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Genetics of Second Flushing in a French Plantation of Coastal Douglas-Fir¹⁾

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Summary

The genetic control of second flushing and its relationships with stem height and forking defects were investigated in a coastal Douglas-fir (*Pseudotsuga menziesii*

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var. *menziesii* [MIRB] FRANCO) progeny test containing 64 open-pollinated families. Mean frequency of second flushing (FSF) in family plots decreased from 0.51 at age 5 to 0.27 at age 10. The estimated family heritability of FSF exceeded 0.60 (mean = 0.68) at ages 5 to 7, but at age 10 was 0.50. At ages 6 and 7, trees were scored for flushing type severity (SFS), based on expected propensity to produce forking defects. Estimated genetic correlations between FSF and SFS were high in both years ($r_A > 0.77$). Mean FSF (over 4 years) had moderate and positive genetic correlations with both height at age 13 (HT13; $r_A = 0.60$) and amount of forking assessed at age 10 (FK10; $r_A = 0.66$). Thus, it is not possible to maximize genetic gain in juvenile height growth without also increasing forking. Fortunately, the genetic correlation between HT13 and FK10 is weak enough ($r_A = 0.53$) that height growth can be improved without increasing forking defects. Nevertheless, expectations based on selection index methods indicate selection for greater juvenile height will increase FSF, even if forking is limited to no change, unless FSF is constrained as well. Constraining FSF, however, would severely limit potential for height-growth gains. The desirability of limiting change in FSF depends on the extent to which increased FSF increases susceptibility to damage from late season drought or early fall frost.

Key words: height increment, lammas growth, heritability, genetic correlation, stem form defects.

FDC: 165.3; 165.5; 174.7 *Pseudotsuga menziesii*; (44).

Introduction

Second flushing (SF), the late-season flushing of recently formed buds which otherwise would not open until the

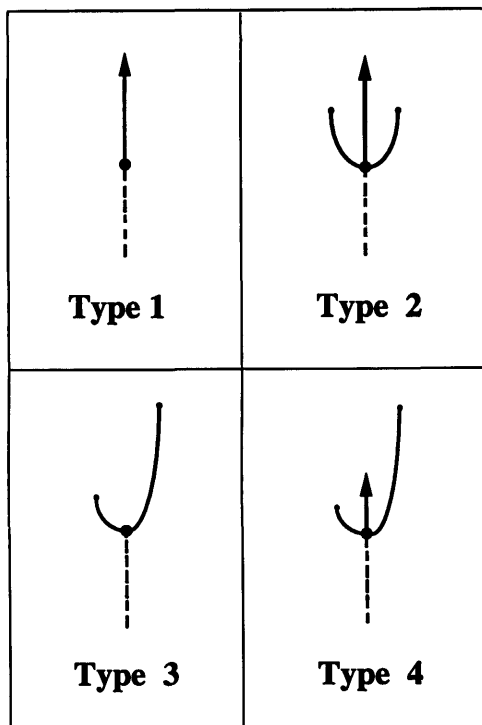


Figure 1. — Flushing types according to DE CHAMPS (1971): Type 1 — only the terminal bud of the leading shoot second flushes; Type 2 — both the terminal and one or more lateral buds at the base of the terminal bud second flush, but lateral shoots are subdominant to the terminal shoot at the end of the growing season; Type 3 — the terminal bud doesn't second flush, but one or more lateral buds do; and, Type 4 — both the terminal and lateral buds second flush, but one or more laterals are dominant at the end of the growing season (dashed lines indicate growth prior to second flushing and solid lines indicate growth following second flushing).

following spring, is a common occurrence in young stands of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [MIRB.] FRANCO). Subsequent Growth of the leading shoot from SF (lammas growth) contributes significantly to yearly height increment in young trees (WALTERS and SOOS, 1961; EHRENBERG, 1963; RUDOLPH, 1964; DE CHAMPS, 1971), and thus, is an important adaptation to early intra- and inter-specific competition.

The frequency of trees which second flush is positively associated with favorable climate and high site fertility, but also varies according to provenance (WALTERS and SOOS, 1961; EHRENBERG, 1963; RUDOLPH, 1964; WALTERS and KOZAK, 1967; DE CHAMPS, 1971; KING, 1986). The presence of a genetic component to SF, along with the positive association of this trait with early stem growth, suggests that SF might be useful for improving height growth in breeding programs, either for the indirect selection of height, or as an axillary trait to improve the efficiency of height growth selection (FALCONER, 1989). The wisdom of doing this, however, may be questioned from several points of view. First, the frequency of SF declines rapidly with age, so its effect on mature tree height is unclear (WALTERS and SOOS, 1961; EHRENBERG, 1963; LOGAN and POLLARD, 1975; POLLARD and LOGAN, 1976). The age at which SF no longer significantly contributes to yearly height increment varies with species and geographical source within species. In Douglas-fir, frequencies of SF in two populations from the state of Washington were 26% and 40% at ages 9 and 10, respectively (JARRET, 1978; ADAMS et al., 1993); but no SF was observed at age 14 in a western Oregon plantation (LI and ADAMS, 1993).

A second reason for questioning the wisdom of selecting for SF to improve height growth is that SF has the disadvantage of contributing negatively to stem form. Second flushing, especially of lateral buds at the base of the terminal bud (called prolepsis, RUDOLPH, 1964), is associated with forking defects, i.e., forks, ramicorns (large, steep angled branches) and multiple tops (WALTERS and SOOS, 1961; RUDOLPH, 1964; DE CHAMPS, 1971; KING, 1986). In an effort to better understand the association between SF and forking defects, DE CHAMPS (1971) described 4 types of SF (Figure 1). Because Types 3 and 4 are most likely to lead to loss of dominance of the terminal shoot, these types are the most severe with regards to risk of leading to forking defects (DE CHAMPS, 1971).

A third potential disadvantage of SF, is that by extending the shoot growth period and delaying shoot hardening, SF increases the susceptibility of stems to damage from late season drought and early fall frost (BÜSGEN and MÜNCH, 1929; RUDOLPH, 1964; CANNELL and JOHNSTONE, 1978; KAYA et al., 1989). Such damage could further exacerbate negative effects of SF on stem form.

The ability to manipulate the frequency of SF in breeding programs for the purpose of either increasing height growth or reducing forking defects, and the indirect impacts of selection for height or stem form on frequency of SF, depend on the strength of inheritance of SF and its genetic relationships with other traits. Little information on the genetics of SF in coastal Douglas-fir is currently available, and that which does exist is limited to results based on only a single growing season and/or small samples of families or parents (JARRET, 1978; KING, 1986; KAYA et al., 1989; ADAMS et al., 1993). Furthermore, results of these earlier investigations do not always agree. For example, while the frequency of SF has been found to be moderately heritable in these studies, its estimated genetic

correlation with stem growth traits has ranged from 0.35 to -0.20. There is only 1 previous report on the genetic correlation between frequency of SF and magnitude of forking defects in Douglas-fir; it was found to be strongly positive (ADAMS et al., 1993).

A coastal Douglas-fir progeny test at the Peyrat le Chateau field station in south-central France has provided excellent data for addressing the genetics of SF in this species. In this test, repeated measurements of SF, height increment, lammas growth and flushing types were made between the ages of 5 and 10. In addition, trees were scored for timing of budburst, stem sinuosity, branching habit, and forking defects. In this paper we report results from analyses of these data. In particular we address the following:

- 1) The genetic control of SF and its repeatability over time.
- 2) The degree to which the severity of second flushing type is correlated with the frequency of SF.
- 3) The genetic relationships of SF with budburst timing, stem growth and sinuosity, branching habit and forking defects.
- 4) The potential implications with regard to breeding.

Methods

Materials

Materials for this study were derived from open-pollinated families of 210 mother trees chosen without regard to growth rate or stem form, in 24 seed stands (mature plantations) in France. The original provenances of these stands are in western Washington and northwest Oregon. Seedlots from each mother tree (families) were sown into flats in the greenhouse in 1975 and transplanted the following year into a replicated design in a bare-root nursery in Orleans. In the spring of 1978, samples of the 210 families were planted at each of 4 test sites. Sixty-four families were planted at Peyrat le Chateau (lat. 45° 49', long. 1° 44' E, 450 m). These families, chosen on the basis of rapid height growth in the nursery and lateness of bud flushing, came from mother trees in all 24 stands (1 to 6 trees per stand).

Seedlings at Peyrat le Chateau were planted according to a cubic lattice design with each family replicated three times in 16-tree square plots. In total, there were 48 incomplete blocks, each with 4 family plots. Trees were originally spaced at 2 m x 1.5 m, but at age 10 (after 7 years in the field), they were systematically thinned to 2 m x 3 m by removing every other row. Survival in the test has been excellent, with survival prior to thinning being 92% and with 95% of the non-thinned positions filled at age 13. We use the convention throughout this paper of numbering growing seasons as years after sowing.

Traits

Thirty-two traits were of interest. These included height increment and length of lammas growth of the leading shoot in each of 4 growing seasons (ages 5, 6, 7, 10) and total tree height (HT13) and circumference (C13) at breast height (1.37 m) at age 13. Date of budburst on the terminal of the leading shoot (first emergence of new needles beyond the bud scales) was recorded at age 7, by scoring trees every 2 to 3 days beginning April 24. These dates, assumed to be the actual dates of budburst, were converted to days after March 31 prior to analysis. Stem sinuosity (stem waviness between internodes) and branch angle were measured once prior to thinning (age 10) and once after-

wards (age 13). Average sinuosity and branch angle over the entire tree were scored visually, with sinuosity scores ranging from 1 (straight) to 5 (very sinuous) and branch angle from 0 (horizontal to bole) to 4 (very acute angle). Branch number and diameter were recorded only at age 13, with branch number being the total number of branches at the main whorl closest to breast height, and branch diameter being the average diameter of the two largest branches at this whorl. The frequency of SF of terminal buds on leader shoots (FSF) was calculated for each family plot in each of the 4 years that lammas growth was recorded. In addition, flushing type (Figure 1) was scored on the leading shoot of each tree in 2 of these years (ages 6 and 7), and plot frequencies for Types 1 to 4 determined. Trees with no SF of terminal or subterminal buds were designated Type 0. Flushing type scores for individual trees were converted into flushing type severity ratings (SFS) based on their expected relative propensity to lead to forking defects: 0 (Type 0), 1 (Type 1), 2 (Type 2), 3 (Type 4), and 4 (Type 3) (DE CHAMPS, 1971). Thus, the greater the magnitude of SFS, the greater the expectation that a forking defect will result from SF. Finally, the magnitude of forking defects in each tree was assessed directly at age 10 (FK10) using a cumulative point system, where trees with no forking defects were scored 0, 5 points were added for each ramicorn present in the crown, and 10 points added for each fork. Forks and ramicorns were defined as branches having a steep (acute) angle with the bole, but with the diameter of ramicorns definitely less than that of the bole, while the diameter of forks is about equal to the bole.

Statistical Analysis

Most analyses were conducted on a plot mean, rather than individual-tree, basis for 2 reasons: 1) the main trait of interest, FSF, was based on plot values and 2) analysis of residuals indicated that all traits conformed well to assumptions of analysis of variance (STEEL and TORRIE, 1980, Section 7.10) when treated as plot means. There were no missing plots and the number of trees per plot was at least 8 prior to thinning (mean = 14) and at least 4 after thinning (mean = 7). Three traits, height and circumference at age 13 and date of budburst (age 7), were also analyzed at the individual-tree level so that estimated genetic parameters could be more readily compared to earlier studies.

A random model for plot means was employed:

$$Y_{ij} = \mu + f_i + b_j + e_{ij} \quad (1)$$

where Y_{ij} is the plot mean of the i^{th} family in the j^{th} incomplete block, μ is the experimental mean, and e_{ij} is the residual error. For individual-tree analyses, this model was expanded by adding a term for block x family interaction. Because of the imbalance in the experimental design, all analyses of variance and covariance were conducted using the GLM procedure of the SAS statistical software (SAS Institute Inc., 1988). Variance and covariance components were estimated from the appropriate mean squares and cross-products using Type III sums of squares and the coefficients of variance and covariance components estimated by the GLM procedure.

The extent of genetic variation in FSF and other traits was quantified by estimating family variances and testing their significance. For all genetic parameter estimation, we assumed that individuals within open-pollinated families were related as half-sibs. Individual (h_i^2) and family (h_f^2) heritabilities and their approximate standard errors were estimated following NAMKOONG (1979). Relationships

Table 1. — Analyses of variance of second flushing, budburst, growth, branching, and stem form traits presented as intraclass correlation coefficients, and estimated means, family ranges and family heritabilities (h_f^2) of these traits.

Trait ^b	Intraclass correlations ^a			Means		h_f^2 (SE)
	Error	Blocks	Family ^c	Overall	Family range	
Second flushing						
FSF5	0.3828	0.1069	0.5103	0.51	0.09-0.87	0.75 (0.06)
FSF6	0.5905	0 ^d	0.4095	0.38	0.09-0.70	0.61 (0.09)
FSF7	0.4845	0.0831	0.4324	0.12	0.00-0.46	0.67 (0.08)
FSF10	0.6842	0.0157	0.3001	0.27	0.04-0.57	0.50 (0.12)
SFS6	0.6160	0 ^d	0.3840	1.22	0.44-2.15	0.59 (0.10)
SFS7	0.5957	0.0824	0.3219	0.40	0.00-1.06	0.55 (0.10)
Budburst	0.2971	0 ^d	0.7029	44.8	37.4-52.5	0.84 (0.04)
Height (HT13, cm)	0.4122	0.2095	0.3783	808.6	653.5-889.9	0.68 (0.08)
Circumf. (C13, cm)	0.3485	0.1641	0.4874	32.5	26.0-38.4	0.76 (0.06)
Branch angle	0.2750	0.1340	0.5910	2.69	2.18-3.35	0.83 (0.04)
Branch number	0.3697	0.4007	0.2296	8.58	6.59-10.50	0.59 (0.10)
Branch dia. (mm/10)	0.6007	0.1612	0.2381	174.8	152.2-203.4	0.48 (0.12)
Stem sinuosity	0.5653	0.1909	0.2438	2.37	1.79-3.22	0.50 (0.12)
Forking (FK10)	0.7098	0.0499	0.2403	3.76	1.60-5.99	0.44 (0.13)

^a) Intraclass correlation coefficients are computed as the ratio of individual variance component estimates to the sum of all components. Degrees of freedom are 81, 47, and 63 for error, blocks and family, respectively.

^b) FSF is the frequency of trees per family plot with second flushing of the terminal bud on the leader shoot and SFS is flushing type severity. Numbers refer to the age at which measurements were taken. Branch number and diameter were measured at age 13. Values for branch angle and sinuosity are means for 2 measurements (ages 10 and 13). See text for details on measurements.

^c) For all traits, the family variance was significant ($p < 0.01$).

^d) Variance components with negative estimates were assumed to be zero.

between traits were examined by estimating phenotypic correlations among family means, genetic correlations (r_A), and the standard errors of these estimates (BECKER, 1984). It should be mentioned that estimates of additive variances and covariances are biased in this study because they are based on data from only a single test site. In particular, heritability estimates are expected to be biased upwards if family x site interactions exist, as was observed for frequencies of SF in Scotch pine (WEST and LEDIG, 1963).

Breeding implications were examined by estimating expected responses in tree height (HT13), forking defects (FK10) and FSF under various selection criteria. For selection of individual traits, we calculated direct and correlated responses according to FALCONER (1989). For multiple trait selection, we used selection index methods (KEMPTHORNE and NORDSKOG, 1959; FALCONER, 1989; COTTERILL and DEAN, 1990).

Results and Discussion

Preliminary calculations indicated that both sinuosity and branch angle scores were highly correlated ($r_A > 0.90$) between ages 10 and 13; thus, only means of these traits were analyzed further. Significant ($P < 0.05$) family differences were expressed for 26 of the 30 remaining traits, with the probability of family F-values less than 0.001 in 21 cases. Low mortality and low site heterogeneity has resulted in the relatively high statistical precision of this test. This precision is further reflected in the individual-tree heritability estimates for HT13 (0.47 ± 0.11) and C13 (0.30 ± 0.09). Although at the high end of h_f^2 estimates reported for growth traits of coastal Douglas-fir at this age (YEH and HEAMAN, 1982; KING et al., 1988; ADAMS and

JOYCE, 1990; LI and ADAMS, 1993), they reflect measurements on only a single test site and of mother trees derived from a fairly broad geographical range of provenances.

Genetic control of SF and repeatability with age

As expected, FSF decreased with age, but not steadily (Table 1). At age 5, approximately half of the trees in each plot second flushed, and by age 7 this percentage was reduced to 12 %, but then increased to 27 % at age 10. Evidently, the effect of tree age is confounded by year-to-year variation in weather conditions, which also strongly influences FSF (EHRENBERG, 1963; WEST and LEDIG, 1963; DE CHAMPS, 1971). Nevertheless, FSF was still relatively substantial in 10-year old trees. There was also considerable genetic variation in FSF; family ranges in FSF each year were large, with some families exhibiting no SF, while in others, FSF exceeded 50 % (Table 1). FSF appears to be under strong genetic control, with estimated family heritabilities exceeding 0.60 between ages 5 and 7. Heritability of FSF may decrease at later ages, however, since at age 10, it was only 2/3 of its magnitude at age 5.

As with FSF, the mean proportion of trees per family plot with second flushing type scores greater than 0 was less at age 7 (0.16) than at age 6 (0.44). At both ages, however, the mean frequency of trees with non-zero flushing types exceeded FSF (Table 1). This is because FSF accounts for SF of terminal buds only, while flushing types include SF of both terminal and subterminal buds (Figure 1). Among trees with flushing type scores greater than 0, Type 2 was the most common over the 2 years (41 %), followed by Type 3 (35 %), Type 1 (14 %) and Type 4 (10 %). In 2 previous studies in France, Type 2 was also

Table 2. — Estimated genetic (above diagonal) and phenotypic (family mean, below diagonal) correlations between frequencies of second flushing (FSF) at four ages^{a)}.

	Age			
	5	6	7	10
5	-	0.69	0.38	0.81
Age 6	0.48	-	0.72	0.74
7	0.31	0.42	-	0.71
10	0.49	0.49	0.43	-

^{a)} Standard errors of genetic correlation estimates ranged from 0.14 to 0.19 (mean 0.17) and from 0.09 to 0.11 (mean 0.10) for phenotypic correlation estimates.

the most common among trees with non-zero scores, at about 40%, but Type 4 was found at frequencies nearly 3 times that in this study (DE CHAMPS, 1971; JARRET, 1978). We have no ready explanation for this difference. However, it is clear in all 3 studies that when SF occurs, it usually (> 80 % of the time) involves SF of lateral buds, whether or not terminal buds second flush.

Mean absolute frequencies of Flushing Types 1 to 4 were less than 0.05 in 5 of the 8 flushing type x age combinations, and in 4 of these cases, family differences were not significant (Types 1 and 3 at age 6, and Types 3 and 4 at age 7). Estimated family heritabilities of flushing type frequencies in the remaining cases where family differences were significant averaged 0.52 (range 0.40 ± 0.14 to 0.65 ± 0.08), somewhat lower in magnitude than observed for FSF in the same years (Table 1).

Estimated genetic correlations in this study were nearly always in the same direction, but of larger magnitude, than phenotypic (family mean) correlations. Thus, only genetic correlations will be discussed, but phenotypic correlations are included in tables for comparison. Genetic correlations between FSF at different ages were positive and moderate in magnitude, averaging 0.67, but exceeding the mean in 5 of the 6 age-pairs (Table 2). In addition, there are no obvious trends in these correlations with age; that is, correlations between consecutive ages were not consistently higher or lower than between ages further apart. These age-age correlations measure the extent to which FSF is controlled by the same genes in different years, and also the extent of family x age interaction in this trait (BURDON, 1977). The generally high magnitude of the correlations suggests there is relatively little family x age interaction in FSF. Thus, families with high frequencies of SF one year seem to be largely those with high frequencies the next year or the year after.

Genetic correlations between ages 6 and 7 in flushing type frequencies could be calculated only for Type 2, since for all other types, family variances were non-significant at one or both ages. The estimated genetic correlation in Type 2 frequencies between ages, however, was quite high (0.80 ± 0.22), suggesting family x year interaction may also be low for flushing type frequencies.

Genetic control of SFS and its relationships with FSF

Estimated family heritabilities of SFS were slightly less than corresponding heritabilities of FSF (Table 1), but

genetic correlations between SFS and FSF were high (0.89 ± 0.06 at age 6 and 0.78 ± 0.11 at age 7). High genetic correlations between these traits indicate that genotypes with the highest propensity for SF are also, in large part, those with the highest average SFS. The estimated genetic correlation between SFS at ages 6 and 7 (0.44 ± 0.21) was considerably lower than between FSF at these ages (Table 2). Thus, FSF appears to provide nearly the same genetic information about flushing type severity as SFS itself, and is more consistent from year to year.

Relationship between SF and budburst timing

Despite selection which favored late-flushing families in the nursery, families at age 7 ranged 15 days in mean date of budburst, and estimated individual-tree (0.64 ± 0.11) and family heritabilities (Table 1) for this trait were strong, as has been reported previously for coastal Douglas-fir (JARRET, 1978; BIROT and CHRISTOPHE, 1983; LI and ADAMS, 1983; ADAMS et al., 1993). Date of budburst was uncorrelated with FSF at age 7 ($r_A = 0.01 \pm 0.17$) when budburst was recorded, but had consistently weak negative genetic correlations with FSF at ages 5 (-0.26 ± 0.15), 6 (-0.07 ± 0.18) and 10 (-0.57 ± 0.17). The lack of correlation at age 7 may be due to the particularly low FSF in this year (Table 1). A negative genetic correlation between date of budburst and FSF in Douglas-fir was also observed by JARRET (1978) and ADAMS et al (1993). Because families that break bud the earliest also have a strong tendency to set bud earlier at this age (LI and ADAMS, 1993; ADAMS et al., 1993), spring buds of early flushing trees may be more mature and better able to flush again should favorable late summer conditions arise.

Relationships between SF and growth

The estimated family heritabilities for height increment in individual growing seasons (ages 5, 6, 7 and 10) ranged from 0.55 ± 0.11 to 0.79 ± 0.05 , but averaged 0.69, which is almost identical to the family heritability for total height at age 13 (Table 1). There was essentially a 1-to-1 correspondence between FSF and amount of lammas growth produced each year (mean $r_A = 0.98$, range 0.96 ± 0.02 to 1.02 ± 0.04), but the genetic correlation between FSF and height increment steadily decreased with age, as the mean proportion of height increment due to lammas

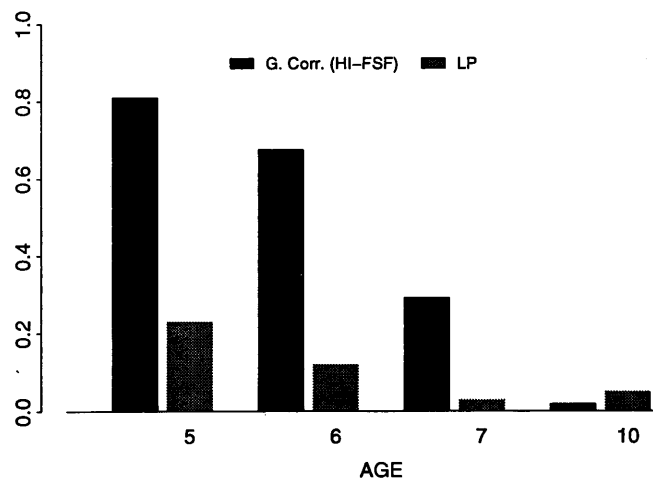


Figure 2. — Estimated genetic correlations between height increment (H) and frequency of second flushing (FSF) in 4 growing seasons (ages 5 to 7 and 10) and mean proportion of HI due to lammas growth (LP) in each season.

Table 3. — Estimated genetic and phenotypic (family mean, in parentheses) correlations of mean frequency (FSF) and severity (SFS) of second flushing (over years scored) and forking score (FK10) with growth, branching and stem form traits*).

Traits ^a	Mean ^b		
	FSF	SFS	FK10 ^c
Height (H13)	0.60 (0.44)	0.90 (0.56)	0.53 (0.34)
Circumf. (C13)	0.49 (0.38)	0.72 (0.47)	0.46 (0.30)
Branch angle	-0.14 (-0.15)	-0.26 (-0.22)	-0.17 (-0.13)
Branch number	0.06 (0.07)	-0.06 (-0.04)	-0.12 (-0.05)
Branch diameter	0.16 (0.04)	0.27 (0.06)	0.22 (0.09)
Stem sinuosity	0.39 (0.26)	0.51 (0.29)	0.22 (0.10)
Forking (FK10)	0.66 (0.45)	0.65 (0.51)	-

^a) Mean FSF over 4 years (ages 5, 6, 7 and 10) and mean SFS over 2 years (ages 6 and 7).

^b) See text for a description of traits.

^c) Experiment means (estimated family heritabilities) for mean FSF and SFS were $0.32 (0.67 \pm 0.06)$ and $0.81 (0.43 \pm 0.09)$, respectively.

^d) Standard errors of genetic correlation estimates averaged 0.17 (range 0.13 to 0.21) for those involving FSF, 0.19 (0.14 to 0.25) for those involving SFS, and 0.25 (0.20 to 0.30) for those involving FK10. The mean standard error for phenotypic correlation estimates was 0.11 (0.09 to 0.12).

growth steadily decreased (Figure 2). At age 5, when 24 % of height increment was due to lammas growth, the genetic correlation between FSF and height increment was 0.81 ± 0.06 ; but by age 10, when lammas growth accounted for only 5 % of height increment, the correlation was only 0.02 ± 0.23 . Thus, the strong phenotypic association between FSF and height increment observed in young (2 to 4 year-old) Douglas-fir plantations by DE CHAMPS (1971) appears to have a strong genetic basis; but, as trees age and FSF diminishes, so does the genetic relationship between these traits. By age 10, most shoot growth in conifers is expected to be predetermined (i.e., due to expansion of the primordial shoot in the overwintered bud) (Figure 2, and VON WÜHLISCH and MUHS, 1986). Therefore, the nearly 0 genetic correlation between FSF and height increment at this age suggests there is little genetic relationship between the propensity to SF and the magnitude of predetermined growth. Results from CANNELL and JOHNSTONE (1978) for 57 Sitka spruce (*Picea sitchensis* (BONG.) CARR. progenies support this conclusion. They found that the amount of lammas growth varied independently of predetermined growth produced in leader shoots during the 8th growing season.

Despite the decrease in genetic correlation between FSF and height increment with increasing age, the estimated correlations of mean FSF (over ages 5, 6, 7 and 10) and mean SFS (over ages 6 and 7) with both height and circumference at age 13 were relatively strong (Table 3). Genetic correlations between HT13 and individual-year values of FSF ranged from 0.22 to 0.67, but were highest at the 2 youngest ages when SF was most frequent. These results are supported by the moderately positive correlation observed between FSF and diameter at breast height in 9-year-old trees from a western Washington population ($r_A = 0.35$), which also involved a large sample (80

of open-pollinated families (ADAMS et al., 1993). In 2 other studies with similarly aged materials, however, the genetic correlation between FSF and total tree height was estimated to be small and negative (-0.20 , JARRET, 1978; -0.14 , KING, 1986). The number of half-sib (or open-pollinated) families included in these studies was limited (15 and 22, respectively), and in the KING study, mean FSF was low ($<13\%$). The extent to which sampling error influences the discrepancy among these genetic correlation estimates is unclear, but when sample sizes are relatively large and SF relatively frequent, the genetic correlation between FSF and stem growth appears to be at least moderately positive.

Mean SFS had higher estimated genetic correlations with HT13 and C13 than mean FSF (Table 3). In addition, genetic correlations between HT13 and individual-year values of SFS at ages 6 and 7 (0.77 ± 0.16 and 0.80 ± 0.19) were higher than corresponding correlations between HT13 and FSF in the same years (0.62 ± 0.17 and 0.46 ± 0.17). Thus, SFS may be a somewhat better predictor of height growth than FSF, but the high standard errors of these estimates prevent a firm conclusion.

Relationships of SF with forking defects, sinuosity, and branching traits

Although 45.4% of individual trees were scored as having 1 or more forking defects at age 10, the estimated family heritability of FK10 (0.49 ± 0.13) was the lowest of any trait in the study (Table 1). This result is compatible with earlier investigations which also found a relatively strong environmental component to phenotypic variation of forking defects in Douglas-fir (JARRET, 1978; BIROT and CHRISTOPHE, 1983; KING, 1986; ADAMS et al., 1993). With the exception of branch angle, heritabilities for branching traits and sinuosity were also somewhat lower than for growth and SF traits. The strong heritability of branch angle in Douglas-fir is well documented in earlier studies (JARRET, 1978; BIROT and CHRISTOPHE, 1983; KING et al., 1992; ADAMS et al., 1993).

The genetic correlation of FSF with forking severity was positive and moderately strong, although because of the low heritability of FK10, the standard error of this estimate is large (Table 3). SFS appears to be no better than FSF for predicting the magnitude of forking defects since its correlation with FK10 was nearly identical to that of FSF. In agreement with ADAMS et al. (1993), correlations of FSF and SFS with sinuosity were positive, but of somewhat lower magnitude than with FK10, while correlations with branching traits were weak. JARRET (1978) reported weak negative genetic correlations between FSF and branch angle, branch number and stem sinuosity ($r_A > -0.26$), but a strong negative correlation between FSF and branch diameter ($r_A = -0.80$). Since the number of families was quite small in JARRET's study (15), his estimates must be subject to very large standard errors.

Consistent with the positive associations of both FK10 and stem growth traits with FSF, a moderately positive genetic correlation between stem growth and forking defects was found (Table 3). This result agrees with ADAMS et al. (1993), but not with KING (1986), who reported that height at age 12 had a weak negative correlation with forking severity ($r_A = -0.17$). Recall, that KING also found FSF and height to have a weak negative correlation, but that both the number of unrelated families and occurrence of SF was low in this study.

Breeding implications

The above results confirm that there is a substantial genetic component to the positive phenotypic associations observed between SF and both stem growth and incidence of forking defects in juvenile stands of Douglas-fir. Thus, selection for faster stem growth in young progeny tests is expected to increase the frequency of SF in the next generation, especially on high quality sites (i.e., sites with high soil fertility and adequate late summer moisture), which will in turn, lead to increased levels of forking. For example, if the top 10% of parents in a population having the same genetic parameters as those in this study, were selected on the basis of the height of their 13 year-old offspring and randomly mated, it is expected that HT13 in the next generation would be improved by 129 cm or 15.9% over the current population mean (selection criterion 1, Table 4). It is also expected that selection based on height alone would indirectly increase forking severity score in the next generation by 1.2 (33.2%) which is equivalent to approximately one additional ramicorn for every 4 trees, or 1 additional fork for every 8 trees. If such increased levels of forking defects are unacceptable to managers, selection for improved stem growth will have to be limited. Fortunately, the genetic correlation between stem growth and magnitude of forking defects is weak enough that both traits could be improved simultaneously. For example, if the goals of both increased HT13 and reduced FK10 were incorporated in a selection index and given equal emphasis in defining net merit (i.e., each trait weighted by the inverse of the standard deviation of its family mean; COTTERILL and DEAN, 1990), it is expected that HT13 would be improved by 11.6 % in the next generation, with FK10 increased by only 1.2 % (criterion 2, Table 4). Using a restriction index (KEMPTHORNE and NORDSKOG, 1959), where the goal is to maximize improvement in HT13 while holding FK10 to no change, is expected to give nearly identical results (not shown).

Because the frequency of SF is strongly inherited and at least moderately correlated with both tree height and forking score, it might be useful in the selection of these traits. One possibility is that FSF could serve as a surrogate for indirect selection of either height or forking, since it is simpler to measure, and perhaps could be assessed at a younger age. For illustrative purposes we use FSF at age 5 (FSF5) because this was the youngest age that SF was scored and because family heritability of FSF was maximum (Table 1). If families are selected for high levels of FSF5, indirect gain in HT13 would be 70 % of that expected if HT13 were selected directly (criterion 3, Table 4), and selections could be made 8 years earlier! FK10, however, would also be increased considerably (31.9 %) under this scenario. In addition, it may be unwise to emphasize increased SF in the selection of improved height growth, since the contribution of SF in young trees to height growth over the entire rotation is unknown. An example where FSF5 might be used instead of FK10, is an index where selection for HT13 is maximized while constraining FSF5 to no change (criterion 4, Table 4). Application of this index is expected to result in nearly 10 % improvement in HT13, which is only a little less gain than expected with the HT13-FK10 equal-emphasis index (criterion 2). Constraining FSF5 under selection criteria 4, however, is less effective than the equal emphasis index in limiting change in FK10.

Table 4. — Expected response in tree height (at age 13, HT13), forking score (FK10), and frequency of second flushing (FSF5) when different selection criteria are used^{a)}.

Selection criteria	Response (%)		
	HT13	FK10	FSF5
1) HT13	15.90	32.23	55.14
2) Equal emphasis HT13 and FK10 ^{b)}	11.63	1.20	34.80
3) FSF5 (positive direction)	11.19	31.94	43.22
4) HT13 and FSF5 (0% change) ^{c)}	9.94	14.14	0
5) Equal emph. HT13 and FK10, FSF5 (0 econ. weight) ^{d)}	12.07	2.72	44.20
6) Equal emphasis HT13 and FK10, FSF5 (0% change) ^{d)}	6.33	-17.13	0

^{a)} Response expected in seed orchard offspring when the top 10% of parental clones (selection intensity (I) = 1.755) are selected on the basis of the various selection criteria given.

^{b)} Net merit of family means is defined as $H = 0.22 \times \text{HT13} - 1.00 \times \text{FK10}$, where the weighting coefficients ("economic weights") are proportional to the inverse standard deviations of family means of HT13 and FK10.

^{c)} Selection index where response in FSF5 is restricted to zero.

^{d)} FSF5 is included in the index to aid in the improvement of net merit (equal emphasis of HT13 and FK10), but is given zero economic weight.

Another possibility is to include FSF in addition to height and forking score in an index. In this case, FSF is used as an aid to determining the breeding values of the other 2 traits (FALCONER, 1989). If FSF5 was included (but given no weight) in an index having the goal to improve net merit based on equal emphasis of HT13 and FK10 (criterion 5, Table 4), response in HT13 is expected to be only slightly greater than if FSF5 were not in the index (criterion 2). In addition, both FK10 and FSF5 would be expected to increase more than under criterion 2. Thus, there seems to be no real advantage to having FSF5 in the index when FK10 is already present. What are the consequences of constraining FSF in an index where improvement of net merit (equal emphasis of HT13 and FK10) is the goal. This is the last selection criterion illustrated in table 4. Expected results of applying this index show that it is possible to make limited gains in both increasing HT13 and reducing FK10, while holding FSF5 constant.

The emphasis to be given forking defects in selection programs depends on their impact on product value and on the ability to deal with them using other silvicultural methods. Little is known about the effects of stem deformations in young trees on product value at rotation, although extreme deformations at this age are likely to have significant economic impact (BLAIR et al., 1974; ZOBEL and KELLISON, 1978). Silvicultural regimes that emphasize high initial planting densities and precommercial thinning, as well as stem pruning, could do much to alleviate stem defects. The costs of these treatments, however, are considerable, especially when they are spread over large areas. It would seem prudent to at least prevent increased incidence of forking defects in breeding programs where improved stem growth is emphasized, since restraining these defects could be accomplished with little impact on the ability to make gains in growth.

It is clear from *table 4* that selection for improved growth in Douglas-fir will lead to increased FSF even when change in forking score is limited, unless change in FSF itself is somehow constrained. Since limiting change in FSF will significantly limit the potential for juvenile growth improvement, the need for including FSF in selection programs needs to be carefully considered. The main concern is the extent to which increasing FSF increases susceptibility of improved varieties to damage from late season drought or early fall frost. Although the timing of SF was not observed in this study, it was recorded recently in a farm field trial in France involving seedling families from mother trees in western Washington (C. BASTIEN, INRA, Centre de recherches d'Orleans). A large proportion of individuals in this test second-flushed shortly after initial budset in late June, but many also had 1 or more second-flushes in August. The extent to which families with late-season SF are among the fastest growers, and the degree to which late final budset influences stem hardening and resistance to cold or drought are unclear, but are important topics for future research.

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Optimum Age for Selection in *Pinus radiata* Using Basal Area under Bark for Age:Age Correlations

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Abstract

Age-related changes in the inheritance of stem diameter in *radiata* pine were studied using discs cut at 1.3 m above ground in trees from a progeny test. Measurements of cross-sectional area enclosed within annual growth rings

yielded annual estimates of basal area. The progeny test was a diallel cross which enabled estimation of genetic parameters such as heritability and genetic correlations between measurements at different ages. The greatest gain per generation would have been obtained through selec-