TREE IMPROVEMENT – PICKING THE WINNERS

AMÉLIORATION DES ARBRES – CHOISIR LES MEILLEURES

PICKING THE WINNERS
EDMONTON
1989

CANADIAN
TREE IMPROVEMENT
ASSOCIATION

PROCEEDINGS
TWENTY-SECOND MEETING
PART 2

EDMONTON, ALBERTA
AUGUST 14-18, 1989

ASSOCIATION
CANADIENNE
POUR L'AMÉLIORATION
DES ARBRES

COMPTES RENDUES
VINGT-ET-DEUXIÈME CONFÉRENCE
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DU 14 AU 18 AOÛT 1989

EDITORS/RÉDACTEURS
F.C.H. YEH, F.I. KLEIN, AND S. MAGNUSSEN

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OF THE
TWENTY-SECOND MEETING
OF THE

CANADIAN TREE IMPROVEMENT
ASSOCIATION

PART 2:
SYMPOSIUM ON
PICKING THE WINNERS

Held in
Edmonton, Alberta
August 14-18, 1989

Editors:

F.C. Yeh, J.I. Klein and S. Magnussen

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DE

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PROCEEDINGS OF THE TWENTY-SECOND MEETING OF THE CANADIAN TREE IMPROVEMENT ASSOCIATION

With the compliments of the Association

Enquiries may be addressed to the authors or to Mr. J.F. Coles, Executive Secretary, C.T.I.A./A.C.A.A., c/o Ontario Tree Improvement Council, Johnston Hall, University of Guelph, Guelph, Ont., N1G 2W1.

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The Twenty-third Meeting of the Association will be held in Ottawa, Ontario, August 19-23, 1991. Speakers will be invited to address the topic of "Maintaining biodiversity, should you be concerned?". Canadian and foreign visitors are welcome. Further information will be distributed in the winter of 1990/91 to all members and to others on request. Enquiries concerning the 23rd Meeting should be addressed to: G. Murray, Forestry Canada, Petawawa National Forestry Institute, Box 2000, Chalk River, Ontario, Canada, K0J 1J0.

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La vingt-troisième conférence de l'association aura lieu à Ottawa, en Ontario, 19-23 le mois d'août 1991. Des orateurs seront invités à adresser le sujet de <<La conservation de la diversité biologique devrait-elle vous préopccuper?>>. Les intéressés au Canada et à l'étranger sont les bienvenus. Des renseignements supplémentaires seront distribués au cours de l'hiver de 1990/91 à tous les membres et à tous ceux qui en feront la demande. Si vous avez des questions à poser concernant la 23^{e} conférence, veuillez les adresser au: G. Murray, Forêts Canada, Institut forestier national de Petawawa, C.P. 2000, Chalk River (Ontario) KOJ 1JO.

À: S. Magnussen, rédacteur, A.C.A.A./C.T.I.A.
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Thanks are due to the planning committee for the 22nd meeting, consisting of Francis Yeh (vice-chairman symposium, University of Alberta), Narinder Dhir (vice-chairman local arrangements, Alberta Forest Service), Bruce Dancik (University of Alberta), and Daryl D'Amico (Blue Ridge Lumber). Invaluable service was rendered by Israel Jiang (University of Alberta) in coordinating registration, and Albert Sproule (Alberta Forest Service) in arranging tour details.

Carrying on the business of the CTIA for the last two years have been the other members of the executive; Jim Coles, executive secretary, and Tim Boyle, Kit Yeatman, and Steen Magnussen, sharing the offices of editor and treasurer.

J.I. Klein, Chairman

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CONFÉRENCIERS INVITÉS
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FORTY YEARS OF TREE IMPROVEMENT - WHERE DO WE STAND?

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ABSTRACT

The critical importance of climate and site of seed origin to plantation success has been recognized in Canada for at least 60 years, yet it is only recently that strict controls over seed collection, registration, and distribution have been exercised in all provinces as a matter of course. The development of knowledge and understanding of underlying genetic variation and patterns of geoclimatic adaptation between and within planted tree species is reviewed, together with advances in application to operational forestation.

INTRODUCTION

> "Tree seed collection was generally considered to be a mere matter of gathering ripe seed in the cheapest way possible" (Thrupp 1927a).

A.C. Thrupp writing in Volume 3 of the Forestry Chronicle drew readers' attention to the wide geographic and climatic distribution of important timber species in Canada and went on:

> "It is therefore very important to state the exact origin -- of seed, the geographic strain -- and to furnish an accurate description of climate -- and, site -- where the parent trees were growing".
>
> He further predicted that "Scientific seed collection will be the basis of silviculture of the future, and will be an important factor in increasing the yield of our forests both in quantity and quality".

It has taken the greater part of the 60 years for "scientific seed collection" to be universally recognized and adopted by public and private forestry agencies in Canada.

Thrupp (1927a, 1927b) was reporting on results of plantation trials of eastern Canadian hardwood species at Salmon Arm, British Columbia. In his conclusions he also referred to 30-year-old plantation trials on the coast of B.C. Two years previously, in the first volume of the Forestry Chronicle, Lyons (1925) emphasized that source of seed, with regard to both physiographic factors and vigour of parental trees, was of "greatest importance" to success of reforestation with white spruce (Picea glauca (Moench) Voss) in Quebec. He strongly advocated collection and use of local seed. These and other documented trials in Canada of species and reforestation dating from the turn of the century were summarized by J.L. Farrar (1969a). It is clear that regional effects on populations of tree species of evolutionary adaptation to climate and soil were appreciated by far-sighted foresters of the time, but their systematic quantification remained for future studies. Numerous authors wrote then, as now, of the need to maintain and improve forest productivity if potential yields were to be realized in successive harvests. How far have we advanced in our understanding? How much better do we manage our forests and employ underlying genetic resources?

Earlier summaries of forest tree breeding in Canada were written by C.C. Heimburger (1954, 1958) and by I.C.M. Place and other authors (1969) in a special issue of the Forestry Chronicle. An unbroken record from 1937 to the present of Canadian research, development, and application in forest genetics and breeding and tree improvement is to be found in the archives of the Canadian Tree Improvement Association, currently retained by Forestry Canada at the Petawawa National Forestry Institute. The record starts with the proceedings of the first five Conferences on Forest Tree Breeding and Propagation prepared by the National Research Council of Canada (1937-38), continues with Proceedings of the Committee on Forest Tree Breeding in Canada and its successor, The Canadian Tree Improvement Association/Association canadienne pour l'amelioration des arbres published by the Canadian Forestry Service (now Forestry Canada) since 1952. These Proceedings, particularly recent issues, should be consulted for detailed information regarding regions, programs, progress, and personnel involved in tree improvement in Canada.

It is the intention of this paper to outline work to date in research and development of forest genetics in Canada, and to highlight advances in scientific knowledge, acceptance of genetic principles by the forestry community, technological developments, and types and levels of genetic management and improvement being applied to forest operations today. In conclusion I will suggest directions I believe research and operations could profitably and logically develop to maintain a broad, flexible, and productive genetic foundation for the future forests of Canada.

The discussion is arranged under the major headings of Research, Operations, Education, and Program Management.

RESEARCH

Genetics research directed to tree improvement focuses on variation and inheritance of survival, growth, and quality of planted trees, and on associated physiological, ecological, anatomical, biochemical, and molecular attributes. Comparisons may be at the level of species, populations within species, or trees within populations, and all levels need to be considered in evaluations at any one of them.

Species Trials

Species introduction and trials have a long history in Canada, beginning with the earliest settlers who introduced seed and plants of familiar species. Scientific and educational collections of native and exotic species were established in public and private arboreta and botanic gardens across the country, largely for horticultural application. In response to the need for cold-hardy, drought-tolerant trees on the prairies, the Federal government, under the Department of the Interior, established a tree nursery at Indian Head, Saskatchewan, in 1901 to produce and distribute seedlings for shelterbelts and farmstead protection. This is continued today at the PFRA Shelterbelt Centre, serving the needs of farmers from Manitoba to Alberta (Agriculture Canada 1989). Currently the Shelterbelt Centre produces 22 hardy species of trees and shrubs.

In eastern Canada, Norway spruce (*Picea abies* (L.) Karst.) found favour for farm shelter in southern Ontario and as a potential plantation species in eastern Canada. It grows vigorously in nursery culture, transplants easily, and is rapid growing on fresh sites of moderate and better fertility. However, early introductions from central Europe were marginally winter hardy in the continental climate of Quebec and Ontario, and the white pine weevil (*Pissodes strobi* (Peck) ravaged the young plantations causing repeated death of leaders on most trees (Holst 1955, 1963). Norway spruce is returning to favour as a plantation species in New Brunswick, Quebec, and eastern Ontario as better provenances are identified and improved weevil tolerance is developed through selection and breeding (Fowler and Coles 1979, Coleman et al. 1987, Corriveau et al. 1988, Hood et al. 1988).

Scots pine (*Pinus sylvestris* L.) was widely planted in eastern Canada in the early decades of this century. Seed was cheap and in plentiful supply from commercial suppliers in western Germany, the species was readily adapted to nursery production, and it survived and grew well when planted on cleared sandy sites too marginal for agriculture (Holst and Heimburger 1969). However, these trees subsequently developed very poor stem and crown form and the species fell into disrepute. Scots pine provenances from the Baltic states, Poland, White Russia, and the Ukraine are well formed and competitive with red pine (*Pinus resinosa* Ait.) or jack pine (*Pinus banksiana* Lamb.) on better sites (Teich and Holst 1970). Southern Siberian sources also show promise in recent trials in Alberta and Ontario (N.K. Dhir, pers. comm., Yeatman et al. 1988). Scots pine is particularly favoured as Christmas trees, especially in southern and eastern Ontario, where selection of provenance and parental type has been for dense foliage, conical form, and good retention of green colour in early winter.

European, Japanese, and Siberian larches (*Larix decidua* Mill., *L. leptolepis* (Sieb. and Zucc. Endl.), *L. sibirica* Lebd.) have attracted attention because of rapid early growth in plantations and high relative density of the wood. European larch of Polish, Sudeten, and Tatra origins is cold-hardy and grows more rapidly in eastern Canada than alternative sources from Austria (MacGillivray 1969). Japanese larch is not winter hardy outside the Maritime provinces and the St. Lawrence lowlands where it has potential on selected sites. Siberian larch may be of value for planting in the boreal forest and for shelter planting in the prairies, as long as slow growing northern provenances are avoided (Boyle et al. 1989, Schroeder 1988).

Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), a close relative of jack pine (*Pinus banksiana* Lamb.), is highly susceptible to sweetfern blister rust (*Cronartium comptonia* Arth.) when planted in the range of jack pine from central to eastern Canada (Yeatman 1974). Lodgepole pine of interior B.C. origin grew well when planted at Lotbiniere, Québec beside the south shore of the St. Lawrence River and outside the natural range jack pine (Beaudoin et al. 1988).

Exotic species and hybrids have captured much attention in research but their use in plantations remains limited. Provenance studies have led to broad application of controls and standards for large-scale seed collection and the distribution of seed and planting stock. Further genetic improvement in productivity, quality, and uniformity of planted trees is sought through diverse breeding programs established within defined breeding zones or regions. Such programs are founded on large genetic variation in economic traits found from tree to tree within selected regional populations. The strategies adopted reflect differences among species in genetic, ecological, physiological, and silvicultural opportunities and constraints; economic factors of value and scale; and the wide range of institutional priorities, perceptions, and human resources.

Hybrids

Hybrids occur naturally among botanical species within tree genera as well as among recognized variants of a single species. Only hybrids between species of conifer are considered here, and include the black-red spruce (*Picea mariana* (Mill.) B.S.P. - *P. rubens* Sarg.) populations of eastern Canada (Morgenstern and Farrar 1964), jack and lodgepole pine (*Pinus banksiana* Lamb. - *P. contorta* var. *latifolia* Engelm.) hybrid swarms in the region of species overlap in western Canada (Moss 1949, Critchfield and Little 1966), the Engelmann - white spruce (*Picea engelmannii* Parry *P. glauca* (Moench) Voss) complex of the interior B.C., and the white spruce - Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and Sitka - Engelmann spruce hybrid populations of the coastal valleys of B.C. (Hosie 1979). The common story is that of past introgression among adjacent populations of sexually compatible species. The viable hybrids occupy habitats intermediate between those of the pure species. Such hybrid swarms are of interest to forestry within their respective regions of occurrence due to adaptation to local forest sites. In some instances the hybrid populations may be of particular value for reforesting sites severely disturbed by cutting and/or fire (Morgenstern and Fowler 1969). In selection and breeding of spruce in the interior of B.C., species designation is ignored within breeding zones for practical purposes (Kiss 1971, 1986).

Creating and testing novel genotypes by forming species hybrids (through controlled breeding) holds a special fascination and may bring about outstanding recombinants. The crossability among species of a genus is also of interest in phylogenetic studies and in interpreting causes and consequences of speciation. Dr. C.C. Heimburger was a pioneer of poplar breeding in Canada (Heimburger 1936, 1940), work he continued for over 30 years (Farrar 1969b) and which laid the foundation for selection, propagation, and planting of poplar hybrids in eastern Canada (Zufa 1969, Barkley 1986, Beaudoin et al. 1988). *Larix eurolepis*, the F_1 hybrid between European and Japanese larches, has frequently demonstrated exceptional vigour although it is intermediate in winter hardiness (Boyle et al. 1989). An extensive and sustained program of hybridization among spruce species has been followed in Ontario by Dr. A. Gordon in pursuit of basic scientific goals of phylogeny and genecology and with the applied objective of discovering hybrids of exceptional adaptability and vigour. Of the many novel combinations, some are both cold hardy and exceptionally vigorous (Gordon 1980, 1988). Attempts to develop blister rust (*Cronartium ribicola* Fisher) resistant hybrids between eastern white pine (*Pinus strobus* L.) and rust resistant species of haploxylon pine from Asia have had only limited success (Zsuffa 1981).

Work with hybrids has advanced knowledge and understanding of the genetics and potential of tree species and, in the example of poplar particularly, the new genotypes have found practical application. Functional, cost effective vegetative reproduction remains the key to exploiting the potential of promising hybrids. Adequate testing is essential for large-scale acceptance so that applications are dominated by genera adapted to short-rotation management.

Provenance

Provenance research has played a key role in ensuring the success of today's large-scale planting programs in Canada by establishing the genetic basis for seed collection and the distribution of seed and plants. Determination of genecological norms and patterns of variation among populations is essential for sound genetic management of seed and the maintenance of existing genetic diversity within species, as well as for the development and deployment of populations improved by breeding. Identification and use of particular populations of generally high genetic value permits immediate gains to be made.

Ying and Morgenstern (1988) provided a comprehensive and up-to-date review of 45 years of provenance research in Canada. Exploratory investigations of geographic variation were initiated in the late 1930s in important native and exotic species in eastern Canada. From 1955 in eastern Canada and from 1960 in the west, new tests were established based on systematic sampling and widespread locations of trials of major species, including cooperative range-wide tests of jack pine, black spruce, and white spruce organized by the Petawawa National Forestry Institute, and the lodgepole pine, coastal Douglas-fir, and Sitka spruce sampling and trials undertaken by the B.C. Forest Service. Provenance investigation of eastern white pine was made in Ontario, and work with western white pine was conducted in the northwestern states of the U.S. Provenance tests of exotic species (Norway spruce, Scots pine, *Larix* species) was concentrated in eastern Canada from Ontario to the Maritime provinces. Limited trials of Scots pine and Norway spruce were planted in Manitoba and Saskatchewan.

Broad adaptive patterns of variation are evident in all species having an extensive geographic and climatic range. The degree of differentiation varies widely by species, but most exhibit broad clinal patterns associated with environmental gradients. The degree and nature of differentiation among population samples may vary markedly in different parts of the range of a species, depending on post-glacial history of migration, isolation, and fluctuation in population size as well as effects of natural selection to climate and soil. Ecotypic variation is most strongly expressed in the coastal provenances of shore pine in the west and jack pine in the east. As pointed out by Ying and Morgenstern (1988), more intensive regional sampling will be required to clarify causes of local differentiation among populations. They also recommended establishing and maintaining large-plot trials of provenances of special interest to follow growth and survival through to rotation age. Electrophoretic analysis of isoenzymes and DNA markers offers powerful tools for examining population structure and breeding systems.

Tree to Tree Variation

Tree to tree variation is the basis of plus tree selection and the foundation of genetic improvement. Breeding programs seek to improve the quantity, quality, and uniformity of wood produced for industrial use in plantations. The silvicultural characteristics that are the focus of selection include growth, stem and crown form, cold hardiness, resistance to insects and diseases, and wood properties. Breeders are concerned with the consistency and inheritance of desirable attributes, which may be qualitative or quantitative in nature. Qualitative traits are usually expressed in distinct phenotypes. They are controlled by gene differences at single or few loci and follow simple Mendelian rules of inheritance. Quantitative characters form a continuum of type that is subject to measurement. Such metric traits depend on genes that have small effects relative to other causes (Falconer 1989). Most differences of interest in tree breeding are quantitative in nature, and must be characterized genetically through carefully designed trials and investigations that yield results capable of rigid statistical analysis.

Thousands of genetic trials have been established, tens of thousands of trees and populations have been sampled, and millions of observations and measurements made by foresters and scientists throughout Canada. This is the essential and expanding database required to quantify and partition genetic and environmental components of variation within and between populations of trees. This information in turn is used to determine and guide current programs of genetic improvement, to predict gains, and to model alternative breeding strategies that may be applied to forest crop species (e.g. Fowler 1986, Klein 1988, Barbour et al. 1989).

Population and Quantitative Genetics

Population genetics refers to observing, recording, and analyzing qualitative traits of individuals within populations. Counts of contrasting phenotypes are summarized as ratios used to characterize the populations sampled in terms of gene and genotype frequencies. Genetic differences among populations may be defined and detected, mating systems inferred or characterized, population structure surveyed, and the evolutionary effects of population size, selection, migration, and mutation studied over distance, time, and generations.

Quantitative genetics is the study of metric characters that exhibit continuous variation that is subject to both genetic effects and those of other causes. Quantitative characters are frequently associated with several to many genes (polygenes), each of small effect. The biometric models employed in quantitative genetics are firmly based in the theory of Mendelian inheritance and genetic characterization developed through population genetics (Falconer 1989).

Both branches have been applied effectively to the genetic characterization of Canadian tree species and to guide and develop regional breeding programs. Morphological markers are the basis of botanical description and differentiation among species, and have been used extensively in population genetic studies, especially of the hybrid swarms referred to above. Similarly, biochemical markers such as terpenes and resins have been employed effectively at this level and have important applications for investigating genetic diversity within species and populations (von Rudloff 1975, von Rudloff and Lapp 1987, 1989). In recent years the advent of new biochemical methods for genetic analyses has greatly facilitated population genetic studies through the direct expression and scoring of co-dominant gene markers (Cheliak et al. 1987, Boyle and Yeh 1988). Electrophoretic analyses give expression to gene markers of enzymes and DNA segments, which provide direct measures of genetic relationships and diversity within and among populations.

Quantitative genetic studies find direct application in developing, testing, and modeling breeding strategies, determining environmental limits for breeding populations and their progeny, selecting traits for genetic improvement, developing selection indices, predicting and quantifying gains, and comparing cost/benefit ratios. Quantitative information on degree and mode of inheritance is gained from both pure research and from applied breeding programs. Both provide course corrections to improvement programs and ensure best possible returns are realized on long-term investments in genetic improvement of Canadian tree species.

Molecular Genetics

Molecular genetics research is the most recent and direct approach to genetic exploration of forest trees. Characterization of nuclear and organelle DNA molecules permits detailed classification of genotypes, identification of genes and assemblies of genes with phenotypic traits, and tracing the inheritance of such traits. Techniques are being explored for transfer of genes from one organism to another by somatic hybridization, direct gene transfer or *Agrobacterium*-mediated uptake

(Dunstan 1988). The potential economic impact of biotechnology is considerable within an integrated system of intensive forest management (Reed 1989).

Technological Research

Genetic improvement relies on a wide array of techniques and technologies from virtually all scientific disciplines applied to forestry. The dominant incentive to developing new, more effective methods is the drive to reduce the long breeding, testing, reselection, reproduction/propagation cycle of most forest trees. Means are sought to propagate and deploy promising and proven genotypes rapidly and in bulk (Bonga 1987, Dunstan 1989). On the one hand rejuvenation of mature trees is attempted to permit rooting of cuttings or propagation from tissue culture not otherwise possible. On the other hand growth acceleration combined with early sexual maturation, is pursued to reduce the period between generations and to bring promising material to volume seed production as early as possible.

Juvenile selection is essential to effective progress in breeding trees, but its effectiveness is critically dependent on the predictive value of early performance with regard to that at rotation age (Magnussen and Yeatman 1988). Rankings of widely different provenances or families commonly change little with time, but early selection is often ineffective among entries of similar genetic and environmental background (e.g. Ying et al. 1989). Determining reliability and effective application of early selection is of highest priority for tree improvement, both in research and in operations.

Control of growth and development is enhanced through increasing knowledge of associated physiological processes, environmental influences, and the biochemical foundations of genetic expression. Early mass screening of material on the basis of physiological response to stress or biochemical constitution offer potential for reducing costs and increasing efficiency of genetic improvement. Intensive developmental studies from embryogenesis to organ differentiation and examination of crown architecture provide increased understanding of age-age relationships. Steady development and adoption of new technology demands anticipation and flexibility in designing current tree improvement strategies (Fowler 1988).

Research contributes to increasing the efficiency of operations such as seed production and collection in seed orchards and seed collection stands; in controlled breeding, pollen management, and cone/seed protection; and in all aspects of seed handling, cleaning, conditioning, testing, and storage.

OPERATIONS

Genetic Management

Genetic considerations are basic to the success of any system of forest management, whether regeneration is by natural or artificial means. Persistent highgrading, excessive reduction in numbers and distortion of distribution of seed trees, planting or seeding of maladapted populations through inattention to seed origin, and elimination and/or replacement of valuable local populations are examples of potential negative influences through inattention to genetic consequences of logging and forest renewal. Such negative effects on tree survival and forest productivity can readily be avoided by applying sound genetic principles to forest management planning and prescriptions, thereby retaining the quality and diversity of forest genetic resources indefinitely. Today, positive practices and regulations widely accepted and applied in Canada include:

- the adoption of standards and rules for large-scale seed collection and distribution with regard to concerns such as crop diversity, stand size, quality, age, and location, accurate labelling of seed origin and collection data, and abiding by environmental limits set for seed and plant distribution;
- the definition, and revision as needed, of seed zones for seed collection and seed transfer rules for administrative practicality and minimum risk of genetic failure;
- determination of requirements, locations, and size of seed production and seed collection areas to ensure future supplies of prime source-identified seed, and developing efficient management prescriptions for such areas and collections;
- adoption of criteria and standards for seed registration for domestic consumption and for official certification, including genetic standards, of tree seed sold for export (Edwards et al. 1988, Portlock 1988);
- designation and management, within existing operations and purposes, of both natural and constructed breeding populations such as gene pools to retain genetic integrity and diversity for conservation of forest genetic resources.

Genetic Improvement - Breeding

Selection and breeding to improve traits of silvicultural importance and economic value is a further stage of applied genetics aimed at improving yields and returns on large plantation investments. As the level of these investments has doubled and redoubled in recent years, Canadian forestry institutions have adopted clear policies to create and support tree improvement programs for those species and in those regions for which it is justified. Genetic enhancement of growing stock is necessarily limited to major commercial species and to regions where tree planting is important to ensure effective forest regeneration and wood production.

The wide range of strategies developed for tree improvement in Canada reflects institutional and economic priorities, environmental and silvicultural opportunities and constraints, and the interests and backgrounds of the people in positions of primary responsibility. Each program must take account of projected requirements for planting stock, genetic and silvical characteristics of species, economic projections of cost-benefit ratios (Thomson et al. 1989), and response over time and generations to accumulated knowledge and changing technology. Breeding zones are initially defined as the target areas for each program to ensure adaptational security of breeding populations and of their progeny. Essential work of field testing, evaluation, and resolution is concentrated by breeding zone, although other aspects of a breeding program may be located elsewhere. The geographic, environmental, and ecological limits of breeding zones are subject to revision on the basis of experience and new information generated by the program itself and by associated research.

Many breeding populations have been created and tens of thousands of plus trees selected to provide clonal or seedling foundation stock for first generation seed orchards, progeny tests, and breeding archives. In the case of hybrid poplar planted in Quebec and Ontario, clones currently in use were selected after extensive testing of diverse material derived from wide arrays of species and genotypes (Vallée 1988, Barkley 1986).

Few breeding programs in Canada have progressed beyond the first generation of selection, testing, and seed production. Many are improving the genetic basis of first generation orchards by roguing the poorer clones or families on the basis of ranking in progeny tests, or by establishing new orchards using only the best-tested clones, the so called one and one-half generation orchards. Further progress depends on the selection among second generation progeny. Much attention is currently being given to determining the intensity of effort to be applied to advanced generation breeding. This may range from low cost, minimal genetic gain mass selection repeated from generation to generation to relatively expensive intensive breeding programs requiring carefully constructed controlled mating designs and extensive progeny testing, but with the expectation of substantial and rapid gains and economic returns. Clearly the choice will depend on the scale of operations for a given breeding zone/species combination and the intensity of silvicultural management to be applied to the planted forests. Economic "engines of growth", the three major commodity forest products of construction lumber, softwood bleached kraft, and standard grade newsprint (Anon 1988) must determine breeding priorities. Where warranted, carefully crafted mating designs and systems are applied over time to rank breeding values and to create new generations of pedigreed stock for further selection, breeding, and propagation for use in plantations.

New technologies are being developed, and old technologies are being applied in novel ways, to improve the efficiency of breeding by increasing rate of gain and decreasing the time between generations. Intensive cultural systems are used for early testing and selection on a progressive program of culling from large numbers of entries (Burdon 1989). Relatively juvenile trees are induced to flower and bear substantial numbers of seed in large enclosed areas -- breeding halls -- where both physical and biochemical environments can be controlled and sequenced at will. Mass vegetative propagation of superior genotypes has been extended to responsive species previously confined to seed propagation. By such means genetic gain may rapidly and progressively be transferred to forest production, while the task of steady genetic improvement and diversification of the breeding populations proceeds in parallel.

EDUCATION

Dr. L. Chouinard initiated the first lectures in forest genetics at a Canadian university in 1953 at the School of Forestry, Laval University, Quebec (Heimburger 1958). It was not until the 1960s and into the 1970s that forest geneticists were appointed full-time in other forestry faculties in Canada. In many cases, these appointments were preceded by special genetics courses and lectures given by adjunct staff or invited speakers. With full recognition, regular courses were available to undergraduates, commonly as an option, and the basic principles and practice of genetics and tree improvement were incorporated into required courses in silviculture. Today, undergraduate training in tree improvement and genetics is available at all forestry faculties, and graduate training to the Ph.D. level can be pursued at most professional schools. Tree improvement principles and technology are also incorporated into the silvicultural training of forest technicians at community colleges across the country.

Academic forest geneticists have attracted strong support from both public and private agencies for research programs so essential to ensure the necessary relevance, recognition, and status of university education. Vigorous educational programs are required to maintain and build momentum and to provide continuity in application and research of genetics in forestry in Canada. Strong links have also been forged with international forestry agencies. Exposure to diverse forest conditions provided by foreign student enrollment and participation in international forestry projects have significantly broadened the base of forestry education in Canada.

PROGRAM MANAGEMENT

The principal support for research and application of genetics in forestry during the period under review came from public agencies: the federal forestry service through its research Institutes and Regional Centres; from federal support for university research; and, variously, by provincial agencies coast to coast. The latter have developed breeding programs to meet provincial needs and priorities, ranging from research, development, to operations.

Private agencies have played a vital role of cooperation in stand (population) sampling and test establishment in the early years and by providing enthusiastic support for plus tree selection and the establishment of breeding populations and seed orchards in later years, as well as for controlled seed production and collection for reforestation. Some larger companies have their own R and D programs for proprietary purposes, and they often join with other agencies, both public and private, in cooperative activities.

Cooperatives under various constitutional arrangements are the major means of implementing operational tree improvement programs. They now number eight, with the recent addition of a new organization in Manitoba (Coles and Simpson 1988).

CONCLUSION

Tree improvement has come of age. The fruits of earlier research are now in common practice. All provinces control seed collection and distribution closely, with few exceptions permitted. Most have designated seed collection/production areas, but with a wide variance in proportion of seed currently coming from such controlled sources or from orchards. Seed orchards are expected to supply ever-increasing proportions of seed for plantation stock. Selected wild stands will continue to be the source of seed for direct seeding and small-scale planting programs. All provinces with major forest economies plan to continue selection and breeding into the second generation and beyond (Personal communication from coast to coast in response to my questionnaire).

Research will concentrate on improving the efficiency of breeding strategies to maximize rate of gain, and reducing the time required to recognize and mass produce superior genotypes for direct use in forestation. Predictions of climatic change call for careful re-examination of provenance tests to determine possible shifts in adaptive norms. Simple yield trials of the products of tree improvement need to be established routinely and followed systematically to quantify progress and to correct direction if required. Foundation genetic resources must be identified and retained as dynamic components of responsible forest management. Both coordination of effort and transfer of technology need to be strengthened and supported at all levels if investments in genetic improvement are to realize their potential.

In 1927 Thrupp concluded his paper thus:

"Scientific seed collection" - in its broadest sense - "will be the basis of the silviculture of the future, and will be an important factor in increasing the yield of our forests both in quantity and quality".

This assertion holds true today.

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TEST RESULTS AND THEIR USE IN PRACTICAL TREE IMPROVEMENT - THE USE OF INFORMATION

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ABSTRACT

Forty years of tree improvement in New Zealand has provided a large data base of progeny test information. This paper discusses how this information has been used to guide the development of the radiata improvement program in New Zealand. In particular it has helped to answer questions regarding: The need to regionalize breeding in New Zealand; How many sites and where to place these sites for further progeny testing? What traits to measure and when for efficient generation turnover? In some parts of Canada there is an extensive enough data base to apply similar quantitative methodology. The New Zealand approach to multiple trait improvement is also discussed.

THE NEW ZEALAND EXAMPLE

I wish to address in this presentation a paraphrasing of the theme topic of this meeting 'Picking the winners'. I will use examples from the radiata pine genetic improvement program in New Zealand, where I have just spent three years, to show how progeny tests results have not only been used for selections to develop the breeding and production populations but have also provided valuable research information to guide the development of the breeding program. Specifically, I would like to demonstrate how effective use of information from progeny tests has helped to answer important questions regarding: (1) GxE interaction and the need to regionalize breeding, (2) the most efficient age for generation turnover, and (3) multiple trait improvement strategies.

The progeny tests in New Zealand are extensive in their distribution, large in scale and many are advanced enough to undergo commercial logging operations. This investment in progeny tests has been important, not just in providing the selection intensities for genetic gain, but also helping to provide a large data base for research. The quantitative procedures used in this research, especially those using highly derived genetic statistics such as genetic correlations, are sensitive to errors. The extent of the New Zealand data base, together with the use of sensitivity analysis, has provided reason for confidence in the results of this research.

The prime methodology used in this research has been index selection and comparisons of expected gains from different alternative strategies. There have been some interesting extensions of index selection applications developed at Forest Research Institute (FRI) in New Zealand (Burdon 1977, Burdon 1979, Burdon 1982, Burdon 1989). The two standard applications of index selection are: (1) for multiple traits, where different traits are assigned different economic values and (2) where multiple classes of relatives are used. Both are common in forest tree breeding (Namkoong 1979). One of Burdon's extensions that is widely used in New Zealand is the use of multi-trait index scoring for information from different sites (Burdon 1979). For instance, diameter growth at site A and site B are treated as separate traits in a multi-trait index. One of the major advantages of using sites as traits in index selection is that validity of the results is not sensitive to heterogeneity of variance between sites. Significant genotype by environment interaction may more reflect different variance structures on sites than a true and repeatable interactive variance.

GxE interaction and the need to regionalize breeding

Until recently, the prevalent view of GxE interaction of FRI was that it justified a regionalized breeding program for radiata pine. Orchards were in place or planned for several regions of the North and South Islands (Shelbourne et al. 1986). This view was based on significant levels of GxE found in progeny tests and the 130 latitude range of radiata pine plantations in New Zealand.

Even where GxE interactions are significant how does one quantify the need to regionalize selections? Shelbourne (1972) suggested where the GxE interaction component reaches 50% or more of the entry component, gains will be seriously impacted. Matheson and Raymond (1984) have suggested using "the loss of potential gain ... as a criterion for decisions about the practical importance of interactions".

Carson quantified the effect of GxE interaction in terms of the increase in gain from regionalized selections over a single set of selections with various criteria for regionalization. Economic weights of 1 or 0 were assigned depending on whether sites were in a region or not. The best realistic regionalization scenarios could only give an additional 14% gain above that of a non-regionalized approach indicating that regionalized selections would not give substantially greater growth than a single set of selections for New Zealand radiata pine (Carson 1988).

Sensitivity analysis for a range of heritabilities, correlations, and phenotypic variances indicated that where correlations are moderate to high ($r_p > .37$), substantial extra gains (50% or greater) would not occur unless both heritabilities are low. In that situation, the correlation statistics are suspect. Even with low ($r_p = .10$), zero or negative correlations, substantial increase in gain from regionalization was not always apparent (Carson 1988).

A different approach was used to investigate the contributions to accuracy of number of sites and choice of sites for progeny testing. A technique termed Binet restriction was used, which assigns zero index weight for sites not being selected, while allowing estimation of indirect response over all sites (Burdon 1989). Three sites were found to provide most (90%) of the information required for total potential gain for as many as 11 sites (Carson in prep., Johnson unpub. data). The efficiency of adding an additional site drops off rapidly after 3 sites. The pumice sites of the central North Island showed good resolution of genetic differences and were well correlated with other NZ sites (Johnson and Burdon in press, Carson in prep.). The decision made for testing of NZ radiata pine is to concentrate 3 tests sites on the central North Island. Selections from these will provide breeding material for all of New Zealand.

Is there any rationale for further considerations of regionalized breeding for New Zealand radiata pine? In regard to GxE interaction in the Australian radiata pine progeny Matheson et al. (1988) suggested that family x site interactions can only be used to advantage if definable causes are responsible. In general this has not been the case and it was concluded that in forest tree breeding, sites may be better considered as random effects (Matheson and Cotterill 1989).

In New Zealand there is evidence, although limited, of definable site types and repeatable interaction effects (Johnson and Burdon in press). Besides the strong correlation among pumice sites, there is a pattern of significant correlations between pumice and clay sites (Johnson and Burdon in press). Justification of regionalized selections for Northland clays, however, is not necessarily warranted as it produces only a few more percentage points of gain above selections that do well across all sites (Johnson and Burdon in press). In the case where progeny tests exist in Northland clays, the marginal costs of using Northland selections in a control-pollinated orchard is minor to the benefits. however, to incur major costs in a further round of breeding and testing on Northland clays may not be warranted and would require a financial analysis to see if benefits outweigh costs.

Relative efficiencies of early selection

The study represents a backwards perspective on an old progeny test. This test, using 588 OP families, has provided the backbone of the New Zealand radiata breeding program (Shelbourne et al. 1986) and was measured at 17 years prior to a commercial thinning operation (31 m man tree height). Besides the retrospective look to determine which direct growth measurements and related auxiliary measurements could best predict age 17 diameter, the data provided the opportunity of looking at forward projections to later commercial rotations (25 and 30 years). The methodology of this research has been published by R.D. Burdon (1989) and the results of this research are currently in preparation. I won't present the details but will mention that an auxiliary trait (in this case a needle cast score) greatly helped in predicting final yields and a selection age of 25-30% of commercial rotation age maximizes genetic gain per year of breeding effort.

Multiple trait improvement

The research of the previous examples has dealt with primarily one trait - volume growth - or related measurement traits such as diameter. What is the current status of multiple trait improvement in New Zealand radiata pine? Selections using progeny test information have in the past emphasized multi-trait index selection, both in the backwards selection of parents and forwards selection of progeny (Shelbourne et al. 1986). Multi-trait indices used diameter growth, freedom from malformation, stem straightness, branching habit, wood density (sometimes) and needle retention.

The emphasis in multiple trait improvement has now changed from reliance on large multi-trait indices to one of using only those traits that will aid in selecting for specific breeding goals (such as diameter and cyclaneusma needle cast for volume growth). one factor in this change has been evidence from realized gain trials that have shown disappointing results for some of the advanced generation seedlots. Improvement for multiple traits, especially those with negative correlations such as volume growth and wood density as a single breeding goal will ensure sub optimal improvement for each individual trait. Another factor has been the development of the control-pollinated seed orchards which allows the flexibility to produce custom seedlots (M.J. Carson 1986). Central to this new strategy is the concept of breed development or multiple breeding populations that emphasize different technical traits. Selections, therefore, are made for parents to fit into a breeding populations based on single or just a few traits. Breeds currently exist for 'growth and form' (volume growth - some culling on form), 'long-internode' (branching habit - for long clears) and 'disease resistance' (FRI 1987). Putative breeds exist for others including wood density.

The advantage of this method of multiple-trait improvement to the breeder is that the breeder does not have to get involved with economic decision making (what is wood density worth compared to volume?) Forest managers make these decisions when they choose orchard seedlots for planting. Breeders just have to provide the breeding value information for the managers.

Implications for Canadian tree improvement

These studies have provided very reliable information for New Zealand radiata pine breeding on the issue or regionalization (there would be little benefit from it), number and location of test sites (three - concentrating on the North Island pumice plateau), duration of progeny tests (7 to 9 years - about 25% rotation age), and choice of traits to measure in progeny tests (for volume growth - diameter and cycalneusma needle cast). I would not suggest that these results are applicable in Canada. Regionalization may be very important in areas of strong environmental gradients (Campbell 1986, Rehfeldt 1989). We may have to look at much lower selection/rotation ages to justify our tree improvement programs. I would suggest, however, that the questions addressed in this research are very relevant in Canada and the methodology is quite applicable here. There is a good deal of progeny test data now available in Canadian tree improvement programs. Whereas before we have had to rely on environmental information to describe breeding regions, genetic information should be added to this for more accurate definition of breeding regions. Likewise age-age correlations can help us define selection ages. Test results can provide a valuable genetic data base to guide practical tree improvement. Breeding values from progeny tests can also provide the basis for multiple population breeding and breed development for commercial Canadian forest tree species.

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SPECIES AND PROVENANCE TESTING: THE OVERLOOKED OPPORTUNITY?

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INTRODUCTION

The objective of species testing is to determine if the array of native species can be enriched by introduction of species from other regions or continents. It must be demonstrated that a new species can thrive under the physical and biotic conditions of a new environment, and that it represents a worthwhile addition to our native flora. As a rule, several provenances of a new species must be tested.

The objectives of provenance testing are more complex, and one could list four objectives:

1) the determination of genetic variation patterns;

2) the designation of seed and breeding zones;

3) the derivation of population parameters useful for the planning of selection programs; and

4) the determination of the best provenances for a given region.

Species and provenance testing and research have been conducted in Canada continuously for the last 40 years, and several review papers have been written (e.g. Fowler 1979a). Two years ago, Dr. Ying and I summarized the results for the major species on the occasion of the last CTIA meeting at Truro, Nova Scotia (Ying and Morgenstern 1988). Today, I will use a different approach. In the first part, dealing with the past, I will give an overview of accomplishments, region by region. In the second part, concerned with the future, I will discuss some problems of past studies and opportunities for future work.

OVERVIEW OF REGIONAL ACCOMPLISHMENTS

This survey of regional accomplishments is primarily concerned with conifers and will be somewhat selective.

Newfoundland

Provenance experiments have been conducted in Newfoundland since 1961 when experiments were established with assistance from Petawawa and the Fredericton federal laboratory. The first geneticist was appointed at the federal forest research centre at St. John's in 1967 (Nicholson 1969).

Studies of native and mainland white spruce (*Picea glauca* (Moench) Voss) and black spruce (*P. mariana* (Mill.) B.S.P.) are underway. Results up to 25 years from seed for white spruce and 15 years for black spruce have been published (Nicholson 1970, Khalil 1974, hall 1986b). The possibility of moving both black spruce and white spruce from the mainland to Newfoundland to increase growth is one of the more important questions considered (Hall 1986a, 1986b). Seed zones based on Rowe (1972) are used.

Exotic species tested in Newfoundland include red spruce (*Picea rubens* Sarg.), Sitka spruce (*P. sitchensis* (Bong.) Carr.), and several species in the genera *Abies* Mill, *Pinus* L., and *Larix* Mill. The introduction of *Larix* species and hybrids appears to be most promising (Hall 1973, Khalil 1977, Hall 1986c, Hall 1988).

Maritime Provinces

As in Newfoundland, the federal forest research centre in Fredericton, New Brunswick is the main agency responsible for basic forest genetics research in New Brunswick, Nova Scotia, and Prince Edward Island. Work was begun by George MacGillivray in the early 1950's (MacGillivray 1956) and has been pursued very actively since that time. Range-wide experiments with red spruce, black spruce, white spruce, tamarack (*Larix laricina* (Du Roi) K. Koch), and jack pine (*Pinus banksiana* Lamb.) have been established, as well as regional experiments with jack pine and white, black and red spruce as part of the cooperative breeding program in the region (Fowler 1979b, Fowler et al. 1986). Variation patterns have been determined for each species and seed and breeding zones established (Fowler and MacGillivray 1967, Morgenstern et al. 1981, Fowler and Park 1982, Fowler et al. 1988a, Park and Fowler 1988).

The major exotic species tested in the Maritimes include Norway (*Picea abies* (L.) Karst.), Japanese larch (*Larix leptolepis* (Sieb et Zucc.) Gord.), European larch (*L. decidua* Mill.) and the European-Japanese larch hybrid (*L. eurolepis* Henry). The Norway spruce experiments have been evaluated and preferred source areas for different geographic areas in the Maritimes have been designated. Plus-tree selection within the best provenances has been undertaken and seed orchards established to develop a land race for the region (Fowler and Coles 1979). Comprehensive analyses of a larch species and provenance trial have been made which included comparisons of growth and wood quality at age 29 years from seed. It appears that Japanese larch, grown in short rotations of about 30 years, produces two to three times more wood than other species commonly grown in the region, and that the wood is suitable for housing construction (MacGillivray 1969, Fowler et al. 1988b).

Quebec

The earliest provenance trials in Quebec date back to 1882 when several provenances of black walnut (*Juglans nigra* L.) were established in the St. Lawrence Valley (Parrot 1971). A favourable constellation of geneticists located at Université Laval, Forêts Canada, and Ministère de l'Energie et des Ressources has existed since the late 1960's and a strong program is maintained (Corriveau and Vallée 1981). Several companies have contributed to this program, especially Canadian Pacific Forest Products (formerly Canadian International Paper Co. Ltd.). One unique feature of the Quebec provenance research program is the establishment of a network of nine arboreta where test plantations are concentrated (Vallée 1971).

The studies of jack pine, red spruce, white spruce and black spruce initiated at Petawawa are all replicated in Quebec and results have been published (Roche 1969a, Corriveau et Boudoux 1971, Yeatman 1976, Morgenstern et al. 1981, Beaulieu et al. 1989). Evaluations have included white spruce wood density (Beaulieu et Corriveau 1985). Seed zones for all species and black spruce breeding zones have been delineated (Service de la Restauration Forestière 1970, Beaulieu et al. 1989).

Combined provenance-family tests of tamarack have been initiated (Stipanicic 1976a). Larches in general have been given much emphasis in Quebec and there appears to be a potential for the production of high volumes of wood in short rotations (Vallée and Stipanicic 1983).

Among the exotic species, Japanese and European larch, Norway spruce and Scots pine (Pinus sylvestris L.) have been tested in many field trials while numerous other species have been planted in small plots in arboreta to determine frost resistance (Beaudoin 1976, Stipanicic 1976b). It seems clear that European and Japanese larch, Norway spruce and Scots pine can be profitably grown in Quebec.

Ontario

Both federal and provincial organizations have maintained strong test programs in Ontario. Significant events were the establishment of a research group under Dr. Carl Heimburger at the provincial Southern Research Station at Maple (now the Ontario Tree Improvement and Foret Biomass Institute) in 1946 and the appointment of Mark Holst as forest geneticist at the federal Petawawa Forest Experiment Station (now the Petawawa National Forestry Institute) in 1950. Many companies, provincial forest districts, and the University of Toronto and Lakehead University have supported the work (Farrar 1969, Morgenstern 1979). Species tested include red pine (Pinus resinosa Ait.), jack pine, white pine (P. strobus L.), red spruce, white spruce, black spruce and tamarack. Significant findings on variation in survival, hardiness, disease resistance and growth have been obtained (Holst and Yeatman 1961, Fowler 1964, Fowler and Heimburger 1969, Morgenstern 1969, Morgenstern and Teich 1969, Teich and Smerlis 1969, Teich and Holst 1974, Yeatman 1974, Yeatman 1975, Dhir 1976, Morgenstern et al. 1981, Boyle 1985, Murray and Skeates 1985). The oldest jack pine provenance experiment at Petawawa, which is properly randomized and replicated, is now 38 years old. A comprehensive analysis at age 34 years from seed indicated significant provenance differences and correlations with latitude of origin for height, diameter and stem volume (Magnussen et al. 1985).

Results from the experiments in Ontario have been used to advance knowledge on population structure and to plan selection programs. Seed zones have been established (Skeates 1979) and breeding zones for black spruce proposed (Boyle 1986). Results from the more recently established range-wide experiments of white spruce and tamarack are not yet available.

The major exotic species tested include Norway spruce, Scots pine, European larch, and the hybrid Larix eurolepis Henry. Large provenance differences have been found in hardiness, growth, form, and insect and disease resistance. Second-generation populations have usually performed better than the first generation (Holst 1963, Holst and Heimburger 1969, Teich and Morgenstern 1969, Teich and Holst 1970, Holst 1974, Holst 1975, Calvert and Rauter 1979, Coleman et al. 1987).

Prairie Provinces

Species and provenance testing in the Prairie Provinces (Manitoba, Saskatchewan and Alberta) was at first essentially limited to federal agencies such as the Prairie Farm Rehabilitation Administration (PFRA) nursery at Indian Head, Saskatchewan, which was established in 1902, and the federal forestry laboratories, but has also been initiated by provincial forest services during the last 10 to 15 years (Cram 1958, Pandila et al. 1988, Dhir et al. 1988). In the older experiments, variation patterns were usually similar to those discovered in eastern Canada such as for red pine (Roller 1968) and black spruce (Segaran 1978a, 1978b). Other species tested are jack pine, lodgepole pine (Pinus contorta Dougl.) and white spruce.

Seed zones for Manitoba have been described (Segaran 1979). In Saskatchewan and Alberta similar guide-lines exist to restrict seed movement (Klein 1979a, 1979b). Breeding districts for jack pine have been defined (Klein 1969, Klein 1982).

Work with exotic species has been given more emphasis recently. The goal is to find trees suitable for shelterbelts and shade trees for the difficult environment of the agricultural plains as well as the forests north of them. in the plains, problems are low and extremely variable precipitation from year to year (about 300-500 mm per year), short hot summers, and long cold winters often without substantial snow cover. Shelterbelts are designed to ameliorate these extreme conditions (Schroeder 1988a). The species tested include the conifers Scots pine, Siberian larch (Larix sibirica Ledeb.), Dahurian larch (L. gmelini (Rupr.) Ledeb.), and Ponderosa pine (Pinus ponderosa Laws.), and among deciduous tree species or shrubs, green ash (Fraxinus pennsylvanica Marsh. var. subintergerrima (Vahl) Fern.), Siberian pea-shrub (Caragana arborescens Lam.), Chinese elm (Ulmus pumila L.), Russian olive (Eleagnus angustifolia L.), the sea-buckthorn (Hippophae rhamnoides L.), and several hybrid poplars (Populus spp.), to name but a few (Dhir et al. 1988; Schroeder 1988a, 1988b; Pandila et al. 1988). Certain provenances of all species mentioned are hardy and some of the shrubs, in addition, provide food for wildlife. Among the trees Siberian larch is consistently one of the most promising tree species and Scots and Ponderosa pine are also acceptable (Roller 1971, Klein 1971, 1979c; Dhir et al. 1988; Schroeder 1988a).

British Columbia

Next to Quebec, British Columbia contains the largest forest area of any Canadian province but leads in standing volume and volume of wood harvested annually (Canadian Forestry Service 1987). British Columbia's geography is also the most complex and its forests the most diversified, containing the largest number of conifer species. The organization of silviculture is therefore more difficult than in all other provinces.

Provenance research in British Columbia has been undertaken both at the University of British Columbia at Vancouver and within the Research Branch of the Ministry of Forests and Lands at Victoria. Field experiments have been largely conducted by the Research Branch with assistance from many forest districts. The federal research centre at Victoria has only occasionally been involved (Piesch 1971). Most provenance research in B.C. began relatively late, namely in the 1968-1974 period.

The biogeoclimatic regions established by Dr. Krajina at the University of British Columbia constitute the basis for seed zones (Konish 1979).

Originally there were 67 seed zones. Provenance research has made a major contribution to the modification and simplification of the seed-zone system, making it possible to revise the system several times during the last two decades. At present there are 21 seed zones in the Interior which apply to all species. At the Coast the number of seed zones for Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) has been reduced from 16 to 4. The other coastal species have 7 zones except Sitka spruce which has 4 as well (Dr. C.C. Ying, pers. comm.).

Another important result obtained at an early stage was the clarification of the taxonomic status of species within the genus Picea. It has been shown that there is a zone of hybridization between white spruce and Engelmann spruce (Picea engelmannii Parry) in middle elevations of the Rocky Mountains and between white spruce and Sitka spruce in north-coastal British Columbia (Roche 1969b). Seed collected within these areas now is not labelled separately by species but designated as being a part of the "spruce complex".

Provenance research has also identified weevil resistant Sitka spruce provenances and productive and stable sources of coastal Douglas-fir in Washington. While the variation pattern of the major species (i.e. Douglas-fir, Sitka spruce and lodgepole pine) is now much better known following the work of Illingworth (1978a, 1978b), Ying and others (Ying et al. 1989), work on several additional species has only recently been initiated (Ying and Morgenstern 1988, Woods and Woon 1988). Overall, much more time is needed to complete the picture of provenance variation in British Columbia. The available information has recently been summarized and interpreted (Lester et al. 1989).

Trials of exotics in British Columbia are rare which is not surprising since this region contains some of the world's fastest growing and valuable species, which have been exported to other countries for nearly two centuries (Mathews 1983). The chances of finding anything better are fairly remote.

THE FUTURE

From this overview and the supporting literature, a number of problems, questions and concerns emerge.

One such problem is the validity of early results. Variation patterns have often been determined from nursery experiments where the test environment was under some control, and the results were clear and could be easily interpreted, as for example in experiments with black spruce (Morgenstern 1978). In contrast, when the same material was tested in the field, the correlations of growth with geographic variables had become much weaker, presumably because "free growth" was no longer an important factor in trees 15 years old (Boyle 1985). Although part of the explanation is the greater diversity of environments, it has also been shown that growth could be related to different levels of outcrossing (inbreeding) in the parental populations (Dr. T. Boyle, pers. comm.). Therefore, superimposed on the general pattern of variation controlled by natural selection, there are deviations related to other genetic processes such as inbreeding, genetic drift, etc. This is really not surprising.

In spite of these complications, a genetic variation pattern related to geographic or climatic parameters will usually persist. Dietrichson (1964) has shown that in a Scots pine experiment, shoot and needle extension could still be related to latitude of origin 22 years after establishment, and that in Norway spruce large differences in late wood percentage were found among provenances 16 years after planting. Langlet (1971) supports this view, pointing out that differences among Norway spruce provenances in volume production have steadily increased in material 70-80 years old.

Secondly, there is a need for more complete analysis of experiments. In many 10-15 year old experiments only height and survival have been assessed. Since volume production depends upon stocking, survival must be followed over a longer time period. Survival is an important indicator of adaptability and sometimes shows geographic trends which are opposite to those for height (Morgenstern and Roche 1969). Insect and disease resistance, wood quality, and volume production per ha are other important traits to be assessed.

Thirdly, studies of exotics have often not been thorough enough. There is a need for continued evaluation of older experiments and joint analysis of groups of experiments with the same species. Furthermore, since the question of adaptation of exotics is really much more critical than for native species, descriptions of test environments (soil, vegetation, local and regional climate) should be regularly included. The inclusion of native species in trials of exotics should be standard practice.

Finally, a number of interesting exotic species have never been properly tested. Only recently have southern provenances of Siberian and Dahurian larch been obtained and these are now being tested in several provinces. Another specie which may have potential is European black alder (Alnus glutinosa (L.) Gaertn.), perhaps as an admixture to hybrid poplar and larch plantations. This is a tree alder which can be utilized for a variety of purposes and is now extensively tested in eastern and central North America (Robison et al. 1978, Genys 1988).

In conclusion, it is clear that species and provenance testing have not been overlooked. In each region, much has been accomplished and good results have been achieved, but we are far from a satisfactory and complete understanding of variation patterns even for our major species. Species and provenance testing must be continued for many years to come.

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CLONAL TESTING AND SELECTION IN CONTEMPORARY TREE IMPROVEMENT

Gilles Vallée

This presentation will not be a literature review of the papers published on the subject. The literature on clonal testing and selection is well covered in the proceedings of meetings held in Sweden in 1981, in the Federal Republic of Germany in 1982, and in Toronto in 1983 (CTIA meeting) cited in reference with other recent papers. Rather, I will try to situate clonal testing and selection in contemporary tree improvement and to make comments on debatable points related to clonal forestry, testing and selection.

To realize this objective, the following subjects will be treated:

- Why clonal forestry?
- Comments on debatable points and limiting factors.
- Clonal selection strategy versus conventional tree improvement program for seed orchard.

Why clonal forestry?

Clonal forestry is a means to answer particular needs of the human society, in the way that intensive agriculture provided answers to the nutritional needs of humanity. If now all agricultural goods were produced on an extensive method as in the Middle Ages, how large would the forest areas be in Europe and North America? I think the natural forest area would be somewhat small considering the present consumption of food.

The same evolution can be applied to forestry. Undoubtedly the needs of humanity in wood will increase in the future. To satisfy them we must intensify wood production in certain areas. This is a necessity if we want to keep large areas of natural forest with no or little management to produce wood in respect to other forest ecosystem products and to keep an equilibrium between the natural ecosystems of the earth.

Large areas of natural forest have already been destroyed for the production of fuel wood, particularly in Africa and Asia. Latest FAO data on forest in China foresee a total elimination of the forest within the next 20 years if the same rate of harvesting or destruction is maintained. In Quebec, nearly all the commercial forest area will be under forest management agreements by April 1990, with exceptions for ecological reserves and certain parks, to answer the needs of the present forest industry.

Clonal forestry proved its potential to meet specific needs a long time ago with poplar, willow and Cryptomeria japonica and more recently with eucalyptus. Then why not go ahead with other species? The timing is good for clonal forestry because in Canada, Western Europe and the United States, there is a surplus of agricultural land part of which is very adequate for the intensive culture of trees.

Comments on debatable points and limiting factors

This presentation is an opportunity for me to give my opinion on certain aspects of clonal forestry and clone selection.

On the limit of clone adaptation to the environment, it is important to understand what a clone is. A clone comprises all ramets reproduced asexually from a common ancestor and having identical genotype. What is genotype? It is the entire genetic constitution, expressed or latent, of an organism. But with the genotype there is also the germplasm, which is "the sum total of the genes and cytoplasmic factors governing inheritance" (Wright, 1976).

All ramets of a clone have the same germplasm constitution, expressed or latent. A new way to improve a clone is somaclonal selection by tissue culture in which cells are forced to express their germplasm differently. It could be the expression of a latent gene or group of genes, or cytoplasmic factors, or the new expression of active genes, etc. If this happens with cells, it can also happen, to a certain limit, with ramets. If the micro-environment surrounding the cells in tissue culture can modify the expression of the germplasm, also the micro and macro-environment around a ramet influence and can force the expression of its germplasm and favor a new expression. A good example of that phenomena is the poplar clone Populus nigra cv. 'Italica' which loses its leaves for the winter season in regions with a temperate climate but keeps them in countries like Chile under a subtropical climate. In Quebec I observed that certain interspecific hybrid poplar clones can adapt their phenology to different growing periods varying from 90 to 120 days.

The conclusion of these first comments is that clones have a certain ability of adaptation to different environmental conditions. Geneticists can select for that flexibility of the germplasm, obtaining clones with larger adaptation related to various germplasm expression. It is true that clone-site matching selection can be done, but I believe it applies more to extreme environmental conditions such as very dry or very wet sites. The rule will rather be the selection of clones for various medium environmental conditions, especially if intensive culture is practised which helps to improve and standardize the cultural conditions. A good example is the clone Populus x euramericana cv. 'Robusta' in France, Belgium and the Netherlands where it has been planted on various sites, from alluvial soils to mesic deep soil deposits, giving good wood production and showing a relatively good resistance or tolerance to pests (Zsuffa, 1983). But for high water table soils in the Poitou region of France, where the soil is very wet, the clone 'Robusta' does not perform well; the clone 'Blanc du Poitou' has been selected for these extreme conditions.

For species like black spruce, jack pine, larches and birches, which have a large ecological adaptability, it would be possible to select clones performing on a wide range of sites excluding the extreme site conditions. This will be more feasible with multiclonal varieties which present more genetic stability and less genotype x environmental interaction because of the combined homeostasis of the individual genotypes belonging to the variety (Bentzer 1988).

Clonal forestry increases the risk of entomological and pathological disasters because of the homogeneity of the genetic stock. This is another assertion we hear very often. But balsam fir natural stands over all of Eastern Canada and the United States have a lot of genetic diversity and every 20 to 30 years, spruce budworm invades nearly all the stands. Someone will counter that it is because of the monospecific culture over large areas that spruce budworm do so much damage. Let us not forget that spruce budworms eat the needles of white, black, Colorado and Norway spruce and also larches. Moreover balsam fir trees are attacked in mixed stands as well as in pure stands!

The hardwood forest stands of southern Québec and Ontario represent a complex of species, tree by tree or in mosaic. This forest is regularly invaded by different insects eating the leaves, which has contributed in part to the decline of that forest in Québec. Also many leaf diseases and cankers are active in that mixed hardwood forest. Besides, one of the largest monospecific cultures of the world, our black spruce forest, does not appear to be too much affected by diseases and insects.

Note that clonal plantations can include more variation in genotype by mixture of clone than some natural stands have where trees show a certain level of inbreeding. By an adequate clonal selection, resistance or tolerance to diseases and insects can be enhanced, improving the ecological production of a given site occupied by a clonal plantation.

Finally, nobody thinks of replacing all the natural forest by clonal plantations. Clonal forestry will be practiced on specific areas, generally the best sites to grow a given species, more or less intensively cultivated on somewhat short rotations to answer particular social needs, as mentioned before.

Clone aging is another limiting factor for clonal forestry and selection. Most of the broadleaf tree species can be rejuvenated by coppicing or suckering and in vitro culture (Périnet et al., 1988, Cornu, 1985), etc. but, inversely, many coniferous species cannot be rejuvenated. Worse, after about 5 to 10 years, clones developed from seedlings start to show problems related to aging like plagiotropism, lower rate of rooting (in cuttings), slower growth, etc. depending on the species.

No treatments are presently known to keep coniferous species juvenile for a long period of time or to truly rejuvenate them. Some treatments have shown appearance of rejuvenation but this was not always proven on a physiological or genetics basis. Ortets of Norway spruce selected from seedlings have been kept at the juvenile stage through repeated pruning for 17 years (Bentzer et al. 1988). Let us hope that in the near future somatic embryogenesis techniques will allow developing and keeping clones at the juvenile stage and that mature trees will be rejuvenated by tissue culture with in vitro micropropagation (Thorpe and Hasnain 1987) without any modification of the chromosome structure and the genotype expression (Fowler, 1987).

For most of the coniferous species, clonal selection strategy must take into consideration this limiting factor of aging and one of the ways to overcome problems is to do early screening using very juvenile stock with a turnover in the clonal stock. Another way to overcome aging problems is to bulk propagate sibs from selected progenies from repeated sowing or repeated controlled crosses (full sibs). These two methods suppose that juvenile mature correlations for growth and other desirable characteristics are high and that these could be evaluated and selected at the juvenile stage.

Every year there is more evidence supporting the generality of these correlations, but not at 100%, particularly or growth which is governed by many genes and highly influenced by ecological conditions.

This juvenile-mature correlation is another limiting factor for clonal selection as it is also for any forest tree improvement strategy when quick results are needed.

One approach to overcome the problems of clone aging and the juvenile-mature correlation for growth is to base our selection strategy on full sib progenies and the following principles:

a) At the juvenile stage, selected full sib progenies must produce cuttings with good rooting ability and the best behavior or response to the propagation system used, such as reaction to shearing, ability to produce cuttings, physiological activities during rooting phases, etc.

b) Full sibs progenies must grow fast at the juvenile stage with low individual variability. Then within the progenies having fast juvenile growth we will select progenies having fast mature growth.

c) By recurrent selection the best growing progenies at juvenile and mature stage will be included in a multi-progenies variety which is a bulk propagation of non-identified clones.

If clonal plantations are managed on shorter rotations than conventional plantations, juvenile growth becomes a very important characteristic. Moreover, the cost of cutting propagation and plant production could be very important in the financial yield of clonal plantations and must be kept as low as possible. In the selection strategy, seedling stage and juvenile behavior of the clones or progenies are as important as mature behavior for clonal forestry systems because of their economic and physiological impacts on the whole system. For example, with the present technology the high cost of in vitro culture prevents its application to forest seedling production for many species.

But if the problem of plagiotropism can be corrected and if juvenile growth loss is accepted, then clone aging is not a limiting factor for certain coniferous species. By successive cycles of cutting propagation and treatment of the donor plant, the rooting ability of the cutting is increased for certain species like black spruce and Eurolepis larch with which I have worked. Plagiotropism can also be partly corrected by successive cycles of cutting but other treatments applied to the donor plant or after rooting are needed to completely correct plagiotropism.

Clonal selection strategy

Before elaborating a clonal selection strategy for a given area, it is primordial (a) to identify the available input to the strategy, which is the background information and biologic material available from past tree improvement programs, (b) to describe the output, that is, the type of clonal plantation desired and, by deduction, the characteristics of the clones desired, and (c) to define the best way to exploit this information and generic material in regard to increasing the probability of obtaining the maximum gain in the output.

Drs. Yeatman and Morgenstern have presented earlier today a general overview of tree improvement for Canada. Figure 1 tries to summarize the principal working steps in most of the tree improvement programs applied in different regions in Canada. some of the output of these programs which can be useful as input in a clonal selection strategy are:

a) Delimitation of tree breeding zones.

b) Identification of the best provenance (populations) for each breeding zone.

c) Evaluation of the potential genetic gains obtainable, by provenances, inter-provenance crosses, interspecific crosses and clonal selection.

d) Evaluation of the heritability level and genetic structure of the populations.

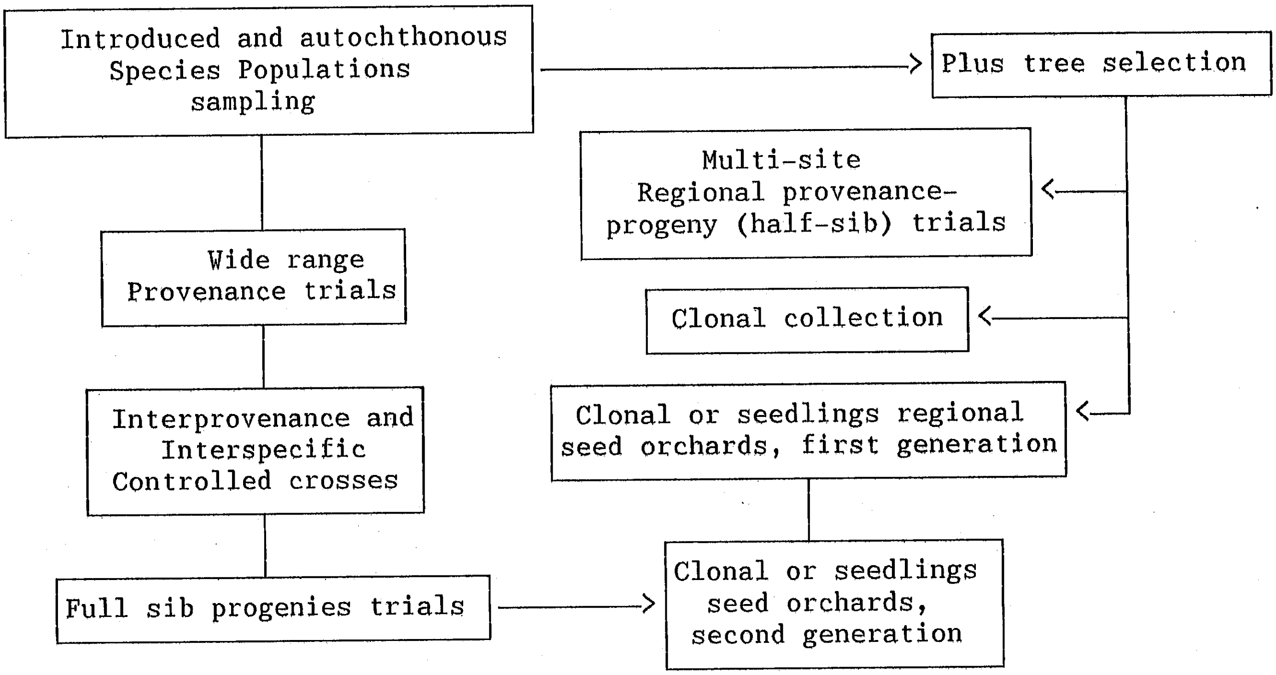
e) Identification of the constraints related to the species such as the use of clone, pest susceptibility, environment sensibility, etc. in regards to reforestation.

f) Identification of the best progenies (half sibs) and the best clones coming from seed orchard programs.

g) Identification of the best interspecific crosses.

Figure 1

Conventional tree improvement strategy: source of informations and biologic material available for clonal selection strategy



Combining the information and biological material available, the intraspecific clonal selection strategy must try to integrate, if not to add, for growth and other desired characteristics, the genetic gains of provenance selection, interprovenance cross heterosis, progeny selection in the inter-provenance full sibs, and clonal selection as shown in figure 2. Interspecific hybrid heterosis is another potential gain to incorporate in a clonal selection strategy. For species like poplar, willow, eucalyptus, larch, etc. interspecific hybrid crossing remains the principal way to obtain clones with high growth heterosis and combining other desired characteristics such as resistance to leaf diseases and canker, wood density, etc. But today most of the clonal selection strategies on poplar include also the conventional genetic improvement of the species to get improved strains which will be used later in interspecific crosses.

The genus Poplar is a typical example of what can be achieved by clonal selection and, especially today, because of available technologies, to produce new clones. Figure 3 summarizes, in French, the activities of a strategy in genetic improvement and clonal selection of poplar. In addition to the traditional sources of clones, it is also possible now with poplar to obtain clones by in vitro culture of haploid tissues, by tissue culture with somaclonal selection, by genetic engineering and by protoplasmic fusion. With the research now going on, there is hope to get in the near future as many sources of clone production for other species as we have for poplar.

Considering the constraints related to clone aging for coniferous species, the tree breeders group working within the Tree Improvement Service of the Quebec Ministry of Energy and Resources has decided for the moment to select multiple full-sib varieties for black spruce, Norway spruce, jack pine and Eurolepis larch (see figure 4). The choice was based on the fact that with breeding hall techniques combined with flower induction treatments, it will be easy to reproduce the selected crosses on a large scale and to replace every year or two the donor seedlings cultivated in greenhouses for the production of cuttings. More gains will be achieved by clonal selection done later in the best selected full sib families. During that period it is hoped that technology of rejuvenation or juvenility maintenance, with no modification of the genotype expression, will be available and will favor clonal selection. That is why for about the next 5 years, the group thinks it is better to concentrate energy and labor on the evaluation of many crosses, with the secondary objective of knowing the specific and general combining ability of the parents. This last information can be useful if a second generation seed orchards, with controlled pollination in a breeding hall, is needed.

Other arguments in favor of this strategy are the necessity to have seedling stock with a certain level of improvement for bulk propagation by cutting and to keep genetic variability. This improvement level is obtained by crossing the good trees of the best provenances for each breeding zone which insure a part of the provenance gain plus the possible gain resulting from the interprovenance crosses. This choice also allows the production of nursery stock with larger genetic diversity obtained through interprovenance crosses between trees of the best provenances from which seeds are not always available in quantity for reforestation.

In the Northern Region of Ontario the strategy for black spruce is to select clones from seedling selection in full sib progenies obtained from controlled crosses between selected trees of the region (Roger, 1988). Selected clones are established in hedges for the production of cuttings (Dewitt, 1988). Clonal selection is done in four steps: the first step is under greenhouse conditions and three other steps under field conditions in which different parameters are assessed with reduction of the number of clones between each step (Archibald, 1988).

In clonal selection, growth performance is not necessarily the first characteristic to select. One of the advantages offered by clonal selection is to help getting cultivars with very special characteristics, which is difficult to obtain from sexual propagation. Clonal selection of poplar is again a very good example of what can be achieved in that respect. Generally the first step in the clonal selection of poplar is for resistance to the most virulent foliar leaf diseases; the second step is for resistance to the most virulent cankers and it is only at the last step that growth, quality of the phenotype and site adaptation can be considered.

Figure 2

Potential gains for growth and production in clonal selection

Clonal selection
must try to integrate the following gains

- Gain of provenance selection
- Gain from the heterosis of interprovenance and interspecific crosses
- Gain of progeny selection in the interprovenance and interspecific full sibs
- Gain of clonal selection made within the best interprovenance and interspecific progenies

The identification of the constraints such as diseases related to a species in clonal plantations is very important for its inclusion in the selection strategy. These constraints are not always expressed in clonal tests or small plantations or with the species in the natural forest. To learn about constraints, somewhat large clonal plantations often favor the expression by allowing, in the case of diseases for example, the development of the inoculum. This is what happens with the plantation of poplar clones susceptible to Septoria musiva canker in southern Quebec and Ontario. At the present time, the selection of clones with low susceptibility to Septoria canker using artificial inoculation has became one step in the clonal selection strategy for poplar in Quebec and Ontario.

Clonal selection can very quickly produce valuable stock for reforestation depending on the desired characteristics. For broadleaf species planted for veneer production, the quality of the phenotype is very important. Straight stem, right angle of branching, very good apical dominance without forks are some of the characteristics needed for planting stock to get plantations which will produce high quality veneer wood. These characteristics are highly heritable and reproducible by cutting propagation. If a thorough selection for these characteristics is made on natural trees having age and growing in forest conditions or in plantation which guarantee a good evaluation of these characteristics, I believe that clonal nursery stock coming from that selection will be superior to any stock coming from seeds, as happened for Prunus avium L. in France (Cornu, 1985).

There are many approaches to clonal testing aimed at evaluating and selecting clones in regards to their growth and other wood production aspects. Many types of statistical layouts are used depending on the strategy, the number of clones tested, species and other constraints. For a first step in selection, it is generally better to start with a large number of clones, tested in small sample plots, as small as one-tree, and with 6 to 10 repetitions per testing site.

The most important step in clonal selection is to determine with high accuracy the growth and production performance of the clone. In many tree improvement trials presently realized on many sites with the same genetic material, I am always perplexed or confused to see the instability in ranking for growth of the provenances, or progenies, or clones, particularly for low requirements species like black spruce and jack pine. As I mentioned before, black spruce has a very wide range of adaptation to different ecological sites and its needs in soil fertility are somewhat low. Moreover black spruce provenances can be transferred northward some 2 or 3 degrees of latitude without suffering frost damage and with gain in growth. If tree growth is the result of many physiological characteristics of a genotype and is controlled by many genes, then is it possible that these genes can express in a compensatory way depending on the environment where the genotype grows?

So why does it seem difficult in multi-site trials to have similar ranking and to find provenances and progenies with general adaptation to different sites and ecological regions?

I believe that in many conventional tree improvement trials done in conditions representative of usual reforestation operational sites, there is uncontrolled ecological microsite variation in soil fertility, drainage, competition, etc. which brings some distortions in the interpretation of the data (Magnussen and Yeatman 1988, Khalil 1987, Boyle 1986, Beaulieu et al. 1989, King et al., 1988, Bentzer et al., 1988). The interactions of microsite ecological variations are not corrected by statistical analysis. Then the evaluation of genotype populations indirectly includes this microsite interaction which may limit expression and ranking of the genotype. I believe that the genotype-environment interaction includes in part that microsite ecological variation which is not related to the true adaptation of clones to a given ecological environment.

One way to eliminate this problem is to do the trials on land well prepared by plowing, disking, draining and fertilizing, making more uniform soil conditions by eliminating as much as possible microsite variations and keeping homogeneity within the test or at least each block. This way to proceed is in correspondence with intensive culture of trees and I think it is also applicable to conventional plantation in a first stage of clonal selection for growth. This first stage of selection for growth can be done in the nursery located in the same ecological region where the clones will be planted, using close spacing and allowing the screening of a large number of clones at a lower cost, on short periods of time depending on growth rate of the species. I will textually repeat here part of the paper submitted by Dr. Park on "Field Testing in Operational Breeding programs" at the 1987 Truro meeting of C.T.I.A., with which I agree completely, and must be applied to clonal testing.

"Site selection, site preparation, and care of field tests are crucially important in obtaining valid and fair estimates. In the past, many of our tests have been established on typical reforestation sites, and several of these tests have had confounding damage and unacceptable levels of mortality. Protection and care of tests from confounding damage and losses will become increasingly important as small-plot designs are adopted. Perhaps homogeneity within the test should be given emphasis. Genetic testing should be done on "testing nursery" or prime sites so that the trees can express optimal potential. One may argue that survival in operational field conditions is important; however, many of our provenance tests indicate that provenance x site interactions are not important, i.e., provenances which survived better on better sites also survived better on poor sites."

"It is generally agreed that genetic testing should be carried out at about one-half the rotation age. However, the information on juvenile-mature correlation is the major factor determining duration of the genetic testing and will be available from family and provenance tests in the near future. If the correlation is sufficiently high such that effective evaluations can be made in 5 to 10 years, trees can be evaluated in a "testing nursery" at a narrow spacing. The use of a narrow spacing in the test reduces the size of the test, which in turn reduces the environmental variation and, thus, increases precision."

I will add that, if some physiological laboratory tests can be used for preliminary screening in tree improvement, why not use intensive soil preparation or culture for testing site in a first field stage screening? Beside the actual typical reforestation sites are probably different of the site in 10 or 20 years from now particularly in regard to soil preparation for which technics are always in evolution.

I believe that clonal selection strategy must be inserted in the conventional tree breeding programs helping to produce useful informations for second generation seed orchards.

But with bulk propagation of selected full sib progenies by juvenile cutting do we need second generation seed orchards?

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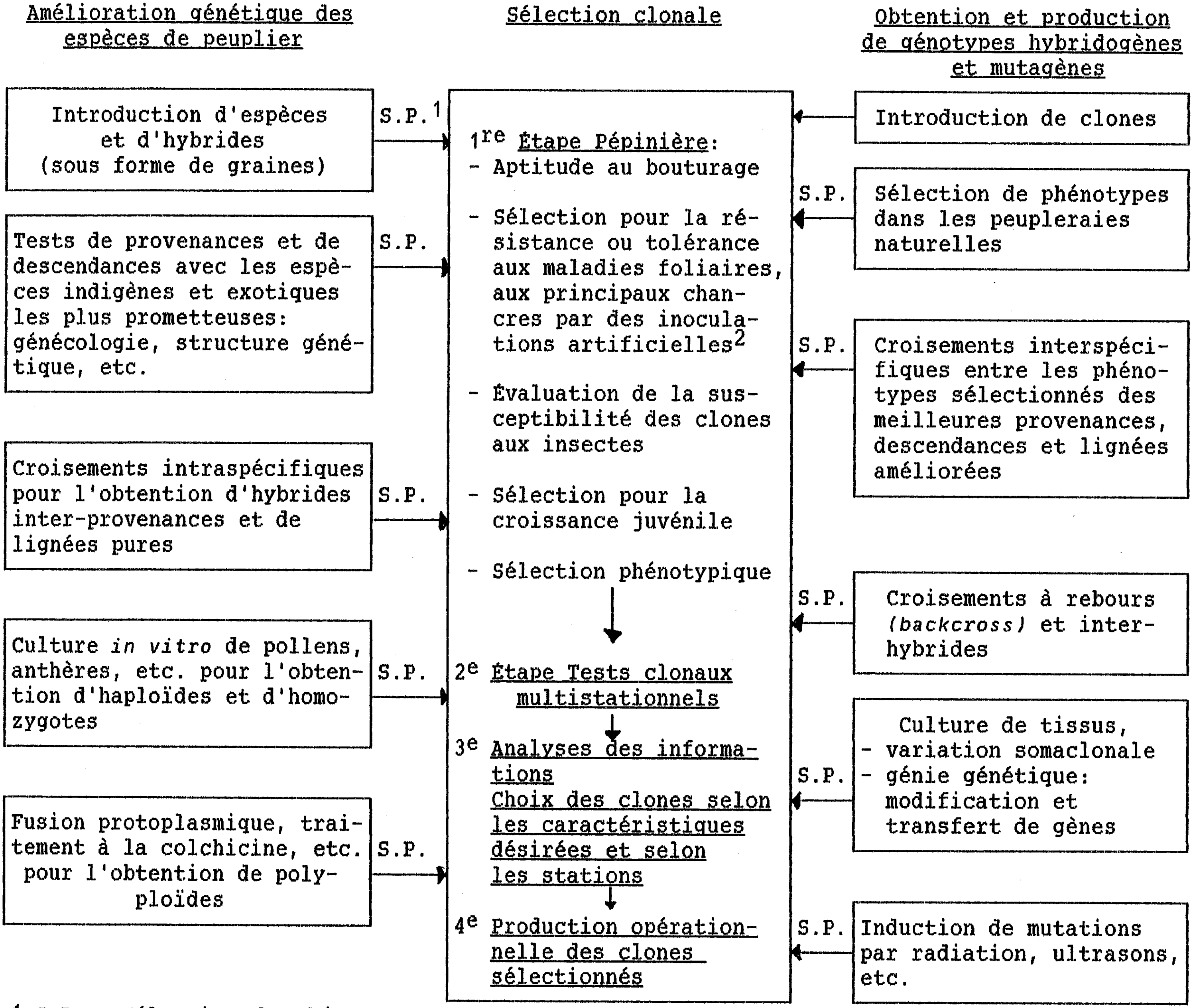
Figure 3

Activités d'une stratégie générale pour l'amélioration des peupliers et la sélection de clones[3]



Amélioration génétique des espèces de peuplier

Introduction d'espèces et d'hybrides (sous forme de graines) — S.P.[1]

Tests de provenances et de descendances avec les espèces indigènes et exotiques les plus prometteuses: génécologie, structure génétique, etc. — S.P.

Croisements intraspécifiques pour l'obtention d'hybrides inter-provenances et de lignées pures — S.P.

Culture *in vitro* de pollens, anthères, etc. pour l'obtention d'haploïdes et d'homozygotes — S.P.

Fusion protoplasmique, traitement à la colchicine, etc. pour l'obtention de polyploïdes — S.P.

Sélection clonale

1re Étape Pépinière:
- Aptitude au bouturage
- Sélection pour la résistance ou tolérance aux maladies foliaires, aux principaux chancres par des inoculations artificielles[2]
- Évaluation de la susceptibilité des clones aux insectes
- Sélection pour la croissance juvénile
- Sélection phénotypique

2e Étape Tests clonaux multistationnels

3e Analyses des informations
Choix des clones selon les caractéristiques désirées et selon les stations

4e Production opérationnelle des clones sélectionnés

Obtention et production de génotypes hybridogènes et mutagènes

Introduction de clones

S.P. — Sélection de phénotypes dans les peupleraies naturelles

S.P. — Croisements interspécifiques entre les phénotypes sélectionnés des meilleures provenances, descendances et lignées améliorées

S.P. — Croisements à rebours *(backcross)* et inter-hybrides

S.P. — Culture de tissus,
- variation somaclonale
- génie génétique: modification et transfert de gènes

S.P. — Induction de mutations par radiation, ultrasons, etc.

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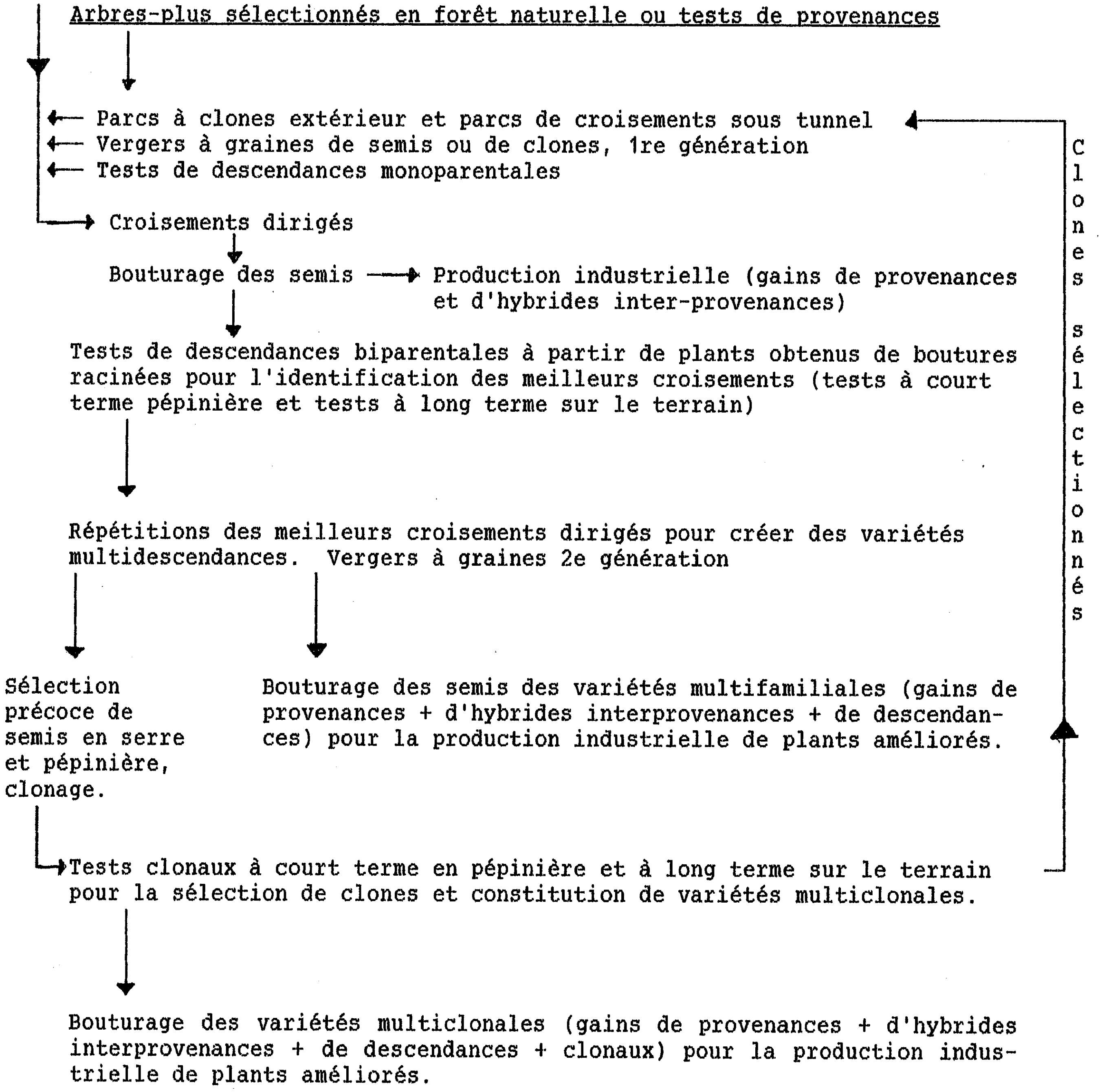
[1] S.P.: Sélection de phénotypes sur la base de leur croissance, leur qualité du port, leur résistance ou tolérance aux maladies foliaires, leur génome particulier, etc.

[2] La sélection pour la résistance ou tolérance aux maladies peut aussi s'effectuer en serre et en culture *in vitro*.

[3] Extrait de: Vallée, G., 1987. *Stratégie d'amélioration du peuplier*. Dans Compte rendu du Simposio sobre sylvicultura y mejorimiento genetico de especies forestales. Buenos Aires, Argentina 6-10 de abril 1987. Centro de investigaciones y experiencias forestales.

Figure 4

Stratégie pour la constitution de variétés
multifamiliales et multiclonales
au Ministère de l'Énergie et des Ressources - Québec



Arbres-plus sélectionnés en forêt naturelle ou tests de provenances

Parcs à clones extérieur et parcs de croisements sous tunnel
Vergers à graines de semis ou de clones, 1re génération
Tests de descendances monoparentales

Croisements dirigés

Bouturage des semis → Production industrielle (gains de provenances et d'hybrides inter-provenances)

Tests de descendances biparentales à partir de plants obtenus de boutures racinées pour l'identification des meilleurs croisements (tests à court terme pépinière et tests à long terme sur le terrain)

Répétitions des meilleurs croisements dirigés pour créer des variétés multidescendances. Vergers à graines 2e génération

Sélection précoce de semis en serre et pépinière, clonage.

Bouturage des semis des variétés multifamiliales (gains de provenances + d'hybrides interprovenances + de descendances) pour la production industrielle de plants améliorés.

Tests clonaux à court terme en pépinière et à long terme sur le terrain pour la sélection de clones et constitution de variétés multiclonales.

Clones sélectionnés

Bouturage des variétés multiclonales (gains de provenances + d'hybrides interprovenances + de descendances + clonaux) pour la production industrielle de plants améliorés.

EARLY SCREENING AND SHORT-TERM TESTS - THEIR USE IN TREE IMPROVEMENT

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ABSTRACT

Early testing methods in forest tree species were evaluated in accordance to the breeding material and analytical methods used in the studies. The directions and magnitudes of juvenile-mature correlations depend on the interaction of several factors such as species, early-testing environments, and the duration of the studies. Recent advances of the effects of endogenous and exogenously applied gibberellic acid on growth rate of several annual and perennial species were discussed in relation to their potential use in early testing and tree improvement programs.

INTRODUCTION

Tree improvement workers, like their colleagues in animal and crop improvement programs, depend on genetic tests to identify and select groups of individuals (genotypes, families, populations) with superior genetic potential for seed and/or propagule production and breeding program. However, measuring the genetic component of "growth potential" of forest trees has been problematical. In addition to the long duration of the field progeny trials, the identification of the genetic effect is formidable because most morphological characters are not only environmentally sensitive, they are also subject to polygenic inheritance and to some degree non-additive gene effects. Thus, tree improvement workers need fast and reliable test procedures which can be applied to juvenile seedlings or saplings. Herein we discuss recent research results that deal with genetic tests based on early growth performance.

We will approach the general strategy of early testings in forest tree improvement programs first by reviewing published and unpublished works. We will then attempt to review various early-testing approaches, in conjunction with their use in various stages of a tree improvement program. Finally, we will provide biological and analytical background information which we believe is pertinent to successful use of early-testing research procedures.

GENETIC TESTS IN TREE IMPROVEMENT PROGRAMS

Recently there has been discussion that the goals of forest tree breeding should be grouped into two categories: long and short terms. in short-term breeding, final realized genetic gains in production forest is the main aim. In long-term breeding, maintenance of a sufficient gene pool, i.e., gene conservation, is the main concern (for a detailed discussion, see Namkoong et al., 1989). Thus, the potential value of early progeny testing in long-term breeding is to accelerate the generation turnover; high juvenile-mature correlations are therefore not important. On the other hand, the function of early progeny testing in short-term breeding activities is directly related to the aim of increasing genetic gain; high juvenile-mature correlations may be thus crucial (Jiang, 1987). In this paper we will concentrate mainly on the importance of early progeny testing in short-term breeding activities.

The aims of short-term genetic tests are to rank trees according to their breeding values and to estimate genetic gain. The reliability of early testing and selection depends on the existence of strong and favorable genetic correlations between juvenile and mature traits (Franklin 1979). On the basis of field progeny trial results reported for Pseudotsuga menziesii (Namkoong et al. 1972), Pinus ponderosa (Namkoong and Conkle 1976) and P. taeda (Franklin 1939), argued that selection for gain in height and volume should be postponed until at least half the rotation age has elapsed. Other workers, however, are more optimistic about the existence of reliable juvenile-mature correlations (e.g. Ying and Morgenstern 1979; Lambeth et al. 1983; Williams et al. 1987). Their results suggested that for the conifers studied the age with the greatest selection gain per unit time lies between 5 and 10 years.

Constraints to yield due to imperfectness of juvenile-mature correlation may become increasingly important for advanced generation breeding. A perfect juvenile-mature correlation for inheritantly superior growth potential can probably never be attained. One must always reduce the expected gain by a correction factor whose size depends on how well one can design and evaluate the tests. More research in this field is required, and we believe that this research should be designed in close collaboration with both growth and developmental physiologists and ecophysiologists. Some of the ideas presented in this paper are currently being applied in Alberta's lodgepole pine progeny testing program.

Two kinds of parental material are usually used by tree improvement workers:

1) In the initial stages of an improvement program open-pollinated seeds are commonly collected from either natural stands or plantations as the founding stock. Progenies raised from these seeds represent samples of a range-wide collection of the species; plants under study are thus unrelated single-tree families (Parental Material A).

2) In contrast, tested and selected individuals in the advanced stages of most breeding programs are derived from control-crosses in various systematic mating designs; plants under study are from complete pedigree matings in which there is a cross-classification structure of the female and male parents (Parental Material B).

CLASSIFICATION OF EARLY-TESTING APPROACHES

Early-testing studies may be classified into three types (Jiang 1987):

Type 1: Age-age correlation studies within adult trees - Existing field-trial data are used to relate growth statistically at different ages.

Type 2: Juvenile performance studies with unknown adult performance - Early tests are made, then followed for several years of observation to determine the effectiveness of the screening procedures.

Type 3: Retrospective tests (Lambeth et al., 1983) -- Juvenile performance studies with known adult performance. using data from existing provenance or progeny tests, young material is grown under various conditions to determine how effectively early prediction might have been.

Jiang (Ibid.) has reviewed in detail literature on the three types of early-progeny testing. In Types 1 and 2, age-age correlations are done on the same individual trees at different ages; data of juvenile and mature performance are taken from the same sites. In Type 3, however, early and mature tests are usually not conducted on the same individuals, nor on the same sites. The most common situation for Type 3 is an established field trial, with stored seed of the same genetic material being used a second time to establish a correlation with the first field test. Early testing environments are usually designed to simulate field-trial environments.

1. Biological Reasoning

Tree performances at different ages are in fact the gene expressions at different growth and development stages. Three levels of genetic variation i.e. at the morphological, biochemical, and molecular levels are directly or indirectly related to the genetic potential of a tree. Advancement of biochemical methods such as electrophoretic and gas chromatographic (GC) analysis has allowed forest geneticists to examine genetic variants at the single-gene level (e.g. Yeh 1986). Most recently, rapid progress in molecular genetics has provided promising opportunities to study genetic variation at the molecular level (Kinlaw et al. 1988). While conventional genetic tests have concentrated on the quantitative genetics approach, e.g. examination of morphological variation such as tree height, stem diameter at breast height, branch angle, above-ground biomass, etc., there is a full spectrum of other useful characters which can be studied in early tests.

We do not yet completely understand why certain tree species grow faster than other species, or within a species why certain families or genotypes excel! However, even without this basic knowledge it is useful for geneticists to know whether the superior growth capacity of certain forest tree 'genotypes' is highly heritable. If so, can these superior 'genotypes' be identified at an early growth stage? Physiologists would like to know, on the other hand, what is the basis for this inherently rapid growth capacity of forest trees. In a recent paper (Pharis et al. 1989), geneticists and physiologists made a collaborative approach to address the above-mentioned questions in a common frame. Our preliminary conclusions were two-fold.

1. Conifer species do indeed exhibit inherently rapid vegetative growth capacity, and this inherent capacity can be identified at quite an early age (3 to 12 months).

2. One working hypothesis as to the basis for inherently rapid growth capacity is that it might be related to the endogenous concentrations of hormones, and specifically gibberellins (GAs); fast-growing genotypes can produce optimal concentrations of GAs, slow-growing genotypes either cannot produce the optimal concentrations or cannot utilize them. This hypothesis has its basis in work with both hybrid maize and trees (Rood et al. 1987, 1988; Pharis et al. 1987 and unpublished works).

Among the Gas thus far tested, GA_4 and GA_7 are the most growth-promotive in Pinaceae tree species (Pharis and Kuo, 1976). It is likely, however, that either or both of GA_4 and GA_7 are precursors of the dihydroxylated GA_1 or GA_3, respectively, the latter being the actual "effectors" of vegetative growth, as is the case for several herbaceous angiosperms (MacMillan and Phinney, 1987, Spray and Phinney, 1987). All of GA_1, GA_3, GA_4, or GA_7 are native to Pinaceae conifers, as are GA_8, GA_9, GA_{15}, or GA_{20} (see Figure 1). It appears likely that Pinaceae (and perhaps all conifers) have the early non-hydroxylation pathway (see Figure 1 and Pharis and King, 1985). If so, this may simplify correlation analysis (see later, and Rood et al. 1988) between endogenous GA concentrations and genetically superior growth performance. Pharis et al. (Ibid.) provided the result on the growth response of both fast-growing and slow-growing families of *Pinus radiata* to exogenous application of the mixture of $GA_{4/7}$. Use of the gibberellins not only caused a differential response between fast- and slow-growing families, but also appeared to have maintained to age six months the good correlation noted earlier for family ranking at age 138 days with the field rating. William et al. (1987) further found that exogenous application of GAs on *Picea mariana* families not only produced different responses in height growth between fast- and slow-growing families, but also promoted growth in slower-growing outcrossed and two selfed families. Pharis et al. (1989) speculated that the very reduced growth of certain selfed and outcrossed families might be due to their inability to synthesize growth-promotive GAs in sufficient amounts to allow for normal vegetative growth. This "working hypothesis" is in reasonable accord with what is known about concentration of GAs (and response to exogenous GAs) in hybrid (heterotic) maize and the less vigorous parental (inbred) maize genotypes (Rood et al., 1988). If the above-mentioned working hypothesis about the relationship between certain classes of gibberellins and inherent growth capacity is validated by future experiments, it may open a new avenue in forest genetics research and in the practice of tree improvement. For example, response of families or genotypes to exogenous application of GAs, and concentration of endogenous GAs in appropriate organs or tissues may enhance the predictive power of early progeny testing for recognizing inherently superior growth performance.

One of the most problematic areas encountered in early testing is the difficulty of measuring early growth. For example, juvenile height growth by itself may often be a poor indicator of later growth in the field because of variation in the allometric distribution of photosynthate to lateral branches among seedlings. The character of lateral branching, like other traits, undoubtedly has genetic, physiological and environmental causes. If we do not have a good understanding of the physiological basis of apical form, and how to deal with the characteristics of lateral branching, either through covariance adjustment or as an expression for total biomass, then the correlations we find between early and late growth may often be poor.

2. Analytical Reasoning

The classification of various early-testing studies based on their testing methods (Methods, 1, 2, and 3) and the genetic material used (Parental Materials A and B), as we discussed in previous sections are in Table 1. Statistical methods that have been commonly used in early-testing studies are: Analysis of Variance, Linear Regression, Linear Correlation and Analysis of Covariance. Some nonparametric methods such as rank correlations have also been used in published reports.

Perhaps the most common statistical methods used in early-testing research are linear correlation and regression. Linear correlation deals with pairs of random variables (juvenile and mature traits) and measures the degree of association between them. On the other hand, in linear regression, juvenile characters are taken as independent variables (regressors) and mature characters as dependent variables which are assumed to be 'fixed' variables without errors. However, this assumption is usually not realistic because the characters investigated in early-testing studies have both inherent variability and measurement error. Nevertheless, the linear regression is still a common approach because of the need for prediction in early-testing studies (e.g. Gill 1978).

The problem in both correlation and regression analyses appears when samples are taken from heterogeneous groups, i.e. provenances, populations, families, etc., which are common in forest genetics studies. The correlations and regressions computed from the pooling of samples from these heterogeneous groups may give researchers a biased picture of juvenile-mature relationships, because each group may have different regression slopes. It is always necessary to check the assumption that the regression slopes among populations are equal (e.g. Freund and Minton, 1979).

When measurements of juvenile and mature characters are made on the same plants in the same environment, linear regression and correlation units are individual plants (Types 1 and 2). when early and mature tests are located in different environments (e.g. Type 3), individual plants cannot be used as regression and correlation units. Genetic group means (e.g. clones, families, parents, etc.) have to be used as units. When group means are used as units in correlation and regression analyses, the problem of sample size arises. In most published works of 'retrospective studies', the number of genetic groups are usually small (say, $n < 15$). For small samples, the estimate of the product-moment correlation is probably biased, and limits statistical power. Olkin and Pratt (1958) recommended an adjusted estimator of the product-moment correlation for such small sample sizes ($4 < n < 15$).

Two-way analysis of variance can be used to test the performance of genotypes at different ages. A serious genotype x age interaction term (in terms of statistical probability and variance components ratio) is an indicator of poor juvenile-mature correlation. This approach is particularly suitable when the early and mature tests are conducted in different environments with unequal ages but relatively the same size and experimental layouts.

Another statistical method, analysis of covariance, which is the combination of analysis of variance and linear regression, may also be used in early-testing studies, especially in complete-pedigree mating designs (Parental Material B). The adjusted estimates of combining abilities in parents from early tests can be used as covariates when analyzing the datasets of mature tests. The prediction power of these covariates may be reflected in the analysis of covariance. A good example is given by Jiang (manuscript in preparation).

In an early-testing study of Type 3 (retrospective study), early-testing environments are usually in nursery, greenhouse, and growth chamber. The common obstacle in these experimental environments is their limited space. Normal complete block designs may not be appropriate for resarchers, because they would like to include a substantial number of genetic entries for statistical power. Some incomplete block designs may be appropriate; howver, their potential values are not yet explotied in published early-testing reports. Currently at the University of Alberta we are conducting a greenhouse study of Pinus contorta; a position-balanced incomplete block (PBIB) design (Montgomery, 1984) was implemented to adjust for the limited space an bench sizes. We believe this particular design not only gives us reliable statistical estimates from adjustments of row and column effects, but it also provides reseachers with the flexibility in measuring a large number of plants (total number of seedlings in this experiment > 2,000). Owing to its single-tre plot configuration, it is not necessary to meaure the whole experiment in one day. Thus, it provides researchers with flexible working schedule.

So far, we have only discussed using single traits as early and mature characters. For example, researchers typically would like to know whether they may use early plant height at month six to predict the final stem volume at rotation stage. Another potential area, howver, is to exploit the possibility of constructing indices as early predictor characters. When performance information of genotypes, families, and populatiojns is accumulated in early-testing and field environments, the opportunity for inclusion of this information in subsequent selection increases. This is analagous to considering the performance of multiple traits in selection. Several procedures exist for exploiting the information on more than one trait and/or from more than one source (Lerner 1958), but the most efficient method is the construction of a selection index (Baker 1986). Land et al. (1987) gave examples for the construction of selection indices incorporating information on individual, family, population, plot, and replication performance in a provenance-family test. In theory, information on early performance could also be included in such an index to improve the accuracy of selection.

CONCLUSIONS

For most long-lived forest trees, the prospect of using early-testing procedures to increasing the efficiency of selection and breeding is very appealing. Research on early tests (several months and up to 3 years) has focussed on procedures to improve the magnitude of phenotypic correlations between early test results and field performancs. In theory, one can increase such correlations by incrasing test precision and/or the use of seedling traits that are highly heritable and have high and consistent genetic correlations with field performances. Despite recent statistical advancements in elucidating the relationship between early test and field performance, the genetic and physiological processes involved in implementation of a successful early-testing program remain largely unrsolved. not only are additional studies on early-testing in clearly defined and controlled environments needed, especially those of a retrospective nature, we also need a better knowledge of the physiological, biochemical, and molecular bases of inherently superior growth (including heterotic growth).

ACKNOWLEDGMENTS

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Table 1. Analytical Approaches in Early Progeny Testing Studies

	Parental Material	
Early-Testing Types	Single-tree families (first generation)	Complete pedigree (advanced generation)
Early and mature performance data are taken on the same individuals (Types 1 & 2)	CORR, REG	CORR, REG
	(on individuals)	
	ANOVA	ANCOVA
Early and mature performance data are taken on the same entries but not on same individuals (Type 3)	CORR, REG	CORR, REG
	(on genetic entry means)	
	ANOVA	ANCOVA

Note: CORR: Linear Correlation; REG: Linear Regulation;
ANOVA: Analysis of Variance; ANCOVA: Analysis of Covariance

CONFÉRENCIERS VOLONTAIRES
VOLUNTARY PAPERS

CONE AND SEED CROP MONITORING

J. Coles

Ontario Tree Improvement Council

Most eastern Canadian seed orchards are approaching or are in the early stages of seed production. Many western clonal orchards are more advanced. These orchards were tremendously expensive to establish and are continuously expensive to manage. To achieve a reasonable return on this investment, it is imperative that both seed production and seed quality be high.

The main objective of cone and seed crop monitoring in an orchard is to improve the efficiency of management activities such that large quantities of high quality seed are produced. Only with constant monitoring of many aspects of flower, cone and seed production, can we determine if problems exist, the nature of the problems and hopefully find solutions to correct the problems.

WHAT IS THERE TO MONITOR, AND WHEN AND WHERE?
AN OVERVIEW OF CONE DEVELOPMENT FOR SPRUCE, LARCH AND PINE

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Three genera of Pinaceae, spruce (*Picea* Dietr.), larch (*Larix* Mill.), and pine (*Pinus* L.), have Canada-wide interest for tree improvement. They represent three subfamilies and have different patterns of shoot and cone development and distribution. Thus, they demand different monitoring procedures. *Picea* produces cones laterally or terminally, depending on shoot vigour. *Larix* may produce cones laterally on long shoots or terminally on short shoots: positioning on parent long shoots depends on shoot vigour and previous occupation of possible positions by cones. *Pinus* produces seed cones in place of lateral long shoots on vigorous parent shoots, and pollen cones in place of proximal short shoots on weak parent shoots. Hence, multiwhorled pines possess more positions where seed cones can occur than do uniwhorled pines. In all cases, pollen cones last only a few weeks in the post-bud condition. Seed cones of *Picea* and *Larix* complete post-bud development to maturity in 3 to 5 months: those of *Pinus* in about 16 months. Developmental differences exist among these three genera in the pollen "catching" and seed-cone closing mechanisms, and in seed-cone orientation at different stages of development.

AN EXAMPLE OF POLLEN MONITORING IN A SEED ORCHARD

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Pollen monitoring was conducted at the Parkindale Clonal Seed Orchard in south-eastern New Brunswick for five years. The species in the orchard of concern are black spruce, white spruce and jack pine. Pollen was monitored to determine background levels before orchard pollen production becomes significant and to determine when background pollen was present compared to female strobili receptivity and pollen shedding within the orchard. Pollen was trapped on microscope slides with double-sided Scotch tape at six stations across the 110 ha orchard site. Daily counts were made for each species by observing eight fields of view at 100X magnification on the microscope slides.

Results show considerable variability from year to year in background pollen levels for the three species. A range of background levels for the orchard over five years has now been established and these will be used to compare with trap catches when the orchard is approaching full production. Comparisons of timing of female receptivity and pollen shedding within the orchard with timing of background pollen presence show that background pollen for white spruce and jack pine is in synchrony with the orchard. Background pollen of black spruce appears to be present slightly ahead of orchard pollen. This is of consequence for clones which develop earlier in the spring as they are likely to be fertilized with non-orchard pollen. Supplemental mass pollination may alleviate this problem.

EFFECTS OF NITROGEN FERTILIZER ON THE QUALITY AND YIELD OF SEED FROM A BLACK SPRUCE SEEDLING ORCHARD

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Ammonium nitrate was applied in 1987 to 8-year-old black spruce (*Picea mariana* (Mill.) B.S.P.) trees in a seedling seed orchard of Fraser Inc. near Plaster Rock, New Brunswick to stimulate flowering and seed production. Tree spacing in the orchard is 2.0 m between and 1.0 m within rows. Fertilizer was applied in a band along the tree rows at the following dosages per 50 metres (50 trees): no fertilizer (control), 2.5 kg on one side, 2.5 kg on two sides, 5.0 kg on one side, 5.0 kg on two sides, 7.5 kg on one side, and 7.5 kg on two sides.

In 1988 all of the cones produced in each 50-tree row were collected and, from the bulk collections, 50 cones were randomly selected. It was found that the fertilizer had no effect on seed weight, but greatly improved seed yields and seed quality. Seed yields from fertilized trees ranged from 35 to 45 seeds per cone as compared to 30 seeds per cone for the control, an increase of 14 to 33%. Although fertilizer had no effect on seed germination, it greatly influenced seed vigour as measured by stress tests and response to prechilling treatment.

PRINCIPLES OF CONE CROP MONITORING

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Cone crop monitoring is a method to inventory and predict cone and seed crop size over time, and to assess the condition and survival of the crop. There are several benefits in having a monitoring program in a seed orchard; some of these include, (1) the ability to predict crop size at different intervals of crop development, (2) identification and quantification of cone and seed losses, (3) the increased ability to estimate work loads and requirements, (4) estimation of the efficacy of control measures, and (5) identification of good and poor crop trees in the orchard. The essential steps in a cone crop monitoring system are as follows: (1) select sample trees in the orchard, (2) count the flowers on the sample trees (whole tree, or a sample), and use this count to estimate the potential number of cones, seeds and seedlings that could be produced (background data or estimates on the seed potential, extraction and germination efficiencies are needed), (3) select and tag branches and cones, (4) visit the tagged cones at periodic intervals (2-3 times minimum during the cone development period), and record the number of healthy and damaged cones (damage by cause if possible). Use this information to update your predictions and take corrective measures (e.g. insect control) when needed to ensure that seed targets will be met, (5) collect cones when mature, and (6) extract seeds, dissect cones, and germinate seed to calculate seed potential, and seed, extraction, and germination efficiencies (this data will then be used to estimate the number of seeds and seedlings in future years- see point (2)). The above six points are fundamental to any cone crop monitoring program. The actual number of clones or families represented in the monitoring program, or the actual number of trees and cones selected, or the number of visits to the tagged cones, etc., will depend on the management objectives of the seed orchard and will include such considerations as the age, number and type of pest problems, accuracy required, cost, and available manpower.

FLOWER INDUCTION DEVELOPMENT TRIALS

Cathy Nielsen

Fast Growing Forests Group
Ontario Ministry of Natural Resources

The Fast Growing Forests Group has been operating a breeding hall since 1985. In the last four years emphasis has been placed on grafting (to provide seed orchard and breeding material), accelerating growth of breeding material and flower induction treatments. The following is a brief summary of the flower induction development work.

WHITE PINE

Developmental trials for flower induction of white pine have emphasized foliar application of $GA_{4/7}$. In 1988, a study was established to determine the optimum time and concentration of gibberellin application for the promotion of female and male strobili. Results indicated that early spring application, at the onset of rapid shoot elongation was the best time for promotion of male strobili. Two concentrations of $GA_{4/7}$ were applied with 500 mg/l providing to be more effective than 250 mg/L. This may be in part due to the later date of the first application, as compared to other workers, who have found 250 mg/l to be adequate. No response for female flowers was observed. The earliest treatment period began May 30th and the latest treatment period ended August 30th. White pine female strobili are not anatomically differentiated until the spring before they appear, although it has been speculated that biochemical differentiation actually takes place in the fall prior to the year of flowering. in order to test this theory, several trials were established to test early spring and fall application of gibberellin. No positive results were obtained from these treatments.

Trials established in 1989 have primarily concentrated on trying to improve the consistency of male response to early spring gibberellin application by combining the $GA_{4/7}$ treatment with root pruning. Trials have also been established to test the application of $GA_{4/7}$ by stem injection in the fall, with the objective of promoting female flowering.

NORWAY SPRUCE

In 1986 and 1987 emphasis was placed on foliar application of $GA_{4/7}$ as a flower promoting treatment, however there was no response observed in these trials. Trials in 1988 and 1989 have concentrated on stem injection of $GA_{4/7}$. The 1988 trial was designed to test the effect of gibberellin applied within a compressed growth cycle (forcing the graft to complete two growth cycles in one calendar year through manipulation of lighting, temperature and moisture). The quantity of $GA_{4/7}$ injected proved to be excessive (60 mg) and toxicity symptoms appeared during the dormancy induction phase of the growth cycle. A trial was established in 1989 to test stem injection of $GA_{4/7}$ as compared to foliar application. Gibberellin applications were made with and without the application of a heat treatment. Results of these trials will be available in 1990.

EXOTIC LARCHES

Trials were established in 1989, in a hybrid larch seed orchard containing both Japanese larch and European larch. The objectives of the trials were to test the effectiveness of branch bending and $GA_{4/7}$ application in conjunction with girdling, for promoting female and male strobili. Results of these trials will also be available in the spring of 1990.

FLOWER INDUCTION WITH GIBBERELLIC ACID 4/7

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Flower induction experiments using $GA_{4/7}$ began in 1985 on white spruce and in 1986 on black spruce. Treatments have been applied as a foliar spray to potted trees in the greenhouse as well as to trees grown in the Parkindale Clonal Seed Orchard. The concentration of $GA_{4/7}$ used is 500 mg/l in a 5% ethanol solution with Aromox C12W as a surfactant (0.02%).

The treatments for both species have resulted in a two- to over ten-fold increase in female strobili production over untreated controls. Male strobili production has generally been enhanced although seldom at a statistically significant level. Flower induction is now being used routinely to promote flowering in both the greenhouse and in the seed orchard in order to complete first generation tree breeding more rapidly. Accelerated growth of grafts is being used along with flower induction treatments in a breeding hall as part of an accelerated breeding strategy. In 1989, significant numbers of controlled pollinations were completed on grafts made in 1986.

CONIFERIN BIOSYNTHESIS AND THE REGULATION OF LIGNIFICATION IN CONIFERS

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Coniferin, the primary storage reserve for guaiacyl lignin monomers in conifer stems, was quantified by gas chromatography (GC) and GC - mass spectrometry (GS-MS) in stem and leaf tissues of *Picea glauca*, *Pinus banksiana*, *Pinus strobus*, and *Larix laricina*. Coniferin was not detectable in mature or developing leaves at any time, nor could it be detected in the stem during dormancy (winter and early spring). Coniferin became detectable in the cambium of all species at an early stage of reactivation, just before resumption of cell-division activity, and accumulated thereafter until lignification of the first-differentiating earlywood tracheids was histochemically detectable. The biochemical pathway to coniferin is shown below. none of the precursors in this pathway occurred at significant levels during the period of coniferin accumulation in early spring, supporting the concept that monolignol (i.e. coniferyl alcohol) biosynthesis is tightly coupled enzymatically.

There is substantial evidence that enzymes 1-9 exhibit elevated activity in response to an auxin - cytokinin combination, and this was investigated using *P. strobus* cambium *in vitro*: endogenous coniferin accumulated and exogenous coniferin was hydrolyzed in response to an auxin - cytokinin combination; however, no convincing evidence for lignification was found in either treatment. The results with whole trees and *in vitro* cambial cultures indicate that although coniferyl alcohol production can occur by auxin - cytokinin promotion of cinnamyl alcohol dehydrogenase and coniferin-specific *beta*-glucosidase, neither of these enzymes can be regarded as lignification specific in conifers. Evidence has been found suggesting a lignin peroxidase is the key enzyme limiting lignification.

SURVEY OF WOOD DENSITY IN FIVE CONIFERS IN THE MARITIME PROVINCES

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About half of the plus trees of five species selected in New Brunswick and Nova Scotia were sampled to determine relative density based on green volume. This work was done by Dr. L.P. Sebastian of the University of New Brunswick and R.L. McIntosh of the New Brunswick Research and Productivity Council. Sample size ranged from 767 trees for *Picea mariana* to 176 for *Larix laricina*. Mean density was: *Picea mariana* - 0.408; *Picea glauca* - 0.366; *Picea rubens* - 0.396; *Larix laricina* - 0.461; and *Pinus banksiana* - 0.398. these mean values were slightly higher than those obtained in a 1964 survey in the Maritimes. Standard deviations were small and ranged from 0.028 for *Pinus banksiana* to 0.033 for *Picea glauca*. Significant correlations (1% level) were obtained between density and Dbh#Age ratio for all species, while correlations of density with age, height, DBH, and latitude and elevation of the place of origin were significant only for some species. Hierarchial analysis of variance attributed an average of 9% of total variation to seed zones, 9% to areas within seed zones, and 82% to trees within areas.

WOOD QUALITY STUDIES IN AN OTTAWA VALLEY JACK PINE PROGENY TEST

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This is an interim report on a study of wood quality characteristics in 55 half-sib families of Ottawa Valley jack pine in a 20-year-old progeny experiment at the Petawawa National Forestry Institute. Characteristics being examined include rate of growth in height and diameter, stem taper, proportion of heartwood, compression wood content, relative wood density, extractives content and longitudinal shrinkage.

Test material for 45 of the families sampled originated from a single plantation at Chalk River. Ten of the families were additionally sampled at two other plantations in the general vicinity. The sample trees contained about 15 growth rings at breast height so that wood properties measured may be characterized as essentially juvenile.

Statistical tests for family association were not significant for tree height, diameter, total volume, compression wood content or longitudinal shrinkage. Significant family associations were indicated for stem taper, heartwood content and relative wood density. The quantities of material removed by extraction with hot water and with an organic solvent will be analyzed by the same procedure.

GENETIC IMPROVEMENT OF VOLUME AND WOOD PROPERTIES OF JACK PINE: SELECTION STRATEGIES

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Six selection strategies aimed at genetically improving volume production and wood quality factors such as density, heartwood content, and stem taper were compared in a 20-year-old jack pine progeny trial at Chalk River, Ontario. Selection indices were computed under various assumptions about economic values of the traits under selection and with constraints in the magnitude and direction of expected genetic gain. Stem taper, wood density, and heartwood content were under strong genetic control; however, the low phenotypic variation of wood density limits its potential for genetic improvement. Heartwood content emerged as a trait amenable to rapid genetic improvement. Despite low heritabilities the prospect of improving size-related traits was promising due to substantial phenotypic variation. Economic weights were important for the selection outcome and good progress was reported in all traits when volume received the highest weight. It was feasible to limit genetic gain in individual traits to predetermined relative levels but the cost in terms of lost progress in unrestricted traits was economically debilitating. Concerns about undesirable concomitant changes in wood density, heartwood, and stem taper when breeding is based solely on growth traits, were not confirmed by our data.

TWO POSSIBLE APPROACHES FOR IMPROVEMENT OF WOOD RELATIVE DENSITY IN TREE IMPROVEMENT PROGRAMS

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Wood relative density is now considered a trait for selection in most B.C. tree improvement programs. Wood quality data from the coastal Douglas-fir and interior lodgepole pine improvement programs, using different types of material and sampling approaches, was used to illustrate two possible approaches for impacting relative density in seed orchard construction using progeny tested clones.

For coastal Douglas-fir, the Pilodyn apparatus has been used to predict parental GCA effects for relative density. A separate study indicated the relationship between family mean relative density and mean pin penetration was $R^2 = 0.85$. From these data, breeding values for growth and relative density can be predicted for each parent, and seed orchards can be tailored by selecting clones which tend to 'break' the negative genetic correlation between growth and relative density.

For lodgepole pine, progeny tests are not old enough for relative density sampling; however, parent trees were assessed for relative density. An examination of the relationship between parent-tree relative density and mean relative density from grafted ramets (of the parents), suggests that parent-tree information may be useful for identifying potential low density clones. The merit of this approach will be pursued once progeny-test information is available.

EARLY SELECTION BASED ON PITH TO BARK PROFILES OF WOOD RELATIVE DENSITY

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A reliable method for predicting the mature wood relative density of a tree based on the relative density of the same tree at a young age is important in the development of appropriate selection procedures for relative density. In this presentation a new method for modelling the relationship between a wood quality characteristic and cambial age is outlined and illustrated using breast height pith to bark profiles of relative density from 60 coastal Douglas-fir trees. The purpose of the modelling was to improve the current prediction methods for this species using the modelled relationship. Results showed that one overall model is not adequate to describe the variability in pith to bark profiles of coastal Douglas-fir relative density. It was concluded that the prospects for using these relationships to refine prediction methods may not be possible for coastal Douglas-fir unless physiological reasons for the different models can be found.

GENETIC CONTROL OF RELATIVE DENSITY BELOW BREAST HEIGHT IN DOUGLAS-FIR

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A 15-year-old Douglas-fir progeny test with two locations in coastal British Columbia was studied to test the value of sampling wood relative density close to the ground in young plantations. This would increase the number of annual rings sampled and would potentially improve the breeder's ability to evaluate wood quality at an early age if the radial relative density profile close to the ground is representative of the breast-height profile. Relative density profiles were compared at three sampling heights (0.4, 0.7 and 1.3 m above the ground) by densitometric analysis of single radial cores. There were at least two more rings of wood at 0.4 m than at 1.3 m. The relative density vs. age profiles differed to age 7 or 8, with the mean relative density decreasing with height in the early years. Heritability estimates were lower at 0.4 m than at 0.7 or 1.3 m, at least until age 8, indicating that in the first 1 to 7 years of growth, environment plays a larger role in relative density at 0.4 m from the ground than at 1.3 m. Genetic correlations among relative densities at the three sampling heights, estimated on a ring by ring basis by cambial age, were all very close to 1.0. Thus there is no evidence that genetic control of relative density changes between breast height (1.3 m) and close to the ground (0.4 m). Wood samples taken at 0.4 m from the ground are likely to yield better information than samples at 1.3 m if the first 6 or 7 rings are discarded.

DEMONSTRATION OF A NEW METHOD FOR WOOD DENSITY MEASUREMENTS

Ernie A. Hamm

Forintek Canada Corp.

A need has existed for a rapid, accurate, field technique for estimation of wood density of parent and progeny trees in tree breeding programs where wood quality is a selection criterion. An instrument to address this need has been developed at Forintek by Ernie Hamm over the past several years. This device operates on the principle that wood substance or cell wall material has a constant density from species to species and therefore the density of a wood sample can be determined from the ratio of bulk to wood substance volume. Wood substance volume is determined in the Forintek wood density gauge by mechanically compressing 5 mm cores and measuring the compressed length and diameter to obtain the volume.

The basic components of the unit consist of a battery powered electro-mechanical actuator to provide the force and displacement to compress the cores, a chamber to hold the cores during compression, a cantilever beam to sense when full compression load has been reached and an electronic scale unit to make the initial and compressed length measurements of the 5 mm core samples. A density tester will be on hand at the meeting to illustrate the components used in its construction and to demonstrate its operation.

GENETIC TRAITS OF DAMAGED AND HEALTHY SUGAR MAPLE AND ASPEN

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Isozyme analysis of two forest tree species was conducted to determine if genetic differences exist between trees tolerant to environmental stress and those susceptible to it. Expanding bud tissue from about 24 damaged and 24 healthy trees was collected within each of 4 mature natural sugar maple stands in southern Ontario. Tree health was determined by the Ministry of the Environment as part of an ongoing monitoring project. Aspen bud tissue was collected from 40 "tolerant" and 39 "susceptible" aspen saplings that were root cloned from aspen collected throughout the United Sates by Dr. D. Karnosky (Michigan Technological University) and scored for sensitivity to ozone fumigation in greenhouse experiments. Polymorphic loci resolved numbered 11 in maple and 10 in aspen. The results in sugar maple indicated allelic heterogeneity in a small proportion of the loci, but no statistically significant differences in heterozygosity levels between the damaged and healthy trees. Further, there was an indication of slightly more inbreeding in populations of damaged trees in comparison to healthy trees. The tolerant and sensitive aspen trees showed similarly low levels of allelic heterogeneity and no statistically significant differences in heterozygosity levels. It is concluded that there is insufficient evidence in these data to indicate genetic heterogeneity between damaged and healthy trees in either maple or aspen. however, it is considered that there is sufficient suggestive evidence to warrant further examination with larger sample sizes.

THE BLACK SPRUCE CLONAL FORESTRY PROGRAM IN NORTHERN ONTARIO

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In 1984, a private greenhouse facility was established in Moonbeam, Ontario, with the objective of producing one million black spruce stecklings per year for regeneration purposes. At that time the limiting factors were aging of donor stock and little experience in large scale (clonal) production. Since then, much progress has been made in techniques for vegetative propagation of this species. An OMNR breeding hall has been established to provide control-pollinated seed for use in the clonal program. The first field screening trials are now four years old. A provincial policy regarding genetic diversity in our tree improvement programs has been developed which will provide guidance for breeding, testing, selection and deployment in the clonal program. Since 1985, approximately 1200 ha of harvested forest land in northern Ontario have been planted with black spruce clonal stock.

Since the last CTIA meeting, the major contributions to the clonal program from the Northern Forest Development Group, OMNR, have been:

1. Providing support for development of a technique for somatic embryogenesis for black spruce and subsequent cryopreservation. This initiative may provide a viable (and superior) alternative to hedge orchards for maintenance of clonal stock;
2. The initiation of a data base management system for the clonal program;
3. The review of clonal plantation performance;
4. The initiation of a new multi-year contract with the private clonal facility, in order to ensure continuity in the clonal program;
5. Provision of support for development of a more cohesive clonal plug through the use of rubberized material;
6. Encouragement of research in related areas, especially in early selection procedures, through provision of clonal materials.

Some of the initiatives likely to be undertaken in the next few years include:

1. Development of a breeding strategy specifically for the clonal program;
2. Revision of current field testing strategies;

3. Rationalization of the role of clonal forestry within the total regeneration strategy in Northern Ontario;
4. Better exploitation of available information and techniques for early selection.

BREEDING POPULATION DEVELOPMENT IN NEW ZEALAND RADIATA PINE

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The fundamental method for the genetic improvement for radiata pine in New Zealand is one of population improvement through recurrent selection for general combining ability. Results from realized gain trials, indicate that over 30% volume gain and comparative form score gains over the unselected New Zealand land race have been achieved through two important stages of seed orchard development. The first reflected a strong emphasis on phenotypic selection, and the second progeny testing for GCA. Both these stages utilized high selection intensities. A third stage builds on selections from the open-pollinated (OP) progeny tests of the second stage. The first three stages were driven primarily to provide orchard clones.

A fourth stage attempts to bring together systematically all current series and generations. Features of this fourth stage include: multiple breeding population, sublines, two complementary mating systems, and separate field designs.

Selection for the next generation breeding population will use combined index selection using the GCA family test and the within family value from the full-sib block. This fourth stage of development is now well under way and selection are being made from family blocks to maintain the continued genetic improvement of radiata pine.

SEED PRODUCTION DEVELOPMENT IN NEW ZEALAND RADIATA PINE

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The genetic improvement program for radiata pine in New Zealand has emphasized the seed production population - seed orchards and related means of delivering gains to production populations. Improvement was first generated through seed collections from select trees. Realized gain trials have shown that this method of mass selection produced significant gains above unselected 'bulk' land race trees. The first seed orchards were propagated from intensively selected plus trees in the late 1950's and early 1960's. Gains of 10% volume growth have been achieved from these orchards. The second stage of orchard development gave less emphasis to the original phenotypic selection but placed emphasis on progeny testing for general combining ability (GCA). Orchards were established from clonal ramets of the best progeny. Advanced generation orchards have also been established. Realized gain trials show considerable gain from these orchards.

Control pollination orchards offer the potential of exploiting specific combining ability (SCA) by selecting for and recombining tested crosses. Low levels of SCA in radiata pine indicate this strategy is not worthwhile and CP orchard strategy is based on mixes of best general combiners.

There has been an active research program in New Zealand to investigate clonal forests as an alternative to conventional seed production. Efforts in clonal forestry are up against the problem of maintaining or restoring juvenility and overcoming the growth losses due to ageing. Even without the problems of juvenility, significant extra gains from clonal selection may not be apparent if an active and aggressive breeding program is followed.

THE ADVANCED GENERATION MATING STRATEGY FOR COASTAL DOUGLAS-FIR IN BRITISH COLUMBIA

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The Douglas-fir breeding program for the largest and most important seed zone in south-western British Columbia has advanced to the stage of selecting second generation populations for seed orchards and breeding. The advanced-generation breeding strategy will utilize a hierarchical population structure, with a small, elite production or orchard group, a larger breeding population and a widely based gene resource population. Each generation the breeding population will advance with a new round of breeding and testing, while the gene-resource population will remain static, to provide a wide genetic base for future contingencies.

Selections are based primarily on an extensive diallel program started in the mid-seventies. Other projects testing various seed sources will also provide some material to the advanced generation population, bringing the total expected number of selections to about 450.

The mating and testing strategy for advancement of the breeding population will utilize a complimentary design to estimate parental breeding values (BV) separately from matings for further selection. BV estimates will be made using material from polycross matings. A uniform pollen mix will be applied to each of the 450 clones in the breeding population. The pollen mix will consist of pollen from 20 males chosen from the diallel mating program. The males will have approximately equal BV that are average or slightly below average for the first generation test population. Using males with approximately equal BV may reduce variation due to the unidentified male component, and bias due to differential reproductive success of different males on different females.

Matings for forward selection of the breeding population for the next generation will utilize small sublines (8 to 16 clones) to help manage coancestry. A partial diallel (double-pair) mating design will be used. This design results in n families from n clones in a subline, and is efficient and flexible. In addition to these matings, a nucleus population will be developed to allow more assortative mating, and to generate elite material that can be used in a limited way in seed orchards or, more extensively, in control-pollinated strategies that are exploited in combination with vegetative propagation methods.

Testing will be done in several series, with each family from the polycross matings tested on three sites using single-tree plots. Full-sib material from the double-pair matings will be tested in family blocks on two sites.

PHENOLOGICAL AND HEIGHT GROWTH VARIATION IN JACK PINE FROM THE NORTH CENTRAL REGION OF ONTARIO

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Five seed zones have been delineated for jack pine (*Pinus banksiana* Lamb.) in the North Central Region of Ontario based primarily on environmental data. To test and refine the number and boundaries of these seed zones, seedlings representing 64 collection sites distributed throughout the region were scored for height growth and date of flushing. Sources were significantly different for 1) height after the first season following outplanting, 2) second year growth increment, 3) adjusted second year growth increment using first year height as a covariate, and 4) date of needle flushing. Generally variation was clinal from southwest to northeast. Trend surface diagrams produced by GIS (Arc/Info) illustrated localized deviations from this clinal pattern. These results support the existence of at least one established seed zone boundary.

EARLY FLOWERING AND SEED PRODUCTION OF A LODGEPOLE PINE SEEDLING SEED ORCHARD IN CENTRAL ALBERTA

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Flowering and seed production of lodgepole pine were studied in a research seed orchard located at Pine Ridge Forest Nursery in Central Alberta. The seed orchard was established in 1980 with seedlings from three West-central Alberta provenances. Planting stock was grown using "accelerated growth (AG)" and "Control" rearing regimes.

Flowering in both stock types began at age 3 years. Percentage of flowering trees increased at a more rapid rate in the "AG" trees than in the "Control" trees. Flowering in the "AG" trees increased steadily from 6% at age 3 years to 99% at age 10 years. Male and female flower production started at the same time. Female strobili production averaged 0.1 strobili per tree at age 3 years and climbed to 66 strobili per tree at age 10 years. Initially male strobili cluster production lagged behind female strobili production. At age 8 years male strobilus production began to increase rapidly. At age 10 years the "AG" trees averaged 153 male strobili clusters per tree. The same general flowering trends were observed in the "Control" trees, however in earlier years, they lagged 2-3 years behind the "AG" trees. At age 10 years the differences in flowering between the "AG" and "Control" trees had almost disappeared. Flowering occurred on 100 percent of the "Control" trees, which produce an average of 59 female strobili and 170 male strobili clusters per tree. Preliminary analyses of flowering data indicates provenance differences are not large.

Average number of cones per tree increased slightly in two study years (1987 and 1988). Cone counts were consistent with flower counts indicating cone abortion is not a problem in this orchard. Number of filled seeds per cone, however, did vary widely. In 1987 number of seeds per cone averaged 10.1 (range 2.3 - 30.9) compared to 5.1 (range 0.5 - 16.8) in 1988. The decrease in seed yield in the 1988 cone crop was attributed largely to a blizzard which occurred on May 18, 1987. Temperatures dropped to -11°C. Germination quality of the seed was consistently good in both years (86.6% and 94.8% in 1987 and 1988 respectively).

It was concluded from the study of flowering and seed production in the lodgepole pine seed orchard that the "accelerated growth" treatment was effective in promoting flowering at an earlier age and in reducing the time required to attain commercial levels of seed production in lodgepole pine seed orchards in Alberta. Cone production, suitable for commercial collections, in lodgepole pine seed orchards can be expected to begin at age 8 to 10 years of age.

PROSPECTS FOR OPERATIONAL USE OF SOMATIC EMBRYOGENESIS

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Somatic embryogenesis has the potential to be used as a cost effect means of multiplying genetically improved seed and subsequently, for the generation of selected clonal lines. Somatic embryogenesis of interior spruce has been optimized with respect to initiation of embryogenic callus, maturation and germination of somatic embryos. The resulting plants have been acclimatized and transferred to an operational forest nursery. Biochemical markers which define explant competence for somatic embryogenesis have been identified. In addition, the developmental response of somatic embryos to culture manipulations has been characterized at the morphological and biochemical level in comparison to zygotic embryos. Improvements in the culture system have resulted in a 55% conversion rate of mature somatic embryos to plants established in the nursery. Two thousand somatic seedlings are currently growing under nursery conditions. Survival and performance of these seedlings appears comparable to seed derived plants; however, substantial variation between clones is observed. The percentage of genotypes which can be captured from selected families will be presented in relation to use of the system in clonal selection.

IN VITRO STUDIES ON ADVENTITIOUS SHOOT FORMATION FROM EMBRYONIC SHOOTS OF BLACK SPRUCE

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Plantlets have been successfully regenerated from embryonic shoots of mature black spruce trees [*Picea mariana* (Mill.) B.S.P.]. The factors that influence the induction and elongation of adventitous shoots were studied. Fifteen-year-old, 27-year-old, 35-year-old, and 100-year-old trees were sampled, one in each age group except two in the 35-year-old group. The trees of the first three age groups responded well. Two 35-year-old trees responded differently indicating a clonal variation. out of six media tried - 1) Murashige and Skoog (MS), 2) Loblolly pine (LM), 3) Schenk and Hildebrandt (SH), 4) Woody Plant Medium (WPM), 5) Gresshoff and Doy (GD), and 6) Aitken-Christie and Thorpe (LP), successful induction occurred only in the last two media. However, LP medium was found to be the best media. Each of the media was supplemented with 5 mg/l of benzylaminopurine (BAP) and 0.2 mg/l naphthaleneacetic acid (NAA). Of the eight monthly incubations carried out from September to April, the best period for sampling was found to be December to March. The embryonic shoots were exposed to continuous light and 16-hour photoperiod and the continuous light induced more number of adventitious shoots per embryonic shoot. One half of the material was transferred to LP medium with charcoal and the other half without charcoal but the addition of charcoal had no advantage in either induction of shoots or elongation. Rooting of adventitious shoots obtained by pulse treatment with LP medium with 3 mg/l indolebutyric acid for four days and then transferred to hormone-free one-half strength LP medium, had a successful rate of only 0.9%.

JACK PINE FLOWERING RESPONSES TO NITROGEN AND GIBBERELLIN TREATMENTS

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Interactions of $GA_{4/7}$ biweekly sprays (400 mg/L) and different levels of soil-applied NH_4NO_3 were examined in jack pine seedling and clonal orchards and in potted trees under polythene shelters. Untreated trees in the seedling or clonal orchard produced similar numbers of female flowers, whereas male flower production was 5- to 9-fold higher in the seedling orchard. $GA_{4/7}$ and NH_4NO_3 treatments enhanced female flowering; the best combination was $GA_{4/7}$ with 400 kg N/Ha. It provided a 2-fold increase in the clonal orchard and a 4-fold increase in the seedling orchard. $GA_{4/7}$ alone increased male flower counts 3-fold in the clonal and seedling orchard. Without $GA_{4/7}$, optimum NH_4NO_3 for male flowering in both orchards was 200 kg N/Ha; with $GA^{4/7}$, male flowering was greatest with no added nitrogen. $GA_{4/7}$ enhanced male and female flowering in potted trees. luxury levels of nitrogen slightly increased female flowering in the presence of $GA_{4/7}$, whereas nitrogen deficiency caused a increase in male flowering.

ONTARIO MINISTRY OF NATURAL RESOURCES NORTHERN REGION TREE IMPROVEMENT

R.D. Ford

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Northern Forest Development Group

The Northern Region alone produces approximately 30% of the volume of wood harvested in the province. Regeneration efforts require 65 million seedlings annually; the potential to reap the benefits of tree improvement is great. The main objective is to produce faster growing and better quality trees by improving the genetic potential of planting stock for artificial regeneration. In 1989, establishment of the first generation program was completed.

The poster display illustrated through the use of photographs, a map and factsheet the general design of the tree improvement program.

The basic steps taken in the program are as follows:

(1) Black spruce and jack pine superior trees were selected from natural stands in 5 black spruce and 4 jack pine breeding zones.

(2) Cones were collected from the trees and the extracted seeds were used to grow seedlings in the Breeding Hall greenhouses for the 5 seed orchard complexes and the 25 associated family tests.

(3) Family tests are assessed to determine which families will be rogued from the seed orchards. The remaining breeding population will provide improved seed for future generations of planting stock.

(4) Scions collected from the superior trees were grafted and are held in 3 clonal archives representing these original plus-tree genotypes. Potted ramets are used in the Breeding Hall.

(5) The Breeding Hall's primary activities relate to vegetative propagation, flower induction and breeding, as well as, growing seedlings for seed orchards and family tests.

The potted grafts representing the plus-tree selections receive flower induction treatments. These treatments provide the strobili required for controlled crosses. Pollination of megastrobilli is carried out annually with pollen of a known source from the same breeding zone.

(6) Seed from the controlled crosses are the framework for the next generation of improvement. In addition, the black spruce seed is used to provide donor trees for the clonal program.

TEMPORAL VARIATION IN NATURAL INBREEDING IN A WESTERN WHITE PINE POPULATION

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Open-pollinated seeds were collected from designated trees in a single white pine stand during three successive seed crops. Analysis of starch-gel electrophoresis data of six independent seed-enzyme loci indicated differences in outcrossing rate among trees across years, although the stand mean did not vary. Some consistent "inbreeders" and "outcrossers" were identified, but outcrossing rates of most trees varied across years, indicating significant differences in pollen dynamics. Although each seed collection produced similar population outcrossing values, the fluctuation of individual-tree values indicates that parental ranking using open-pollinated seeds should be based on pooled seed collections from 2-3 years, and that statistical adjustments of stand parameters may misrepresent the true genetic value of a parent.

DEVELOPING TECHNIQUES FOR AN OPERATIONAL ACCELERATED BREEDING PROGRAM

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Ontario Ministry of Natural Resources

Acceleration of a breeding program translates into greater gain per unit time. The Fast Growing Forests Group is committed to developing accelerated breeding techniques for white pine, Norway spruce, tamarack, Japanese larch and European larch for the Tree Improvement Program in the Eastern Region, O.M.N.R.

Reduction in the time from grafting to completion of controlled crosses is achieved through accelerating the growth of grafts in a potted breeding orchard, followed by application of flower induction treatments. Early testing techniques are being developed to reduce the time from progeny trial establishment to the time when information can be used for selection of the production population and the second generation breeding population.

Vegetative propagation techniques facilitate earlier production of improved stock and the possibility of greater genetic gain as compared to the clonal seed orchard approach. Vegetative propagation techniques have been established for Norway spruce and the larches, however development work continues for white pine.

EASTERN WHITE CEDAR: EVIDENCE OF LOW OUTCROSSING

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The levels of effective outcrossing were determined for three natural populations of eastern white cedar (*Thuja occidentalis* L., family *Cupressaceae*) using starch-gel electrophoresis. Four unlinked loci (Me, Mdh-1, Pgm and 6Pg-2) were examined in paired megagametophyte and embryo tissues of 20 seeds from each of 20 trees per population. Multilocus estimates of outcrossing (t_m) for the three populations were 0.507, 0.652 and 0.745. There was no heterogeneity among single-locus estimates (t_s) within populations and differences between t_s and t_m were small indicating consanguineous matings other than selfing were not an important factor contributing to the low estimates of t. The low levels of outcrossing observed in these eastern white cedar populations may be a reflection of selfed embryo survival which may be higher than in some other conifers. Although a significant amount of selfing was apparent in the mating system of eastern white cedar, no deviations from Hardy-Weinberg equilibrium were observed in the mature parental populations. This suggests that considerable selection may occur through the life cycle.

FLOWER INDUCTION OF WHITE PINE

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The W.R. Bunting Tree Improvement Centre services several tree improvement programs in southern Onario. In our breeding hall we are testing hormonal and cultural treatments to promote early and enhanced flowering of 3- to 5-year-old potted conifer grafts. We have completed three flower induction studies with white pine, with the primary goal being to determine the optimum treatment period and concentration for gibberellin $A_{4/7}$ application. Treatments consisted of four or six weekly foliar spray applications at specific times during the growing season, with concentrations ranging from 0 to 800 mg GA/L.

The results of these trials suggest that appropriately timed applications of gibberellin $A_{4/7}$, carried out in the breeding hall, can significantly enhance pollen cone and, to a lesser extent, seed cone production of potted white pine grafts. The optimum concentrations (of those tested) included 400 and 500 mg GA/L. The optimum treatment period for pollen cone production was from mid-May to mid-June (which roughly coincided with the latter portion of shoot elongation). Gibberellin application after this period did not enhance pollen cone production. The optimum treatment period for seed cone production was mid-August to mid-September. Late-winter/early-spring applications did not enhance seed cone production.

USE OF DNA PROBES FOR THE ANALYSIS OF HYBRID AND MIXED SEEDLOTS OF SPRUCE

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Spruce seedlots containing species mixes and hybrids of Sitka spruce (*Picea sitchensis*) and interior spruce (*Picea glauca* (Moench) Voss/*P. engelmanni* (Parry)) produce seedlings of unacceptable stock type under operational nursery growing regimes in British Columbia. We have investigated the utility of chloroplast DNA (cpDNA) restriction fragment length polymorphisms for identification of the species composition of these seedlots. A BamHI library of Sitka spruce cpDNA was constructed in pUC8. Two clones were selected by hybridization with a 10.5kb BamHI fragment of white spruce cpDNA which is unique to interior spruce. One of these (pSS4) containing a 4.3 kb BamHI fragment was tested in screening of pure and mixed seedlots of Sitka and interior spruce. The results show that this probe can be used to screen total DNA samples to reliably identify and quantify the cpDNA composition of two week old germinants using a sample size of 0.5 g and allows less than 5% species contamination to be detected. Analysis of seedlings from a hybrid seedlot showed that both chloroplast types could be found in some individuals. This result demonstrates the occurrence of hybrid individuals in seedlots and suggests that chloroplasts can be biparentally inherited in *Picea* spp. Seedlot identification obtained with the cpDNA probe agreed with the recommended growing regimes based on the nursery performance of the seedlings.

ACCELERATED AGING IS EFFECTIVE IN PREDICTING SEED STORAGE POTENTIAL

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Seed aging is a natural, irreversible metabolic process. The rate of aging, however, depends on the inherent seed longevity of the species, seed quality prior to storage, and the influence of environment during storage. Vigour testing methods have been developed to monitor changes in physiological and genetic quality of seedlots in storage.

In our research we used an established vigour test called "accelerated aging" technique to evaluate its applicability for detecting seed vigour and predicting seed storage potential of pine and spruce seedlots. Our results indicate that white spruce seeds from individual trees within and between populations aged differently, even though they were collected, handled, and processed uniformly. Also, we found that when the germinability of bulk seedlots decline from near 100% to less than 50%, it may only represent a much reduced population from the original collection.

Our findings show that the accelerated aging technique is effective in predicting seed storage potential of lodgepole pine seedlots with different histories based on their calculated rate of aging.

INDUCTION OF HAPLOIDS IN POPULUS MAXIMOWICZII BY ANTHER CULTURE

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Inbreeding to develop homozygous lines is not fruitful with forest trees due to their long generation cycle, inbreeding depression and high initial levels of heterozygosity. Therefore, anther culture and subsequent chromosome doubling are techniques with great potential for the development of homozygous lines, especially in dioecious trees. Anthers of Populus maximowiczii clone MD-1 with microspores at the mononucleate stage were subjected to a cold preculture treatment for 4 days at 4°C. Subsequently anthers were cultured on agar-solidified MS medium supplemented with three levels each of 2,4-D (0.5, 1.0 and 2.0 mg/L) and kinetin (0.1, 0.5 and 1.0 mg/L) in a factorial fashion and exposed to darkness at 20°C. After four weeks, unusual globular to oblong calli with smooth surfaces were observed. These calli consisted of expanding microspores surrounded by a gel-like substance. After two weeks of transfer of anthers with these calli to MS medium with three levels of BAP (1.0, 2.0 and 5.0 mg/L) meristematic areas within the globular calli were observed. These meristematic nests developed into heart-shaped embryoidal structures and germinated precociously without developing into embryos. Adventitious shoots could be harvested from these roots which then could be rooted in half-strength MS and 0.025 mg/L NAA. Chromosome counts after two years of induction revealed that 47% of obtained plantlets were haploid (n=19) and a further 25% were dihaploids originating spontaneously. Dihaploids could be separated from somatic diploids through the use of an isozyme assay of a heterozygous locus in the donor genotype. Anther response to this mode of haploid induction was 11% over three years. Embryogenic calli were also observed with one other donor genotype of this species, although at lower frequencies.

OPERATIONAL CONE INDUCTION TRIALS IN BLACK SPRUCE SEEDLING SEED ORCHARDS

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Cone production in individual young black spruce (Picea mariana (Mill.) B.S.P.) trees has been successfully increased through applications of ammonium nitrate. However, fertilization schedules for operational cone induction in seed orchards have yet to be determined. Therefore in 1987, a five-year cooperative experiment was established in three New Brunswick black spruce seedling seed orchards ages six to nine with the objective to determine the optimum rate(s), and frequency of fertilizer applications.

Trees fertilized before the middle of June in 1987 produced two to five times the numbers of cones in 1988 than did the controls and those fertilized after June 15. In general, the older the orchard trees, the higher was the fertilization rate at which cone production was maximized.

Preliminary results from one orchard in 1989 include:

(1) The same general timing pattern occurred (trees fertilized after June 10/88 showed little or no increase in cone production).

(2) A slight carryover effect into the second year, but only for trees receiving 7.5 kg on one or both sides.

(3) Trees fertilized in both 1987 and 1988 produced more cones in 1989 than those fertilized only in 1987 or 1988.

MASS SELECTION SEED ORCHARDS FOR NORTHERN MANITOBA

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The Manitoba Forestry Branch expressed interest in a cooperative program within the Canada-Manitoba Forest Renewal Agreement to develop genetically improved jack pine for the interlake and northern regions of the province. Because annual planting in each of these regions is less than 2.5 million trees, an inexpensive program seemed appropriate. The program established in 1986 pursues genetic gain at two levels. Genetic variation among trees within stands is sought by progressive mass selection among closely spaced trees from the same stand. Genetic variation among stands can be captured by assessing performance of stand progenies, followed by use of the best stands as seed collection areas.

Seed was obtained from at least 10 good phenotypes in each of 32 stands in each region. Equal numbers of viable seeds from each tree within a stand were mixed to form each stand lot. Following enhanced site preparation, seedlings were planted at 1-m spacing in stand plots of 48 trees (northern) or 24 trees (interlake). Plots are separated by 4-m aisles. Stand lots are randomized within replications. There are 6 replications on each of two sites for the northern region and 25 replications on one site for the interlake region, owing to unavailability of a second site.

Plots will be thinned progressively to 2 trees (northern) or 1 tree (interlake) for seed production. Thinning will be done before crowding occurs, to favor selection of trees able to grow well before canopy closure, and to encourage early seed production. Cone harvest may begin at about 12 years, and mass selection should be completed at about 15 years. Surviving trees will be measured periodically, and the data analyzed for selection of the best source stands, beginning at about 8 years. Control-pollinated progenies will be produced from survivors of mass selection for recurrent selection.

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