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Breeding Design Considerations for Coastal Douglas-Fir

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Abstract

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The basic principles of designing forest tree breeding programs are reviewed for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Pacific Northwest. Breeding populations are discussed given current and future breeding zone sizes and seed orchard designs. Seed orchard composition is discussed for potential genetic gain and maintaining genetic diversity in the forest. Mating and field testing designs are described and compared. Recommendations of the Breeding Zone Evaluation and Restructuring Cooperatives Working Group of the Northwest Tree Improvement Cooperative are presented.

Keywords: Douglas-fir, multiple populations, sublines, breeding population, gene resource populations, mating designs, selection, seed orchard.

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Introduction

Tree improvement activities started in the Pacific Northwest in the 1950s, with large-scale operational breeding programs for coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) beginning in Oregon and Washington in the 1960s (Adams and others 1990). Many of these programs are entering the second generation of breeding and are now starting to develop or revise tree improvement strategies. This paper reviews some of the basic principles of forest tree breeding so that foresters can better understand the challenges in developing the next generation of breeding in the Pacific Northwest. Also included in this report are the general recommendations of Breeding Zone Evaluation and Restructuring Cooperatives Working Group of the Northwest Tree Improvement Cooperative (NWTIC). (A glossary of terms is provided for words in bold print at the end of this report; also terminology used in this paper is from Burdon and Namkoong [1983]).

The two main objectives of a breeding program are to (1) improve economic traits and (2) ensure that the resulting breeding populations are well adapted and have sufficient genetic variation for gain to continue in subsequent generations. These two objectives are contradictory because to increase gain, selection intensity must be increased (fewer selections made of only the best), which in turn reduces genetic variation.

Breeders overcome this dilemma by structuring their selections so that both objectives can be met. Burdon (1988) describes three populations to consider when designing a breeding program. The **breeding population** is the group of selections that will be used to produce offspring for the next generation of selection. Usually selections are control-pollinated to produce **full-sib** families, but in many first-generation programs, open-pollinated families were used. The **production population** produces propagules for the forest, either as seed or clonal donor stock. The production population is a subset of the best breeding population selections. The **gene resource population** is all the extant individuals of a species that might potentially be selected for inclusion in the breeding population. It is usually large enough to maintain **alleles** that are at low frequency so that they are not lost for future use. The gene resource population includes the breeding population but often encompasses a much larger population.

Besides providing improved plants, a breeding program also must supply information for making decisions. Therefore, besides (1) providing improved selections for the following generation and (2) ensuring sufficient genetic variation is available for the future, a breeding program also must (3) provide **breeding value** estimates for the next generation of selections, and (4) provide information on the parental population for roguing orchards. No one mating design will maximize these four objectives simultaneously (Burdon and Shelbourne 1971). Therefore, one must prioritize the objectives before designing a breeding program. The breeding program must address every facet of breeding, including the mating design; the number, size, locations, and field design of progeny tests; timing of operations; and methods of selection. Campbell (1989) developed a decision tree to help design breeding programs. This paper will examine specific aspects of the decision tree presented by Campbell (1989); in particular, this paper discusses the structure of the breeding population, crossing design considerations, and field test design considerations.

Population Structure

Subpopulations

Breeding populations can be subsetted into subpopulations to (1) conserve genetic variation, (2) increase gain by putting more effort into the better selections, and (3) restrict inbreeding in the production population (seed orchard).

Multiple populations—Multiple populations refer to subpopulations designed to maintain genetic diversity in the breeding population. The concept was introduced to forestry by Namkoong (1976) and was developed because of the uncertainty of the future value of the traits selected. The idea is that each multiple population is selected for different traits (or different weightings), thereby providing more options (genetic variation) in the future.

Genetic diversity can be of two types: **intrapopulation diversity** or **interpopulation diversity**. The current NWTIC breeding programs are using intrapopulation (i.e., intrastand and intrabreeding zone variation) to improve growth genetically. For traits controlled by many genes (polygenic), such as growth, gains should be possible for many generations. For example, in corn breeding, increases (and decreases) in oil content have continued after 76 generations of breeding (Dudley 1977). The key to continued gains is in maintaining genetic variation. Mutation will maintain this at some level (Lande 1995, Lynch 1995), the level being dependent on population size.

Interpopulation diversity, that associated with variation among **breeding zones** (populations), is associated with adaptation to different environments and to processes of **genetic drift** (i.e., random loss of genes). Currently, this type of diversity is being maintained by restricting breeding programs to relatively small breeding zones.

Both types of variation (diversity) may supply genetic variation for unknown traits that may be needed in the future (e.g., resistance to a new pest or the need for a different wood property). A recent example is resistance to Swiss needle cast. Resistance is associated with distance to the coast (though not exclusively). If the disease becomes a problem farther inland and resistance is needed, it may be predominately found in more coastal breeding zones (interpopulation), yet some selections (although at a lower frequency) may be present farther inland (intrapopulation for those zones).

Namkoong and others (1989) point out that multiple populations, each selecting for different traits, will conserve genes better than one single breeding population. In fact, this is the only way to ensure the conservation of interpopulation diversity, because interpopulation diversity may require the conservation of gene combinations in addition to the conservation of individual genes. Multiple populations, however, also can be used to maintain intrapopulation diversity when the multiple populations are being selected for different sets of traits. This intrapopulation diversity can provide the variation needed to improve new traits that may be needed. A drawback to multiple populations is that overall gain for a single trait is normally greater for a single large population than the average of the multiple populations. If sufficient multiple populations are present, it would be possible that one of the populations was better than the large single population. This superior single population, however, would have to have enough unrelated clones to stock a seed orchard fully (or other production option) to achieve all the gain in that population. More important, if the multiple populations are selected for different criteria (different weightings of traits), there is a greater possibility that one population has the appropriate weightings for future economic weightings, as these can change with time (Namkoong 1976).

Stratified breeding populations—Nucleus breeding refers to the stratification of the breeding population into two groups, an elite and a main population, based on estimated genetic value. The key idea of this strategy is to concentrate more of the breeding effort on the **elite population,** where maximum gain is expected, with less emphasis placed on the **main population**, which is the primary source of genetic variation for the long term. This system was initially used in sheep breeding (James 1977) and has since been incorporated into forest trees by Cotterill (1989). The main population serves in both breeding population and gene resource population roles. An example is the North Carolina State University-Industry Tree Breeding Cooperative where they have a main breeding program and small elite populations for accelerated short-term gain.

Lindgren and Matheson (1986) proposed a strategy using a similar concept regarding seed orchards, suggesting that clones be used in proportion to their breeding value. In the context of breeding populations, the better clones (parents) would be used to make more crosses than the poorer clones.

Sublines—Sublining refers to the partitioning of the breeding population into unrelated groups (sublines). Each group is bred for a similar purpose (unlike multiple populations). The idea was first introduced to forestry by van Buijtenen and Lowe (1979) when they put forward the idea of "breeding groups." Unrelatedness across sublines is maintained generation-to-generation in the breeding population by only crossing within sublines. Production seed is produced by crossing among sublines, thus inbreeding depression cannot occur because related individuals do not mate in the production of commercial seed. The alternative to avoid inbreeding depression in an unsublined population is to carefully monitor the crossing in the breeding population and place restrictions on related crossing (distance between clones in a seed orchard) in production populations. Eventually, after many generations of breeding, inbreeding will occur in an unsublined population; the key is to allow it to happen gradually and practice selection along the way.

Choice of how one uses the production population impacts the feasibility of sublining a breeding population. In open-pollinated seed orchards, one must have as many sublines as the number of unrelated clones desired for the orchard. This can result in many small sublines that may restrict making specific cross combinations in breeding. For example, if sublines had less than 10 individuals, crosses among high wood density selections might not be possible, because more than one high-density selection might not be present in a subline if volume is the primary selection trait. If the production option is control-pollinated seed or clonal forestry, one would need only two sublines to allow for unrelated crosses. The Cooperative Forest Genetic Research Program breeding program (University of Florida) and the North Carolina State University-Industry Cooperative Tree Improvement Program use sublines for open-pollinated orchard strategies, whereas the New Zealand Radiata Pine Breeding Cooperative and Southern Tree Breeding Association (Australia) have fewer sublines because they use control-pollinated orchard strategies.

Sublining has both advantages and disadvantages. Disadvantages are (1) it may be difficult to divide the breeding population into unrelated groups; this is especially true for programs that are already in their second or third generation of breeding, (2) any new selections brought into a breeding population must maintain the integrity of the sublines, (3) inbreeding will occur at a faster rate in sublined populations because relatedness is proportional to the number of selections; therefore (4) loss of fecundity

can be a more severe problem within a subline than within a larger unsublined population, and (5) the crosses made for breeding may not be suitable for making selections for clonal or full-sib family deployment because of increased inbreeding depression within sublines.

The advantages to sublining are (1) the operational simplicity in production of commercial seed and (2) complete control of inbreeding depression. In sublining, the option always exists to unsubline the population; the converse is seldom true. This flexibility is one reason many programs have opted to subline their breeding populations as they begin their second or third generation of breeding.

Considerations When Structuring a Breeding Population

Questions that must be asked before structuring breeding populations include the following:

- What should be considered a breeding zone?
- What is considered as the gene resource population?
- How large of a breeding population is needed?
- What will the commercial seed-plant propagation system be?
- How many clones must be in a seed orchard to maintain diversity in the commercial forest, yet achieve genetic gain?
- What traits or trait combinations will be selected on?

Breeding zone size—The NWTIC breeding programs were initially established with relatively small breeding zones to ensure the adaptiveness of the resulting improved material. The complex environmental patterns of the region did not provide large areas of uniform climate to allow for large breeding zones as are found in most other breeding programs in the United States. Subsequent research has shown that Douglas-fir shows considerable local adaptation based on variation in seedling and tree characteristics (Campbell 1986, Campbell 1991, Campbell and Sugano 1993, Silen and Mandel 1983, Sorensen 1983). Although research confirmed that local adaptation is present, other results suggest that the original breeding zones may have been too small. Randall (1996) has reviewed the data and proposed new seed transfer zones that are longer in the north-south direction than the old ones. The small breeding zones ensured adaptiveness but also limited the return on investment because the results of any one breeding program had limited application.

The return on investment opportunities have been diminished further because the USDA Forest Service and USDI BLM reduced harvest on their lands. Land owners are now combining breeding zones to decrease breeding costs and increase the area over which gains can be capitalized. Indirect evidence has suggested that this could be possible in some areas. Weyerhaeuser[1] studies (Stonecypher and others 1996) have shown that, on their lower elevation sites, there is a set of improved families that performed well in all four of their Washington breeding zones, at least in the short

[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

term. Data from NWTIC trials also have shown significant correlations among zones; full-sib progeny performance at the J.E. Schroeder Seed Orchard near St. Paul, Oregon, was reasonably correlated with progeny performance in the field (midparent values of open-pollinated (trials) in four cooperatives (Snow Peak r = 0.68, Molalla r = 0.59, Umpqua Coast r = 0.43, and Vernonia r = 0.41) (Silen 1995). In another study (Johnson, in press), distance of plantation separation was not correlated with the genetic correlation among pairs of sites. Conversely, Campbell (1992) showed significant genotype-by-environment interaction in several breeding zones throughout Oregon.

Care must be taken in interpreting data from these studies because none used trees of rotation age. Maladaptation can take many years before it shows itself in the field. The Stonecypher and others (1996) data only examined mild sites, and the other data are limited to relatively small breeding zones (Johnson, in press).

Gene resource population—To alter a trait through traditional breeding, genetic variation must be present. For example, one can only breed for resistance if the genes (alleles) for resistance are present. The land area that could offer potentially beneficial genes to a breeding zone include more than the breeding zone being considered. Neighboring zones could offer genes of interest with perhaps minimal impact on adaptability. In addition, gene resource populations are more than just the progeny tests and parental selections currently in the breeding programs. Trees in the forest are also potential contributors of favorable genes.

To a limited extent, the whole species range could be considered as a source for potential genes, but this would not be the norm. At this point, transferring single genes is impossible; therefore for the Pacific Northwest to use a gene from the Southwest, we also must incorporate the maladaptation associated with trees from there. In this paper, a gene resource population will be considered as the land area from which the breeding population was drawn. This includes existing stands and *ex situ* resources available through breeding programs (e.g., progeny tests, seed orchards, and breeding orchards) throughout an ecoregion. An ecoregion is defined as a group of first-generation breeding zones that have similar climatic and ecological conditions.

Breeding population size—Before determining the size of a breeding population, “breeding population” must first be clearly defined. In the past, a breeding population was considered as the selections made in a single breeding zone. Some breeding cooperatives have already combined zones, and breeding populations are now composed of multiple first-generation breeding zones. For this discussion, we will consider a breeding population to be the pool of individuals from which we would consider selecting a clone to use in advanced generation breeding, not just for use as a seed orchard candidate.

Breeding population size is important because the rate at which genes (alleles) are lost to **random drift** is a function of population size. Genes that are at low frequency in the population are most prone to being lost if population sizes are too small. Loss of genes can affect potential gain in current traits of interest and in traits that may be of interest sometime in the future.

Gain from selection is affected by initial gene frequencies; breeding gains come predominately from genes with moderate frequencies (Namkoong 1979). In later generations, it will be important that low-frequency genes have increased in frequency to take the place of what were once genes with moderate frequency, genes that have since increased in frequency such that they no longer provide the bulk of the gain.

To have the flexibility to breed for new traits, it also is important to maintain neutral alleles because they may become valuable in the future. If a program has to find genes for a new trait in the gene resource population, any gain achieved in the breeding population for other traits will be reduced because the gene resource population will have a reduced level of gain (sometimes no gain at all).

Eventually, most low-frequency alleles will be lost from the population through random drift. Kang (1979) computed the necessary **effective population size** needed to maintain neutral alleles (those not under selection pressure) for 30 generations for varying allele frequencies (table 1). Effective population size represents the number of individuals that would give rise to the rate of inbreeding for the population in question. If individuals do not produce equal numbers of offspring or individuals are closely related, the effective population size is less than the census number.

It is virtually impossible to conserve all genes; even nature loses genes to random drift. A population with an effective population size (Ne) of 50, however, would conserve most genes with a frequency of 0.05 or greater for an extremely long time. The 30-generation time period in table 1 would encompass more than 300 years for most forest tree breeding programs.

Namkoong and Roberds (1982) point out that neutral alleles may be **linked** to alleles being selected against, in which case, the rate of allele loss would increase. They suggest doubling the population number needed to maintain unlinked neutral alleles to account for this. An effective population size of 100 to 200 should be adequate to maintain most neutral alleles.

Forest tree breeding programs tend to have 300 to 400 parents (White 1992). These numbers are larger than what is available in breeding programs for some agronomic crops, but much less than that suggested for conserving populations in the wild. An Ne of 500 proposed by Franklin (1980) and Soulé (1980) has traditionally been accepted as the number needed to maintain variability in quantitative traits by those in the conservation biology realm. Recently, Lynch (1995) has proposed increasing this number to 1,000, and Lande (1995) has proposed 5,000. These estimates are based on the effects of mutation, selection, and random drift.

White (1992) provides an excellent review of the literature and a discussion on population sizes and concludes that effective population sizes of 20 to 50 can sustain several generations of breeding (see also Namkoong and others 1989). Several hundred to more than a thousand parents, however, may be required to sustain long-term (20 to 50 generations) gain. One-hundred-fifty to two hundred selections (census number, not Ne) should maintain sufficient diversity to maintain rate of gain in the breeding program for at least 10 generations if the selections are made with some forethought; i.e., by limiting the number of selections from any one family, the resulting Ne of the breeding population can be maintained at a reasonable level (50 to 100).

Table 1—Effective population size (Ne) necessary to maintain neutral alleles for 30 generations with initial frequency p

p	0.005	0.01	0.02	0.03	0.04	0.05	0.10	0.20	0.50
Ne	282	161	94	69	56	48	29	19	11

Source: Kang 1979.

Production population—The current production populations for most Douglas-fir programs in the Pacific Northwest are open-pollinated seed orchards containing more than 30 unrelated selections (**clones**) or families. Some orchards have in excess of 100 clones. Having such a large number of clones reduces the potential genetic gain but ensures diversity. Thirty sublines would be required to ensure 30 unrelated clones in future generations. If one can rely on supplemental mass pollination (SMP) or controled-pollinated orchards in the future, then much fewer (two) sublines are necessary to control inbreeding in the production population.

Production population size—The size of the production population impacts a breeding program in many ways. The most obvious impact is on realized gain. It is important for an organization to realize the impact that increasing the number of orchard clones has on potential genetic gain and resulting genetic diversity. Secondly, as previously mentioned, the number of sublines is affected by size of the production population. Elite population sizes also are influenced by the size of the production population. If the production population is considered a subset of an elite breeding population, then larger production populations can result in larger elite breeding populations.

One way to look at genetic diversity is to examine the genetic variation that comes from a seed orchard. The theoretical genetic variation resulting from a given number of clones in the orchard can be calculated. The formula for calculating the percentage of the potential **additive genetic variation** for any number of clones is (Falconer 1960, p. 266):

$$\text{Percent of total additive genetic variation} = 1\text{-}F\ , \qquad (1)$$

where

F = the inbreeding coefficient.

If each clone in an orchard contributes equal numbers of seed and pollen, and all matings are at random (panmixous), then (Falconer 1960, p. 69),

$$F = 1/(2N)\ , \qquad (2)$$

where

N = the number of orchard clones (if all clones are unrelated).

Thus the expected percentage of all possible additive genetic variation expected from a clonal orchard is,

$$\text{Percent of total additive genetic variation} = 1\text{-}(1/(2N))\ . \qquad (3)$$

Equation (3) assumes that selfing takes place and that there is no inbreeding depression. If one assumes no selfing, the reduction in variation is greater because certain gene combinations are limited (i.e., a very large proportion of homozygotes for rare alleles are the result of selfing). To approximate this relation, the F-value is replaced with the probability of an individual being inbred for a monoecious species, resulting in,

$$\text{Percent of total additive genetic variation} = 1-(1/N)\ . \qquad (4)$$

The results from equation (4) are more realistic, in that a two-clone orchard (a full-sib family) has half the expected additive genetic variation of that found in the population. This is in line with quantitative genetics because the additive genetic variation within a full-sib family is one-half the population total.

Comparable formulae for nonadditive genetic variation are complex because they are dependent on gene frequencies. Because most of the genetic variation is additive (Yanchuck 1996), this discussion will not address the nonadditive portion of genetic variation.

The equations above assume all mating is at random and all clones provide equal seed and pollen to the final seed crop; this does not occur in orchards. The effective population size (Ne) needs to be used for N in the equations to adjust for the imbalance. This imbalance must be considered when discussing the "optimum" number of orchard clones. By using data approximated from El-Kassaby and Askew (1991), the effective inbreeding population size (Ne) of a Douglas-fir orchard was estimated by using Robertson's (1961) formula,

$$Ne = (\sum u_i)^2 / \sum u_i^2\ , \qquad (5)$$

where

u_i = the number of offspring contributed by $clone_i$ ($family_i$ in this case).

The effective population size (Ne) of the full-sib family orchard examined by El-Kassaby and Askew (1991) was about two-thirds of the actual population size. The reduction calculated in the full-sib orchard may underestimate the reduction for clonal orchards because clonal seed production has been shown to be more skewed than open-pollinated family orchards (El-Kassaby and others 1989). The amount of skewness also is dependent on crop year. El-Kassaby and others (1989) found that in good cone years, the genetic contribution of each parent was more similar to one another. Kjær (1996) found that the variance effective population number (Ne relative to genetic drift) decreased in poor flowering years in a Norway spruce (*Picea excelsa* Link) orchard, thereby resulting in less genetic variation than good flowering years. Variance Ne varied from 37 percent of the census number (N) in the poor flowering year to over 100 percent of N in the year with abundant flowering. In Scots pine (*Pinus sylvestris* L.), Muona and Harju (1989) found Ne to be 66 percent and 93 percent of N for two seed orchards in Finland. Siegismund and others (1996) estimated variance Ne to be 121 percent of N (the inbreeding Ne was 65 percent of N) for a noble fir (*Abies procera* Rehd.) orchard in Denmark.

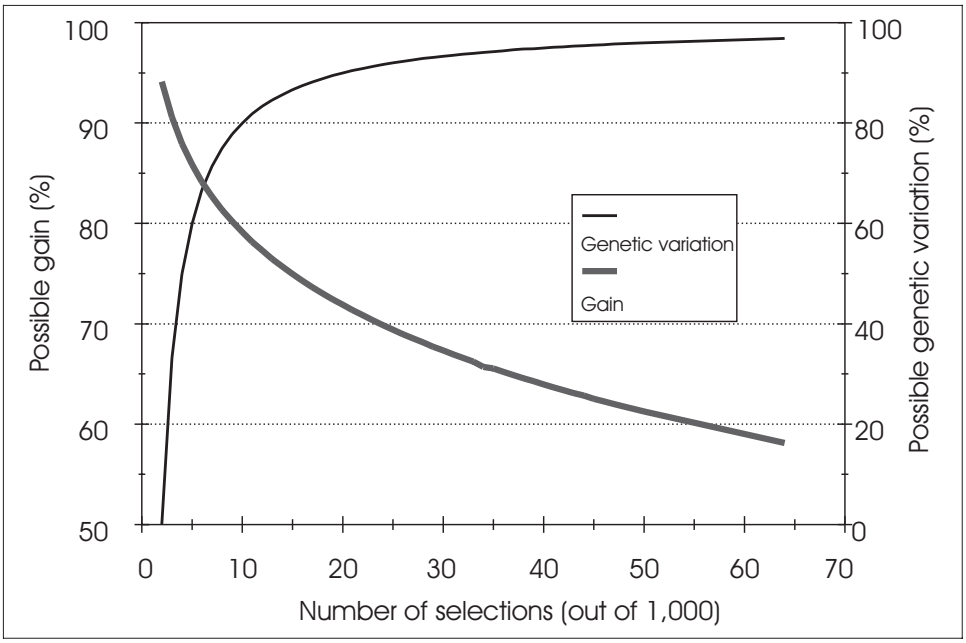

Figure 1—Genetic gain and percentage of total additive genetic variation as a function of number of seed orchard parents under the assumption that Ne = 0.5 N.

A conservative estimate of Ne in an orchard would be half the census number (N) based on the literature. This differs greatly, however, from year to year. If we want 90 percent of the potential genetic variation in an orchard, therefore, we would want 2 x 10 = 20 clones. Figure 1 shows the relation between gain and genetic variation when selecting from 1,000 individuals and setting Ne = ½N. After 20 to 25 clones, the genetic variation in the resulting seed changes little, but gain still decreases noticeably.

Rare (low-frequency) genes (alleles) are valuable in breeding populations but have limited benefits in plantations. If the gene is in the breeding population, it may or may not be in the production population. A low-frequency gene in the breeding population also will be at a low frequency in a seed orchard (if at all) and therefore also will be at a low frequency in the forest. An optimistic case study would be to assume that one clone in a 33-clone orchard was homozygous for a rare desirable gene. Theoretically, the gene would be transmitted to 6 percent of the orchard progeny (3 percent of orchard seed from the clone and 3 percent of the pollen). If we assume this is a dominant gene and the only source of resistance to a new disease, then resulting stands will have a maximum stocking after a major disease outbreak of only 6 percent. From a practical standpoint, 6 percent stocking is not any better than 0 percent; the stand would have to be replanted in either case. The gene will be of much more value in the next generation where it can be used in the breeding population to produce many resistant selections for a new seed orchard.

It has been well documented that selfing is detrimental in most coniferous species and should be avoided in the production of commercial seed. The theoretical selfing rate under panmixia is 1/n, where n is the number of orchard clones. Table 2 shows

Table 2—Theoretical percentage of self-pollinations from a seed orchard with varying numbers of unrelated clones and panmixia

Clones	Self-pollination	Clones	Self-pollination	Clones	Self-pollination
	Percent		*Percent*		*Percent*
1	100.0	11	9.1	21	4.8
2	50.0	12	8.3	22	4.5
3	33.3	13	7.7	23	4.3
4	25.0	14	7.1	24	4.2
5	20.0	15	6.7	25	4.0
6	16.7	16	6.3	26	3.8
7	14.3	17	5.9	27	3.7
8	12.5	18	5.6	28	3.6
9	11.1	19	5.3	29	3.4
10	10.0	20	5.0	30	3.3

that when the number of clones is below six, the percentage of inbred seed is 20 percent or more. Not until the number of clones is above 10 does the percentage drop to below 10 percent. Because the effective population size is probably less than the actual size, the clonal numbers in table 2 may need to be increased to approximate a more realistic model. Many selfed seeds, however, are not filled (Sorensen 1982), and orchard management techniques can reduce inbreeding rates. These factors must be considered when examining potential inbreeding in an orchard (El-Kassaby and Davidson 1991). Inbreeding will pose more of a problem in orchards where related individuals are included in the orchard. In such cases, the inbred seed resulting from sib-crossing would have less seed abortion and may not be culled in standard nursery practices. Proper orchard design can mitigate this problem to some degree. For a more thorough discussion, see Sorensen and Miles (1982).

Orchards with relatively short lifespans would need fewer clones than orchards with long lifespans because they would contribute to a smaller fraction of the reforestation base over time. If rotation age is 60 years and the orchard production life is 15 years, then four separate orchards will contribute to the genetic variation in the operational forest. If the orchard production life was 30 years, then only two orchards would contribute to the genetic variation. Orchards will be related from generation to generation, but not entirely. Genetic variation across the landscape, therefore, will be larger when orchards have shorter lifespans.

A final orchard (production population) of 25 clones after roguing should be adequate given the above considerations. It would produce forest stands with over 90 percent of the potential genetic variation of a 200-clone orchard and should produce less than 10 percent selfed seed. Twenty-five sublines would be required to ensure complete unrelatedness in future seed orchards if open-pollinated orchards will be the standard. If the future holds the possibility of control-pollinated orchards by using some aspect of supplemental mass pollination, then only two sublines would be needed.

Possible multiple populations—With current information, multiple populations could be generated in most programs for growth, wood density, and to some degree, stem form. Other traits now being assessed by companies include forking, straightness, and resistance to Swiss needle cast. Additional multiple populations will be possible in the future.

If one were to view Douglas-fir breeding in western Oregon, Washington, and British Columbia as one large breeding program, the current breeding zones would represent multiple breeding populations. Each breeding zone is breeding for volume in a particular zone. This will maintain the interpopulation diversity associated with adaptability.

Conclusions

The breeding population for a local cooperative should include a minimum of 100 selections but will probably be more than 150 because genetic diversity is of high importance. The effective population would probably be close to 100 if total population size is near 150 selections because many advanced-generation selections are apt to be related.

Breeding zones will be combined for biological and economic reasons to form **deployment zones** (combinations of old breeding zones with the intention that one production population will suffice for the area) and **testing zones** (area over which a group of organizations test the same families). Additional testing will be needed to confirm that increased maladaptation does not result. The new seed transfer zones (Randall 1996) can provide some general guidelines to establishing deployment zones. Combining old breeding zones will increase genetic diversity because breeding populations will contain the variation from multiple first-generation breeding zones. However, this does not necessarily translate to a better adapted population. This can only be determined with long-term testing. In nature, gene flow occurs among seed zones through the movement of pollen; there is no reason we should eliminate this natural process. Any maladapted selections would be removed from the breeding population through testing. The frequency of maladapted reforestation seedlings should be extremely rare because only tested clones will be allowed in the production populations.

Crossing Designs

Types of Designs

The primary purpose of the crossing design is to produce a population (pedigreed preferred) from which selections can be made, and from which breeding value data can be estimated. It also can provide information on genetic parameters, but this information is only crucial when the parameters are unknown. Information on most genetic parameters is readily available for Douglas-fir (heritabilities, **general combining ability/specific combining ability** (GCA/SCA) ratios, etc.), but the availability of information on genetic correlations across breeding zones is extremely limited.

Crossing designs fall into four broad categories:

1. Random matings
2. Assortative and nucleus matings
3. Structured designs (diallels, factorials)
4. Complementary mating designs

Random matings produce families for selection purposes but provide relatively poor information on parental performance. **Assortative** and **nucleus mating designs**, which use the better parents in more crosses, can improve gain minimally (increase efficiency by 5 to 10 percent), but also can reduce effective population size drastically (King and Johnson 1993). A preferable way to increase gain in the breeding population is to increase the number of families produced in the crossing design. Increased use of better parents is more beneficial in the seed production population where effective population size need not be as large. Random designs usually do not have the appropriate structure needed to estimate the GCA and SCA variance components. Variance component estimation, however, is usually a secondary objective, and open-pollinated orchards cannot use SCA to generate gain.

Diallel and **factorial mating designs** are structured designs that provide an adequate selection population and can estimate GCA and SCA variance components. In forest tree breeding, these designs are limited to partial and disconnected diallels and disconnected factorials because complete designs would be too large for practical programs. The major drawback to these designs is that they can take a considerable amount of time to complete. Factorials also have the problem in that unbiased parental breeding values cannot be produced. In a factorial, the tester parents differ among disconnected groups and between females and males, thus limiting unbiased comparisons to within small groupings. Comparable, unbiased parental breeding values are difficult (and sometimes impossible) to produce with incomplete disconnected diallels. Balanced partial diallels appear to be relatively efficient in ranking parents (Burdon and van Buijetenen 1990).

Complementary mating designs are being used by an increasing number of breeding programs because a single mating design cannot simultaneously optimize all objectives (Burdon and Shelbourne 1971). The most common combination of designs is a polycross (male or female testers) combined with full-sib families planted either in replicated trials or family blocks. The replicated polycross trials provide information on breeding values of parents and can be used to estimate breeding values of the control-pollinated families by use of midparent values. Only programs that can capitalize on SCA must test full-sib families in replicated trials.

The complementary design offers advantages and disadvantages. A major disadvantage lies in the fact that the polycross trees are not readily available for use as selections for the next generation. This is because (1) the tester parentage is commonly unknown (unless genetic markers are used or full-sibs are bulked to make the half-sib tester family), (2) only a limited number of unrelated selections would be available, and (3) the tester parents are usually not part of the subline. This reduces overall selection intensity because a large percentage of the population is not available for selection. Another potential drawback is that there is no possibility to examine gains by using SCA if the full-sib families are only planted in family blocks.

The advantages of a complementary design are as follows:

1. Accurate GCA estimates of parents
2. Parents are tested as outcrossed individuals
3. The potential for more precise within-family selection in family blocks
4. Simple data analysis

Use of a polycross test ensures that each parent is tested with similar, if not identical, tester parents. This leads to comparable breeding values for all parents. Breeding values would then be used to estimate the genetic value of the full-sib crosses that will provide selections for the next generations. If the “polycross” is comprised of bulked full-sib families (as is the case for female testers), each tester also can be monitored and any tester exhibiting unusually high SCA effects can be replaced. Female testers also would eliminate any bias from seed size or other maternal effects.

Testing parents as outcrossed individuals is especially important in sublined breeding populations. Because inbreeding depression differs by clone, it is possible that breeding values established by using inbred families will not accurately represent the true breeding value of an outcrossed individual. This problem can be overcome with an outcrossed GCA test. Tester parents could be chosen that are unrelated to individuals in all sublines or use different testers for each subline. The former offers the advantage of using poorer genotypes as testers. This can allow for better GCA precision for some traits if dominance masks GCA values (e.g., rust resistance in loblolly pine [*Pinus taeda* L.], see Byram and others 1987). Using unique testers for each subline would allow one to use superior testers. These crosses would produce trials of superior trees that could be used for clonal selections and provide for better public relations.

The effectiveness of GCA testing relative to directly testing the full-sib families are shown in appendix 1. When dominance is not present, midparent values are 90 to 95 percent as effective as directly testing the full-sib families. When dominance variation is half the additive variation, the two methods are identical. If the relative effectiveness is about equal, then the testing design that provides for the highest selection intensity (i.e., produces the most full-sib families while maintaining reasonable within-family selection) would yield the highest gain.

Intuitively it seems that choosing a single mating design (such as disconnected diallels) would produce more full-sib families than if a complementary design were used (two mating designs with only one for making selections). If one assumes a constant number of trees per design, this is always the case. The operational constraints, however, are far greater on the single mating design.

Regardless of the number of full-sib families, the number of families to be tested in replicated field trials remains constant with the complementary design (i.e., the number of parents). If one were to produce twice as many families as parents, the replicated field trials for the complementary design would be half the size of a single trial design. This also could lead to better test precision because replication size would be reduced. Because pollen or female testers are usually readily available, time required to complete the crossing for the GCA test should be less than that for the complete full-sib test. Because full-sib blocks for the complementary design do not have to be replicated and the field layout is simple, more seedlings can be planted as full-sib blocks than as replicated trials.

Within-family selection in blocks is much simpler than when members of a family are scattered among sites and replications. One can visually compare the members of a family, which is a tremendous aid in selection.

Cotterill and Jackson (1989) examined seed orchard gains arising from several breeding strategies. They found that half-diallels produced the greatest gains but were followed closely by single-pair mating with open-pollinated progeny tests (a complementary design), then by single-pair mating. They emphasized the fact that if one were to consider the time needed to complete crossing, the more simple designs may result in greatest gain per unit of time.

The decision on the crossing design is dependent on the economic model one wishes to use. If one wishes to maximize the return on a given "minimal" investment, the single design may be the one of choice, especially if land resources were not sufficient to establish both replicated field tests and full-sib blocks. The capital costs of establishing full-sib blocks would be minimal because replication is not necessary, but suitable land is still a requirement. If one wished to invest until the marginal return was below a certain level, the complementary design may be the option of choice.

Number of Crosses to Use in the Breeding Populations

Gain can be more readily achieved through family selection than through within-family selection. The **heritability of family means** for most traits ranges from 0.6 to 0.9. This indicates that between 60 and 90 percent of the variation observed in family means is attributable to genetic differences. The heritability of within-family selection usually ranges from 0.05 to 0.20. The efficiency of within-family selection is considerably lower than that of family selection. Despite the lower heritability for within-family selection, the intensity of selection (a function of the proportion selected) is usually much greater. Genetic gain is a function of both heritability and selection intensity, so the interaction of these two must be considered when selecting the number of families and number of individuals per family to produce in a crossing design. Other important considerations include practical limitations and the need to maintain the effective population size at a reasonable level.

Table 3 shows how gain is affected by increasing the level of family selection for three levels of heritability. The example illustrates a fixed progeny test population size of 6,000 trees that are the result of crossing 60 selections. These 60 selections are the best two individuals from the best 30 families. A total of 30 families is created if a single-pair mating design is used. Because 30 families are chosen in the next generation, there is no family selection, and all the gain is from within-family selection (the best 2 out of 200 trees per family). As the number of families produced increases, the overall gain increases; but at a decreasing rate. At some point, there are so few individuals within a family that the decrease in family-mean heritability results in a lowering of gain (family means of only a few individuals are relatively unstable because of the small sample size). By doubling the number of families from 30 to 60, gain increases 82 to 117 percent (1.49/0.82, 1.24/0.58). Doubling the number of families again (60 to 120) only increases gain 21 to 23 percent. Increasing families from 125 to 250 only increases gain 5 to 7.7 percent. If one were to use a model that assumed a constant family size and allowed for increasing the number of tested trees, the gain would be somewhat larger for additional crosses.

Increasing families comes at a cost, because more breeding is usually required. An appropriate economic analysis is required to optimize the number of families. Intuitively, it would seem that the minimum number of families to be produced is somewhere between the number of selections (parents) and twice the number of selections. This is equivalent to two to four crosses per selection.

Table 3—Gain associated with family and within-family selection by selecting the best 2 individuals from the best 30 families (60 selections)[a]

Number of crosses	Number of trees per cross	Family i[b]	Within family i	$h^2 = 0.20$		$h^2 = 0.15$		$h^2 = 0.10$	
				Gain	Relative gain	Gain	Relative gain	Gain	Relative gain
30	200	0.000	2.580	0.82	0.55	0.71	0.51	0.58	0.46
40	150	.414	2.478	1.19	.80	1.08	.78	.94	.76
50	120	.634	2.400	1.37	.92	1.26	.91	1.13	.91
60	100	.788	2.328	1.49	1.00	1.38	1.00	1.24	1.00
70	86	.906	2.267	1.58	1.06	1.47	1.06	1.33	1.07
80	75	1.001	2.217	1.65	1.10	1.53	1.11	1.39	1.12
90	67	1.081	2.174	1.70	1.14	1.59	1.15	1.44	1.16
100	60	1.149	2.127	1.74	1.17	1.63	1.18	1.48	1.19
120	50	1.258	2.052	1.81	1.21	1.69	1.22	1.53	1.23
125	48	1.286	2.035	1.82	1.22	1.70	1.23	1.54	1.24
150	40	1.390	1.957	1.87	1.26	1.75	1.27	1.58	1.27
175	34	1.475	1.889	1.91	1.28	1.78	1.29	1.61	1.29
200	30	1.545	1.829	1.93	1.30	1.80	1.30	1.62	1.30
225	27	1.606	1.781	1.95	1.31	1.82	1.31	1.63	1.31
250	24	1.658	1.726	1.96	1.31	1.82	1.32	1.62	1.31
300	20	1.746	1.638	1.97	1.32	1.82	1.32	1.62	1.30

[a] The number of progeny tested trees is held to 6,000. Assumes a single progeny test site.
[b] i represents selection intensity.

One must also consider that in addition to increasing gain, increased family selection results in increased inbreeding and decreased effective population sizes. One way to overcome this problem is to increase the family selection intensity by increasing the total number of families and leaving the number of families selected constant. The inbreeding problem can be addressed through sublining to some extent (see above), and multiple populations can assist in maintaining low-frequency alleles. In the end, the costs and benefits of increased family selection must be considered.

Appendix 2 examines gain over generations for several options. If low-frequency alleles are not necessary in the next eight generations, then intense family selection maximizes gain. If, through high family selection, a low-frequency allele is lost that is later needed, then more expensive options such as open-nucleus breeding or multiple populations need to be considered.

Field Testing Design Considerations

Cotterill and James (1984) examined field testing designs in some detail, and a review was done by Mikola (1993). Cotterill and James (1984) examined the tradeoffs between increased family selection intensity and decreased family-mean heritabilities given a fixed number of progeny to test. Their results showed that the optimum was between 10 and 20 trees per family depending on heritability. This provided sufficient numbers to estimate family means and provided many families for selection. The NWTIC progeny tests serve not only to rank families but also to provide information for delineating breeding zones. Each test, therefore, must provide reliable estimates of family means on each site; each site must be able to stand alone. The earliest NWTIC trials did not have sufficient numbers of trees per family to characterize sites, but the large number of sites allowed for a reliable ranking of families overall. The Cotterill and James optimum also implies undamaged, living trees. Progeny tests, therefore, should have a minimum of 20 trees per family per site.

It is important that progeny tests be established on multiple sites to ensure that family rankings are stable over sites (i.e., test for the presence of genotype-by-environmental interaction). Multiple sites also are needed to help delineate appropriate breeding zones; the new NWTIC testing zones have not been shown to represent appropriate deployment zones. From a selection point of view, the benefits from adding additional sites decreases as site numbers increase. Figure 2 shows the expected gain from using different numbers of progeny test sites (see Jognson, in press). The figure was generated by using data from five breeding units. After four sites, the additional gain from adding additional sites is minimal. The minimum four-site gain was 80 percent of the average four-site gain; the minimum five-site combination was not far off the five-site mean. Based on this data, four sites seem adequate for an existing breeding unit. If one site is lost, there still would be three sites, which, on average, is over 85 percent as efficient as six sites. Where multiple first-generation breeding zones have been combined and new deployment zones cannot be verified, it would be wise to have at least two progeny test sites in each first-generation breeding zone. This would ensure a minimum of two sites in a deployment zone if first-generation breeding zones are, in fact, the most appropriate deployment zones. The other progeny test sites would still contribute some information because the correlation across sites would not be zero; therefore, total gain would reflect more than the two-site gain in figure 2.

The sets-in-reps field design allows for better comparisons among sets of families than the reps-in-sets design originally used. Unbalanced designs, as developed by Patterson and Williams (1976), could further improve the comparisons among all families.

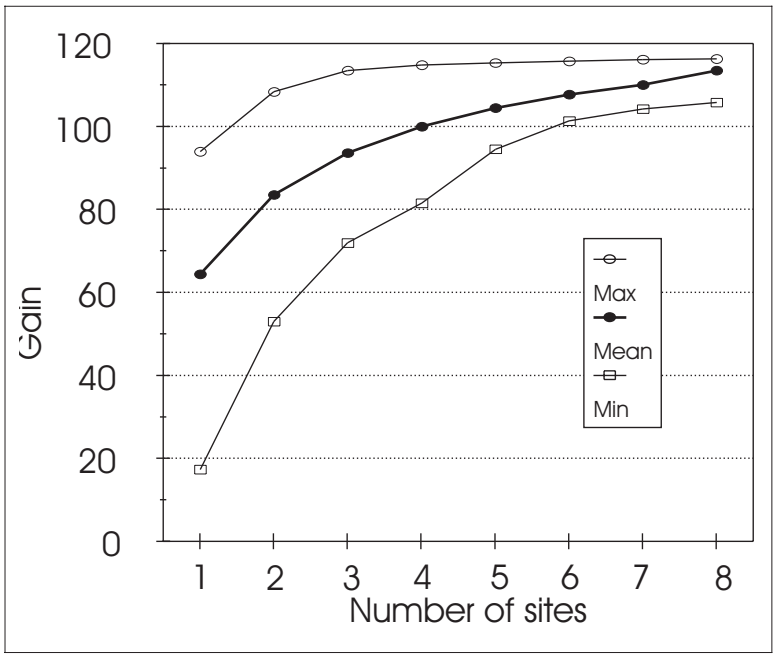

Figure 2—Mean, minimum, and maximum gain from using different numbers of progeny test sites. Source: Johnson, in press.

Noncontiguous and single-tree plots are the most efficient for ranking families (Cotterill and James 1984, Lambeth and others 1983, Loo-Dinkins and Tauer 1987) and should be continued by the NWTIC.

The noncontiguous plots are not optimal for examining gains on a per-acre basis or for within-family selection. The primary purpose of progeny testing is to rank families, next of importance is within-family selection, and lastly is the quantification of gain. Full-sib blocks could simplify within-family selection because all trees of a family could be viewed at a single location. To use full-sib blocks to quantify gain, they would need to be replicated. Blocks for within-family selection would not need replication, except for ensurance purposes.

Conclusions

The major question yet to be answered in the Pacific Northwest is the appropriate size of deployment zones. Until more information is available, breeding designs should provide flexibility for the future. Now is the time to design flexibility into a program; by the third generation, designating sublines will be nearly impossible. If second-generation testing zones are too large and as a result third-generation population sizes are too small, additional selections will have to be made in first-generation tests, thereby reducing gain in the later generations.

Flexibility costs money, and to offset these costs, testing and deployment zones will be larger than in the first generation. Organizations will try to obtain more gain from their investment by spreading their breeding results over a larger land base—perhaps even more so if the Federal agencies continue to reduce their harvest levels and inputs into tree breeding. Testing costs also could be reduced by combining first-generation breeding zones because fewer trials and smaller breeding populations would be required for one breeding program than for many. Again a lack of information exists about which zones could be combined into a single testing program. If the testing zone is too large and a seed orchard is developed for the whole testing zone, maladapted growing stock will result.

The key to the next generation will be to develop programs that are structured so that, as more information becomes available, the programs can be easily modified to accurately represent well-founded deployment zones. This requires having sufficiently large population sizes and enough trials in the ground.

Obviously, providing flexibility conflicts with maximizing short-term gain, especially when limited breeding resources are available. The former requires large investments into maintaining large populations, whereas the latter depends on emphasizing only the best selections (although at a higher risk). A compromise can be reached by structuring a reasonably sized breeding population and establishing progeny tests on a sufficient number of sites to allow for the worst case scenario of going back to the old breeding zones as future deployment zones.

Recommendations

The following overall recommendations were developed by the Breeding Zone Evaluation and Restructuring Cooperatives Working Group of the NWTIC.

Population Structure

The general recommendations for population structure are as follows:

- Within each first-generation breeding zone, construct a minimum of two unrelated breeding groups from second-generation selections and the best first-generation parents.
- Testing zones will incorporate larger areas than previous breeding zones; new zones are to be based on any available data or observations.
- Breeding populations will utilize breeding groups from a wide range within an ecoregion. These will include selections from outside the testing zone. As selections are considered from areas outside the testing zone, only the best parents and families will be considered.
- Elite populations can be developed to increase gain in the next few generations.

Within each of the first-generation breeding zones, the best available first- and second-generation selections should be placed in unrelated breeding groups based on parental origin. These breeding groups will function in a dual role as both sublines and multiple populations. Crossing to produce full-sib families for the next generation

will be limited to crosses within a breeding group. They will serve as multiple populations because breeding groups from different breeding zones may have somewhat different sets of genes that influence growth and other traits. They also will function as sublines that can be used in control-pollinated production populations. In the worst case scenario of having to use the old breeding zones as deployment zones, the multiple populations can serve as elite populations.

New testing zones will test families produced from breeding groups that span a relatively broad range within an ecoregion and be “rolling zones.” Breeding groups that originate near a progeny test site will be completely represented on the site. Breeding groups located farther away from a progeny test site would have only their better crosses tested. Such a test design should provide a sufficient number of superior parents for a breeding zone. The design is similar to the continuous zone suggestion of Rehfeldt (1990).

By using the best selections from breeding groups outside the testing zone, a more intensely selected group of parents is tested within a testing zone. This will increase selection intensity and maintain a relatively large effective population size. The risk of producing maladapted families will increase because some families will be produced from parents that originated from outside the testing zone. Selections from these families, however, would never be used in the production population until they had been tested in the testing zone. If after testing, some breeding population selections are not suitable for a breeding zone, additional second-generation selections could be infused into third-generation programs to increase the effective population sizes of third-generation breeding populations. This would reduce gain in the breeding population, but the production populations in the next few generations could still capitalize on gain made by the high selection intensity in the families that were adapted.

An added advantage of testing the best parents and families over a broad range is that information will be available for the next generation to help better define breeding and testing zones. A subset of families will be tested over many testing zones and provide an excellent population from which to examine the stability of performance over the landscape.

Breeding group size should be between 20 and 30. This provides sufficient genetic variation for many generations and is large enough that inbreeding depression should not be a problem in the next few generations. Because there is a minimum of two breeding groups from each first-generation breeding zone, actual breeding numbers from an old zone would be 40 or more. In the worst case scenario, when only the old local zone is appropriate for breeding, sufficient third-generation seed orchard selections would be available from the two local breeding populations.

Additional elite populations could be formed if there is interest in increasing the rate of genetic gain over the next three to four generations. These elite populations would be used for intense breeding over the next few generations to increase gains in the production population. Greater gains could arise from a rapid turnover of generations, a different crossing design, more intense field testing, and testing for adaptive traits in the nursery. Elite populations could be based on specific combinations of traits (e.g., fast growth, high wood density, disease resistance, and form). An elite population would consist of the best 30 to 40 selections from various breeding groups. This

would allow for two sublines to be formed to prevent the occurrence of inbreeding in the production population. Thirty to forty selections would provide a sufficient number of production population (seed orchard) selections and allow for at least five generations of breeding. Any fewer selections would require that additional selections from the "main" populations be used in future seed orchards to maintain an effective population size of > 20 in the orchard. The use of too many "main" population selections in an orchard would dilute the gain made from the elite breeding.

Mating and Crossing

Each selection should be used in a minimum of two crosses so that some level of family selection can be practiced. Any selection used in a seed orchard should be used in a minimum of three crosses if a GCA test is not used and roguing information is needed. Three crosses per parent should provide sufficient parental GCA information in a balanced crossing design (Burdon and van Buijtenen 1990) but four crosses may be necessary if there is a large degree of imbalance. Crossing should be limited to within breeding groups and be dictated by operational constraints, not by preplanned designs such as diallels or factorials. Although preplanned designs provide good estimates of genetic variation patterns and provide better breeding values for parents, they often take considerably more time to complete.

Complementary crossing designs will be necessary in future generations to test parents as outcrossed individuals but are not necessary in this generation because inbreeding is not yet a problem in the breeding population. To use GCA tests this generation, different testers would be required for each testing zone. This would limit the usefulness of these tests in examining family performance over a wide geographic range because a tester family would be restricted to a single testing zone.

A complementary design is recommended for elite populations because gain could be increased by several methods: (1) a polycross mating design could be completed faster than the full-sib crosses, thus reducing generation interval; (2) nursery tests could screen GCA families for some adaptive traits (bud set, flushing, cold hardness, etc.) to provide additional information that could be used in helping deploy the next generation of commercial seed; (3) more trials (of smaller size) could be planted in the region to increase the precision of family rankings; and (4) a quicker and more accurate assessment of parental breeding values would be available to rogue second-generation seed orchards.

Field Design

Previously it had been suggested that a cross should be tested on at least four sites overall. Assuming that a cross will be tested in its first-generation breeding zone of origin and in at least two others, it is recommended that each first-generation breeding zone have at least two progeny test sites. This should ensure adequate testing even if breeding zones cannot be combined because the four test sites outside the old zone still provide some information for ranking families within an old breeding zone.

Instead of a "reps-in-sets" or "sets-in-reps" design, an imbalanced (alpha) design (Patterson and Williams 1976) could improve comparisons among families. Software is readily available for setting up and analyzing such designs (CSIRO/BioSS 1996).

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Appendix 1

Modeling the Difference in Efficiency Between Testing Full-Sib Families and Using Midparent Values From GCA Tests

Complementary mating designs must depend on selecting full-sib families based on midparent values that come from polycross trials if the full-sib families are only planted in family blocks. The objective of this section is to examine the efficiencies of midparent values.

Three crossing designs are examined for selecting the best full-sib families:

1. Full-sib families produced at random; individual family means are used to select families.

2. Full-sib families produced at random; midparent values from GCA tests are used to select families.

3. Double pair-matings, both full-sib and half-sib families values are used to select families.

Gain was computed by examining predicted gain as a result of using selection indices. Two sets of genetic parameters were examined: no SCA (dominance) variation and SCA variation = ½ GCA (additive). This exercise assumes 78 progeny are planted in progeny tests and no GxE interactions. The variance components were set to:

Variance component	No SCA	SCA = ½ GCA
σ^2_a	560	560
σ^2_d	0	280
σ^2_e	2000	2000
$\sigma^2_{\text{full-sib family}}$	309	382
$\sigma^2_{\text{half-sib family}}$	171	175

Gain was calculated as,

$$\text{Gain} = i\, G_{ai}\, V_i^{-½} = i\, b'\, G\, (b'Pb)^{-½} = i\, (b'Pb)^{½}\,, \qquad (6)$$

where

i = selection intensity,

G_{ai} = covariance between the breeding value (a) and the index (I),

V_i = variance of the index,

b = the index coefficients = $P^{-1}G$, and

P = the variance covariance matrix of the family means used to predict the breeding value.

The matrices for the indices were as follows:

	Test design					
	FS family	**GCA**	**Testing**	**Double-pair crosses**		
P matrix	309	171	0	309	0	140
(no SCA)		0	171	0	309	140
				140	140	309
P matrix	382	175	0	382	0	140
(SCA = ½ GCA)		0	175	0	382	140
				140	140	382
G' array	280	140	140	140	140	280

The results show little difference in estimated gain for a given selection intensity (i) (table 4). Therefore the option that could produce the most families for a given cost would produce the most gain.

Table 4—Gains estimates calculated as $(b'Pb)^{½}$ for 3 breeding options and 2 levels of dominance (SCA) variation[a]

	GCA[b]-SCA variation	
Crossing design	No. of SCA	SCA = ½ GCA
Random full sib	15.92	14.33
Random GCA	15.14	14.98
Double pair	15.98	14.67

[a] SCA = Specific combining ability.

[b] GCA = General combining ability.

The random full-sib crosses were examined in more detail by Monte-Carlo simulation in a manner similar to that described in King and Johnson (1993). Sixty parents were generated with additive genetic variance (σ^2_a) of 560. These 60 selections were crossed in a double-pair crossing design. Combinations were selected at random. Full-sib and half-sib family (phenotypic) means were generated for full-sib and half-sib families as follows,

$$\text{Full-sib mean} = ga3 + gd3 + fsvar, \text{ and}$$

$$\text{Half-sib mean} = (ga2 / 2) + hsvar\ , \qquad (7)$$

where

ga3 = additive genetic value of the full-sib family in generation 3 = (gm + gf)/2;

gm = additive genetic value of mother (ga2);

gf = additive genetic value of father (ga2);

ga2 = additive genetic value of parent selections in generation 2 (it is divided by 2 to represent a pollen mean of 0);

gd3 = dominance genetic value of the full-sib family, this number was produced randomly as $(\frac{1}{4}\sigma^2_d)^{\frac{1}{2}}$ * rannor, where rannor is a normal random variable with mean 0 and variance 1;

fsvar = deviation of a full-sib family mean from its actual value; this was produced as $[(\frac{1}{2}\sigma^2_a + \frac{3}{4}\sigma^2_d + \sigma^2_e) / 78]^{\frac{1}{2}}$ * rannor; and

hsvar = deviation of half-sib family mean from its actual value, this was produced as $[(\frac{3}{4}\sigma^2_a + \sigma^2_d + \sigma^2_e) / 78]^{\frac{1}{2}}$ * rannor.

Midparent values were estimated for each full-sib family as the average of the parental half-sib family means. The efficiency of the GCA tests (half-sib families) and the full-sib family means were compared by examining the correlations of the phenotypic means (full-sib mean and midparent value) with the actual additive genotypic value of the full-sib family (ga3) and the genotypic value of the full-sib family (ga3 + gd3). Twenty-five simulations were run to produce 1,500 family means for which correlations were calculated. Specific combining ability (dominance) variation was examined at the values of 0 and ½ GCA variation as in the previous example.

When SCA variation was not present, the correlation between the full-sib family mean and the full-sib breeding value was marginally larger than the correlation between the midparent value and the full-sib breeding value (table 5). When SCA variation was one-half the GCA variation the midparent value and full-sib family mean had identical correlations with the full-sib breeding value (table 5). This corresponds to the index selection estimates of gain (table 4).

Table 5—Correlation of full-sib family means and midparent values from a GCA test with the additive and total genetic value of the family[a]

	No SCA[b]		SCA variance = ½ GCA	
Estimate type	Additive value	Genetic value	Additive value	Genetic value
Full-sib	0.966	0.966	0.894	0.965
Midparent	.905	.905	.909	.835

[a] GCA = general combining ability.

[b] SCA = specific combining ability.

Appendix 2

Modeling the Value of Different Mating Designs in Preserving Low-Frequency Alleles

How much gain is lost if a needed gene is lost from the breeding population through the process of intense selection over generations? This exercise will examine the gains from breeding scenarios and the impact of gene loss. The four breeding scenarios are:

1. Five subpopulations, each with 30 parents (selections) that produce 30 families by way of double pair matings. The best individual is selected from each full-sib family. Gain is only made from within-family selection. Effective population size (Ne) is 30 in each subpopulation. Total Ne = 150.

2. One elite breeding population of 30 parents. These 30 parents make 150 full-sib families. Selection is made by using family and within-family selection. The best individual is chosen from the best 30 families. It is assumed that the effective population size is reduced to 15 because of the family selection; this implies that several half-sibs are selected.

3. This scenario is similar to scenario 1, in that there are five subpopulations, each with 30 parents. These 30 selections produce 60 full-sib families. Only half as many individuals are tested per family. Selection is then based on family (30/60) and within-family (1/45) selection. Ne is estimated as 25 per subpopulation because minimal family selection is applied. Total Ne = 100.

4. This scenario is a nucleus breeding program that uses scenario 2 as its nucleus and has a 200-family open-pollinated breeding population as the main population. The best two individuals from the best 95 families are chosen out of the main (the other 10 families come from the nucleus top 10 selections). The best three main population selections are added to the nucleus each generation. For the nucleus, Ne was estimated at Ne = 15; a conservative estimate as main selections are introduced to the nucleus each generation. The main Ne was estimated at 150.

The genetic variation (σ^2_a) was reduced (1-F) each generation. This reduction was spread equally among and within families. This is an oversimplification but will suffice for this comparison. Inbreeding values (F) for each generation were calculated as (Falconer 1960, p. 62),

$$F_t = 1 / 2Ne + (1 - 1/Ne)F_{t-1} , \qquad (8)$$

where

F_t = inbreeding value in generation t, and

F_{t-1} = inbreeding value in generation t-1.

Inbreeding values for each generation were estimated as follows:

	Generation							
Inbreeding values	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
F for (1)	0	0.017	0.033	0.049	0.065	0.081	0.096	0.111
F for (2) and nucleus (4)	0	.033	.066	.097	.127	.156	.184	.211
F for (3)	0	.020	.040	.059	.078	.096	.114	.132
F for main (4)	0	.003	.007	.010	.013	.017	.020	.027

The initial variance components were set to $\sigma^2_a = 560$ and $\sigma^2_e = 2000$. Gain calculations assumed three progeny test sites of 30 individuals per family in single-tree plots for options 1 and 2, and no genotype-by-environmental interaction. The variance of full-sib family means would therefore equal $0.5\sigma^2_a + (0.5\ \sigma^2_a + \sigma^2_e)/n$, where n is the number of individuals per full-sib family. The within full-sib family variation would equal $0.5\ \sigma^2_a + \sigma^2_e$. Gains from family selection were estimated as $i\ 0.5\ \sigma^2_a / \sigma_p$, where σ_p is the square root of the variance of family means for family selection and the square root of the within-family variation for within-family selection. Gains for the half-sib families in option 4 required modifying the equations to represent 1/4 of the additive genetic variation being among families and 3/4 being within families. Total gains were calculated as the sum of the family and within-family gains (i.e., not index selection, but family and within-family selection). Gains for open-nucleus breeding were estimated by first calculating gains in the nucleus and main without accounting selections being moved between populations. Final gains were calculated by weighting the gains by the contribution each population made to the subsequent population; i.e., final gains for the nucleus were 27/30 of the nucleus gain plus 3/30 of the main gains. Cumulative gain over 8 generations was estimated as follows:

	Generation							
Options	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1	14.5	28.7	42.8	56.6	70.2	83.6	96.7	109.7
2	36.8	72.7	107.7	142.0	175.4	208.1	240.0	271.2
3	24.7	49.1	73.0	96.6	119.9	142.8	165.3	187.5
4 nucleus	34.6	68.3	99.6	128.8	156.3	182.2	206.7	230.0
4 main	16.2	33.2	50.9	69.1	87.7	106.6	125.8	145.0

In generation eight, a disease is devastating the Douglas-fir plantations of the Pacific Northwest. A single gene gives resistance, but it is at a low frequency in the population. Because of their relative large Ne, options 1 and 3 still have the gene in one of their subpopulations, but it was lost from option 2. In option 4, the gene is still in the main population but has been lost from the nucleus. Where does each breeding option stand?

Options 1 and 3 use the existing gene in the population and do not reduce gain.

Option 2 must go back to the wild and find the gene, thus reducing its gain by half.

Option 4 must go to the main for half of the gain for the next generation. Gain is therefore the average of the two.

The resulting estimated gains are as follows:

Option	**Gain**
1	109.7
2	135.6
3	187.5
4	187.5

Option 1 with no family selection is the big loser. If the disease had never come, it gave 40 percent of the option 2 gain and 57 percent of the option 3 gain. Even with the disease, it will produce only 81 percent of the option 2 gain. This points out the need for family selection; it is the major source of gain. If the gene had occurred by mutation in either the breeding population or plantations established from seed orchard seed, gain would be reduced by half the amount of improvement in the last generation, thus making option 2 the better choice because gain would be 255.6.

The choice between options 2 through 4 requires a study in risk management and is not addressed here. Questions that must be asked are What is the probability of a devastating disease? and At what frequencies would we find resistant genes? Option 4 is the highest cost and maximizes gain in the most severe case and is the second best in the no-disease scenario. Is the added cost worth the ensurance?

The risk of losing genes could have been reduced if option 2 had been the nucleus of a nucleus breeding program.

Glossary

Definitions come from various sources, including Falconer (1960), Wright (1962), and Snyder (1959).[1]

Additive genetic variation—The variation associated with the additive gene action effects. The additive gene action effects are those associated with offspring being like their parents. For example, the additive variance is the variation associated with regressing full-sib family means on the midparent value of the parents.

Alleles—Members of a series of genes producing different effects on the same developmental process. An allele (gene) is located at a particular locus (place on a chromosome). Because Douglas-fir has two of each chromosome, it has two alleles (genes) that affect the outcome of a trait at each locus.

Assortative mating designs—Mating designs that use the breeding value of a selection to determine with whom it will be mated. In positive assortative mating, the best individuals are mated together, thereby increasing the probability of producing a superior full-sib family. It also can mean that the number of times a selection is used in a crossing program is related to its breeding value.

Breeding population—The group of selections that will be crossed to produce offspring for the next generation of selection for a particular deployment zone.

Breeding group—Within the context of the NWTIC, this is a group of 20 to 30 selections that will be used to generate full-sib families. Selections within a breeding group are from the same geographic area; therefore, they are expected to have similar adaptational characteristics because, presumably, they have evolved under similar selection pressures. Breeding population crosses are made within breeding groups; therefore, breeding groups also serve as sublines.

Breeding value—The estimated genetic value of a selection. The breeding value for a parent is judged by the performance of its progeny. For open-pollinated families, the parental breeding value is calculated as twice the deviation of the progeny mean from the population mean. The value of the progeny is half due to the identified parent and half due to the population mean (for open-pollinated families), thus the need to multiply the deviation by two.

Breeding zone—A geographic-elevational subdivision of a local first-generation NWTIC cooperative program.

Clone—A group of plants derived from a single individual (ortet) by asexual reproduction (e.g., grafts or rooted cuttings). All members (ramets) of a clone have the same genotype.

Complementary mating design—A combination of mating designs, different designs for different objectives. The most common combination is a polycross (male or female testers) to estimate general combining abilities, combined with full-sib families planted either in replicated trials or family blocks to be used as the selection population.

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[1] Definitions also were obtained from the document "Northwest Tree Improvement Cooperative–BZERC Working Groug proposal for Restructuring the Molalla and Snow Peak Co-ops for a second-generation–Northern Oregon Cascades Tree Improvement Cooperative ("NOCTIC")." The document is available from Jess Daniels, Daniels and Associates, Inc., 1143 West Roanoke Street, Centralia, WA 98531-2023.

Deployment zone—The planting area (i.e., a set of planting environments) for which a landowner (or group of cooperators) chooses to develop a production population (e.g., a seed orchard).

Diallel mating design—A mating design in which a group of parents are crossed in every way possible. Modifications include half-diallels, where reciprocal crosses are ignored, and partial diallels which only have a subset of the crosses. Below is an example of a five-parent half-diallel (without selfs); the x's are created crosses:

	< - - - - - - Parent - - - - - - >				
Parent	**A**	**B**	**C**	**D**	**E**
A		x	x	x	x
B			x	x	x
C				x	x
D					x

Ecoregion—Within the context of the NWTIC, it is a subdivision of the range of coastal Douglas-fir, which is perceived to be significantly different from other such subdivisions in terms of overall climatic and ecological conditions influencing the general adaptational character or status of resident populations. Although there is genetic variation among populations within an ecoregion, the range of variation is expected to be much narrower within than among ecoregions. For example, the coastal areas of Oregon and Washington might be considered as one ecoregion.

Effective population size—The number of individuals that would give rise to the sampling variance or rate of inbreeding appropriate to the population and mating design being considered, if they were to randomly mate and contribute equal numbers of gametes (seed and pollen). For an overview of these concepts, see Caballero 1994. As an example, if 40 percent of the seed (and pollen) in an orchard seed lot came from each of two unrelated parents, and four other unrelated parents each contributed 5 percent of the seed (and pollen), the census number (N) would be 6, but the calculated effective population size (Ne) would be 3.

Elite populations—A subset of the breeding population, which is comprised of the best selections. Elite populations generally are used to accelerate breeding efforts by putting more resources into breeding the elite population relative to the larger breeding population (sometimes referred to as the **main population**).

Factorial mating design—A mating design in which one group of parents (selections) is used as females and another group is used as males. For example:

	< - - ♀ Parents - - >			
♂Parents	**A**	**B**	**C**	**D**
E	x	x	x	x
F	x	x	x	x
G	x	x	x	x
H	x	x	x	x
I	x	x	x	x

Full sibs—Trees with both parents in common.

General combining ability (GCA)—The average performance of parents in crosses. The GCA variation is associated with a full-sib family mean relative to the breeding values of its parents.

Gene resource population—All of the extant individuals of a species which might potentially be selected for inclusion in a breeding population.

Genetic diversity—In this paper, genetic diversity means the variation in a character that is associated with the different genotypes in a population.

Genotype—The genetic constitution of an individual (or clone) as determined by its genes.

Half sibs—Trees with one parent in common.

Heritability—The proportion of the observed variation associated with genetic factors; a measure of the relative degree to which a character is influenced by heredity as compared to environment; the ratio of genetic variation to phenotypic variation. The higher the heritability, the more an individual's phenotype (what it looks like) is indicative of its genotype (its genetic makeup).

Heritability of family means—The proportion of the variation of family means associated with genetic variation.

Interpopulation diversity—genetic diversity associated with the genetic variation among breeding zones (populations).

Intrapopulation diversity—Genetic diversity associated with the within-breeding zone genetic variation.

Linkage—The association of alleles from one generation to the next because they are located near one another on a chromosome.

Multiple populations—Groupings of the breeding population designed to maintain genetic diversity.

Nucleus mating design—A mating design that places more emphasis on an elite population.

Nucleus breeding—Nucleus breeding places more emphasis on the very best selections (the nucleus population [elite population]) by using two different mating and testing programs, one for the nucleus and one for the main (a larger, more genetically diverse population). The first nucleus-breeding program in forestry (Cotterill and others 1989) used an intensive control-pollinated mating design in the elite population and an open-pollinated mating design to breed the larger main population. Genetic variation was maintained in the elite population by bringing up the best selections from the main population every generation.

Panmixia—Panmixia means that any individual has an equal chance of mating with any other individual within the population; random mating.

Production population—A group of selections used to produce improved operational reforestation stock (e.g., seed orchard clones and clonal donor stock).

Random drift—The change in gene frequency resulting from sampling of small populations.

Specific combining ability—The part of the genetic variation that represents the variation associated with a full-sib family mean being different from the parental midparent value.

Sublining—Refers to the partitioning of the breeding population into unrelated groups (sublines). Unrelatedness across sublines is maintained generation-to-generation in the breeding population by only crossing within sublines. Production seed is produced by crossing among sublines, thus inbreeding depression cannot occur in the production of commercial seed because related individuals do not mate.

Johnson, Randy. 1998. Breeding design considerations for coastal Douglas-fir. Gen. Tech. Rep. PNW-GTR-411. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 34 p.

The basic principles of designing forest tree breeding programs are reviewed for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Pacific Northwest. Breeding populations are discussed given current and future breeding zone sizes and seed orchard designs. Seed orchard composition is discussed for potential genetic gain and maintaining genetic diversity in the forest. Mating and field testing designs are described and compared. Recommendations of the Breeding Zone Evaluation and Restructuring Cooperatives Working Group of the Northwest Tree Improvement Cooperative are presented.

Keywords: Douglas-fir, multiple populations, sublines, breeding population, gene resource populations, mating designs, selection, seed orchard.

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