

Genetic Parameters of Stem Form Traits in a 9-Year-Old Coastal Douglas-fir Progeny Test in Washington¹⁾

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Summary

The genetic control of stem form traits was investigated in a 9-year-old progeny test comparing 80 open-pollinated families, located in a fertile Pacific coast site in Washington. In addition to stem form traits (internode sinuosity, and number of forks and ramicorns per tree), stem volume (height and DBH), bud phenology (earliness of budburst and budset), and occurrence of second flushing on the leader shoot (9th growing season) were measured. Trees with at least one fork or ramicorn were frequent (26% and 46%, respectively), as were trees with second flushing (26%). Most of the trees exhibited sinuosity of limited magnitude. Due to strong differences among family means and at least modest family heritabilities (0.35 to 0.66), all traits were found to be amenable to genetic improvement. The estimated genetic correlation (r_A) between numbers of forks and ramicorns was relatively strong (0.54), and both forking defects traits exhibited similar genetic associations with other traits. Forking defects were strongly and positively associated with frequency of second flushing, a trait which in turn is positively and moderately correlated with both DBH (0.32) and earliness of budburst (0.39). These results are consistent with previous findings. Breeding consequences for simultaneous improvement of both stem volume and form are discussed.

Key words: *Pseudotsuga menziesii*, forking defects, lamas growth, genetic correlation, index selection.

FDC: 165.3; 181.6; 181.8; 232.1; 815.5; 174.7 *Pseudotsuga menziesii*; (797).

Introduction

As in many conifers, coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (MIRB.) FRANCO) breeding programs have mainly emphasized adaptation and stem volume, with less emphasis on stem form and branching traits (WOODS, 1993). Part of the lack of concern for stem form and branching habit is that old Douglas-fir stands are usually characterized by trees with straight-stems and good form. Nevertheless, young plantations of this species, especially those on favorable sites, often exhibit high frequencies of stem defects, especially forking and stem waviness or sinuosity (CAMPBELL, 1965; WALTERS and KOZAK, 1967; DE CHAMPS, 1978; KING, 1986; ADAMS and BASTIEN, 1994). Stem defects lower the quality of trees removed in early commercial thinnings and, although these defects may be covered by subsequent wood growth and thus masked in older trees, the economic value of wood in the lower logs of these trees is still negatively impacted (CAMPBELL, 1965). Silvicultural manipulations such as high planting densities, precommercial thinning, and stem pruning can do

much to alleviate stem defects; nevertheless, these treatments are expensive. The inclusion of stem form traits in tree breeding programs of Douglas-fir may be essential if these traits are unfavorably correlated with stem growth or other characters of interest (ADAMS and BASTIEN, 1994).

In order to account for stem defects in a breeding program, it is important first to define goal traits (types of defects, location in tree and magnitude) according to their impact on wood quality. Stem defects are most detrimental when they occur in the lower logs of trees. Therefore, goal traits can be defined as stem defects expressed at a relatively young age (10 to 15 years), when they are most easily visible. Determining acceptable levels of defects for wood utilization depends on the intended end products, the veneer industry being the most exacting, followed by lumber and then pulp (EHRENBERG, 1969).

Forking defects (forked stems and ramicorn (steep-angled) branches) are probably the most serious stem-quality problems in coastal Douglas-fir. Forked stems reduce wood yield and increase difficulty of pruning. Ramicorn branches are also difficult to prune and produce very large knots that reduce lumber strength and quality. Forking defects arise from loss of apical dominance in the terminal shoot, due to damage either to the terminal bud or to the leader shoot by insect attack, bird perching, early season frost, or they result from second flushing (WALTERS and SOOS, 1961; DE CHAMPS, 1971; KING, 1986; ADAMS and BASTIEN, 1994). BUJON (1994) showed that loss of apical dominance is most marked, increasing the risk of persistence of forking defects, when lateral realize one more growth cycle than the terminal shoots during a growing season. DE CHAMPS (1971), however, found that only one-third of observed forking defects in young Douglas-fir trees in France were due to second flushing.

Among the types of stem straightness defects (e.g., general lean, sweep, crook, SHELBOURNE, 1969), sinuosity (stem waviness or crookedness totally within inter-whorl segments) is the most common in Douglas-fir (CAMPBELL, 1965). Severe deviations from straight stems will lead to high proportions of compression wood and spiral grain (SHELBOURNE, 1969), significantly reducing structural strength of lumber (SHELBOURNE, 1969; TIMELL, 1986). There is a lack of knowledge, however, on the effects of sinuosity on amount and severity of compression wood in Douglas-fir. This knowledge will be necessary in order to define acceptable limits of sinuosity with respect to wood utilization.

There have been only a few previously published accounts of the genetics of stem form traits in coastal Douglas-fir (JARRET, 1978; BIROT and CHRISTOPHE, 1983; ADAMS and HOWE, 1985; KING, 1986; ADAMS and BASTIEN, 1994). In this paper we report on progeny test data collected on a fertile site in western Washington which exhibits a high frequency of forking defects. In addition to forking defects and sinuosity, a number of growth and growth phenology traits were measured. These data enabled us to address the following questions regarding the genetics of stem form traits in Douglas-fir:

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1) How much genetic variability and what degree of genetic control exists for stem form traits?

2) What are the genetic relationships among stem form traits and between stem form traits and other characters of interest? In particular, is stem form in this population unfavorably associated with either stem growth or bud phenology?

3) What are the implications of answers to 1) and 2) for breeding coastal Douglas-fir? For example, how readily can both stem growth and form be improved simultaneously in this species?

Materials and Methods

The materials consisted of 80 families derived from open-pollinated seed of trees phenotypically selected in numerous natural low elevation stands within the Grays Harbor breeding zone, located on the Olympic Peninsula close to the Pacific ocean in western Washington. Two progeny test sites within this zone were included in the study, but the frequency of stem form defects was high enough (>20% of trees) in only one of these to warrant their measurement. Thus, this report is restricted to the results from this one site. Planting of the test took place in 1984 with 1-0 plug seedlings at a density of 3453 trees/ha. The 80 families were allocated at random to 2 sets of 40, each 40-family set being evaluated in a separate randomized complete block experiment with 5 replications. Within each block, families were represented by 4-tree noncontiguous plots, with trees assigned to planting spots at random. Planting success was very high, so that no replacement trees were necessary. At the time of measurement (1991, age 9 from seed), survival of original planted trees was 98% and the stand was approaching canopy closure.

Trees were measured for 8 traits. First, timing of budburst and budset were assessed by scoring the presence or absence of budburst (or budset) on a single day midway in the bud flushing (or bud setting) period of the test site (i.e., when about half the trees have flushed or set) (LI and ADAMS, 1993). These assessments were made for the terminal bud of a lateral branch on the fourth whorl from top of the tree. At this height, buds were fully exposed to sunlight, but still easily reached from the ground. Budburst was defined as the presence of green needles emerged beyond the bud scales; and budset as the presence of brown scales at the terminal. The frequency of trees in a family that burst (or set) bud midway in the flushing (setting) period has a strong negative genetic correlation with mean date of family budburst (budset) ($|r_A| > 0.80$, LI and ADAMS, 1993). After stem growth ceased in the fall, trees were measured for total height, diameter at breast height (DBH, 1.37 m), presence of second flushing (1991) in the terminal shoot (terminal or lateral buds), stem sinuosity and forking defects. Sinuosity score (SIN) was recorded visually from the ground, for the interwhorl between the first 2 whorls below the leader, as the number of displacements from a straightbole times the width of the maximum displacement. Displacement width was expressed in units of one-half the bole diameter at the point of maximum displacement. Restricting measurements to the first interwhorl below the leader was shown by ADAMS and HOWE (1985) to be nearly as efficient as measuring sinuosity on the 3 top interwhorls of the tree and averaging the result. Forking defects, number of forks (FO) and ramicorns (RA), were recorded as the total number of occurrences in branch whorls below the two top whorls of the tree. A ramicorn was defined as a branch diverging less than 30 degrees from the main stem, with a diameter less than half that of the main bole. A similarly steep-angled branch with diameter greater than half that of the bole was defined as a fork.

All traits were analyzed at the plot level, with presence-absence traits being expressed as frequencies [i.e., frequencies of trees per plot which burst or set bud on the respective scoring dates (BB or BS), and frequencies of trees per plot which second flushed (FSF)]. Families with higher proportions of BB or BS are those that have a tendency to break or set bud earlier than other families.

Analyses of variance-covariance were first conducted for each set of 40 families separately. Genetic correlations among traits were very similar between sets. In addition, a KULLBACK test (LEGENDRE and LEGENDRE, 1984) indicated that residual and family variance-covariance matrices were homogeneous between sets ($p < 0.05$). Therefore, combined analyses of variance-covariance of plot means (frequencies) for the 2 family sets were carried out with the following linear model:

$$y_{ijk} = \mu + s_i + f_{j(i)} + b_{k(i)} + e_{jk(i)}$$

where μ is the overall mean,

s_i the fixed effect of the i th set,

$f_{j(i)}$ the random effect of family j within set i ,

$b_{k(i)}$ the fixed effect of block k within set i ,

$e_{jk(i)}$ the residual.

Function MODLI (KOBINSKY, 1990) of statistical software Splus was used to compute type II sum of squares and crossproducts. No plots were missing. Variance (covariance) components were estimated by equating mean squares (cross-products) for each effect with its expectation. Assumptions of analysis of variance were checked. The following transformations of plot means proved adequate to circumvent problems due to non-normality of residuals and mean-residual variance dependency: square root transformation of FO, RA and FSF, and log transformation of SIN. Means of non transformed variables are given in table 1.

The amount of genetic variation in the traits was quantified by estimating family variances and testing their significance. Family (h^2_f) heritabilities, used for computing genetic gains from backward (i.e. parent-tree) selection, were estimated as: $h^2_f = 1/4 \sigma_A^2 / \sigma_{Pf}^2$, where σ_A^2 is the additive genetic variance and σ_{Pf}^2 the phenotypic variance of family means. $\sigma_{Pf}^2 = \sigma_f^2 + \sigma_e^2 / n_b$, where σ_f^2 is the family within sets variance, σ_e^2 is the residual variance, and n_b is the number of blocks per set. Because open-pollinated progenies are expected to be more closely related than half-sibs, we estimated σ_A^2 as $3 \sigma_f^2$ (CAMPBELL, 1979). Confidence intervals for family heritabilities were calculated according to GALLAIS (1990). To evaluate the genetic relationships between traits, we estimated genetic correlations (r_A) and the standard errors of these estimates (BECKER, 1984).

Breeding implications were examined by estimating responses (ΔG) of individual traits to backward selection on progeny mean values: $\Delta G = 2 i h^2_f \sigma_{Pf}$, where i is the intensity of family selection. This response is appropriate to gain expected in the progeny of a clonal seed orchard after roguing clones on the basis of their open-pollinated families in a progeny test (VARGAS-HERNANDEZ and ADAMS, 1991). To evaluate multiple-trait selection, we used selection index methods (reviewed by WHITE and HODGE, 1991). As a priori definition of economic weights is difficult, our approach was to compute selection indices that enable the breeder to obtain expected genetic gains (ITOH and YAMADA, 1988).

Results

The high quality of the test site is evident in the excellent growth; trees averaged about 6 m in height at age 9 (Table 1). Forking defects, however, were very common in the test,

Table 1. – Estimates of test means (ranges in family means), family heritabilities (h^2_f), and genetic response (ΔG , % of overall mean) for study traits at age 9.

Trait	Means ^a)		h^2_f ^b) [95% confidence interval]	Expected genetic gain (%) ^{b,c})
	Overall	Family range		
Number of ramicorns (RA)	0.73	0.06 - 1.89	0.43 [0.32 - 0.52]	-49
Number of forks (FO)	0.30	0 - 0.83	0.35 [0.20 - 0.46]	-46
Stem sinuosity index (SIN)	0.86	0.11 - 2.9	0.39 [0.26 - 0.49]	-48
Earliness of budburst (BB) (% per plot)	39	0 - 100	0.66 [0.63 - 0.69]	<-100
Second flushing (FSF) (% per plot)	26	0 - 68	0.42 [0.31 - 0.52]	-61
Height (HT) (cm)	6.0	4.6 - 6.9	0.56 [0.49 - 0.61]	+12
Diameter at breast height (DBH) (cm)	7.2	4.4 - 8.8	0.55 [0.48 - 0.61]	+14

^a) Phenotypic family means, for non transformed variables.

^b) Heritabilities and genetic gain for all traits except height and DBH were calculated for transformed variables (see text).

^c) Expected genetic gain (% of test mean) when the top 10% of the parental clones are selected for the designated trait only. It is assumed that both lower frequencies of budburst (later budburst) and second flushing are desirable.

especially ramicorns, with 46% of trees having at least one ramicorn, 26% at least one fork, and 15% both types of defects. Among trees with ramicorns or forks, most had only one (60% and 80% respectively), but individuals with as many as 7 ramicorns and 4 forks were observed. Twenty-six % of the trees produced second flushing on the leader shoot in 1991. In comparison to forking defects, sinuosity was less prevalent. Sinuosity score was 0 in 51% of the trees and only 1 in 30% of the trees.

Family differences were significant for all traits measured ($p < 0.01$) and ranges among family means were considerable (Table 1). For example, mean number of forks per tree range from 0 to nearly 1, while DBH ranged 2-fold among the 80 families. Thus, given that estimated family heritabilities were all greater than 0.35, the potential for improving either stem form or growth in this population by family selection is great.

As observed in previous studies of similarly aged Douglas-fir (JARRET, 1978; BIROT and CHRISTOPHE, 1983; LI and ADAMS, 1993), estimated genetic correlations between DBH and height and between BB and BS were high (0.82 and 0.70, respectively). For this reason, only one stem growth (DBH) and one bud phenology (BB) trait are considered further with regard to genetic associations among traits in this test.

Although the estimated genetic correlation between RA and FO was positive, it was not particularly strong (Table 2),

indicating that the 2 forking defects are only partially controlled by the same genes. In previous investigations in Douglas-fir, forks and ramicorns were combined into a single score (JARRET, 1978; BIROT and CHRISTOPHE, 1983; ADAMS and BASTIEN, 1994).

Both forking defects and stem sinuosity were unfavorably (positively) correlated with stem growth (DBH), although the estimated relationship between stem sinuosity and stem growth was weak (Table 2). Forking defects and stem growth were positively correlated with frequency of second flushing; the relationships between FSF and forking defects were particularly strong. FSF, however, was not associated with SIN. Positive associations of FSF with both increased stem growth and forking defects have previously been observed at both the phenotypic and genetic levels in Douglas-fir (DE CHAMPS, 1971; WALTERS and SOOS, 1961; JARRET, 1978; BIROT and CHRISTOPHE, 1983; ADAMS and BASTIEN, 1994).

Although earliness of budburst timing was not associated with stem growth in this study, it was positively correlated with FSF and forking defects (Table 2). Earlier budburst, and subsequently earlier budset, may provide more time for spring buds to mature and flush again if favorable weather permits (ADAMS and BASTIEN, 1994). In addition, earlier budburst and budset increases the likelihood of favorable weather and soil moisture at the time of budset, thus increasing the frequency of second flushing. Trees that break bud earlier are more

Table 2. – Estimates of additive genetic correlations (standard errors) between study traits.

Trait	DBH	Number of ramicorns (RA)	Number of forks (FO)	Sinuosity score (SIN)	Frequency of second flushing (FSF)	Earliness budburs (BB)
RA	0.42 (0.15)					
FO	0.59 (0.18)	0.54 (0.19)				
SIN	0.24 (0.18)	0.28 (0.21)	0.10 (0.26)			
FSF	0.32 (0.17)	0.72 (0.11)	0.93 (0.18)	0.09 (0.20)		
BB	-0.05 (0.13)	0.42 (0.13)	0.56 (0.17)	0.10 (0.16)	0.39 (0.15)	

susceptible to spring frost damage (AITKEN and ADAMS, 1995) which can result in loss of dominance of the leader, followed by development of forks and ramicorn branches.

Breeding Implications

It is clear from the results of this investigation that selection for fast growth in young trees will indirectly increase the frequency of stem defects in coastal Douglas-fir. Thus, if 10% of parent trees in each 40-family set were selected on the basis of mean family DBH, we would expect not only increased mean DBH the next generation, but also increased forking, ramicorn branching and stem sinuosity (Index 1, *Table 3*).

Table 3. – Expected genetic response (ΔG , % of overall mean) in diameter at breast height (DBH), number of ramicorns (RA) and forks (FO) per tree, sinuosity index (SIN) and frequency of second flushing (FSF) using various selection indices for backward selection.

A selection rate of 10% is assumed.

Target(s) of selection (constraints)	ΔG				
	DBH	RA	FO	SIN	FSF
1. DBH	14	23	34	14	24
2. DBH, RA and FO (no change on RA and FO)	8.6	0	0	8.1	-18
3. DBH and FSF (no change on FSF)	13	11	20	13	0
4. DBH and earliness of budburst (BB) (-50% ΔG in BB)	13	15	26	13	14

The weak to moderate associations between growth and stem form traits suggest, however, that it is possible to improve growth rate in Douglas-fir tree improvement programs without increasing the frequency of stem defects. Allowing for the potential of silvicultural improvement in stem straightness and the relatively low frequency of sinuosity defects in this population, we computed a selection index with the goal of improving DBH without changing the mean number of forks and ramicorns in the next generation (Index 2). In this scenario, the expected gain in DBH would be about 60% of that when only improved DBH is the target of selection, and stem sinuosity would be increased relatively little.

Given that forking defects are caused in part by second flushing and by cold damage to early flushing terminals, an alternative strategy for increasing stem growth while limiting stem form defects might be to select for DBH while holding FSF to no change (Index 3), or while constraining frequency of budburst to a negative genetic gain (i.e., later budburst, Index 4). The genetic correlations of FSF with forking defects are much stronger than with DBH. Indeed, selection for DBH, while holding FSF constant is expected to result in nearly the same response in DBH, while reducing adverse responses in forking defects, relative to selection for DBH alone. Nevertheless, the expected increases in RA and FO may still be larger than managers are willing to tolerate. Because BB and DBH are uncorrelated in this population, DBH can be effectively increased while simultaneously selecting for later BB (Index 4). Such a selection regime, however, would do little to stem increases in forking defects associated with rapid stem growth.

The results of this study confirm earlier reports in Douglas-fir that genetic improvement in stem growth cannot be maximized without increasing the occurrence of stem form defects, at least on higher quality sites (ADAMS and BASTIEN, 1994; KING, 1986). Fortunately, genetic correlations between stem growth and the propensity to produce forks and

ramicorns is low enough that good progress can be made in improving growth, while limiting forking defects, as long as both stem volume traits and forking defects are measured and included in selection indices. Although both second flushing and early budburst are indirect causes of forking defects, selection against these traits, while trying to improve stem volume, is not very effective in holding forking defects in check. Among important issues remaining with regards to the genetics and physiology of stem form defects in coastal Douglas-fir, is the degree to which these traits are expressed in different environments (e.g., site fertility, moisture regimes) and are subject to genotype x environment interaction. Further investigations are also needed on the degree to which various patterns of free growth in young trees influence the propensity for forking defects (ADAMS and BASTIEN, 1994; BUJON, 1994; KAYA et al., 1994), including magnitudes of continuous free growth (i.e. free growth without setting a temporary bud) and second flushing, as well as the distribution of second flushing between terminal and lateral buds.

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Genotype by Environment Interaction and Genetic Correlation of Greenhouse and Field Performance in *Pinus contorta* ssp. *latifolia*

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Summary

Family by site interaction from 4 progeny test sites for 9-year height and its impact on estimation of genetic correlation between greenhouse traits and 9-year height were investigated in 110 families of *Pinus contorta* ssp. *latifolia* from Alberta, Canada. Significant family by site interaction, site and family effects were observed in 9-year height among 4 progeny test sites. The estimated narrow-sense heritability was from 0.127 to 0.277 for individuals and was from 0.247 to 0.475 for family means. 25 greenhouse seedling traits (height, diameter, bud, branch and biomass) in 2 growing seasons were jointly studied with 9-year tree height at the 4 progeny test sites. The genotype by site interaction had a significant impact on greenhouse-field family-means and genetic correlations. Only 9-year tree height in the best site (site B), which had more similar growing conditions to the greenhouse, had significant family-mean and genetic correlations with greenhouse seedling traits. Seedling traits of height increment at the dormancy induction period between 2 growing seasons (HG1, $r_g = 0.52$), height at the second growing season (H3, $r_g = 0.36$), and height ($r_g = 0.37$) and diameter ($r_g = 0.42$) at harvest, had the highest and significant family-mean and genetic correlation. The pattern of greenhouse-field family-mean and genetic correlations among 4 sites indicates that early testing should be conducted under simulated field conditions. The implications of genotype by site interaction on early selection were discussed for lodgepole pine.

Key words: Genotype by environment interaction, juvenile-mature correlation, type-B genetic correlation, early selection, lodgepole pine.

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Introduction

Lodgepole pine (*Pinus contorta* ssp. *latifolia* ENGLM.) is one of the most widely distributed trees in Western Canada, and is a commercially important conifer, native to Alberta. It is valued for its growth potential, good form characteristics, timber quality and relative freedom from major pests. It is the second most important tree species and accounts for 22.3% or 3.37 million hectares of the productive forest in Alberta (DHIR and BARNHARDT, 1993). Variability in economic traits such as growth, form and wood quality is expressed both within and among populations (CRITCHFIELD, 1980; REHFELDT, 1985; YANCHUK, 1986; FRIES, 1987). Therefore, lodgepole pine is a prime candidate for genetic improvement through selective breeding to increase plantation forest productivity and quality in Alberta.

Improvement of *P. contorta* ssp. *latifolia* in Western Canada has generally included phenotypic mass selection in wild stands and use of this material for seed production in clonal or seedling seed orchards. The selection criteria invariably emphasized height and diameter growth and form traits, and additive genetic effects were assumed (WHEELER, 1979; FRIES, 1986, 1989; CARLSON, 1990). In Alberta, phenotypic selection for growth and form traits among trees within stands was initiated in the late 70's by the Alberta Forest Service (DHIR, 1983; DHIR and BARNHARDT, 1993). Progeny tests of the phenotypic selections were established to select genetically superior families for reforestation and for further breeding purposes.

The lower limit of rotation age of *P. contorta* ssp. *latifolia* in Alberta was about 70 years (SMITHERS, 1961). Waiting for one-half rotation age for final evaluation and selection of families, as commonly recommended (ZOBEL and TALBERT, 1984), would be very inefficient in terms of genetic gain per unit time. Thus, the method of early selection, particularly, early greenhouse