotypic variation present

indicate moderate gains from selection and breeding programs are possible for stem growth, while lesser gains can be achieved for stem form and branching traits.

Genetics of Stem Volume, Stem Form, and Branch Characteristics in Sapling Noble Fir

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INTRODUCTION

Noble fir (Abies procera Rehd.) is an important forest tree species in the Pacific Northwest where it occurs at upper elevations (1000 - 1700 meters) in the Cascade Mountains in Oregon and Washington and on isolated peaks in the Oregon Coast Range and the Willapa Hills in southwestern Washington. It is valuable for timber, Christmas trees, and greenery products (Franklin 1981, Douglass et al. 1986).

There are a number of noble fir breeding efforts in the Pacific Northwest (Qualm 1988), including several USDA Forest Service tree improvement programs. By 1991, the Forest Service programs included 990 parent tree selections, 164 ha (405 acres) of progeny test sites, and 26.3 ha (65 acres) of seed orchards (USDA Forest Service 1991). Noble fir is also of interest as an exotic in Europe and Canada, where provenance evaluations are underway in Great Britain, Germany, and British Columbia (Fletcher and Samuel 1990, Ruetz et al. 1990, Ying 1990). In addition, a small progeny test to assess christmas tree value has been established in the Willamette valley in Oregon (Brown and Proebsting 1987). Despite all this activity, within population genetic variation in only early height growth, mortality, and christmas tree grade have been reported in the literature to date (Brown and Proebsting 1987, Fletcher and Samuel 1990, Ruetz et al. 1990, Ying 1990). Geographic variation in noble fir has also been investigated to a certain extent (Zavarin et al 1978, Sorensen et al 1991), and strong family differences reported for nursery traits such as early height growth, date of bud set, and extension period (bud flush to final bud set) (Sorensen et al 1991).

Bole volume is of primary economic importance and has historically been the main focus of tree improvement programs. Stem form and branch characteristics, however, are also important because of their influence on product value (Faulkner 1970, Shelbourne 1970, Bendtson 1978, Kellogg and Warren 1984). Branch size, number of branches, and the angle at which branches are attached to the bole influence the size and number of knots

formed, and consequently grade of lumber and plywood. Stem crookedness, forking, and the presence of large ramicorn branches decrease lumber yields and increase the amount of compression wood in the stem, which lowers pulp yields and lumber quality. Straight stems with little taper have lower handling costs and higher recovery values for lumber and plywood (Shelbourne 1970, Kellog and Warren 1984, Zobel and Talbert 1984).

The goal of most tree improvement programs is to combine rapid stem volume growth with high quality stems (i.e. straight boles with small limbs) to produce well adapted superior trees for lumber and pulp (Shelbourne 1970, Zobel and Talbert 1984). Only a few traits, however, can effectively be improved at one time and, thus, breeders must narrow the choice of traits upon which selections are based. The decision as to which traits to focus selection in tree improvement programs depends upon their influence on the economic value, cost of measurement, potential response to selection, and genetic interrelationships with other traits.

To efficiently achieve desired results in a breeding program requires estimates of a variety of genetic parameters, including levels of phenotypic variation, heritabilities, interrelationships among traits, and the degree to which the relative performance of genotypes remains the same in different environments (Birot 1981). Heritability, or the strength of inheritance, is important because to a large degree it determines the extent to which selection will be successful in improving traits. Genetic correlations, or interrelationships between traits, indicate the magnitude and direction of changes which will occur in one trait as the result of selection in another trait (Zobel and Talbert 1984).

Individual tree heritabilities of branching and stem form traits vary in conifers. Heritability estimates for branch length and diameter adjusted for tree size, and the number of branches per whorl were low to moderate (.1 - .3) in Douglas-fir (Pseudotsuga menziesii (Mirb.)Franco), yet branch angle was highly heritable (>.7) (King et al. 1993). Branch length, branch angle, and the number of branches per whorl all had high heritabilities in jack pine (Pinus banksiana Lamb.) (Polk 1972). Conversely, number of branches per whorl, branch diameter, and branch angle all had low to moderate (.12 - .26) heritabilities in Scots Pine (Pinus sylvestris L.) (Poykko 1982). In White spruce (Picea glauca

(Moench) Voss), Merrill and Mohn (1984) found heritability for branch angle moderate (.4), for branch diameter low (.16), and were unable to estimate heritability for number of branches per whorl because family differences for this trait were not significant. Heritabilities for branch length and diameter were low (<.18) in Slash pine (Pinus elliotti Engelm.), while branch angle was moderately heritable (.3) (Strickland and Goddard 1965).

Genotype-by-environment interaction (GxE) occurs when the relative performance of genotypes differs in different environments. Such interactions are important if they involve changes in family ranking in different environments, since conclusions concerning 'best' genotypes in one environment will be invalid for other environments (Shelbourne 1972). Conversely, when families have stable rankings across environments, selected families will perform well over a broad range of environments. Evaluation of GxE is complicated by the fact that the amount of interaction may differ for different traits. It is important to know which commercially important traits are most sensitive to GxE interaction, and what environments bring about interaction. Large production losses may result in operational forestry if GxE interaction is ignored (Zobel and Talbert 1984).

This study was undertaken to :

1) Quantify the amount of genetic and phenotypic variation for stem and branching traits in sapling noble fir, the strength of inheritance of these traits, and their genetic interrelationships.
2) Determine the extent to which families are stable for stem and branching traits across test environments.
3) Examine the implications of 1) and 2) with regard to breeding programs in this species.

To accomplish these objectives, a variety of stem (e.g. volume, taper, and sinuosity) and branching traits (e.g. branch diameter, branch angle, and number of branches per whorl) were measured on 11 year-old trees of 60 families growing in three progeny test sites located in the Gifford Pinchot National Forest, in the State of Washington.

MATERIALS and METHODS

Materials

In 1981 the Cowlitz Tree Improvement Cooperative in southwest Washington planted 11 Noble fir progeny test sites to evaluate 120 open-pollinated progenies (families) of 'roadside' parent tree selections. The criteria for selecting parents were simply that they be well formed dominant or co-dominant trees and have evidence of past cone production. These parents were located in the upper elevations of the Cowlitz and Lewis River drainages (Figure 1). The families were subdivided into four thirty-family sets for the purposes of testing, with families assigned to sets randomly. Sets one and three (60 families total) were randomly chosen for this study. Mean elevation of parents in these sets is 1191 meters (range is from 1067 to 1433 meters).

Seeds for the progeny test were sown at the Industrial Forestry Association greenhouse facilities near Olympia, Washington, grown as container seedlings in Leach 'supercells' for one year, transplanted to larger 'd-pot' containers for another year, and then outplanted to the field sites. Each field site has a split-plot design replicated within each of three blocks, with sets as main plots and families nested within sets as subplots. Each family subplot consisted of four trees assigned at random to planting spot within the main plot (i.e. four tree non-contiguous subplots). Blocks, main plots, and subplots were used to reduce environmental variation. Trees were planted on a grid at 2.8 m spacing.

Three of the eleven sites were selected for measurement based on high survival (Table 1). At time of measurement, trees on these sites had full crowns which extended to the ground and were not competing for light. Age of the progeny trees at the time of measurement was 11 years from seed. The Lonetree and Section12 sites are at intermediate elevations for Noble fir in the region, on moderate slopes (0-15%) facing south to southwest. At both of these sites the previous stand was a mixture of Douglas-fir, western hemlock (Tsuga heterophylla (Raf.) Sarg.), noble fir, and Pacific silver fir (Abies amabilis (Dougl.) Forbes). Natural regeneration has been primarily noble fir, Douglas-fir, and western hemlock . The Bishop site is about 250 meters higher in elevation and

slopes steeply (55%) to the northeast, resulting in lower year-round temperatures, more snow in the winter, and a shorter growing season than at the other two sites. Trees at this site were damaged by a cold, dry winter in 1982-83, however, by the time of measurement (fall, 1989) they had recovered to the point where they had full crowns. The previous stand at Bishop consisted of Pacific silver fir and western hemlock, and natural regeneration has primarily been of these two species. Soils at all three sites are well drained and of volcanic origin.

Measurement Methods

Thirteen traits were measured, including three related to stem growth, five related to stem form, and five related to branching habit (Table 2, Figure 2). Typically a large number of measurements must be made in selection programs, and techniques used must be simple and inexpensive to apply yet must be reasonably accurate in reflecting the traits of interest. Methods for estimating bole volume and branch traits were developed from intensive measurements made on 35 trees in the Section 12 plantation (see Appendix A for details). For bole volume, a volume equation was derived by estimating total bole volume as the summed volume of all interwhorl stem segments, then using multiple regression analysis and stepwise elimination techniques to choose predictor variables and to estimate regression coefficients (model R^2 =.98). Branch trait measurements were developed by first estimating as precisely as possible an average value for the tree based on the set of intensive measurements ('best measure'). The extent to which various simpler and less expensive measures were related to the 'best measure' was then determined by correlation analysis. Simple measures which were sufficiently correlated with the 'best measure' were chosen for use in the remainder of the study. Taper was assessed as the change in diameter over a given section of stem (King 1986). The stem segment comprised of interwhorls three through six was used in this study because the required measurements could readily be made from the ground and this section of the stem was generally free from deformities due to snow. Sinuosity was measured in the second interwhorl using the scoring system of Adams and Howe (1984). Fork, crook, and

ramicorn branching were measured simply as the number of occurrences of each defect along the entire stem, as the entire stem was readily visible from the ground.

Statistical Methods

To achieve Objective 1, all thirteen traits were subjected to Analysis of Variance (ANOVA) and all pairs of traits to Analysis of Covariance (ANCOVA). Analyses were carried out on both the combined data set (all sites) (Table 3) and on the data for individual sites (essentially the same as Table 3, but with terms involving sites deleted). Analyses were done on plot means, with within plot variances estimated separately for each plot and pooled. Because of the high survival on all sites there were no missing plots. Effects were judged significant when their probabilities were less than 0.05. Quasi F ratios for site and set effects were calculated using Satterthwaite's method (Steel and Torrie 1980).

Data for taper, sinuosity, ramicorn branching, fork, and crook were transformed prior to analysis. Transformation was needed to meet the assumptions of ANOVA (i.e., independent errors, normally distributed with constant variance). Taper was transformed to LOG(Taper+1); sinuosity, ramicorn branching, fork, and crook were transformed to SQRT(Trait+.5) (Steel and Torrie 1980). Unless otherwise noted, means were backtransformed prior to presentation in tables and text.

Variance components were estimated by equating observed mean squares to those expected and solving for the desired component. Components of covariance were estimated by a similar procedure, only mean crossproducts were used instead of mean squares.

Genetic variability and interrelationships between traits (Objective 1) were quantified by estimating additive genetic variances, individual and family heritabilities, and genetic and phenotypic correlations between traits. Genetic parameter estimates were not calculated in cases where family variances were not significant. Referring to Table 3 for definitions, additive genetic variance was estimated as (Falconer 1981)

$$\sigma^2_A = 4\sigma^2_{f(s)} ,$$

total phenotypic variation on an individual tree basis as

$$\sigma^2_{PI} = \sigma^2_w + \sigma^2_e + \sigma^2_{f(s)p} + \sigma^2_{f(s)} ,$$

and total phenotypic variation on a family basis as

$$\sigma^2_{PF} = \frac{\sigma^2_w}{(hn)(r)(p)} + \frac{\sigma^2_e}{(r)(p)} + \frac{\sigma^2_{f(s)p}}{p} + \sigma^2_{f(s)} .$$

Narrow-sense individual (h^2_i) and family heritabilities (h^2_f) were estimated according to Falconer (1981):

$$h^2_i = \frac{\sigma^2_A}{\sigma^2_{PI}} \quad \textit{and} \quad h^2_f = \frac{\sigma^2_f}{\sigma^2_{PF}} .$$

Additive genetic correlations were estimated as

$$r_A = \frac{cov_{f(xy)}}{\sqrt{\sigma^2_{f(x)}\sigma^2_{f(y)}}}$$

where $cov_{f(xy)}$ is the family component of covariance between traits x and y, and $\sigma^2_{f(x)}$ and $\sigma^2_{f(y)}$ are the respective family components of variance (Falconer 1981). Phenotypic correlations between family means were calculated as product-moment correlations (Steel and Torrie 1980). Standard errors of heritabilities and genetic correlations were approximated according to Becker (1984).

In order to evaluate the implications of the above genetic parameter estimates with regards to breeding programs (objective 3), expected genetic gains and correlated responses to selection were calculated. Genetic gain was estimated as the amount of improvement expected in the progeny of a seed orchard consisting of clones of parent trees selected on the basis of the performance of their open pollinated offspring (Namkoong 1979):

$$\Delta G_F = 2ih_f^2\sigma_{PF} ,$$

where i is the selection intensity. Correlated response to selection (CR_y) is the amount of change in a trait (y) resulting from selection in another trait (x) (Falconer 1981):

$$CR_y = 2ir_A\sqrt{h^2_{f(y)}h^2_{f(x)}\sigma^2_{PF(y)}} ,$$

where $h^2_{f(x)}$ and $h^2_{f(y)}$ are the family heritabilities for traits x and y respectively.

Family stability across environments (GxE) (Objective 2) was examined for each of the traits in three ways:

1) The size and significance ($p<.05$) of the Family(Set) x Site variance component ($\sigma^2_{f(s)p}$, Table 3) was used to evaluate the magnitude of interactions. While this gives some idea of the magnitude of interaction, GxE variance can be significant without rank changes occurring.

2) Genetic correlations between the same traits expressed in different sites evaluate the extent to which GxE influences the ability to select in one environment for performance in another and, thus, reflect stability of family performance. If the correlation is low, then families selected in one environment will not be the best families for the other environment. Conversely, if the correlation is high, then families selected in one environment will perform well in the other environment as well. Also, by comparing the magnitude of correlations between pairs of sites, one can determine whether one site contributes more to interaction than others. Genetic correlations between sites were calculated for each of the three pairwise combinations of sites (Burdon 1977):

$$r_{g_{ab}} = \frac{COV_{f(ab)}}{\sqrt{\sigma^2_{f(a)}\sigma^2_{f(b)}}} ,$$

where $cov_{f(ab)}$ is the family component of covariance for the trait expressed on sites a and b, and $\sigma^2_{f(a)}$ and $\sigma^2_{f(b)}$ are the respective family components of variance.

3) Comparison of family rank changes gives some idea of the degree of

interaction. Also, calculation of overall rank change for each family helps in evaluating the extent to which a few families may be contributing to most of the interaction. To calculate the overall rank change for a family, the absolute deviations of the rankings at each site from the overall mean ranking of a family were totalled and averaged (Matheson and Raymond 1984).

RESULTS and DISCUSSION

Site and Set Effects

Site means differed significantly for most traits related to growth (Table 4, Appendix Table B.1). Trees were considerably smaller at the Bishop site, which was higher and colder than Section12 and Lonetree (Table 1). Trees also had greater average branch length ratio and stem taper at the Bishop site, while branch angle was flattest at Lonetree. Sites did not differ significantly for the remaining traits (Table 4).

Set effects were non-significant for all traits. This is not surprising, as families were assigned to sets randomly.

Genotype-by-Environment Interactions (GxE)

Family(Set) x Site interaction was significant ($p<.05$) for all stem growth traits (volume, height, and stem diameter), branch length ratio and sinuosity (Table 5, Appendix Table B.1). Shelbourne (1972) gives as a rule of thumb that if the interaction variance component reaches fifty percent or more of the family component, GxE interaction will likely have serious effects on a breeding program. However, interaction effects can be of two kinds - scale effects and/or rank changes. Family x Site interactions do not cause serious problems in breeding programs unless they involve rank changes, i.e. families rank differently on different sites.

To assess for rank changes, the average change in height ranking of each family was calculated (Table 6). Family ranks often change greatly between sites; e.g., while Family 150 is ranked 28th overall, it is ranked 9th at Lonetree, 14th at Bishop, and 58th at Section12, and has an average rank change of 21.00. Other families are very stable; e.g., Family 334 has an overall rank of 60, it is ranked 55th at Bishop and 60th at both Section12 and Lonetree. Often the greatest rank changes are between Bishop and the other two sites.

To determine if interaction is due primarily to one site, genetic correlations between pairs of sites were calculated for all traits with significant family X site interaction across all sites and significant family differences within sites (Table 7). Genetic correlations for stem

height and diameter were highest between Section12 and Lonetree, lowest between Bishop and Section12, and intermediate between Lonetree and Bishop. These results indicate that much of the interaction is due to the Bishop site. Genetic correlations for volume and sinuosity could only be calculated for Section12 and Bishop, but in both cases they were very low (.22 and -.18), providing further support to the above perception. For branch length, the remaining trait showing significant GxE, the genetic correlation was still the lowest between Section12 and Bishop, but was higher between Lonetree and Bishop than between Section12 and Lonetree.

Since most of the interaction appears to be due to Bishop, and this site is higher in elevation than the other two, it was of interest to determine if rank changes are associated with the elevation of the seed source, i.e. whether rank changes reflect adaptation of families to elevation of origin. Multiple regression was used to evaluate the extent to which variation in family growth can be accounted for by variation in family origin and/or interactions between family origin and site (Morgenstern and Teich 1969). When family means for different growth traits were plotted against elevation of parent tree, slight linear trends were observed; thus the effect of elevation on growth was assumed to be linear. Family means for all plantations were regressed on elevation of parent trees and two dummy variables (orthogonal contrasts) to account for the effects of plantation site. The full regression model was:

$$y_i = \beta_0 + \beta_1 X_A + \beta_2 X_B + \beta_3 X_E + \beta_4 X_E X_A + \beta_5 X_E X_B + \varepsilon_i$$

Where: y_i = family mean at a site.

X_A = Dummy variable contrasting performance at Bishop to performance at Section12 and Lonetree (-2 if site = Bishop, 1 if site = Lonetree or Section12).

X_B = Dummy variable contrasting performance at Section12 to performance at Lonetree (-1 if site = Lonetree, 1 if site = Section12, 0 if site = Bishop)

X_E = Elevation of parent tree in meters.

Stepwise procedures (Wiseberg 1985) were used to select independent variables from the full model for the final model. Significance levels for entry and deletion of variables were $p<.15$ and $p<.05$, respectively.

Regressions for the three growth variables examined (height, volume, and stem diameter) were very similar, so only the final model for height is shown (model R-square = .64):

$$y_i = 112.77 + 11.61(X_B) + .09(X_E) + .02(X_E X_A)$$

Elevation of the parent tree alone explains only a small (partial R-square = .05) amount of the variation in family means. The coefficient for this effect, however, is positive, indicating that families from higher elevation sources tend to be taller or larger, on average, than families from low elevation sources at all planting sites. Supporting this is the fact that the five highest ranking families overall (Table 5) are from over 1280 meters elevation, the upper range of parent tree elevations. The contrast between Section12 and Lonetree also explains only a small amount of variation (partial R-square = .05). The interaction between source elevation and the dummy variable contrasting performance at Bishop to performance at the other two sites was strong (partial R-square = .53) and accounted for the largest portion of variation in family means. Although a positive association between growth and elevation of source is apparent at all sites, the slope of the relationship is twice as great at Section12 and Lonetree than as at Bishop (Figure 3). If interaction reflected adaptation of families to elevation of origin, one would expect a negative relationship between growth and source elevation at Section12 and Lonetree, and an opposite, or positive relationship at Bishop.

The positive relationship between parent tree elevation and height growth at all sites is surprising. The higher elevation selections are located in the northern part of the area, such that the correlation between latitude and elevation was .67. Site or stand characteristics where the higher elevation parents were selected may have resulted in more effective tree selection (e.g. even-aged stands growing in more uniform environments). Alternatively, there may be moisture gradients positively associated with elevation during the growing season in the sampling area. Family performance could be reflecting genetic response to increasing moisture stress with decreasing elevation. Moisture stress could be due to increasing plant competition at lower elevations. Also, higher elevations are nearer melting snowpack during the growing season, and more moisture

would be available here than at lower elevations.

The fact that the slope of the regression at the lower elevation sites is not opposite to the slope at Bishop indicates that elevation of seed source is not a factor in rank changes among families, and other unknown factors must be involved. Bishop is located at the upper elevational limits of noble fir in the area (only two parent trees were from higher elevations) and is on a Northeast facing slope, resulting in a colder environment than at Section12 and Lonetree. Indeed, this site may be too cold for noble fir. Noble fir was not part of the original stand, nor is it part of the natural regeneration on the site. Although noble fir is considered a high elevation species, it shows a preference for warmer microclimates at upper elevations (Franklin 1981).

Because Bishop appears not to be representative of sites where noble fir should be planted, the remainder of analysis addresses this site separately from the pooled data for Section12 and Lonetree. The pooled analysis for Section12 and Lonetree data (Appendix Table B.3) is probably representative of typical noble fir planting sites. Analysis is also carried out for the Bishop site data (Appendix Table B.4) because it is of interest to see how the harsher (high elevation) environmental conditions at this site affect genetic parameter estimates.

Genetic Variability and Inheritance

For both data sets, within plot variance accounted for the bulk of variance (>84%) of all traits, while plot error variance was usually zero (Table 8).

Although the magnitude of Family X Site interaction was usually less when only the two low elevation sites were analyzed (Table 8) than when all three sites were considered together (Table 4), it was still significant for three traits (stem diameter, branch length ratio, and branch angle). Genetic correlations between Section12 and Lonetree for branch length ratio and stem diameter are .78 and .77 (Table 7), suggesting that family rankings are relatively consistent between the two sites, despite the significant interaction. The estimate of genetic correlation between Section12 and Lonetree for branch angle, however, was

low (.38) indicating family rankings on one site are quite different from those on the other.

Significant family differences were detected for stem growth traits in both analyses, however the proportion of phenotypic variance due to family effects was usually higher for Bishop. Family variance estimates are probably inflated in the analysis of one site because family-by-site effects are not removed. Taper and most branching traits showed significant family differences only in the Section12-Lontree analysis. This could be for two reasons: 1) the ANOVA on two sites has more precision for detecting family differences (mean square sampling error is higher for these traits at Bishop); and 2) family differences for these traits are better expressed at sites which are typical for noble fir and are more productive.

One trait, sinuosity, showed significant family variation at Bishop, but not at the lower elevation sites. The ability to detect significant family differences at Bishop is probably due to the higher frequency of trees with sinuosity (sinuosity score>0) on this site (39.6%) than on the other sites (12.3%). Bishop also has a higher frequency of crooks (18% vs. 9%). The crooks at Bishop occurred just below the whorl formed in 1983, indicating the tops of trees were killed during the winter of 1982-83 (possibly by winter desiccation, as this was a year with a very low snowpack). At Bishop, families were able to express variation in the ability to maintain straight stems in a harsh winter climate. This may help explain why most branch traits did not show significant family differences; that is, damage to stems and crowns obscured family differences in branching characteristics. These traits which are expressed in one environment and not the other underscore the importance of measuring traits where they can be expressed.

Narrow sense individual heritabilities (Table 8) are low to moderate for all traits where estimates were possible. Family heritabilities are often twice the magnitude of individual heritability estimates. Where comparable, both individual and family heritabilities in the lower elevation sites were similar to those found at Bishop.

Individual tree heritabilities range four-fold among traits, with the highest heritability being for branch length ratio (h^2_i = .49). This

is higher than what generally has been observed in other conifers for adjusted and unadjusted branch length (h^2_i .12 - .20, Strickland and Goddard 1966, Poykko 1982, King et al 1993), although Polk (1972) found heritability for branch length to be high in jack pine, as well. Heritabilities for adjusted branch diameter, branch number, and knot index in noble fir are comparable to what researchers have found in other species (King et al 1993, Poykko 1982, Eriksson et al. 1982, Merrill and Mohn 1984, Strickland and Goddard 1966) . Branch angle heritability appears to vary a great deal in conifers. While it is high in Douglas-fir (h^2_i = .73, King et al. 1993) and White spruce (.44, Merrill and Mohn 1984), it is lower in Slash pine (.33, Strickland and Goddard 1966) and in noble fir (Table 1.8).

Heritability estimates were similar for the three stem growth traits, and are comparable to those reported for other species (King et al. 1988, Eriksson et al. 1987, Zobel and Talbert 1984). Consistent with Douglas-fir (King et al. 1993) and Scots pine (Eriksson et al. 1987), taper is weakly heritable in noble fir. Heritability of sinuosity in noble fir is similar to Douglas-fir (h^2_i= .39, Birot and Christophe 1983).

Interrelationships Among Traits

Phenotypic and genetic correlation estimates (Table 9) followed similar trends in both test environments, although where comparable, genetic correlations were somewhat higher at Bishop. This agrees with the observation by Lambeth et al. (1983) that higher genetic correlations occur in traits with greater genetic control.

Genetic and phenotypic correlations among stem growth traits were all large and positive (≥0.73), which agrees well with findings in other species (King et al. 1988, Eriksson et al. 1987). The moderate negative genetic correlation of taper with height (-.56) agrees with findings in Douglas-fir, as do the weak correlations of stem diameter and volume with taper (King et al. 1993). Sinuosity had positive phenotypic and genetic correlations with stem growth at the high elevation site; the larger faster growing trees were more sinuous. This relationship agrees with results in Douglas-fir and Scots Pine (Eriksson et al. 1987, King 1986),

although the correlations between sinuosity and stem growth traits are somewhat higher than what have been reported in these other species.

Phenotypic and genetic correlations between branch traits and stem growth traits were generally weak and negative, although associations involving branch diameter ratio and knot index could be considered moderate (Table 9). Branch number was an exception, having weak positive correlations with growth traits. Larger trees appear to have a slight tendency to have more branches which are smaller relative to stem diameter and which intersect the stem at a steeper angle. These relationships among branching traits and stem growth traits are similar to results in Douglas-fir and Scots pine, where stem size was found to be positively associated with the production of numerous fine branches (King et al. 1993, Eriksson et al. 1987). The negative correlations of stem growth traits with knot index indicate, however, that the amount of branch area per unit stem area decreases as stem size increases. Taper was negatively correlated with all branch traits, which agrees with results in Scots pine (Eriksson et al. 1987) but contrasts with the weak positive correlations found between these traits in Douglas-fir (King et al. 1993).

Not surprisingly, phenotypic and genetic correlations among branch diameter ratio, branch length ratio, and knot index were moderate to strong and positive (.75 to .93). Branch angle correlations with other branch traits were generally weak and negative, an exception being the positive correlation between branch angle and branch number. Branch number correlations with other traits were generally weak and positive.

Implications for Breeding

The significant amounts of GxE and rank changes suggest the breeding population may need to be subdivided if sites sampled in this study are representative of sites which will be planted with noble fir. This study underscores the need to test breeding populations under the full range of planting site conditions, particularly when considering noble fir for planting in non-native environments. Although most of the GxE interaction was between the two lower elevation sites and the one higher elevation site, one cannot conclude that elevation alone is the reason for the

interactions. The regression analysis did not support the idea that interaction was due to maladaptation of lower elevation sources to higher elevation planting sites and visa versa.

An alternative to subdivision is to maintain one breeding population for all planting sites and select for broadly adapted genotypes. This may be difficult given the strength of interaction observed in this study and the low frequency of families which rank high at all sites. Another alternative may be to apply the breeding program only to the lower elevations of the breeding zone, where higher growth rates may justify the investment. Higher elevations could be regenerated with seed from wild stand collections, seed production areas, or plantations suitable for mass selection (Zobel and Talbert 1984). Also, the cold, high elevation sites may be better suited to reforesting with other species, such as Pacific silver fir, Englemann spruce (Picea engalmannii Parry), or Mountain hemlock (Tsuga mertensiana (Bong.) Carr.).

The amounts of genetic and phenotypic variation in noble fir indicate breeding programs would be successful in improving a variety of stem and branching traits. Ten of the thirteen traits originally examined showed significant genetic variance in at least one planting environment. Expected genetic gains from selection of parents based on the mean performance of their progeny at the Lonetree and Section12 sites indicate moderate responses are possible for volume, height, branch length ratio, and knot index (10.6 to 15.9%), while low to moderate gains could be achieved for taper, diameter, branch diameter ratio, branch number, and branch angle (Table 10).

The genetic interrelationships among traits in Noble fir indicate there would be few unfavorable responses in stem quality and branching habit if selection was applied to only stem volume at the low elevation sites. Although selection for volume alone is expected to slightly increase the number of branches per whorl, there would be essentially no impacts to branch length ratio or branch angle, and stem taper and knottiness would decrease.

It appears that stem diameter might be an acceptable trait for indirect volume selection in Noble fir. Genetic correlations between diameter and volume were very high ($\geq$ .92) and diameter is easy to

measure. However, the height of the trees in this study averaged less than 2.5 meters, while similar recommendations for Douglas-fir were based on trees greater than six meters (King et al. 1988). The relationship between stem diameter and volume may weaken in older trees, and, thus it may be too early to draw conclusions about the value of stem diameter for indirect selection of stem volume.

Additional Research

This was the first study in Noble fir emphasizing topics related to selection of growth, stem form, and branching traits for breeding programs. There are many important areas where future research is needed. The large amount of GxE found in this study warrants more attention. More sites and families need to be included in tests to: 1) sample a greater range of environments; 2) determine if family rank changes continue to occur in the same pattern across sites; and 3) validate the trend of increasing growth performance with increasing parent tree elevation. Environmental factors such as temperature and moisture need to be measured at test sites to determine what influence they may have on interactions.

Specific gravity is an important wood quality trait influencing wood strength and pulp yields which was not evaluated in this study, and needs to be examined. High heritability and phenotypic variation exist for this trait in other tree species (Zobel and Talbert 1984). Also, if a negative genetic correlation between wood specific gravity and stem growth is found, such as in Douglas-fir (King 1986, Vargas-Hernandez and Adams 1991), it will probably be necessary to include specific gravity in noble fir selection programs.

The material used in this study should be maintained and evaluated periodically in the future. The trees in this study were only eleven years old, and substantial changes may occur in heritabilities, family stability, and interrelationships of traits over time.

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Table 1. Description of the three test sites included in this study.

	Site		
	Section 12	Lonetree	Bishop
Elevation (meters)	1158	1128	1402
Latitude	46° 01' 00"	46° 29' 00"	46° 26' 00"
Longitude	121° 51' 00"	121° 47' 00"	121° 41' 00"
Survival[a] (%)	87.9	92.6	88.1

[a] Survival at time of measurement (11 years from seed).

Table 2. Description of traits.

Stem Growth Traits.

Height(cm): Total height of the tree (HGT), using a telescoping pole.

Diameter(mm): Stem diameter outside bark at the bottom of interwhorl six (DOB), using vernier calipers. Interwhorls (Figure 1.2) were numbered from the top of the tree down, beginning with the leader.

Volume(cm^3): Calculated using the formula: $VOL = .0035(HGT)^{1.1653}(DOB)^{1.6391}$.

Stem Form

Taper(mm/cm): Decrease in stem diameter over a given stem length. Derived from height and diameter measurements using the formula TAPER = (DIA6-DIA3)/(HGT3-HGT6), where DIA6 is stem diameter (mm) outside bark at the bottom of interwhorl six (DOB), DIA3 is stem diameter (mm) outside bark at the top of interwhorl three, HGT3 is height (cm) at the top of interwhorl three, HGT6 is height (cm) at the bottom of interwhorl six.

Ramicorn branching: Presence of a branch intersecting the stem at an angle less than 30^0 and definitely smaller in diameter than the main stem in size at the same height (Figure 1.2). Measured as the total number of ramicorn branches in a tree.

Fork: Presence of one or more stems diverging at an angle less than 30^0 from the main stem and of about equal diameter as the main stem at the same height (Figure 1.2). Measured as the total number of forks in a tree.

Crook: Major bend in the main stem resulting from loss or death of the leader at a point in time corresponding to formation of major bend (Figure 1.2). Measured as the total number of crooks in a tree.

Sinuosity: Deviation from straightness, or crookedness, of the main stem within an interwhorl (Figure 1.2). Scored visually from the ground in the second interwhorl as the maximum deviation from straightness (amplitude) in units of one half stem diameters at the point of displacement.

Branching

Branch diameter ratio(mm/mm): Diameter (mm) of the largest branch on the tree adjusted for tree size by dividing by DOB.

Branch length ratio(cm/mm): Length (cm) of the longest branch on the tree adjusted for tree size by dividing by DOB.

Table 2 (continued).

Branch angle(^{0}): The average vertical angle of main whorl branches from the mainstem in the whorl nearest mid-crown height and the next lower whorl, visually estimated to the nearest 5^0 using a clear plexiglass guide.

Branch number: Average number of main whorl branches in the whorl nearest midcrown height and the next lower whorl.

Knot index(mm^2/mm^2): Ratio of the branch cross sectional area to stem cross sectional area (KI) estimated using the average number of branches in a whorl (BRN), diameter of the largest branch on the tree (BDIA, mm), and DOB: KI=[BRN*((BDIA/2)^2*3.1416)]/((DOB/2)^2*3.1416).

Table 3. Form of the analysis of variance on multiple sites.

Source	degrees of freedom	Expected Mean Squares[a]
Sites	p-1	$\frac{\sigma_w^2}{hn} + \sigma_e^2 + f\sigma_{r(p)s}^2 + r\sigma_{f(s)p}^2 + rf\sigma_{ps}^2 + fs\sigma_{r(p}^2 + fsr\sigma_p^2$
Sets	s-1	$\frac{\sigma_w^2}{hn} + \sigma_e^2 + f\sigma_{r(p)s}^2 + r\sigma_{f(s)p}^2 + rf\sigma_{ps}^2 + rp\sigma_{f(s}^2 + rpf\sigma_s^2$
Sites X Sets	(p-1)(s-1)	$\frac{\sigma_w^2}{hn} + \sigma_e^2 + f\sigma_{r(p)s}^2 + r\sigma_{f(s)p}^2 + rf\sigma_{ps}^2$
Reps(Sites)	p(r-1)	$\frac{\sigma_w^2}{hn} + \sigma_e^2 + f\sigma_{r(p)s}^2 + fs\sigma_{r(p)}^2$
Sets X Reps(Sites)	(s-1)p(r-1)	$\frac{\sigma_w^2}{hn} + \sigma_e^2 + f\sigma_{r(p)s}^2$
Families(Sets)	s(f-1)	$\frac{\sigma_w^2}{hn} + \sigma_e^2 + r\sigma_{f(s)p}^2 + rp\sigma_{f(s)}^2$
Families(Sets) X Sites	s(f-1)(p-1)	$\frac{\sigma_w^2}{hn} + \sigma_e^2 + r\sigma_{f(s)p}^2$
Plot error	s(f-1)p(r-1)	$\frac{\sigma_w^2}{hn} + \sigma_e^2$
Within plot error	$\sum^{psrf} n-1$	σ_w^2

[a] For analysis of covariance, variances are substituted with covariances. σ_p^2 -variance due to sites (p sites),

Table 3 (continued).

σ_s^2 -variance due to sets (s sets); σ_{ps}^2 -variance due to site-by-set interaction; $\sigma_{r(p)}^2$ -variance due to replications-within-sites (r replications within each site); $\sigma_{r(p)s}^2$ -variance due to set-by-rep(site) interaction; $\sigma_{f(s)}^2$ -variance due to families-within-sets (f families within each set); $\sigma_{f(s)p}^2$ -variance due to family-within-set-by-site interaction; σ_e^2 -variance due to subplots (sfpr plots); σ_w^2 -variance due to individual trees within subplots (hn - harmonic mean of trees within each subplot).

Table 4. Site means for all traits.

Trait	Site Section12	Lonetree	Bishop
Volume(cm^3)**	1465.6	1093.2	698.7
Height(cm) **	255.2	233.6	181.7
Stem Diameter(mm)*	49.9	44.2	39.7
Taper(mm/cm)**	.2365	.2190	.2624
Ramicorn Branch (count)	.14	.05	.26
Fork (count)	.10	.01	.04
Crook (count)	.09	.09	.18
Sinuosity (Score)	.16	.04	.46
Branch Diameter Ratio(mm/mm)	.36	.32	.35
Branch Length Ratio(cm/mm)*	1.67	1.64	1.95
Branch Angle (degree)*	76.3	83.7	76.5
Branch Number (count)	4.3	4.8	4.5
Knot Index (mm^2/mm^2)	.57	.49	.56

*, ** Site effects significant at p=.05 and .01 levels, respectively (see Appendix Table B.1).

Table 5. Estimated variance components (expressed as intraclass coefficients), total phenotypic variances, and narrow sense heritabilities for thirteen traits measured at three test sites.

Trait	Variance Components (%)[a]				Phenotypic[b] Variance	Heritabilities (± SE)	
	Family	Family X Site	Plot	Within Plot		Individual	Family
Volume	2.87**	3.14*	0	93.99	427052.87 (62.1)	.11 ± .05	.41 ± .19
Height	4.86***	2.99*	0	92.15	3487.87 (26.4)	.19 ± .07	.55 ± .19
Diameter	2.75**	4.82***	0	92.43	108.40 (23.3)	.11 ± .06	.37 ± .19
Taper	0.81	0	0.36	98.84	.007540 (40.5)	–[c]	–
Ramicorn Branch	0.54	0	3.46	96.00	.061306 (30.9)	–	–
Fork	0.40	0	0	99.60	.021196 (19.6)	–	–
Crook	0.26	.06	0	99.68	.038177 (24.8)	–	–
Sinuosity	0	6.53***	0	93.47	.069615 (31.3)	–	–
Branch Diameter Ratio	2.33**	2.38	0	95.29	.006655 (23.8)	.06 ± .05	.27 ± .21
Branch Length Ratio	6.50***	3.00*	0	90.50	.127641 (20.4)	.20 ± .07	.54 ± .19

[a] Negative estimates set to zero.
[b] Total phenotypic variance on an individual basis (phenotypic coefficient of variation given in parentheses).
[c] Genetic parameters not estimated when Family effects are not significant.
*, **, *** - Corresponding variance significant at the p=.05, .01, and .001 levels, respectively.

Table 5 (continued).

Trait	Variance Components (%)[a]				Phenotypic[b] Variance	Heritabilities (± SE)	
	Family	Family X Site	Plot	Within Plot		Individual	Family
Branch Angle	6.00***	1.29	0	92.70	57.894 (9.7)	.17 ± .06	.56 ± .18
Branch Number	2.46**	0	0.54	97.00	1.1182 (23.3)	.10 ± .04	.44 ± .18
Knot Index	2.68**	2.41	0	94.91	.08074 (52.6)	.11 ± .05	.41 ± .19

[a] Negative estimates set to zero.
[b] Total phenotypic variance on an individual basis (phenotypic coefficient of variation given in parentheses).
[c] Genetic parameters not estimated when Family effects are not significant.
*, **, *** - Corresponding variance significant at the p=.05, .01, and .001 levels, respectively.

Table 6. Family ranks and average rank changes for height.

Family	Rank overall	Rank at Bishop	Rank at Section 12	Rank at Lonetree	Average rank change
1	3	15	5	2	5.00
4	15	7	43	13	12.67
32	1	2	3	1	1.00
33	18	38	15	21	8.67
35	2	29	1	3	9.67
36	4	13	7	4	4.00
48	20	31	24	20	5.00
49	21	49	21	14	11.67
111	47	26	51	38	11.33
118	5	11	20	8	8.00
119	10	8	26	15	7.67
141	46	47	16	55	13.33
143	39	44	48	23	10.00
146	24	10	33	35	11.33
147	52	52	45	42	5.67
149	59	53	59	53	4.00
150	28	14	58	9	21.00
152	38	36	9	54	15.67
153	53	42	31	59	13.00
154	51	34	42	57	10.67
157	7	43	2	7	13.67
158	29	27	19	41	8.00
159	44	56	28	33	13.00
160	55	30	56	58	9.67
162	22	22	39	17	7.33
165	45	57	14	45	14.33
169	27	4	52	29	16.67
170	12	12	18	22	5.33
171	42	54	41	16	13.00
172	58	50	54	56	4.67
173	54	48	50	40	8.00
174	42	37	44	36	4.33
175	11	17	12	18	4.67
176	36	3	46	44	17.00
177	25	24	49	12	12.67
178	37	19	40	39	7.67
188	13	5	37	10	11.67
191	32	6	53	30	16.33
193	30	41	34	25	6.67
194	26	9	10	52	19.67
196	19	23	11	34	9.00
197	43	59	25	32	15.00
220	6	35	4	6	10.33
221	9	16	35	5	12.33
222	14	25	23	11	7.67
229	16	39	6	19	12.00
294	8	1	17	24	10.67
325	31	28	32	31	1.33

Table 6. (continued).

Family	Rank overall	Rank at Bishop	Rank at Section 12	Rank at Lonetree	Average rank change
326	56	51	57	50	4.00
327	49	33	47	47	6.67
328	23	18	8	46	14.33
329	33	45	30	27	7.00
330	41	32	29	49	9.67
331	34	21	36	37	6.00
332	48	40	38	48	6.33
333	57	58	55	51	3.00
334	60	55	60	60	1.67
335	35	46	27	28	8.67
336	50	60	13	43	18.00
353	17	20	22	26	5.67

Table 7. Estimated genetic correlations between sites.

Trait	Lonetree - Section12	Lonetree - Bishop	Bishop - Section12
Volume	~[a]	~	.22
Height	1.18	.66	.31
Stem Diameter	.77	.46	.30
B. Length	.78	.92	.53
Sinuosity	~	~	-.18

[a] Family effects not significant at one or both sites.

Table 8. Estimated variance components (expressed as intraclass coefficients), total phenotypic variances, and narrow sense heritabilities for thirteen traits measured in low (A) and high (B) elevation test environments.

Trait	Test[a] Env.	Variance Components (%)[b] Family	Family X Site	Plot	Within Plot	Phenotypic[c] Variance	Heritabilities (± SE) Individual	Family
Volume	A	4.15**	1.80	0	94.05	570399.90 (59.0)	.17 ±.08	.43 ±.20
	B	6.51**	–	0	93.49	214768.04 (66.3)	.26 ±.12	.41 ±.19
Height	A	7.31***	0.41	.29	91.99	3933.53 (25.7)	.29 ±.20	.61 ±.20
	B	8.29***	–	0	91.71	2592.11 (28.0)	.33 ±.12	.47 ±.18
Diameter	A	4.32**	3.86*	0	91.82	108.36 (22.1)	.17 ±.09	.41 ±.20
	B	6.37**	–	0	93.63	108.52 (26.2)	.25 ±.12	.40 ±.20
Taper	A	2.27*	0	0	97.73	.005192 (35.1)	.09 ±.05	.33 ±.17
	B	0	–	4.25	95.75	.012914 (48.8)	–[d]	–
Ramicorn Branch	A	0	1.44	0	98.55	.036806 (25.1)	–	–
	B	0	–	4.79	95.21	.110870 (38.2)	–	–
Fork	A	0.28	0	0	99.72	.022882 (20.3)	–	–
	B	0.48	–	0	99.52	.017663 (18.0)	–	–
Crook	A	0.18	0	0	99.82	.033551 (23.8)	–	–
	B	3.32	–	0	96.68	.049130 (26.9)	–	–

[a] A consists of two test sites (Section12 and Lonetree), B is the Bishop test site.
[b] Negative estimates set to zero.
[c] Total phenotypic variance on an individual basis (phenotypic coefficient of variation given in parentheses).
[d] Heritabilities not estimated when Family effects are not significant.
*, **, *** - Corresponding variance significant at the p=.05, .01, and .001 levels, respectively.

Table 8 (continued).

Trait	Test Env.	Variance Components (%)[b] Family	Family X Site	Plot	Within Plot	Phenotypic[c] Variance	Heritabilities (± SE) Individual	Family
Sinuosity	A	0.20	2.33	0	97.48	.069616 (31.3)	-	-
	B	8.13*	-	0	91.87	.141850 (38.4)	.33 ±.13	.47 ±.18
Branch Diameter Ratio	A	3.71*	2.85	4.05	89.40	.005567 (22.2)	.15 ±.09	.37 ±.22
	B	2.25	-	0	97.75	.009374 (27.8)	-	-
Branch Length Ratio	A	12.23***	3.71*	0	84.06	.095293 (18.6)	.49 ±.13	.67 ±.19
	B	3.07	-	0	96.93	.194680 (22.7)	-	-
Branch Angle	A	4.19*	3.34*	0	92.47	50.268 (8.9)	.17 ±.08	.40 ±.20
	B	6.93**	-	0	93.07	73.607 (11.2)	.28 ±.11	.42 ±.17
Branch Number	A	2.38*	0	0.75	96.87	1.0048 (21.9)	.10 ±.06	.33 ±.21
	B	0.46	-	0	99.54	1.3205 (25.6)	-	-
Knot Index	A	3.37*	3.04	1.11	92.48	.06637 (48.5)	.13 ±.08	.35 ±.22
	B	3.42	-	0	96.59	.11194 (59.8)	-	-

[a] A consists of two test sites (Section12 and Lonetree), B is the Bishop test site.
[b] Negative estimates set to zero.
[c] Total phenotypic variance on an individual basis (phenotypic coefficient of variation given in parentheses).
[d] Heritabilities not estimated when Family effects are not significant.
*, **, *** - Corresponding variance significant at the p=.05, .01, and .001 levels, respectively.

Table 9. Genetic (below diagonal) and phenotypic (above diagonal) correlations between traits measured in low (A) and high (B) elevation environments.[a,b]

		VOL	HGT	SDIA	TAP	SN	BDIA	BLEN	ANGL	BNUM	KI
VOL	A[c]	1.00	.92	.93	-.62	.36	-.51	-.19	-.11	.27	-.39
	B	1.00	.90	.95	.17	.57	-.41	-.38	-.03	.05	-.41
HGT	A	.93*	1.00	.80	-.44	.43	-.39	.03	-.03	.29	-.26
	B	.93*	1.00	.81	.08	.54	-.40	-.15	.13	.05	-.38
SDIA	A	.92*	.73*	1.00	-.04	.30	-.66	-.38	-.15	.27	-.55
	B	.99*	.89*	1.00	.24	.53	-.45	-.54	-.14	-.02	-.49
TAP	A	-.13	-.56*	.16	1.00	-.16	-.07	-.29	-.27	-.14	-.13
	B	-[d]	-	-	1.00	.07	.08	-.18	-.10	.04	.03
SN	A	-	-	-	-	1.00	-.06	.20	-.02	.09	-.05
	B	.54*	.54*	.49*	-	1.00	-.10	-.02	-.22	.04	-.10
BDIA	A	-.41	-.29	-.65*	-.15	-	1.00	.66	.03	-.15	.90
	B	-	-	-	-	-	1.00	.50	-.23	-.21	.90
BLEN	A	-.04	.17	-.30	-.44*	-	.75*	1.00	.05	.00	.64
	B	-	-	-	-	-	-	1.00	.40	.06	.57
ANGL	A	-.07	-.01	-.15	-.80*	-	-.32	-.16	1.00	.02	.04
	B	-.20	-.06	-.25	-	-.43	-	-	1.00	.18	-.12
BNUM	A	.23	.33	.23	-.35	-	-.05	.23	.40	1.00	.21
	B	-	-	-	-	-	-	-	-	1.00	.26
KI	A	-.28	-.10	-.56*	-.30	-	.93*	.84*	-.13	.30	1.00
	B	-	-	-	-	-	-	-	-	-	1.00

[a] A consists of two test sites (Section12 and Lonetree); and B is the Bishop site.

[b] Key to traits: VOL=Stem Volume: HGT=Height; SDIA=Stem Diameter; TAP=Taper; SN=Sinuosity; BDIA=Branch Diameter Ratio; BLEN=Branch Length Ratio: ANGL=Branch Angle: BNUM=Branch Number; KI=Knot Index.

[c] Phenotypic correlations with an absolute value greater than or equal to .25 are statistically significantly different from zero at the .05 probability level.

[d] - means estimates not calculated because the family variance was not significant for one or both traits ($p<.05$).

* Absolute value of correlation exceeds twice it's Standard Error.

Table 10. Expected genetic gains when selection is applied directly to individual bole and branching traits, and correlated gains in these traits when selection is applied to bole volume.[a]

Trait	Direct Gain[a]	(%)[b]	Correlated Gain	(%)
Volume (cm^3)	202.8	(15.85)	202.8	(15.85)
Height (cm)	26.5	(10.83)	20.7	(8.46)
Diameter (mm)	2.8	(5.85)	2.6	(5.58)
Taper (mm/cm)	.0155	(6.81)	-.0109	(4.77)
Branch Diameter Ratio (mm/mm)	.0174	(5.17)	-.00777	(2.31)
Branch Length Ratio (cm/mm)	.1772	(10.70)	-.00565	(0.34)
Branch Angle (degrees)	1.8	(2.31)	-.013	(0.17)
Branch Number (count)	.18	(3.88)	.047	(1.02)
Knot Index (mm^2/mm^2)	.0561	(10.57)	-.01731	(3.26)

[a] Gain per unit of selection intensity, when parent trees are selected on the basis of mean progeny performance.

[b] Gain relative to population mean before selection.

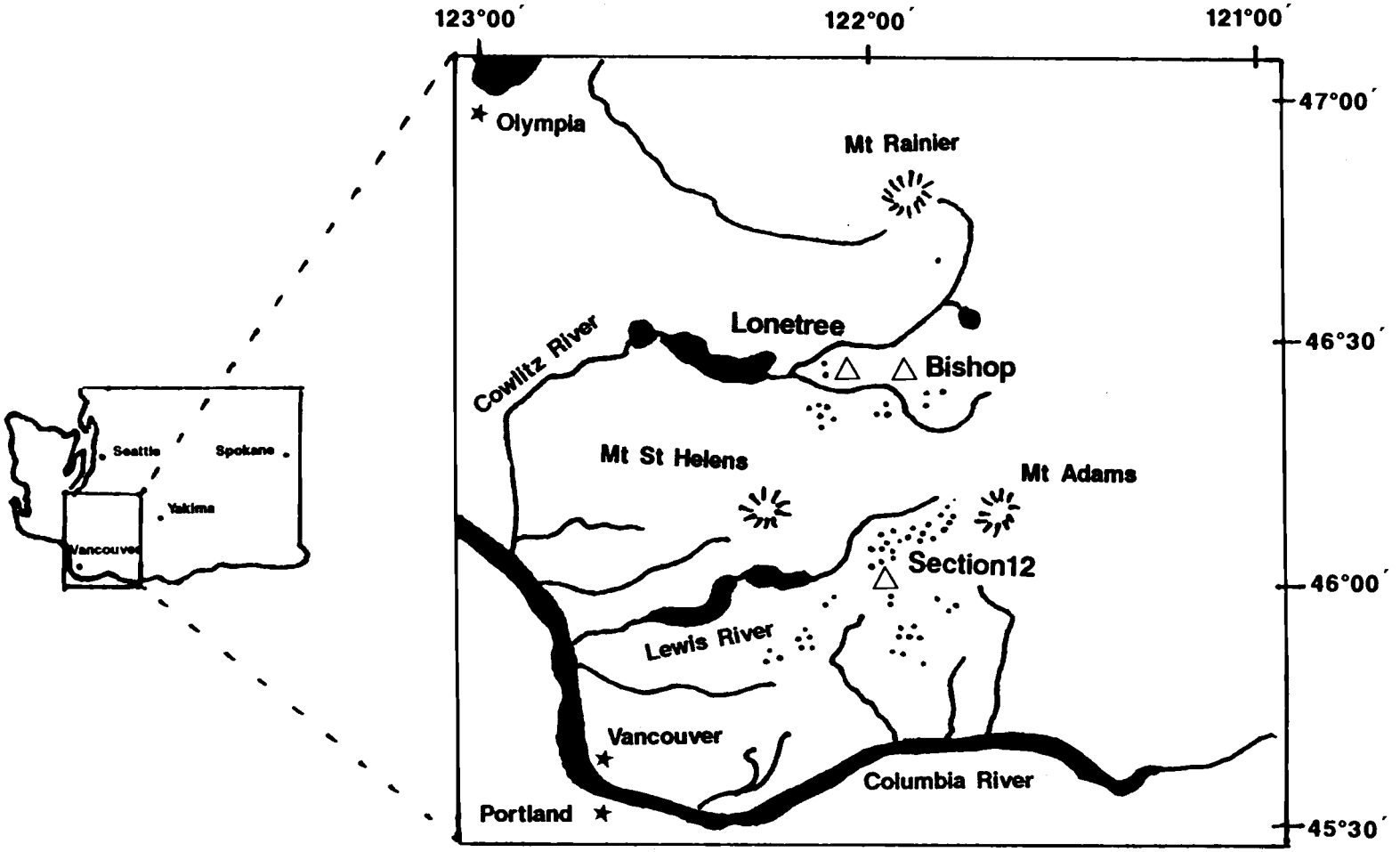
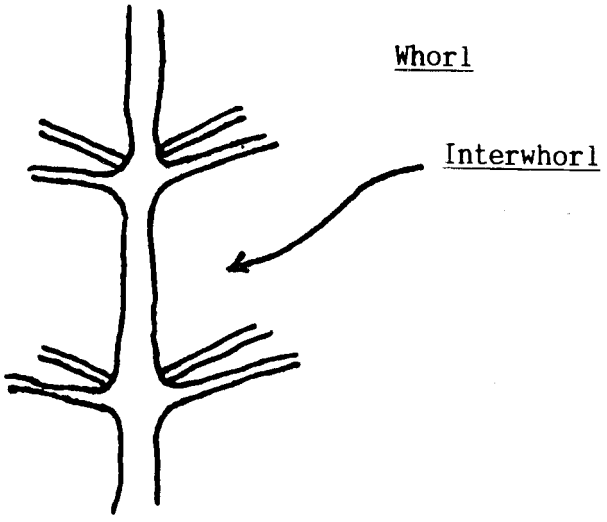
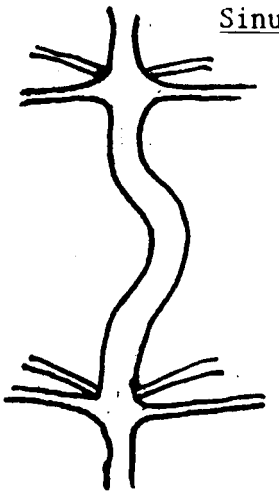


Figure 1.1. Locations of the three test sites (△) and sixty parent trees (•) included in this study.





Deviation from straightness within an interwhorl (in units of one half stem diameters). In this example sinuosity would have a score of 2.

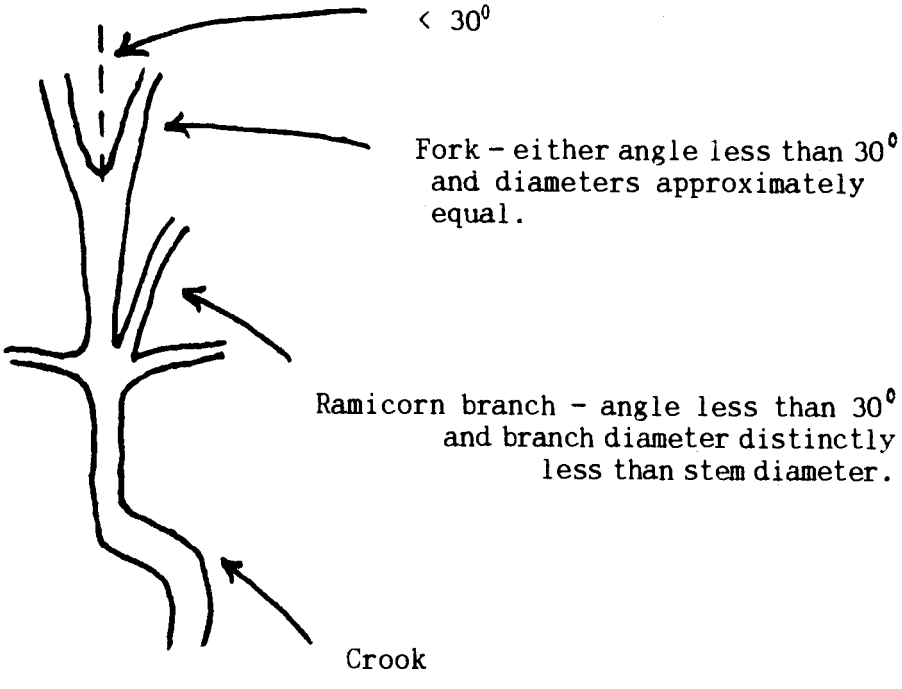


Figure 1.2. Illustrations of terms used in defining branching habit and stem form in noble fir. (See also Table 1.2).

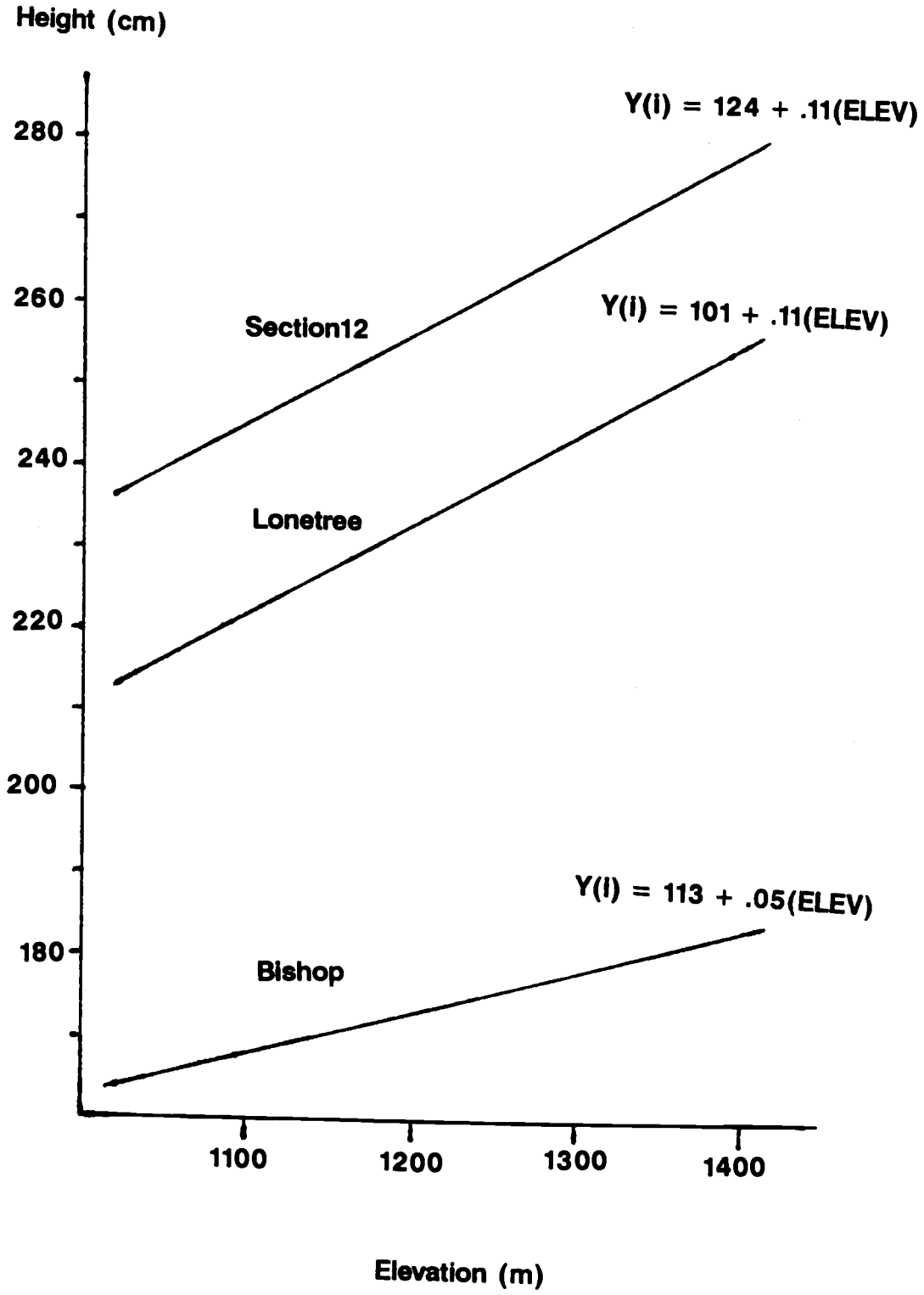


Figure 1.3. Predicted relationship between family mean height (Y(i)) and elevation of parent tree (ELEV) at three sites.

APPENDICES

APPENDIX A.
RAPID MEASUREMENT TECHNIQUES FOR BOLE VOLUME AND BRANCHING TRAITS.

INTRODUCTION

In order to be useful in tree improvement programs, branching and stem form traits must be measured accurately and inexpensively. While most tree breeders agree on what constitutes desirable crown and stem form for wood quality (small, short, straight branches and straight stems with little taper), there is little agreement on how to quantify these characteristics. Methods range from a single aggregate score for overall form to direct measurement of each component trait (Raymond and Cotterill 1990, Busby 1983). When quality is estimated as an aggregate trait, e.g. when a subjective score is used to summarize crown and stem form, heritability of the score and response to selection is often low (Raymond and Cotterill 1990). The expense of measurement and unknown genetic properties of quality traits however, may make some breeders reluctant to include individual quality traits in breeding programs.

Due to the nature of genetic analysis, traits are generally measured on every tree in an evaluation plantation. Directly measuring every component of each trait, e.g. the diameter of every branch in each whorl to determine average branch diameter, would be very costly and time consuming. In addition, boredom and fatigue lead to measurement and recording errors. Conversely, the reliability of parameter estimates may be questionable if based on only one measurement for an individual. Presumably the more measurements of a trait for which multiple measurements are possible, such as branch diameter or length, the more accurate the assessment of that trait. Yet, there must be a reasonable compromise between the precision needed and the cost involved.

Briefly, the approach used in this study was:

1) Measure as accurately as practical each trait (i.e. the 'best' measure of the trait) on 35 trees located at one site. This was done for volume, branch diameter, branch length, branch angle, and branch number.
2) Simpler measures were then compared to the 'best' measure using

correlation analysis to identify measurement techniques which were quicker and easier to employ, yet were reasonably accurate.

MATERIALS and METHODS

Materials

The thirty-five trees chosen for measurement are found on the Section12 progeny test site located approximately 20 miles N of Carson, Washington. Section12 is an operational test of open-pollinated families originating from parent trees selected in the upper elevations of the Cowlitz and Lewis River drainages. The site is at an intermediate elevation for noble fir in the area (1158 meters) and slopes gently (0-15%) to the Southwest. The trees were planted at 2.4 meter spacing and at the time of measurement (August, 1989), were ten years old from seed and had full crowns. Mean tree height at age 10 was 225.7 cm. (range 126 - 352 cm.) and is average for noble fir plantations in the area. Trees were randomly selected for measurement with no regard for family affiliation, size, or location within the test site. The only criterion was that trees with severe damage (that which impacted growth severely or affected more than one whorl of branches) were excluded.

Estimation of Tree Values

For this study, main branch whorls are defined as the whorls of branches originating from lateral buds adjacent to the terminal bud on the main bole. Interwhorl sections are the stem segments between main branch whorls. Whorls and interwhorls are numbered from the top of the tree down, such that whorl one is the last whorl formed, whorl 2 is the whorl formed the previous year, etc (Figure 1.2).

Bole volume is the total volume of wood in cm^3 contained in the stem of the tree. The best measure for bole volume was estimated by summing the volume of interwhorl sections one through six and the stem section between whorl six and ground level. Interwhorls one through six were relatively open and stem measurements easy to take; but. below whorl six the stem was crowded with branches, making it difficult to identify stem segments. To estimate the volume of interwhorl stem segments, heights (measured from

ground level) to all main branch whorls one through six were measured to the nearest centimeter using a telescoping measuring pole. Stem diameters were measured to the nearest mm at the midpoints and bottoms (just above any nodal swelling) of interwhorl segments one through six and at the base of the tree using vernier calipers. Volumes of interwhorl segments and the stem section below whorl 6 were calculated as volumes of a cylinders with heights equal to interwhorl distances and diameters equal to stem diameters at the midpoints of the segments.

To estimate branching traits, the number of branches per whorl, lengths, diameters, and vertical angles of all live branches in whorls one through six were measured. All branches in these whorls were accessible from the ground and measurements relatively easy to take. Branches below whorl six were not measured because below this point branch size was differentially influenced by shading (Snyder 1961) and snow load. Branch lengths were measured to the nearest cm from the main stem using a meter stick, and diameters were measured to the nearest mm approximately 1 cm from the intersection of the branch with the bole using vernier calipers. Vertical angles were estimated to the nearest 5^0 using a plexiglas viewing guide.

To determine the best measure for branch diameter and length, a ratio was calculated between the value for the trait and the stem diameter at the bottom of the interwhorl immediately above the whorl where the branch was located. This was done to reduce size effects due to age and environment (King et al. 1993, Eriksson et al. 1987). The mean of all ratios in the middle third of the crown (whorls four through six) was used as the best measure for branch diameter and length. Only midcrown whorls were utilized because in the upper whorls relative branch size changed rapidly from one whorl to the next, and seemed largely a function of tree growth rate. In addition, the difficulty of reaching the upper crown and small size of branches and main stem make accurate measurements difficult.

The best measure for branch angle was calculated as the average of the mean whorl values in whorls one through six. The best measure for branch number, however, was calculated as the mean number of branches in whorls one through five. Branch numbers per whorl remained relatively consistent for each tree throughout these whorls.

Derivation of simple measures

For all traits except bole volume, the approach was to find a single simple measure which best predicted the best measure of a trait. This was done by computing Pearson correlation coefficients between simpler measurements and the best measure. The simpler measurements chosen had to be highly correlated ($r>.80$) with the best measure, yet quick and easy to perform.

For bole volume, a combination of whorl height and interwhorl diameter measurements which best predicted bole volume was chosen using multiple regression analysis. Three height and diameter measurements with the highest correlations (Pearson correlation coefficient) with volume were chosen for inclusion in the full regression model. Stepwise elimination procedures (Weisberg 1985) were then used to eliminate variables which were not significant in the regression model at the .05 probability level. A LOG transformation was applied to independent and dependent variables to achieve a normal distribution of the data and independence of error.

RESULTS AND DISCUSSION

Bole volume

Diameter outside bark (DOB) at the bottom of interwhorl six had the highest correlation with total tree volume ($r^2 = .93$) of any single field measurement. Other measurements also used as predictor variables in the linear regression model were: total tree height ($r^2 = .90$) and DOB at the ground level ($r^2 = .83$). The reduced regression model (model $r^2 = .98$) was:

$$LOG(Bole\ Volume) = -5.70 + 1.17\,(LOG(HGT)) + .59\,(LOG(DOB))$$

Where: HGT = Total tree height (partial $r^2 = .93$)

DOB = Diameter outside bark at the bottom of interwhorl six (partial $r^2 = .05$).

This model requires two field measurements, total tree height and

DOB at whorl six. Total tree height is not difficult to measure at this age in noble fir, however identifying whorl six does take time. Measuring DOB at mid tree height would be faster, because it does not require identifying a particular whorl location. When this measure was used with total tree height the model obtained was (model r^2 = .95):

$$LOG(Bole\ Volume) = -7.11 + 2.23(LOG(HGT)) + .59(LOG(DOBH))$$

Where: HGT = Total tree height (partial r^2 =.93)

DOBH = DOB at one-half tree height (partial r^2 = .02)

Although the r^2 in this model is slightly less than the above model, the independent variables require less measurement time and it does a good job of predicting the best estimate of stem volume.

Branch length and diameter

Results of correlation analyses between simple and best measures for branch length ratios (BLR) and branch diameter ratios (BDR) were very similar, although the magnitudes of the correlations for BDR were somewhat less (Table A.1). Previous studies have shown that the size of the largest branch in a whorl is often well correlated with the mean of all branches in the whorl (Adams and Howe 1984), therefore the use of the largest branch (or two branches) was examined.

In general, correlations increased when the largest branch in more than one whorl was averaged, but not greatly. For example, the highest correlation for BLR with one branch was .958 (whorl five) and the correlation of the mean of the largest branches in whorls four through six with BLR was .987. Only one largest branch measurement from either whorl five or whorl six for BDR and BLR is needed to obtain correlations greater than .80, although some improvement can be made by taking the two largest branches. Branches in whorl six are essentially the largest branches on the tree (below this whorl branch size decreased) and are easily identified. Consequently, the most suitable simple measure for BDR and BLR in plantations of about this size and age would be the single largest branch on the tree and diameter of the stem just above the point of attachment.

Branch angle

Branch angle correlations also increased when more measurements were used (similar to the trend found in branch size), but were smaller in magnitude than branch size correlations (Table A.1). One or two branch angles representative of the whorl average, estimated visually, were investigated for use as simple measurements. Simple measures from the middle section of the crown (whorls three, four, five, and six) were examined because these whorls were easier to reach from the ground and it is easier to identify angles representative of the whorl average in these whorls.

Only one measurement of branch angle from the middle part of the crown is needed to achieve a correlation with the best measure greater than .80, however, not all single measures had correlations greater than .80 (i.e., r=.733 for whorl four). As with branch size, some improvement can be obtained by averaging two branch angles, either from the same whorl or from different whorls, but not much. The whorl closest to midcrown height (usually whorl three in these trees) is easily identified, relatively open, and readily accessible for angle measurement. Thus, a suitable simple measurement for branch angle would be to measure a representative branch angle from the whorl closest to midcrown height.

Branch number

The simplest measure considered for branch number was the count of mainwhorl branches in one whorl. More intensive measures consisted of averaging counts of more than one whorl. As with the other branch traits, correlations increased between simple measures and the best measure for branch number as more measurements were added.

The highest correlation of any single measure with the best measure of branch number was .704 (branches in whorl one), two measurements were required to achieve a correlation of .80. As with branch angle, the whorl closest to midcrown height is easily identified, relatively open and the number of branches easily counted. When the number of branches in this

whorl (whorl three) and the next lower whorl were averaged, the correlation with the best measure increased to .797. Thus, the best compromise operationally for measuring branch number is to take the average branch number in the whorl nearest midcrown height and the next lower whorl.

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Table A.1. Correlations between best measures of branch traits and rapid measures. (p-values for all correlations are < .001.)

Measure	Correlation	r^2
A. Branch Diameter Ratio		
Largest branch in whorl 4	.735	.54
Largest branch in whorl 5	.901	.81
Largest branch in whorl 6	.882	.78
Average of 2 largest branches in whorl 4	.820	.67
Average of 2 largest branches in whorl 5	.914	.84
Average of 2 largest branches in whorl 6	.988	.98
Average of largest branches in whorls 4 and 5	.924	.85
Average of largest branches in whorls 5 and 6	.963	.93
Average of largest branches in whorls 4 and 6	.939	.88
Average of largest branches in whorls 4, 5, and 6	.981	.97
B. Branch Length Ratio		
Longest branch in whorl 4	.902	.81
Longest branch in whorl 5	.958	.92
Longest branch in whorl 6	.933	.87
Average of 2 longest branches in whorl 4	.921	.85
Average of 2 longest branches in whorl 5	.961	.92
Average of 2 longest branches in whorl 6	.945	.89
Average of longest branches in whorls 4 and 5	.975	.95
Average of longest branches in whorls 5 and 6	.987	.97
Average of longest branches in whorls 4 and 6	.965	.93
Average of longest branches in whorls 4, 5, and 6	.987	.97
C. Branch Angle		
Single branch angle from whorl 3	.824	.68
Average of 2 branch angles from whorl 3	.832	.69
Single branch angle from whorl 4	.733	.54
Single branch angle from whorl 5	.845	.71
Single branch angle from whorl 6	.819	.67
Average of branch angles from whorls 4 and 5	.889	.79
Average of selected angles in whorls 4, 5, and 6	.904	.82
D. Branch Number		
Branches in whorl 1	.704	.50
Branches in whorl 3	.584	.34
Branches in whorl 5	.568	.34
Average of branches in whorls 1 and 2	.856	.73
Average of branches in whorls 3 and 4	.797	.63
Average of branches in whorls 4 and 5	.767	.59
Average of branches in whorls 3, 4. and 5	.904	.82
Average of branches in whorls 2,3,4, and 5	.942	.86

APPENDIX B.

ANALYSES OF VARIANCE FOR STEM AND BRANCHING TRAITS

This appendix contains Analysis of Variance tables for thirteen stem and branching traits measured on sapling Noble fir. Analyses are presented for data pooled over all three sites (Table B.1), data pooled over two of the three sites (Table B.2; Section12 and Lonetree), and for data from the third site (Bishop) alone (Table B.3). Estimated variance components from the Section12-Lonetree and Bishop analyses are also presented (Table B.4).

Table B.1. Analyses of variance for traits at all sites.

A. Volume

Source	df	SS	MS	F	prob.
Site	2	52953597.7	26476798.8	10.424	0.0103
Set	1	3009345.3	3009345.3	1.922	0.2686
Site X Set	2	2744214.8	1372107.4		
Rep(Site)	6	8112303.8	1352050.6		
Set X Rep(Site)	6	11514677.5	1919112.9		
Family(Set)	58	16056308.1	276832.9	1.735	0.0062
Site X Family(Set)	116	18509131.1	159561.5	1.366	0.0165
Plot error	348	40637026.7	116773.1		
Sampling error	1393	594884649.5	427052.9		

B. Height

Source	df	SS	MS	F	prob.
Site	2	513878.5072	256939.2536	12.671	0.0095
Set	1	65645.4227	65645.4227	4.490	0.1245
Site X Set	2	24294.6827	12147.3414		
Rep(Site)	6	55313.0132	9218.8355		
Set X Rep(Site)	6	82680.7624	13780.1271		
Family(Set)	58	159124.7246	2743.5297	2.252	0.0001
Site X Family(Set)	116	141290.2050	1218.0190	1.346	0.0212
Plot error	348	314855.8275	904.7581		
Sampling error	1393	4477039.2333	3213.9549		

C. Stem Diameter

Source	df	SS	MS	F	prob.
Site	2	9356.1965	4678.0983	7.074	0.0203
Set	1	348.8342	348.8342	1.027	0.4115
Site X Set	2	623.6430	311.8215		
Rep(Site)	6	2394.0830	399.0139		
Set X Rep(Site)	6	2102.9651	350.4942		
Family(Set)	58	4059.7064	69.9950	1.622	0.0141
Site X Family(Set)	116	5006.3300	43.1580	1.571	0.0010
Plot error	348	9562.5085	27.4785		
Sampling error	1393	139561.7500	100.1879		

Table B.1 (continued).

D. Taper[a]

Source	df	SS	MS	F	prob.
Site	2	0.1116	0.0558	10.119	0.0059
Set	1	0.0154	0.0154	4.153	0.0589
Site X Set	2	0.0034	0.0017		
Rep(Site)	6	0.0246	0.0041		
Set X Rep(Site)	6	0.0176	0.0029		
Family(Set)	58	0.1436	0.0025	1.284	0.1283
Site X Family(Set)	116	0.2238	0.0019	0.871	0.8092
Plot error	348	0.7709	0.0022		
Sampling error	1392	10.3735	0.0075		

E. Sinuosity[b]

Source	df	SS	MS	F	prob.
Site	2	5.5112	2.7556	7.850	0.0593
Set	1	0.1114	0.1114	0.462	0.6456
Site X Set	2	0.5592	0.2796		
Rep(Site)	6	0.4572	0.0762		
Set X Rep(Site)	6	0.2244	0.0374		
Family(Set)	58	1.8141	0.0313	0.966	0.5501
Site X Family(Set)	116	3.7558	0,0324	1.730	0.0001
Plot error	348	6.5227	0.0187		
Sampling error	1393	90.6437	0.0650		

F. Crook[c]

Source	df	SS	MS	F	prob.
Site	2	0.3368	0.1684	1.139	0.4184
Set	1	0.0363	0.0363	0.391	0.6808
Site X Set	2	0.2166	0.1083		
Rep(Site)	6	0.4110	0.0685		
Set X Rep(Site)	6	0.1979	0.0330		
Family(Set)	58	0.6586	0.0114	1.085	0.3502
Site X Family(Set)	116	1.2140	0.0105	1.010	0.4722
Plot error	348	3.6174	0.0104		
Sampling error	1393	53.0112	0.0381		

[a] Transformed for analysis as LOG(Taper+1).
[b] Transformed for analysis as SQRT(Sinuosity +.5).
[c] Transformed for analysis as SQRT(Crook +.5)

Table B.1 (continued).

G. Ramicorn Branching[d]

Source	df	SS	MS	F	prob.
Site	2	1.6989	0.8495	13.642	0.0070
Set	1	0.0867	0.0867	1.919	0.2383
Site X Set	2	0.0693	0.0347		
Rep(Site)	6	0.1775	0.0296		
Set X Rep(Site)	6	0.1604	0.0267		
Family(Set)	58	1.0888	0.0188	1.187	0.2167
Site X Family(Set)	116	1.8346	0.0158	0.815	0.9024
Plot error	348	6.7493	0.0194		
Sampling error	1393	81.9866	0.0589		

H. Fork[e]

Source	df	SS	MS	F	prob.
Site	2	0.3349	0.1674	1.078	0.4820
Set	1	0.0908	0.0908	0.592	0.5351
Site X Set	2	0.3122	0.1561		
Rep(Site)	6	0.0058	0.0010		
Set X Rep(Site)	6	0.0110	0.0018		
Family(Set)	58	0.3332	0.0057	1.155	0.2546
Site X Family(Set)	116	0.5772	0.0050	0.834	0.8757
Plot error	348	2.0769	0.0060		
Sampling error	1393	29.4072	0.0211		

I. Branch Diameter Ratio

Source	df	SS	MS	F	prob.
Site	2	0.1596	0.0798	4.933	0.0742
Set	1	0.0228	0.0228	1.537	0.3080
Site X Set	2	0.0252	0.0126		
Rep(Site)	6	0.0393	0.0065		
Set X Rep(Site)	6	0.0885	0.0147		
Family(Set)	58	0.2150	0.0037	1.603	0.0162
Site X Family(Set)	116	0.2683	0.0023	1.258	0.0585
Plot error	348	0.6397	0.0018		
Sampling error	1386	8.7901	0.0063		

[d] Transformed for analysis as SQRT(Ramicorn Branch +.5)
[e] Transformed for analysis as SQRT(Fork +.5)

Table B.1 (continued).

J. Branch Length Ratio

Source	df	SS	MS	F	prob.
Site	2	10.2984	5.1492	8.374	0.0431
Set	1	0.5280	0.5280	0.982	0.4100
Site X Set	2	0.9282	0.4641		
Rep(Site)	6	1.0538	0.1756		
Set X Rep(Site)	6	1.2457	0.2076		
Family(Set)	58	6.8008	0.1173	2.754	0.0000
Site X Family(Set)	116	4.9394	0.0426	1.369	0.0160
Plot error	348	10.8264	0.0311		
Sampling error	1386	160.1061	0.1155		

K. Branch Angle

Source	df	SS	MS	F	prob.
Site	2	6428.1730	3214.0865	8.404	0.0322
Set	1	502.6685	502.6685	1.706	0.2925
Site X Set	2	513.5510	256.7755		
Rep(Site)	6	820.5756	136.7626		
Set X Rep(Site)	6	559.2886	93.2148		
Family(Set)	58	2731.4439	47.0939	2.977	0.0000
Site X Family(Set)	116	1834.8855	15.8180	1.165	0.1477
Plot error	348	4723.2052	13.5724		
Sampling error	1385	74333.1667	53.6702		

L. Branch Number

Source	df	SS	MS	F	prob.
Site	2	19.6414	9.8207	3.205	0.1052
Set	1	0.3774	0.3774	.307	0.8225
Site X Set	2	3.2371	1.6186		
Rep(Site)	6	10.6945	1.7824		
Set X Rep(Site)	6	6.4836	1.0806		
Family(Set)	58	30.7163	0.5296	1.877	0.0021
Site X Family(Set)	116	32.7341	0.2821	0.864	0.8232
Plot error	348	113.6920	0.3267		
Sampling error	1385	1502.2208	1.0846		

Table B.1 (continued).

M. Knot Index

Source	df	SS	MS	F	prob.
Site	2	0.6479	0.3239	1.900	0.2156
Set	1	0.2548	0.2548	2.213	0.2012
Site X Set	2	0.1611	0.0805		
Rep(Site)	6	0.7589	0.1265		
Set X Rep(Site)	6	0.4161	0.0693		
Family(Set)	58	2.7320	0.0471	1.703	0.0078
Site X Family(Set)	116	3.2081	0.0277	1.268	0.0528
Plot error	348	7.5910	0.0218		
Sampling error	1385	106.1341	0.0766		

Table B.2. Analyses of variance for traits at Lonetree and Section 12.

A. Volume

Source	df	SS	MS	F	prob.
Site	1	12477947.4	12477947.4	4.083	0.1437
Set	1	3615943.1	3615943.1	1.609	0.3912
Site X Set	1	2038106.8	2038106.8		
Rep(Site)	4	6814913.1	1703728.3		
Set X Rep(Site)	4	11195957.5	2798989.4		
Family(Set)	58	18554167.8	319899.4	1.801	0.0134
Site X Family(Set)	58	10303457.9	177645.8	1.209	0.1656
Plot error	232	34084121.7	146914.3		
Sampling error	939	503723853.6	536447.1		

B. Height

Source	df	SS	MS	F	prob.
Site	1	41943.2532	41943.2532	2.091	0.3181
Set	1	61413.7798	61413.7798	2.760	0.3016
Site X Set	1	19820.0567	19820.0567		
Rep(Site)	4	38802.6949	9700.6737		
Set X Rep(Site)	4	79108.7919	19777.1980		
Family(Set)	58	164065.7060	2828.7191	2.561	0.0002
Site X Family(Set)	58	64063.6360	1104.5454	1.046	0.3988
Plot error	232	245093.3217	1056.4367		
Sampling error	939	3397815.9500	3618.5473		

C. Stem Diameter

Source	df	SS	MS	F	prob.
Site	1	2922.4852	2922.4852	3.828	0.1327
Set	1	560.2938	560.2938	1.254	0.4383
Site X Set	1	410.9166	410.9166		
Rep(Site)	4	1908.3342	477.0836		
Set X Rep(Site)	4	1907.9223	476.9806		
Family(Set)	58	3875.7407	66.8231	1.725	0.0200
Site X Family(Set)	58	2247.4440	38.7490	1.478	0.0232
Plot error	232	6081.0702	26.2115		
Sampling error	939	93429.5500	99.4989		

Table B.2 (continued).

D. Taper[a]

Source	df	SS	MS	F	prob.
Site	1	0.0184	0.0184	9.125	0.0268
Set	1	0.0049	0.0049	2.687	0.1090
Site X Set	1	0.0005	0.0005		
Rep(Site)	4	0.0070	0.0018		
Set X Rep(Site)	4	0.0082	0.0021		
Family(Set)	58	0.1003	0.0017	1.693	0.0235
Site X Family(Set)	58	0.0592	0.0010	0.820	0.8688
Plot error	232	0.2727	0.0012		
Sampling error	938	4.7595	0.0051		

E. Sinuosity[b]

Source	df	SS	MS	F	prob.
Site	1	0.5382	0.5382	1.361	0.4556
Set	1	0.2468	0.2468	.615	0.5849
Site X Set	1	0.4082	0.4082		
Rep(Site)	4	0.0584	0.0146		
Set X Rep(Site)	4	0.1484	0.0371		
Family(Set)	58	0.6941	0.0120	1.035	0.4484
Site X Family(Set)	58	0.6708	0.0116	1.26	0.1178
Plot error	232	2.1259	0.0092		
Sampling error	939	31.4812	0.0335		

F. Crook[c]

Source	df	SS	MS	F	prob.
Site	1	0.000013	0.000013	.542	0.7142
Set	1	0.009627	0.009627	.546	0.7068
Site X Set	1	0.023472	0.023472		
Rep(Site)	4	0.210302	0.052576		
Set X Rep(Site)	4	0.164986	0.041246		
Family(Set)	58	0.454511	0.007836	1.050	0.4271
Site X Family(Set)	58	0.433006	0.007466	.780	0.8666
Plot error	232	2.214547	0.009545		
Sampling error	939	31.446323	0.033489		

[a] Transformed for analysis as LOG(Taper+1).
[b] Transformed for analysis as SQRT(Sinuosity +.5).
[c] Transformed for analysis as SQRT(Crook +.5)

Table B.2 (continued).

G. Fork[d]

Source	df	SS	MS	F	prob.
Site	1	0.3293	0.3293	1.286	0.4598
Set	1	0.1466	0.1466	0.580	0.5923
Site X Set	1	0.2560	0.2560		
Rep(Site)	4	0.0030	0.0008		
Set X Rep(Site)	4	0.0034	0.0009		
Family(Set)	58	0.3196	0.0055	1.074	0.3927
Site X Family(Set)	58	0.2974	0.0051	0.783	0.8654
Plot error	232	1.5193	0.0065		
Sampling error	939	21.4267	0.0228		

H. Ramicorn Branch[e]

Source	df	SS	MS	F	prob.
Site	1	0.3277	0.3277	3.801	0.1814
Set	1	0.0840	0.0840	1.326	0.4404
Site X Set	1	0.0620	0.0620		
Rep(Site)	4	0.1379	0.0345		
Set X Rep(Site)	4	0.1558	0.0389		
Family(Set)	58	0.6089	0.0105	0.872	0.6984
Site X Family(Set)	58	0.6984	0.0120	1.153	0.2315
Plot error	232	2.4236	0.0104		
Sampling error	939	34.0613	0.0363		

I. Branch Diameter Ratio

Source	df	SS	MS	F	prob.
Site	1	0.1416	0.1416	10.581	0.0291
Set	1	0.0019	0.0019	0.425	0.7998
Site X Set	1	0.0061	0.0061		
Rep(Site)	4	0.0364	0.0091		
Set X Rep(Site)	4	0.0761	0.0190		
Family(Set)	58	0.1965	0.0034	1.576	0.0430
Site X Family(Set)	58	0.1247	0.0022	1.284	0.1018
Plot error	232	0.3886	0.0017		
Sampling error	934	4.6481	0.0050		

[d] Transformed for analysis as SQRT(Ramicorn Branch +.5)
[e] Transformed for analysis as SQRT(Fork +.5)

Table B.2 (continued).

J. Branch Length Ratio

Source	df	SS	MS	F	prob.
Site	1	0.0668	0.0668	0.248	0.9050
Set	1	0.1917	0.1917	0.234	0.7600
Site X Set	1	0.8556	0.8556		
Rep(Site)	4	0.9613	0.2403		
Set X Rep(Site)	4	0.8180	0.2045		
Family(Set)	58	5.9490	0.1026	3.143	0.0000
Site X Family(Set)	58	1.8926	0.0326	1.48	0.0225
Plot error	232	5.1080	0.0220		
Sampling error	934	74.8124	0.0801		

K. Branch Angle

Source	df	SS	MS	F	prob.
Site	1	4899.4593	4899.4593	38.968	0.0022
Set	1	28.3829	28.3829	1.199	0.3343
Site X Set	1	8.2255	8.2255		
Rep(Site)	4	483.4262	120.8566		
Set X Rep(Site)	4	522.6160	130.6540		
Family(Set)	58	1716.5132	29.5951	1.744	0.0181
Site X Family(Set)	58	984.3141	16.9709	1.423	0.0363
Plot error	232	2766.8605	11.9261		
Sampling error	933	43367.7500	46.4820		

L. Branch number

Source	df	SS	MS	F	prob.
Site	1	18.5451	18.5451	5.081	0.2029
Set	1	0.1796	0.1796	0.123	0.9742
Site X Set	1	3.2190	3.2190		
Rep(Site)	4	2.7788	0.6947		
Set X Rep(Site)	4	5.3573	1.3393		
Family(Set)	58	23.8279	0.4108	1.538	0.0521
Site X Family(Set)	58	15.4972	0.2672	0.917	0.6442
Plot error	232	67.5758	0.2913		
Sampling error	933	908.1458	0.9734		

M. Knot Index

Source	df	SS	MS	F	prob.
Site	1	0.5492	0.5492	3.571	0.1271
Set	1	0.0338	0.0338	1.363	0.2686
Site X Set	1	0.0048	0.0048		
Rep(Site)	4	0.6990	0.1748		
Set X Rep(Site)	4	0.3681	0.0920		
Family(Set)	58	2.2094	0.0381	1.544	0.0505
Site X Family(Set)	58	1.4312	0.0247	1.324	0.0765
Plot error	232	4.3228	0.0186		
Sampling error	939	57.2650	0.0614		

Table B.3. Analyses of variance for traits at the Bishop site.

A. Volume

Source	df	SS	MS	F	prob.
Set	1	99510.19	99510.19	.624	0.5122
Rep	2	1297390.74	648695.37		
Set X Rep	2	318719.93	159359.97		
Family(Set)	58	5707813.59	98410.58	1.7	0.0059
Plot error	116	6552904.93	56490.56		
Sampling error	454	91160795.88	200794.70		

B. Height

Source	df	SS	MS	F	prob.
Set	1	8706.2690	8706.2690	4.875	0.1579
Rep	2	16510.3183	8255.1591		
Set X Rep	2	3571.9705	1785.9852		
Family(Set)	58	72285.5876	1246.3032	2.07	0.0005
Plot error	116	69762.506	601.401		
Sampling error	454	1079223.283	2377.144		

C. Stem Diameter

Source	df	SS	MS	F	prob.
Set	1	1.2667	1.2667	0.130	0.9197
Rep	2	485.7487	242.8743		
Set X Rep	2	195.0428	97.5214		
Family(Set)	58	2942.8517	50.7388	1.69	0.0086
Plot error	116	3481.4383	30.0124		
Sampling error	454	46132.2000	101.6128		

D. Taper[a]

Source	df	SS	MS	F	prob.
Set	1	0.0134	0.0134	2.868	0.2324
Rep	2	0.0176	0.0088		
Set X Rep	2	0.0094	0.0047		
Family(Set)	58	0.2079	0.0036	.83	0.7762
Plot error	116	0.4982	0.0043		
Sampling error	454	5.6139	0.0124		

[a] Transformed for analysis as LOG(Taper+1).

Table B.3 (continued). E

Sinuosity[b]

Source	df	SS	MS	F	prob.
Set	1	0.0155	0.0155	0.408	0.5883
Rep	2	0.3988	0.1994		
Set X Rep	2	0.0760	0.0380		
Family(Set)	58	4.2050	0.0725	1.91	0.0016
Plot error	116	4.3968	0.0379		
Sampling error	454	59.1625	0.1303		

F. Crook[c]

Source	df	SS	MS	F	prob.
Set	1	0.2198	0.2198	13.374	0.0673
Rep	2	0.2007	0.1003		
Set X Rep	2	0.0329	0.0164		
Family(Set)	58	0.9851	0.0170	1.40	0.0619
Plot error	116	1.4029	0.0121		
Sampling error	454	21.5649	0.0475		

G. Ramicorn Branch[d]

Source	df	SS	MS	F	prob.
Set	1	0.0100	0.0100	4.306	0.1737
Rep	2	0.0395	0.0198		
Set X Rep	2	0.0046	0.0023		
Family(Set)	58	1.6162	0.0279	0.747	0.8905
Plot error	116	4.3256	0.0373		
Sampling error	454	47.9252	0.1056		

H. Fork[e]

Source	df	SS	MS	F	prob.
Set	1	0.0004	0.0004	0.101	0.7805
Rep	2	0.0028	0.0014		
Set X Rep	2	0.0076	0.0038		
Family(Set)	58	0.2935	0.0051	1.053	0.4009
Plot error	116	0.5575	0.0048		
Sampling error	454	7.9806	0.0176		

[b] Transformed for analysis as SQRT(Sinuosity +.5).
[c] Transformed for analysis as SQRT(Crook +.5)
[d] Transformed for analysis as SQRT(Ramicorn Branch +.5)
[e] Transformed for analysis as SQRT(Fork +.5)

Table B.3 (continued).

I. Branch Diameter Ratio

Source	df	SS	MS	F	prob.
Set	1	0.0401	0.0401	6.454	0.1263
Rep	2	0.0029	0.0015		
Set X Rep	2	0.0124	0.0062		
Family(Set)	58	0.1622	0.0028	1.292	0.1224
Plot error	116	0.2511	0.0022		
Sampling error	452	4.1420	0.0092		

J. Branch Length Ratio

Source	df	SS	MS	F	prob.
Set	1	0.4089	0.4089	1.912	0.3009
Rep	2	0.0925	0.0462		
Set X Rep	2	0.4276	0.2138		
Family(Set)	58	3.8986	0.0672	1.364	0.0799
Plot error	116	5.7183	0.0493		
Sampling error	452	85.2936	0.1887		

K. Branch Angle

Source	df	SS	MS	F	prob.
Set	1	979.6111	979.6111	53.425	0.0183
Rep	2	337.1494	168.5747		
Set X Rep	2	36.6725	18.3363		
Family(Set)	58	1862.5022	32.1638	1.907	0.0017
Plot error	116	1956.3448	16.8650		
Sampling error	452	30965.4167	68.5076		

L. Branch Number

Source	df	SS	MS	F	prob.
Set	1	0.2159	0.2159	0.383	0.5990
Rep	2	7.9157	3.9578		
Set X Rep	2	1.1264	0.5632		
Family(Set)	58	24.1254	0.4160	1.046	0.4113
Plot error	116	46.1162	0.3976		
Sampling error	452	594.0750	1.3143		

Table B.3 (continued).

M. Knot Index

Source	df	SS	MS	F	prob.
Set	1	0.3772	0.3772	15.722	0.0581
Rep	2	0.0599	0.0299		
Set X Rep	2	0.0480	0.0240		
Family(Set)	58	2.2996	0.0396	1.40	0.0607
Plot error	116	3.2682	0.0282		
Sampling error	452	48.8691	0.1081		

Table B.4. Estimated variance components from the Section12-Lonetree and Bishop test site analyses.

Trait		Family	Family X Site	Plot	Within Plot
Section12 and Lonetree					
Volume		23708.94	10243.84	-7984.79	536447.13
	SE	11134.43	11720.88	15345.14	24731.31
Height		287.36	16.04	11.58	3618.55
	SE	92.40	74.69	108.90	166.82
Diameter		4.679	4.179	-2.529	99.499
	SE	2.351	2.493	2.762	4.587
Taper[a]		.01180	-.00514	-.02910	.50741
	SE	.00611	.00719	.01280	.02341
Sinuosity[a]		.00671	.08006	-.05172	3.3526
	SE	.05064	.07584	.09575	.1546
Crook[a]		.00618	-.06933	-.01245	3.3489
	SE	.03293	.05413	.09887	.1544
Fork[a]		.00636	-.04736	-.00401	2.2819
	SE	.02290	.03716	.06774	.1052
Ramicorn Branch[a]		-.02572	.05315	-.00274	3.6274
	SE	.04861	.08004	.10798	.1672
Branch Diameter[a]		.02063	.01584	.02253	.49766
	SE	.01221	.01407	.01687	.02300
Branch Length[a]		1.1656	.35382	-.13152	8.0099
	SE	.3275	.20986	.23036	.3703
Branch Angle		2.1040	1.6816	-1.6247	46.482
	SE	1.0381	1.0963	1.2682	2.150
Branch Number		.02394	-.00803	.00751	.97336
	SE	.01491	.01857	.02996	.04502
Knot Index[a]		.22362	.20142	.07396	6.1377
	SE	.13811	.16077	.19111	.2839

[a] X .01.

Table B.4. continued.

Trait		Family	Family X Site	Plot	Within Plot
Bishop					
Volume		13973.34	-	-4342.80	200794.70
	SE	6471.38		8385.64	13297.95
Height		214.97	-	-118.79	2377.14
	SE	80.21		91.68	157.43
Diameter		6.909	-	-.773	101.613
	SE	3.351		4.407	6.729
Taper[a]		-.02369	-	.05486	1.2365
	SE	.02869		.06117	.08189
Sinuosity[a]		1.1532	-	-.15772	13.031
	SE	.47088		.55845	.863
Crook[a]		.16300	-	-.22968	4.7500
	SE	.11592		.18405	.3146
Fork[a]		.00844	-	-.00519	1.7578
	SE	.03719		.07183	.1164
Ramicorn Branch[a]		-.31415	-	.53084	10.556
	SE	.23441		.52966	.699
Branch Diameter[a]		.02107	-	-.06204	.91637
	SE	.01944		.03370	.06082
Branch Length[a]		.59736	-	-.80486	18.870
	SE	.46163		.74615	1.253
Branch Angle		5.0996	-	-3.9537	68.508
	SE	2.0898		2.5943	4.547
Branch Number		.00613	-	-.00186	1.3143
	SE	.03063		.05815	.08724
Knot Index[a]		.38250	-	-.46819	10.812
	SE	.27050		.42672	.718

[a] X .01.