very old (some trees are older than 200 years) and has always been safeguarded because of its protection of the village beneath against avalanches. It also showed the highest value of heterozygosity, conferming the adaptive role of the latter.

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General and Specific Combining Ability from Disconnected Partial Diallels of Coastal Douglas-fir

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Summary

General and specific combining ability (GCA and SCA, respectively) were examined in 36, 6-parent disconnected partial diallels across 4 different experimental series in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* Dougl.) to examine the ratios of the 2 genetic variances, the distribution of GCA and SCA effects, and estimates of genetic gain from GCA and SCA for 3 growth traits. Height at age-7 and height and volume at age-12 were measured on approximately 150 trees per full-sib family in each diallel, across 11 different test sites within each series. The average percentage ratio of SCA variance to GCA variance was 36%, across all series and the 3 growth traits, with a range of 19% to 65%. GCA and SCA variances did not appreciably change for height growth from age 7 to age 12. Diallel set effects were generally negligible. From theoretical considerations assumed for the diallel model, clear separations of additive and dominance effects (*vis-a-vis* the assumptions of selecting on GCA and SCA variances) are likely not possible: the effects are subject to degrees of dominance, epistasis and linkage in the population. However, these genetic details did not manifest themselves in any

noticeable pattern or correlation among GCA and SCA effects. While these results confirm current strategies in Douglas-fir breeding to select primarily on GCA, there are opportunities to utilize SCA variance in the production population. Controlled matings for elite production populations are now common in coastal Douglas-fir improvement programs, and controlled crossing with specified parents could i) elevate gains by as much as 3.0% in 12-year volume (assuming competition effects have not biased volume estimates), and ii) access additional sets of parents that would otherwise be disregarded. Gains for height growth from utilizing SCA are lower, which reflect either, i) lower SCA variances associated with height, or ii) competition has biased upward volume SCA variance by age 12 (relative to height).

Key words: Pseudotsuga menziesii, Douglas-fir, diallels, general combining ability, specific combining ability, genetic gain.

FDC: 165.3; 165.4; 232.11; 174.7 *Pseudotsuga menziesii.*

Introduction

The terms general combining ability (GCA) and specific combining ability (SCA) were first used by SPRAGUE and TATUM (1942) to describe the concept of the *average performance of parents in crosses* (i.e., GCA) versus that of *deviations of individual crosses from the average of their expected performance* (i.e., SCA). Tree breeders have long been interested in examining the proportions of the total genetic variance, for some trait of commercial interest, that can be attributed to SCA relative to that of GCA (e.g., BALOCCHI et al., 1993; BOYLE, 1987; COTTERILL et al., 1987; FOSTER and BRIDGWATER, 1986; KRIEBEL et al., 1972; WILCOX et al., 1975; YEH and HEAMAN, 1987). This is considered important because the relative magnitudes of these 2 types of genetic variance would influence the choice of breeding and production population improvement strategies.

(Where appropriate for the remainder of the paper, GCA and SCA variance will be denoted as σ^2_{gca} and σ^2_{sca}, and GCA and SCA effects (i.e., GCA and SCA means expressed as deviations from a mean) will be denoted as GCA_e and SCA_e.)

While analysis of variance approaches are useful for describing the general importance of σ^2_{sca} relative to σ^2_{gca} in the test population, the distribution of SCA_e and GCA_e *per se* are also important. Little has been reported in this regards in forest trees because: 1) typically not enough parents have been used in controlled-crossing programs to adequately represent the reference population, and 2) operational problems of using σ^2_{sca}, relative to that of σ^2_{gca}, are generally viewed as being unsuitable for current breeding methods (VAN BUIJTENEN, 1988).

To expand on this later point made by VAN BUIJTENEN (1988), some examples of specific problems of using σ^2_{sca} in tree breeding programs are as follows.

1) Since any SCA_e would be unique to a particular full-sib family, the SCA_e can only be captured by re-making the specific cross. Seed production systems were not able to handle large-scale controlled crossing among specified pairs of parents. This barrier, however, is quickly being overcome by cost-effective improvements in vegetative amplification techniques, and in operational controlled breeding systems.

2) SCA_e are not estimated as well as GCA_e (GILBERT, 1958) (e.g., in a 6-tree diallel mating, GCA_e is estimated from all

progeny among 5 other parents, whereas an SCA_e is based on progeny from only 1 of the 5 parents), so SCA_e have larger standard errors.

3) σ^2_{sca} can vary from negligible to as great as 7 times that of σ^2_{gca} in terms of total genetic variance (FOSTER and BRIDGWATER, 1986). In Douglas-fir, the ratio of $\sigma^2_{sca}/\sigma^2_{gca}$ has previously been reported to be one-quarter (YEH and HEAMAN, 1987). Moreover, σ^2_{sca} typically decreases, relative to σ^2_{gca}, with age and is therefore thought to be a less important form of genetic variance over time (BALOCCHI et al., 1993).

4) Most breeding programs are based on the concept of recurrent selection and the premise that gains will be cumulative over a number of generations. Across generations, additive genetic variance is the only important source of variation, as non-additive variance can only originate from the effects of gene pairs.

Hence, breeders have justifiably avoided attempts to incorporate σ^2_{sca} into their breeding and production programs because σ^2_{gca} is larger and more conducive to simpler improvement techniques (CARSON, 1985). SPRAGUE and TATUM (1942) also concluded that σ^2_{gca} is more important for previously unselected material, which is largely the case in tree breeding programs.

The objectives of this study were to examine the relative magnitudes of σ^2_{gca} and σ^2_{sca}, and the distribution of mid-parent GCA_e and SCA_e in a large test population of coastal Douglas-fir parent trees tested in a diallel mating design for 3 traits related to juvenile growth performance. Findings are then discussed in the context of utilizing σ^2_{sca} from 2 selection and genetic gain scenarios.

Assumptions of the Model

The genetic variances for GCA and SCA arise from the expectations of the covariance among half-sibs and full-sibs. From the diallel mating design (the basic design of this study), the components for GCA variance (σ^2_{gca}), which is equivalent to the covariance among half-sibs (Cov(HS)), is:

$$\sigma^2_{gca} = 1/4\ \sigma^2_A + 1/16\ \sigma^2_{AA} + 1/64\ \sigma^2_{AAA} + \text{etc.} \tag{1}$$

The SCA variance (σ^2_{sca}) is equivalent to the covariance among full-sibs (Cov(FS)) minus 2 times the covariance among half-sibs (2 x Cov(HS)) (MATZINGER and KEMPTHORNE, 1956), which results in the following components of genotypic variance:

$$\sigma^2_{sca} = 1/4\ \sigma^2_D + 1/8\ \sigma^2_{AA} + 1/8\ \sigma^2_{AD} + 1/16\ \sigma^2_{DD} + 3/32\ \sigma^2_{AAA} + 1/16\ \sigma^2_{AAD}$$
$$+ 1/32\ \sigma^2_{ADD} + 1/64\ \sigma^2_{DDD}, \text{etc,} \tag{2}$$

where subscripts "A" and "D" denote additive and dominance genetic variance, respectively, and their various epistatic interactions of increasingly higher order (in both [1] and [2]).

Potential Biases of Diallel Analyses with Forest Trees

Diallel crossing schemes are common mating designs in forest tree breeding. However, many of the genetic assumptions of the diallel model are not met, and are typically assumed not to be present. While examples of specific violations to the assumed genetic model for diallels are rare, it may be useful to review the potential biases that may be present.

The widely-simplified expectation is that σ^2_{gca} is purely a function of additive genetic effects and that σ^2_{sca} is purely a function of dominance genetic effects; however, if epistasis is present, epistatic variance contributes to both σ^2_{gca} and σ^2_{sca} (GRIFFING, 1956a). As noted by MATZINGER and KEMPTHORNE (1956), and in [1] and [2], σ^2_{gca} includes not only additive variance but portions of higher-order, additive-type epistatic variance. σ^2_{sca} includes dominance and portions of all types of epistatic variance: if epistasis is present, the sum of these epistatic interactions could be large.

Epistasis is typically ignored or assumed to be zero; however, it is clear that this is not a safe assumption (BAKER, 1978) and this is supported by empirical evidence (BARKER, 1979; BENSON and HALLAUER, 1994; GEIGER, 1988). As suggested by GILBERT (1958), multiplicative gene action should be expected and metabolic relationships are usually nonlinear rather than additive (DEAN et al., 1988). Furthermore, FALCONER (1981) suggests that additive variance does not carry with it an indication that genes necessarily act additively; additive variance can arise from any degree of dominance or epistasis. If all genetic variance is additive, all we can conclude is that the genes show no dominance or epistasis. Thus, the overriding conclusion is that σ^2_{gca} and σ^2_{sca} cannot be simply equated to σ^2_A and σ^2_D, respectively. Besides epistatic variance likely being present, it is well known that other assumptions concerning the analysis of variance tables of diallels are violated (BAKER, 1978), such as no reciprocal effects, intermediate gene frequencies, and no linkage disequilibrium (LD).

It may be worthwhile to consider LD in slightly more detail, since the literature cited earlier is somewhat unclear as to how it effects quantitative genetic parameters. Disequilibrium between pairs of alleles at different loci will introduce a covariance between additive and dominance gene action (MELCHINGER, 1988). YANG and BAKER (1990) and Barker (1979) reported that linkage disequilibrium (LD) can cause epistatic-like responses (and vice versa), and that the relationship between the 2 is complex.

Considering the above discussion, it is likely that any one of the single 6-parent diallel units is in some LD because of 1) genetic sampling effects (NASSAR, 1965) caused by random assignment of parents to a diallel; 2) by the mixing of previously isolated and genetically different populations (i.e., from populations with different gene frequencies) (BARKER, 1979), and 3) selection (BULMER, 1971). Selection is known to generate LD, so the effects of plus-tree selection in the wild, and the magnitude of LD it has created, may be important but unknown.

BAKER (1978) reported conflicting results in the literature as to whether LD will bias estimates of σ^2_{gca} or σ^2_{sca}. The linkage phase in the population (or diallel) for the trait of interest is important: if genes are in coupling phase, estimates of σ^2_A will be biased upward and, if in repulsion phase, estimates of σ^2_D will be biased downward (HALLAUER and MIRANDA, 1981). Considering this, any unidirectional effects of LD on overall variance estimates may actually be small, since it could be "averaged" across diallel units, if approximately half of the diallels are in repulsion and half are in coupling (which would be expected by chance if parent-tree selection has not modified the linkage phase greatly). FRANKLIN and LEWONTIN (1970) suggested that LD is probably the norm, and could have larger effects than 2-locus theory could predict. Very recently, however, TURELLI and BARTON (1994) have shown that with the infinitesimal model, LD does not significantly contribute to departures from classical gain equation predictions. This was particularly true of higher order linkage, but two locus LD and

epistasis remains a problem. BULMER (1985) also suggested that LD in species with more than four chromosomes may not be important.

In summary, there appears to be no simple way to separate the effects of LD, epistasis, or dominance on the observed SCA effects of individual crosses. Even with more control of the genetic make-up of lines being studied (e.g., inbred lines), clear separations of the effects of LD, epistasis, or dominance are not straightforward (BARKER, 1979; BAUMAN, 1959; HALLAUER, pers. comm., 1994; YANG and BAKER, 1990). For Douglas-fir, STONE-CYPHER and McCULLOUGH (1986) reported epistatic variance to be zero after height growth at age-4 in a cloned 12-parent diallel study. However, MULLIN et al. (1992) have reported large epistatic variance for early height growth in *Picea mariana,* and PARK et al. (1994) have reported very large epistatic variance for several traits in the somatic embryogenesis technique in *Picea glauca*.

Materials and Methods

From 1976 to 1986, 7 series of 6-parent-tree disconnected half-diallel tests were established as the test and selection population for the genetic improvement of coastal Douglas-fir in British Columbia (HEAMAN, 1978). Preliminary results of the first series (first 10 diallels) have been reported by YEH and HEAMAN (1987). Each of the 7 series of 6-parent disconnected diallels were established on 11 different forest sites, with each full-sib family represented by four-tree row plots in four replicates on each site. Crosses were fully randomized within replicates (i.e., diallels were not blocked in replicates). Actual establishment of the seven series occurred over a 10-year period (1975 to 1985). Each diallel is balanced (i.e., no missing crosses); however, one cross in Series I was removed from the analysis, as it was established one year after all others in the series. This was the only missing cross (cell) in any of the diallel tables, but 64 reciprocal crosses (out of the 539 present in the study) were used when specific female x male combinations were not possible. Reciprocal effects, and their potential bias, were considered small. This was confirmed by examining 62 of the 539 crosses having the other cross combination present; i.e., correlation coefficients between the "female x male" and "male x female" full-sib means was 0.94 for HT12, indicating reciprocal effects were minimal. Due to the relatively small number of reciprocal crosses present across the diallel tables, inclusion of reciprocal effects in the analysis of variance model was not considered appropriate.

Height at age 7 (HT07), height at age-12 (HT12), and breast-height diameter at age-12 was measured on all trees. Diameter and height at age-12 was converted to an estimate of volume at age-12 (VOL) by the formula presented by OMULE et al. (1987) for small-diameter Douglas-fir trees.

Data from four series are reported in this study, as they were the only series with complete measurements to age 12 (from planting) as of 1992. In total, this allowed for an examination of 539 full-sib families from 216 parents in 36 diallel units (Appendix).

Analysis of variance was carried out with a modified version of the SCHAFFER and USANIS DIALL program (PARK and FOWLER, 1982), which incorporates diallel set effects into the analysis of variance table (with nesting of GCA and SCA within diallel sets). This removes any problems due to averaging variance components across disconnected diallel sets when diallels are analyzed separately (especially when a set may have a σ^2_{gca} less than or equal to zero). The analysis of variance table for the diallel model is shown in *table 1*.

GCA$_e$ and SCA$_e$ were generated from arithmetic means within each diallel set as shown by FALCONER (1981). HUBER et al. (1992) has recently re-examined the ordinary least squares (OLS) solutions for the diallel model, but because of the extreme balance in this experiment, arithmetic based effects, when checked against OLS, were less than 2% different and not biased in any one direction. Therefore, arithmetic effects were used because of the relative computational ease.

Finite population corrections (*fpc*) for 6-parent diallels were made for each GCA$_e$. This equalled $(p-2)/(p-1) = 1.25$ (FALCONER, 1981) (where p = number of parents in the diallel), for the 6-parent diallel case. This *fpc* of 1.25 is equivalent to that obtained from the formula in GRIFFING (1956b) when derived from sums. The sum of the 2 corrected GCA$_e$ were subtracted from the full-sib family mean effect to derive the SCA$_e$: i.e., SCA$_e$ = full-sib mean$_{ij}$ – $((GCA_{e(i)} + GCA_{e(j)}) + Diallel_{mean})$, where subscripts denote the effects of parents i and j. Without the use of the proper *fpc* factor GCA$_e$ and SCA$_e$ are not orthogonal. This suggests that with unbalanced matings (missing cells) in diallel tables, SCA$_e$'s will likely be biased as covariances between GCA$_e$ and SCA$_e$ may not equal zero. All further references to GCA$_e$ assume they have been corrected with the *fpc* of 1.25.

As pointed out by MATHER and JINKS (1971, p.49), SCA$_e$ relative to GCA$_e$, may be biased or affected by scale differences and can be corrected by scale transformations. A normality check of all GCA$_e$ and SCA$_e$, using the SHAPIRO-WILK test (SAS, 1990), confirmed that the effects were normally distributed, so transformations were not necessary.

6-parent diallels are subject to "sampling drift" which may cause significant genetic differences among diallels. If diallel effects are significant, an adjustment can be made to all GCA$_e$ and SCA$_e$ by adding a "diallel effect," which would need to be multiplied by some estimate of "diallel repeatability." Diallel repeatabilities were approximated by "h^2_{Dial}" = $\sigma^2_d/(MS_d/k_6)$, from parameters shown in *table 1* and the Appendix. Diallel variance components were generally negative or very low, but varied among the 3 traits and the 4 series (Appendix). Adjustments, which may be appropriate in an operational context, were therefore ignored as they would not affect the main interpretations of the results.

Since GCA$_e$ and SCA$_e$ do not represent exact "genetic means" or breeding values (BV) for additive and non-additive effects, respectively, an appropriate heritability for each type of effect is needed to act as regressor (i.e., to "regress out" experimental and environmental noise). For GCA, h^2_{GCA} was approximated by $h^2_{GCA} = \sigma^2_{gca}/(MS_{gca}/k_3)$ and, similarly, a "heritability for SCA" (h^2_{SCA}) was approximated by $\sigma^2_{sca}/(MS_{sca}/k_1)$, from parameters presented in *table 1* and Appendix. More exact formulae exist for heritability of genetic entry means (e.g., h^2_{GCA}), but these approximations give results which are very close to more detailed calculations.

Genetic gain estimates for GCA, expressed as a percentage of the diallel mean (i.e., GCA$_{BV\%}$), were made by simply multiplying h^2_{GCA} by the sum of the 2 parental GCA: i.e., GCA$_{BV\%(ij)} = h^2_{GCA} \times (GCA_{e(i)} + GCA_{e(j)}) \times (100/\bar{X}_{DM})$, where $\bar{X}_{DM}$ is the grand mean of the diallel. Genetic gain estimates from the use of SCA for a particular cross, again expressed as a percentage (i.e., SCA$_{BV\%(ij)}$) of the diallel mean, were approximated from $h^2_{SCA} \times (SCA_{e(ij)}) \times (100/\bar{X}_{DM})$. With the use of effects, covariances between GCA$_e$ and SCA$_e$ are effectively zero so gain predictions from the 2 types of genetic variance can be viewed as orthogonal and therefore equivalent to that obtained from matrix solutions.

An analysis of genotype x environment interaction was not an objective of this study, but could be a source of bias to the results reported here. This would occur if GCA$_e$ was correlated with any SCA$_e$ by environment interaction, due to epistatic deviations being expressed only in certain environmental conditions (BAUMAN, 1959). GCA x environment and SCA x environment interactions were not included in the analysis of variance due to the technical difficulties in computing a full ANOVA table. These interactions would have added 1540 degrees of freedom to the main effects of the model (but removed 1540 from the error degrees of freedom). It was assumed that although significant GCA x site and SCA x site interactions might be present (YEH and HEAMAN, 1987), any bias present, in terms of a covariance between GCA and SCA, would

Table 1. – Outline of the analysis of variance table used for each trait (HT07, HT12, VOL) in each of the 4 series of diallels in coastal Douglas-fir. MS (mean squares) and k coefficients for each series are presented in Appendix.

Source	DF	MS	EMS
Site	s-1	MS$_s$	
Rep (S)	s(r-1)	MS$_{r(s)}$	
Diallel	d-1	MS$_d$	$\sigma^2_e + k_4\sigma^2_{sca} + k_5\sigma^2_{gca} + k_6\sigma^2_d$
GCA (D)	d(p-1)	MS$_{gca}$	$\sigma^2_e + k_2\sigma^2_{sca} + k_3\sigma^2_{gca}$
SCA (D)	dp(p-3)/2	MS$_{sca}$	$\sigma^2_e + k_1\sigma^2_{sca}$
Error		MS$_{error}$	σ^2_e

where; s = number of sites (S), r = number of replications (Rep), d = number of diallels (D), and p = number of parents in each diallel. GCA refers to general combining ability (terms in brackets denote nested effects) and SCA refers to specific combining ability.

be minimal and not affect genetic interpretations of the main results. GCA x site and SCA x site interactions will be reported in another study.

Ratios of genetic variances for inbred lines are sometimes expressed as $2\sigma^2_{gca}/(2\sigma^2_{gca} + \sigma^2_{sca})$; this is because the total genetic variance would be equal to $2\sigma^2_{gca} + \sigma^2_{sca}$ in the population of inbred line crosses (GRIFFING, 1956b) (due to the fact that there is no segregation variance within families of the F_1 crosses among inbred lines). Since the parents in this study were not inbred the value of expressing the variances in this form would not to be any more informative than simply dividing σ^2_{sca} by that of σ^2_{gca} as a general measure of the magnitude of σ^2_{sca}.

Since progeny from any full-sib family are not inbred, genetic sampling effects can occur which may bias family means. However, each full-sib family is represented by approximately 150 individuals, likely making genetic sampling effects minimal. KEMPTHORNE (1968) suggested that tests of significance are not as important as the ratios themselves; nevertheless, they do reflect upon the reliability of variance estimates. Because of this, and for the sake of brevity, the discussion will deal primarily with the $\sigma^2_{sca}/\sigma^2_{gca}$ ratios, but standard errors for both types of genetic variance and effects were calculated as shown by GRIFFING (1956b), for each of the 4 series, and are presented in the Appendix.

Results and Discussion

Variance Components

Values of heritability were very high for h^2_{GCA}, ranging from 0.79 to 0.91, which is likely due to the large amount of genetic variation present in Douglas-fir and the large number of offspring per family in the experiment. As expected, h^2_{SCA}'s were lower, ranging from 0.50 to 0.69, reflecting the fewer numbers of trees that composed full-sib family mean.

Over the 4 series, the ratio of $\sigma^2_{sca}/\sigma^2_{gca}$, averaged 36% for all 3 traits, varying from 19% (Series III for HT07) to as high as 65% (Series V for VOL)(Table 2). The large differences between $\sigma^2_{sca}/\sigma^2_{gca}$ ratios for height and volume measures suggest that diameter might have more σ^2_{sca} associated with it than does height. However, this was only noticeable for Series IV and V (Table 2), which may suggest that this is due to some genetic sampling effects, or competition effects may be influencing diameter and causing more "SCA" in VOL measurements (see discussion below). Series IV and V did not have the highest mean height, so this competition may not be an adequate explanation.

Ratios did not generally become lower from HT07 to HT12, except for a 15% reduction in Series V. This suggests that in this linear growth phase (i.e., ages 7 to 12) in coastal Douglas-fir, the ratios of the 2 genetic variances have not changed substantially. Competition among trees and plots in field tests can obviously bias genetic variance estimates (MAGNUSSEN, 1993), but this did not seem to be a factor as σ^2_{sca} for height growth did not change in any one direction across the 4 series.

BALOCCHI et al. (1993) reported that σ^2_{sca} was initially larger than σ^2_{gca} until age 12, then remained constant as σ^2_{gca} continued to increase. It is important to note that these changes may be affected by σ^2_{sca} being composed of both non-genetic and genetic effects (e.g., greenhouse effects, maternal effects), which diminish over time. On the other hand, BOYLE (1987) reported that in black spruce σ^2_{sca} increased over time, relative to σ^2_{gca}. It should be noted, however, that competition effects could also create this phenomenon particularly with large, multi-tree plot field designs. Interpretations of σ^2_{sca} changing over time should be viewed with caution; they need to be measured over a long period of time and in competition-free experiments which minimize environmental covariances.

Forms of dominance variance, through the presence of inbreeding depression in seed and growth traits in coastal Douglas-fir, is well known (ORR-EWING, 1976; WOODS and HEAMAN, 1989; WOODS, pers. comm.). However, the presence of inbreeding depression does not carry with it a direct indication of what the magnitude of non-additive genetic variance, in the form σ^2_{sca}, will be. This is because relatively few genes may be the cause of the obvious (or even small quantitative) inbreeding depression which may not contribute substantially to σ^2_{sca} estimates in a large outcrossed population. The magnitude of dominant loci that cause inbreeding depression, which also affect estimates of σ^2_{sca}, will be determined by the degree of dominance, gene frequencies of dominant and recessive alleles, and the number of loci affecting the trait. For σ^2_{sca} to change over time, and for the change to be of a true genetic origin, relevant loci affecting HT07, for example, would have to be different from those affecting HT12, or else dominance is somewhat transient over that period of time. Therefore, it is not be surprising that σ^2_{sca} did not appreciably change over the 5-years reported here.

GCA Effects, SCA Effects and Genetic Gain

While the ratios of σ^2_{sca} to σ^2_{gca} are of general interest an important question is: *how are the effects themselves distributed?* For each cross within each diallel $SCA_{BV\%(ij)}$ effects were plotted against mid-parent $GCA_{BV\%(ij)}$ for VOL, HT07, and HT12 (*Figure 1 to 3*). This was done for convenience in examining the distribution of the effects, but expressed in units that easily translate into expected gain. As anticipated, no correlations were present between $GCA_{BV\%(ij)}$ and $SCA_{BV\%(ij)}$ for any of the traits (*Figures 1* to *3*). Of interest, HALLAUER and MIRANDA (1981, p. 441) suggested that better GCA parents also tend to have positive SCA effects, but this trend is not apparent here. Although a zero correlation is present between $GCA_{BV\%(ij)}$ and $SCA_{BV\%(ij)}$, 2 selection scenarios become obvious: 1) is to select on $GCA_{BV\%(i)}$ alone (i.e., simply selecting the top GCA parents), or 2) try to combine selection on $GCA_{BV\%(ij)}$ plus $SCA_{BV\%(ij)}$. The later approach imposes some technical difficulties (i.e., specific crosses have to be made), but the advantages may outweigh the inconveniences in particular situations.

If we assume that the top 22 parents (approximately 10% proportion selected), based on $GCA_{BV\%(i)}$ across all diallels in all four series represents the selected population for scenario 1, and these parents are allowed to interbreed at random (i.e.,

Table 2. – $\sigma^2_{sca}/\sigma^2_{gca}$ ratios (in %) from 4 diallel series of coastal Douglas-fir for 3 traits (HT07, HT12, VOL).

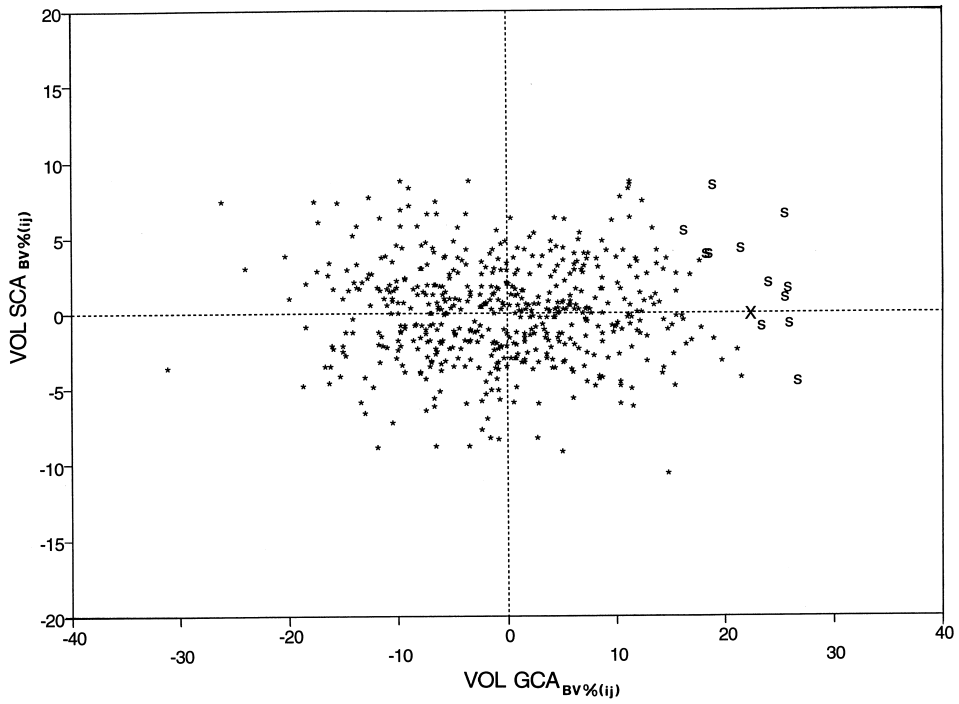| Trait | SERIES | | | | |
	I	III	IV	V	*mean*
VOL	35	25	46	65	*43*
HT07	33	19	36	46	*34*
HT12	29	24	42	31	*32*
mean	32	23	*41*	*47*	*36*

Figure 1. – Relationship between mid-parent general combining ability (GCA$_{BV\%(ij)}$) and specific combining ability effects (SCA$_{BV\%(ij)}$) for volume at age 12 (VOL) for 3 different cross-types from 36 six-parent disconnected diallels, expressed as a % of the grand mean across the 4 series. *) indicate a "non-select" cross, S indicate the 12 to 13 full-sib crosses selected for mid-parent GCA$_e$ plus SCA$_e$, and χ is the location of the mean for the top 22 parents based on GCA$_e$ alone.

Figure 2. – Relationship between mid-parent general combining ability (GCA$_{BV\%(ij)}$) and specific combining ability effects (SCA$_{BV\%(ij)}$) for height at age 7 (HT07) for 3 different cross-types from 36 six-parent disconnected diallels, expressed as a % of the grand mean across the 4 series. *) indicate a "non-select" cross, S indicate 1 of 12 to 13 full-sib crosses selected for mid-parent GCA$_e$ plus SCA$_e$, and χ is the location of the mean for the top 22 parents based on GCA$_e$ alone.
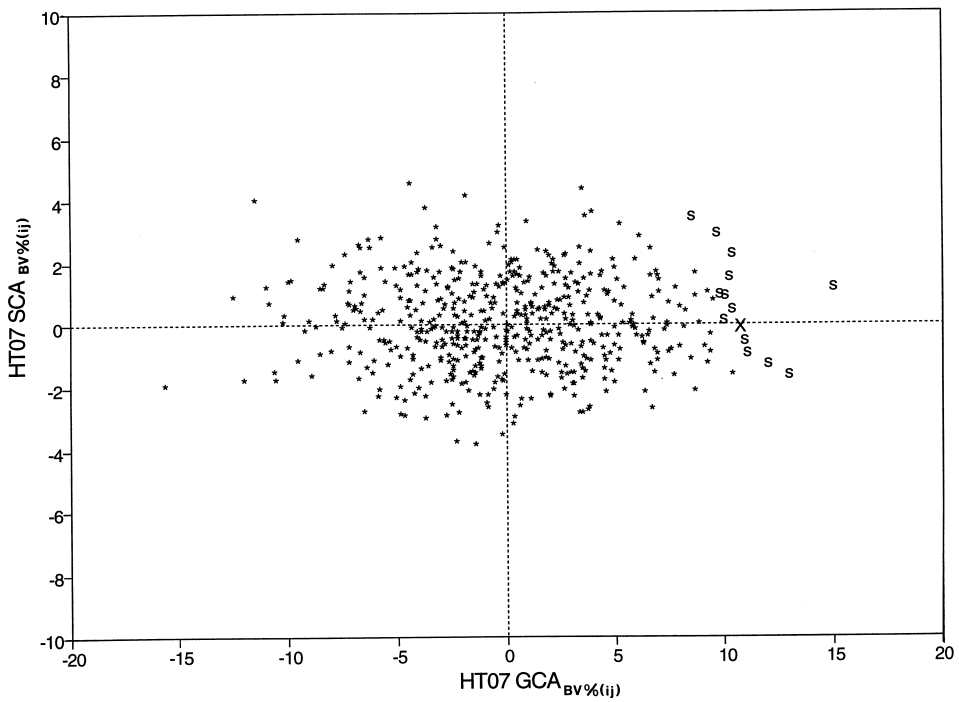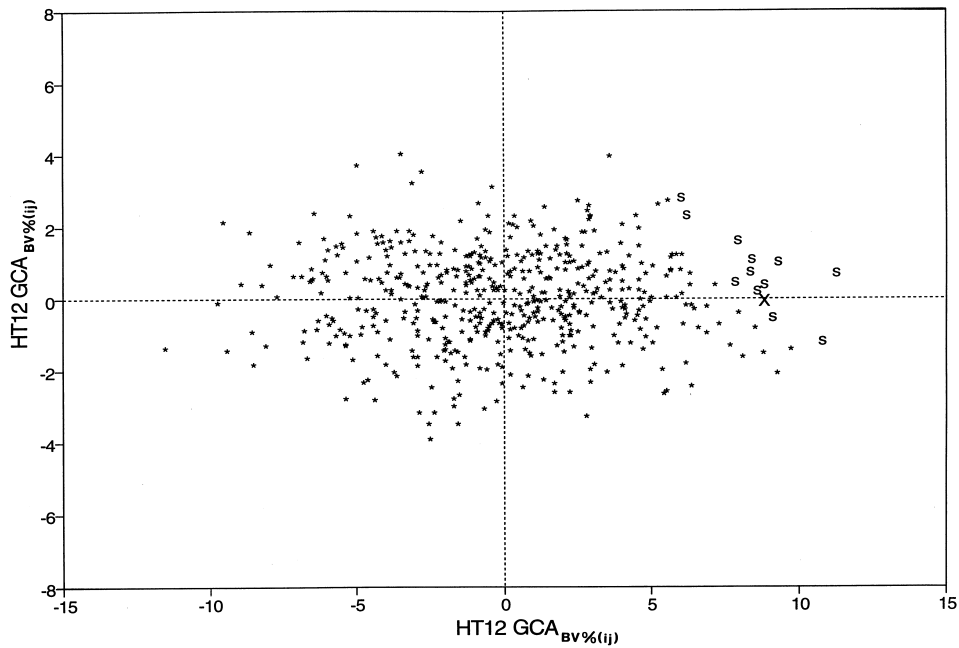
Figure 3. – Relationship between mid-parent general combining ability ($GCA_{BV\%(ij)}$) and specific combining ablility effects ($SCA_{BV\%(ij)}$) for height at age 12 (HT12) for 3 different cross-types from 36 six-parent disconnected diallels, expressed as a % of the grand mean across the 4 series. *) indicate a "non-select" cross, S indicate 1 of 11 full-sib crosses selected for mid-parent GCA_e plus SCA_e, and χ is the location of the mean for the top 22 parents based on GCA_e alone.

open-pollinated orchards or polymix outcrossing systems), genetic gain in age-12 VOL is expected to be 22.4% (expressed as a percent of the grand mean across all 4 series)(*Table 3*). The "X" in *figures 1* to *3* indicate where the expected gains for the $GCA_{BV\%(i)}$ lie on the horizontal axis. To utilize SCA in the production population (i.e., scenario 2), and for an equivalent comparison to selecting the top 22 parents based on GCA alone (i.e., scenario 1), the same number of "effective" parents were chosen (i.e., 11 full-sib crosses). In most cases this was comprised of the top 12 or 13 crosses, and not 11, as some parents where present in more than one full-sib family. With this approach, based on the sum of mid-parent $GCA_{BV\%(ij)}$ plus the $SCA_{BV\%(ij)}$ for the selected crosses (which are denoted by "S"'s in *Figures 1* to *3*), some crosses with negative $SCA_{BV(ij)}$ are included but gain was expected to be 25.2%, a difference of 2.8%. However, for HT07 and HT12, these gain estimates from selection scenario 2 were only 1.0% and 0.6% higher, respectively. Although gain was higher with the use of SCA for all three traits, the difference was very small, particularly for

Table 3. – Mean differences in predicted genetic response (%) relative to the grand mean of all 4 series by cross "type" which reflects 2 selection scenarios. "x" type crosses are gains expected from selection of the top 22 parents based only on $GCA_{BV\%(i)}$, where i and j denote 2 parents as mid-parents, or i as a single parent, times 2. "S" type crosses are gains expected from selection of the top 11 mid-parent crosses based on $GCA_{BV\%(ij)}$ plus $SCA_{BV\%(ij)}$ (*Figures 1 to 3*).

Trait	Mean Response (genetic gain in %) of Group Cross	
	Cross type "S"	Cross type "X"
VOL	25.2%	22.4%
HT07	11.7%	10.7%
HT12	9.4%	8.8%

the two height traits. This reflects the smaller σ^2_{sca} associated with both height measures, relative to volume.

The advantage of utilizing σ^2_{sca} from specific-cross pairs for VOL may not be based on the small additional gain as much as the fact that, of the 22 parents selected based on GCA_e alone, nine are common to the crosses which would be selected on mid-parent $GCA_{BV\%(ij)}$ plus $SCA_{BV\%(ij)}$. Additional parents may not be needed for gain in growth traits in the production population, as much as they may be useful for other traits that have i) non-linear economic values (BURDON, 1990) and ii) family specific responses to full-sib breeding or vegetative propagation technologies. Access to additional families, with similar levels of gain, may become the advantage of specific-pair breeding rather than increases in gain *per se*. Furthermore, the specific crosses exist in current trials and can be evaluated for specific traits; obtaining similar estimates based on GCA_e would require sampling many half-sib families to get adequate genetic sampling for GCA_e.

MAGNUSSEN and YANCHUK (1993) have recently quantified certain risks of early selection in Douglas-fir. Although many parameters need to be considered in juvenile-mature correlation predictions, family selection at age 12 (as described above for the 2 gain scenarios), should be quite robust. Predictions based on equation 5 in MAGNUSSEN and YANCHUK (using an average of the four regression parameters indicated in *table 1* in MAGNUSSEN and YANCHUK), and assuming a mature age of 60, the family juvenile-mature correlation would be approximately 0.7. This would further reduce putative gains from using σ^2_{sca}, reinforcing the value of obtaining additional parents for the production population, and not genetic gains *per se*.

Conclusions

A summary of the findings and implications of this study, as it relates to the diallel analysis in forest trees, is as follows:

1) Estimates of σ^2_{gca}, σ^2_{sca}, GCA_e and SCA_e (i.e., variances and means) may be affected by degrees of dominance, LD and epistasis, but no population trend was present for Douglas-fir, even though individual crosses may be affected by it.

2) Estimates of σ^2_{sca} and σ^2_{gca} should only be considered as very general indications of what type of gene action (additive, dominance, epistasis, multiplicative, etc.) is present for these 3 growth traits. The zero correlation between SCA_e and GCA_e effects suggests epistatic or LD does not contribute any unidirectional affects on SCA_e estimates and that there is an independence of alleles among parents.

3) In general, σ^2_{sca} relative to σ^2_{gca} was approximately 36%, which is similar or slightly higher to values reported for many other conifers. It did not decrease for height growth from age 7 to 12.

4) Although σ^2_{sca} was approximately 36% of that estimated for σ^2_{gca} a program that includes only the best general combining parents in seed production systems may only lose an additional 3.0% in VOL gain by not making specific pair crosses. Additional gain from using σ^2_{sca} for height growth was lower, in the order of 1%. However, the advantage that is obtained from full-sib breeding is that 13 of the 22 parents used are different than the ones used in the outcross breeding based on GCA_e alone. While this may not be necessary for gain *per se* in growth traits, the advantages of using other families may be important for other traits not being directly assessed for SCA_e in the field tests (e.g., rooting ability, somatic embryogenesis, form, wood properties). These concerns are becoming more relevant daily in operational programs of Douglas-fir, as many production facilities in Douglas-fir are moving towards controlled matings.

5) Gains in height growth traits from using SCA were lower than for VOL suggesting either i) SCA in height growth is lower and the only advantage it provides is access to additional sets of families to provide similar levels of gain, or ii) SCA for VOL growth may be biased upwards due to competition effects by age-12 unduly affecting diameter growth. Gains reported here were predicted for juvenile growth traits, and need to be adjusted down by a factor which would reflect a reasonable juvenile-mature correlation.

Acknowledgments

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Appendix

Appendix. – Descriptive statistics and genetic parameters for 4 series (series I, III, IV and V) of disconnected partial 6-parent diallels of coastal Douglas-fir for 3 growth traits, height at age 7 (HT 07), height at age 12 (HT 12) and volume at age 12 (Volume).

Series	I	III	IV	V			I	III	IV	V
Parameter						**Volume**				
# of diallels	10	9	8	8		mean(dm³)	2.29	1.89	1.40	1.98
# of crosses	149	135	135	120		h^2_{Dial}	0.00	0.32	0.08	0.00
# of sites	11	11	11	11		h^2_{GCA}	0.88	0.89	0.83	0.79
						h^2_{SCA}	0.64	0.50	0.55	0.63
Degrees of Freedom						σ^2_{gca}	0.0511	0.0269	0.0130	0.0195
Diallels	9	8	8	7		σ^2_{sca}	0.0180	0.0068	0.0059	0.0126
GCA(D)	50	45	45	40		s.e.$(\sigma^2_{gca})^c$	0.0114	0.0063	0.0032	0.0051
SCA(D)	89	81	81	72		s.e.(σ^2_{sca})	0.0042	0.0019	0.0019	0.0022
Error	23553	20823	19103	18168		s.e.$(GCA_{e(ij)})^d$	0.046	0.037	0.032	0.039
						s.e.$(SCA_{e(ij)})^e$	0.078	0.063	0.054	0.067
Volume										
$MS_d{}^a$	73.46	66.03	22.62	29.09		**HT07**				
MS_{gca}	36.74	18.86	8.91	14.92		mean(cm)	270.95	239.07	193.88	245.69
MS_{sca}	4.44	2.10	1.54	3.07		h^2_{Dial}	0.00	0.10	0.33	0.00
MS_{error}	1.60	1.04	0.70	1.15		h^2_{GCA}	0.89	0.91	0.86	0.85
						h^2_{SCA}	0.55	0.53	0.55	0.65
HT07						σ^2_{gca}	165.93	116.83	58.43	97.42
MS_d	258692	212723	136714	130126		σ^2_{sca}	54.46	22.67	21.17	44.97
MS_{gca}	117353	79500	38569	69710		s.e.(σ^2_{gca})	36.59	26.35	14.11	23.85
MS_{sca}	12653	6651	5432	10584		s.e.(σ^2_{sca})	11.83	12.75	10.42	22.83
MS_{error}	4066	3130	2420	3729		s.e.$(GCA_{e(ij)})$	2.32	2.05	1.88	2.26
						s.e.$(SCA_{e(ij)})$	3.93	3.48	3.19	3.83
HT12										
MS_d	1049241	824632	367841	470072		**HT12**				
MS_{gca}	445063	359341	200146	261191		mean(cm)	678.40	625.21	535.97	621.52
MS_{sca}	42064	30166	27049	27698		h^2_{Dial}	0.00	0.00	0.00	0.00
MS_{error}	13198	10746	8710	9397		h^2_{GCA}	0.91	0.92	0.86	0.89
						h^2_{SCA}	0.69	0.65	0.68	0.66
$k_1{}^b$	157.95	155.41	142.40	152.55		σ^2_{gca}	637.5	527.8	305.0	384.4
k_2	158.52	156.04	143.22	152.13		σ^2_{sca}	182.8	125.0	128.8	120.0
k_3	632.12	623.65	570.72	607.49		s.e.(σ^2_{gca})	138.4	119.1	73.1	89.0
k_4	158.75	155.76	143.46	153.07		s.e.(σ^2_{sca})	39.3	57.8	51.8	59.7
k_5	1583.00	1555.53	1428.70	1527.63		s.e.$(GCA_{e(ij)})$	4.20	3.79	3.56	3.58
k_6	2372.67	2332.80	2141.06	2290.46		s.e.$(SCA_{e(ij)})$	7.10	6.44	6.06	6.08

[a] MS indicates mean squares from analysis of variance table (*Table 1*).
[b] k values correspond to those in *table 1* for each series.
[c] s.e.$(\sigma^2_{gca}$ or $_{sca})$ is the standard error of the variance component.
[d] s.e.$(GCA_{e(i)})$ is the standard error of the midparent GCA effects for the $_i$th and $_j$th parents.
[e] s.e.$(GCA_{e(ij)})$ is the standard error of the SCA effect for the $_{ij}$th parents.