UTILIZING GENETIC RESOURCES OF CONIFERS IN BRITISH COLUMBIA

D.T. Lester

RR 93001-HQ

R·E·S·E·A·R·C·H

REPORT

Internal Reports of the Ministry of Forests
Research Program

Ministry of Forests

Utilizing Genetic Resources of Conifers in British Columbia

D.T. Lester

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Research Program

1993

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This publication is RR 93001-HQ

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31 Bastion Square
Victoria, B.C.
V8W 3E7

Citation:

Lester, D.T. 1993. Utilizing genetic resources of conifers in British Columbia. B.C. Min. For., Victoria, B.C. Research Report 93001-HQ.

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SUMMARY

Genetic variation in the conifers of British Columbia is a legacy to be maintained and to be utilized. Genetic variation is being maintained through an extensive network of legally protected reserves and parks (a report on that network has been submitted to Ministry of Forests), and through frequent use of natural regeneration for harvested forests. Further maintenance is represented in the hundreds of thousands of trees in genetic test plantations.

Utilization of genetic variation for increased productivity and quality of wood, where tree planting is the chosen form of forest regeneration, is the focus of this report. Research on genetic variation and genetic improvement is in progress for 11 coniferous species. The oldest program has been in operation for over 30 years; the newest was initiated 5 years ago. Production goals for genetically improved seed, by species, range from more than 60 million to less than 2 million. Eighty-one seed orchards have been approved for establishment and most are currently in place.

This report describes the linkage between breeding and orchard development, and research results on provenance variation, inbreeding, and reproductive biology. The program for each species is reviewed in terms of elements that are common to all tree breeding programs. Expected timing of establishment, development, and full production is presented for each orchard, and average timing of major activities includes three generations of genetic improvement for each species.

Based on this review, seven recommendations are presented. They emphasize the need for clearer priorities in research on genetics and improvement of trees within the Ministry of Forests, the placement of tree improvement in a broader context of gene resource management, and the increased integration of activities to achieve genetic improvement of conifers in British Columbia.

PREFACE

This report summarizes programs for the utilization of genetic variation in the conifer species of major commercial importance in British Columbia. It provides an overview of activities and timelines in an integrated system of genetic improvement, from selection of parents to delivery of genetically improved seedlings for reforestation.

Although existing programs follow a similar general strategy of recurrent selection with production of genetically improved seed in wind-pollinated, soil-based seed orchards, technical details vary somewhat among species.

Each of the breeding programs and most of the supporting research efforts have been recently reviewed by peer committees. Most of the technical details, therefore, will be omitted and emphasis will be on a current view of program structure for each species through the third generation of breeding. Given the availability of peer review comments, the primary intent of this report is to illustrate the links between breeding and production of genetically improved seed, both in terms of timing and of technical complementarity.

ACKNOWLEDGEMENTS

Eighteen employees of private industry and the Ministry of Forests were interviewed in preparing this report. Particular appreciation goes to Maartin Albrecht who provided copious data and to Mike Crown from whose memory came many details.

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1 INTRODUCTION

Forest tree improvement has been described as being ‘‘applied when the control of parentage is combined with other forest management activities, such as site preparation and fertilization, to improve the overall yields and quality of products from forest lands’’ (Zobel and Talbert 1984). Increased production of wood products, whether through reduction in losses from pests and weather effects or through increased growth rate and wood quality, continues to provide the main justification for tree improvement. Changing social expectations for forests and forestry, however, require that tree improvement be assessed and presented in a broader context. Increased productivity through the application of genetic principles is more important than ever, given rising demands for wood products from a diminishing forest land base. At the same time, public concerns over biodiversity at the ecosystem level and genetic diversity at the level of species and forest stand require that the genetic implications of tree improvement are understood by those who choose to use the option.

Perhaps of equal importance is the need to educate those who are not knowledgeable in genetics about genetic implications of alternatives to tree improvement. The expanded public awareness of genetic issues in forestry also needs to be supplemented with an awareness of the relatively large base of information on genetic variation supporting most tree improvement programs.

Forest tree species are among the most genetically diverse organisms studied to date (see summary by Carlson and Yanchuk 1990). Based on the expectation that wide genetic diversity usually is associated with variable environments, the genetic variation observed in trees is not surprising. Each tree is stationary in an environment that changes within a day, within a year, and often between years — if not systematically over decades. In addition, most tree species are widely distributed geographically so that different populations are exposed to substantially different ranges of environmental variation. This is especially true in British Columbia where the combination of a vast geographic area and extensive mountain ranges presents a landscape of great variety.

Although there is much to be learned about the relationship between genetic variation in trees and their environments, the major activity in forest genetics and in tree breeding is field testing for the identification of genetic differences. Across British Columbia, hundreds of thousands of trees are being tested in plantations designed to estimate genetic effects. Among these plantations are many that are at least 20 years old. In this regard, geneticists working with forest trees bring much more information to issues of genetic resource management than do most other participants in the debate over how to manage genetic resources of forest organisms.

The extensiveness of genetic variation provides the basis for genetic improvement through seed source choices and breeding. Experimental plantations (provenance research) in British Columbia, in which trees are grown from seed collected in different parts of the species’ range, have demonstrated patterns of genetic variation associated with geography. For several species this has allowed the identification of geographic sources of seed that offer much improved growth rate (B.C. Ministry of Forests 1990) or, as in Sitka spruce, much reduced injury from pests (Ying 1991).

Where individual trees have been selected and tested by growing their progeny in experimental plantations, tree-to-tree genetic differences have been demonstrated (e.g., Yeh and Heaman 1987; Kiss and Yanchuk 1991). These differences provide the basis for culling seed orchards to leave only those parents with the most desired economic traits, and for choosing parents to cross for development of higher levels of genetic gain.

Recurrent cycles of testing and selection are expected to yield incremental genetic gains, by changing gene frequencies through emphasis on genes that favourably influence certain traits. Levels of genetic variation are high enough in most forest tree species that genetic gains should be substantial for several generations without creating populations at risk from reduced genetic variation.

Genetic variation provides the raw material for genetic gain, but tree improvement needs to be viewed in the larger context of total gene resources for each species being improved. One way of monitoring changes in genetic resources is to compile reforestation data in the format of Table 1A. This table at a glance, reveals the general potential impact of planned genetic changes in each seed planning zone. Of course, reforestation is rarely in a random pattern in time and space, so some additional consideration would need to be given to areas where reforestation is concentrated. Table 1B, a comparison of hectares reforested naturally or by planting, demonstrates the use of currently available data to show the potential relative impact of tree improvement by species and seed planning zone on the basis of reforested area. Data of this type are useful in planning how to maintain a wide array of genetic variation, mostly of unknown current value, as a basis for potential future changes in trait emphasis or environment.

Tree improvement programs can be a major part of the maintenance of genetic resources. Provenance research contributes by maintaining plantations from seed collections of very diverse origin; tree breeding programs contribute by maintaining genes (including those selected against in breeding programs) in clone archives and progeny tests. In addition, collections maintained by tree improvement programs can be integrated with the provincial system of protected wildlands to reduce the probability of loss of potentially important genes.

The identification of useful genetic variation is only the first step in achieving genetic improvement. Packaging and delivering genetic gain are additional elements that link selection to the realization of genetic benefits in practice. The several-step process includes seed orchard management, seed processing, nursery culture, planting stock allocation, and stand tending. For this report, only those elements up to nursery culture will be included.

TABLE 1. Formats for an inventory of deployment of genetic variation in reforestation by seed planning zone. Data are entered separately by species. A. Comprehensive format, data to be entered as hectares planted and hectares planted as a percentage of total area reforested using seed of the indicated origin. B. Data for 1991 summarized by species for four seed planning zones (data as defined above).

A.

Species:	**Reforestation method**									
Seed planning zone	**Natural seeding**		**Locally collected seed**		**Better provenances**		**Untested orchards**		**Tested orchards**	
	ha	**%**	**ha**	**%**	**ha**	**%**	**ha**	**%**	**ha**	**%**
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.										
.										

B.

Species	**Seed planning zone**							
	Okanagan Dry		**McGregor**		**Quesnel Lakes**		**West Kootenays**	
	ha (M)	**%**	**ha (M)**	**%**	**ha (M)**	**%**	**ha (M)**	**%**
Interior Douglas-fir	15.4	22	1.3	94	15.7	55	9.2	50
Western larch	1.0	48	0	0	0	0	2.0	59
Lodgepole pine	12.1	40	15.7	94	16.5	72	3.8	47
Interior spruce	10.5	70	68.7	93	88.5	82	23.2	65

2 DEVELOPING THE GENETIC RESOURCE

2.1 Breeding

Tree improvement began in British Columbia in the mid-1950's. It used a model of intensive selection in wild stands followed by collection of scions for the establishment of clonal seed orchards and clonal archives. The archives maintain selected genotypes, and provide the opportunity for crossing to produce seed needed in progeny testing. This model has been continued as species have been successively added to the list of those for which a formal breeding program was approved.

The principal changes in tactics have been the use of wind-pollinated seed for progeny testing of first-generation selections and the use of data from provenance testing showing that local populations do not always have the greatest potential for genetic gain. The acceptance of wind-pollinated progeny testing reflects evidence to date, both from British Columbia and elsewhere, that additive genetic variation is the predominant type of genetic variation in early generations of tree breeding. Additive genetic variation is the genetic variation measured by average performance of progeny after a parent is crossed with several other parents, and is the basis for genetic gain from wind-pollinated seed orchards.

Although selection of parents for a second generation of improvement has been completed only for coastal Douglas-fir, several programs are nearly ready to begin the formation of new populations from which second-generation parents will be taken. These new populations will require close control of pedigree and, as a result, mating designs for the production of control-pollinated progenies are planned. Recurrent selection for additive genetic variation, however, is the planned strategy for the next few generations.

At present, tree breeders are planning to make initial selections at an age of 5 or 6, years with a final validation of those selections at ages 10–12 years. While this is now common practice in tree breeding, the validity of selection at about ⅒ of rotation age remains controversial. Some of the oldest progeny tests will have to be measured at older ages to verify the relative development of progeny from parents that currently are the best.

The use of early selection, combined with great improvements in promotion of cone and pollen formation, suggests that one generation of tree breeding can be completed in about 15 years. With the expense and lag time to full productivity of seed orchards, establishment of a seed orchard for each breeding generation may not be reasonable. That issue has been addressed in a a separate report (Lester 1992).

2.2 Seed Orchards and Reproductive Biology

Knowledge and experience in seed orchard management, as in tree breeding, has grown rapidly over the nearly 30 years since the first orchard was established in British Columbia. On the positive side, the importance of warm, dry environments for cone initiation has been recognized and used to advantage, graft-compatible rootstock has been developed, regimes for maintaining the health of hundreds of thousands of grafted trees have been implemented, the morphology and phenology of receptivity have been described in detail, techniques for promotion of seed and pollen cones have been implemented, and a variety of alternatives to the traditional soil-based, wind-pollinated orchard are under consideration. Guidelines for pollen collection, processing, storage, and application have extended the alternatives available for increasing genetic value in orchard seed. The increasing availability of estimates of genetic value for specific orchard parents has been important in helping us re-think ways to enhance the genetic value of orchard seed.

On the negative side, it is clear that the seed orchards do not, and probably never will, meet the expectation of equal opportunity for mating among all parents. Large differences in production of seeds and pollen among parents mean that genetic gain is partly a function of how much each parent contributes to a given seedlot. The issue of imbalance in parental contributions strongly influences genetic diversity of orchard seed as well. Genetic contamination from pollen outside the orchard can represent another serious impact on genetic value of orchard seed. Proposals for ameliorating these problems seem feasible, but represent an added cost for orchard seed.

A shift in emphasis from increasing the quantity of orchard seed to improving its genetic quality is occurring where orchards are approaching expected production targets. A series of protocols with which to assess the genetic quality of orchard seed has been developed for the collection of data required to predict genetic gain. These protocols and the necessary calculations have been applied to the 1991 seed crop on the coast. It is expected that the system of rating for genetic quality, with some refinements, will be adopted for all orchards licensed under provincial policies for reforestation of Crown lands.

3 PROVENANCE RESEARCH

For several of the species, research on genetic variation associated with geographic origin (provenance) of seed has strongly influenced the structure of tree improvement. Those cases are noted in the discussion of specific breeding programs, below. In addition, provenance tests have provided genetically superior parents and identified provenances from which superior seed could be collected as an interim measure until seed orchards are productive. One view of provenance testing is that it provides the geographic framework within which genetic improvement is implemented.

Although most breeding programs are now implementing strategies that accommodate provenance variation, the need to continue monitoring existing provenance tests is compelling. For most species, provenance tests represent a broader range of genetic variation than progeny tests and most provenance tests of British Columbia conifers are appreciably older than progeny tests. For these reasons, provenance tests can validate the geographic structure imposed on progeny testing or sound an early warning of potential problems as tests age. In the latter case, the issue of climatic warming is especially relevant.

The larger range of genetic variation usually seen in provenance tests may be valuable in studies of the physiological basis of genetic superiority. In addition, provenance tests sample a wider range of environments than progeny tests, and therefore contribute useful information on provenance-by-environment interaction.

Responsibility for provenance research is distributed among several scientists in a variety of ways. A formal provenance program includes a large number of tests of wide-ranging bulked seed collections. In some breeding programs, the selection of several parents in each of many stands should allow detection of provenance effects if such effects are substantially larger than variation among progenies for individual trees. Short-term tests, including nursery testing and laboratory testing in controlled environments, are being conducted to provide quick and often inexpensive, identification of patterns of genetic variation associated with geography.

An increasing commitment of provenance research in hardwoods promises to provide basic information on genetic variation, which will be valuable in assessing genetic resources and in structuring breeding programs if such programs are developed.

4 IMPROVEMENT PROGRAMS BY SPECIES

4.1 General Format

Each tree species has a biology and genetic architecture that is unique, and each is found in a somewhat different range of environments. The history of breeding program development likewise varies from the early concentration on coastal Douglas-fir in the late 1950's to initial breeding efforts with Sitka spruce in the 1990's. Seedling demand for a given species also varies with time.

Despite these differences, several issues are common to nearly all tree breeding programs. These issues are grouped under the headings of "Genetic Resources," "Breeding Strategy," and "Genetic Benefits." Concerns over improvement plans for specific species are noted following the description of each program. Recommendations and comments more generally applicable to tree improvement in British Columbia, as a whole, are presented in a separate section.

Species differences also extend to the timing of seed orchard development. In some cases, orchards were established without the assurance that there would ever be a supporting breeding program. More recently, orchard establishment has been delayed until early progeny test results are available and only the better parents will be included in an orchard. Over the time scale of three generations of improvement, however, most of these variations in program initiation tend to be reduced as the cyclical pattern of selection becomes apparent.

For this report, all first-generation orchards are presented on a timeline that anticipates a period of orchard development leading to seed production at the level for which the orchard was designed. The lag period before full production varies by species, being 6 years for yellow cypress and 16 years for western larch (Appendix 1). This variation represents biological differences between species, as well as the state of knowledge about cone induction. No accommodation is made for the possible influence of different orchard sites on the speed with which full production is reached. The total lifetime of a given orchard is arbitrarily chosen to be 20 years beyond the date when full production is expected. The decision to phase out an orchard will relate to its demonstrated productivity, availability of a higher level of genetic improvement, seed demand, and, presumably, the balance of these elements with cost considerations.

To illustrate relationships between breeding and seed production, activities of a typical program are presented on a timeline that includes three generations. The timelines for existing first-generation orchards compared with those of the typical orchard will provide a sense of the variation around a schedule of typical activities.

4.2 Interior Spruce (*Picea glauca*, *P. engelmannii*, *P. sitchensis*, and hybrids)

Planting is expected to be the principal means of regeneration for interior spruce. Up to 90 million seedlings are planted annually, making interior spruce the most commonly planted "species" in the province. Planned production of orchard seed will provide the major part of anticipated seed needs (Tables 2 and 3). Seed with significantly improved genetic potential, however, will not be available in substantial quantities until after 1994 (Table 2).

The area of interest for planting of interior spruce covers about 8° of latitude and 1500 m of elevation. Although provincial seed planning zones have been mostly followed in structuring the breeding and orchard programs to date, progeny test and clonebank results suggest that interior spruce may possess a flexibility that will allow substantial movement of parents from their geographic origin.

Tree breeding in interior spruce was initiated in 1968. The first series of parent-tree selections was made in the late 1960's and progeny testing was under way in the early 1970's. A second series of selections was made in the early 1980's and testing of their progeny began in 1984.

Seed orchards were first established in 1980 with the objective of securing a reliable seed supply that was geographically representative. Genetic improvement was not a substantial expectation because opportunities for intense selection were rare in forests containing spruce. Progeny testing was not planned. Table 2 lists 10 orchards that are existing first-generation orchards. Their design probably precludes roguing of more than 50% of parents based on progeny testing. They are providing substantial quantities of seed, as well as staff experience in spruce orchard management. A second list of orchards (Table 3) includes those that will be rogued to 50% of the original parents before trees are established in an orchard. An additional roguing to about 25% of the original population will use data from progeny tests at an older age.

TABLE 2. First-generation seed orchards of interior spruce by seed planning zone with timelines and annual projected yield of seedlings from orchard seed at full production after roguing at about 50%

Seed planning zone	Orchard number	Year 1980 1990 2000 2010 2020 2030 2040	Seedling numbers[a] (M)
Central Plateau (Low)	205	: +++++∗∗∗∗∗∗∗∗∗∗[b]	2.1
Central Plateau (High)	206	: +++++∗∗∗∗∗∗∗∗∗∗	1.7
West Kootenay (Low)	301	: +++++∗∗∗∗∗∗∗∗∗∗	2.5
West Kootenay (High)	302	: +++++∗∗∗∗∗∗∗∗∗∗	3.1
Bulkley Valley (Low)	207	: +++++∗∗∗∗∗∗∗∗∗∗	1.5
Bulkley Valley (High)	208	: +++++∗∗∗∗∗∗∗∗∗∗	1.7
Quesnel Lakes	209	: +++++∗∗∗∗∗∗∗∗∗∗	2.1
Shuswap/Adams (Low)	305	: +++++∗∗∗∗∗∗∗∗∗∗	1.3
Shuswap/Adams (High)	306	: +++++∗∗∗∗∗∗∗∗∗∗	1.3
Thompson/Okanagan	303	: +++++∗∗∗∗∗∗∗∗∗∗	3.6

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg (400 000), and plantable seedlings per seed (0.65).

[b] : = planting; + = developing; ∗ = at targeted production. (Each denotation equals a 2-year period.)

TABLE 3. First-generation seed orchards of interior spruce by seed planning zone with timelines and annual projected yield of seedlings from orchard seed at full production after roguing at about 75%

Seed planning zone	Orchard number	Selection unit	Year 1980 1990 2000 2010 2020 2030	Seedling numbers[a] (M)
North Central	217	Prince George/Smithers	: +++++∗∗∗∗∗∗∗∗∗∗[b]	2.1
Mica East	304	East Kootenay	: +++++∗∗∗∗∗∗∗∗∗∗	5.2
Bowron Lakes	214	Prince George	: +++++∗∗∗∗∗∗∗∗∗∗	11.3
Nass/Skeena	229	Smithers/Prince George	: +++++∗∗∗∗∗∗∗∗∗∗	2.2
Finlay	210	Finlay	: +++++∗∗∗∗∗∗∗∗∗∗	9.1
McGregor	211	McGregor	: +++++∗∗∗∗∗∗∗∗∗∗	6.5
Hudson Hope	212	Hudson Hope	: +++++∗∗∗∗∗∗∗∗∗∗	7.8
Mt. Robson	213	Mt. Robson	: +++++∗∗∗∗∗∗∗∗∗∗	0.7

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg (400 000), and plantable seedlings per seed (0.65).

[b] : = planting; + = developing; ∗ = at targeted production. (Each denotation equals a 2-year period.)

In the early 1980’s, it was decided that all subsequent spruce orchards would be progeny tested. With that decision, the breeding program provided tested parents for several orchards to represent the areas included in progeny testing of the earliest selections and, in addition, initiated testing of selections from four additional seed planning zones.

The breeding plan for interior spruce applies recurrent cycles of selection and testing (at about 20-year intervals) to populations that largely represent existing seed orchard planning zones.[1] Initial population sizes range from about 130 to over 200 parents. While these populations are smaller than the average for most other species, the apparent ability of interior spruce to grow well in a range of environments probably will allow an increase in population sizes through combinations of parents from different zones. The timing of general activities through three generations of selection and orchard development is shown in Table 4.

TABLE 4. Generic breeding and seed production cycles for interior spruce and lodgepole pine

INTERIOR SPRUCE

```
                                    Year
Generation         1980 1990 2000 2010 2020 2030 2040 2050

                                                PPPPPPPPPP[a]
     3                                    DDDDDD
                                         SS
                                   TTTTTTT
                                  CC

                                       PPPPPPPPPP
                                 DDDDDD
     2                          SS
                          TTTTTTT
                         CC

                              PPPPPPPPPP
                        DDDDDD
     1                 SS
                TTTTTTTT
              SSS
```

LODGEPOLE PINE

```
                                    Year
Generation         1980 1990 2000 2010 2020 2030 2040 2050

                                               PPPPPPPPPP
                                        DDDDDDD
     3                                 SS
                                    TTTT
                                  CC

                                 SS
     2                        TTTT
                            CC

                                   PPPPPPPPPP
                            DDDDDDD
     1                     SS
                        TTTT
              SSSSSSS
```

[a] S = selection and grafting; T = progeny testing; C = crossing of new selections; D = developing orchard; P = orchard producing at targeted levels.

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[1] Kiss, G.K. 1991. Interior spruce breeding program in British Columbia. Unpubl. man. 15 p.

The following elements of a typical breeding plan apply to interior spruce:

Genetic resources

Levels of intensity for tree improvement: Multi-generational breeding is planned for all seed orchard planning zones where tree improvement is practised.

Role of provenance research: Results from extensive transfer of grafts and seedlings of interior spruce across several degrees of latitude suggest that spruce genotypes will grow over a wide range within southern and central British Columbia. Genetic differentiation associated with elevation, however, is more obvious and elevation transfers are more restricted, especially in northern parts of the region (B.C. Ministry of Forests, undated). Existing formal provenance studies are limited and no new studies are planned.

Population management: The proposed strategy for the generation of new populations for selection calls for mating in a series of 4 × 4 disconnected diallels. The proportion of selected families will be 50% for breeding populations and 25% for orchard populations combined with selection of the best tree in 100 within families. The implications of this strategy, as applied to populations currently available within seed planning zones for interior spruce, are outlined in Appendix 2A.

Availability of new genetic material: The success of spruce grafts and seedlings planted across several degrees of latitude suggests that a wide range of material not currently integral to each breeding population may be available for future breeding. In addition, the promising performance of white spruce from eastern Canada may provide a much larger gene resource and some genes from Sitka spruce could be useful in some areas.

Breeding strategy

Traits: Major emphasis is on volume and resistance or tolerance to spruce weevil. Relative density of wood may be important. Evidence for a genetic relationship between diameter and relative density is ambiguous at present.

Early testing: Phenotypic correlations indicate generally stable relative performance for height between ages 6 and 15. Decisions on genetic worth of progenies for growth traits could be made at age 10, but response to spruce weevil infestation may require waiting until age 15. Initial results show that early rapid height growth is associated with reduced weevil injury, and validation of that relationship may allow earlier selection. Early testing of growth rate in ‘‘farm field’’ environments is planned.

Cone enhancement: An anticipated breeding cycle of 20 years assumes that advanced generation parents, selected at 10–15 years of age, will be capable of sexual reproduction. Research to assure that capability may be required.

Effects of partial inbreeding: Parents with the necessary relatedness to produce a series of progenies with different degrees of inbreeding are currently unavailable. They may be produced as a by-product of recent controlled crosses. No plan for initiating partial inbreeding studies is available.

Impact of new technology: Implementation of the indicated breeding cycle may depend on whether techniques for early identification of weevil resistance or tolerance can be achieved. Early testing using caged weevils, for example, may be useful in shortening the breeding cycle. Somatic embryogenesis or rooted cuttings may be appropriate for producing planting stock for areas where intensive silviculture is to be practised. The breeding plan does not specifically address breeding for vegetative propagation.

Genetic benefits

Predicted gains: Following the strategy of selection and breeding outlined in the breeding plan,[2] genetic gains in height at age 15 can be predicted (Appendix 3A). With a multiplier of 2 to transform height to volume and an age:age correlation of 0.3 (Lambeth 1980) for selection at an age of 10 years and harvest at an age of 110 years, average predicted genetic gains in volume at harvest are about 11% per improve-

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[2] Kiss, G.K. 1991. Interior spruce breeding program in British Columbia. Unpubl. man. 15 p.

ment cycle. This estimate assumes that the improved trees perform relatively the same in all environments where they are planted (i.e., there is no genotype by environment interaction).

Validation of predicted gains: Seedlots representing operational seed collections (checklots) are not included in progeny tests. Plantings — including crosses among the best parents, orchard seedlots, and bulked wild stand seed collections — are planned in a row-plot design to demonstrate genetic improvement and in a design of 100-tree square plots to estimate area yields. Plantings are scheduled for 1994. No studies address issues of the interaction of silvicultural practice and genetic improvement.

Timing of improved seed production: The impact of the tree improvement program on seedling supply is dramatic: seedling production is projected at 16 million for 1992, 29 million for 2000, and 66 million for the year 2010 using estimates of seed production for developing orchards (Appendix 1). Anticipated production of improved seedlings represents about one-third of estimated total seedling needs for planting in the year 2000 (82 million). The year 2010 is the last scheduled year of seed production for several orchards (Table 2), so either orchard life will have to be extended or new orchards must be in place if the supply of improved seedlings is to continue at the indicated level.

Comments

- The assumption that interior spruce is very broadly adapted is central to present and future breeding plans. A continued validation of that assumption through longer-term assessment of a subset of progeny tests is desirable. A recently established test of crosses among the most promising parents in each of several geographically different populations is represented across a wide range of environments. This test will contribute to questions of transferability of spruce parents between orchard planning zones.
- Flexibility in moving parents between seed planning zones offers large advantages in structuring breeding and orchard populations. Exercise of that flexibility, however, has potential implications for genetic diversity. A system is needed for tracking where specific genotypes are being used and the degree to which that use influences genetic diversity.
- Application of the stated mating and selection strategy with the apparent numbers of parents available in several seed planning zones leads to reductions in population size that are unacceptable under current recommended provincial guidelines for genetic diversity.

4.3 Lodgepole Pine (*Pinus contorta* var. *latifolia*)

Although natural regeneration is more easily achieved for lodgepole pine than for most commercial conifers of British Columbia, demand for planting stock remains high, with up to 70 million seedlings planted annually. At full production, orchard seed is expected to be available for most seedling demands in areas where a tree improvement program is available.

The area represented by lodgepole pine breeding programs is similar to that for interior spruce. The exceptions are the higher elevations, the southeastern seed planning zones of the Kootenays, Mica, and Bush, and the submaritime area of Skeena/Nass.

Tree breeding for lodgepole pine was initiated in 1975, with wild stand selections representing four geographic areas in central British Columbia.[3] Progeny testing was intended to be with progenies generated by controlled crossing on grafted parents and orchard establishment was to be delayed until progeny-tested parents could be included. The absence of pollen on grafted parents led to the collection of wind-pollinated seed from as many of the early selections as possible, and progeny testing was initiated in the mid-1980’s. Additional selections, especially in the southern part of the province, were added to the total program as well. Initial breeding populations range from 250 to 300 selections, with about one-half from within a seed planning zone and about one-half from other areas including those represented in provenance tests. The apparent ability of superior provenances and progenies to grow well in a variety of environments suggests that some current breeding populations may be combined in the future.

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[3] Carlson, M. and J. Murphy. 1986. Lodgepole pine breeding plan. B.C. Min. For., Victoria, B.C. Unpubl. man. 33 p.

First-generation seed orchards for lodgepole pine are of three types. Four early orchards (Table 5) were established with untested parents selected for tree breeding in Sweden. These are considered to be interim sources of seed and will have minimal opportunities for upgrading based on progeny testing. A second category is represented by selections made in a large provenance-progeny test at Prince George. It is expected that individuals selected from the better progenies within the better provenances will offer opportunities for genetic gains sooner than the conventionally tested orchards. Because several assumptions underlie this approach, these orchards were designed to provide only about 25% of the seed needed for reforestation in each planning zone. The balance of the required seed will come from progeny-tested parents selected in a given planning zone and in adjacent zones. Table 6 shows the orchard planning zones and targets for seedling production from each of the ‘‘progeny-tested’’ orchards.

The timing of tree improvement activities through three generations for a typical orchard planning zone is shown in Table 4.

The following elements of a typical breeding plan apply to lodgepole pine:

Genetic Resources

Levels of intensity for genetic improvement: Advanced-generation breeding and orchard development are planned for 7 of the 16 seed planning zones where lodgepole pine is planted. For the remaining zones, local seed or seed from provenances that have shown outstanding growth across representative environments is recommended.

Role of provenance research: An unusually comprehensive network of provenance tests has provided the basis for identification of certain areas that produce seed with superior genetic potential for growth. This information has been used for wild stand seed collection and development of seed transfer guidelines, for the structuring of the breeding program, and for the selection of seed orchards and breeding populations.

Population management: The proposed strategy for generation of new populations specifies mating in 3×3 disconnected factorials. Unpublished revisions in the breeding plan, including reduced intensity of family selection and acceptance of some inbreeding in the third breeding cycle, will allow the production of seed orchards with sufficient parents to meet current guidelines for minimum effective population size. Alternatively, information from progeny tests may allow some breeding zones to be combined to increase population size while maintaining higher intensities of selection and preventing inbreeding. Appendix 2B illustrates the plan for population management.

Availability of new genetic material: The apparent flexibility of lodgepole pine may make accessible much of the gene pool present in the species in south and central British Columbia. Gene resources from outside that area are not of great promise at present. The range-wide collection of provenances available in an extensive network of provenance tests could provide ‘‘exotic’’ germplasm if required.

Breeding Strategy

Traits: Total height will be the principal trait used in selection. Relative density of wood may be used in a second-stage selection.

Early testing: Roguing is planned in two stages for orchards. At a progeny-test age of 5 years, 30% of the parents represented will be included in orchards and 50% will be included in the breeding population. In a second roguing, an additional 50% of the orchard parents will be removed, based on measurements of progeny at age 10 years. Early testing in ‘‘farm-field’’ environments is in progress.

Cone enhancement: Initial attempts have not been promising and no work is currently planned.

Effects of partial inbreeding: Initial crosses have been made and completion of the mating design awaits reproductive maturity in controlled crosses.

Impact of new technology: None is foreseen.

TABLE 5. First-generation seed orchards of lodgepole pine by seed planning zone with timelines and annual projected yield of seedlings from orchard seed at full production after minimal roguing. These orchards are scheduled for roguing of the worst parents only, based on 5-year progeny performance.

Seed planning zone	Orchard number	Year	Seedling numbers[a] (M)
		1970 1980 1990 2000 2010 2020 2030 2040	
Omineca/Pinchi	201[b]	: ++++++**********[c]	1.3[d]
Dawson/Peace	202[b]	: ++++++**********	0.3[d]
Willow/Bowron	203	: ++++++**********	0.7[d]
Smithers (Bulkley)	204	: ++++++**********	0.8[d]
Nass/Skeena	230	: ++++++**********	2.6[e]

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg (270 000), and plantable seedlings per seed (0.65).
[b] Numbers 201 and 202 may be combined.
[c] : = planting; + = developing; * = at targeted production. (Each denotation equals a 2-year period.)
[d] Seedling numbers are estimated on the basis of 50% roguing, which is higher than planned.
[e] No progeny testing is planned for this orchard.

TABLE 6. First-generation seed orchards of lodgepole pine by seed planning zone with timelines and annual projected yield of seedlings from orchard seed at full production after roguing at about 75%

Seed planning zone	Orchard number	Type	Year	Seedling numbers[a] (M)
			1980 1990 2000 2010 2020 2030 2040	
Bulkley Valley	228	1.75[b]	: ++++++**********[c]	3.1
	219	1.50[d]	: ++++++**********	10.5
Central Plateau/Finlay	223	1.75	: ++++++**********	2.0
	218	1.50	: ++++++**********	8.4
Finlay	224	1.50	: ++++++**********	3.8
Shuswap/Adams	307	1.75	: ++++++**********	2.6
	313[e]	1.50	: ++++++**********	1.9
	314	1.50	: ++++++**********	0.4
Thompson/Okanagan	308	1.75	: ++++++**********	2.3
	310[f]	1.50	: ++++++**********	3.8
	311	1.50	: ++++++**********	2.0
	312	1.50	: ++++++**********	0.4
Willow/Bowron	220	1.75	: ++++**********	2.8
	222	1.50	: ++++++**********	4.2

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg (270 000), and plantable seedlings per seed (0.65).
[b] 1.75 identifies orchards as containing parents selected from an existing provenance-family test plantation. Total genetic gain should include gain from family selection and within-family (forward) selection.
[c] : = planting; + = developing; * = at targeted production. (Each denotation equals a 2-year period.)
[d] 1.5 identifies orchards as containing parents based on performance of their progeny (backward selection).
[e] Numbers 313 and 314 may be combined.
[f] Numbers 310, 311, and 312 may be combined.

Genetic Benefits

Predicted gain: Following a strategy of selection and breeding modified from the breeding plan (M. Carlson, pers. comm., Jan. 1992) , predicted genetic gains in height are shown in Appendix 3B. Using a multiplier of 2 to transform height to volume and an age:age correlation of 0.25 (Lambeth 1980) for selection at an age of 6 years with harvest at an age of 70 years, average predicted genetic gains in volume at harvest are about 6% per improvement cycle. This estimate assumes that the improved trees perform relatively the same in all environments where they are planted (no genotype by environment interaction). Interaction has been detected in some orchard planning zones (M. Carlson, pers. comm., March 1992) and the gain estimate here is thus inflated by the extent of interaction.

Validation of predicted gain: Several unimproved seedlots from collections used in operational reforestation have been included in progeny tests. Single-pair crosses have been made among parents in the top 20% of each of two seed planning zones to represent seed from rogued orchards. These crosses will be compared with several unimproved seedlots from collections for operational reforestation. Row plots for demonstration and block plots for area yield estimation are scheduled for planting in 1994. Block plots will be planted in configurations to allow comparison of large, small-row, and single-tree plots. Interactions of genotype with planting stock type and spacing are being tested.

Timing of improved seed production: Expected seed production will result in 13 million seedlings in the year 2000 and 53 million in 2010. This production represents about 20% and 80% of anticipated total seedling demand, respectively. The estimates are conservative because roguing cannot be as heavy as planned for orchards 201 and 202.

Comments

- Flexibility in moving parents between seed planning zones offers large advantages in structuring breeding and orchard populations. Exercise of that flexibility, however, has potential implications for population size and genetic diversity. A system of tracking where specific genotypes are being used and the degree to which that use influences genetic diversity is needed.

4.4 Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca)*

Interior Douglas-fir is the third component of the spruce-pine-fir lumber market of interior British Columbia. The area of interest for planting is the southeastern one-quarter of the province where Douglas-fir is a component of the Interior Cedar−Hemlock, and Montane Spruce biogeoclimatic zones. About 8 million trees are expected to be planted annually by the year 2010.

The breeding program was initiated in 1982.[4] Selection in eight seed planning zones has been followed by prompt initiation of wind-pollinated progeny testing. Seed orchards are to be established with progeny-tested parents only. The schedule for establishing seed orchards is shown in Table 7.

The timing of general activities through three generations of selection and seed orchard development for a typical program are shown in Table 8. A breeding cycle of about 15 years is anticipated, with initial selection at age 6 years and validation at age 10 years.

Genetic Resources

Levels of intensity for tree improvement: Multi-generational breeding is planned for five seed planning zones. For the Central Plateau, McGregor, and East Kootenay zones, tree improvement will probably culminate with an untested seed orchard developed from selections within first-generation progeny tests.

Role of provenance research: There has been no comprehensive provenance testing of interior Douglas-fir in interior British Columbia, although the selection of several parent trees in each stand will provide an estimate of regional provenance effects in progeny test results. Interior provenances represented in tests in

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[4] Jaquish, B.C. 1984. Breeding strategy for Douglas-fir in the British Columbia interior. B.C. Min. For., Victoria, B.C. Unpubl. man. 27 p.

central Canada and Europe have shown substantial provenance variation and generally superior performance from provenances in the "wet belt" of interior British Columbia. Extensive provenance research in the U.S Rocky Mountains suggests that Douglas-fir is closely adapted to local environments where elevational gradients are steep (Rehfeldt 1984). Seed collections in the province have been made to test elevation effects, but no plans are in place to initiate such tests. Some evidence for elevational effects is present in progeny test data.

TABLE 7. First-generation seed orchards of interior Douglas-fir by seed planning zone with timelines and annual projected yield of seedlings from orchard seed at full production after roguing at about 75%

Seed planning zone	Orchard number	Year 1980 1990 2000 2010 2020 2030 2040	Seedling numbers[a] (M)
Central Plateau	225	:+++++**********[b]	0.7
Cariboo Transition	226	:+++++**********	0.6
Shuswap/	321[c]	:+++++**********	0.8
Adams	322	:+++++**********	0.8
West Kootenay (Low)	323	:+++++**********	0.4
West Kootenay (High)	324	:+++++**********	0.7
Mt. Robson	227	:+++++**********	0.1
Mica (Low)	329[d]	:+++++**********	0.5
Mica (High)	330	:+++++**********	0.3
East Kootenay	331	:+++++**********	0.2

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg (86 400), and plantable seedlings per seed (0.65).

[b] : = planting; + = developing; * = at targeted production. (Each denotation equals a 2-year period.)

[c] Numbers 321 and 322 may be combined.

[d] Numbers 329 and 330 may be combined.

The one major provenance experiment with Douglas-fir in interior British Columbia has yielded exceptionally interesting results. If maintained, the early vigour (age 15 years) of provenances from the zone of transition between Coast and Interior will have a major influence on strategy of the breeding program. Support for the usefulness of genes from the transition zone comes from performance of coast-interior hybrids (Rehfeldt 1984), and from performance of transition-zone checklots included in progeny tests (B. Jaquish, pers. comm., 1992).

Population management: The proposed strategy for generation of new populations specifies mating in 3 × 3 disconnected factorials. If the standards of selection remain at 50% of selected parents to be advanced to the next breeding population and 25% of selected parents to be used in the next seed orchard — and if selections are to be unrelated — seed orchards acceptable by current standards of population size cannot be formed after the second generation unless parents from different seed planning zones are combined. Appendix 2B illustrates the calculations. To circumvent the apparent problem, it is planned that populations will be increased by pooling parents from different seed planning zones.

Availability of new material: The expectation that interior Douglas-fir shows relatively strong adaptation to local environment led to the breeding program being structured strictly along the lines of seed planning zones, although a few non-local progenies have been included. From this design, it may not be clear whether exchanges of superior parents are advisable.

The current focus for new genetic material is on genes from the coast-interior transition or even from coastal trees. Initial crosses of interior and transition parents have been made to test performance of pedigreed material in the Interior. The areas expected to be most suitable for coast × interior hybrids would be lower-elevation (milder) sites of southern British Columbia.

TABLE 8. Generic breeding and seed production cycles for interior Douglas-fir and western larch

Interior Douglas-fir

Generation	Year							
	1980	1990	2000	2010	2020	2030	2040	2050
						PPP	PPPPP	PP[a]
					DDDDD	DD		
3				SS				
				TTTT				
			C	C				
			SS					
2			TTTT					
		C	C					
				PPPP	PPPPP	PP		
		D	DDDDD	D				
1		SS						
	TT	TT						
	SS							

Western Larch

Generation	Year							
	1980	1990	2000	2010	2020	2030	2040	2050
								PPPP
						DDDD	DDDDD	
3					S	S		
					TTTT			
					CC (?)			
						PPP	PPPPP	PP
				DD	DDDDD	DD		
2				SS				
			TT	TT				
			CC					
				PPPP	PPPPP	P		
		DDD	DDDDD	D				
1			SS					
		TT	TT					
		SSSS						

[a] S = selection and grafting; T = progeny testing; C = crossing of new selections; D = developing orchard; P = orchard producing at targeted levels.

Breeding Strategy

Traits: Initial selection will emphasize height in traditional progeny tests, plus information on growth rhythm from ‘‘farm-field’’ tests. Selection will be for stem volume when orchards are rogued at a progeny-test age of about 10 years. Relative density of wild-stand parents will be used in selection for parents in first-generation orchards and in crossing for second-generation breeding populations.

Early testing: ‘‘Farm-field’’ testing, including measurements of growth rhythm, is in progress. There are no older tests from which to estimate age:age correlations.

Cone enhancement: No research is in progress or planned. It is expected that extensive experience with coastal Douglas-fir will apply to interior Douglas-fir.

Effects of partial inbreeding: There are no materials with which to initiate a study of partial inbreeding and it will be several years before materials become available.

Impact of new technology: Minimal impact is foreseen, although wide implementation of machine stress rating could dramatically increase emphasis on relative density. Advances in resistance to insects and root diseases could influence tree improvement planning.

Genetic Benefits

Predicted gain: Following the strategy of selection and breeding outlined in the breeding plan,[5] predicted genetic gains in height at age 6 are shown in Appendix 3C. Based on a multiplier of 2 to transform height to volume and an age:age correlation of 0.33 (Lambeth 1980) for selection at an age of 6 years with harvest at an age of 60 years, average predicted genetic gains in volume at harvest are about 12% per improvement cycle. This estimate assumes that the improved trees perform relatively the same in all environments where they are planted (no genotype by environment interaction). This estimate should be applied only to low-elevation sites because data from some progeny testing shows changed rankings of parents (interaction) at higher elevations (B. Jaquish, pers. comm., March 1992).

Validation of predicted gain: Checklots from seed collections for operational reforestation have been included in progeny tests. Row plots and block plots to validate genetic differences between crosses among better families and seedlings from wild-stand seed collections will be planted in 1995. Block plots will be configured to allow comparison of progeny-test plots (4-tree row) and larger plots.

Timing of improved seed production: By the year 2000, orchards are expected to produce seed for 1.2 million seedlings (15% of demand) and by 2010 (at full targeted production), 5.1 million seedlings (60% of demand).

Comments

- Based on available evidence of geographic variation, the improvement program for interior Douglas-fir is appropriately the most conservatively structured of British Columbia programs. Unless demand for planting stock increases substantially, however, mutually exclusive breeding efforts for 10 seed planning zones results in traditional seed orchards of 1 ha or less. Contiguous orchards would allow for economies of scale while compromising the genetic integrity of individual orchards. Alternatives to the traditional orchards should be considered. Expanded testing of the degree to which parents from different seed planning zones can be combined might alleviate the problems of scale in the program.
- Extension of the stated breeding strategy does not allow an acceptable seed orchard to be produced beyond the second generation. The proposed solution is to add parents from different breeding zones.

4.5 Western Larch (*Larix occidentalis*)

Western larch is of increasing interest for reforestation in southern British Columbia. Rapid growth, high relative wood density, and relatively low susceptibility to root diseases are factors in the choice of larch planting stock. Lack of seed supply from wild stands, however, limits availability for planting as well as for natural regeneration, especially in milder areas of the West Kootenay and Shuswap-Adams zones.

Tree improvement efforts will be concentrated on the southeastern corner of the province, although there is interest in the potential of western larch north of its native range. The two seed planning zones of most interest are the East and West Kootenays.

Tree breeding was initiated for western larch in 1987 with wild-stand selections in four seed planning zones.[6] Selection is continuing and the formation of initial breeding populations with 250–300 parents is expected to be completed within the next few years. Central to the structure of the breeding program is the

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[5] Jaquish, B.C. 1984. Breeding strategy for Douglas-fir in the British Columbia interior. B.C. Min. For., Victoria, B.C. Unpubl. man. 27 p.

[6] Jaquish, B.C. 1987. A breeding plan for western larch (*Larix occidentalis* Nutt.) in British Columbia. B.C. Min. For., Victoria, B.C. Unpubl. man. 31 p.

view that larch does not exhibit strong local adaptation (Rehfeldt 1984). The East Kootenay and West Kootenay seed planning zones, however, are considered different enough (based on field tests in the U.S. and early observations in British Columbia tests) to warrant development of separate breeding programs.

First-generation seed orchards were established in 1990 with about one-half of the parents expected to form initial breeding populations (Table 9). Progeny tests have been established for all orchard parents from the East Kootenays, and all orchard parents from the West Kootenays will be under test by 1993.

The timing of tree improvement activities through three generations is illustrated in Table 8. Uncertainty about the period required before reproductive maturity in larch results in a somewhat longer tree improvement cycle than for other species.

TABLE 9. First-generation seed orchards of western larch by seed planning zone with timelines and annual projected yield of seedlings from orchard seed at full production after roguing at about 75%

Seed planning zone	**Orchard number**	**Year** **1980 1990 2000 2010 2020 2030 2040**	**Seedling numbers[a] (M)**
West Kootenay	332	: + + + + + + + * * * * * * * * * *[b]	1.1[c]
East Kootenay	333	: + + + + + + + * * * * * * * * * *	1.8

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg (86 400), and plantable seedlings per seed (0.65).

[b] : = planted; + = developing; * = at targeted production. (Each denotation equals a 2-year period.)

[c] Includes seed for high and low elevations in West Kootenay and Shuswap-Adams zones.

The following elements of a typical breeding plan apply to western larch:

Genetic Resources

Levels of intensity: A multi-generational breeding program is planned for two seed planning zones, with distribution of seed from the West Kootenay zone to two adjacent zones. Seed production areas for an interim supply of seed have been established over the last 30 years but have not been productive to date. Establishment of seed orchards before all parents have been selected reflects the focus on seed production.

Role of provenance research: One range-wide provenance test has been established. Some provenance information for the seed planning zones of interest will be provided from progeny-test data as a consequence of the selection of several parents from each sampled stand. Seed for range-wide provenance testing is available, but financial resources are needed to initiate testing. Elevation of seed origin is not considered to be an important variable because the species distribution is limited to a relatively narrow range of elevations and seed transfer guidelines are relatively broad.

Population management: In the mid-1990's, 3 × 3 disconnected factorial crosses are to be used in progeny tests to provide material for advanced-generation selection. If the breeding plan is similar to that of interior Douglas-fir, details of population management will be similar to those shown in Appendix 2B.

Availability of new material: The most likely source of new material will be the Inland Empire Tree Improvement Cooperative. The apparent ability of superior larch families to grow well in a variety of environments may allow substantial exchanges of genotypes between programs. Seed from U.S. parents has been obtained along with data from early testing. Such exchanges may provide genetic benefits beyond those that could be justified by the size of the U.S. and British Columbia programs individually.

Breeding Strategy

Traits: Volume will be emphasized. Increasing use of machine-stress rating in lumber production is raising interest in relative density.

Early testing: No "farm field" testing is planned due to the small size of the program.

Promotion of early flowering: A co-operative (U.S. Forest Service and B.C. Ministry of Forests) study on promotion of flowering in wild stands of larch at about 20 years of age has been initiated. Lack of flowering in young material may be a constraint to rapid progress in advanced generations and may delay achievement of seed production targets in first-generation orchards. A study of container culture for promotion of flowering in larch is in progress. Given the relatively small size of the larch improvement program, the research priority for induced flowering will depend on how severe the delays are. Co-operative efforts with the U.S. may be warranted.

Effects of partial inbreeding: Unless successful techniques for promotion of early flowering are developed, it will be decades before parents with the appropriate relatedness can be produced for the necessary crosses. The longer generation interval for larch and a low self-compatibility further reduce the urgency of estimating partial inbreeding effects.

Impact of new technology: Greater use of machine-stress rating of lumber is expected to raise the demand for larch planting stock. A relative density comparable to Douglas-fir, combined with faster growth, are the principal reasons.

Somatic embryogenesis could be especially useful as a consequence of poor seed availability.

Genetic Benefits

Predicted gain: Following the strategy of selection and breeding outlined in the breeding plan,[7] predicted genetic gains in height at age 8 are shown in Appendix 3D. Using a multiplier of 2 to transform height to volume and an age:age correlation of 0.36 (Lambeth 1980) for selection at an age of 8 years with harvest at an age of 60 years, average predicted genetic gains in volume at harvest are about 11% per improvement cycle. This estimate assumes that the improved trees perform relatively the same in all environments where they are planted (no genotype by environment interaction). As data from only one plantation were available, interaction could not be estimated and the predicted gain is inflated by the extent of interaction.

Validation of predicted gain: The larch improvement program is too new to have identified genetically superior families for demonstration planting or realized gain trials.

Timing of improved seed: Western larch orchards may be producing seed for an average of 0.5 million seedlings in the year 2000 and 2.9 million in 2010. This would represent 30% of expected demand in the year 2000 and more than expected demand in 2010. Projections in western larch, however, are the most uncertain of interior species due to late reproductive maturity and the virtual lack of experience with cone production in seed orchards.

Comments

- Extension of the stated breeding strategy leads to an inability to produce an acceptable seed orchard for the third generation.
- Unless demand for planting stock increases substantially, traditional seed orchards for western larch will be very small. Contiguous orchards would allow for economies of scale while compromising the genetic integrity of individual orchards. Alternatives to the traditional orchards should be considered.

4.6 Coastal Douglas-fir (*Pseudotsuga menzsiesii* var. *menziesii*)

Planting is expected to be the principal method of regenerating coastal Douglas-fir to maintain forest land in an early seral stage with a species of high value in the structural lumber market. About 8 million seedlings are expected to be planted annually. The wide availability of seed orchard seed and the current development of British Columbia’s only second-generation seed orchards provide further incentives to plant.

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[7] Jaquish, B.C. 1987. A breeding plan for western larch (*Larix occidentalis* Nutt.) in British Columbia. B.C. Min. For., Victoria, B.C. Unpubl. man. 31 p.

Recent revision of seed transfer rules for coastal Douglas-fir (B.C. Ministry of Forests 1990) have reduced the number of seed planning zones to three to cover the area of coastal and coast-interior transition where the species will be planted. Of these, only two are represented in tree improvement because seed transfer from the wet maritime zone to the Georgia Lowland will be permitted. Historically, breeding efforts have been concentrated on one zone, the wet maritime zone (and its earlier subdivisions), due to timber value and planting demand.

Tree improvement began for coastal Douglas-fir in 1957 with phenotypic selections in wild stands. At the time, intensive phenotypic selection was expected to result in substantial genetic gain in orchard seed. As a consequence, progeny testing was not the principal objective of mating designs that produced material for more than 100 test plantations over a period of 10 years.

Seed orchards were established periodically starting in 1963, as interest in tree improvement grew and participation by private companies added resources to the effort (Table 10). These early orchards have provided very important information on orchard site location and management, in addition to substantial amounts on seed. Likewise, the extensive network of plantations resulting from controlled pollination of parents selected for orchards has provided essential information of genotype-environment interaction, types of genetic variation, and breeding values on which to base the removal of poor orchard parents.

TABLE 10. First- and second-generation seed orchards of coastal Douglas-fir by seed planning zone with timelines and annual projected yield of seedlings from orchard seed at full production. Initial roguing, based on progeny testing, has been applied in some orchards.

Seed planning zone	Orchard number	Year 1960 1970 1980 1990 2000 2010 2020 2030	Seedling numbers[a] (M)
Maritime: Low			
Quinsam	101	: +++++**********[b]	2.6
Saanichton	109[c]	: +++++**********	1.0
Koksilah	114	: +++++****	—
Snowden	115	: +++++***	—
Nootka	111	: +++++**********	2.2
Saanichton	121	: +++++**********	4.2
Harmac	122[d]	: +++++**********	1.1
Harmac	124	: +++++**********	1.1
Mt. Newton	134	: +++++**********	1.6
Mt. Newton	154	: +++++**********	1.4
Bowser I	149	: +++++**********	1.5
Bowser II	149		2.5
Maritime: High			
Saanichton	110[c]	: +++++**********	2.6
Sechelt	116	: +++++**********	1.4
Harmac	123	: +++++**********	1.1
Sub-maritime: Low			
Surrey	146	: +++++**********	0.7
Sub-maritime			
Dewdney	120	: +++++**********	6.8

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg (108 000), and plantable seedlings per seed (0.7).

[b] : = planting; + = developing; * = targeted production. (Each denotation equals a 2-year period.)

[c] Numbers 109 and 110 are scheduled to be combined.

[d] 300–800 m.

TABLE 11. Generic breeding and seed production cycles for coastal Douglas-fir

Generation	Year									
	1960	1970	1980	1990	2000	2010	2020	2030	2040	2050
							PPPPPPPPPP[a]			
						DDDDDD				
3						SS				
					TTTTT					
				CC						
					PPPPPPPPPP					
2				DDDDDD						
			SSS							
			PPPPPPPPPPPP							
		DDDDD								
1		TTTTTTT								
		CCCCC								
	SSSSS									

[a] S = selection and grafting; T = progeny testing; C = crossing of new selections; D = developing orchard; P = orchard producing at targeted levels.

The plantations resulting from a large program of controlled pollination have provided excellent material for proceeding to advanced generation orchards. The Ministry of Forests and some forest companies are taking advantage of this opportunity.

A draft breeding plan has been prepared[8] and reviewed. Timing of tree improvement activities through three generations is shown in Table 11. Breeding strategy has been modified to reflect experience both in British Columbia and elsewhere. The principal modifications are: reduction in the scope of progeny testing; establishment of separate plantations for parental testing and for producing populations from which outstanding parents will be chosen for a new level of genetic improvement; and structuring of the breeding populations to provide control of inbreeding.

The following elements of a typical breeding plan apply to coastal Douglas-fir:

Genetic Resources

Levels of tree improvement: Multi-generation breeding is planned as a single breeding program for the two seed planning zones along the coast (wet maritime and Georgia Lowland). For the sub-maritime zone, more restrictive seed transfer rules create the potential for several seed planning zones. Most of the seed demand, however, is for lower elevations in the southern part of the sub-maritime zone and a program of progeny testing for parents selected in wild stands is planned. Improvement may not extend beyond a tested first-generation orchard. Because of low seed needs, progeny testing is not considered to be worthwhile for the other areas.

Role of provenance research: Provenance research has provided the basis for seed transfer rules, for the current structure of seed planning zones, and for the identification of the potential of northward seed transfer for improved volume growth. Provenances from the maritime zone are well represented in tests that are fairly well distributed in the maritime zone. Testing in the sub-maritime zone is inadequate with two tests at low elevation on the western margin of the zone.

Population management: Multi-generation breeding is planned for only one seed planning zone. This, combined with the availability of several hundred tested parents, allows great flexibility in choosing how to manage improved populations. The breeding plan shows that a second-generation population of about 500 parents will be divided into 8-parent sublines (current plans are for 12-parent sublines). A complementary design will be used with polycross mating for progeny testing and a circular mating design to generate progeny from which selections will be made for the next orchard and breeding population. Although

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[8] Heaman, C. and J. Woods. 1989. The coastal Douglas-fir breeding program in British Columbia: Summary of past, present and future activities. B.C. Min. For., Victoria, B.C. Unpubl. man. 42 p.

emphasis in most sublines will be on volume, a few sublines will emphasize other traits, specifically relative density and stem quality. This plan is supported by calculations that show that, by the fourth generation, inbreeding will reach a level at which the combining of sublines is required. A study quantifying effects of partial inbreeding also supports the chosen strategy of population management.

Availability of new material: There are a large number of trees in provenance and progeny tests, in addition to trees represented in the formal breeding program. Provenance tests indicate a marked increase in growth when seedlings are grown from some sources in the state of Washington. Genetic differentiation at the family level, however, receives most emphasis in breeding. Some U.S. parents are being progeny tested and are included in orchards now being established. Discussions on exchanges of tested parents with U.S. programs are in progress.

Breeding Strategy

Traits: Juvenile volume will receive principal emphasis, while relative density will be held at a level similar to that in plantations of unimproved trees. There will be some attention paid to stem quality in recognition of quality problems on sites of extremely high growth potential.

Early testing: Data from the large number of progeny tests indicate reliable selection at age 7 for performance at age 12. A retrospective test using the ‘‘farm field’’ approach is being analysed for correlations with performance at earlier ages. Orchard roguing will be based on progeny assessments at ages 5 and 10 years.

Cone enhancement: Induction in orchards is now routine on an operational basis. Some additional research may be required for young material provided after forward selection.

Effects of partial inbreeding: A comprehensive study has produced estimates of the impact of partial inbreeding on seed production and nursery performance. Field tests have been established.

Impact of new technology: Recent progress in vegetative propagation may influence breeding strategy.

Genetic Benefits

Predicted gain: Gains were predicted by Loo-Dinkins (1990) in a report on simulated advanced-generation breeding. Volume gains, at a rotation age of 60 years, are 8% for the second cycle and 7% in subsequent cycles where selection is at age 12 (J. Woods, pers. comm., Jan. 1992). Predicted gains are somewhat lower than for other species presumably as a consequence of plans to maintain wood density at the level of comparable trees in unimproved plantations.

Validation of predicted gain: Seedlots from unselected trees were not included in progeny tests. Plantings to demonstrate genetic variation and to estimate gain on an area basis are planned for 1992. Genetic categories to be included are ‘‘best’’ crosses, ‘‘poor’’ crosses, orchard seed, and wild-stand seed.

Timing of improved seed production: In the maritime zone, seed production capacity of existing seed orchards exceeds expected seed demand and will continue to do so. In the sub-maritime zone, about 50% of the seed need will be met by the Dewdney orchard in 1995 and about 75% will be met when an orchard for the central sub-maritime zone is producing in 2005. From current plans for Douglas-fir, about 85% of the seedlings used for reforestation will be from orchard seed by 2005.

Comments

- While current evidence is fully supportive of a breeding strategy that in British Columbia ignores provenance effects in coastal areas, existing provenance tests and some progeny tests should continue to be assessed to validate the current program strategy.
- Increased confidence in the desirability of northward transfer of Douglas-fir genes might result from a review of European literature on provenance variation, and from short-term testing of growth rhythm.

- Patterns of genetic variation associated with geography in the harsher environments of the sub-maritime seed planning zones are unlikely to be similar to patterns on the Coast. Given the size of expected seed demand for the sub-maritime zone (compared with both the coast and interior areas), it is difficult to reconcile the lack of genetic research in the sub-maritime zones.
- With relatively small seed demand and a lumber product of relatively high value, alternatives to the traditional wind-pollinated seed orchard might enhance genetic gain.

4.7 Western Hemlock (*Tsuga heterophylla*)

Planting, as a method of regenerating western hemlock, is subject to greater uncertainty than for most other conifers of commercial importance in British Columbia. As a major representative of the later stages of forest succession in much of the wet maritime zone, hemlock will likely be common as advanced regeneration on many unburned cutblocks and will often become established from natural seeding as well. Planting, however, remains a common choice where rapid establishment of growing stock is desired with greater certainty or where a change of species is planned. Planting demand is projected to be about 5 million seedlings annually by the year 2010.

Tree breeding for western hemlock was initiated in the late 1970's with selection of parent trees in the many seed zones recognized at the time. Testing of many of the selected parents is in progress. After a period of inactivity in the program, a new commitment was made in 1988 and a new strategy is being developed.[9] In general, the new strategy emphasizes high genetic gain through intensive roguing in a large breeding population. The intent is to "regionalize" genetic resources by including superior parents from the northwestern U.S. with British Columbia parents, while maintaining some local structure in crossing, testing, and selecting parents. Such a return to a more local approach would not require large-scale program revision. At present, a specific plan for hemlock breeding in the province awaits the outcome of negotiations among potential co-operators on equitable distribution of genetic material, which varies widely in validation of genetic value.

The first seed orchard was established in 1980 and several additional orchards followed (Table 12), each with a general focus on specific seed zones at the time. A combination of advances in techniques for induction of cones, changed seed transfer guidelines, and reduced seed demand makes a substantial excess of hemlock seed apparent. Existing orchards would become substantially less attractive if regional co-operation were to give British Columbia access to U.S. parents that have been through a more advanced progeny testing program. Timing of tree improvement activities for three generations is illustrated in Table 13.

The following elements of a typical breeding plan apply to western hemlock:

Genetic Resources

Levels of intensity for tree improvement: Several elements combine to focus improvement on high gain in one seed planning zone through a multi-generational program of breeding and selection. If exceptional benefits from tree improvement become apparent, the option of natural regeneration may become less attractive and the demand for seed may increase.

Role of provenance research: Provenance information is largely lacking for hemlock. Early progeny tests do not indicate substantial effects of seed origin except in seed collected at higher elevations. Small test plantings of provenances will be established adjacent to some progeny tests.

Population management: Initial emphasis will be on recurrent selection and breeding within the several seed planning zones that currently represent hemlock tree improvement in British Columbia and the U.S. Simultaneously, crosses among the very best genotypes, regardless of geographic origin, will be made to

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[9] King, J.N. and D.W. Cress. 1991. Breeding plan proposal for western hemlock cooperative tree improvement. Unpubl. man. 14 p.

create populations with high genetic gain for specific traits. Maintenance of a “local” structure to the program will allow testing of a proposed aggregation of genotypes into a common breeding population. In addition, maintenance of local populations could provide a basis for future sublines.

TABLE 12. First-generation seed orchards of western hemlock by seed planning zone with timelines and annual projected yield of seedlings from orchard seed at full production. Progeny testing is in progress.

Seed planning zone	Orchard number	Year 1980 1990 2000 2010 2020 2030 2040	Seedling numbers[a] (M)
Maritime: Low			
Nootka	136	: ++++**********[b]	2.0
Lost Lake	127	: ++++**********	1.7
Lost Lake	126	: ++++**********	2.9
Sechelt	133	: ++++**********	0.6
Harmac	150[c]	: ++**********?	1.3
Lost Lake	156[d]	: ++++**********	0.6
Saanichton	165	: ++++**********	1.4
Maritime: High			
Yellow Point	132	: ++++**********	0.9
Mt. Newton	130	: ++++**********	4.1
Harmac	163[c]	: ++********?	0.4
South Quinsam	143	: ++++**********	1.5

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg (530 000), and plantable seedlings per seed (0.5).

[b] : = planting; + = developing; * = at targeted production. (Each denotation equals a 2-year period.)

[c] Container orchard. Life is indefinite with re-propagation.

[d] Seed to be used north of 50°N. Lat. (Transfer of seed from all other hemlock orchards is limited by seed transfer guidelines to ranges of 6° of latitude between 46° and 53°N.)

TABLE 13. Generic breeding and seed production cycles for western hemlock

Generation	Year 1970 1980 1990 2000 2010 2020 2030 2040 2050
	PPPPPPPPPP[a]
	DDDDDDD
3	SS
	TTTT
	CC
	PPPPPPPPPP
	DDDDDDD
2	SS
	TTTT
	CC
	PPPPPPPPPP
	DDDDD
1	SS
	TTTTTT
	SSSSSS

[a] S = selection and grafting; T = progeny testing; C = crossing of new selections; D = developing orchard; P = orchard producing at targeted levels.

Three options for advanced-generation breeding, representing different levels of expense and long-term commitment, have been presented.[10] The option recommended by the authors creates a second-generation breeding population representing 240 parents. If the breeding population is treated as single population, the problem of adequate genetic diversity noted in Appendix 2 will be postponed for one generation under the same standards of selection. It is not clear, however, how an overlay to maintain local population structure would influence breeding population size.

Availability of new genetic material: Well-tested parents from the U.S. represent an exceptional opportunity to infuse new material early in the program. No other sources of promising new material have been identified.

Breeding Strategy

Traits: Emphasis will be on height, with some interest in relative density and possible interest in wood traits related to pulping.

Early selection: Initial selection is planned at age 5 years, with verification at age 10. No ‘‘farm field’’ testing is planned. Studies of the physiological basis for genetic superiority in growth may be undertaken by the adaptive physiologist.

Cone enhancement: Hemlock responds very well to gibberellin treatment and such treatments are operationally routine.

Effects of partial inbreeding: No parents representing the appropriate genetic relationships are available for developing a study of partial inbreeding. With the population sizes expected to be available, in the absence of a subline population development, partial inbreeding studies can probably be delayed for this species.

Impact of new technology: Vegetative propagation for increasing the number of plants from crosses among high selected parents may be attractive.

Genetic Benefits

Predicted gain: Gain estimates were based on extensive progeny tests at an age of 10 years.[11] From a geographically aggregated population of 1800 tested parents, selection of the best 3% produced an expected volume gain of 13% at rotation age without adding gains from selection of wild-stand parents. Combined selection among and within families in the second generation would result in a predicted additional gain of 9% in volume at rotation age.

Validation of predicted gain: Check lots from wild-stand seed collections, along with crosses among genetically superior parents, are included in the most recent progeny tests. Ten-hectare square plots are being planted in 1992 to compare realized gain from crosses among the best parents with conditions in unimproved seedlots.

Timing of improved seed production: Current and projected seed yields from orchards exceed anticipated seedling demand at least until 2014 (Table 12).

Comments

- A formal breeding plan is needed as soon as negotiations on access to U.S.-tested parents are completed. That plan will need details of population management to illustrate how an adequate genetic base will be maintained if local population structure is to be maintained.
- After a formal breeding plan is available, recommendations should be made for rationalizing current excess seed production capacity with opportunities for greater genetic gain. King and Cress (1991) have made suggestions about this.
- A formal discussion of the issue of planting versus natural seeding with hemlock would help to rationalize the hemlock improvement program.

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[10] King, J.N. and D.W. Cress. 1991. Breeding plan proposal for western hemlock cooperative tree improvement. Unpubl. man. 14 p.

[11] Ibid.

4.8 Sitka Spruce (*Picea sitchensis*)

Planting of Sitka spruce is largely tied to the issue of reducing impacts of the spruce weevil. Although Sitka spruce has the potential for high productivity in coastal environments where moisture is ample, seedling demand will remain low (<2 million) unless injury by the weevil can be reduced.

Breeding activity has been limited to clonal testing of resistance to spruce weevil. Testing of open-pollinated progeny from populations in the Georgia Lowland is planned following the next seed year. Interest in material from the Georgia Lowland is based on provenance research that shows a much higher frequency of resistant individuals in that area.

Seed orchards were started in the 1976–1980 period (Table 14) and were among the first to produce ample crops of seed. Seed production has exceeded seed demand for several years.

TABLE 14. First-generation seed orchards of Sitka spruce by seed planning zone with timelines and annual projected yield of seedlings from orchard seed at full production. Progeny testing is not planned.

Seed planning zone	**Orchard number**	**Year** **1980 1990 2000 2010 2020 2030 2040**	**Seedling numbers[a] (M)**
Maritime: South			
Hovey Road	118[b]	: ++++**********[c]	2.5
Maritime: Mid			
Lost Lake	157	: ++++**********	0.4
Maritime			
Lost Lake	142	: ++++**********	2.0
Quesnel Road	144	: ++++**********	1.1

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg (414 000), and plantable seedlings per seed (0.5).

[b] Scheduled to be reduced to a clonebank.

[c] : = planting; + = developing; * = at targeted production. (Each denotation equals a 2-year period.)

At the current level of tree improvement activity, only a few of the elements of a typical tree breeding program are applicable:

Genetic Resources

Levels of intensity: A breeding plan for Sitka spruce will not be feasible until the degree of genetic control over weevil resistance has been estimated.

Role of provenance research: A network of provenance tests representing maritime and sub-maritime environments has revealed geographic patterns of variation in weevil resistance, growth rate, and cold hardiness. In addition to drier parts of the distribution of Sitka spruce being promising areas for locating genetic resistance to weevil, the potential for large increases in growth rate has been shown from the northward transfer of seed (accompanied by a increased risk of cold injury).

Population management: There is insufficient information on genetic control of weevil resistance to determine whether a breeding program for Sitka spruce is warranted. Collection of material from threatened populations in the areas of apparently higher resistance to weevil is of high priority.

Availability of new material: Sitka spruce from the Georgia Lowland currently offers the most promise for locating genetic resistance to weevil injury. Outstanding increases in growth rate are evident in coastal provenances from Oregon and Washington, but currently these provenances are useful only in the Queen Charlotte Islands. Material from drier parts of the species range in Oregon and Washington may show a combination of increased resistance and growth. As knowledge of the inheritance of weevil resistance increases, resistance may be combined with increased growth rate.

Breeding Strategy

Traits: Current interest is almost exclusively on weevil resistance. There is substantial variation in growth rate, both at the level of provenance and the level of individual family (Yeh and Rasmussen 1985).

Early testing: As with interior spruce, the age at which response to the weevil can be reliably assessed will determine the rate at which genetic improvement of Sitka spruce could proceed. At present, field testing of progeny would seem to require at least 10 years.

Cone enhancement: Grafts from older trees have flowered relatively quickly and copiously. Younger material is expected to respond to hormonal treatments for cone induction.

Impact of new technology: With current evidence for clonal differences in weevil resistance, vegetative propagation could be an attractive option for the production of planting stock. Progress has been made in somatic embryogenesis, and a field test of trees produced through the technique is planned for 1992. Techniques to allow the early identification of resistance to the spruce weevil could accelerate an improvement program.

Genetic Benefits

Predicted gain: If protection against the spruce weevil can be provided, substantial genetic gains in growth rate are available through genetic improvement of Sitka spruce. Provenance tests at age 10 years indicate an average gain of 9% in volume per degree of northward seed transfer (C. Ying, pers. comm., May 1989). Genetic variation comparable to that of other forest tree species (Yeh and Rasmussen 1985) indicates that similar rates of genetic improvement would be expected from a multi-cycle program of selection and breeding.

Validation of predicted gain: A test of grafts from provenances resistant or susceptible to weevil has verified the presence of large provenance differences in response to exposure to the spruce weevil (Ying 1991). A second clonal planting to verify apparent genetic differences is being established in 1992 at a location that will be useful for demonstration purposes.

Timing of improved seed production: Orchard seed production exceeds anticipated seedling demands through 2004. It should be noted, however, that reduction of Orchard #118 to a clonebank reduces the principal source of orchard seed for Vancouver Island and the Lower Mainland. Seed from the smaller orchard #157 could be used in that area.

Comments

- Genetic improvement is largely exploratory at this point and is tied to estimation of the degree of genetic control of resistance or tolerance to the spruce weevil.
- If breeding for weevil resistance appears to be promising, combining resistance with the exceptional growth potential demonstrated in the northward transfer of genetic material will be an important activity.

4.9 Yellow Cypress (*Chamaecyparis nootkatensis*)

Yellow cypress has a limited natural distribution which, in turn, limits the area where it is recommended for planting. The range of environments where cypress can be profitably grown, however, is unknown. The high value of cypress wood has prompted interest in expanding the apparent ecological amplitude of the species and in regenerating by planting. Demand is expected to be at about 1 million trees per year.

Tree breeding with yellow cypress began in 1990 with development of a breeding plan.[12] Breeding will concentrate on the wet maritime seed planning zone, which includes more than 90% of anticipated planting. Progeny testing will be with cloned seedlings to provide estimates of genetic variation available for breeding, and to allow selection of clones for use in planting.

Seed orchards were started in 1983 (Table 15) and soon produced large numbers of cones following hormonal treatments. Unexpected problems with premature cone ripening, however, have reduced the yield of viable seed, and a combination of seedlings and cuttings has been used to fill planting requirements. It is expected that seed production will meet seed requirements in 1992. Timing of selection and development of improved planting stock is shown in Table 16.

The following elements of a typical breeding plan apply to yellow cypress:

Genetic Resources

Levels of intensity: Given the relatively small demands for planting stock, tree improvement may be conducted through only one cycle of crossing and testing to produce rogued first-generation seed orchards. These may be replaced by second-generation hedge orchards for the production of rooted cuttings.

Role of provenance research: Little is known of geographic variation in yellow cypress and a substantial program of provenance research, both short and long term, accompanies the breeding program.

Population management: The desirability of multi-generational breeding in yellow cypress is not clear at present. A tentative proposal for breeding through the second generation[13] uses a circular mating strategy in 24 groups of 8 parents each. Extension of selection and breeding beyond a third generation would raise the problems of genetic diversity illustrated in Appendix 2.

Availability of new genetic material: Based on early provenance test results, some increase in growth rate can be achieved if seed is moved northward.

Breeding Strategy

Traits: Growth rate and relative density of wood are the traits of current interest, although the uniformity of yellow cypress wood is attracting interest from pulp makers. A variety of traits — including stem form, rooting ability, fungitoxic components of wood, and resistance to browsing — may be more important than growth rate in this species.

Early testing: Studies of controlled freezing and of controlled drought have been conducted. The development of age:age correlations will have to wait for field plantations (planted in 1991) to become older.

Cone enhancement: Yellow cypress is expected to respond well to gibberellin treatment.

Effects of partial inbreeding: Unless a multi-generational breeding program is planned in the future, partial inbreeding studies will not contribute to tree improvement.

Impact of new technology: Any improvements in vegetative propagation (somatic embryogenesis, anther culture, rooting) would fit well with an improvement plan focused on clonal testing and the clonal production of planting stock.

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[12] Russell, J. 1990. Yellow-cedar genetic improvement plan. Unpubl. draft man. 17 p.

[13] Ibid.

TABLE 15. First-generation seed orchards of yellow cypress by seed planning zone with timelines and annual projected yield of seedlings from orchard seed at full production. Progeny testing is planned.

Seed planning zone	Orchard number	Year 1980 1990 2000 2010 2020 2030 2040	Seedling numbers[a] (M)
Maritime			
Mt. Newton	138	: ++ * * * * * * * * * * ?[b]	0.6
Yellow Point	137	: ++ * * * * * * * * * * ?	0.3
Saanichton	164	: ++ * * * * * * * * * * ?	0.5

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg (220 000), and plantable seedlings per seed (0.5).

[b] : = planting; + = developing; * = at targeted production. (Each denotation equals a 2-year period.)

TABLE 16. Generic breeding and seed/cutting production cycles for yellow cypress

Generation	Year 1970 1980 1990 2000 2010 2020 2030 2040 2050
3	PPPPPPPPPP[ab]
	DD
	SS
	TTTT
	CC
2	PPPPPPPPPP[b]
	DD
	SS
	TTTT
	CC
1	PPPPPPPPPP[c]
	DDD
	SSSSSS

[a] S = selection and grafting; T = progeny testing; C = crossing of new selections; D = developing orchard; P = orchard producing at targeted levels.

[b] Container hedge orchards for production of cuttings. Orchard life span is limited only by success of container culture.

[c] Soil-based orchards for production of seeds.

Genetic Benefits

Predicted gain: Inadequate data are available to justify gain predictions at present. A provenance experiment including seedlings from individual-tree collections has shown levels of genetic variation comparable to those in most other west coast tree species (Russell 1992).

Validation of predicted gain: No validation is currently planned.

Timing of improved seed production: Seed production is expected to meet seedling demand in 1992 and in subsequent years. A switch to full clonal production of planting stock will be possible by the year 2000.

Comments

- A better rationalization of the genetic improvement program awaits genetic information from current tests and from tests of the species in environments where it does not occur naturally.

4.10 Western White Pine (*Pinus monticola*)

The place of western white pine in British Columbia forestry has some similarities with Sitka spruce in that a pest problem (blister rust) severely limits use of the species in reforestation. Surveys of future seedling demand show a consistent interest in western white pine when availability of disease-resistant stock is assumed. The substantial history of attempts to circumvent the disease problem by a variety of options has led to acceptance of breeding for resistance as the most promising option at present.

Initial efforts to provide seed with some potential resistance involved importation of seed from the U.S. resistance breeding program in Idaho. A small plantation from U.S. seed was established at Skimikin Nursery in 1979, along with a second plantation including mostly seedlings from a few largely infection-free stands in British Columbia. These plantations produced small seed crops after about 10 years. Additional activity in tree improvement for western white pine includes selection by the Nelson Forest District, and selection and orchard development by private industry (Westar).

A program of screening for resistance to blister rust was initiated in 1984 with administration and technical expertise located at the Pacific Forestry Centre. Program plans have been presented for 4-year periods, the most recent being for 1990/91 to 1994/95.[14] Several hundred trees have been selected in coastal and interior stands and these selections are being screened by artificial inoculation for response to the pathogen. Several demonstration plantings have been established to test response of different seedlots to the pathogen and to environmental variation. Research on the genetics of host and pathogen is also part of the program at the Centre.

To accelerate access to seed with an expected genetic potential for improved resistance, the Ministry of Forests collected scions from about 50 tested parents in the U.S. program in 1990. Grafts have been made and await establishment in a seed orchard to produce seed for reforestation in the Interior. For the Coast, a seed orchard is planned, using coastal trees screened in the program at the Pacific Forestry Centre.

A co-ordinated plan for tree improvement of western white pine has not been developed. Seedling needs may not justify an extensive effort in breeding, especially if genotypes developed in the U.S., combined with those identified in British Columbia, can provide an adequate level of disease resistance and growth under British Columbia conditions.

4.11 Other Species

Table 17 lists species for which seed orchards have been established without supporting breeding programs. Research is in progress to determine whether adequate genetic variation exists in western redcedar to justify a program of genetic improvement. Seed orchards of western redcedar have produced copious amounts of seed at an early age, especially in response to treatment with gibberellic acid. For Pacific silver fir, orchards have grown very slowly and there has been no seed production.

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[14] Hunt, R.S. and M.D. Meagher. 1989. White pine blister rust four-year plan 1990/1 to 1994/5. Forestry Canada, Victoria, B.C. Unpubl. man. 15 p.

TABLE 17. Seed orchards for species without supporting breeding programs by seed planning zone, with timelines and annual projected yield of seedlings from orchard seed at full production for first-generation orchards of coastal species

Seed planning zone	Orchard number	Year 1970 1980 1990 2000 2010 2020 2030	Seedling numbers[a] (M)
Western redcedar			
Maritime: South			
Lost Lake	128/158	: +++**********[b]	2.3
Mt. Newton	140	: +++**********	0.9
Mt. Newton	152	: +++**********	0.8
Harmac	139[c]	: ++**********?	0.7
Maritime: North			
Lost Lake	155	: +++**********	1.1
Pacific silver fir			
Maritime: Low			
Nootka	160	: +++++++**********	0.3
Mt. Newton	129	: +++++++**********	0.8
Maritime: High			
Yellow Point	135	: +++++++**********	0.5
Engelmann spruce			
Cobble Hill	131	: ++++++**********	13.3

[a] Seedling numbers were calculated as the product of expected seed production (kg), number of seeds per kg, and plantable seedlings per seed. Seeds per kg were 884 000 for redcedar, 34 000 for Pacific silver fir, and 436 500 for Engelmann spruce. Seedlings per seed were 0.5 for cedar and fir, 0.4 for spruce.

[b] : = planting; + = developing; * = targeted production. (Each denotation equals a 2-year period.)

[c] Container orchard. Life is indefinite with re-propogation.

5 DELIVERING GENETIC IMPROVEMENT, FROM ORCHARD TO FOREST

5.1 Orchard Management

Cone and seed development: Extensive studies of the anatomy, morphology, and phenology of cone and seed development have provided a basic understanding of seed production for all of the British Columbia conifers currently under improvement.

Cone enhancement: Research has guided the development of cultural treatments (ranging from root-pruning to hormonal sprays) that are now practiced on an operational basis for several species. For selections from older trees, some refining of treatments remains to be done, but the focus in cone enhancement is expected to shift toward balancing sex expression so that adequate pollen is produced. Additional work on quantitative control of cone induction and on physiological processes in induction need attention.

With advanced-generation orchards, selected parents will be from young trees and the issue becomes one of accelerating reproductive maturity in addition to switching on a reproductive ability that is already present. Experience with coastal Douglas-fir is available outside the province. Interior spruce will require research effort in British Columbia.

Crown control: There has been some experience with different approaches to crown control in orchards of coastal Douglas-fir, but there seems to be no agreement on whether — or how — to control crown height or shape. Only one study on the impact of crown control on cone production in Douglas-fir has been done (M. Crown, pers. comm. 1992). The impact of crown control on sex expression seems not to have been considered. For the Interior, studies of topping are in progress for large and small lodgepole pine, interior spruce, and western white pine. Also in progress is a test of the trade-off between smaller seed crops and ease of cone harvest from the ground when orchard trees are grown at closer-than-normal spacing.

Alternatives to soil-based, wind-pollinated orchards: Container orchards for three species have been more difficult to manage and less productive than expected. Container culture may be most useful for accelerating crossing in breeding populations. Orchards with clonal rows and control of pollen are of current interest. No installations have been tried.

Pollen handling: Work on pollen handling has been largely completed for species with many orchards. Progress will be summarized.

Tracking of cone development: On the Coast, information on the fate of cone buds between the time of bud surveys and the time of cone collection is lacking except for a few species at Canadian Pacific Forest Products (CPFP) (El-Kassaby *et al*. 1992). In the Interior, no tracking of buds has been done.

Genetic efficiency: Many of the issues that must be dealt with to ensure that orchard seed contains the genetic potential represented by orchard parents have been presented (El-Kassaby 1989). A start has been made on assuring that the genetic quality of orchard seed is adequately estimated for operational purposes. This is the result of efforts to develop a genetic rating system which, in turn, is co-ordinated with the provincial policy statement on orchard seed. Much testing of assumptions in the rating system remains to be done.

Orchard design with genetic efficiency in mind could alleviate some of the difficulties faced in existing orchards. Use of data on reproductive phenology and fecundity could result in orchards that more closely meet the assumptions under which wind-pollinated orchards are established.

Adaptation in orchard seed: Studies are in progress of interior spruce to estimate whether production of seed at off-site locations has significant negative implications for operational planting.

5.2 Seed Biology

Most of the current effort in the Ministry of Forests is on wild-stand collections because most of the problems of germination are related to cone collection. Detailed studies for specific orchards are being done at CPFP. The degree to which those results can be extrapolated needs to be determined.

5.3 Nursery Management

Sowing practices: Genetic variation in germination rate has been clearly demonstrated (El-Kassaby *et al*. 1992). The impact of thinning in multiple-sown cavities on delivery of expected genetic benefits in the nursery crop has received only preliminary attention. To the extent that orchard seed behaves differently than wild-stand seed (i.e., exhibiting heterogeneity of germination and growth), nursery managers may need new guidelines for growing protocols.

Stock culling practices: Genetic consequences of culling rules based on a fixed size for seedlings have been demonstrated, but implications for delivery of the expected genetic benefits in the nursery crop are only beginning to be addressed (El-Kassaby 1992).

5.4 Deployment of Improved Nursery Stock

No consideration has been given to the impact of site quality or expected silvicultural practice on the expected benefits from a genetically improved nursery crop. The implications of site class for the quantity of wood produced from different combinations of genetic gain over three cycles of breeding have been estimated for coastal Douglas-fir and interior spruce (Lester 1992).

6 RECOMMENDATIONS

Tree improvement in British Columbia is characterized by the high energy, enthusiasm, and commitment of those who plan and then implement those plans. The technical merit of plans has been verified through extensive review by committees that include specialists from outside the program and outside British Columbia. Progress is represented in the guidelines for seed transfer, the dozens of seed orchards in place, thousands of selected trees, and hundreds of thousands of progeny in test plantations.

Co-ordination of tree improvement efforts has improved markedly over the last 15 years. The following comments are intended to note areas where additional co-ordination may be beneficial.

- Recommendation: Develop a structured process for making program decisions that commit, currently or in the foreseeable future, substantial program resources.

  Comment: Peer review committees are asked to address the question of how best to produce genetically improved trees. There should be a better process for determining whether to produce improved trees wherever the opportunity exists. Economic efficiency, as well as allocation of finite program resources, should be a part of the decision process. Examples of some of the issues involved are in Lester (1992).

- Recommendation: Establish a management structure to encourage a focus on the whole process of producing improved seed.

  Comment: The interaction between different components of research and between research and operational seed production remains a source of complaint. The proposed re-orientation of some physiology research toward seed production, rather than the individual components of seed production, reflects an awareness of needed changes. An even broader perspective would be useful. The contribution that the training and experience of tree breeders can make would not seem to end with the delivery of selected genotypes for grafting. Similarly, the contributions that physiology researchers could make in support of tree improvement would seem not to be necessarily limited to intervention when major problems are encountered. Decisions to make the process of seed production more technologically sophisticated should be accompanied by the commitment to provide the necessary technical support. Containerized seed orchards may be an example of a less-than-well co-ordinated process.

Options for encouraging closer integration of components in tree improvement could include assignment of the responsibility to one position, or creation of a standing committee or small committees assigned to species or specific issues. Network diagramming or other techniques for laying out complex processes might be useful for illustrating the required sequencing of information and action to produce improved seed in a specific program.

Among the technical issues that such focus might uncover are apparent unrealistic expectations for the timing and quantity of results from short-term research in adaptive physiology. Another issue is the question of whether cone enhancement techniques developed on scions from reproductively mature trees would be equally effective on the reproductively immature trees being selected in advanced generations.

Among the administrative issues that plague efficient tree improvement province-wide are the uncertainties surrounding the role of forest industry. While resolution of this uncertainty would be beyond the jurisdiction of the administrative structure suggested above, a focus on an integrated tree improvement process would highlight the need for clarification of roles.

- Recommendation: Broaden the context of tree improvement to include gene resource management.

Comment: Tree breeders and geneticists have the most appropriate training, experience, and knowledge to plan for the maintenance and use of genetic variation in trees. Their responsibility could be extended beyond production of genetically superior genotypes into questions of the conservation of important natural populations, the balance between natural and artificial regeneration, and the deployment of improved seed.

At present, an assessment of the representation of British Columbia conifers in protected forest lands (ecological reserves, parks) is in progress, with the objective of producing a provincial plan for gene conservation. As that plan develops, the role of tree improvement in gene conservation should be developed and identified in the plan.

For hardwoods, provenance testing is being started and clonal testing of poplar hybrids is in progress. Both will contribute to an information base for gene resource management.

- Recommendation: Require additional planning for the genetic management of breeding and orchard populations for some species.

  Comment: The degree to which issues of population composition and size, selection intensity, inbreeding, and associated genetic questions have been addressed varies widely among species. While any plan may change with new information, and all breeding programs will be producing new information almost continuously, there are certain fundamental genetic issues that every tree breeding program must confront as soon as initial breeding populations have been selected. Decisions about these issues strongly constrain future options and ought to be documented with the explicit evidence that future impacts have been considered.

- Recommendation: Review whether the current balance of effort in research and in operational tree improvement is the most appropriate for efficient advancement of tree improvement.

  Comment: The current organizational model for tree improvement in British Columbia seems to be relatively decentralized. This leaves the individual tree breeder largely responsible for all of the technical details as well as the operational details of generally large programs. While this has the advantage of keeping technical expertise near operational activities, it leaves breeders with little time for research. A more centralized model would enlarge the allocation of resources to research, at the same time shifting operational responsibilities to less technically trained employees.

- Recommendation: Develop explicit plans to validate the effectiveness of early selection and represent the cost of those plans in budget projections.

  Comment: Tree breeders in British Columbia and elsewhere are implementing plans to identify genetic value at ages that represent less than ⅒ of the expected rotation age. While most evidence supports the feasibility of such plans, very little research has extended observations of genetic variation to even half of rotation age.

- Recommendation: Consider whether a shift from a focus on quantity in tree improvement to a focus on quality may be appropriate.

  Comment: Initial selection, progeny testing, and production of genetically improved seed has progressed to a point where substantial tangible progress is evident. For orchard seed production, interest is shifting from getting the seed production “machinery” in place to issues of the genetic quality of seed being produced. It may be appropriate to shift some focus in tree breeding from numbers of seed planning zones served and numbers of parents under test, to a broader understanding of available genetic variation and the implications of selection for height on other traits. The trade-off (with finite resources) could be between greater knowledge of value in genetic improvement for planning zones with large planting needs or a generally higher level of risk in tree improvement for more planning zones.

APPENDIX 1. Projected rates of approach to targeted seed production for eight species in developing orchards as a percentage of target

Year after orchard establishment	Species[a]							
	Si	Pl	Fdi	Lw	Fdc	Hw	Ss	Cy
4	0	0	0	0	0	0	0	20
6	10	0	10	0	10	20	20	60
8	30	15	30	15	30	70	70	100
10	60	30	60	30	60	100	100	100
12	100	75	100	50	100	100	100	100
14	100	100	100	75	100	100	100	100
16	100	100	100	100	100	100	100	100

[a] Si = interior spruce
Pl = lodgepole pine
Fdi = interior Douglas-fir
Lw = western larch
Fdc = coastal Douglas-fir
Hw = western hemlock
Ss = Sitka spruce
Cy = yellow cypress

APPENDIX 2. Generic details of selection from advanced-generation breeding plans for four species

A. Interior spruce

Breeding population					
Generation	Number of			% selected	
	Parents	Sets[a]	Families	Parents or families	Individuals in families
1	800?	-	-	25?	-
	200[b]	-	-	50	-
2	100	25	150	33-[c]	1
3	50	12	75	33-[c]	1

Breeding population			Orchard population		
Generation	Selection intensity		Number of parents	Selection intensity	
	i1[d]	i2[e]		i1[d]	i2[e]
1	1.3	-	-	-	-
	0.8	-	50	1.3	-
2	1.1-[c]	2.3	25	1.3	2.3
3	1.1-[c]	2.3	12	1.3	2.3

[a] Sets are 4 × 4 disconnected half-diallels.

[b] Several breeding zones have substantially fewer than 200 parents.

[c] Selection %, if unrelated crosses only are taken, will usually be much larger than 33% (⅔) because after the first cross is chosen, there is only one other unrelated cross in a 4 × 4 disconnected half-diallel.

[d] Selection intensity for family.

[e] Selection intensity for individual within family.

B. Lodgepole pine, interior Douglas-fir, and western larch

Breeding population					
Generation	Number of			% selected	
	Parents	Sets[a]	Families	Parents or families	Individuals in families
1	3000[b]?	-	-	10[b]?	-
	1200[c]?	-	-	25[c]?	-
	300[d]	-	-	50	-
2	150	25	225	67[e]	1[f]
3	150[e]	25	225	67[e]	1[f]

Breeding population			Orchard population		
Generation	Selection intensity		Number of parents	Selection intensity	
	i1[g]	i2		i1	i2
1	1.8	-	-	-	-
	0.8	-	75	1.3	-
2	0.5[h]	2.3	50	1.3	2.3
3	?	?	50[h]	1.3[f]	2.3[f]

[a] Sets are 3 × 3 disconnected factorials.

[b] Lodgepole pine.

[c] Interior Douglas-fir and western larch.

[d] Several breeding zones have substantially fewer than 300 parents.

[e] Inbreeding cannot be avoided at this point because there are only *three* unrelated crosses in a 3 × 3 disconnected factorial and the breeding plan calls for selection of *six* families per factorial.

f More than one tree per family may be selected in balancing inbreeding and genetic gain. Actual selection intensities may, therefore, be somewhat different than indicated.

[g] i1 = selection intensity for family; i2 = selection intensity for individual within family.

[h] Inbreeding will be present at this point.

APPENDIX 3. Prediction of genetic gain from three cycles of improvement for four species

Formulae

Genetic gain = $i\sigma^2_A/\sigma_P$

σ^2_{A2} = $(0.9)\sigma^2_{A1}$ (see Bulmer 1971)

σ_{P1} = $2(\sigma^2_P)^{1/2}$ (Phenotypic variance in wild stands is assumed to be twice that in progeny tests)

$\sigma_{P2,P4,P8}$ = $((0.5)\sigma^2_{A2}+(\sigma^2_{PF}-\sigma^2_F)+\sigma^2_D/4)^{1/2}$

$\sigma_{P5,P9}$ = $((\sigma^2_P-(\sigma^2_{A1}-\sigma^2_{A2}))^{1/2}$

Definitions

i = selection intensity
σ^2_A = additive genetic variance
σ^2_F = variance component for family means
σ_P = phenotypic standard deviation for individuals (σ_P) or families (σ_{PF})
σ^2_D = dominance genetic variance (assumed to be one half of σ^2_A)

A. Interior spruce

Gain parameters

Parameters[a]	Subscript number								
	1	2	3	4	5	6	7	8	9
i	1.3[b]	1.3	0.8	1.3	2.3	1.1-[c]	2.3	1.3	2.3
σ^2_A	1500	1350	N/A[d]	1350	1350	N/A	N/A	1350	1350
σ_P	108[e]	31[f]	N/A	31	75[g]	N/A	N/A	31	75

[a] Values are based on open-pollinated progeny at age 15 years, 3 seed planning zones averaged (A. Yanchuk, pers. comm., Jan. 1992).
[b] i1 is assumed to be 1 tree in 4; subsequent values for i are from the breeding plan.
[c] Selection intensity is likely to be lower than that specified in breeding plan.
[d] N/A = not applicable.
[e] $108 = (2)(5800)^{1/2}$.
[f] $31 = (675+(463-338)+(675/4))^{1/2}$.
[g] $75 = ((5800)-(1500-1350))^{1/2}$.

Gain prediction

Cycle	Population	Gain equation	Calculation	Gain[a]	
				cm	%
1	Wild-stand selections	$i1\ \sigma^2_{A1}/\sigma_{P1}$	(1.3) (1500)/108	18	7
	Rogued orchard	$i2\ .5\sigma^2_{A2}/\sigma_{P2}$	(1.3) (.5)(1350)/31	28	11
2	Breeding population	$i3\ .5\sigma^2_{A2}/\sigma_{P2}$	(0.8) (.5)(1350)/31	17	7
	Rogued orchard :				
	Family select.	$i4\ .5\sigma^2_{A4}/\sigma_{P4}$	(1.3) (.5)(1350)/31	28	11
	Individual sel.	$i5\ .5\sigma^2_{A5}/\sigma_{P5}$	(2.3) (.5)(1350)/75	21	8
3	Breeding population :				
	Family select.	$i6\ .5\sigma^2_{A4}/\sigma_{P4}$	(1.1-)(.5)(1350)/31	<24	<9
	Individual sel.	$i7\ .5\sigma^2_{A5}/\sigma_{P5}$	(2.3) (.5)(1350)/75	21	8
	Rogued orchard				
	Family select.	$i8\ .5\sigma^2_{A8}/\sigma_{P8}$	(1.3) (.5)(1350)/31	28	11
	Individual sel.	$i9\ .5\sigma^2_{A9}/\sigma_{P9}$	(2.3) (.5)(1350)/75	21	8

[a] Gain in height at age 15 years; starting mean is 2.6 m.

APPENDIX 3. (Cont'd.)

B. Lodgepole pine

Gain parameters

Parameters[a]	Subscript number								
	1	2	3	4	5	6	7	8	9
i	1.8[b]	1.3	0.8	1.3	2.3	0.5	2.3	1.3	2.3
σ^2_A	120	110	N/A[c]	110	110	N/A	N/A	110	110
σ_P	35[d]	10[e]	N/A	10	24[f]	N/A	N/A	10	24

[a] Values are based on open-pollinated progeny at age 6 years; parameters were averaged from 8 progeny tests in 3 breeding zones (M. Carlson, pers. comm., Jan. 1992).

[b] i1 is assumed to be 1 tree in 10; subsequent i values are from the breeding plan.

[c] N/A = not applicable.

[d] $35 = (2)(610)^{1/2}$.

[e] $10 = (55+(54-30)+15)^{1/2}$.

[f] $24 = (610)-(120-110))^{1/2}$.

Gain prediction

Cycle	Population	Gain equation	Calculation	Gain[a]	
				cm	%
1	Wild-stand selections	i1 $\sigma^2_{A1}/\sigma_{P1}$	(1.8) (120)/35	6	6
	Rogued orchard	i2 $.5\sigma^2_{A2}/\sigma_{P2}$	(1.3)(.5)(110)/10	7	7
2	Breeding population	i3 $.5\sigma^2_{A2}/\sigma_{P2}$	(0.8)(.5)(110)/10	4	4
	Rogued orchard :				
	Family select.	i4 $.5\sigma^2_{A4}/\sigma_{P4}$	(1.3)(.5)(110)/10	7	7
	Individual sel.	i5 $.5\sigma^2_{A5}/\sigma_{P5}$	(2.3)(.5)(110)/24	5	5
3	Breeding population :				
	Family select.	i6 $.5\sigma^2_{A4}/\sigma_{P4}$	(0.5)(.5)(110)/10	3	3
	Individual sel.	i7 $.5\sigma^2_{A5}/\sigma_{P5}$	(2.3)(.5)(110)/24	5	5
	Rogued orchard				
	Family select.	i8 $.5\sigma^2_{A8}/\sigma_{P8}$	(1.3)(.5)(110)/10	7	7
	Individual sel.	i9 $.5\sigma^2_{A9}/\sigma_{P9}$	(2.3)(.5)(110)/24	5	5

[a] Gain in height at age 6 years; starting mean is 1.0 m.

APPENDIX 3. (Cont'd.)

C. Interior Douglas-fir

Gain parameters

Parameters[a]	Subscript number								
	1	2	3	4	5	6	7	8	9
i	1.3[b]	1.3	0.8	1.3	2.3	0.5	2.3	1.3	2.3
σ^2_A	280	250	N/A[c]	250	250	N/A	N/A	250	250
σ_P	42[d]	15[e]	N/A	15	29[f]	N/A	N/A	15	29

[a] Values are based on open-pollinated progeny at age 6 years; parameters were averaged from 8 progeny tests in 3 breeding zones (B. Jaquish, pers. comm., Jan. 1992).

[b] i1 is assumed to be 1 tree in 4; subsequent i values are from the breeding plan.

[c] N/A = not applicable.

[d] $42 = (2)(889)^{1/2}$.

[e] $15 = (125+(127-63)+31)^{1/2}$.

[f] $29 = ((889)-(280-250))^{1/2}$.

Gain prediction

Cycle	Population	Gain equation	Calculation	Gain[a]	
				cm	%
1	Wild-stand selections	$i1 \quad \sigma^2_{A1}/\sigma_{P1}$	(1.3) (280)/42	9	8
	Rogued orchard	$i2\ .5\sigma^2_{A2}/\sigma_{P2}$	(1.3)(.5)(250)/15	11	10
2	Breeding population	$i3\ .5\sigma^2_{A2}/\sigma_{P2}$	(0.8)(.5)(250)/15	7	6
	Rogued orchard:				
	Family select.	$i4\ .5\sigma^2_{A4}/\sigma_{P4}$	(1.3)(.5)(250)/15	11	10
	Individual sel.	$i5\ .5\sigma^2_{A5}/\sigma_{P5}$	(2.3)(.5)(250)/29	10	9
3	Breeding population :				
	Family select	$i6\ .5\sigma^2_{A4}/\sigma_{P4}$	(0.5)(.5)(250)/15	4	4
	Individual sel.	$i7\ .5\sigma^2_{A5}/\sigma_{P5}$	(2.3)(.5)(250)/29	10	9
	Rogued orchard				
	Family select.	$i8\ .5\sigma^2_{A8}/\sigma_{P8}$	(1.3)(.5)(250)/15	11	10
	Individual sel.	$i9\ .5\sigma^2_{A9}/\sigma_{P9}$	(2.3)(.5)(250)/29	10	9

[a] Gain in height at age 6 years; starting mean is 1.06 m.

APPENDIX 3. (Cont'd.)

D. Western larch

Gain parameters

Parameters[a]	Subscript number								
	1	2	3	4	5	6	7	8	9
i	1.3[b]	1.3	0.8	1.3	2.3	0.5	2.3	1.3	2.3
σ^2_A	1490	1340	1340	N/A[c]	1340	1340	N/A	N/A	1340
σ_P	92[d]	33[e]	N/A	33	64[f]	N/A	N/A	33	64

[a] Values are based on open-pollinated progeny at age 8 years; parameters are from 1 progeny test at 1 location in Idaho (Rehfeldt 1992).

[b] i1 is assumed to be 1 tree in 4; subsequent i values assume a breeding plan similar to that for interior Douglas-fir.

[c] N/A = not applicable.

[d] $92 = (2)(4210)^{1/2}$.

[e] $33 = ((670+(572-335)+168)^{1/2}$.

[f] $64 = ((4210)-(1490-1340))^{1/2}$.

Gain prediction

Cycle	Population	Gain equation	Calculation	Gain[a]	
				cm	%
1	Wild-stand selections	i1 $\sigma^2_{A1}/\sigma_{P1}$	(1.3) (1490)/92	21	6
	Rogued orchard	i2 $.5\sigma^2_{A2}/\sigma_{P2}$	(1.3)(.5)(1340)/33	26	8
2	Breeding population	i3 $.5\sigma^2_{A2}/\sigma_{P2}$	(0.8)(.5)(1340)/33	16	5
	Rogued orchard :				
	Family select.	i4 $.5\sigma^2_{A4}/\sigma_{P4}$	(1.3)(.5)(1340)/33	26	8
	Individual sel.	i5 $.5\sigma^2_{A5}/\sigma_{P5}$	(2.3)(.5)(1340)/64	24	7
3	Breeding population :				
	Family select.	i6 $.5\sigma^2_{A4}/\sigma_{P4}$	(0.5)(.5)(1340)/33	10	3
	Individual sel.	i7 $.5\sigma^2_{A5}/\sigma_{P5}$	(2.3)(.5)(1340)/64	24	7
	Rogued orchard				
	Family select.	i8 $.5\sigma^2_{A8}/\sigma_{P8}$	(1.3)(.5)(1340)/33	26	8
	Individual sel.	i9 $.5\sigma^2_{A9}/\sigma_{P9}$	(2.3)(.5)(1340)/64	24	7

[a] Gain in height at age 8 years; starting mean is 3.4 m.

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