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BREEDING STRATEGIES OF IMPORTANT TREE SPECIES IN CANADA

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Abstract

Breeding programs and strategies for four major tree species of Canada are presented, including Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), jack pine (*Pinus banksiana* Lamb), the larch species (*Larix* spp.), and black spruce (*Picea mariana* (Mill.) B.S.P.). The proposed breeding strategies for the species incorporate several new concepts and techniques for advanced-generation breeding plans.

Résumé

Des programmes et des stratégies d'hybridation pour les quatres espèces principales au Canada sont présentés, à savoir le Douglas taxifolié (*Pseudotsuga menziesii* (Mirb.) Franco), le pin gris (*Pinus banksiana* Lamb), l'espèce des laricins (*Larix* spp.), et l'épinette noire (*Picea mariana* (Mill.) B.S.P.). Les stratégies d'hybridation proposées pour les espèces incorporent plusieurs concepts et techniques nouveaux pour des plans d'hybridation des générations anticipées.

Foreword

By the late 1970s, operational tree improvement programs had been initiated in all regions of Canada. These programs are often carried out cooperatively with industrial and governmental organizations and universities. They deal with major commercial species for the region; genetically improved seed is currently being produced for reforestation. Also, many of these programs are now initiating advanced-generation breeding plans.

During the 24th Canadian Tree Improvement Association meeting, issues concerning advanced-generation breeding will be discussed under the general theme of "Future Forests: Options and Economics." While the symposium will address a broader issue, we thought it would be an opportune time to organize a workshop to learn about the specific tree breeding programs and strategies for important tree species in Canada. Due to time constraints, we could include only four major species: Douglas-fir, jack pine, the larch species, and black spruce.

The authors present outlines of advanced-generation breeding plans for the species. The breeding strategies incorporate several new concepts and approaches, such as using modified genetic testing procedures, breeding population management using sublines, and vegetative propagation techniques. All the breeding strategies are aimed at obtaining an optimal genetic gain under biological constraints and economic realities.

It is also recognized that the breeding plans presented relate to the specific programs, and that further refinement may be necessary as we gain more information and experience. Following the four lead presentations, discussions on the issues and problems concerning tree breeding activities are expected to take place. The purpose of this workshop is to exchange ideas and views in implementing operational tree improvement programs for advanced generations.

We appreciate the contribution of the authors and the reviewers. Additional review comments were provided by D.P. Fowler and C.B. Talbert. We thank Caroline Simpson for editing and publication of this report.

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BREEDING PROGRAMS AND STRATEGIES FOR DOUGLAS-FIR IN NORTH AMERICA

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Abstract

Douglas-fir breeding programs in western North America are discussed and compared. The existing programs have followed one of two basic strategies in the first generation; diallels or open-pollinated testing. Large differences in breeding zone size exist between programs. Advanced-generation strategies have been developed and are in progress for some programs. Where these strategies are fully designed, a complementary mating design is being implemented to estimate second-generation parental breeding values separate from material for forward selection. The integration of the breeding programs with operational planting is an important factor in breeding strategy, particularly with regard to subline structure.

Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has a wide natural geographic distribution in western North America, ranging from 55 degrees in central British Columbia to as far south as 20 degrees in Mexico (Harlow and Harrar, 1969). It is one of the most important timber species on the continent.

Douglas-fir wood is strong and highly valued as dimension lumber. The first logging and reforestation efforts on the west coast of British Columbia, Washington, and Oregon were directed at Douglas-fir. This resulted in genetics research as early as 1912 (Munger and Morris, 1936) in Washington and Oregon. In British Columbia, inbreeding and wide crossing work began in the mid 1950s (Orr-Ewing, 1965; Orr-Ewing *et al.*, 1972). These early studies shaped the understanding of Douglas-fir genetics, but contributed little material to later efforts to produce genetically superior reforestation stock.

Efforts to understand the genecology of Douglas-fir, in support of reforestation programs, began in the 1950s (Schmidt, 1973; Ching and Hinz, 1978; Illingworth, 1978; Rehfeldt, 1989; Sorensen, 1983; Campbell, 1986). This work added greatly to the knowledge of the genetics of Douglas-fir, and has influenced the strategies of breeding programs in different parts of the range.

The Players

Breeding and seed orchard programs for Douglas-fir are structured around a variety of agencies and cooperatives, with varying levels of exchange between them. In British Columbia, most forest land is publicly owned and forest companies work through license arrangements. Under this ownership pattern, cooperatives have developed for the coast and interior of the province, through which all agencies meet to set goals and priorities. The British Columbia Forest Service (BCFS) operates separate coast and interior Douglas-fir breeding programs for public land through the cooperatives.

In western Washington and Oregon, there is a much larger percentage of privately owned forest land than in B.C. Most forest companies and public agencies involved in Douglas-fir tree improvement activities do so through the Northwest Tree Improvement Cooperative (NWTIC), encompassing 35 organizations. The United States Forest Service (USFS), the Bureau of Land Management, and the Washington State Department of Natural Resources are members of the NWTIC, but carry out testing independently when they are the only landowner in a breeding zone.

Another significant player is Weyerhaeuser Company. Their 1.1 million-ha land holdings in western Washington and Oregon are primarily suitable for growing Douglas-fir, and they have been involved in an aggressive improvement program since the late 1960s.

In eastern Washington, Idaho, and western Montana, tree improvement efforts are coordinated by the Inland Empire Tree Improvement Cooperative (IETIC). Testing is done primarily by the USFS with other cooperators participating relative to their own needs and objectives. Seed orchard establishment is done independently by cooperators.

Breeding Zones

Breeding zone sizes differ substantially between coastal U.S. and B.C. programs. In coastal B.C. parent-tree selection and seed orchard planning were originally based on seed zones that delineated major climatic regions. A number of studies were established to investigate source-related differences, including wide-crossing work by Orr-Ewing *et al.* (1972), early provenance testing by Ching (Ching and Hinz, 1978), followed by more provenance testing by Schmidt and Illingworth (Illingworth, 1978). These led to the observation that source-related genetic differences were not strongly exhibited among coastal populations and maladaptation did not appear to be a problem unless interior sources were used.

At present, both provenance and progeny test data support the use of a single large Maritime zone (west of the Coast mountains, below 650 m and on sites ecologically suitable for Douglas-fir). This zone ranges from 48.4 degrees on southern Vancouver Island to about 50.7 degrees. In the transition area between the coast-interior climates (Coast mountains), seed movement is more restrictive as few data are available to suggest otherwise.

In western Washington and Oregon, provenance research began as early as 1912 (Munger and Morris, 1936). Later work was carried out by Ching (Ching and Hinz, 1978), Campbell, Sorensen (Campbell, 1986; Campbell and Sorensen, 1978), and also by Weyerhaeuser Company. The range of Douglas-fir in western Washington and Oregon is substantially larger than in B.C. (over 7 degrees in latitude) and encompasses a wide range of physiographic and climatic types. Results from early provenance studies influenced the Western Forest Tree Seed Council to take a conservative approach to seed zonation (Anonymous, 1966). This is supported by the short-term genecological work of Campbell and Sorensen, particularly in south-west Oregon. Weyerhaeuser results, however, show that broader movement of select families is acceptable across moderate environments (Stonecypher, 1990). There is currently interest within the NWTIC to consolidate some breeding zones to reduce testing costs.

Weyerhaeuser geneticists originally established six low elevation (<650 m) seed zones in western Washington and Oregon to govern deployment of improved planting stock on their lands. Deployment of first-generation families continues to be primarily within these zones. Work is also ongoing to screen parents for adaptive traits and link this information to risk on specific sites (Wheeler *et al.*, 1990). As this information becomes more complete, their deployment strategy will focus more on matching families to sites, both within and across zones, but with continuing controls over the allowable "environmental distance" from origin to planting site.

The genecology of interior Douglas-fir in the U. S. has been intensively studied by Rehfeldt (1989). His work led to the delineation of breeding zones based on geographic and elevational criteria. Pro-

Table 1. Comparative statistics for the five principle Douglas-fir genetic improvement programs in western North America.

Activity	Program[a]				
	BC coast	Weyco.	NWTIC[b]	BC int.	IETIC[c]
No. Breeding zones	2	6[d]	73	8	13
1st-generation parents in test	560	2700	20569	1700	2855[e]
Types of 1st-generation tests	diallel, O.P., factorial	diallel, polymix, singl. pr.	O.P., singl. pr.	O.P.	O.P.
No. 1st-generation tests	130	400	630	32	41
Primary traits	Volume, density	Volume, form	Volume, form	Volume	Frost, volume
Secondary traits	Form, frost	Density, frost	Density	Density, frost	Pests, form

a. Describes only principal programs by administrative group or agency; some programs are excluded, including USFS programs outside cooperatives.
b. Source; 1992 Progress Report for Local Cooperative Programs, prepared by L. Ray, Daniels and Assoc., 1143 W. Roanoke St., Centralia, WA. 98531.
c. Source; Inland Empire Tree Improvement Cooperative, Sixteenth Progress Report, by L. Fins, M. Rust, and C. Amonson, Univ. of Idaho, Moscow, ID. 83843.
d. Will be moving toward the consolidation of some zones in advanced generations.
e. Actual number is somewhat less, as some families planted in greater than 1 zone.

grams within the IETIC follow Rehfeldt's guidelines.

In the interior of British Columbia, little work was done to determine breeding zones prior to 1980. Delineation of areas for testing and seed orchard establishment were based on results from Rehfeldt's work and on biogeoclimatic classification (Pojar *et al.*, 1987). There are currently eight breeding zones and testing has proceeded within each.

Breeding Strategies

Genetic improvement strategies differ among programs due to test age, cooperative structures, and agency goals. Table 1 contrasts the programs for several important criteria.

Traits

Douglas-fir is valued for dimension lumber and veneer. It is also used for pulp and paper, but its fiber characteristics for these products are not as desirable as many other species which share its range. Pests such as root rot (*Phellinus weirii* and *Armillaria ostoyae*) and, Douglas-fir tussock moth (*Orgyia pseudotsugata*), spruce budworm (*Choristoneura* spp.), and Douglas-fir needle cast (*Rhabdocline pseudotsugae*) are a problem in some areas, but they are generally considered to be better controlled through cultural manipulation than through breeding. Therefore, with the exception of the IETIC program, the focus is on yield traits (height or stem volume), and quality traits (wood density, stem form). Frost hardiness is also considered where appropriate. Due to their more extreme environments, the IETIC program is placing a higher emphasis on adaptive traits such as frost hardiness and susceptibility to spruce budworm.

Selection of First-Generation Parents

Base populations for all the breeding programs, were selected from natural stands within the breeding zones. The B.C. coastal program also included trees from western Washington. Selection criteria varied, but generally base population parents were selected for form and size characteristics relative to other trees in an even-aged stand. Geographic coverage of the zone was a priority, and avoidance of co-ancestry was achieved with minimum distances between trees. The earlier coastal programs put significant effort into the selection of base populations, but gains are estimated to be small due to low individual tree heritabilities in natural stands. Consequently, later programs have put relatively less effort into this phase.

First-Generation Breeding and Testing

Early test strategies varied among the coastal programs, depending upon the material available. On the B.C. coast, intensive parent-tree selection and clonebanks provided material for controlled matings. In the early 1970s, a six-tree half diallel mating design (without selfs) was initiated to estimate parental general combining abilities (GCA) and variance components, and to make material available for second-generation selections. Beginning in 1975, diallels were grouped in annual series, and each series planted on 11 test-sites. The large number of sites reflect uncertainty regarding genotype by environment interactions. Three-hundred and seventy-two parents are currently in test across 88 test sites. An additional group of 161 parents from Washington state are being tested, using open-pollinated progeny, across five sites each. These, in combination with various other tests, bring the total number of tested parents for the coastal area (Maritime seed zone) to about 560.

Weyerhaeuser Company began their testing in 1973 with polymix crosses and single-pair matings, but switched to six-tree half diallels in 1980. Their program encompassed six breeding zones, and there are currently about 2700 low-elevation Douglas-fir parents in test. Their objectives are similar to those of the coastal B.C. program, but they are generally testing each parent on three to four sites, complemented by extensive research trials across zones.

With the exception of the Weyerhaeuser and B.C. coastal programs, virtually all first-generation testing by other programs has been with open-pollinated seed. This strategy reflects the desire to quickly obtain GCA information for orchard establishment or culling. As shown in Table 1, the NWTIC program is a massive effort with 73 breeding zones and 20,569 parents in test. The interior programs also show substantial efforts, with about 1700 and 2800 parents in the B.C. Forest Service and IETIC programs, respectively.

Progeny test designs differ somewhat among the various first-generation programs. With the exception of some USFS tests within the IETIC, all programs choose homogeneous logged areas within the breeding zone. Site preparation is usually minimal, and trees are planted in non-contiguous or small row plots. Weed and browse control are used in various forms to allow the trees to become free-to-grow. Within the IETIC, some tests are established as described above, but the USFS is also using farm-field early-selection trials (Carlson, 1990) with intensive site preparation.

Interpretation and Deployment of First-Generation Test Results

Most programs have, or will establish, untested first-generation clonal or seedling seed orchards. The decision to use seedlings in some early coastal orchards was based on high mortality due to graft incompatibility (Copes, 1982). Within the IETIC, some cooperators made a strategic decision to avoid the cultural problems associated with grafts and to take advantage of early test data by using better seedlings from within better families. For all coastal programs, graft incompatibility problems are now held to acceptable levels through the use of compatible rootstock.

Decisions to establish non-tested orchards on the coast were, in some cases, due to unrealistic expectations of genetic gains from parent-tree selection in wild stands. As parental breeding value data become available, many of these early orchards are being culled or replaced and orchard management techniques such as supplemental mass pollination or controlled matings are being implemented to increase gains.

In the B.C. interior, orchard establishment is being delayed until 6-year test results are available. At that time, the better 50-75% of the test clones will be put in an orchard. Further culling will proceed as tests age.

Weyerhaeuser Company has adopted a more aggressive strategy to obtain the highest possible genetic gains for growth and quality traits based on their test results (usually age 8). Using technology developed for the production of rooted cuttings, they are able to vegetatively amplify seed from controlled crosses among better parents. They are also collecting and deploying wind-pollinated orchard seed by female parent.

Selection of Advanced-Generation Breeding Populations

The different breeding programs are at different stages of development, and varying levels of attention have been given to advanced-generation selection strategies. The coastal BCFS and the Weyerhaeuser programs have fully developed strategies that are currently being implemented, whereas strategies are not yet fully developed for the BCFS interior, IETIC, and NWTIC programs.

Current plans for the BCFS interior program are to select parents represented in open-pollinated tests (backward selections) based on 6-year heights. A later evaluation for wood density will lead to some independent culling of clones with low breeding values.

The USFS, within the IETIC, is using early-selection trials to screen populations based on an adaptation index for shoot phenology. This reflects the highly variable conditions within this zone and the problems with frost damage. Advanced-generation breeding and testing strategies are being developed, and the expectation is that selections from this material will be based on yield characteristics and possibly resistance to diseases or insects.

Within the organizational structure of the NWTIC, 12 second-generation Co-ops have been organized. Plans and test ages differ somewhat among cooperators and breeding zones, however, breeding populations are derived primarily from forward selections within existing open-pollinated progeny tests. Selections are based on stem volume and wood density, with independent culling based on stem form. To date, all 12 second-generation programs plan tests that will allow an expansion of breeding-zone boundaries and the merging of concurrent programs operating in the same geographic area.

The coastal BCFS and the Weyerhaeuser Company programs are both currently selecting second-generation populations. In B.C., selections are primarily from the diallel test series, while Weyerhaeuser Company selections are currently from tests with polymix and single-pair matings. Diallel tests will contribute more in the coming years. Many similarities exist among the advanced-generation strategies for Weyerhaeuser Company and the BCFS, however, there are some important differences which relate primarily to agency goals and the administrative structure of each organization.

For most of their first-generation test series, Weyerhaeuser established check lots which provided a common base for comparison of selections. Analyses were developed to estimate breeding and index selection values for all forward selection candidates, as well as their parents, across all test series relative to this common check. Current selection traits include stem volume, ramicorn branching, stem sinuosity, and wood density, with frost hardiness considered at the deployment stage. A "main" population is being developed that emphasizes volume and quality, while smaller "elite" populations are being set up emphasizing low defect and high wood density. Candidates are identified on paper and then field verified. Family and within-family selection is employed for volume, ramicorn branching, and sinuosity. A mass-selection approach is being used for wood density. Forward selection within these first-generation tests is progressing, and the ultimate goal is to select 150 trees from each of the two original Oregon zones and 300 across all four of the original Washington zones.

The coastal B.C. breeding program is also selecting from within a variety of test projects. Different deployment goals and mating strategies than those of Weyerhaeuser, result in less need to bring breeding value estimates and index selection values to a common base. Most selections are being made from the diallel test series using an index based on 12-year stem volume and wood density. Short-lists of candidate trees are developed based on their index value and on goals for co-ancestry control within sublines. Candidates are then viewed in the field, and some trees are rejected if form characteristics are not satisfactory.

Trait improvement goals for the coastal B.C. program are to develop a general breed for high volume production, without losses in wood-density or stem-form potential. Index weights for selections within diallel sets vary based on the genetic variances and correlations for volume and density. This partially subjective procedure is designed to take best advantage of each diallel set towards meeting the overall population goal.

A total breeding population of 450 parents is planned for the Maritime seed zone. This will likely be reduced following a generation of testing all selections using a common procedure.

Advanced-Generation Mating Designs

The various breeding programs can be categorized into two groups: 1) programs with open-pollinated tests, moving to selections and matings for full-sib tests, and on to the selection of pedigreed breeding populations (BCFS-interior, IETIC, NWTIC and USFS programs), and 2) programs with full-sib tests in the first generation, that are making forward selections for a second-generation population (BCFS coastal, Weyerhaeuser). As programs in category 1 are in an earlier stage, advanced-generation mating, testing, and deployment strategies are not yet fully developed. These will be discussed only briefly. Programs in category 2 have more complete plans at this point, and a more thorough discussion of these strategies follows.

Programs in category 1 are making both forward and backward selections from parental populations, and mating these using designs such as small factorials or diallels to develop full-sib material for within-family selections. Subline structure will be imposed at this point. Genetic variances and correlations will be estimated using this full-sib material, and will guide decisions related to further selection and testing. The NWTIC and interior BCFS programs are making selections primarily on stem yield and quality traits, but due to their environments, the IETIC programs will continue a heavier focus on adaptive traits.

The programs in category 2 are illustrated in Figure 1. Both the Weyerhaeuser and BCFS coastal programs are using the following general procedure: a) subdivide the advanced-generation population into sublines, b) use separate complimentary mating designs to estimate parental GCA and to generate pedigreed material for selecting the next generation, c) test using inten-

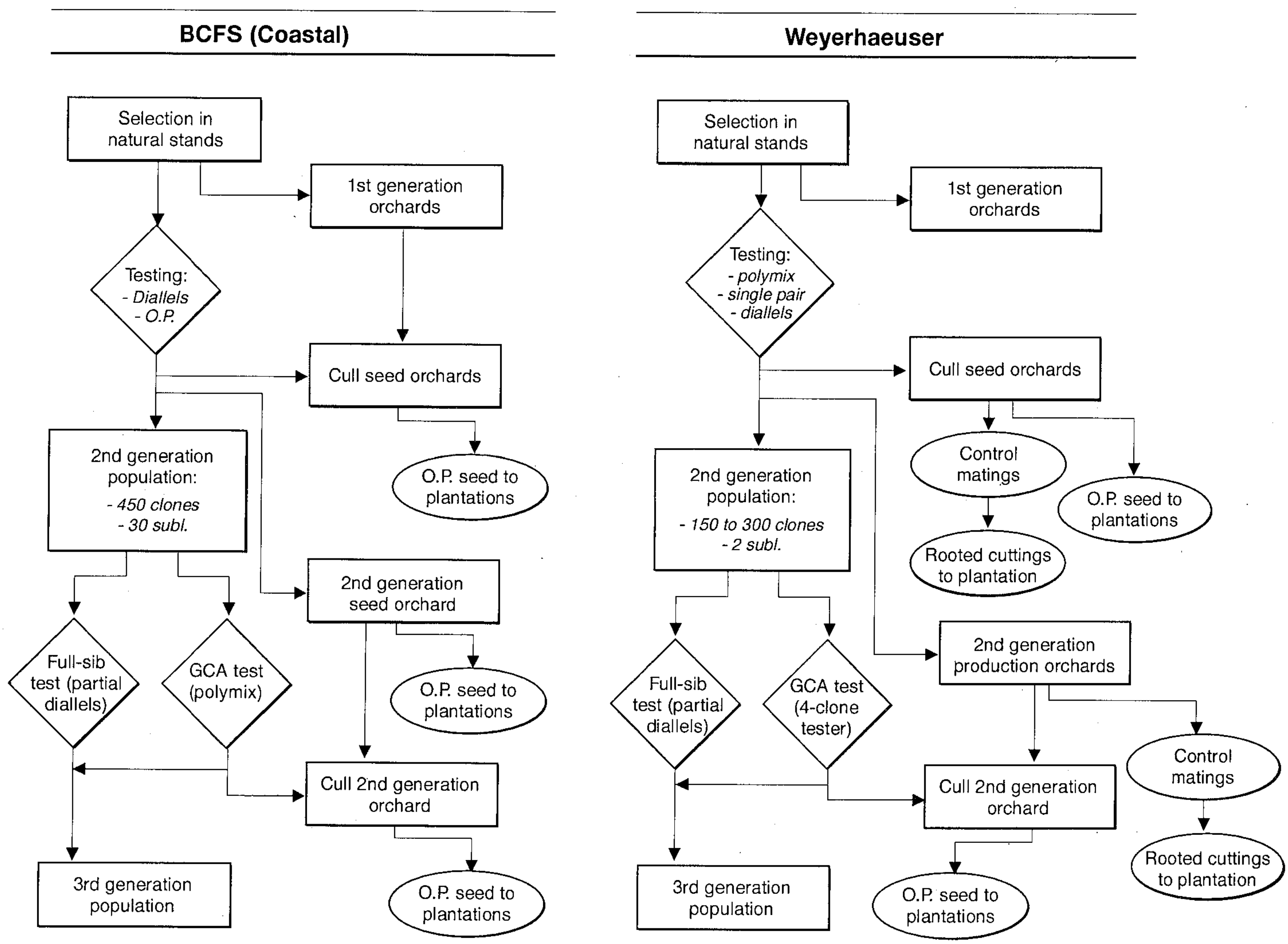

Figure 1. Flow charts of the coastal Douglas-fir breeding program strategies being implemented by the B.C. Forest Service and Weyerhaeuser Company.

sively prepared and managed field trials, and d) carry a main growth and quality breed, with associated breeds for specific traits of interest. Differences in how these steps are being carried out relate to different deployment strategies.

Weyerhauser is selecting second-generation populations of about 150 to 300 individuals per breeding zone. Within each original breeding zone, selections are divided into two sublines (eight sublines in the consolidated Washington zone). Selections within each subline are divided into four quartiles based on rank. Full-sib mating is carried out using a mating design that is assortative in that crosses are carried out within, but not generally between quartiles. Trees in the top quartile are crossed four times each, three times in the next quartile and so on. Elite breeds for various traits such as high stem quality, wood density, and frost tolerance will be made between the best individuals across sublines. In general, however, sublines will be kept separate. This subline strategy is designed to maximize gain within sublines, but requires a controlled cross deployment strategy (discussed later) to avoid inbreeding in plantation stock.

Matings for GCA testing will use a four-parent tester design, in which each breeding population selection will be crossed as either a male or female (whichever can be most quickly accomplished for the clone) to four common testers. These testers will be used for all selections within a breeding zone and for testing in future generations. The tester design will allow all GCA tests to be done without the confounding of inbreeding depression.

In the BCFS program, a breeding population of about 450 clones is being selected and subdivided into small sublines of about 12 to 16 clones. All co-ancestry is contained within sublines. Breeding population clones (for the second generation and beyond) are mated using a polymix of 15 clones. These 15 clones are not related to any clones in the breeding population, and are purposely selected as having stem volume and wood density breeding values that are close to zero. Breeding values for these polymix clones are nearly equal to reduce the impact of differential success of certain male-female combinations. As with the Weyerhaeuser program, inbreeding will not influence GCA testing.

Within sublines, crosses are made using a double-pair circular mating design. Clones are crossed assortatively based on their estimated breeding values, with better clones put in more crosses when feasible. A restriction is placed on crosses to limit inbreeding for any given cross to less than F=0.125. This may be relaxed in future generations when inbreeding effects are better understood.

Most sublines (about 80%) are being bred towards the goal of maximizing stem volume while maintaining stem form and wood density at existing levels. Selections from first-generation diallel groups that are exceptional for wood density or stem form will be put in separate sublines to develop specialty breeds. Selections in these sublines will be for the appropriate specialty trait, with some exchange with the main breed sublines, over generations. The small subline structure is designed to control inbreeding in subsequent seed orchard populations, but will be reviewed when better data are available on inbreeding effects.

Advanced-Generation Testing Strategies

This section will only describe the strategies for the Weyerhaeuser and BCFS coastal programs. Both these programs are using complementary breeding designs, and will have separate tests to meet specific objectives. GCA testing for both programs will use non-contiguous plots, on three or four sites representing the higher site qualities within the respective ownerships. These sites will be distributed throughout the breeding zone. Experience has shown that better sites allow faster and more precise expression of genetic worth, and correlate well with poorer sites. Also, stem sinuosity and ramicorn branching are more strongly expressed on high site-index areas, and cannot be assessed adequately on poor sites.

Candidate sites will be evaluated on an individual basis for site preparation needs but, in general, testing will be done on areas cleared of stumps and debris and then cultivated to homogenize soils. Spacings will be narrower than those normally used in operational forestry. Weyerhaeuser plans 2x2 m spacing and the BCFS plans 1x1 m spacing, although this will be modified depending on the site. Interlocking rep designs may be used (modifications of Libby and Cockerham, 1980) to allow thinning. Correlations between early data (3- or 4-year) from this type of site and later data (13-year) on more widely spaced field sites are high for both volume and wood density (BCFS unpublished data). Standard checks of natural stand and test crosses to known clones will be included.

For the BCFS program, a thinning will be performed at age 4 from seed (after measuring height and diameter) for the purpose of estimating wood density GCA from the thinned material.

Each full-sib family from the circular mating design will be deployed in two 25-tree blocks for the BCFS program. These will provide material for within-family (forward) selections for the following generation.

Full-sib families in the Weyerhaeuser program will be outplanted in a non-contiguous plot design on four sites, paired where possible with the GCA test. The test will be interspersed with blocks of check lots for demonstration purposes. Non-contiguous plots rather than family-block plots are planned to allow specific combining ability effects to be considered when choosing full-sib families for deployment. It is felt the loss of efficiency for forward selection will be minimal with good site selection and maintenance.

Deployment of Improved Genotypes

All of the Douglas-fir programs use or plan to use seed orchards to deploy improved material. These orchards take various forms relative to the stage of the various programs and the amount of data available for culling. In addition, management varies according to agency goals, from low levels with little activity outside cone collection, to intensively managed with supplemental mass pollination, controlled matings and overhead irrigation for phenology delay and compression. Seed collection also varies from bulk to maintaining seed separate by female parent.

Advanced-generation deployment strategies differ between the BCFS and Weyerhaeuser programs, and account for most of the breeding strategy differences. Weyerhaeuser plans to use the best available material from the breeding program, at any given time, to produce controlled crosses that will be vegetatively amplified through rooted cuttings (some open-pollinated orchard seed will also be used by family). These cuttings will then be deployed to plantations in family blocks using families that meet the site conditions and plantation objectives. Foresters within the company will order specific families based on known performance data. This aggressive strategy makes possible the use of two sublines per breeding zone without the concern of inbreeding becoming a problem in the production population, as all co-ancestry is kept within sublines.

Due to a mix of land tenures, ownerships, seedling production facilities, and plantation management objectives, the BCFS program is less able to match specific families to sites as is done by Weyerhaeuser Company. Consequently, program objectives are to produce a general, stable breed for growth, density, and form. The exceptions will be the relatively minor use of good form or high density breeds in some areas. Rooted cuttings or other clonal options will not replace orchard seed in the foreseeable future. As seed will continue to be used, the breeding program and subline structure are designed to produce sufficient unrelated selected clones (about 30), for an orchard, to maintain genetic diversity, allow a continuum of reproductive phenologies and result in little or no inbreeding. As discussed above, when more data on inbreeding are available, sublines may be joined and some relatedness allowed in production populations. At present, the BCFS has one second-generation orchard established that will provide most of the Douglas-fir seed for public land over the next 15 to 20 years.

The use of rooted cuttings of specific families and the careful matching of genotypes to sites will allow Weyerhaeuser foresters to obtain more gain per unit time and breeding effort than in British Columbia. This strategy, however, requires a well-defined wood production goal and efficient management to ensure accurate and fast delivery of research results to operational programs. On public land in British Columbia, the mixture of tenures and management goals precludes such a deployment strategy. The use of a general breed is simpler and more acceptable within the context of integrated resource management. The exception may be the use of good form or high wood-density families on specific sites.

Tracking Long-Term Performance

As breeding programs progress and more selected material is established in operational plantations, the need to track progress increases. One such need is to link performance estimates based on single-tree assessments (as in progeny tests) with performance on a unit-area basis, particularly for yield traits. The performance lifts must also be linked to growth and yield models used for forest management purposes.

Realized-gain trials, in some form, have been established by Weyerhaeuser, the BCFS coastal program and some cooperators in the NWTIC. More are planned in all programs. Within the BCFS program, such area-based plots will be used to monitor long-term performance of improved material at key times as the breeding program proceeds through generations. This will involve comparing a small set of the best available material every one or two generations with natural stand checks. These trials will be maintained for a full rotation to monitor progress being made with the early-selection and fast generation turn-over of the breeding population.

Conclusions

The selection and breeding of Douglas-fir with genetically superior economic potential is receiving substantial effort in western North America. The many programs involved have been successful in exchanging knowledge, but each have a different set of economic, organizational, and biological constraints and opportunities that direct the methods and progress. This is particularly demonstrated by the different deployment strategies used by the Weyerhaeuser and BCFS coastal programs.

The time taken to progress through the first generation of breeding will be greatly reduced in advanced generations, as early selection and breeding techniques continue to be refined. In addition, the knowledge of genetic parameters, including genotype by environment interactions, will allow programs to progress more efficiently in the future.

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AN ADVANCED GENERATION BREEDING STRATEGY FOR JACK PINE IN ONTARIO

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Abstract

The foundation of the proposed advanced-generation breeding strategy is based on: the conservation of adaptive gene complexes by ensuring that breeding populations and zones are biologically sound, the maintenance of a minimum effective population size of 100 for managing inbreeding, and the inclusion of marginal gains analyses in determining the optimum selection age. A nucleus breeding system together with a simple mating design will be used to promote continued rapid genetic gains while minimizing the human and financial resource required. Farm-field testing procedures will be used for assessing genetic potential and small-scale field performance tests used for estimating realized gain. A pilot breeding population will be used to work out the details for implementation.

Introduction

Over the last 3 years, tree improvement efforts in Ontario have been revitalized through the establishment of an association of operational cooperatives. In spite of substantial industrial and government commitment to tree improvement, fiscal constraint and limited manpower are likely to continue for the foreseeable future. Budgeting decisions will go beyond simple cost/benefit analyses to include consideration of the opportunity costs — every dollar spent on tree improvement is a dollar that is not available for other programs. As a result, the goal of all advanced-generation breeding efforts in Ontario will be to optimize genetic gain in traits of commercial interest per unit time and dollar spent. Because of marginal costs, the optimum selection age is likely to be earlier than the age that maximizes gain per unit time.

In recognition of these realities, this paper describes the general approach to advanced-generation breeding envisioned for Ontario's jack pine (*Pinus banksiana* Lamb.) breeding populations. Although timing, goals, and selected traits may vary among programs, the proposed strategy is viewed as the basic design for all jack pine breeding populations. This paper begins by considering some basic biological and economic principles and how they apply to breeding programs. Then, recent theoretical and technological advances in the individual components of the breeding cycle are presented as the philosophical basis for the advanced-generation breeding strategy for jack pine.

Adaptation

When breeding zones and populations are rigorously constructed with regard to adaptive gene complexes, the importance of genotype by environment interaction will be greatly reduced and substantial efficiencies in genetic testing can be realized (Rehfeldt, 1984). However, even when breeding zones and populations are biologically sound, selection decisions must consider correlated responses in growth rhythm to ensure adaptive gene complexes do not deteriorate in advanced generations (Rehfeldt, 1992). Genecology studies of jack pine, designed to identify the patterns of adaptive variation, are currently in progress in Ontario. Testing procedures for Ontario's genecology program follow Rehfeldt (1986). The resulting information on adaptive variation will be used to ensure that breeding populations and the landbase they service are biologically sound. Such information provides the foundation for building an efficient advanced-generation program.

Effective Population Size

One of the primary concerns of multiple generation breeding strategies is the maintenance of a broad genetic base in order to manage the effects of inbreeding. Population genetics theory, as applied to conservation biology, provides valuable insights for tree breeders when considering the size of a breeding population. Frankel and Soule' (1981) refer to the 1% rule as the "basic rule of conservation genetics." This rule states that selection for performance and fertility can balance the effects of inbreeding depression if the increase in the inbreeding coefficient is no more than 1% per generation. There is a simple relationship between population size and the change in the inbreeding coefficient (delta F).

$$\text{Delta F} = 1/(2Ne)$$

Where Ne is the effective population size, *i.e.*, the size of an "ideal population" that is subject to the same degree of genetic drift as the actual population being considered. "Ideal" refers to a population that has random mating, a 1:1 sex ratio, and the number of progeny per family are randomly distributed. Deviations from this ideal reduce the effective population size below that of the actual population.

Therefore, the minimum effective population size for managing inbreeding is approximately 50. If a slightly more conservative criterion for the inbreeding coefficient where applied (*e.g.*, delta F = 0.5%) the minimum effective population size becomes 100 individuals. A second study identified the conservation goal as the retention of 90% of the original genetic variation after 200 years, and considered the impact of generation length (Hedrick and Miller, 1992). They found that when the generation interval was 10 years, an effective population size of between 50 and 100 would be required.

Genetic testing in advanced generations will emphasize within-family selection because family selection reduces the effective population size. As a result, beginning with the second generation, genetic tests will have fewer families and a greater number of individuals per family. Based on this information, an effective population size of 100 will be used as the initial standard for advanced-generation programs.

Economics

Over the last 15 years, a great deal of work has been devoted to identifying the optimum selection age for beginning the next breeding cycle. While substantial advances have been made in this area of study, the work has largely been a biological comparison of the trade-offs between gain per generation versus gain per unit time. However, a recent study (White and Hodge, 1992) examined optimum selection ages from a new perspective. The principles of marginal gains and economic discounting were included in the identification of optimum selection ages for slash pine (*Pinus elliottii*). They found that the discount rate had a large impact on selection efficiency (gain per year) and optimum selection age (Figure 1). At a zero discount rate (*i.e.*, no economic weighting of time), selection efficiency increased with increasing age through to age 10. Although the relative efficiency was less than for direct selection (volume at 15 years), the optimum selection age was estimated to be at 9 years, because of the ability to turn over generations more quickly. As the discount rate increased, early selection became more efficient than direct selection, and the optimum selection age decreased. A discount rate as low as 3%

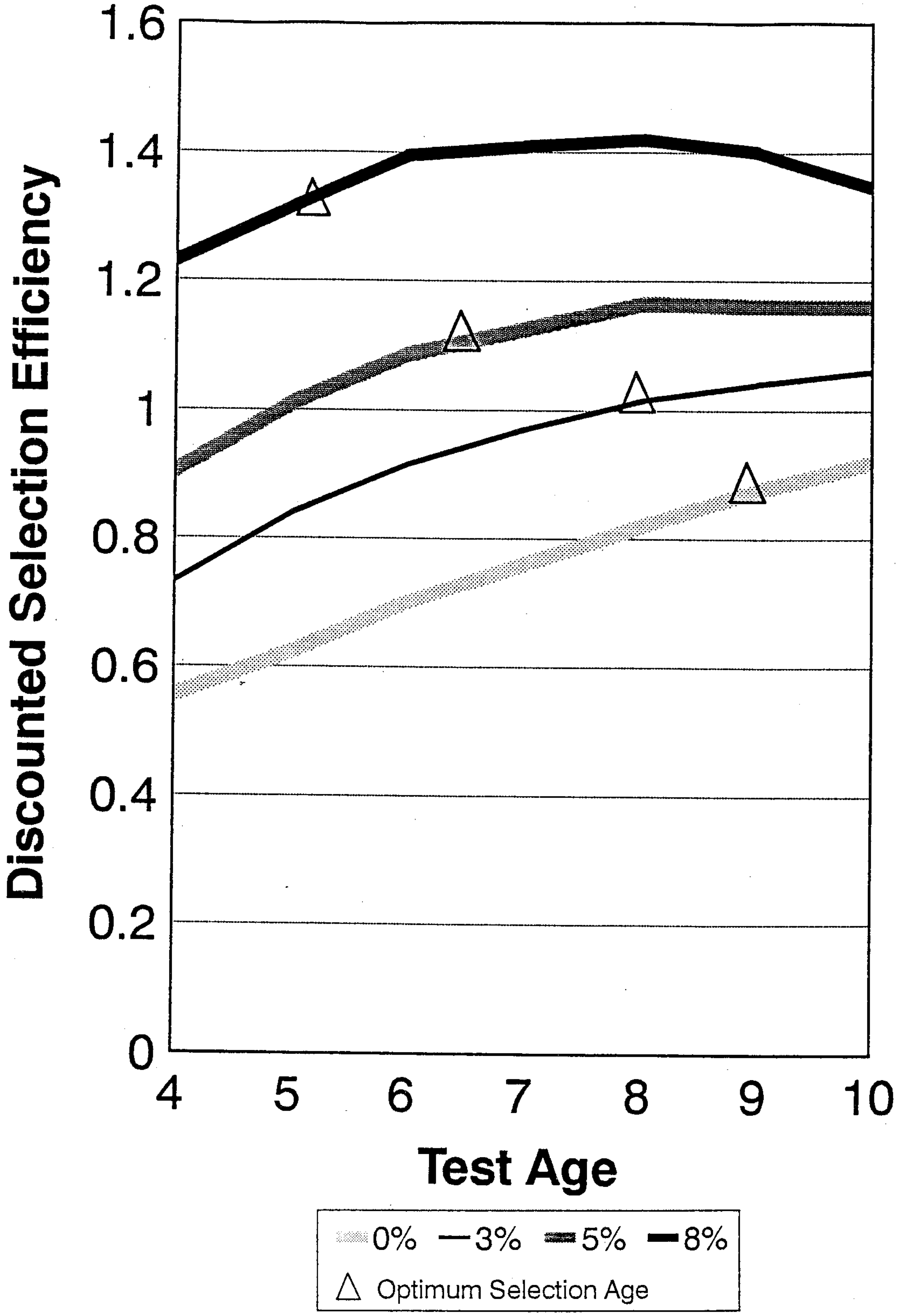

Figure 1. Discounted selection efficiency (0, 3, 5, and 8%) for improvement of 15-year volume in slash pine Efficiency is calculated on the basis of 12 test sites with good precision, *i.e.*, high heritabilities (From White and Hodge, 1992.)

resulted in early selection being more efficient than direct selection at age 15. That is, even for a single generation, the gains from direct selection were lower than from early selection. The authors concluded that there appeared to be little operational value in maintaining tests past age 10, as they become increasingly costly to measure with little incremental genetic benefit to the operational program.

The consideration of marginal gains will become part of the decision-making process for determining optimum selection ages for all advanced-generation breeding in Ontario.

Ontario's Jack Pine Program

There are several attributes of jack pine that make it an ideal choice for applied tree improvement and for forest genetics research purposes (Rudolph *et al.*, 1989). Jack pine is noted for its rapid juvenile growth and responsiveness to silviculture (Yeatman, 1984). Jack pine occurs in extensive even-aged stands throughout Ontario and is second only to black spruce in the size of the planting program. Flowering can occur at very young ages, with significant flowering by age 7. The high phenotypic variability in jack pine make it a promising candidate for genetic improvement in growth and form (Magnussen and Yeatman, 1987; Polk, 1972; Rudolph and Yeatman, 1982).

A tree breeder's goal is to change allele frequencies in economically important traits, while conserving allelic variation in adaptive traits. For ease of presentation, however, height growth will be used to illustrate the strategy. In practice, correlated responses in other traits will be considered when estimating breeding values. Although not explicitly identified at this time, the breeding goal for jack pine is likely to be oriented toward improved growth rate and form, while holding wood quality and phenology constant.

Since the early 1980s, 27 jack pine seed orchards have been established in Ontario. Each orchard contains seedlings from approximately 400 plus trees (Ontario Ministry of Natural Resources, 1987). At final roguing (no later than age 20), each orchard will contain no more than the best 25% of the trees. Several orchards have already been partially rogued to remove the poorest families.

Table 1. Heritability estimates for total tree height from field performance tests for four operational jack pine tree improvement programs (approximately 400 families in each program).

Age	Program				Mean
	1	2	3	4	
Individual Tree Heritability					
3	0.19	.13	-	-	0.160
5	.12	.11	.17	-	.133
6	-	-	-	.14	.14
7	.14	.13	-	-	.136
Family Heritability					
3	0.42	.29	-	-	0.345
5	.32	.25	.52	-	.363
6	-	-	-	.32	.32
7	.35	.28	-	-	.315

These roguings have been based on height (at ages 5 to 7) information obtained from between two and three genetic tests. Family heritabilities from field performance tests have averaged about 0.35 with a range between 0.25 and 0.52 (Table 1). These relatively low heritabilities are, at least in part, due to high levels of damage, especially as a result of white pine weevil. A typical test has fewer than 30% of the trees scored as undamaged.

Propose Advanced-Generation Breeding Strategy For Jack Pine

Selection

The selection of individuals to form the breeding population for the next generation will be based on ranking individuals based on their genetic worth, or breeding value. The efficiency of this selection is strongly dependent on the models, methodology, and techniques used to calculate breeding values. Theory and practice has shown that index selection is the most efficient method of selection (*e.g.*, Cotterill and Jackson, 1985). White and Hodge (1989) have described an index methodology, Best Linear Prediction, that maximizes the relationship between predicted and true breeding values for tree improvement programs where data are frequently unbalanced and messy.

Best Linear Prediction procedures are currently used to guide seed orchard roguing decisions in Ontario. These procedures will be extended to support the establishment of second-generation breeding populations that maximize selection efficiency. Second-generation breeding populations will include both backward and forward selections when warranted by breeding values estimates.

Mating Design

There are a number of mating designs of varying complexity available for advanced-generation breeding. The mating design, however, has considerably less impact on efficiency of gain than does the selection methodology and the time required to complete the breeding. For example, Cotterill (1986a) compared half-diallel mating with single-pair mating and found that while the more elaborate diallel mating provided the maximum gain per generation, the single-pair mating design provided greater gains per unit time because the controlled crosses could be completed in less time. Reductions of as little as 1 year in the generation interval had a marked influence on gains per unit time (Cotterill 1986b). The author noted that ambitious plans can destroy a tree improvement effort when executed poorly, and that it is much better to do a good job of a simple strategy than to make a mess of an elaborate design. When all else is equal, respect for Murphy's Law suggests the wisdom of keeping the mating design simple.

Given the limited resources available for controlled pollination work, the relative efficiencies of simple mating designs, the information available on parental breeding values, and the focus on within-family selection, controlled pollinations will be limited (between 50 and 100) and will not follow a rigid design. Rather, a "best mate" index will be used to predict the most promising crosses (Cotterill 1989).

Breeding System

Although sublining is the traditional approach to advanced-generation breeding, the financial returns under this system are diluted by spending limited resources on extensive controlled crosses across a relatively large breeding population. For example, a sublining system with 400 selections (Ontario's standard program size) would require a minimum of 200 controlled crosses with a single-pair mating design. When multiplied by the 27 jack pine breeding populations in Ontario the minimum number of controlled matings required per generation using a sublining approach is 5,400. It is highly unlikely that the limited staff in the province can manage the logistics of such a large controlled mating effort, especially when the tree improvement programs for other species are added in.

An innovative breeding system has recently developed for sheep improvement cooperatives in Australia. Referred to as a "nucleus breeding system", it focuses investments on the best genetic material (Jackson and Turner, 1972; James, 1977, 1978; Rae, 1977). The nucleus breeding system as adapted to radiata pine and eucalyptus, reduces the number of controlled crosses substantially while retaining the potential for continued rapid genetic gains (Cotterill *et al.*, 1988).

The nucleus breeding system reorganizes the traditional breeding population structure into a two-tier population consisting of a large "main" population and a smaller elite "nucleus" population For radiata pine, the main population is regenerated via selection from open-pollinated progeny, while the nucleus selections result from controlled-pollinations (Cotterill *et al.*, 1988). Each generation, a portion of the nucleus is derived from the best individuals in the main population, and a portion of the nucleus is returned to the main population to promote more rapid improvement of the main population. The nucleus breeding system promotes rapid genetic gains each generation by focusing financial resources and breeding effort on a relatively few individuals with the highest breeding values.

For radiata pine, the main population contains 300 female parents resulting from open-pollination mating and mass selection, and a nucleus population of 40 elite parents regenerated each generation via a circular mating design (Cotterill *et al.*, 1988). While exact numbers for jack pine have not been determined, the intention is to have a nucleus population no larger than 100 trees. This together with a simple mating design would result in minimal number of controlled crosses per generation (*e.g.*, single-pair mating, 50 crosses). The main population is not likely to exceed 300 selections and will be based on open-pollinated tests and mass selection.

Testing

Genetic testing is a costly, yet essential component of the breeding cycle. If the establishment of biologically sound populations is the foundation, then a well planned testing program is the cornerstone for a program where genetic gains are realized efficiently. A careful evaluation of the duration, type, and number of genetic tests is one of the keys to optimizing genetic gains per unit time and dollar spent. Decisions regarding financial investment in genetic tests should reflect the age at which information is needed and the expected precision of the tests at those ages.

Duration: While the ultimate goal of a tree improvement program is to improve the quantity and/or quality of yield at an economic rotation, the costs of maintaining and measuring appropriately designed genetic tests for generating high quality parameter estimates at ages of even 40 years is impractical. In any case, mensurationists have shown that, in the absence of severe environmental events, a growth curve of a single form characterizes tree growth beyond ages 10 to 15 years (Rehfeldt, 1984). As a result, assessment of optimum selection ages in jack pine will be based on age-age correlations with 20-year-old trees, rather than at a poorly defined harvest age (with its questionable parameter estimates). Because of the effect of generation interval, the reduction of the reference age to 20 years carries with it the requirement that age-age correlations be stronger if the optimum selection age is to remain constant (Lambeth, 1983).

Type of Test: Traditionally, tree improvement programs have been based on "field performance tests" that are established on sites representative of the target deployment environment and are managed extensively, and performance data (*i.e.*, genetic potential as modified by extraneous random environmental events) collected at multiple year intervals. The limitations of this type of testing include low precision in the first few years while trees are getting established, and variable test precision at later ages. The primary arguments put forward for field performance testing as the standard include: 1) a need for multiple tests representing the range of target environments for evaluating genotype by environment interactions, and 2) information regarding performance at older ages is required in order for selection to be efficient. However, the careful construction of biologically sound breeding populations greatly limit genotype by environment interactions (Rehfeldt, 1984). And, with the recognition that optimum selection ages are generally less than 10 years (Lambeth, 1980), the role of field performance testing (with its emphasis on long-term results) relative to other types of tests must be carefully evaluated.

Over the last 15 years, there has been substantial emphasis on short-term testing and identification of optimum selection ages (*e.g.*, Burdon, 1989; Carter *et al.*, 1990; Lambeth, 1980, 1983; Magnussen and Yeatman, 1987; Riemenschneider, 1988). Age-age correlations have been shown to be predictable across species and optimum selection ages are less than age 10 for rotation ages as high as 50 years (Lambeth, 1980). The work in short-term testing has resulted in higher precision shorter term testing procedures being available to tree breeders. These modified testing procedures are generally referred to as "farm-field tests."

The primary focus of farm-field testing is on generating high quality information on genetic potential between the ages of 3 and 10. Farm-field testing is based on selecting a site that fosters vigorous growth, practising clean cultivation, and a design that emphasizes close initial spacing and the ability to conduct thinnings as trees grow larger. In addition, an explicit commitment is made to minimize random environmental effects and to statistically purge damaged trees before analyses. The age-age correlations for height of individual trees, families, and provenances in Douglas-fir, western white pine, lodgepole pine, and ponderosa pine at young ages in such farm-field tests and heights in older field performance tests have tended to be high, r = 0.8 (Rehfeldt, 1984).

For example, Carlson (1990) reported on 6-year results of farm-field tests and their companion field performance tests (Table 2). He found the farm-field tests provided greater precision for estimating family means and produced higher family heritabilities than the associated traditional field

Table 2. Family heritabilities for 2- to 6-year heights for four farm-field tests (two separate programs) and for 6-year height in five associated field performance tests (60 families). From Carlson (1990).

Farm-Field Test	Age 2	3	4	5	6	Field Performance Tests
Program 1						
Skimikin	.91	.88	.91	.91	.93	0.71
Grandview	.92	.79	.79	.80	.80	0.36
Program 2						
Willow Cr.	0.88	.81	.71	.73	.73	0.64
Red Rock	.86	.77	.32	.38	.49	0.59
						0.41

Table 3. Heritability estimates for 1-, 2- and 3-year height from an operational black spruce farm-field test in Ontario (400 open-pollinated families).

	Heritability	
Age	Individual Tree	Family
1	0.48	0.68
2	.60	.79
3	.45	.76

tests. The results from the farm-field tests were also more stable across tests and populations. The oldest farm-field test in Ontario has completed three growing seasons, and contains a full complement of black spruce plus tree selections (400). Heritabilites for total height, thus far, have been quite strong (Table 3). The gain estimate (i = 1.0) for 3-year height from the farm-field test is 4.1%. Average heritabilities for height at ages 3, 5, 6, and 7 from field performance tests have been considerably weaker (Table 1). As a result, the mean estimated gain in 3-year height from field performance tests (i = 1.0) is 2.5%. While age-age correlations have not been factored in, these numbers demonstrate the importance of the improved precision obtainable from farm-field testing.

Number of Tests: The last topic to consider under testing is the optimum number of tests. Carson (1991) reported on a study of the relationship between the number of tests and selection efficiency using data obtained from genetic tests of radiata pine on 11 sites in New Zealand. The author found that on average, the results from one test site provided approximately 66% of the maximal estimated gain obtained from the full 11 test sites. The mean relative efficiency of estimated gains increased to approximately 82, 89 and 93% for 2, 3, and 4 test sites, respectively. From a purely marginal gains perspective, the use of more than two test sites seems questionable.

A recent study of selection efficiency in slash pine demonstrates the importance of test quality over quantity (White and Hodge, 1992). The authors modified parameter estimates to represent the increased precision associated with improved testing techniques and compared the results with the original first-generation parameter estimates. Under this "improved testing" scenario, the number of test sites required for a given selection efficiency was reduced by approximately 50%. Also, within-family selection, which will be emphasized in advanced generations, favors increased test size (*i.e.,* more trees per family) over an increased number of tests.

Testing in advanced generations will consist of a minimum of two farm-field tests for assessing genetic potential, and a series of small carefully designed realized gain trials (*i.e.*, block plantings in field performance tests) to translate estimated gains into growth and yield data. The advantages of converting one or both farm-field tests into seed orchards will be considered when developing the plan for passing gains on to production plantings.

Next Steps

The Genetic Resource Management Program in the Ontario Forest Research Institute will be working with operational program staff to identify an operational breeding population to use as a "pilot" for implementing the advanced-generation strategy. The knowledge gained from this pilot program will guide implementation on a broader scale. In general, implementation plans include (See Figure 2):

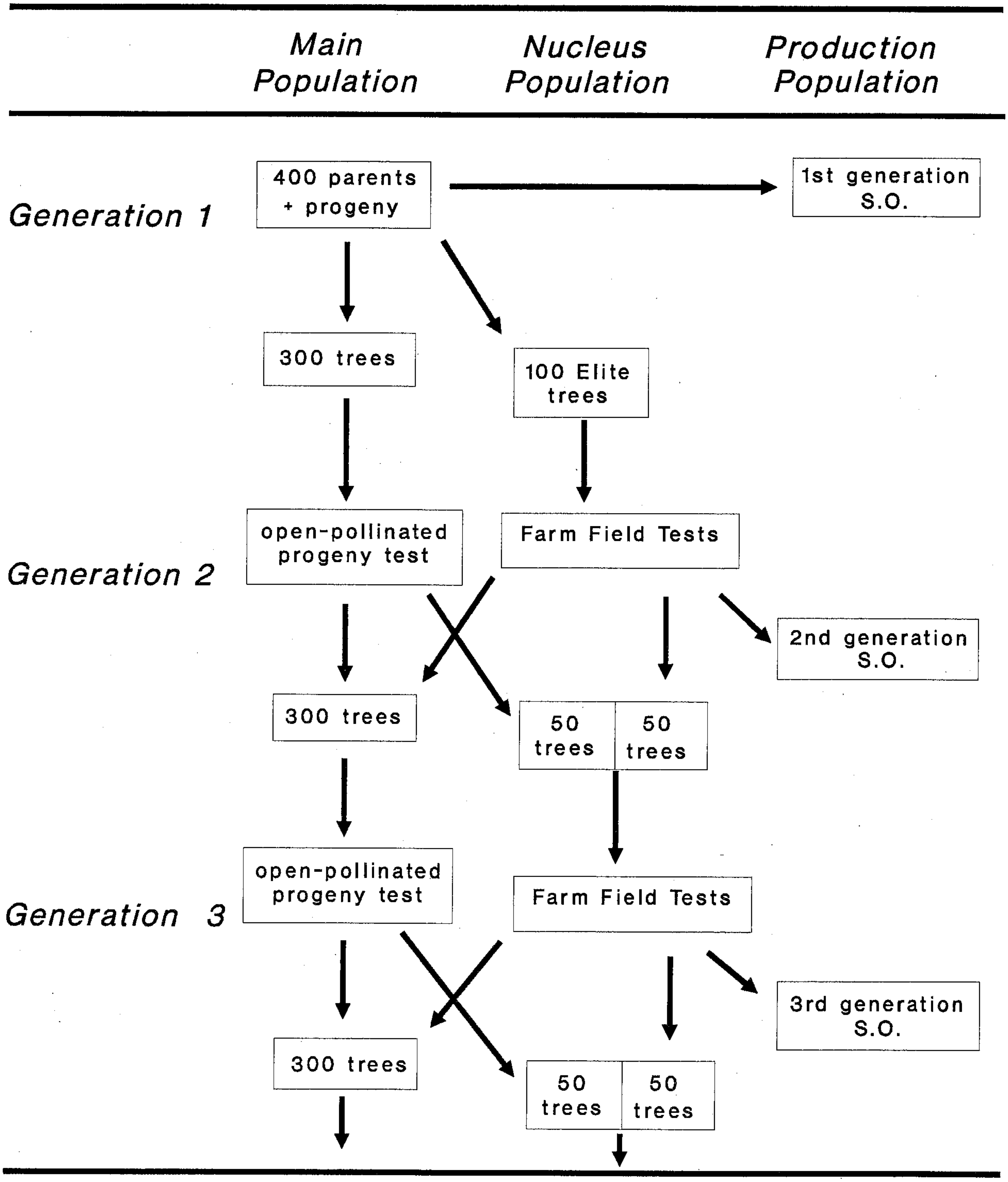

Figure 2. The nucleus breeding strategy for jack pine in Ontario

1) Use genecological information to evaluate and, if required, modify the selected operational breeding population to ensure biological soundness.

2) Use Best Linear Prediction to rank parents and offspring as to their aggregate breeding value, and make 100 elite selections for the nucleus breeding population.

3) Make an additional 300 selections for establishing the main breeding population. Collect open-pollinated seed for testing purposes.

4) Develop a "best mate" index, identify the optimal number of controlled crosses that can be supported, and implement the mating design for the nucleus.

5) Establish a minimum of two farm-field tests for assessing genetic potential. Consideration of the third farm-field test will be based in part on a marginal gains analyses. Tests will be rogued after 5 years, and realized gain trials (field performance tests) will be established based on 5-year information. Final measurements in farm-field tests will be no later than at age 10, depending on results of marginal gains analyses of optimum selection age.

6) Select best 50 individuals from the farm-field tests and an additional 50 individuals from the main population progeny test for the next nucleus population.

7) Convert farm-field tests into seed orchards.

Many questions and concerns will undoubtedly arise as the proposed strategy is implemented. The Genetic Resource Management staff at the Ontario Forest Research Institute will take the lead in developing answers to the questions that arise. The information needs are largely the same as those under any other breeding strategy. The primary information needs are likely to include:

1) age/age correlations based on high quality data at all ages from farm-field tests.

2) Economic analyses of marginal gains associated with delayed selection.

3) Developing an efficient testing protocol for the "main population."

4) Developing an understanding of the benefits and risks (genetic gain *vs.* effective population size) associated with multiple-tree selections from the best nucleus families.

5) Determining optimal timing and roguing levels in multiple-stage selection.

6) Monitoring correlated responses in various traits.

7) Efficient design for realized gain trials.

8) Determining optimal designs for the production population (*i.e.*, how and when are orchards to be established, especially if farm-field tests are not converted to orchard).

Summary

Obviously, there is a lot of work still needed to translate the advanced-generation breeding strategy described into an operational program. But, the key attributes of the proposed strategy include:

1) Breeding zones and populations that are biologically sound.

2) Selection decisions based on predicted breeding values generated by the Best Linear Prediction methodology.

3) A nucleus breeding system that focuses limited resources on the best genetic material.

4) A combination of farm-field tests for evaluating genetic potential and a design that supports within-family selection, and small scale field-performance tests for estimating realized gains.

5) Optimal selection ages based on marginal gains economic analyses.

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A REVIEW OF BREEDING PROGRAMS AND STRATEGIES FOR LARCH SPECIES

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Abstract

An outline of the present and future status of larches in Canadian reforestation programs and the lumber industry. The most important pest problems are enumerated, and breeding programs and strategies are described by province. Breeding programs described deal with western larch (Larix occidentalis Nutt.) in British Columbia and Alberta; tamarack (L. laricina (Du Roi) K. Koch) in Alberta, Ontario, Quebec, New Brunswick, Prince Edward Island, and Newfoundland; Siberian larch (L. sibirica Ledeb.) in Alberta, Saskatchewan, and Manitoba; and European larch (L. decidua Mill.), Japanese larch (L. kaempferi (Lamb.) Carr) and their hybrids in Ontario, Quebec, and the Maritimes. For western larch, tamarack and Siberian larch the breeding strategy is based on clonal or seedling seed orchards combined with half-sib progeny tests to evaluate general combining ability. For European larch, Japanese larch, and their hybrids, the breeding strategy is based on intra- and inter-specific mating designs between selected trees to make intraspecific improvement and to evaluate specific combining ability for the production of interspecific hybrids.

Introduction

This report briefly reviews breeding programs for larch species in Canada and outlines the breeding strategies employed in each program. Information presented in this report was gathered by means of a circular letter sent to 23 tree breeders and geneticists in Canada asking for details on the status of larch breeding programs in their regions. Also, the circular letter asked for information on the status of larch species in the reforestation program, use of wood, and disease and pest problems. All the information reported in this paper, on breeding program and larch species status in Canada, has been supplied by correspondents, whose names are listed in the Acknowledgments (references were not always available).

In Canada, the principal larch species and hybrids included in breeding programs are: European larch (*Larix decidua* Mill.), Japanese larch (*L. kaempferi* (Lamb.) Carr), Siberian larch (*L. sibirica* Ledeb.), tamarack (*L. laricina* (Du Roi) K. Koch), western larch (*L. occidentalis* Nutt.), and the hybrid European/Japanese larches.

This paper does not attempt to review all available information on the genetics of larch *spp.*; that has been covered by many other authors (Anonymous (1992a and b), Boyle *et al.* (1989), Fowler (1986a), Fowler (1986b), Fowler *et al.* (1988), Morgenstern *et al.* (1984), Ying and Morgenstern (1991), *etc.*).

Larch Species in Reforestation Programs

The number of larch seedlings planted in Canada in 1991 was about 5.0 million. Except for Prince Edward Island, where larch seedlings represented 12.9% of the total, the proportion of larch seedlings varied from 3.5% to less than 1%. In British-Colombia, Ontario, and Quebec, between one and two million seedlings per year are planted. For all the other provinces, the figure is less than 500 000 seedlings. Reforestation levels with larch seedlings are, in general, very low for all regions of Canada and the increase forecast for the next few years will only double that number.

Larch Wood Use

Results of the survey concerning larch wood use in Canada are as follows:

In Newfoundland, less than 5% of total industry consumption used for newsprint pulp is larch; locally, there is a demand for lumber in small quantities, but no increase is forecast within the next 10 years.

Prince Edward Island's producers ship 3 500 m^3/year of larch pulp wood to the mainland. Locally, lumber is used for seed potato boxes and ship building (12 000 m^3/year), for domestic firewood (22 000 m^3/year), and for institutional heating as fuel chips (10 000 g tons). In the next 10 years, consumption should remain constant, but an increase in use is foreseen in about 20 years as plantations produce superior quality material.

New Brunswick's and Nova Scotia's industries use larch wood for kraft pulp and in mixture (small proportion) for other pulping processes. It is used for lumber and is awarded the "north species" lumber grade. Larch wood use is not expected to increase.

Quebec's industry uses a small quantity in mixture for kraft pulp; locally, it is used for lumber in small quantities and it sells at the same price as spruce or fir lumber. Larch wood use is not expected to increase in the near future.

Ontario's industry used 1 477 m^3 for pulp, 480 m^3 as sawlogs, and 660 m^3 as tree lengths (probably as poles) in 1991-92. Larch wood use in the future will not change and it will remain a minor species as it is now (2 617 m^3 compared to a total of 18 million m^3 harvested in 1991-92).

Manitoba and Saskatchewan: no information was received on larch wood use.

Alberta's industry does not presently use larch wood, but this kind of wood is desired for fence posts. No change is expected in larch wood use over the next 30 years or so because of unchanged supply status.

In British Colombia, western larch wood is easily marketed as a structural product in the Douglas-fir/larch species group. Specialty end uses include glue-laminated beams and trusses, which command excellent prices. The annual harvest of western larch is approximately 500 000 m^3 and it represents a small proportion of the total harvest in the province. Little change in use is expected over the next 10 years.

From this survey on larch wood use in Canada, it can be concluded that larch spp. make only a small contribution to the forest industry. There are two explanations for this low use of larch wood:

a) natural stands of larch are, in general, a minor component of the natural forest and are often very scattered over a large territory;

b) for pulp and paper products and for sawed products, the wood characteristics restrict use in mixture with other softwood species that are more important in the natural forests and thus more used by industry.

To obtain a greater degree of use, larch wood must be processed separately but the available volume of wood is very often too small to justify the full operation of a typical mill in most of the regions of Canada. To increase larch wood use, products other than the traditional ones must be created, with particular consideration given to higher value products to counterbalance the higher costs of logging resulting from the dispersal of the stands.

Pest Problems in Larch Plantations

The most important pest problems mentioned by the correspondents are: a) Meria needle blight (*Meria laricis* Vuill.), larch casebearer (*Coleophora laricella* Hbn.), and dwarf mistletoe (*Arceuthobium laricis* [Piper] St. John) for western larch forests and plantations in British Colombia; and b) larch sawfly (*Pristiphora erichsonii* Hartig.), larch casebearer, eastern larch beetle (*Dendroctonus simplex* Lec.), larch shoot borer (*Argyresthia laricella* Kft.), cone midge (*Resseliella* spp.), and porcupine (*Erethizon dorsatum* L.) for eastern larch and other exotic larch species. Also, European larch canker (*Lachnellula willkommii* Hartig) has been introduced in the Maritime provinces.

Breeding Programs and Strategies in Canada

British Columbia

In British Columbia, three natural species of larch occur: tamarack in the boreal forest; subalpine larch (*Larix lyallii* Parl.) at the timberline of the Rocky and Columbia Mountains below 52° Lat. and in the northern Cascade Mountains; and western larch, which forms a serial major component throughout the upper Columbia river basin and into the Okanogan highlands. Only western larch attains commercial significance, but it is a minor component of the province's forest resource.

Within its natural range, western larch is an important timber species and has several characteristics that make it an attractive reforestation species. Reforestation with western larch has been constrained by seed supply (infrequent flower crops damaged by spring frost, low seed yield, *etc.*), but it is hoped that these problems will be overcome in seed orchards (soil-based or greenhouse). Western larch is the only larch species considered in the tree breeding program for the Nelson and Kamloops Forest Regions of British Columbia. The objective of the program is to develop well-adapted trees with improved height, diameter, and volume growth and quality, while maintaining acceptable levels of genetic diversity and wood quality.

The program is based on a clonal seed orchard established with grafts of plus trees selected from natural stands. The target is 550 parent trees. To date, over 350 parent trees (five trees per stand) have been selected and established by field-grafting in two seed orchards, including 176 and 147 clones with respect to two breeding zones delimited on the basis of biogeoclimatic information.

In 1993, a progeny test with 332 wind-pollinated families from the selected plus trees will be established across nine sites. Each family is included on a minimum of four high-quality sites within its zone of origin. This test will permit recurrent selection for general combining ability within the clones in the seed orchards. A gain of about 20% in height is expected varying from 11 to 35% based on breeding values for 7-year height and 10% selection intensity, as was obtained in the U.S.A. with western larch (B. Jaquish, pers. comm.).

In addition, a provenance trial of 128 seed sources from a range-wide collection is underway as part of a cooperative USFS/ BCFS western larch ecological genetics research project. The main objective of this joint project is to describe patterns of genetic variation for growth and adaptive traits, in order to refine existing seed transfer rules and breeding zone boundaries. Other research includes flower induction, pollen manipulation, potted or land-based seed/breeding orchards, somatic embryogenesis, and juvenile-mature wood relative density relationships.

Alberta

In Alberta, three larch species are included in the breeding program: tamarack, Siberian larch, and western larch. Each species has its own specific objectives.

For tamarack, genetic improvement for growth, yield, stem straightness, and wood quality are desired. The program also aims to develop an understanding of population variation in Alberta, to determine seed zonation, and to identify superior seed sources for reforestation, where feasible. The breeding strategy for tamarack is based on (1) natural seed collection from designated seed source areas; and (2) mass selection of superior trees in natural stands and development of a small clonal orchard for the central Alberta breeding region. Seven trials of 20-22 seed sources were established during 1985-87 across Alberta and one clonal seed orchard (0.75 ha), including grafts from nine selected trees (more will be added later). An annual production of 5 kg of improved seed is projected for the central region. It is expected that this program will be expanded to other regions depending on industry participation.

For Siberian larch, provenance testing is used to identify suitable seed sources for various ecoregions as well as for genetic improvement by selection and breeding. The improvement strategy is based on (a) seed source testing for mass introduction in various regions in Alberta combined with (b) tree selection within the Raivola provenance of Finland and within local plantations. To date, four provenance trials with 12 seed sources from the USSR, two tests of 20-30 open pollinated families, and two plantings with 19 and 56 full-sib and selfed families have been established. These trials and other young plantations in Alberta will supply selected superior trees from which grafts will be made to supplement a seedling seed orchard (1.2 ha) made with seed obtained from a seed orchard originating from the Raivola provenance. The production of improved seed forecast from that orchard is 10 kg annually. Early results of field trials have shown that, in northern Alberta, Siberian larch grows 30% faster in height than tamarack, but site selection is critical.

For western larch, the strategy is to improve cold hardiness by the establishment of a clonal seed orchard for southwestern Alberta and the mountain forest ecoregions, with the selection and propagation of hardy trees found in fringe populations of the species in Alberta. From scions of these hardy trees, a clonal seed orchard for an annual production of 5 kg of improved seeds will be established. To date, 15 ortets have been propagated and it is planned to outplant 300 grafts in 1994. Note that in a trial with eight British Colombia seed sources established in 1980, all trees suffered severe winter damage and nearly 100% mortality.

Saskatchewan and Manitoba

In Saskatchewan and Manitoba, the only larch breeding program is being conducted by the Prairie Farm Rehabilitation Administration Shelterbelt Centre at Indian Head, Saskatchewan. Siberian larch is the principal species considered by the program, initiated in 1983 (Schroeder, 1987). The objectives of the program are to develop trees with superior growth rates, insect resistance, and drought tolerance for planting in field and farmstead shelterbelts for wind protection, micro-climate enhancement, and wildlife habitat. Crown form and density are characteristics considered for selection.

Seedling seed orchards are established using progenies of superior phenotypes selected from populations of Siberian larch at the Shelterbelt Centre (particularly from a plantation established in 1912 originating from near the Ural mountains). To enlarge the genetic diversity of seed sources, collections were made in Siberia. Twenty provenances in 10 trials and 62 half-sib families in two trials; as well as other plantation types of Siberian larch and seven other larch species are now being tested in Alberta, Saskatchewan, and Manitoba. Ultimately the establishment of a progeny-tested clonal seed orchard to capture the genetic gains among provenances based on selection within the best provenances is planned.

Ontario

The larch breeding program in Ontario is active only in zone 6 of the six tree improvement zones defined for Ontario by the Ontario Tree Improvement Board (B. Elliott, pers. comm.). Zone 6 comprises the Southern Region, and the Parry Sound, Algonquin Park, Pembroke, and Bancroft Districts of the Central Region. The tree improvement program of zone 6 is presently under revision and the information on the larch breeding program reported here is based on past initiatives. Tamarack, European, and Japanese larch are considered in the breeding program.

For tamarack, the program consists of a base component and an intensive component. The objectives of the base program are gene conservation and seed source control for artificial regeneration. For the intensive program, the aim is to improve growth, stem form, and rooting ability of cuttings. Due to the ease of rooting and the difficulty experienced in obtaining seed for reforestation, the long-term strategy for improvement aims at developing a bulk propagation of cuttings from seedlings obtained from selected families inside repeated cycles of selection, breeding, and testing. The families will be produced by a polycross mating design within a population of 200 plus trees selected in zone 6, cloned by grafting, and allocated to the breeding hall and archives. The families will be tested in both short- and long-term trials. Based on short-term test results, the top-ranked 10 clones will be used in crosses to produce donor stock for the cutting propagation program. Short-term test results will be also used to assign clones in an assortative mating scheme to produce selection material for the next generation of breeding. A annual production of 500 000 rooted cuttings is planned and it is hoped that 18% gain (probably in volume) will be achieved as reported in the literature.

Aside from that strategy, a 3.2-ha clonal seed orchard has been established in the eastern region of Ontario. Also the short-term program propagation of superseedlings tested as clones in a 5-year nursery screening trial is being considered.

The breeding program strategy for European and Japanese larch is to test the intra-specific crosses of plus trees and, from progeny tests results, use the best plus trees in inter-specific crosses to produce hybrid seedlings. These will feed a cutting propagation system for the production of stecklings. Hybrid crosses will be made in a breeding hall and, at this time, the project is to proceed only with the first generation.

Based on the observation that several clones consistently produce female flowers every year and that male flowers can be induced easily by branch bending, the use of the female tester mating scheme was retained to evaluate the breeding values of the cloned plus trees.

A hybrid larch clonal seed orchard was established in 1983 to produce *L.* x *eurolepis* seed. The orchard includes 677 grafts at a spacing of 8x8 m on 5.2 ha. The design was intended to allow production of hybrid larch seed by completely surrounding the self-sterile European larch by Japanese larch.

E.B. Eddy Forest Products Ltd. from Espanola, Ontario also established, in 1989, a small clonal seed orchard comprising 288 ramets of tamarack (72 clones x 4 repetitions). The company is currently planting 50 000 larch seedlings per year.

In Ontario, genetic research work on larch spp. is also being carried out by scientists at the Petawawa National Forestry Institute of Natural Resources Canada. A synthesis of all the species, provenance, and progeny tests of the genus *Larix* has been published (Boyle *et al.*, 1989), giving valuable information and results, especially on European, Japanese, Siberian, tamarack, and hybrid larches. Research work on somatic embryogenesis and genetic engineering are being conducted at the Institute. The Institute has contributed to the establishment of tests in other provinces by planting the tests itself or by distributing seedlings or seed to provincial or other federal regional agencies. The Institute has also contributed to provincial and company larch breeding programs by supplying scientific and technical information, scions of selected trees, and by establishing seed orchards.

Quebec

In Quebec, despite the current low interest in planting larch species, the Ministry of Lands and Forest agreed 20 years ago to start a breeding program. Larch was considered as a fast-growing species that could compete with the southern pines planted in the southeastern U.S.A. The breeding programs principally concern tamarack, European, Japanese, and hybrid larches. Siberian larch and its hybrids with Japanese and European larches are tested for the northern region of Quebec (balsam fir and black spruce climax).

Tamarack is the preferred larch species for planting in the northern region of Quebec and on wet sites in southern Quebec, because European and Japanese larch have a very low survival rate when they are planted on hydromorphic soils. On mesic and somewhat dry sites, European, Japanese, and hybrid larches produce more wood than tamarack for the same number of trees per hectare because they have a better growth in diameter (Vallée and Stipanicic, 1983).

For tamarack, the breeding program is based on a seedling seed orchard with half-sibs or a clonal seed orchard depending on the distribution, the importance of the area, and the origin of the natural populations of the region covered by the orchard. In regions where we found many large stands of tamarack with a low possibility of inbreeding, open-pollinated seed was collected from plus trees. For each seedling seed orchard, there are one to three progeny tests depending on the ecological variation of the region to be serviced by the orchard.

One clonal seed orchard has been established in the Gaspésie region. In this region, tamarack populations are distributed in a narrow strip along the north shore of Baie-des-Chaleurs and follow the settlement of the land. Many stands come from a few trees left after the settlement and the larch sawfly infestation, and they present a high risk of inbreeding. This orchard will probably be rogued twice: once based on the phenotype of the clone and again based on a half-sib progeny test of all clones present in the seed orchard. Four seed orchards have been established, for a total of 13.5 ha with a potential production of 4.2 million seedlings annually (Lamontagne, 1992).

Because of the low number of tamarack seedlings planted presently, no second-generation orchard is planned. Nevertheless, 80 selected trees from one provenance test have been grafted and included in a clonal bank.

In addition to the standard seed orchard, two progeny trials planted in 1982 will be converted to seed orchards. They include 403 and 459 half-sib families collected, respectively, in 30 and 31 provenances of Quebec located between latitudes 45° to 49°. These trials are located in the Lac Saint-Jean and Estrie (Eastern Townships) regions and are combined with two provenance trials established in 1977; one in the Quebec region with 71 provenances and another in the Gaspé region with 60 provenances. These trials will be used to delimit seed zones and provenance regions for the province of Québec.

The breeding strategy for European, Japanese, and hybrid larches has two steps. In the first step, clonal and seedling orchards were established using grafts and half-sib families collected from plus trees in Quebec and Ontario. Generally, the plus trees were selected in the best plantations known and in the best-tested provenances or progenies. The Quebec Ministry of Forests has established three European and one Japanese seed orchards covering 8.9 and 1.8 ha, respectively. The Japanese seed orchard has been established in collaboration with Canadian Pacific Forest Products Company.

To produce the hybrid, experimental orchards have been made using seedlings of known provenances or selected clones, with a special design to expose the mother trees to the pollen of selected fathers. For example, in an orchard to produce the hybrid *L. decidua* x *L. kaempferi*, each mother tree of *L. decidua* was surrounded by four lines of Japanese larch. Verification of the production of hybrid seeds has not been made because of the low production of cones. One clonal orchard and two seedling orchards have been established based on that design.

In a second step, presently underway, inter-specific crosses between selected European and Japanese clones will be done to identify the clones having the best specific combining ability. The best crosses evaluated from progeny tests will be reproduced to supply a limited quantity of hybrid seed for producing donor plants for cuttings production. Until now, the crosses have been made in outside clone banks, however, ramets from 20 selected clones of each species are presently being established in a breeding hall. Half diallel crosses within clones of each species and full diallel interspecific crosses will be made and the progeny tested to evaluate the specific combining ability. The seedlings of the best families of pure species and hybrids will be bulk propagated by cuttings or, if available technology permits, mass production of seed of the best crosses will be done in an indoor seed orchard. In support of the breeding program of European and Japanese larches, many provenance and progeny tests have been established in Quebec. Genotypes will be selected from them in the future.

New Brunswick and Prince Edward Island

For New Brunswick and Prince Edward Island, Fowler (1986a) suggests two very comprehensive breeding strategies for tamarack. The first strategy is based on a clonal seed orchard with three successive generations over a period of 36 years, and is designed to capture only the general combining ability (GCA). The other strategy is based on the bulk propagation by cuttings of seedlings of the best identified progenies obtained by polycrosses from the first generation and by a disconnected half-diallel design for the subsequent generation to capture the specific combining ability as well. The two strategies start with the selection of 300 plus trees in New Brunswick and the surrounding regions of Prince Edward Island and Maine. The New Brunswick Tree Improvement Council has proceeded with the clonal seed orchard strategy; 269 plus trees were selected, grafted, and planted into the orchards and breeding gardens of cooperators by 1987. The strategy is presented in the flowchart of Figure 1 taken from Fowler (1986a).

In a first step each clone obtained from a plus tree will be crossed with a standard pollen mix (polycross) to produce seedlings for a progeny tests. These tests will provide GCA information for roguing the clonal seed orchard and identification of superior full-sib families obtained by single pair mated crosses of clones of the same seed zone. The seedlings from single pair matings are planted into selection plantations to provide material for second-generation selection and breeding. From these plantations, 400 best phenotypes (*i.e.*, four from each of the 100 best families) will be selected and divided into 20 20-tree breeding groups, with related trees from the same seed zone being assigned to the same group. Based on family test rankings, the phenotypically best 30-40 unrelated clones will be selected within the 400 to establish a second-generation clonal seed orchard.

These 20 20-tree breeding groups will be used for the second cycle of breeding where polycross and partial diallel crosses designs will provide information for roguing the second-generation seed orchard and for subsequent breeding generations (Figure 1).

The objective of the tamarack breeding program is to improve growth rate, stem straightness, and, perhaps, relative density of wood. To date, three cooperators have established seed orchards: New Brunswick Department of Natural Resources and Energy (one of 9.0 ha), J.D. Irving, Ltd. (one of 9.8 ha), and the Prince Edward Island Department of Energy and Forestry (two orchards, 2.0 ha). Only one generation is planned for now. Progeny tests

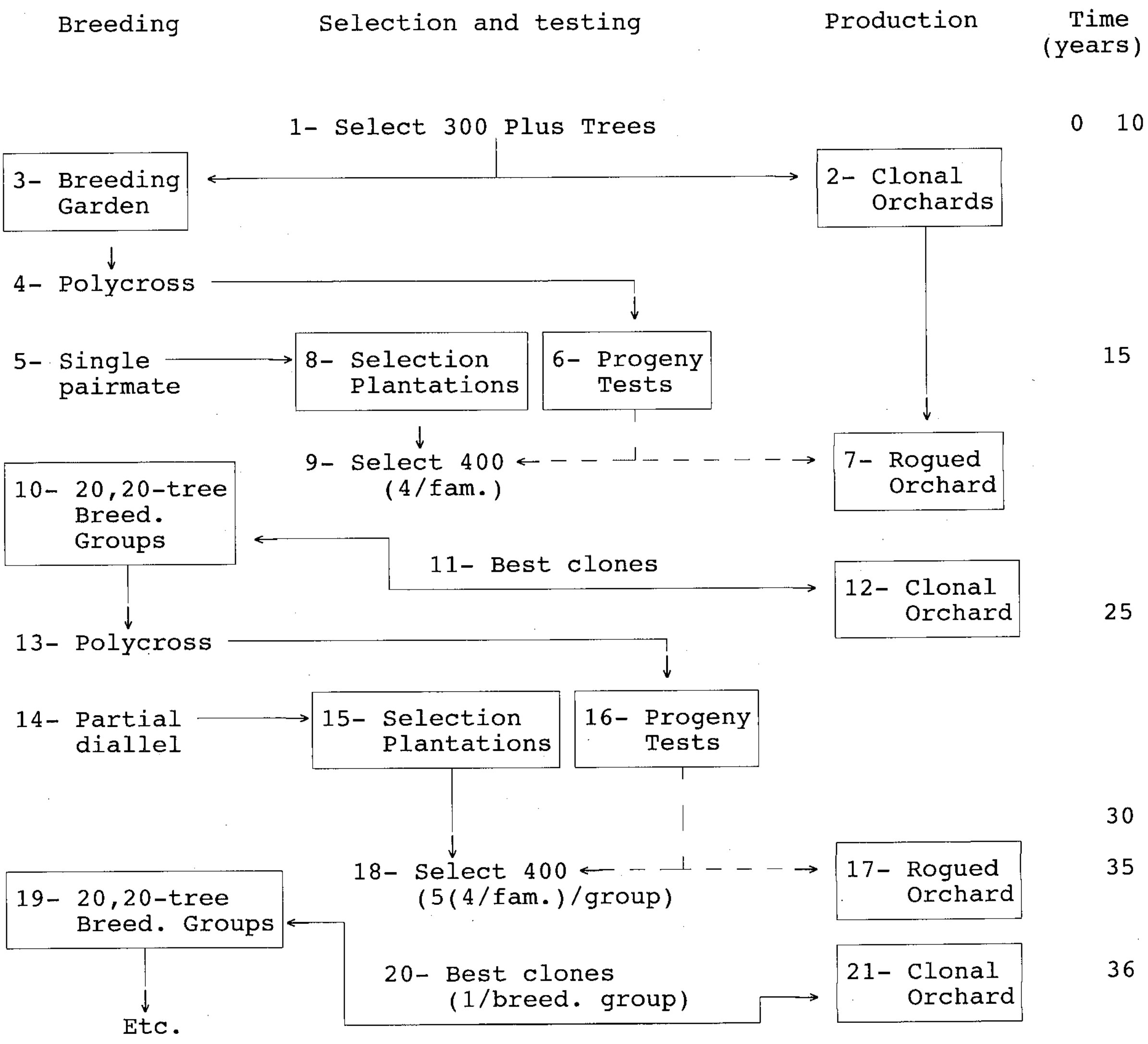

Figure 1. Flowchart for tamarack improvement strategy NBTIC Program, initiated 1977 (taken from Fowler 1986a).

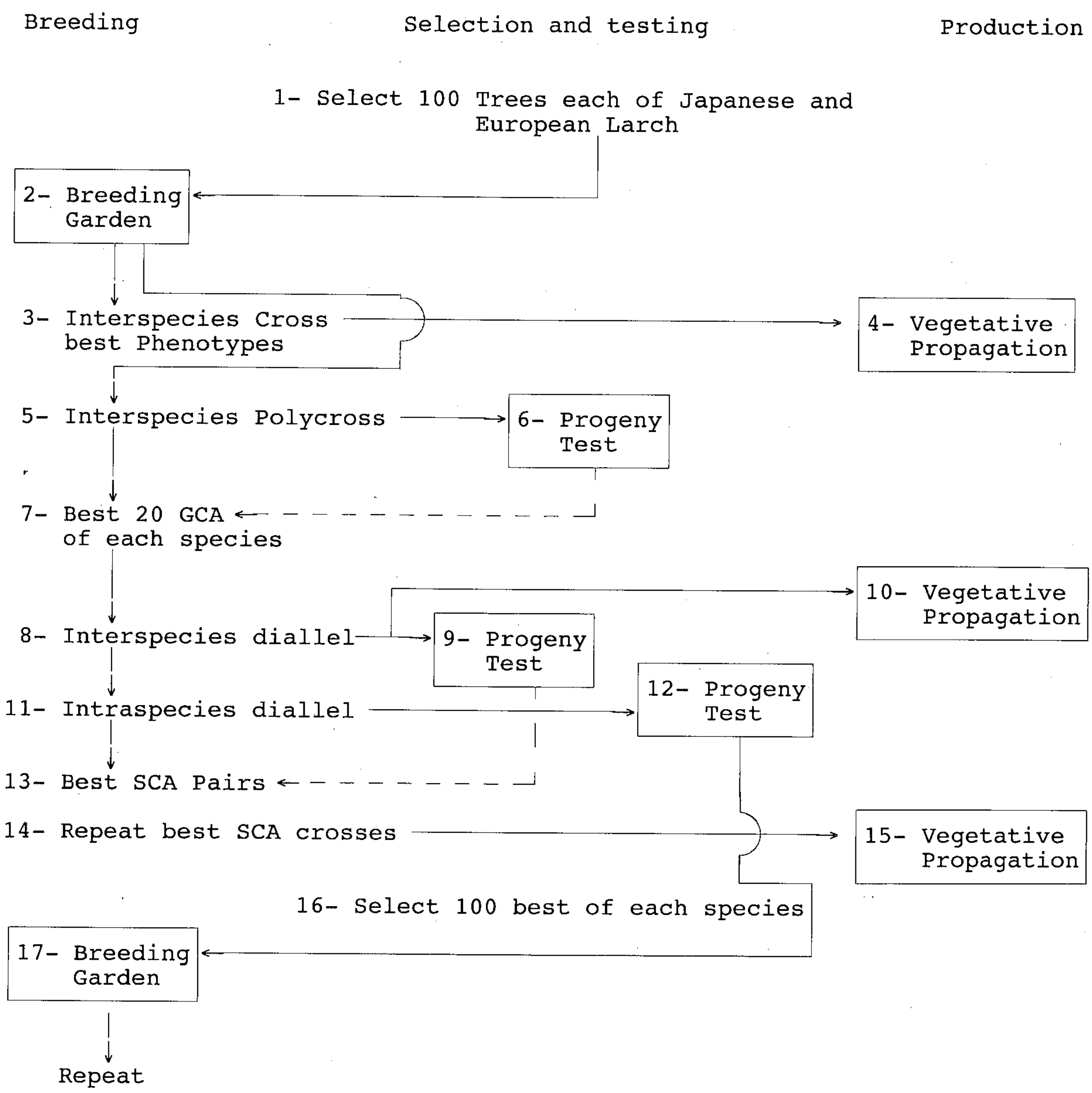

Figure 2. Flowchart for the production of improved *Eurolepis* hybrid larch (taken from Fowler 1986b).

are being conducted with most of the cooperators. Fraser Inc. has established a small clone bank of about 50 clones that may be used to produce control-pollinated seed in the future, if required.

In the Maritime provinces, good provenances of Japanese larch and hybrid larch outperform tamarack on upland sites (Fowler, 1986b). But even more important, the hybrid proved to be more resistant to the larch canker (*Lachnellula willkomii* (Hartig) Dennis), which is now present in part of the Maritime provinces. Fowler (1986b) has also suggested a very complete breeding strategy for the improvement of Japanese and European larches with the production of improved hybrids over several generations. The strategy elaborated by Fowler (1986b) is presented in a flowchart in Figure 2.

In summary, the strategy suggested by Fowler (1986b) is based on the improvement of each species by the identification within the 100 selected trees of each species of those having the best interspecific general combining ability in a first step and the best specific combining ability in the subsequent steps. The 20 selected trees of each species having the best GCA and SCA are interspecific crossed to identify those having the best specific combining ability. The same trees are intraspecific crossed in a half diallel design and progeny tested to provide the 100 best trees of each species to form the second breeding population. Then intraspecific improvement permit to supply improved genotypes at each step for the improvement of the interspecific hybrid.

Considering the information available, Fowler (1986b) suggests selecting for quality within the parental species, relying on the hybrid vigor to obtain improvement in growth.

To date in the answers received from the correspondents, there is no information from the New Brunswick Tree Improvement Council on breeding programs for European, Japanese, and hybrid larches. For these species and other larch species, the principal work underway is species trials. However, one small Japanese larch clonal orchard has been established by Valley Forest Products Ltd., including 22 clones selected in a provenance trial. But the company no longer intends to manage larch and has not collected cones since 1984. The Prince Edward Island Forestry Branch has proposed planting European, Japanese, and hybrid larches to meet a shortage in sawlog and studwood supply around year 2020 (information gathered in a draft report of W.M. Glen).

Natural Resources Canada is carrying out a breeding program on hybrid larches and other studies on tamarack in the Maritimes. The objectives are (a) to produce and test Japanese and European hybrids to evaluate performance of hybrids in relation to either parental species and to identify superior crosses, and (b) to investigate population structure of natural stands of tamarack and to determine genetic variation patterns. It is surprising that there is so little interest from industry and provincial agencies with regard to Japanese and hybrid larches, considering their production potential. Fowler *et al.* (1988) reported a production of 12 m^3/ha per year at age 25 years for the best provenance of Japanese larch compared to 4 m^3/ha per year for tamarack. They conclude that Japanese larch, managed over short rotations, is capable of producing two to three times more wood than other conifer species commonly planted in the Maritimes region of Canada. Moreover, in this study on yield and wood properties, Fowler *et al.* (1988) found that "the Japanese larch sawed, dried, and machined well. It appears suited to general construction use and may be eligible for a stress grade."

Many other joint projects on larch are being conducted in New Brunswick and Prince Edward Island by Natural Resources Canada and the University of New Brunswick. These include species trials, clonal selection and variation experiments, provenance trials with population and genetic structure, and investigation of genetic variances among clones and the implications for clonal forestry (Park and Fowler, 1987; Fowler *et al.*, 1988; Morgenstern *et al.*, 1984; Morgenstern, 1986; Morgenstern, 1987; Ying and Morgenstern, 1990, 1991; Carswell and Morgenstern, 1992).

Nova Scotia

The Nova Scotia Department of Natural Resources does not have a breeding program for larch species, but the Department is evaluating the potential for larch. In the meantime, a cutting orchard of hybrid larch derived from the same clones of seed orchard established by Valley Forest Products Ltd., New Brunswick, has been realized and will supply material for vegetative propagation if desired.

Scott, Canadian Timberlands company of Nova Scotia has a breeding program for Japanese, European, and hybrid larches. The company planted 135 000 larch seedlings in 1993; this represents 7% of the reforestation program. Within 5 years, this proportion will increase to 25%. Larch wood is used for kraft pulp. The objectives of the program are "to establish a Japanese/European hybrid orchard to produce a high percentage of hybrid seed, test each specific cross, and to expand the orchard with material whose crosses exhibited the highest degree of hybrid vigor based on growth and yield" (Tom Matheson, Scott Worldwide Inc., pers. comm.). The strategy of the breeding program is based on 20 tested Japanese larch clones that were the best clones evaluated by polycross and untested European larch clones. The clones come from provenance tests at the Acadia Forest Experiment Station, New Brunswick. Partial diallel crosses will be made to test hybrid vigor. The projected clonal orchard will consist of 30 clones of Japanese (30 ramets each); and 30 clones of European (10 ramets each). The orchard will be based on a miniature orchard design, where all material will be deployed in clonal rows. Pollen will be supplied with supplemental mass pollination to ensure a high degree of hybridization and a low degree of selfing. Production is expected to be between 750 000 to 1 000 000 viable seed per year from that orchard and a genetic gain is expected in the order of 25% in height by selecting the best crosses. Selection for a higher degree of resistance to larch canker may be incorporated into the program in the future.

Newfoundland

Tamarack is the only larch species in a breeding program in Newfoundland. However, other larch species like Japanese, European, Siberian, and hybrids are in trials (Harrison, 1986). The objective of the breeding program is to provide larch seed for reforestation that is of better quality and greater productivity than that gathered from wild stands. The principal characteristics to improve will be growth rate and stem straightness. The strategy proposes two clonal seed orchards for the province, one catering to Labrador and the Northern Peninsula and the other to the rest of the island. Both will be located at Wood Dale Provincial Tree Nursery, near Grand Falls.

The strategy is based simultaneously on clonal seed orchard and vegetative propagation of 100 cloned plus trees for each area. The strategy combines two alternative strategies suggested by Fowler (1986a), (Figure 3). The breeding values of the clones will be checked by half-sib progeny tests. The tested progenies obtained from partial diallel and polycross with 100 new plus tree selection will produce material for the second-generation seed orchard and vegetative propagation. This material is then divided in breeding groups of 20 x 20 trees, and bred to partial diallel and polycross to prepare the next generations. It is hoped that the first-generation seed orchard will produce at least four million seed in a good seed year between year 2005 and 2010. A minimum genetic gain of 10% is envisioned for growth rate, a greater gain for straightness and probably a 5% gain for branch size and angle. However, plantations of Japanese larch show promising results with a 20% improvement in both growth rate and stem straightness compared to native tamarack, at least on the

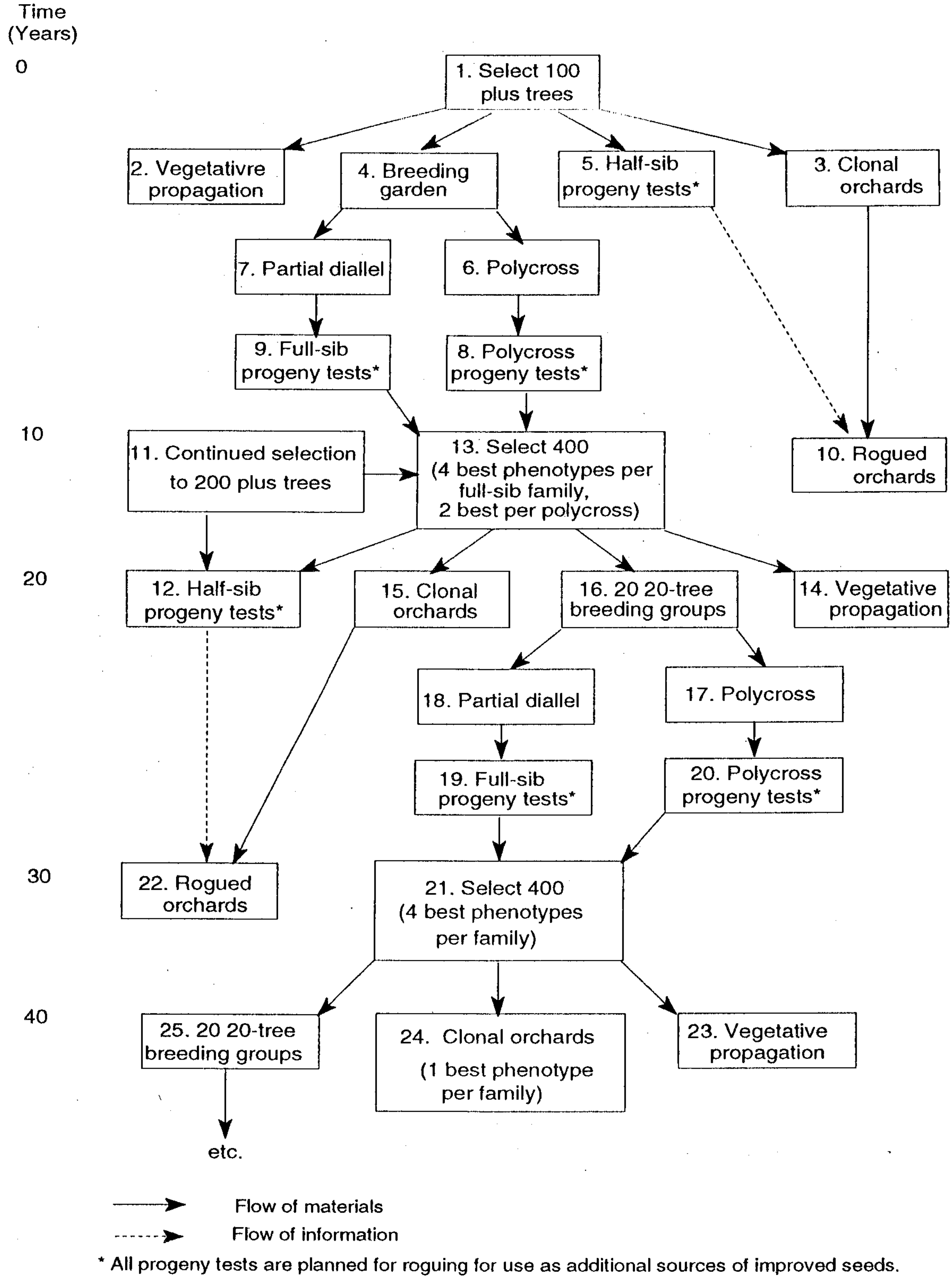

Figure 3. Flowchart for tamarack tree improvement in Newfoundland and Labrador (supplied by C. Harrison).

main land mass of the island (Charles M. Harrison, pers. comm.).

Northern United States

In the Northern Regions of United States, larch breeding programs are conducted by cooperatives. The U.S. Forest Service/Inland Empire Tree Improvement Cooperative are conducting a breeding program on western larch with a strategy based on selection of plus trees, clonal orchard, and recurrent selection from results of half-sib progeny tests.

The University of Minnesota/Institute of Paper Science and Technology Aspen/Larch Genetics Cooperative operates a breeding program for European, Japanese, and hybrid larches only because they outperform tamarack on upland sites in the north central and northeastern U.S. and Canada (Wyckoff *et al.*, 1992). The strategy is based on recurrent selection for general combining ability to improve pure European and Japanese larch species. The objective is to increase the adaptability and growth rate of the two species for commercial plantations. The European larch plus tree selections will be divided into breeding groups according to their seed source origins to maintain genetic diversity and avoid inbreeding in future generations. Because of budget limitations and the relatively small natural distribution and variation within species for Japanese larch, a single population will be used for the recurrent breeding program (Wyckoff *et al.*, 1992).

For the hybrid larch breeding, a single hybrid population consisting of 160 full-sibs obtained from single-pair matings will be created and will serve as a base breeding population for future improvement using recurrent selection. "Subsequent generations of hybrids will be selected from crossings within the hybrid base population, and no further hybridization between the two species will be made in the future generations" (Wyckoff *et al.*, 1992). This strategy for a hybrid is based on information from maize breeding and pitch pine (*Pinus rigida* Mill.) loblolly pine (*Pinus taeda* L.) hybrid breeding programs. In the meantime, based on field test results, seed of the best hybrid full-sib families will be produced for commercial planting by controlled crosses, establishing hybrid seed orchards or supplemental mass pollination in the breeding orchard. Wyckoff *et al.* (1992) do not exclude vegetative propagation of superior hybrid trees in subsequent generations, to capture all genetic gain from the hybrid program and to produce uniform hybrid plantations.

Discussion and Conclusion

From this brief review, it appears that many breeding programs for larch spp. have been initiated in Canada and the U.S.A. Tamarack and western larch are the native species considered in the breeding programs. Of the exotic species, European and Japanese larches and their hybrids are the ones on which most breeding work is done, followed by Siberian larch in the Prairie provinces.

Surprisingly, despite the existing breeding programs, consumption of larch wood and reforestation with larch are generally at very low levels relative to spruce and pine. The low use of larch wood can be explained by the scarcity of the natural stands of larch in most provinces. But knowing the potential for wood production of larch plantations and the multiple uses of the wood, why is there no major program of reforestation with larch, as happened with southern pines in the southeastern U.S.A.?

With their growth and production on short rotation (20-30 years), larch spp. are the "southern pines" of the northern regions. Reforestation with larch and other fast-growing species like poplar is an opportunity to create new resources of wood on abandoned farm lands using short-rotation management and, at the same time, create jobs for people in rural regions facing a very bad economic situation.

Another point is also surprising: why create breeding programs for tamarack when it has been demonstrated that European and Japanese larch and their hybrids produce a lot more than tamarack (Loo-Dinkins *et al.*, 1992; Boyle *et al.*, 1989)? In the Maritime provinces, southern Québec, and Ontario, the hybrid can produce two to three times more than tamarack on mesic to somewhat dry upland sites.

Moreover, Pâques (1992) reported the potential of the hybrid *L. laricina* x (*L. decidua* x *L. kaempferi*): at 8 years it has a height that is 19% superior to tamarack and 12% lower than the *eurolepis* hybrid. Besides its exceptional vigor, this hybrid was one of the best for rooting ability.

It may be possible for Newfoundland, the northern regions of Quebec, Ontario, and the Prairie provinces to develop this type of hybrid which has good frost resistance and higher production than tamarack. To get the same production with tamarack, it may take more than one generation of improvement. Other hybrids are potentially interesting using Siberian larch and genotypes of European and Japanese larch which show frost resistance and good performance in some trials done in northern Quebec. Provenances of European larch from high elevations in the Alps may also give better adaptation to the boreal ecological conditions. Considering the potential of the *eurolepis* hybrid, there is a need to get a better sampling of the alpine populations of European larch.

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AN UPDATED BREEDING STRATEGY FOR BLACK SPRUCE (*PICEA MARIANA* (MILL.) B.S.P.) IN NEW BRUNSWICK

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Abstract

As an alternative to the current conventional seed orchard breeding, strategies using controlled breeding followed by vegetative multiplication procedures are proposed for implementing the first set of second-generation black spruce selections. The 80 parents are divided into four 20-tree sublines, one of which is an elite subline consisting of the best 20 parents. One purpose for using the elite subline is to use the best parents intensively in the production population. A two-tiered breeding and testing scheme is followed, involving the elite subline and the regular sublines. Within the elite subline, a disconnected diallel mating is used to produce progeny for genetic testing, including clonally replicated, accelerated tests in a greenhouse. For the regular sublines, an assortative mating is carried out within each subline to produce material for the third generation. Conventional progeny tests, including the families from the elite subline, will be carried out and, subsequently, converted to selection plantations for the third-generation selection.

Introduction

Black spruce (*Picea mariana* (Mill.) B.S.P.) is one of the most widely distributed tree species in Canada, ranging from Newfoundland to the Yukon Territory. It is an important commercial species for pulp and paper industries owing to its favorable wood density and fiber characteristics. Increased utilization of forest resources has led to the development of large-scale reforestation programs in many parts of Canada. East of Manitoba, it is the most frequently planted species (Smyth and Brownright, 1986). Coinciding with these reforestation programs, selection and breeding were begun in some provinces as early as about 1960. Since about 1975, large-scale tree improvement programs have begun in all provinces where the species is important. It is a major species for tree improvement in the Maritimes (Coles, 1979).

The development of efficient breeding strategies requires detailed genetic information. At the time these improvement programs were initiated, however, there was a general lack of such information. The initial development of breeding strategies for black spruce was based on experiences with other species and on currently available information on genetic and biological characteristics, but the need for flexibility to accommodate new information and technological advances was recognized (Fowler, 1986, 1987). During the past 15 years, since the beginning of regional black spruce breeding programs, more detailed genetic information has become available and many new technological advances have been made, such as vegetative multiplication of juvenile seedlings by rooted cuttings, techniques for accelerated breeding and testing, and propagation by somatic embryogenesis and cryopreservation.

The purposes of this paper are: 1) to review progress of the black spruce breeding program in New Brunswick, and 2) to propose an updated breeding plan for advanced generations using the most recent genetic information and techniques.

Breeding Strategies for the First Generation

The breeding strategy adopted for the first generation was a "seedling seed orchard" approach, where plus-tree selections were made in wild stands based on individual phenotype followed by planting of "seedling seed orchards" and family tests using open-pollinated seeds of the selected trees. This strategy is generally simpler and cheaper than a "clonal seed orchard" approach practised for many species world-wide. The early flowering habit of black spruce, which can begin at age 6 years (Morgenstern and Fowler, 1969), was also an important reason for adopting this strategy (Morgenstern and Park, 1991).

A detailed breeding strategy for black spruce has been developed for the New Brunswick Tree Improvement Council (NBTIC) (Fowler, 1986); however, some modification or change may be necessary after the first generation. A total of 1200 plus trees was selected over a 10-year period for establishment of open-pollinated family tests (Simpson, 1992). As the trees generally have a straight stem, narrow crown, and short branches, selection efforts focused on superior height growth (Coles, 1979). To date, a total of 85 ha of seed orchards and 63 family tests have been established. The seedling seed orchards were planted using single-tree plots at a narrow spacing (1x2 m), and each family was represented by about 100 trees randomized within the orchards. The family tests were usually established at five locations using 10 randomized blocks of four-tree row-plots at each location. These family tests serve two purposes: 1) to rank the performance of families for roguing of seedling seed orchards, and 2) to select the best 400 individuals for second-generation breeding.

Advanced-Generation Breeding

In 1990, NBTIC began the second-generation improvement program of black spruce following the strategy outlined by Fowler (1986), which begins with the best tree from each of the best 400 families (*i.e.*, 400 clones). Also, these 400 clones are subjected to a polycross test to determine their general combining ability (GCA) values. At the same time, these 400 clones are single-pair mated to produce 200 full-sib families to select the best 400 trees (four best trees per family) and form 20 20-tree sublines for third-generation improvement. Subsequently, for each generation, polycrossing will be used to determine GCA values of clones, while a partial diallel mating system will be used to produce the next generation breeding population. In each generation, new clonal seed orchards are established, which are subsequently rogued on the basis of the polycross test.

Since the selection of plus-trees was carried out over a 10-year period, the strategy is implemented in phases with overlapping generations. By 1993, the first four series of family tests had been evaluated for 10-year performance. Based on the results of the family tests, the corresponding seedling seed orchards have been rogued, and 176 trees in total have been selected from the family tests for second-generation breeding. The best 40 clones from the oldest series of family tests are currently used to establish clonal seed orchards.

Alternative Breeding Strategies Using Clonal Propagation

As an alternative to the current conventional seed orchard breeding procedure, strategies using "breeding-cloning" procedures are being implemented on a pilot scale to produce improved planting stock for reforestation. Although conventional seed orchard breeding will likely continue to satisfy a significant portion of reforestation requirements, there is great potential to capture even greater gain through the use of cloning tech-

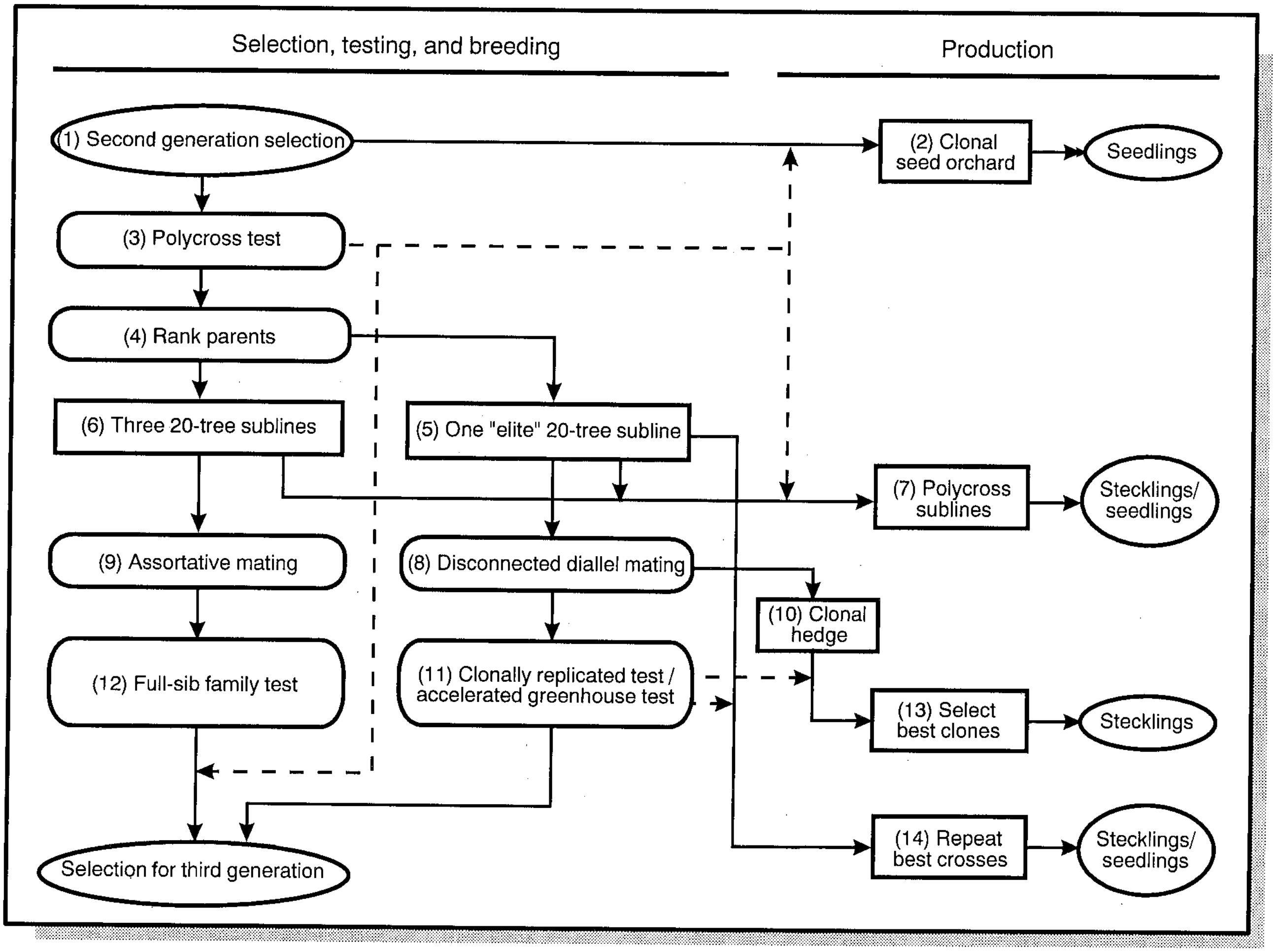

Figure 1. Flowchart of the second-generation black spruce breeding plan for New Brunswick. Solid lines represent material flow; dotted lines represent information flow.

nology and recent advances such as flower induction, improved rooting of cuttings, somatic embryogenesis, and cryopreservation.

Over the next several years, it is anticipated that vegetative multiplication using rooting of cuttings from juvenile plants and somatic embryogenesis will become a viable alternative for the mass production of planting stock for most northern conifers (Park and Bonga, 1993; Park *et al.*, 1993). Currently, for black and white spruce (*Picea glauca* (Moench) Voss), vegetative propagation on a large scale is possible using cuttings from juvenile donor seedlings albeit at about 1.5 times the cost of comparable seedling stock (White, 1992; Nova Scotia Dept. Natural Resources, pers. comm.).

The proposed alternative breeding strategy for black spruce, and possibly for white spruce as well, is based on incorporation of vegetative propagation as a means of producing planting stock. In a study to investigate factors that should be considered in making choices for seedling and clonal options for breeding and reforestation for New Brunswick, Mullin (1992) indicated that vegetative multiplication of seeds produced in controlled-pollinated orchards may be an economically viable method, even at a high rate of interest.

The general outline of the proposed alternative breeding strategy, including theoretical genetic gains, is described by Mullin and Park (1992). In this paper, however, we describe operational details of the strategy for possible implementation in New Brunswick.

General Overview

A flow chart for an alternative breeding strategy for the first set of second-generation selections is presented in Figure 1. In this first set, 80 clones selected from the family tests (best tree from each of the 80 best families) are used (1). Also, as part of the existing NBTIC plan, conventional clonal seed orchards have been established using the 40 best clones (2). All 80 selections are polycrossed with a standard polymix and progeny tests are established (3). Based on the results of a polycross test in a nursery, the parents are ranked (4). This information is used to form four 20-tree sublines and possibly for low level roguing in the clonal seed orchard. One of the four sublines will consist of the best 20 GCA parents, namely, the "elite" subline (5) as described by Williams and Lambeth (1992). In the other three sublines, the ranked parents are assigned uniformly across sublines (6). The controlled polycross within the elite subline as well as the best 5-10 trees from each of the remaining sublines, are polycrossed among different sublines (7) and the resulting seeds are bulked, seedlings grown and vegetatively propagated using serial rooting of cuttings for reforestation. A disconnected diallel mating is performed within the elite subline in a breeding hall, producing 30 full-sib families (8). Assignment of parents for mating will be random within the elite subline. For the remaining three sublines, a scheme of assortative mating will be performed based on their GCA rankings. Progeny from the disconnected diallel mating (30 full-sib families from elite subline) are raised in a greenhouse for progeny testing. In addition, the 10 tallest seedings in each of the families are clonally replicated. The seedling donors (ortets) are maintained by hedging (10), while the clonal replicates are used in progeny testing (11). The progeny test will include an accelerated greenhouse test (Sulzer *et al.*, 1993) as well as a conventional full-sib progeny test, that will be used for subsequent selection. The progeny resulting from the other three sublines will be used for establishing family tests (12), from which subsequent selections for the third generation will be made. When test results become available at the various stages of progeny testing, the information will be used to modify the polycross scheme (7) used to produce stecklings. When the progeny test identifies superior full-sib families, such crosses may be repeated in the breeding hall (14) and resulting seedlings vegetatively multiplied using serial rooting of cuttings. Optionally, as the clonally replicated test develops, the best clones within the elite subline may be vegetatively multiplied (13) by using the ortets in the clonal hedges (10). Based on the results of the progeny and family testing, the best 20 clones within each subline, a total of 80 clones, are selected for the third-generation breeding population.

Polycross Test

The polycross test (Fig 1,(3)) is used to assess GCA of the second-generation selections. A pollen mix consisting of equal volumes of pollen from 20 unrelated trees is used. This pollen mix excludes pollen from parents being tested, and the same pollen mix is used for testing all the parents. The pollen mix is maintained for future testing, as recommended by Fowler (1986).

The polycross progeny tests are established at six field locations using 15 blocks of two-tree plots, including one nursery test. The field tests are evaluated at 5-year intervals and the results will be used to rogue the conventional clonal seed orchards. The nursery test will be conducted for 3 years, and the parents ranked according to the nursery test to form subsequent sublines. Alternatively, an accelerated progeny test in a greenhouse may be substituted, which would result in a time saving of about one year. Currently, the first series of nursery tests is nearing completion and the second-generation selections will soon be ranked.

Table 1. Composition of sublines represented by the rankings of the clones based on the polycross test.

Subline 1:	1,	2,	3,	4,	5,	6,	7,	8,	9,	10,
(Elite subline)	11,	12,	13,	14,	15,	16,	17,	18,	19,	20
Subline 2:	21,	26,	27,	32,	33,	38,	39,	44,	45,	50,
	51,	56,	57,	62,	63,	68,	69,	74,	75,	80
Subline 3:	22,	25,	28,	31,	34,	37,	40,	43,	46,	49,
	52,	55,	58,	61,	64,	67,	70,	73,	76,	79
Subline 4:	23,	24,	29,	30,	35,	36,	41,	42,	47,	48,
	53,	54,	59,	60,	65,	66,	71,	72,	77,	78

Sublining

All second-generation selections will be divided into sublines as suggested by van Buijtenen and Lowe (1979) by assigning 20 trees per subline. For this series, the assignments are based on the GCA rankings for height from the nursery test. The first subline is formed by assigning the best 20 to develop the "elite" subline. The main reason for developing the elite subline is to use the best parents intensively in the production of planting stock. For the remaining three sublines, the assignments are evenly distributed (Table 1). However, in the future, sublines may also be developed according to some specific constraints, such as a subline that is frost hardy or suitable for specific planting zones. The management of multi-generation breeding populations using sublines will allow for flexibility while achieving progressive genetic gain. In any multi-generation breeding program, inbreeding is an inevitable consequence. The use of sublines makes control of co-ancestry conveniant by confining inbreeding within each subline. Inbreeding is eliminated in the production population by crossing among different sublines. It is also possible to develop highly inbred sublines to use inbreeding as a breeding tool, as suggested by Lindgren and Gregorius (1977).

Breeding-Cloning Strategies

The alternative breeding strategy proposed here is focused on controlled breeding followed by vegetative multiplication, namely "breeding-cloning" strategies. The potential for genetic gain from breeding and deployment of clones is expected to be greater than conventional seed orchard breeding and planting of seedlings. For example, an increase in genetic gain for black spruce was due to capturing a greater portion of additive variance as well as substantial non-additive variance (epistatic variance) (Mullin *et al.*, 1992). Although advantages of clonal reforestation have been recognized (Carson, 1986; Libby and Rauter, 1984; Libby, 1990), the implementation of clonal reforestation is limited by several factors. Perhaps the most important one is our inability to propagate true-to-type at a reasonable production rate, which results from aging of donor plants. This can only be partially controlled through serial propagation of young hedged seedlings less than 5 years old (Dekker-Robertson and Kleinschmit, 1991). Currently, operational true-to-type propagation in black spruce is possible with very young seedlings via rooting of cuttings.

Operational production of clonal black spruce planting stock using the rooted cuttings has been

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
A		X	X	X																
B			X	X																
C				X																
D																				
E						X	X	X												
F							X	X												
G								X												
H																				
I										X	X	X								
J											X	X								
K												X								
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N															X	X				
O																X				
P																				
Q																		X	X	X
R																			X	X
S																				X
T																				

Figure 2. Disconnected diallel mating design for the elite subline to produce progeny for testing and selection. Parents are assigned randomly within the subline.

carried out on a limited scale in Ontario (Rogers, 1990), Quebec (Beaudoin *et al.*, 1991) and Nova Scotia (Levy, 1983). For implementation of clonal reforestation strategy in New Brunswick, we consider three possible options of breeding-cloning strategies as described by Mullin and Park (1992), *i.e.*, (1) backward GCA selection and polycrossing, (2) backward specific combining ability (SCA) selection and repeat crossing and (3) forward clonal selection.

Mating Designs

For the elite subline, a disconnected diallel mating scheme will be used to produce offspring populations for progeny testing and selection for the third generation. Within the subline, five sets of four-parent half diallels will be used resulting in 30 full-sib families (Fig 2). The parents are assigned randomly among and within the diallel sets. The use of disconnected sets within a subline can be viewed as "sublines within a subline", which may be useful for managing sublines and selection of the next generation breeding population. Since the mating design is balanced, it is expected to provide sound estimates of GCA and SCA from progeny testing. In addition, the progeny derived from the elite subline are used to provide material for clonal selection and deployment in reforestation.

For the remaining three sublines, a scheme of assortative mating will be used. Within each sub-

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1		x	x																	
2			x																	
3				x																
4					x	x														
5						x	x													
6							x													
7								x												
8	x	x																		
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14															x					
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16									x											
17	x																			
18			x																	
19					x															
20							x													

Figure 3. An assortative mating scheme within a subline for full-sib progeny test and selection. The parental numbers correspond to their GCA ranking.

line, the parents are arranged according to their GCA ranking, and controlled mating will be performed. For the top eight parents, three crosses per parent will be made among them, and, among the middle eight parents, two crosses per parent will be made. The bottom four parents will be pair mated with any one of the top eight parents. An example of the mating scheme is shown in Fig 3, and the mating scheme will result in 24 full-sib families.

Considerable breeding work is required to carry out the proposed assortative and disconnected diallel mating designs. To perform the required crosses in a reasonable timeframe, it is important that accelerated breeding techniques be employed as described by Greenwood *et al.* (1991).

Progeny Testing

Progeny testing is an expensive and critical component of any tree improvement program. It is often constrained by cost and logistical problems and requires some compromises. For example, increased number of genotypes in the test may result in reduced number of test sites. Also, if the test plantations are used for selection of next generation breeding material, further trade-offs may be necessary. Three types of progeny testing will be carried out: (1) full-sib progeny test involving all four sublines; (2) clonally replicated test involving the elite subline; and (3) accelerated greenhouse-nursery test of the elite subline with clonal replicates.

The full-sib progeny test involving all four sublines will be established at two or three different locations in New Brunswick. A total of 102 families are available for progeny testing. At each test location, ten blocks of four-tree plots will be planted. The test will be evaluated at 5-year intervals. After evaluation of the test at 10 years, selection for next generation breeding population will be carried out in a test plantation. It is likely that the test locations with least environmental variability will be used for selection. Since the selection for next generation will be carried out in the test plantations, the test site must be chosen and prepared carefully to reduce environmental variability.

Both clonally replicated field and accelerated greenhouse tests are conducted for the elite subline. Seeds from the full-sib families derived from the disconnected diallel mating are raised in a greenhouse, and the ten tallest seedlings from each of the 30 families are selected and designated as clones, thus, resulting in a total of 300 clones. These clones are vegetatively propagated as described by Park and Fowler (1987) and Mullin *et al.* (1992). Two cycles of serial rooted cuttings may be necessary to produce sufficient number of clonal replicates (ramets) for the tests.

The clonally replicated field test will be established at one or two locations where operational clonal forestry is expected to be practised. At each location, ten blocks of single-tree plots will be planted. Like the seedling progeny test, the test will be measured at 5-year intervals.

Accelerated greenhouse testing as described by Sulzer *et al.* (1993) will be carried out using the clonal replicates. It has been shown that the best family correlation of 10-year field height in the shortest time was obtained with potted greenhouse studies with controlled growing seasons. The seedlings will be potted after initial growth (6 months). After a dormant period, the seedlings will be grown for two growth cycles in "long growing season" conditions to promote free growth.

The implementation of an effective clonal strategy will require accurate genetic information. Shaw and Hood (1985) explored the benefits of using clonal replicates to increase precision in rankings of individuals within families for selection and concluded that clonal replicates should increase the cumulative genetic gain obtained during each breeding cycle. To predict genetic gains from clonal strategies, it is necessary to obtain both additive and non-additive variances including epistatic variance. Mullin and Park (1992) used cloned ramets from full-sib crosses to resolve non-additive variance due to dominance and epistatic effects. Clearly, the efficiency of clonal selection will benefit from detailed information on the magnitude of genetic variances in the cloned population involving the elite subline.

In addition to the clonally replicated tests described above, the original ortets and the first cycle rooted cuttings (*i.e.*, ortets for second cycle rooted cuttings) will be maintained in clonal hedges until clonal test results become available. Twenty best clones in the hedge will be used as donor plants for production of steckling stock for reforestation. The clones in the hedge will be vegetatively propagated every 3 years to maintain juvenility. This process also allows for comparison of ramets from different cycles of propagation to determine the extent of possible c-effects (Lerner, 1958).

Production of Stecklings for Reforestation

Backward GCA selection and polycrossing is easiest to practise and can commence soon after establishment of sublines, as shown in Fig 1, (7). The breeding values of parents are determined by a preceding polycross progeny test in the nursey. The ten best-GCA parents from each of the sublines are selected for use in controlled polycrossing, hence the terms "backward GCA selection

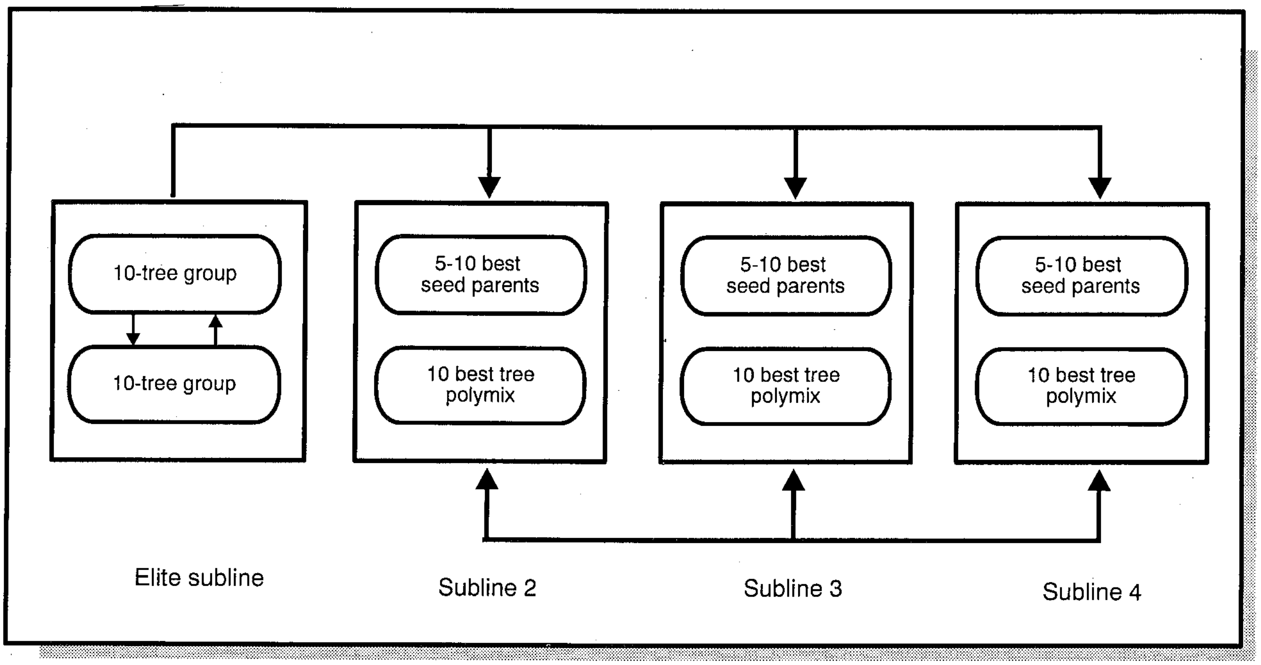

Figure 4. An example of "backward general combining ability selection and polycrossing" scheme to produce seeds for vegetative multiplication.

and polycrossing." To take advantage of the elite subline, the parents are divided into two groups (ten trees each) and controlled polycrossing will be carried out between them. Also, the polymixes of the elite subline are used for polycrossing the selected parents of the three regular sublines. In addition, the selected parents of one subline are polycrossed with a polymix of selected parents of another subline; an example of a possible polycross scheme is shown in Fig. 4. The limited quantities of seedlings produced by the polycrosses are then vegetatively multiplied using serial rooting of cuttings from young seedlings. This strategy is equivalent to a conventional rogued clonal seed orchard, but without most of the inefficiencies associated with wind-pollinated seed orchards such as pollen contamination and nonsynchronous flowering. Since the initial phase of this strategy is based on 3-year nursery test results, the scheme may have to be revised as new information becomes available from the periodic evaluation of field polycross tests and progeny tests, especially when there are significant rank changes among parents. Thus, this strategy is readily adaptable to changing needs and more flexible than land-based seed orchards.

Based on the results of progeny tests involving the elite subline, the parents that produced the best SCA pairs will be identified and the crosses will be repeated, hence "backward SCA selection and repeat crossing", to produce seeds for steckling production. Genetic gain from this strategy depends on the amount of SCA variance (*i.e.*, dominance effect) within the elite subline. With absence of SCA variance, the gain from this strategy is likely to be similar to that of backward GCA selection and polycrossing.

The greatest genetic gain will be obtained from forward clonal selection and vegetative multiplication of selected clones because this strategy utilizes total genetic variance including epistatic variance. Clonally replicated progeny tests from the elite population will identify the best clones for reforestation, hence "forward clonal selection."

Vegetative multiplication of these clones will be carried out from the clonal hedges where juvenility was maintained by serial rooted cuttings. This strategy is commonly referred to as "clonal forestry", and many studies demonstrate that the strategy yields consistently higher genetic gains. The practice of this strategy is contingent on the performance of rooted cuttings from clonal hedges compared with that of seedling stock. Thus, the success of this strategy depends on how effectively we arrest the maturation of donor plants during clonal testing as well as how economically we can produce steckling stock compared to that of seedlings.

Selection for Next Generation

Selection for the third-generation breeding population will be carried out from the full-sib progeny test. Twenty clones each from the 24 or 30 full-sib families, derived from the assortative or disconnected diallel crosses within subline, respectively, will be selected and form a new subline for the third-generation. The selection will be made using an index based on perfomance of individuals weighted with parental GCA information from the polycross test.

Lindgren (1986) suggested a linear deployment of clones based on GCA values for seed orchards and breeding, including the mating designs, to obtain optimal gain. As mentioned previously, the mating design employed was a scheme of assortative matings. Also, the disconnected diallel mating scheme used in the strategy has a subline structure within a subline (*i.e.*, disconnected diallels within each subline). Differences among the five disconnected diallels will be compared, and possibly, a linear deployment of clones from different diallels may be practised. For example, more clones are selected from best diallel sets than poor ones.

Controlling Genetic Diversity

The objective of any breeding strategy is the efficient transformation of genetic variation into gain, and requires that the strategy conserve as much genetic variance as possible (Dempfle, 1990). The design of the breeding strategy must consider the paradox that selection methods that are efficient for gain are not efficient for preserving diversity (Wei and Lindgren, 1991). As mentioned earlier, subdividing the breeding population into sublines will assist in retaining variation across the entire population, although the combined effects of inbreeding and random drift may cause the rapid loss of variability within sublines. Random drift will cause neutral alleles to be lost or fixed within the small sublines, although subdivision will reduce the effects of drift over the population as a whole. Drift can be effectively countered by the occasional introduction of new, unrelated selections into the sublines (Lacy, 1987).

While polycrosses made *between* sublines will always be out-crossed (assuming that all of the original selections were unrelated), crosses made *within* sublines will result in accumulated inbreeding. This accumulation is accelerated by methods such as positive assortative mating and combined-index selection which are designed to increase levels of gain. Selection in future generations may be adversely affected if deleterious inbreeding is permitted to accumulate to unacceptable levels. Furthermore, since clones from these within-subline crosses are to be tested for possible deployment, it is important that co-ancestry be controlled to minimize the effects of inbreeding on clonal performance. Provided that pedigree records are maintained, computerized techniques for the calculation of inbreeding coefficients (*e.g.*, Meuwissen and Luo, 1992; Tier, 1990) make it easy to calculate inbreeding coefficients of all individuals in the breeding population and all possible crosses. Co-ancestry can, therefore, be controlled by constraints on the number of related selections made in each generation, or by controlling the levels of inbreeding in mating designs that produce progeny and clones for selection. The efficiency of co-ancestry control strategies to minimize inbreeding and the loss of genetic diversity requires further investigation (Wei and Lindgren, 1993). A simulation study currently in progress is developing the necessary data to fine-tune co-ancestry controls to achieve efficient gain while minimizing inbreeding and loss of diversity (T.J. Mullin, unpublished data).

Anticipated Problems and Opportunities

The alternative breeding strategy discussed here is based on controlled-pollinations followed by steckling production for reforestation. Since the plan is implemented on the first set of materials of the second-generation breeding program, our progeny testing scheme encompassed several objectives, which may result in some trade-offs. For example, the mating design was intended for production of progeny for next generation selection, as well as for progeny testing. Three different testing schemes, *i.e.*, a full-sib progeny test using seedlings, a clonally replicated test, and an accelerated test, are used at an increased cost. However, breeding and testing is the most important part of the strategy, and the information and experience gained from this plan will help implement the next set of the second-generation material. For example, if there is no substantial SCA variance, backward SCA selection and the repeat crossing scheme may not be practised for the next set.

Since stock production in the strategy is by rooting of cuttings, it is essential that the stock plants grow like seedings. This does not appear to be a problem for the backward selection schemes where very young seedlings are used as donor plants. It is, however, less certain that the procedure used to maintain juvenility during the progeny test will also eliminate cumulative c-effects (Lerner, 1958; Libby, 1976) in the forward clonal selection. Dekker-Robertson and Kleinschmit (1991) found that by using serial propagation of Norway spruce, no serious problem due to maturation occurred until after seven or eight cycles of propagation spanning about 20 years.

Somatic embryogenesis (SE) techniques may hold future promise of a vegetative multiplication system with greater efficiency, especially in conjunction with cryopreservation (Klimaszewska *et al.*, 1992). Since the first reports of successful SE (Nagamani and Bonga, 1985; Hakman *et al.*, 1985), rapid progress has been made and plants produced by SE (emblings) are routinely produced with relatively high success rates (Park *et al.*, 1993, Adams *et al.*, 1993). SE fits well into our strategies. Especially, it will have a great impact on the forward clonal selection strategy because SE offers the opportunity to maintain clones in a juvenile state by cryopreservation while field testing is being carried out. SE is still labor intensive; however, research is being actively conducted at Natural Resources Canada, in Fredericton, to develop automated embling culture systems

As mentioned, a total of 400 clones selected for the second generation will be used in an overall breeding program at different times because the first-generation family tests are spread over 10 years. The current breeding strategy involves only 80 selections from three family-test series established during 1979 - 1981, thus bringing the selections made during this period together. We expect that implementation of the second-generation breeding program will take a total of four stages spanning the next 10 years, and, at each stage, four to six sublines (80-120 clones) will be implemented. It is also likely that third-generation breeding may commence before implemention of second-generation material has been completed, and therefore, it is possible to develop breeding plans for overlapping generations of breeding material.

The updated breeding plans proposed here will provide practical information and experience in implementing the next sets of sublines or the next-generation breeding material. If the pilot-scale implementation proves to be efficient, the conventional breeding strategy is likely to be replaced by appropriate alternative strategies. For example, if most of the genetic variance is due to additive effects with a lack of SCA variance, implementation of backward SCA selection and a repeat crossing scheme is not warranted. Furthermore, implementation of sublines at different times permits the adoption of different strategies flexible enough to meet changing goals when necessary.

Several researchers have also advocated inbreeding as a tool for breeding (Lindgren and Gregorious, 1977; Lindgren, 1986). This idea may deserve further exploration. Breeding using sublines will increase the rate of inbreeding primarily due to subline size. Lindgren (1986) indicated that inbreeding releases genetic variance and makes it available for selection albeit at a cost in time and difficulty. He suggested using only the top-ranking genotypes for intentional inbreeding. Our elite subline may be a good candidate for this. It may be divided into two sublines to develop highly inbred sublines and backcrossed to the sublines of the previous generation.

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