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Genetic Parameters of Somatic Clones of Coastal Douglas-fir at $5^1/_2$-Years across Washington and Oregon, USA

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Abstract

Five genetic tests involving 70 somatic clones of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) were planted March-April 1999 in Weyerhaeuser plantations across western Washington and Oregon states, USA. Four of the tests are in Longview and Twin Harbors regions of Washington, and one test is in Springfield, Oregon. Each test is based on single-tree plots with 12 randomized complete-blocks. The 70 coastal Douglas-fir clones were propagated by somatic embryogenesis from two full-sib families that had the same female parent. Results are reported for survival, height, diameter at breast-height (DBH) and volume growth at $5^1/_2$-years.

These tests provide evidence of acceptable growth and survival of somatic trees of coastal Douglas-fir across a range of site conditions. Height had a clonal heritability of 0.25 ± 0.01, DBH 0.21 ± 0.01 and volume 0.20 ± 0.01. The growth traits were all strongly genetically associated with clonal correlations of 0.92 to 0.99.

Clonal performance for growth proved quite stable across tests with an overall between-test correlation of 0.84 ± 0.04. There was little variance due to clone x test interactions.

Key words: Coastal Douglas-fir, somatic embryogenesis, adaptability, clonal heritabilities, clonal stability.

Introduction

Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) is one of two varieties of *P. menziesii*; the other being Rocky Mountain Douglas-fir (*P. menziesii* var. *glauca*). The natural range of coastal Douglas-fir extends south from central British Columbia, Canada, along the Pacific Coast Ranges of northwest USA and into California and Mexico (HERMANN and LAVENDER, 1999). Coastal Douglas-fir is among the most important commercial forest tree species in North America and,

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since the early 1960s, has been the focus of genetic improvement programs.

Weyerhaeuser Company manages one of the most advanced genetic improvement programs of coastal Douglas-fir. Initial selections were made by Weyerhaeuser in 1956 with grafting of trees that had survived a major freeze event in 1955 (WOFFINDEN, 1955). In 1962 Weyerhaeuser began a more extensive and structured selection, breeding and testing program to improve plantation growth, form and wood quality (STONECYPHER *et al.,* 1996); a process now well into its third generation. A core part of Weyerhaeuser's advanced-generation improvement strategy is the use of somatic embryogenesis and manufactured seed technologies to bring more concentrated investment on elite genotypes in nucleus populations (DEAN, 2007).

Somatic embryogenesis (SE) is an *in vitro* tissue culture technique that involves repeating the normal conifer polyembryony process in zygotic seed embryo development to produce genetically identical embryos that can be grown as clonal trees for genetic testing and plantation establishment (DUNSTAN, 1988; CHELIAK and ROGERS, 1990; TAUTORUS *et al.,* 1991; ROBERTS *et al.,* 1995; GROSSNICKLE *et al.,* 1996; GROSSNICKLE, 1999; BENOWICZ *et al.,* 2002; GROSSNICKLE and FOLK, 2005). NAGMANI *et al.* (1991), GUPTA *et al.* (1994) and BENOWICZ *et al.* (2002) report various aspects of SE technologies applied specifically to cloning Douglas-fir.

Authors such as BENOWICZ *et al.* (2002), ALLAN (2003), HÖGBERG (2003), SUTTON (2002) and GROSSNICKLE and FOLK (2005) have commented that compared with other propagation systems such as cuttings, SE applied to forest trees offers the advantages of: (i) Long-term storage of embryo tissue through cryopreservation with no loss of juvenility or propagation capacity of genotypes (CYR *et al.,* 1994; PARK *et al.,* 1998) and (ii) Prospects for automatic handling of somatic embryos. Other micropropagation methods may also use the cryopreservation option, but most of the development has been done on embryogenic cultures (HÖGBERG, 2003).

Integration of SE technologies into conventional genetic improvement programs raises possibilities of enhanced genetic gain from selection and breeding; together with more rapid and flexible deployment of superior genotypes into plantations. Thorough analyses of genetic improvement strategies with SE requires reliable estimates of genetic parameters including clonal heritabilities, clonal genetic variances and clonal correlations. The literature appears to contain no estimates of these clonal genetic parameters for somatic clones of Douglas-fir.

In 1999 Weyerhaeuser established five tests of 70 somatic clones of coastal Douglas-fir across Washington and Oregon, Pacific Northwest USA. The principal objectives of these genetic field tests were to evaluate: (i) Survival and performance of somatic trees in plantations; (ii) clonal genetic parameters such as variances, heritabilities and correlations; and (iii) stability of clonal performance across tests. This paper presents results of these tests for growth of somatic clones at $5\frac{1}{2}$-years.

Experimental Details

Sites, Establishment and Silviculture

The five genetic tests were planted March–April 1999 in Weyerhaeuser Company plantations across western Washington and Oregon states, and included 70 clones of coastal Douglas-fir propagated from two full-sib families using SE. Tests identified as LV01 and LV02 are in the Longview region of Washington; TH03 and TH04 in Twin Harbors, Washington; and SP05 in Springfield, Oregon. The tests were planted by hand using containerized seedlings at 3,020 trees per hectare (1.82 m x 1.82 m). Site and establishment details of all five genetic tests are summarized in *Table 1*.

Genetic Material

The 70 coastal Douglas-fir clones were propagated by SE from two full-sib families that had the same female parent: 43 clones were propagated from family AxB

Table 1. – Details of site and establishment of genetic tests LV01 and LV02 (Longview, Washington); TH03 and TH04 (Twin Harbors, Washington); and SP05 (Springfield, Oregon).

	LV01	LV02	TH03	TH04	SP05
Site Parameters:					
Plantation	Hemlock Creek	Ostrander Creek	Dryad-Dell Creek	Goat Mtn – J Line	Anderson Creek
Region	Longview	Longview	Twin Harbors	Twin Harbors	Springfield
Elevation (m)	320	460	180	180	370
Slope	10%	Level	10%	15%	30-40%
Soil association	Morgan	Morgan	Newlund	Astoria	Nekia
Soil texture	Clay loam	Clay loam	Silty clay	Silt loam	Clay
Site index	130	130	140	140	120
Establishment:					
Planting date	March 99	April 99	March 99	March 99	March 99
Spacing (m)	1.82x1.82	1.82x1.82	1.82x1.82	1.82x1.82	1.82x1.82

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(female A x male B); and 27 clones from family AxC. The three parents (A, B and C) were all first-generation plus trees selected in the mid-1960s from 60- to 80-year old natural stands of coastal Douglas-fir growing below 600m in the Longview region of Washington. The original plus tree selection was on superior phenotype for stem diameter and branch habit.

Families AxB and AxC were part of Weyerhaeuser's first-generation breeding of coastal Douglas-fir and had demonstrated superior stem quality (notably stem sinuosity and branch habit) in seedling genetic tests. These two full-sib families were part of a high stem quality breeding population in which selection was not constrained by growth performance.

Somatic Embryogenesis Technology

The somatic seedlings used in this study were produced using early SE procedures for Douglas-fir from research at the beginning of the 1990s (described in GUPTA *et al.,* 1994). The protocol started with excising immature zygotic embryos from variable numbers of seeds of each of the AxB and AxC full-sib families. Embryonic suspensor masses (ESM) were then initiated *in vitro* from the individual excised embryos using a semi-solid medium containing mineral nutrients, sucrose and vitamins. The next step involved multiplication of the ESM cultures by weekly subculture in fresh liquid medium. An *in vitro* development step followed in which mature somatic embryos were produced on pads soaked in high osmolality liquid development medium containing abscisic acid, gibberellic acid and activated charcoal.

Good quality embryos were selected by hand from the development medium with the aid of a stereo microscope. The selected embryos were transferred onto semi-solid medium and incubated for the first 5–7 days in the dark followed by transfer to light for eight weeks to produce germinants with cotyledons.

The germinants were then transferred to *ex vitro* nursery conditions. This transfer involved the individual selection of good quality somatic seedlings with epicotyls. These seedlings were transplanted into a mixture of peat, vermiculite and perlite in 164 cm^3 "supercell" containers. All somatic seedlings were grown in the same greenhouse for one year and had morphology and growth rates within the normal range exhibited by zygotic seedlings in nurseries.

Field Design

Each of the five genetic tests are based on single-tree plots of the 70 somatic clones randomised across 12 complete-replicates; that is, 12 trees planted per clone per test. An attempt was made to minimise site variation by careful site preparation and placement of replications.

Measurements

In fall 2004 ($5\frac{1}{2}$ years after planting) all surviving trees in all tests were measured for height using poles; and stem diameter over-bark at breast-height (DBH at 137cm) using callipers. Stem volume over-bark was calculated from diameter and height for each tree using the small-tree volume equation developed by BRUCE and DEMARS (1974).

Statistical Methods

(1) STATISTICAL PACKAGE: ASREML (GILMOUR *et al.,* 2006) was used for all data analyses. ASREML is based on "Restricted Maximum Likelihood" methodology (PATTERSON and THOMPSON, 1971; SEARLE *et al.,* 1992). The program makes optimal use of all available information, has considerable flexibility in the range of models that can be fitted and its solutions are BLUP (Best Linear Unbiased Prediction).

(2) GENERAL MODEL: Three variations of the following GENERAL MODEL were fitted to the $5\frac{1}{2}$-year data for the 70 somatic clones pooled across the five genetic tests LV01, LV02, TH03, TH04 and SP05 – (1)

$$\begin{aligned} \text{Trait}_{ijklm} = \mu + \text{TEST}_i + \text{REP}_{ij} + \\ \text{FAMILY}_k + \text{CLONE}_{kl} + \\ \text{FAMILY.TEST}_{ik} + \text{CLONE.TEST}_{ikl} + \\ \text{RESIDUAL}_{ijklm} \end{aligned} \quad (1)$$

where Trait_{ijklm} is the observation on the m*th* tree of the l*th* somatic clone from the k*th* full-sib family and growing in the j*th* replicate at the i*th* test; μ is a fitted mean; TEST_i is the effect of the i*th* test site (i = 1–5), assumed to be a fixed effect; REP_{ij} is a random effect of the j*th* replication nested within the i*th* test (j = 1–12); FAMILY_k is the fixed effect of the k*th* full-sib family (k = 1, 2); CLONE_{kl} is the random effect associated with the l*th* somatic clone nested within the k*th* full-sib family (l = 1–43 in one family and 1–27 in the other); FAMILY.TEST_{ik} is the interaction of family and genetic test; CLONE.TEST_{ikl} is the interaction of clone and test; and RESIDUAL_{ijklm} is a residual error among the m*th* trees within the l*th* clone. The effect of FAMILY_k is considered fixed in this GENERAL MODEL because two families are not sufficient to reliably estimate a variance component for this effect.

Any so-called "c-effects" present in this study are completely confounded with CLONE_{kl}. C-effects refer to propagation effects associated with particular clones but not of genetic origin.

(3) MODEL 1: In preliminary analyses of the $5\frac{1}{2}$-year growth data from the five genetic tests and using the GENERAL MODEL described previously, the interaction of family x test (FAMILY.TEST_{ik}) was found to be negligible. MODEL 1 is the GENERAL MODEL (defined by Equation 1) with the FAMILY.TEST_{ik} effect omitted; and has been used to estimate variance components and overall clonal heritabilities across the five tests. Effects in MODEL 1 were estimated separately for each trait in a series of univariate analyses.

MODEL 1 was used to estimate variance components for the effects of REP_{ij} (denoted σ^2_R), CLONE_{kl} (σ^2_C), CLONE.TEST_{ikl} interaction (σ^2_{CT}) and the RESIDUAL_{ijklm} within-clone error (σ^2_e). Overall phenotypic variance (σ^2_P) was calculated as – (2)

$$\sigma^2_P = \sigma^2_C + \sigma^2_{CT} + \sigma^2_e \quad (2)$$

Broad-sense clonal heritabilities (H^2_C) were defined as the ratio of between-clone (within-family) variance to phenotypic variance – (3)

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$$H^2_C = \sigma^2_C / \sigma^2_P \quad (3)$$

The H^2_C is actually a repeatability parameter that provides an indication of the degree to which a somatic clone's superiority is repeatable, relative to other clones from the same family. The terms "clonal heritability" and "clonal repeatability" are both commonly used to describe H^2_C; in this study the "clonal heritability" term is used.

Clonal variance (σ^2_C) and heritability (H^2_C) were also estimated with the effect of families ($FAMILY_k$) omitted from MODEL 1. In this case σ^2_C is variance among clones ignoring the fixed effects of families, and H^2_C the repeatability of a clone's superiority ignoring family.

(4) MODEL 2: Was used to analyse data from each of the individual tests. $FAMILY.TEST_{jk}$ interaction was omitted from MODEL 2 and the $CLONE_{kl}$ (σ^2_C) and $CLONE.TEST_{ikl}$ (σ^2_{CT}) variances were partitioned into separate but correlated $CLONE_{kl}$ (σ^2_C) components for each test. Separate residual variances were then fitted to each test to allow site-specific estimates of clonal heritability.

(5) MODEL 3: Is a variant of MODEL 1 and was used to estimate between-trait clonal correlations by adding an extra dimension to each term to accommodate bivariate structures, and also excluding the interaction term. Independent variance components were fitted for replicate, while separate but correlated variances were fitted to both the clone and error terms. Thus MODEL 3 accommodates the two trait vector/matrix of effects while MODEL 1 is univariate.

Results and Discussion

General

Total numbers of somatic trees measured, and their average survival and growth at 5½-years of age across the five genetic tests (LV01, LV02, TH03, TH04 and SP05) are given in *Table 2*. It is evident that survival was acceptable (92–99%) across all tests. In particular, there was very high survival (97–99%) of somatic trees at 5½-years across the three tests at Twin Harbors and Springfield (*Table 2*). These Twin Harbors and Springfield tests also exhibited the fastest growth to 5½-years with the somatic trees reaching mean heights of 3.83m at SP05, Anderson Creek Plantation, Springfield; and 3.85 m and 3.47 m, respectively, at TH04 (Goat Mountain) and TH03 (Dryad-Dell Creek) in Twin Harbors (*Table 2*). Test LV02 at the colder, higher elevation (460 m, *Table 1*) site in Ostrander Creek Plantation, Longview, grew the slowest with mean height of 2.90 m (and 94% survival).

SE is viewed as a relatively new technology by many in the forest industry and authors such as BENOWICZ *et al.* (2002), HARRINGTON (2003), and GROSSNICKLE and FOLK (2005) emphasise the need to continue assessing performance of somatic plants under operational nursery and plantation conditions. Until now BENOWICZ *et al.* (2002) seem to provide the only published evaluation of performance of somatic trees of coastal Douglas-fir in the field. These authors evaluated 192 each of somatic and zygotic seedlings in a single field test location on Vancouver Island, British Columbia over two growing seasons. Both stock types of Douglas-fir were found to be comparable in attributes such as frost hardiness (including both spring bud break and fall assessments of tissue damage and conductivity after freezer testing) as well as physiological attributes (such as net photosynthesis). Development of frost hardiness in both spring and fall can, of course, be extremely important for survival and production of Douglas-fir plantations (WHEELER *et al.,* 1990; BENOWICZ *et al.,* 2002). This current study provides strong evidence that somatic plantations of coastal Douglas-fir are capable of good survival and growth across the range of site conditions studied in Washington and Oregon.

GROSSNICKLE and FOLK (2005) conducted a nursery stock evaluation of somatic seedlots of spruce crosses (*Picea glauca* (MOENCH) VOSS, *P. engelmannii* PARRY ex. ENGELM.). The somatic plants met all operational grading criteria for plantable seedlings as defined by the British Columbia Ministry of Forests; including seedling height, root collar diameter and root growth.

Clonal Variances and Heritabilities

Table 3 presents variance components and heritabilities for growth of somatic clones of coastal Douglas-fir across the five tests studied, which were derived by fitting the ASREML MODEL 1. The clonal heritability (or repeatability) of growth of the somatic clones to 5½-years across the five Washington and Oregon tests were in the 0.20–0.25 range and all had very low standard errors. Height growth had the highest clonal heritability of $H^2_C = 0.25 \pm 0.01$. DBH and stem volume had marginally lower heritabilities of 0.21 ± 0.01 and 0.20 ± 0.01, respectively (*Table 3*).

The estimates of H^2_C presented in *Table 3* reflect the ratio of the variance between-clones within full-sib fami-

Table 2. – Number of Douglas-fir somatic trees planted, trees measured and percent survival at 5½-years across genetic tests LV01 and LV02 (Longview, Washington); TH03 and TH04 (Twin Harbors, Washington); and SP05 (Springfield, Oregon). Also given is mean stem height and volume (± standard errors) at 5½-years of all the somatic trees in each test.

	LV01	LV02	TH03	TH04	SP05
Measured (no)	772	786	818	834	813
Survival (%)	92%	94%	97%	99%	98%
Stem height (m)	3.33±0.07	2.90±0.07	3.47±0.07	3.85±0.07	3.83±0.07
Stem volume (dm^3)	2.73±0.16	2.13±0.16	3.03±0.16	3.99±0.16	3.85±0.16

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Table 3. – ASREML estimates and standard errors (SE) determined with fitted MODEL 1 for overall means, variance components and clonal heritabilities for stem height, diameter at breast-height (DBH) and volume for coastal Douglas-fir somatic clones at $5^1/_2$-years across the genetic tests LV01, LV02, TH03, TH04 and SP05.

	Height (m)	DBH (mm)	Volume (dm^3)
Overall Means:			
Mean ($\mu \pm$ SE)	3.46 ± 0.05	38.7 ± 0.7	3.10 ± 0.10
Variance Components:			
Clones within-families ($\sigma^2_C \pm$ SE)	0.11 ± 0.02	23.5 ± 4.5	0.42 ± 0.08
Clone x test interaction ($\sigma^2_{CT} \pm$ SE)	0.02 ± 0.00	5.4 ± 1.1	0.11 ± 0.02
Within-clone residual ($\sigma^2_e \pm$ SE)	0.27 ± 0.01	77.6 ± 1.8	1.56 ± 0.04
Phenotypic variance (σ^2_P) [A]	0.40 ± 0.02	106.4 ± 4.8	2.09 ± 0.09
Pooled Heritabilities (No Units of Measurement):			
Clonal heritability ($H^2_C \pm$ SE) [B]	0.25 ± 0.01	0.21 ± 0.01	0.20 ± 0.01

[A] Phenotypic variance (σ^2_P) estimated as sum of variance between clones within-families (σ^2_C), clone x test interaction (σ^2_{CT}) and between-trees within clones (σ^2_e).

[B] Clonal heritability (H^2_C) is estimated as the ratio of variance between clones within-families (σ^2_C) over phenotypic variance (σ^2_P); and reflects the repeatability of clonal performance.

lies (σ^2_C) divided by the phenotypic variance (σ^2_P; Equations 2 and 3). As already mentioned, these clonal heritabilities give an indication of the degree to which a somatic clone's superiority across tests is repeatable, relative to other clones from the same family. It is important to note that c-effects associated with non-genetic propagation factors are completely confounded with σ^2_C in this study, and these effects may lead to substantial upward bias in the genetic parameter estimates.

In analyses not reported here, clonal heritability was also determined using a σ^2_C component estimated as variance between-clones ignoring families (*i.e.* with $FAMILY_k$ omitted from MODEL 1). These estimates of H^2_C ignoring family were almost identical to those presented in *Table 3*. This observation reflects the similarity of the two particular full-sib families involved in this study with respect to average performance of their clones. As already mentioned, two full-sib families of common female parentage does not represent a sufficient sample to estimate variance for the effect of family. The current study is not sufficient to reach conclusions about the influence of family on performance of somatic Douglas-fir clones.

Table 4 presents ASREML estimates with fitted MODEL 2 of clonal heritabilities (or repeatabilities) and standard errors of growth of the somatic clones to $5^1/_2$-years in each individual genetic test. While the magnitude of the heritabilities is higher in the individual tests, compared with estimates in *Table 3*, the H^2_C for each trait are remarkably consistent across tests (*Table 4*). The somewhat slower growing tests in the Longview region of Washington (namely LV01, LV02) also displayed strong heritabilities for growth.

The literature appears to contain no previous published estimates of clonal genetic parameters for growth of coastal Douglas-fir in field tests. There are published genetic parameter estimates for zygotic trees in field tests. For example, DEAN and STONECYPHER (2006) estimated individual heritabilities of 0.18–0.22 for height of coastal Douglas-fir between four and 17 years after planting across polymix family tests in Weyerhaeuser plantations in Oregon that had similar silviculture to the somatic tests reported here. The heritability of stem diameter age-for-age of those zygotic trees was consistently much lower than for height. CAMPBELL *et al.* (1986), KING *et al.* (1988), NAMKOONG *et al.* (1972),

Table 4. – ASREML estimates with fitted MODEL 2 of clonal heritabilities (or repeatabilities) and standard errors (SE) for stem height, diameter at breast-height (DBH) and volume for coastal Douglas-fir somatic clones at $5^1/_2$-years in the each of the genetic tests LV01, LV02, TH03, TH04 and SP05. Pooled between-test clonal correlations are also shown.

Genetic Test	Height	DBH	Volume
LV01 (Longview, Washington)	0.32 ± 0.05	0.29 ± 0.05	0.27 ± 0.04
LV02 (Longview, Washington)	0.34 ± 0.05	0.26 ± 0.04	0.23 ± 0.04
TH03 (Twin Harbors, Washington)	0.34 ± 0.05	0.29 ± 0.05	0.26 ± 0.04
TH04 (Twin Harbors, Washington)	0.31 ± 0.05	0.25 ± 0.04	0.23 ± 0.04
SP05 (Springfield, Oregon)	0.32 ± 0.05	0.28 ± 0.04	0.28 ± 0.04
Between-test clonal correlation	0.84 ± 0.04	0.84 ± 0.04	0.84 ± 0.04

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ADAMS and JOYCE (1990) and JOHNSON *et al.* (1997) also present estimates of genetic parameters for field growth of zygotic coastal Douglas-fir progeny tests. The individual heritability estimates of CAMPBELL *et al.* (1986) and KING *et al.* (1988) ranged between 0.12–0.21 for height growth of zygotic coastal Douglas-fir at five to 13 years after planting.

The substantial levels of clonal variation and heritability (repeatability) reported here suggest that selection among SE clones of coastal Douglas-fir can provide strong gains in growth (assuming c-effects are not large). This between-clone variation, together with the potential of SE technology, for propagating clonal lines (that can be cryogenically stored) offer new possibilities for the continued genetic improvement of Douglas-fir. Options range from using SE clones in establishing seed orchards to large-scale clonal forestry. As already mentioned, the clonal variances and heritabilities reported here are indeed confounded with some level of c-effect, and if these propagation effects are large they will cause substantial upward bias in the estimated genetic parameters and gains.

Clonal Stability

Stability of clonal performance across tests was high for all growth traits with between-test correlations of 0.84 ± 0.04; derived from fitting MODEL 2 (*Table 4*). A between-test correlation of unity implies that clones rank the same across each of the five tests. A correlation of zero implies that there is no correspondence at all between rankings across the tests.

The stability of genetic expression that is evident from the high between-test clonal correlations is reinforced by the low levels of variance due to clone x test interactions. Indeed, the variance between-clones within families (σ^2_C) is more than four times greater than variance due to clone x test interaction (σ^2_{CT}) for growth of the somatic clones to $5\frac{1}{2}$-years across the five tests in Washington and Oregon (*Table 3*). Intuitively, one might expect clones to exhibit more genetic x environment interaction than say families or populations due to the genetic uniformity of clonal lines (KLEINSCHMIT, 1983). The stability of SE clones in this current study is encouraging for future clonal forestry applications in coastal Douglas-fir.

Table 5. – ASREML estimates with fitted MODEL 3 of clonal and phenotypic correlations among stem height, diameter at breast-height (DBH) and volume of coastal Douglas-fir somatic clones at $5\frac{1}{2}$-years across the genetic tests LV01, LV02, TH03, TH04 and SP05. Correlations are above the diagonals, standard errors below.

	Height	DBH	Vol
Genetic correlations:			
Height		0.92	0.94
DBH	0.02		0.99
Volume	0.02	0.01	
Phenotypic correlations:			
Height		0.90	0.90
DBH	0.01		0.97
Volume	0.01	0.01	

Correlations among Traits

Height, DBH and volume were all closely genetically correlated at the clonal level (correlations of 0.92–0.99; *Table 5*). The clonal genetic correlation between height and DBH at $5\frac{1}{2}$-years was 0.92 ± 0.02.

Conclusions

Following are the main conclusions from analyses of five genetic tests of 70 somatic clones developed from two full-sib coastal Douglas-fir families; and measured at $5\frac{1}{2}$ years –

(1) Survival and Growth: The somatic trees showed generally acceptable survival and growth across the field conditions studied. These site conditions are representative of many lower elevation (below say 600 m) plantations in the Pacific Northwest USA. The most challenging site studied here was Ostrander Creek (LV02; elevation 460 m) at Longview that had acceptable average survival of 94% at $5\frac{1}{2}$ years.

(2) Genetic Parameters: Clonal heritabilities of growth traits at $5\frac{1}{2}$ years were moderately high with low standard errors. Heritability of height was $H^2_C = 0.25 \pm 0.01$, DBH 0.21 ± 0.01 and volume 0.20 ± 0.01. Height, DBH and volume were all closely genetically correlated at the clonal level. The estimated clonal parameters are confounded with any c-effects due to propagation.

(3) Clonal Stability: Clonal performance for growth was quite stable across tests with between-test correlations of 0.84 ± 0.04. The stability of genetic expression that is evident from the high between-test clonal correlations is reinforced by low levels of variance due to clone x test interactions.

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