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# CANADIAN TREE IMPROVEMENT ASSOCIATION

## PART 2

**Symposium**

# TREE IMPROVEMENT: ITS CONTRIBUTION TO SUSTAINABLE DEVELOPMENT

Sainte-Foy, Québec
August 18-21, 1997

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J. Beaulieu and J.D. Simpson

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## 2e PARTIE

## Colloque

# L' AMÉLIORATION DES ARBRES POUR UN DÉVELOPPEMENT DURABLE

Sainte-Foy, Québec
18-21 août 1997

Rédacteurs
J. Beaulieu et J.D. Simpson

# TABLE OF CONTENTS / TABLE DES MATIERES

Page

## INVITED SPEAKERS

## CURRENT KNOWLEDGE OF TREE BREEDING

## FUTURE DIRECTIONS AND CONTRIBUTIONS TO SUSTAINABLE DEVELOPMENT

## BIOTECHNOLOGY AND MOLECULAR POPULATION GENETICS

## PHYSIOLOGICAL GENETICS AND PEST RESISTANCE

## FIELD TESTING AND GENETIC GAINS

## TREE SEED WORKING GROUP WORKSHOP

## POSTERS

# Conférenciers invités/Invited Speakers

De gauche à droite/From left to right: J. Beaulieu, M.J. Lechowicz, W.J. Libby, S.E. McKeand, B. Zobel, G.W. Adams, M. Bonnet-Masimbert, A.D. Yanchuk, J.P. van Buijtenen. Absents/Not present: K.J. Tosh, F.E. Bridgewater, L. Kucera, D.B. Neale, J.C. Mercier, G.Vallée.

# CURRENT KNOWLEDGE OF TREE BREEDING

# OVERVIEW OF PROGRESS IN TREE BREEDING IN QUÉBEC WITH EMPHASIS ON WHITE SPRUCE AND BLACK SPRUCE

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## ABSTRACT

Research in forest genetics in Québec began in the mid-1950's and was aimed at learning more about genetic variation due to geographic origin. Provenance trials were set up as well as in the early 1960's. Results showed the presence of a high level of variation and its potential for increasing wood production. Tree breeding programs were set up in the early 1970's and some were headed by breeders attached to the Canadian Forest Service (CFS) while others were under the responsibility of the geneticists attached to the Service d'amélioration des arbres of the ministère des Ressources naturelles (MRN) du Québec. In 1996, after a program review conducted by the federal government, it was decided that the CFS would withdraw from tree breeding programs, transfer its responsibility in tree improvement to the MRN, and focus on advanced genetics and biotechnology research. Hence, all tree breeding activities are now carried out by the MRN and other agencies, such as CFS and Université Laval, are collaborating on basic research in forest genetics.

Since the inception of tree breeding activities in Québec, there have been many important achievements which are described in this paper. Major steps in the improvement of white spruce and black spruce are also presented but in more details. Future prospects for tree breeding in the new context of sustainable development are expressed.

## LAND TENURE AND CONTEXT OF FOREST MANAGEMENT IN QUÉBEC

In Canada, most of the land is in the public domain and in the province of Québec the situation is no different from that in the rest of the country. Hence, more than 85% of the inventoried forest land, where harvesting is allowed, is owned by the government (Table 1), and more than 70% is occupied by the boreal forest (Table 2). Since 1986, forest management on public land, which is a provincial responsibility, is regulated by the

"Forest Management System" and is based on the following principles (Robitaille 1997):

1) do not harvest more than the potential yield of the forest,
2) protect the forest ecosystems and their components,
3) use all the available resources while respecting the needs of each class of user, and
4) allow the public and interested groups to comment on land management practices.

A strategy aimed at protecting forest resources was put in place in 1994. Hence, use of chemical brushkillers and insecticides is now minimized and will be banned by 2001, and harvesting with protection of advance regeneration and soil promoted. From the early 1980's to 1994, a large reforestation program was implemented for lands that had not regenerated adequately after harvesting or forest fire. Since then, all the backlog has been eliminated and the reforestation program has decreased considerably. In 1995, for instance, 76 000 hectares were reforested (CCCF, 1997), which is equivalent to about 0.1% of the total inventoried forest land. Just for the sake of comparison, on average, forest fire destroyed 73 000 hectares annually during the last decade.

Table 1. Inventoried forest land [1] in Québec and land tenure [2]

| Land tenure | Total land area ($km^2$) | Percentage (%) | Productive land area (aspect 0% to 40%) ($km^2$) | Percentage (%) |
|---|---|---|---|---|
| Provincial Crown | 652 717 | 85 | 447 541 | 86 |
| Federal Crown | 4 573 | 1 | 3 069 | 1 |
| Private | 107 460 | 14 | 65 991 | 13 |
| Total | 764 750 | 100 | 516 601 | 100 |

[1] Where harvesting is permitted
[2] Source: Parent, B. 1996. Ressource et industrie forestières. Portrait statistique. Édition 1996.

Table 2. Vegetation zones in southern Québec

| Vegetation zones | Percentage of forest land (%) |
|---|---|
| **Deciduous forest** | **14.9** |
| Sugar Maple / Hickory ecological domain | 1.3 |
| Sugar Maple / Basswood ecological domain | 4.4 |
| Sugar Maple / Yellow Birch ecological domain | 9.2 |
| **Mixed forest** | **11.4** |
| Balsam Fir / Yellow Birch ecological domain | 11.4 |
| **Boreal forest** | **73.7** |
| Balsam Fir / White Birch ecological domain | 14.0 |
| Balsam Fir / White Spruce ecological domain | 1.7 |
| Balsam Fir / Black Spruce ecological domain | 58.0 |

On the other hand, the Québec government, through its Forest Act, has made a commitment to provide the seedlings required to reforest public and private land. Thus, the involvement of the private sector in tree improvement activities is minimal. Only a few large companies continue, through collaboration with public research organizations, to invest in forest genetics and tree improvement. Furthermore, unlike elsewhere in Canada and the United States, there are no cooperatives that represent the interests of all organizations involved in tree improvement activities.

It is in this context that tree breeding is currently evolving in Québec. The least that can be said is that the golden era for tree improvement in Québec, with a large reforestation program for producing wood fibre more efficiently, is yet to come. But the situation could evolve rapidly. Moreover, means to produce more wood fibre while decreasing the pressure on natural ecosystems must be found. The benefits of tree improvement are now promoted more actively and as results of past research speak for themselves, it is easier to convince the population of their value.

## EVOLUTION OF FOREST GENETICS AND TREE IMPROVEMENT

Early research in forest genetics in Québec began in the mid-1950's and was aimed at learning more about genetic variation in growth traits due to geographic origin. Various provenance trials with native and exotic species were set up under the direction of geneticists at the Petawawa National Forestry Institute (PNFI). In the early 1970's, after regionalization of research at the Laurentian Forestry Centre and a local agreement with the Ministère des Ressources naturelles du Québec (MRN), breeding programs were set up, and some were headed by breeders attached to the Laurentian Forestry Centre while others were under the responsibility of the geneticists attached to the Service d'amélioration des arbres of the MRN. Other organizations have also been involved in forest genetics and tree improvement research activities. Among these, the most important are Université Laval since 1960, Université du Québec from the 1980's and a few forest companies such as Avenor Inc., Abitibi-Consolidated Inc., Tembec Inc., and Cartons St-Laurent Inc.

Since the inception of tree breeding activities, there have been many important achievements (Table 3). Because of the extent of the breeding programs, 21 arboretums and populetums, covering a total area of 6 000 ha, were put aside as soon as 1969 for establishing the genetic tests. Over a couple of decades, this led to the creation of a network of *ex situ* conservation sites grouping together more than 750 experimental designs made up of clones, families, and provenances of 157 exotic and native species. Eighty-one first-generation seed orchards were established by the MRN to mass produce seed for 12 commercial conifers and new ones are now in preparation for white and black spruce. Furthermore, information gathered over the years made it possible to select and recommend the best provenances and clones for reforestation, to delineate breeding zones for three commercially important conifer species, to set up breeding populations, and to initiate the second generation of genetic improvement.

Since last year, after a program review conducted by the federal government, it was decided that the Canadian Forest Service (CFS) would withdraw from tree breeding programs, transfer its responsibility in tree improvement to the MRN, and focus on advanced genetics and biotechnology research. Hence, all tree breeding activities are now carried out by the MRN and other agencies are collaborating on basic research in forest genetics.

Table 3. Major achievements in forest genetics and of tree breeding programs in Québec

1. Setting up of a network of 19 arboretums, 2 populetums, and 150 protected experimental areas grouping together more than 1 000 experimental designs
2. Conversion of 132 good stands into seed stands of plus trees for 16 species
3. Establishing a network of 81 clonal and seedling seed orchards for 12 coniferous species with 75 progeny tests
4. Delineation of seed zones for commercial conifer species
5. Delineation of breeding zones for white spruce, black spruce, and Norway spruce and establishment of breeding populations
6. Selection and recommendation of the best provenances and families for major conifers
7. Selection of 50 clones of hybrid poplar and recommendations for reforestation
8. Building of greenhouse, grafting, and rooting cutting complexes
9. Development of vegetative propagation methods (grafting, cuttings, somatic embryogenesis)
10. Development of methods for flower induction in conifers
11. Setting up of seed and pollen banks (more than 18 000 seedlots and 1 000 pollen lots for 52 different species)
12. Development of molecular markers for the management of genetic resources and marker-aided selection

## WHITE SPRUCE (*Picea glauca* [Moench] Voss.)

White spruce has been known for many years to have a high potential for genetic improvement (Corriveau and Boudoux 1971; Nienstaedt and Teich 1971) and it is one of the three major species for reforestation in Québec, as more than 40 million seedlings are planted annually (Parent 1996). As for other conifers, the earliest research directed at understanding the genecology of white spruce dates back to the late 1950's and early 1960's. About a dozen provenance trials were established in Québec during that period. In addition, half-sib progeny tests including open-pollinated families from Québec and Ontario were established during the 1970's and the 1980's for the same purpose. Numerous studies have been conducted since then using this material in order to quantify the level of genetic variation present in white spruce and the strength of genetic control on adaptive and growth traits (Beaulieu and Corriveau 1985; Corriveau *et al.* 1987; Corriveau *et al.* 1991; Desponts *et al.* 1993; Li *et al.* 1993; Li *et al.* 1997).

Results obtained so far for the old provenance trials originating from the Great Lakes and St. Lawrence region revealed, similarly to what was observed elsewhere with the same provenances, the presence of a superior gene pool for white spruce in southwestern Québec and southeastern Ontario (Table 4). These results, after 25 years of testing, led to recommendations for reforestation with a first group of seven provenances from Ontario. Their average volume totalled 154 $m^3$/ha and 243 $m^3$/ha in Drummondville and Harrington, respectively, for a superiority of 28.5% and 56.9% over the average values for the Québec seed sources tested. A second series of seven provenance trials, including seed sources from the same region, was initiated in the early 1960's. Five provenances showed superior growth in each of these tests. They are Peterborough (ON), Beachburg (ON), Cushing (Qc), Beloeil (Qc) and Grandes-Piles (Qc). Their average yield, 20 years after planting, exceeded the Québec seed sources by an amount varying from 15% to 30% depending on the site. These results, as well as those from later studies (Li *et al.* 1993), confirmed that the GxE interaction was relatively low in white spruce and it was possible to select generalist genotypes for developing material adapted to a wide variety of conditions. Hence, a first group of 100 superior genotypes from the 12 superior provenances recommended for reforestation were grafted and placed in a breeding orchard for breeding work.

Provenance trials make it possible to study genetic variation at the geographic level but not to estimate either the heritability of each trait to improve or the genetic gains following selection and breeding work. Hence, in the late 1970's and early 1980's, two series of genecological tests using over 400 Québec and Ontario progenies were established. Genetic structure and patterns of genetic variation among the provenances were examined and mathematical models describing patterns of variation were developed and permitted the delineation of two provisional breeding zones (Figure 1) and provide new rules for seed transfer (Li *et al.* 1997). Breeding values were also estimated, using the best linear prediction (BLP) method, for each parent tree in 1992, i.e. about 15 years after sowing. Forward selection was performed. Families with the highest breeding values were selected first and then mass selection was made within these families to complete the first-generation breeding population for each breeding zone. Hence, as a first step, 360 plus-trees belonging to 89 families were mass selected and grafted in 1994. This number will be reduced by two-thirds at the final stage based on early flowering and wood density. Expected genetic gains in height growth at 15 years of age after family selection are about 16%. This figure could increase when the breeding populations attain their final size.

A breeding strategy was implemented for white spruce (Beaulieu 1996) based on the strategy proposed by van Buijtenen and Lowe (1979) for controlling related matings. Hence, the two breeding populations, each including 240 genotypes, have been divided into 11 separate breeding groups, 10 of which include 20 trees, and the last one is made up of the 40 best trees and forms an elite population. General combining ability of each genotype is estimated through progeny testing with families obtained by polycross mating. A partial diallel, with each genotype being crossed with two others, is used to generate full-sib families from which will be selected the genotypes for the next generation to create the breeding groups again.

Table 4. Superiority of white spruce seed sources from which parent trees were selected for the breeding populations, compared with the average values for Québec seed sources tested in Drummondville and Harrington

| Seed source origin | Drummondville[1] | | Harrington Forest Station | |
|---|---|---|---|---|
| | Height at 20 years (m) | Volume at 25 years ($m^3$/ha) | Height at 20 years (m) | Volume at 25 years ($m^3$/ha) |
| **Seed sources from Québec** | | | | |
| Maniwaki | 5.23 | 98 | 5.30 | 144 |
| L'Annonciation | 5.73 | 97 | 4.80 | 149 |
| St-Donat | 5.90 | 106 | 5.19 | 148 |
| Harrington | 5.37 | 114 | 4.02 | 102 |
| St-Zénon | 5.17 | 101 | 5.04 | 134 |
| St-Charles-de-Mandeville | 5.75 | 110 | 4.98 | 144 |
| St-Maurice | 5.75 | 108 | 4.93 | 150 |
| Rivière-aux-Rats | - | - | 5.16 | 195 |
| Average | 5.58 | 105 | 4.93 | 155 |
| **Recommended seed sources** | | | | |
| Algonquin Park 1, Ont. | - | - | 6.28 | 261 |
| Algonquin Park 2, Ont. | - | - | 6.53 | 249 |
| Carnarvon, Ont. | 6.48 | 139 | 4.26 | 164 |
| Sundridge, Ont. | 6.53 | 131 | 5.93 | 210 |
| Monaghan, Ont. | - | - | 6.24 | 303 |
| Rama Twp, Ont. | 6.27 | 126 | 5.64 | 225 |
| Petawawa Nat. For. Inst., Ont. | 7.00 | 145 | 6.35 | 288 |
| Average | 6.57 | 135 | 5.89 | 243 |
| Superiority (%) | 17.8 | 28.5 | 19.6 | 56.9 |

[1] Total volume after a 50% thinning

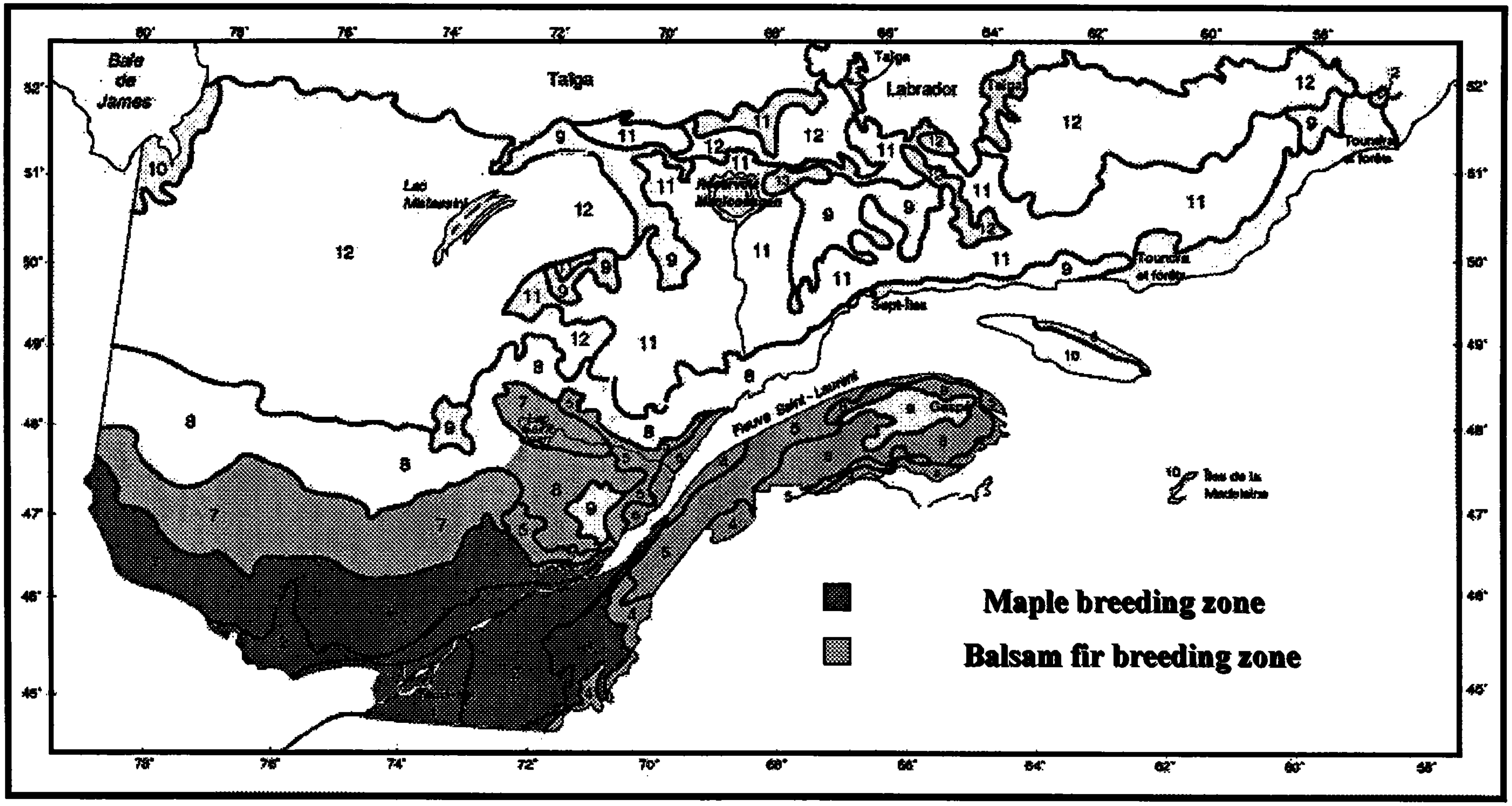

Figure 1. White spruce breeding zones in Québec.

Hundreds of control crosses have already been carried out for the breeding groups made up of the genotypes selected in the provenance trials. Seven progeny tests were recently established in southern Québec for estimating general combining ability of these selected trees. Seedlings from full-sib families were also produced and two tests are already established. Two others will be set up within a couple of years. The first second generation genotypes are expected to be selected within five to ten years from now.

A clone bank of the 3 500 plus-trees mass selected in natural forests in the early 1980's by the MRN for building up 17 first-generation regional clonal seed orchards has also been set up. These trees form an alternate genetic diversity pool that could be used in the future for increasing the level of genetic diversity in the existing breeding populations or could be used for implementing a multiple breeding population strategy.

Breeding values estimated for the parent trees of open-pollinated families evaluated in the genecological tests established in the late 1970's were also used for selecting trees to establish new clonal seed orchards. So far, five trees from the 25 best families have been selected and grafted for each of the two breeding zones delineated. For the Maple Forest Breeding Zone, the genetic gain expected in height growth at 15 years of age from the family selection varies from 15% to 21% over the local sources, depending on the site, while it is about 16% for the Balsam Fir/Yellow Birch Breeding Zone.

Vegetative propagation of white spruce, either by somatic embryogenesis or rooting cuttings, has become relatively easy and permits us to consider increasing the genetic gains by clonal deployment. So far, various studies have been initiated for comparing vegetative propagules and seedlings and for predicting the genetic gain expected from clonal propagation. Clonal trials of full-sib families as well as genetic tests including full-sib families represented by seedlings and vegetative propagules are now established and should very soon help to make a decision as to whether it is worth investing more effort in clonal forestry. Furthermore, the pair-matings that should be given priority to produce the genetically superior seedlots needed for large scale cuttings production will be identified from these tests.

A series of investigations on genetic variation in wood density of white spruce (Beaulieu and Corriveau 1985; Corriveau *et al.* 1987; Corriveau *et al.* 1990; Corriveau *et al.* 1991) has also been carried out. A high level of genetic variation with strong genetic control (Corriveau *et al*. 1991) was revealed. On average, relative wood density is about the same in natural stands and provenance trials (Table 5). This seems to indicate that physical properties of wood of white spruce grown in plantations might not be very different from that produced in natural stands. A study aimed at comparing dried wood physical properties of trees growing in both types of stands was recently initiated. Results will also allow us to estimate the extent of effects of provenance on wood properties in plantation-grown trees.

Table 5. Wood density of white spruce growing in natural stands and plantations in Québec

| Stand type | Number of provenances | Age[1] | Basic wood density[2] (kg/m$^3$) |
|---|---|---|---|
| Natural | 80 | 39 | 344 (24) |
| Grand-Mère provenance trial | 28 | 24 | 326 (23) |
| Harrington provenance trial | 23 | 24 | 344 (24) |

[1] Average age for the natural stands

[2] Standard deviation in parentheses

Knowing the heritability of wood density was relatively high in white spruce (Corriveau *et al.* 1991), one expects to find markers associated with genes controlling that trait which could explain a part of the variation observed. Thus, a collaborative research program aimed at finding molecular markers associated with mature wood density to be used in a marker-aided selection program at an early stage has been initiated (Isabel *et* *al.* 1994). So far, a 4% genetic gain in mature wood density could be expected in using four putative molecular markers, which corresponds to an increase of 13 kg/m$^3$. Further benefits could be achieved by using these markers in tandem selection for mature wood density and growth. A research program for finding molecular markers associated with the capacity to produce somatic embryos in white spruce was also initiated, as this character is also under strong genetic control (Park *et al.* 1994). Such markers would help in decreasing the cost of the vegetative propagation technique by putting only embryos from high potential families on culture medium.

## BLACK SPRUCE (*Picea mariana* [Mill.] BSP)

Black spruce is a commercially important species in Québec. More than 92 million seedlings were planted in 1993-1994. While that figure has decreased since then, as it has for other species, the reforestation program for black spruce remains the largest. The first research program on the genetics of black spruce goes back to the early 1970's. A range-wide provenance trial, including 100 provenances from Alaska to Newfoundland, was established in 1974 and 1975 on six sites in Québec by the CFS under the direction of Dr. E.K. Morgenstern from PNFI. Based on results obtained 12 years after planting and on vegetation zones covering southern Québec (Thibault and Hotte 1985), and administrative considerations, five provisional breeding zones (Figure 2) were delineated (Beaulieu *et al.* 1989 modified, M. Villeneuve unpublished). For each of these zones, 25 superior provenances were recommended. They showed a height growth superiority of 6% and 15% over the local sources in the two southernmost breeding zones, 16 years after sowing. Provenances that performed the best are in many cases very remote from the region for which they were recommended (Table 6). For the long term, any adaptation problems are not expected because black spruce is a very frost tolerant species and has already adapted to a variety of harsh environmental conditions.

The breeding strategy developed for this species aims at taking advantage of the ease with which cuttings of young black spruce seedlings can be rooted. Hence, for the first generation, mass selection was carried out within the best provenances for each breeding zone in which at least one provenance trial was located and the superior phenotypes were mated. Full-sib families were then bulked up by rooted cuttings. Farm-field tests as well as conventional tests were established. Results obtained so far show that an increase of 56 m$^3$/ha can be expected in 35-year-old plantations, which corresponds to an actual increase in value of $560 per ha (M. Villeneuve unpublished). However, in view of the fact that producing rooted cuttings is more expensive than seedlings, research on mass pollination aimed at increasing the number of seeds produced while partially controlling the contamination was initiated. If the benefit/cost ratio, i.e. the genetic gain over the cost of mass pollination, is higher than that obtained by bulking up the controlled crosses, then the breeding strategy could be revised.

The deployment of first-generation seed orchards was initiated in the early 1980's (Lamontagne 1992). Mass selection was carried out in natural stands and a network of 24 regional seedling seed orchards with 42 progeny tests was completed in the late 1980's. So far, roguing has been conducted in 11 of these seed orchards after the analysis of data collected in the progeny tests. On average, a 5% genetic gain is expected from the rogued orchards, which corresponds to a gain of 6 m$^3$/ha in addition to the 126 m$^3$/ha expected after 35 years from the local sources. Since 1996, new seed orchards are being developed. Trees were selected in first-generation progeny tests after spatial adjustment for family effects. These elite trees were vegetatively propagated by rooted cuttings to produce the planting stock for the second-generation orchards for breeding zones D and N (see Figure 2). The expected genetic gains in height at 12 years is around 20% in both cases. The same strategy is being implemented for the other breeding zones.

As for white spruce, a collaborative research program aimed at finding molecular markers associated with mature wood density to be used in a marker-aided selection program was initiated (Isabel *et al.* 1997). This program is too recent to know its real potential. However, genetic gains of at least the same order as with white spruce are expected.

Table 6. List of black spruce seed sources recommended for the Appalachian breeding zone and superiority over the local sources

| Seed source origin | Average 16-year height (m) | Superiority over the local sources (%) |
|---|---|---|
| Perthuis, Portneuf | 2.81 | 20.3 |
| Matagami, Abitibi-Est | 2.74 | 17.3 |
| Rivière-aux-Rats, Laviolette | 2.77 | 18.5 |
| Péribonka, Roberval | 2.73 | 16.8 |
| Chute-aux-Galets, Chicoutimi | 2.74 | 17.3 |
| Madawaska, N.B. | 2.77 | 18.5 |
| Rivière Caraquet, N.B. | 2.85 | 22.0 |
| R. Tweedie, N.B. | 2.73 | 16.8 |
| Timmins, Ogden, Ont. | 2.76 | 18.1 |
| Tour, Sioux, Ont. | 2.84 | 21.5 |
| Parc Chibougamau, Roberval | 2.54 | 8.7 |
| Parc Chibougamau, Lac-St-Jean | 2.68 | 14.7 |
| Bas Mattawin, St-Maurice | 2.64 | 13.0 |
| St-Michel-des-Saints, Berthier | 2.52 | 7.8 |
| Normandin, Roberval | 2.56 | 9.6 |
| Mars Ha! Ha!, Chicoutimi | 2.60 | 11.3 |
| Lac Parent, Abitibi-Est | 2.57 | 10.0 |
| Lac Doré, Maskinongé | 2.62 | 12.1 |
| CFB Gagetown, N.B. | 2.70 | 15.5 |
| Penobscot Co., Maine | 2.57 | 10.0 |
| Bancroft, Hastings, Ont. | 2.53 | 8.3 |
| Chalk River, Renfrew, Ont. | 2.65 | 13.4 |
| Ipsala, Ont. | 2.68 | 14.7 |
| Minaki, Ont. | 2.61 | 11.7 |
| Whiteshell Prov. Park, Man. | 2.71 | 16.0 |
| Average of recommended seed sources | 2.68 | 14.7 |

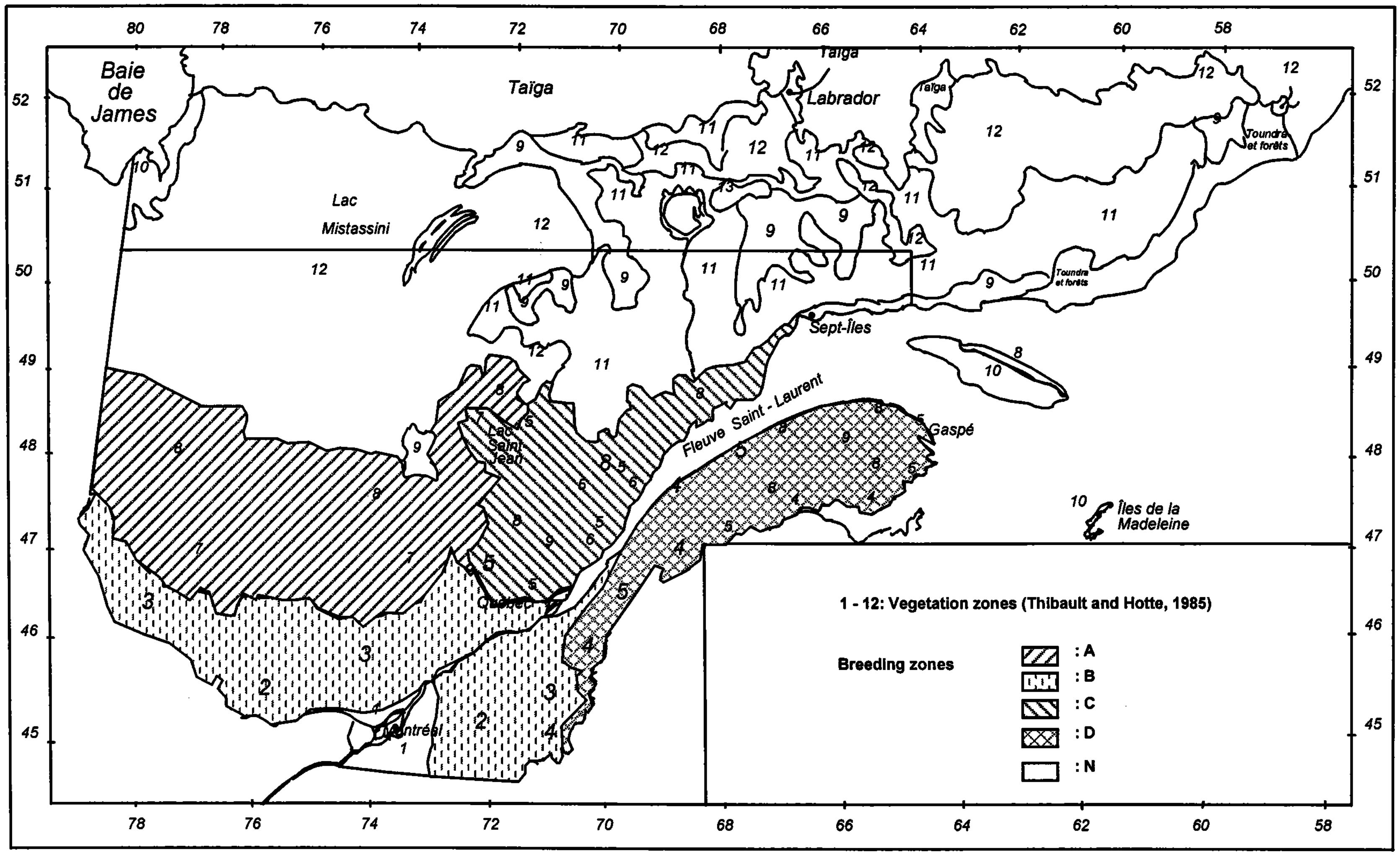

Figure 2. Black spruce breeding zones in Québec.

# FUTURE PROSPECTS FOR TREE BREEDING

In Québec, as well as in other provinces and countries, the demand for forest products has increased considerably over the last decades. This trend will continue as the human population is expected to double and reach 10 billion by 2070 (Ehrlich and Ehrlich 1988). Hence, there is a need to have access to more resources to meet the demand for wood fibre while providing better access to forest land for other activities such as hunting and fishing. On the other hand, sustainable forest management must be implemented and a larger portion of the forest ecosystems set aside as a reservoir of biodiversity for future generations.

Even though in Québec there are strong commitments for preserving biodiversity and implementing forest practices that ensure sustainable development (Gouvernement du Québec 1996), the recent trend in productivity causes some concern (Figure 3). Indeed, while the number of cubic metres produced per working hour was almost stable or increased during the last 12 years in New Brunswick, Ontario and British Columbia, it decreased in Québec. The forest industry is now harvesting mature stands in northern Québec where the volume per hectare is lower than it is for forest stands in the southern part of the province. Lesser productivity means a decrease in competitiveness and a larger area harvested to meet the demand for forest products.

Tree breeding can certainly make a major contribution to improving the situation with regard to productivity and pressures on natural ecosystems. As demonstrated for white and black spruce, yield can be considerably increased. Results obtained with fast growing species are also impressive. The recommended hybrid poplar clones can produce about 200 $m^3$/ha in 20 years with a 3 m x 3 m spacing. This corresponds to about four times the volume of the best aspen stands and three times that of the best indigenous poplar clones. Significant results were also achieved from exotic and hybrid larch. For instance, the production of a Japanese larch plantation reached 334 $m^3$/ha at 35 years. Breeding programs for these two species are well under way but could be expanded and accelerated.

The forest industry recently showed a renewed interest in reforestation using genetically improved material. Companies like Tembec Inc., Cartons St-Laurent Inc., Avenor Inc., and Forex St-Michel Inc. among others have begun to invest in reforestation to ensure their future supply and decrease the cost of the raw material in the long term. The higher volume per hectare that will be obtained will make it possible to decrease the pressure on the natural forest by reducing the area to be harvested. This is a major contribution to the preservation of biodiversity and sustainable development. With the current reforestation program, production of more than half of the actual annual potential yield in conifers would be easily achievable with a 50-year harvesting cycle using only 5% of the productive land area.

Future prospects for tree breeding in Québec are positive. Major forest companies cooperate in research and are more actively involved in operational activities. Strong links between federal and provincial research organizations and universities have been developed over the past years. Research on tree biotechnology is progressing rapidly and creates, along with traditional breeding, new opportunities for improving wood supply while promoting and ensuring sustainable development.

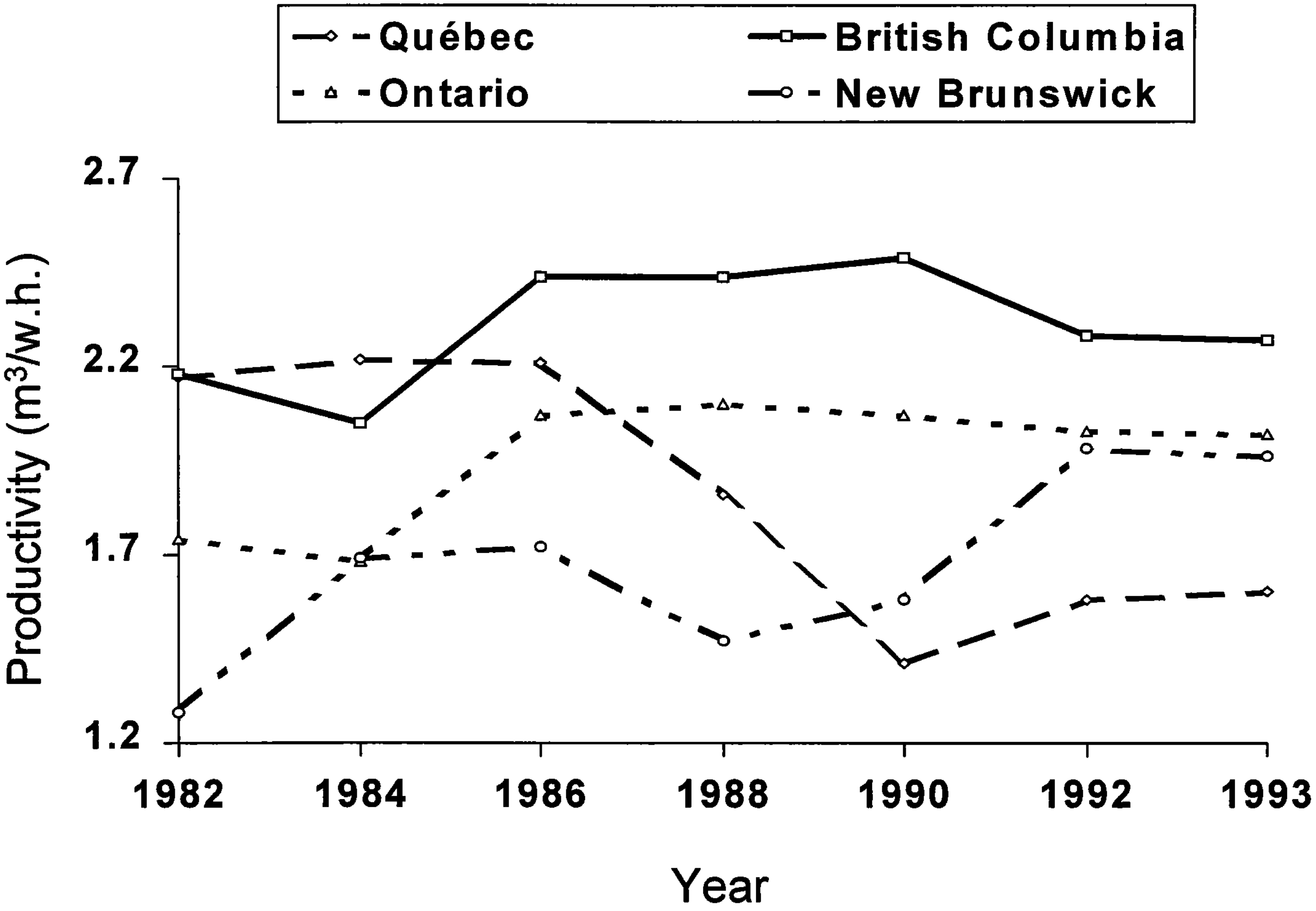

Figure 3. Comparison of number of cubic metres harvested per working hour over the last 12 years in four Canadian provinces.

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# TWO GENERATIONS OF GENETIC GAINS WITH LOBLOLLY PINE IN THE SOUTHEASTERN UNITED STATES

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## ABSTRACT

The North Carolina State University-Industry Cooperative Tree Improvement Program has completed two cycles of breeding with loblolly pine (*Pinus taeda* L.). The estimated gains for height from 2nd-generation seed orchards ranged from 6% to 10% over unimproved checklots in different regions. When these height gains were projected to rotation-age volume improvement, the gains were substantially higher, ranging from 13% to 21%. Roguing seed orchards to the best 30% of the parents could boost the gains to as much as 13% to 16% in height growth and 26% to 35% improvement in volume production at harvest. A substantial number of 2nd-generation selections have not only demonstrated outstanding growth but also had less rust infection, with R-50 values of 20% to 25% below the unimproved checklots. The best family from each population was generally 10-20% above the 1st-generation seed orchard mix in height growth, indicating additional gain above the first-generation selections. Although genetic gain for stem straightness is difficult to quantify, most of the 2nd-generation families had a higher percentage of trees with above average straightness than the checklots.

**Keywords:** Genetic gain, growth and yield, open-pollinated family, *Pinus taeda*, rust infection, second-generation, seed orchard.

## INTRODUCTION

The southern United States has long been a major wood producing region for both domestic and export markets. The southern yellow pines are the most common species used in the 11 million ha of plantations. Although only 15% of the commercial forests are in plantations, almost 50% of the timber harvest will soon come from them (Kellison 1997). Tree improvement with loblolly pine has had a major impact on the productivity of many of these plantations. Members of the North Carolina State University-Industry Cooperative Tree Improvement Program (NCSU-ICTIP), currently 16 industries and five states, annually plant 600 000 000 trees on 350 000 ha, accounting for 37% of the tree planting in the country. Essentially every seedling is a product of one of the tree improvement programs.

Even modest improvement in productivity and quality makes investments in tree improvement profitable because of the economies of large-scale regeneration programs. From the first generation of improvement in the Cooperative, average volume estimates of 8-12% were projected for improved seedlings compared to unimproved seedlings. Returns on investment were estimated to be 18-19% (Talbert *et al.* 1985). When the most responsive families are deployed, volume gains of 2-3 times the average are possible (McKeand *et al.* 1996).

Second generation seed orchards were established in the 1970's and early 1980's with the best individuals from the best crosses of first-generation parents. Each year that a cooperator established a block of seed orchard, the best clones available in that region were used. Many clones were shared among cooperators, and across the 10-15 years when most orchards were established, over 500 clones were used. Although many of these clones are related, there is a huge amount of genetic diversity in these orchards. Initial evaluations have indicated there is a wide range of performance among the open-pollinated families for all traits evaluated.

In this paper we summarize the performance of families from second-generation seed orchards to compare earlier predictions of performance to what has been evaluated to date. We also use other trials where large block-plots of different genetic entries are evaluated.

## MATERIALS AND METHODS

Second-generation selections were made from progenies of incomplete factorial matings of the 1st-generation parents where each of 20 to 30 females was mated to four to six males. These selections were grafted to establish 2nd-generation seed orchards by each cooperative member. Open-pollinated seeds from each seed orchard were collected and 2nd-generation progeny tests were established by each member organization throughout the Southeast. Since open-pollinated loblolly pine families generally show little genotype by environment interaction and high family stability in performance across a wide geographic area (Li and McKeand 1989, McKeand *et al.* 1990), the tests were grouped into four general geographic regions: 1) Virginia and northern North Carolina with 124 families in 5 test series, 2) Atlantic Coastal of North Carolina, South Carolina and Georgia with 131 families in 5 test series, 3) Piedmont regions of North Carolina, South Carolina and Georgia with 285 families in 12 test series, and 4) Lower Gulf region with 83 families in 3 test series.

Details of the data analysis and genetic gain predictions for height are given by Li *et al.* (1997). Briefly, best linear unbiased prediction (BLUP) was used to estimate parental breeding values because the data are unbalanced with different parents, ages, and test qualities (Huber 1993). The BLUPs for parental general combining abilities (GCA) were estimated and then breeding values were calculated using the GCA estimates. Breeding value estimates were based on 8-year height. For ranking parents within a given geographic region, percent genetic gain over local checklots was calculated from the predicted breeding values for height. Breeding values for rust infection at a 50% infection level (R-50) were also calculated for ranking parents for rust resistance.

Volume gains at rotation were estimated using methods described by Talbert (1982) and Talbert *et al.* (1985). Percentage height gains at age 8 years were assumed to equate to percentage changes in site index at age 25 years. Using the growth and yield model first developed by Hafley *et al.* (1982), we estimated the volume in unthinned plantations at age 25 years. We made the simplifying assumption that the shape of height over age curves are essentially equivalent for all families and that selection has little impact on other parameters of stand growth and yield such as mortality functions and height-diameter relationships. Work by Buford and Burkhart (1987) suggest that these assumptions are reasonable for many situations, but there are exceptions (e.g. Knowe and Foster 1989).

## RESULTS

Genetic gains for height, expressed as a percentage over local unimproved check seedlots, are summarized in Table 1. It is evident from these estimates that 2nd-generation selections have produced substantial gains over unimproved checklots. The genetic gain for all families in a region is representative of the gain from two generations of breeding, testing, and selection in the Cooperative. The genetic gain for 8-year height from the top 30% of families is the estimated gain from intensively rogued seed orchards. Height gain averaged 8% above the local checklots for Virginia/North Carolina (VA/NC), 8% for the Lower Gulf, 6% for the South Atlantic Coastal Plain, and 10% for the Piedmont region. Volume gains over unimproved checklots ranged from 13% to 21% for unrogued orchards and 26% to 35% for the top 30% of families. As discussed by Talbert *et al.* 1985, volume gains are much greater than those based on height. These estimates indicated that, in general, second-generation breeding and selection has been effective for improving loblolly pine growth even with the limited selection intensity due to the tester mating design used in the 1st-generation breeding program.

Table 1. Summary of second generation loblolly pine genetic gain predictions for 8-year height and volume at rotation age of 25 years. Gains are expressed as percentage over local, unimproved checks. For rotation volume, the gain is based on expected volume on a site index (base age 25 years) of 60 feet (18.3 metres) for unimproved seedlings

| | Average of all families in region | | Average for top 30% of families | |
|---|---|---|---|---|
| Region | % height gain | % volume gain | % height gain | % volume gain |
| VA/NC | 8.1 | 17.0 | 12.7 | 27.0 |
| S. Atl. Coast | 6.1 | 12.8 | 12.4 | 26.3 |
| Lower Coast | 7.7 | 16.0 | 14.6 | 31.2 |
| Piedmont | 9.9 | 20.7 | 16.0 | 34.9 |

Rust infection (R-50) was generally lower for 2nd-generation families than for the checklots. For example, in the Atlantic Coastal population, about 80% of the families had lower R-50 breeding values than all three checklots. The top ranked 30% of families for rust in the Atlantic Coastal population had an R-50 of 29.6%; significantly lower than the three checklots (above 63%). Similar differences in R-50 were observed for the Piedmont population which averaged 28% for the best 30% families and 56% for checklots. No strong correlations were found between height growth and R-50 breeding values except in the Lower Gulf population. While rust infection was generally high for tests in the Lower Gulf, the R-50 was moderately correlated (r=-0.48) with height growth. Because of this favorable correlation, it is possible to select fast growing families with relatively low R-50 values.

Much greater genetic gains can be expected from utilizing the best families since large differences were observed among 2nd-generation families. The best Atlantic Coastal family had 31.6% height gain and 71.6% volume gain over the unimproved checklots of North Carolina and 17.1 height gain (37.3% volume gain) over the checklots of South Carolina (SC), while the best Piedmont family had 29.3% height gain (66.2% volume gain) over the unimproved checklots of SC. The best family from each population generally had 10-20% height advantage and 21-44% volume gain above the checklot of 1st-generation seed orchard mix, indicating additional gains above 1st generation selections. Although genetic gain for stem straightness is difficult to quantify because of different ages and scoring systems in different tests, it is evident that most of the 2nd-generation families had a higher percentage of trees with above average straightness than the checklots.

## DISCUSSION

Based on estimates from first generation tests (Talbert *et al.* 1985), expectations for improvement in the Cooperative's second generation were in the range of 6% to 8% over unimproved checks. This would equate to two generations of breeding, each yielding 3-4% height gain. These expectations were met or exceeded in each region where data are currently available. Because of the large number of clones in orchards, substantial gain can be realized by roguing to the best clones.

Often in tree improvement programs, projected gains and actual gains are not the same. There are several reasons why this might happen. Gain predictions are based upon genetic and environmental components of variance and covariance and must be accurate and reasonably precise to give reliable gain estimates. If tests are poorly designed, then precision will be low. If the genetic sample in the tests is not large enough and representative of all the families, then genetic values will be biased no matter how precisely they are estimated.

For many species, long-term trials through rotation are not available and the correlation of juvenile and mature performance cannot be estimated. Gain estimates at juvenile ages are often inflated above what will be realized at rotation even if age-age correlations are high. If there is significant rank change in genotypic performance, then early gain estimates would be erroneous. For most loblolly pine trials, juvenile-mature correlations are generally high, and early selection appears to be effective (Li *et al.* 1996).

Fortunately genotype by environment (G x E) interactions among open-pollinated families of loblolly pine are minor and of little practical concern for growth traits (Li and McKeand 1989, McKeand *et al.* 1997). If G x E is important, then gain estimates based on an inadequate sample of test sites will not be reliable. Likewise if tests of realized gain are established on too few sites, then operational gains may not be similar to estimated gains.

Finally, the greatest absolute gains came from the combination of intensive silviculture and use of the best genotypes. Even when family rank changes are small, the greatest gains are most evident on the best sites (McKeand *et al.* 1997). If foresters are not judicious with the appropriate deployment of families on the appropriate sites, then little actual gain will be seen at the mill.

The simplifying assumptions made in these analyses about genetic improvement of volume at rotation may not be appropriate. For example, in *Pinus radiata* improvement programs in New Zealand, much more improvement in basal area compared to height has been observed (Carson 1996). With loblolly pine, there is evidence that height-age relationships vary not only for the asymptote but also for rate and shape (Knowe and Foster 1989), so equating early percentage height differences to percentage change in site index may be erroneous for some families. However, in a recent trial of large blocks of loblolly pine families, growth differences, especially height, were large among twelve different families (Svensson *et al.* 1997). Percentage differences in height at 4-5 years were maintained through 11 years and the genetic correlation of early height with volume at age 11 was very high.

There is an urgent need for more growth and yield trials with different families of loblolly pine. While many companies have these types of experiments installed with limited numbers of families, trials that are in the public domain are rare. As tree improvement programs become more advanced and families are more intensively selected, the likelihood of selecting genotypes with different growth and yield patterns will increase. This is particularly true with selection of full-sib families and clones for deployment where the level of genetic homogeneity within the genetic entries are much lower than with open-pollinated families. Only with knowledge about the growth and development of these families in block-plot trials will breeders be able to identify optimal selection criteria in progeny tests.

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# GENETIC DIVERSITY FOR CLONAL FOREST PLANTATIONS

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## ABSTRACT

Diversity is discussed in general with a focus on random-pair identity, a measure being developed to index deployed genetic diversity in clonal plantations. Manipulation of census number, relatedness, and deployment proportions is discussed in terms of adjusting deployed genetic diversity. Pedigree-based measures of genetic diversity do not wholly substitute for long-term field-based experiments that measure adapted and adaptive diversity.

## SOME RELATIVELY NEW CONSIDERATIONS FOR PLANTATION ESTABLISHMENT

In the last two decades, consideration of both genetic and ecosystem diversity has spread from a few early thinkers on these topics to become a part of routine plantation planning and evaluation. In general, foresters have been better than farmers in such diversity considerations. This is partly because plantation foresters have a much longer time frame of concern than do farmers planting annual crops, or raising relatively short-lived animals. Another contributing factor is that foresters generally can impose much less control on the plantation environment than can farmers on their farms. Thus, foresters were more likely to include genetic diversity in their plantation planning, in order to cope with greater environmental variation and uncertainty; many plantation foresters managed ecosystem diversity simply because complex ecosystems generally developed between planting and final harvest.

Although foresters managing plantations of a few taxa (such as *Cryptomeria* and hybrid poplars) have long routinely considered how best to deploy available clones, such deployment considerations have recently become important for many additional forest species. In some, family forestry is leading the way as seed-orchard and control-pollination technologies become better, and as the several considerable advantages of family forestry are appreciated (Carson 1986). Meanwhile, a better understanding of maturation (Hackett *et al.* 1992; Bonga and von Aderkas 1993; Greenwood 1995) has allowed deployment of clones with increasingly-known performance records. Continuing developments in tissue culture and somatic embryogenesis are likely to make this clonal option even more available (Ahuja and Libby 1993a).

### Diversity

Does diversity equate to sustainability? This is an attractive idea, but it may not invariably be true. However, the postulated dependence of sustainability on diversity is currently politically correct and it is therefore important. Furthermore, genetic diversity is clearly necessary for long-term breeding and it is an important component of shorter-term risk management. So how do we begin to characterize and deal with diversity? This is a formidable task.

At one level, we can consider the diversity of species on a given site. In some cases, this begins with identifying and then counting the species present (Kiester *et al.* 1996). This can then be refined by weighting the species by their frequency, or biomass, or some judgement as to their "importance".

At another level, some of these species are sufficiently important so that we characterize the amounts and patterns of their within-species diversity (Libby and Critchfield 1987). It is clear that such studies cannot be done for all species in every ecosystem, at least not in the near future. So, which ones DO we study?

Keystone species seem sufficiently important to warrant such detailed knowledge and, in many ecosystems, tree species qualify as keystone. In forest plantations, the planted trees and their subsequent management surely are dominant factors in the development of the plantation ecosystem, and thus the plantation trees surely deserve such attention. Other species in plantation ecosystems that have received, or probably soon will receive, such attention are: 1) threatened and endangered species, 2) various charismatic species, 3) and species judged to be biologically and/or economically important, for example, pests and beneficial symbionts.

With respect to the amounts and patterns of associated diversity that develop in plantation ecosystems, I recommend a recent proposal by Stelzer (1997). He has suggested the establishment of research plantations that are designed to contain various levels and patterns of genetic variation in the planted trees. These should then be monitored to evaluate the associated diversity that develops in these contrasting plantation ecosystems.

## Clonal deployment

While I will focus on clonal deployment, it seems likely that the principles discussed will apply with somewhat less force to deployment of full-sib families and some may even apply to deployment of open-pollinated families. As an introduction to this increasingly available clonal option, the following are among the several topics to consider when planning the deployment of clones.

*Interactive vs Broadly-adapted Clones* For awhile, it was popular to believe that many of the most productive clones would be interactive *prima donnas*, namely, a clone capable of outstanding performance under conditions favorable for it but likely to perform poorly where conditions are suboptimal for it. Thus, getting the right interactive clones to the right sites seemed likely to be the best strategy with respect to harvest productivity. However, this was easier said than done. A major problem was foresters' inability to adequately characterize sites in advance of planting, compounded by the rather fine-grained heterogeneity of many plantation sites. We also began to wonder if meaningful climate changes might occur at a time scale shorter than the period from planting to harvest. These factors have combined to shift the preference from potentially productive interactive clones to more conservative broadly-adapted clones.

One sometimes hears the argument that clones are more interactive than seedlings. Although it is hard to prove, this seems unlikely. Genotype-by-environment interactions can be clearly demonstrated in clones because they can be grown in more than one environment, while seedlings can be investigated only indirectly by the performance of their relatives on contrasting sites. Zobel (1993, and follow-up personal communication) has noted that about 50% of the second round of gain in the Aracruz eucalyptus program was probably achieved by replacing seedlings (many of which were probably interactive and by chance in the downside environments for their genotypes) with proven broadly-adapted clones.

*Breeds and Ideotypes* Here, as an example of our developing future, I describe some examples from radiata pine. During its 40+ years' existence, the New Zealand tree-improvement program (now co-op) has developed and characterized several different breeds. Seedlings, families, and clones of the GF (growth and form) breed are deployed to permissive sites, where they typically grow large volumes of wood with greatly improved form and good harvest index. The slower-growing LI (long interwhorl) breed features long bolts of clear wood in the valuable second log. However these LI trees often develop stem-form problems on the more fertile sites. The LI breed, therefore, is generally deployed to less-fertile sites. On sites where red-band needle-blight (caused by *Dothistromi pini*) is likely to be a problem, deploying the DR (*dothi*-resistant) breed reduces or even avoids the need for chemical countermeasures. The development of both higher-density and lower-density breeds reflects a diversity of uses for the wood, with their relative deployments reflecting judgements of likely future needs.

Within each of these breeds, cooperating companies and institutions clonally test promising families and search for outstanding clones. In some cases, these outstanding clones are among the very best of their respective breeds. But in other cases, the clonal ideotype departs from the general breed specifications. Some of these latter are correlation breakers, with good performance in one or more of the breed's weaknesses (for example, a long-interwhorl clone with robust good form on fertile sites). In others, the clone (or family) exhibits a desirable expression of a trait not normally included in the breed description (for example, unusually low energy requirements for mechanical pulping). One important result of this testing-and-selection strategy is great genetic diversity among the known families and clones available for deployment within the several New Zealand organizations and regions planting radiata pine.

*WIMPs vs MOMS* When there are several clones that are suitable for a given site, there are two main spatial deployment options. One is to deploy them in intimate mixtures (either random or sequenced) on many or all appropriate sites in the regional ownership (Widespread Intimately Mixed Plantations). The other is to deploy them in similar frequencies, but as Mosaics Of (relatively small) Monoclonal (or monofamily) Stands. There are substantial theoretical and demonstrated differences between these options (Ahuja and Libby 1993b), some of which I'll mention here.

As indicated in Harper's (1977) review and by the few subsequent reports of clonal experiments with poplars and other forest clones, even random WIMPs generally produce more biomass per unit area than do the same clones in MOMS. Such differences may be even greater if clones with known complementarities are specifically sequenced in WIMPs (Libby 1987a, b).

There are several advantages to MOMS compared to WIMPs. These include: 1) more effective management throughout the growing period, from nursery practices tailored to each clone, 2) through more precise applications (timing, amount, and formulation) of such things as fertilizers and pesticides, 3) the timing of silvicultural practices such as thinning, pruning, and harvest, 4) the ability to effectively salvage killed or damaged clones, and 5) to the more effective marketing and utilization of clones with non-trivial differences in wood properties (Zobel 1993).

A common perception of the likely progression of deployment options as clonal programs mature begins with random WIMPs, as many inadequately-tested clones become available. Such mixture allows the poorer clones (phenotypes) to be removed in early thinnings. As clonal test results accumulate, the next step is to use a smaller set of better-known clones deployed as MOMS. Then, when enough is known about the requirements and performances of some of these, one might deploy clones in specifically sequenced WIMPs (Libby 1987a,b). Those with different root-growth patterns would more efficiently use the site if neighbors, and particularly those with similar height-growth, silviculture, and end-uses could be grown and marketed together.

Now, in the context of this meeting, I suggest another possible consideration. If complementary clones deployed in either random or sequenced WIMPs indeed utilize the site more completely (perhaps the main reason they produce more biomass per unit area), there is less ecological space for associated plant species in the developing ecosystem. Thus, if total ecosystem diversity is an important consideration, MOMS may develop richer ecosystems than either form of a WIMP. (Although WIMPs perhaps would provide more local host-niches for pests, pathogens, and other organisms that live directly on the trees than would these same clones deployed im MOMS.) Stelzer's proposed experiments would provide some data.

## GENETIC DIVERSITY AT THE WITHIN-PROVENANCE OR WITHIN-PROGRAM LEVEL

While the pattern of genetic variation within an entire species is of academic and scientific interest (Libby and Critchfield 1987), in a regional program it is only the portion of the species' variation likely to be deployed that is of interest. This is a good place to point out that too much genetic diversity can be at least as bad as too little. As two examples, deploying a mixture including a high proportion of trees from inappropriate provenances, or increasing mutation rates by renewed atmospheric testing of nuclear weapons, would both substantially increase deployed genetic diversity. But both would decrease the adapted diversity in the deployed population.

The interest in genetic diversity appropriate to the tree species used in a regional plantation program generally focuses on three levels of concern: 1) the genetic diversity among the clones (or families) to be (or being) deployed, 2) that in the breeding population(s) from which the plantation trees are drawn, and 3) that in the genetic-conservation reserves and collections underpinning the breeding populations (Figure 1).

While there is some merit in counting clones or families or unrelated parents in each of these levels of concern, there is strong agreement that it is adapted and adaptive diversity that is important, both in natural populations and in plantations. Figure 2 is an attempt to show that considering the amount of adapted diversity among propagules deployed in a region's plantations may provide a very different perspective than that of simply counting genotypes (Figure 1). Such adapted and adaptive diversity is more likely to fit the Figure 2 conceptualization if it is a stated goal of the plantation program to maintain or enhance adaptedness, with implemented actions to achieve it.

While there may be relatively few parents in the breeding populations, and very few clones or families being deployed (Figure 1), their effective adaptive and adapted diversity can be as great or greater than that available in a typical large natural population. This is more likely to occur if the breeding population(s) are drawn from many natural stands within the general population considered appropriate for the region. A broad range of adaptive diversity is enhanced if multi line breeding is employed (Namkoong 1997), particularly if the multi lines are differentiated into contrasting breeds, as in the New Zealand radiata pine program.

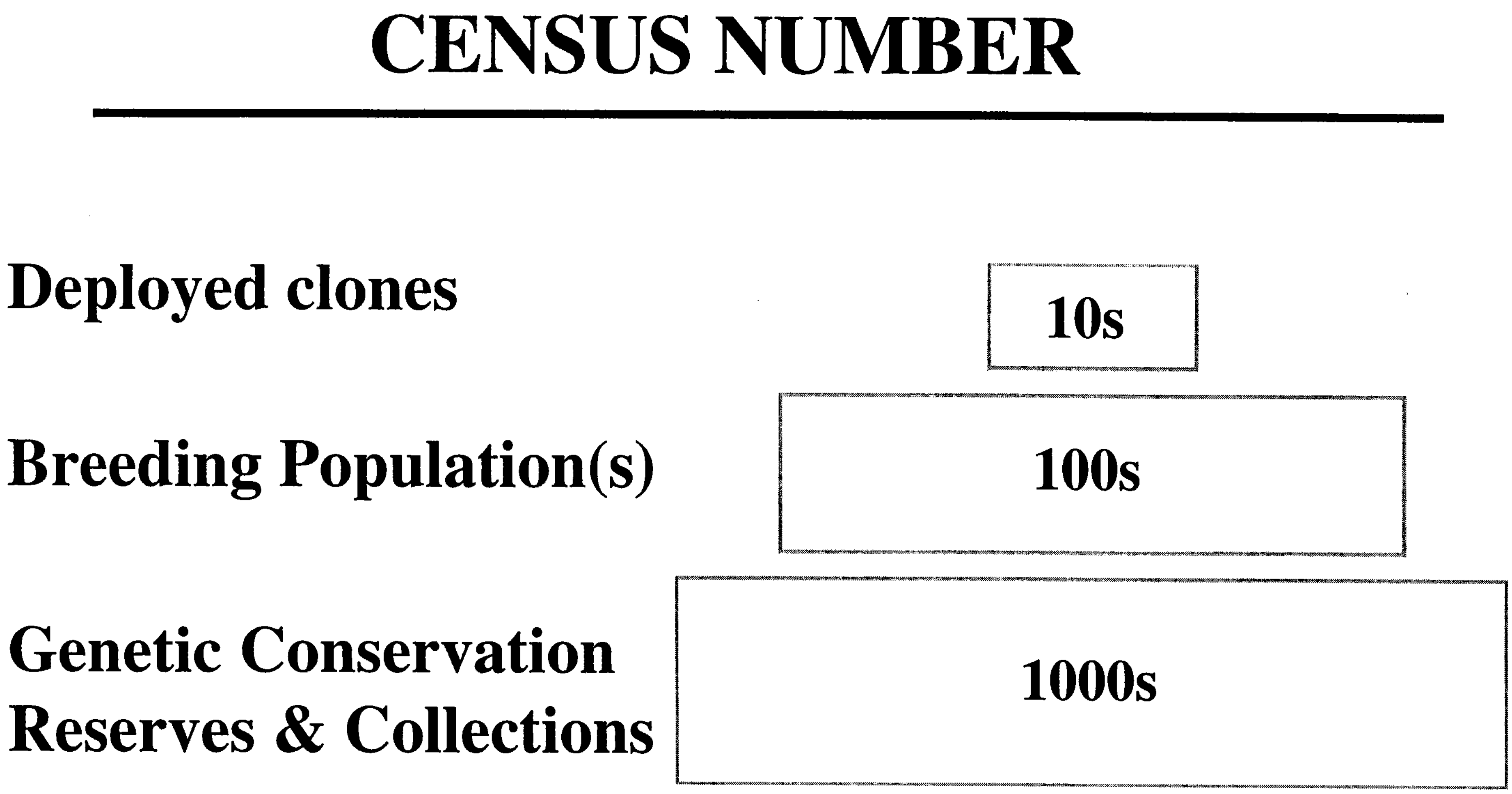
An important conclusion of the 1994 Southern Regional Information Exchange Group meeting was that biochemical and molecular markers do not index adaptive traits well, if at all (Libby *et al.* 1997). Deployment decisions based on biochemical markers alone, in many documented cases, would have been seriously in error (Libby and Critchfield 1987; discussion led by Millar and Skrøppa, as reported in Libby 1995). In short, adapted variation in plantations is best indexed by information based on extensive long-term field experiments (such as reciprocal common-garden experiments) and on extensive field experience, and it is best accomplished by the application of well-thought-out deployment principles. One of the most important of these is to deploy genetic diversity in anticipation of unknown physical and biotic problems, rather than to breed too closely for the current known problems.

## MEASURES OF GENETIC DIVERSITY

Here I present three ways to measure and monitor genetic diversity. All three rely on estimating some number characterizing the population that is equal to "the size of an 'equivalent' population composed of unrelated, non-inbred individuals" (definition by T.J. Mullin offered during this meeting).

### Effective Number (*Ne*)

Effective number as variously defined and calculated is a well-established concept in the literature and in practice. One can trace its development from the early work of S. Wright in the 1930s on an "idealized population" (Wright 1938), through its exploration and formulation by J. Crow, M. Kimura and A. Robertson in the 1960s (Robertson 1961; Kimura and Crow 1963; Crow and Kimura 1970) to a wider understanding (and sometimes misunderstanding) and application since then (Falconer 1960, 1981, 1989). Briefly, it substitutes an "effective number" for the "census number" of individuals in a population by considering their degree of relatedness (and/or inbreeding) and their relative numbers of offspring.



# CENSUS NUMBER

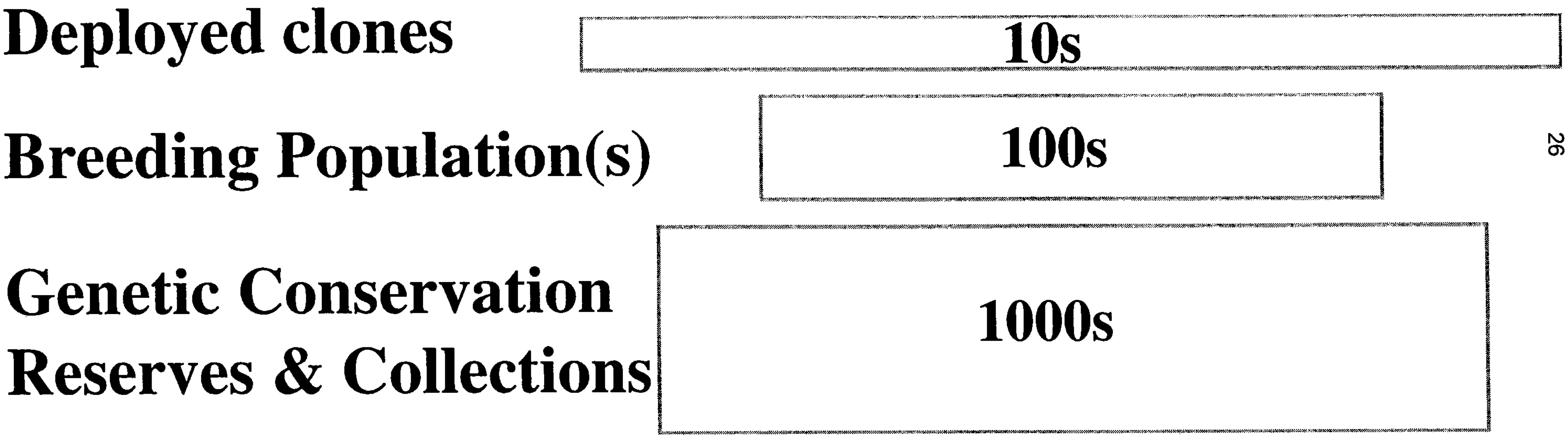
**Deployed clones** — **10s**

**Breeding Population(s)** — **100s**

**Genetic Conservation Reserves & Collections** — **1000s**

Figure 1. A conceptualization of common opinions as to the numbers of unrelated genotypes that appropriately should be used or maintained. These numbers are in the 10s in the deployed set (perhaps as low as 7), in the 100s in the breeding populations(s), and in the 1,000s or even 10,000s in the genetic-conservation reserves and collections.

# ADAPTIVE DIVERSITY



**Deployed clones** 10s

**Breeding Population(s)** 100s

**Genetic Conservation Reserves & Collections** 1000s

Figure 2. A conceptualization of adapted and/or adaptive variation, shown in two dimensions but representing an n-space landscape of components of adaptedness. In general, the goal is to deploy adapted genetic diversity in plantations while maintaining adaptive genetic diversity in the breeding and genetic-conservation populations.

### Status Number (*Ns*)

Status number has been developed in the 1990s (Lindgren *et al.* 1997). It is meant to be a "snapshot in time" and has been focused on the breeding population, giving its status with respect to genetic diversity at that moment. It takes into account the coancestry of members of the breeding population, allows all possible crosses among them including selfs, and divides by 2 to preclude the possibility that status number might exceed census number.

### Random-pair Identity (*Nri*)

While working with Fletcher Challenge Forests in 1994, I developed an index number based on random-pair identity to deal with clonal deployment. It takes the approach of using the relatedness of the gametes that produced the clones (A. Robertson similarly used gametes).

### Safe and Comfortable Numbers

I won't present details of formulas or applications for any of these measures of genetic diversity here. Rather, I will discuss the factors that contribute to them, with a focus on deployed clonal diversity. But first, I have a short digression on "safe" and "comfortable" numbers.

Figure 1 shows deployed numbers "in the 10s", a pretty broad range. While a case can be made for a "safe" deployed number as low as 7 unrelated clones (Libby 1982), most experienced breeders and population geneticists cluster answers to the question "What is a comfortable number?", in the neighborhood of 20. This is not a sharp boundary, indicating that 19 is inadequate and 21 is excessive. Rather, it is a neighborhood in which, as numbers increase through it, the force of selection becomes more important than drift in influencing genetic change in a population. In other words, at *Ne* or *Nri* of 20 or above, you're not likely to lose adapted variation in the population, nor by chance fail to change the traits you are selecting for in the desired direction.

The "comfort range" for status number is likely to be relatively lower than for *Ne* or *Nri*. This appears to be due to the joint effects of including selfs in its calculation (when in fact selfs may not be used in a breeding program, and generally would not be deployed even if used for breeding), and of dividing by 2. Although *Ns* is meant to reflect the current status of a population, it can be and has been used to evaluate the future status in each of several generations of various breeding designs (Lindgren *et al.* 1996, 1997). In most such evaluations, the calculated value of *Ns* drops rapidly in very few generations. This could create a political problem if *Ns* is used by opponents of intensive plantation programs, particularly if they do not (or choose not to) understand some of the reasons for the sharp *Ns* drop in tree-breeding programs being evaluated

## FACTORS AFFECTING DEPLOYED GENETIC DIVERSITY

In calculating *Nri*, or when using similar tools for measuring and monitoring deployed genetic diversity, there are three component variables that should be considered: 1) census number, 2) relatedness, and 3) proportional deployment.

### Census Number and Relatedness

Census number is straightforward; one counts the clones (or families) being deployed. Relatedness may be defined as: *the proportion of alleles shared by recent common descent.* This is more complicated than census number, but is nevertheless fairly clear and not too hard to calculate. I'll return later to the problems that may be posed by *recent* in the definition.

Before calculating *Nri*, one may first calculate a so-called "equivalent number", namely the census number of clones modified by the proportion of their genomes not related by recent common descent. This then becomes a reference number of the equivalent number of clones, if non-inbred and unrelated, that would contain the same amount of genetic variability as is contained in the clones being deployed. Here, the trick is to calculate the genomic proportion of different (non-shared) genetic variability that each deployed clone (or family) brings to the deployed set. This is done by determining the proportion of its genome shared by one or more other clones in the deployed set, and subtracting that from 1.00 to weight its addition to genetic diversity in the deployed set. The census number is thereby adjusted to an "equivalent number of unrelated clones" by the proportion of their genes NOT shared by recent common descent.

The approach we use to calculate *Nri* is similar to that for status number and leads to a similar relationship, namely that the effective number is a function of the inverse of the average coancestry among all deployed ramets in the set of deployed clones. Calculation of *Nri* takes into account the deployment frequencies of each clone. Furthermore, rather than dividing by 2, it multiplies by two, and thus does not force *Nri* below *N*, the census number. It is a nice concept that plantation foresters can improve on Mother Nature with respect to deployed genetic diversity and, as indicated by *Nri*, sometimes exceeding *N*, I think we can.

One first determines whether each clone is inbred or not. (Most programs have a policy to NOT deploy inbred clones, making things simpler at this step.) Then, using a handy computer protocol, compare all individuals from each deployed clone to all other individuals in the deployed set with respect to the expected parts of their genomes shared by recent common descent.

The critical principle in calculating *Nri* for deployment planning is: *Two planted trees share heritable risks because they have the same alleles.* If they do not share alleles by recent common descent, then they are no more at shared risk than any two trees randomly drawn from the reference population. But if they have recent common descent, then some of their alleles are shared at frequencies dependent on the degree of relatedness, rather than on the frequencies of those alleles in the reference population.

### Proportional Deployment

Note that the third variable, proportional distribution of clones, is already accounted for by comparing all possible random pairs (the computer protocol actually does this by using deployed frequencies of each clone). Thus, members of commonly-deployed clones (or families) will be randomly paired with members of their same clones (or families) more often than will members of clones (or families) deployed in low frequencies. If the clones (or families) are all non-inbred, and unrelated, the genetic diversity of that particular deployed set will be maximized (at twice the census number) if all clones (or families) are deployed in exactly equal numbers (proportions). The calculated *Nri* should equal the census number if clonal distribution conforms to a Poisson distribution. That underlying concept of idealized deployment is the reference condition in which many breeders and population geneticists are comfortable with numbers in the vicinity of 20. That does not mean that such a distribution is particularly desirable. It does mean that, for a given "equivalent number", the deployed clones will have more, or less, "effective" deployed genetic variation than indexed by that "equivalent number" of clones deployed as a Poisson, depending on which direction actual clonal deployment deviates from a Poisson.

To the degree that the calculated *Nri* is greater or less than the calculated "equivalent number", it tells you something about how much your clonal deployment allocation is more or less effective (with respect to deployed genetic diversity) than a Poisson-shaped deployment allocation would be. The following is meant to give you some back-of-the-neck sense of how your deployment is influencing the effective genetic diversity of your deployed clones (or families). Please recall that, in the concepts developed by Wright, Crow and Kimura, and others, census number equals *Ne* when the deployment distribution of families (if non-inbred and unrelated) conforms to a Poisson distribution and it is about half of *Ne* when all families (if non-inbred and unrelated) are deployed in equal proportions.

Since my work with Fletcher Challenge Forests has elements of confidentiality, I'm unable to provide actual data. Table 1 has fabricated data, which however are similar to data from several clonal programs I've seen. It shows how a census number of 50 clones might be distributed early in a clonal program, then how those same 50 clones might be distributed later and includes a calculated distribution of those 50 clones that fits a Poisson. In all three cases, the total number of plants out the nursery gate and into plantations that year is 5 million.

Figures 3 and 4 plot that same data, in Figure 3 by classes based on units of 10,000 ramets, in Figure 4 cumulatively. (Note that, with these large numbers, the Poisson distribution is nearly normal.) By such plots of your own data, you can get an easy, quick and fairly accurate feel for whether and how much the census number of your deployed clones (adjusted for relatedness and for inbreeding if you allow inbreds to be deployed) differs from the effective number that indexes deployed genetic diversity.

In the fabricated cases plotted, early deployment is much flatter than the Poisson in Figure 3 and it begins above and finishes below it in Figure 4. This indicates that the genetic diversity in your early deployment proportions is substantially less than one would expect based only on your census number adjusted for relatedness. Such an early proportional distribution is due to such things as greatly different success in propagating the clones, with some clones achieving abundant production much earlier than others. A calculated *Nri* for such "early" deployment would be smaller than the calculated "equivalent number". This lets you know you don't have as much genetic diversity in your plantations as you might have thought, based on the genetic diversity available in your deployed clones.

Plotted distributions of the later deployment are squeezed inside the Poisson except near its peak in Figure 3 and begin below and finish above it in Figure 4. This indicates that your deployed diversity is actually greater than what one would expect based on that same relatedness-adjusted census number. A calculated *Nri* for such "later" deployment would be larger than the calculated "equivalent number". This not only quantifies an index of your deployed genetic diversity, but it also tells you that your deployment allocation is better than Wright's idealized approximation to Mother Nature at getting genetic diversity into your forest.

Such a later distribution picture characterizes a clonal program in a steady state. Details of propagation technique are pretty well ironed out for the deployed set, and clonal performances are well known. The approximately two-fold differences between the most popular and least popular clones in the deployed set reflect differences in their performance values, in the available appropriate sites for each clone that year, and in anticipated market demand for each ideotype. In reality, there might be a few clones in any "dynamic steady state" year deployed in much lower frequencies than the rest, as new clones are being scaled up and older poorer-performing clones are being phased out. These can be ignored in your diversity evaluation, as low-frequency clones add little to deployed diversity.

## Manipulating Your Deployment Set

The nice thing about understanding the three variables, census number, relatedness, and proportional distribution, is that it allows you to sensitively adjust your program. Suppose, for example, that either legal regulations or organizational policy requires you to have an *Nri* of 22 (comfortable and a bit conservative). This year's monitoring of your nursery-gate deployment showed an *Nri* of 19. You can increase this next year by increasing your census number (add a few clones from the most promising under current test), or by substituting clones (if you are deploying clones from full-sib or half-sib families, replace the poorer in some families with unrelated clones), or by making deployment proportions more similar.

Alternatively, you might find that this year's *Nri* is 26. You could drop a few of your least valuable or more-difficult-to-propagate clones, thus increasing gain and/or lowering costs. Or, you could substitute a few additional clones from excellent families that already have clones in your deployment set, thus increasing gain without unacceptably increasing risk. Or, you could increase the deployment proportions of your most valuable clones at the expense of the poorer clones in your deployment set, which would increase overall gain and value.

Such adjustments can be iteratively entered into your computer's *Nri* calculation table until your *Nri* for the next deployment allocation is comfortably near 22.

Table 1. Comparison of two distributions of 50 clones to an expectation based on a Poisson distribution based on units on 10 000 ramets, mean =10 (100 000)

| Classes | Number of clones | | | Number of Ramets | | | Cumulative Number of Clones | | |
|---|---|---|---|---|---|---|---|---|---|
| | Poisson | Early | Later | Poisson | Early | Later | Poisson | Early | Later |
| <0.5 | 0.00 | 13 | 0 | 5 | 30,000 | 0 | 0.00 | 13.00 | 0.00 |
| 1 | 0.02 | 1 | 0 | 217 | 10,000 | 0 | 0.02 | 14.00 | 0.00 |
| 2 | 0.12 | 2 | 0 | 2,319 | 40,000 | 0 | 0.14 | 16.00 | 0.00 |
| 3 | 0.38 | 0 | 0 | 11,304 | 0 | 0 | 0.52 | 16.00 | 0.00 |
| 4 | 0.94 | 2 | 0 | 37,679 | 80,000 | 0 | 1.46 | 18.00 | 0.00 |
| 5 | 1.89 | 5 | 0 | 94,560 | 250,000 | 0 | 3.35 | 23.00 | 0.00 |
| 6 | 3.15 | 1 | 1 | 189,121 | 60,000 | 60,000 | 6.50 | 24.00 | 1.00 |
| 7 | 4.51 | 0 | 3 | 315,491 | 0 | 210,000 | 11.01 | 24.00 | 4.00 |
| 8 | 5.63 | 3 | 6 | 450,411 | 240,000 | 480,000 | 16.64 | 27.00 | 10.00 |
| 9 | 6.25 | 1 | 8 | 562,797 | 90,000 | 720,000 | 22.89 | 28.00 | 18.00 |
| 10 | 6.25 | 1 | 14 | 625,330 | 100,000 | 1,400,000 | 29.14 | 29.00 | 32.00 |
| 11 | 5.69 | 0 | 9 | 625,692 | 0 | 990,000 | 34.83 | 29.00 | 41.00 |
| 12 | 4.74 | 2 | 5 | 568,666 | 240,000 | 600,000 | 39.57 | 31.00 | 46.00 |
| 13 | 3.64 | 4 | 2 | 473,816 | 520,000 | 260,000 | 43.22 | 35.00 | 48.00 |
| 14 | 2.60 | 1 | 2 | 364,184 | 140,000 | 280,000 | 45.82 | 36.00 | 50.00 |
| 15 | 1.73 | 2 | 0 | 259,769 | 300,000 | 0 | 47.55 | 38.00 | 50.00 |
| 16 | 1.09 | 0 | 0 | 173,904 | 0 | 0 | 48.64 | 38.00 | 50.00 |
| 17 | 0.64 | 0 | 0 | 108,400 | 0 | 0 | 49.27 | 38.00 | 50.00 |
| 18 | 0.36 | 1 | 0 | 63,910 | 180,000 | 0 | 49.63 | 39.00 | 50.00 |
| 19 | 0.19 | 1 | 0 | 35,795 | 190,000 | 0 | 49.82 | 40.00 | 50.00 |
| 20 | 0.09 | 0 | 0 | 18,840 | 0 | 0 | 49.91 | 40.00 | 50.00 |
| 21 | 0.05 | 0 | 0 | 9,891 | 0 | 0 | 49.96 | 40.00 | 50.00 |
| >21.5 | 0.04 | 10 | 0 | 7,900 | 2,530,000 | 0 | 50.00 | 50.00 | 50.00 |
| Sum | 50.00 | 50 | 50 | 5,000,000 | 5,000,000 | 5,000,000 | | | |

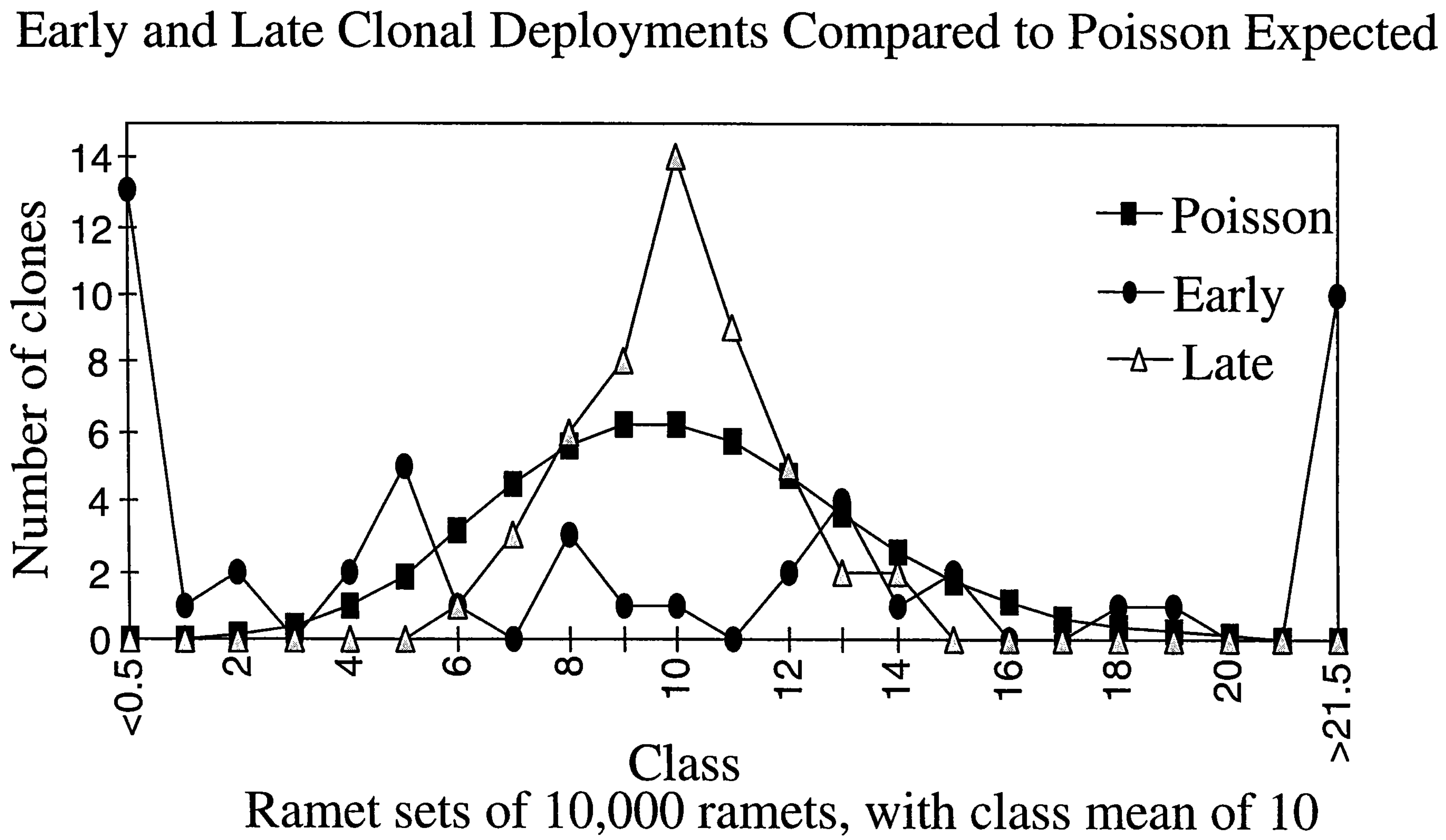


Figure 3. The distribution of 50 clones (data in Table 1) early in a clonal program, the same clones deployed later as the program reaches a steady state, and those same 50 clones as they might be deployed to fit a Poisson distribution. Deployment numbers per clone are presented by units of 10,000 ramets. In the early deployment, 13 clones were deployed in numbers under 5,000 ramets per clone, only one clone was in the 95,000-to-105,000 ramets class, and 10 clones were deployed in numbers exceeding 215,000 ramets per clone. In the later period, none of these clones were deployed in numbers fewer that 55,000 ramets per clone, nor in numbers greater than 145,000 ramets per clone, and 14 were deployed at numbers of ramets per clone between 95,000 and 105,000.

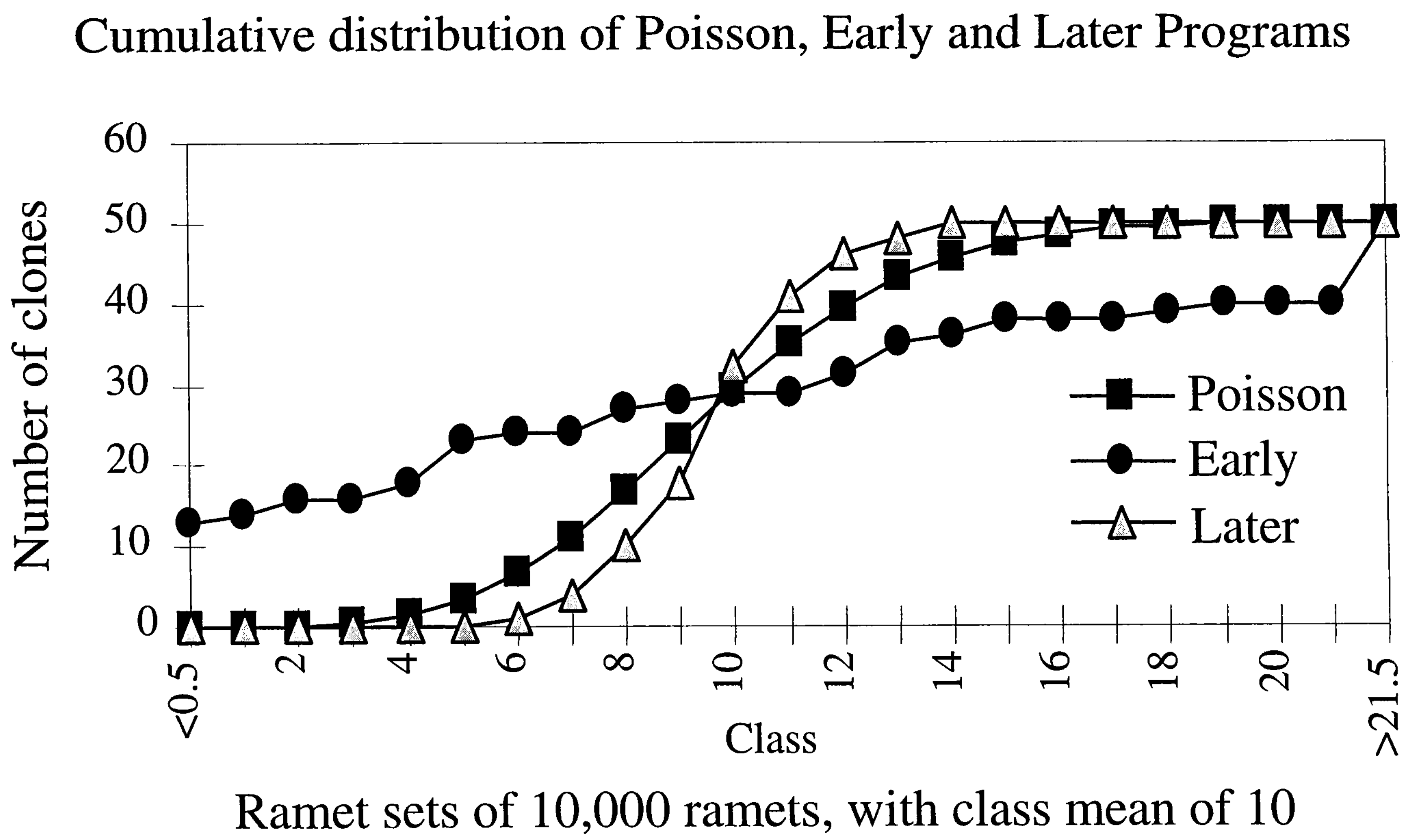


Figure 4. The Table 1 and Figure 3 data plotted by class mid-point in cumulative distributions.

## RISKS

Risks tend to fall into three classes.

### Physical Risks

Although varying substantially from place to place and from year to year, physical risks such as drought, flooding, high or low temperature, wind, fire, and nutrient imbalances tend to be static with respect to the adapted diversity among the deployed clones.

### Biotic Risks

In contrast to physical risks, some elements of biotic risks can be dynamic. For example, short-lived pests and pathogens can themselves adapt to be able to successfully attack widely-deployed previously resistant clones, perhaps forcing retirement of clones whose defenses have been solved.

Given the long-term nature of the enterprise and the great range of physical and biotic events that can harm various segments of the deployed set, keeping a broadly-based and diverse set of clones in the plantations is a good, although not impregnable, strategy. With wisdom and a little luck, most of the plantations will biologically survive the great majority of realized risks and the plantation enterprise is thus more likely to survive economically as well.

### Market Risks

Market risks involve inaccurate future-guessing. The "portfolio approach" seems a good response to future market uncertainty ( R. D. Burdon, pers. comms.,1993-97, New Zealand Forest Research Institute, Rotorua). This is analogous to an investment strategy in which the portfolio includes different kinds of stocks and bonds. For a plantation strategy guarding against market risk, it involves deploying some contrasting ideotypes, for example some clones with long-interwhorls and others with short interwhorls, some with high-density and some with low-density wood, etc. The genetic diversity maintained by such a market-risk strategy seems likely to be compatible with the diversity appropriate for coping with physical and biotic risks.

## SOME PROBLEMS IN ASSESSING DEPLOYED DIVERSITY

### Pre-pedigree Relatedness

Here, we return to what is implied by "*recent common descent*". In most tree-improvement programs, pedigree records currently go back only one or two generations. Thus, there is pre-pedigree uncertainty about the diversity and relatedness of trees selected for breeding. This is particularly a problem in programs with exotic trees in which some or all of the selections are made from previously-established land races.

For many land races, there is little reliable documentation of the number of imported trees or open-pollinated families that founded the land race, as well as of the spatial distribution of the parents of those founding families within native stands, among stands within regional populations, and among regional populations. A diversity-index value based only on recent known pedigrees does not account for whether the breeding population was selected from a broadly-founded land race or a narrowly-founded land race. Yet, there should be more genetic variability among trees derived from the broadly-founded land race.

Furthermore, it is possible, even likely, that some of the parents selected from such land race populations have "pretty recent" common ancestors. The likelihood of this is influenced by the number of families that founded the land race populations. If the trees chosen for the breeding population are selected on similar criteria (for example, growth rate, stem form, branch form, and tree health), the probability that they are related is increased. To the degree that pre-pedigreed trees are related but assumed to be unrelated, the calculated diversity indexes will overestimate the "effective numbers" that index genetic diversities in the deployed set, breeding population, and/or genetic-conservation reserve.

For breeding populations drawn from native stands, it has been common (and excellent) practice to choose no more than one tree from any given stand or neighborhood. If pedigree is then maintained, estimates of pedigree-based diversity indexes will be essentially free of the problem of possible recent but unknown common ancestry. Furthermore, such multi-stand founding of the breeding population should result in a greater amount of genetic diversity than when the parents come from a single stand, even though a pedigree-based "effective number" of some sort might indicate that they are the same.

### Organelle Genes

Diversity indexes such as *Ne*, *Ns*, and *Nri* are based on nuclear genes following Mendelian rules of inheritance. However, organelle genes are inherited largely or exclusively from only one parent. How important is diversity of alleles of chloroplast and mitochondrial genes? If deploying two clones from a good full-sib family, should we prefer them to be from reciprocal crosses?

### Pedigree

Open-pollinated and polycross families have been widely used in various tree-improvement programs. They often seem cost-effective. However, they are a major pain when it comes to tracking genetic diversity. If measuring or monitoring deployed diversity is (or is likely to be) important in your program, I strongly recommend high-fidelity controlled crosses in your breeding lines and to produce your deployed families and clones. By high-fidelity, I mean using techniques that allow little or no pollen contamination, with fingerprinting backup, so that accurate pedigrees can be maintained.

Fingerprinting is an important and valuable role for molecular biology. As these molecular fingerprinting techniques improve, they may even be able to sort out some of the relationships in our breeding and deployed populations that trace back to their pre-pedigree or incomplete-pedigree histories.

### Adapted and Adaptive Diversity

Please recall that it is adapted diversity in the deployed set and adaptive diversity in the breeding lines and genetic-conservation reserves that are important. Number-based indexes such as *Ne*, *Ns* and *Nri* merely provide a tool to aid in wise development and implementation of genetic-conservation, breeding and deployment strategies. They do not substitute for the knowledge and skills of field-experienced breeders and plantation foresters in monitoring the health and general performance of the families and clones being deployed and under test.

## THE GOAL OF ALL THIS

There are of course several goals when estimating and monitoring genetic diversity, including those of satisfying academic and scientific curiosity and proactively blunting likely criticism. I recommend the following, however, as primary goals that are highly practical and highly ethical. To maintain and deploy amounts and structures of genetic diversity such that: 1) our clonal plantations will have a lower risk of unacceptable loss than did our seedling plantations, and 2) our clonal plantations will have a lower risk of unacceptable loss than do natural stands.

These are currently politically-incorrect statements, as it is common *belief* that plantations and particularly clonal plantations have greater risk than do natural stands. Nevertheless, if we give intelligent attention and sufficient institutional support to these goals, I think that we can reliably meet them.

## ACKNOWLEDGMENTS

I acknowledge with thanks the organizers of the 1997 Canadian Tree Improvement Association meeting for inviting me to present these ideas; Fletcher Challenge Forests for their support and interest in evaluating the genetic diversity in their clonal program; and colleagues, particularly R. Burdon, L. Gea, J. King, D. Lindgren, and T. Mullin, for fruitful discussions on these topics.

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# BREEDING FOR RESISTANCE TO FOREST PESTS: TOWARDS THE DEVELOPMENT OF LOW RISK STRATEGIES

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## INTRODUCTION

With a theme of a conference such as "Tree Improvement: Its Contribution to Sustainable Development," there can be little doubt that genetic strategies to combat forest pests must, at some point, be a critical part of the discussion. Throughout the history of civilization, pests have lived with our crops and it continues to be a major task to keep their share of the crop down to an acceptable level. Forests and forest tree plantations are not much different in this regard, but they do present special challenges to remain "sustainable."

While I am grateful to the organizers of this conference for asking me to address some of the issues in pest resistance breeding in tree improvement, this is an intimidating task. Several IUFRO working parties exist and meet annually to deal with this topic, and at least three major conferences have been held, one in 1964 (Gerhold *et al.* 1966), one in 1969 (Bingham *et al.* 1972), and the other in 1980 (Heybroek *et al.* 1982). It seems the time is appropriate for another conference but it may be worthwhile, in the mean time, to touch upon a few issues that have developed since the last one in 1980. The area of molecular genetics has grown immensely, as has some developments in agriculture and general theory, but it is surprising that many of the main ideas used today still originate from those three earlier meetings.

## OBJECTIVES

The objectives of this paper are to attempt to review and present some current thoughts on:

1) the **types of resistance mechanisms** we expect are working in forest trees,
2) how breeders of forest trees should consider these **mechanisms in breeding** (both classical recurrent selection schemes and the use of molecular techniques) and their utility in breeding and production populations, and
3) considerations for **deployment strategies of improved pest resistance material.**

There is, of course, a danger in attempting to provide an overview and a synthesis of these three topics. There is a large diversity of host-pathogen interactions and there is no general answer to any of the questions; each must be studied individually in considerable depth in order to have any real value (Johnson 1992). Molecular genetic studies of many well known gene-for-gene mechanisms have shown some remarkable findings, and the details of the biochemistry and physiology of the resistance are becoming better understood (e.g., Mendgen *et al.* 1995; Staskawicz *et al.* 1995; de Wit 1996). However, it may be useful to summarize a few "across-organism concepts" that are present at this point in time as they relate to pest resistance breeding for forest trees.

## TYPES OF RESISTANCE MECHANISMS

The classic reference on the types of resistance exists in Vanderplank (1963). In this reference he introduced the two most famous terms; vertical resistance (VR) and horizontal resistance (HR). Since then, several authors have tried to expand on the actual meaning of these two terms but the basic assumptions remain similar (Nelson 1982).

VR infers a "gene-for-gene" mechanism, that is, products of a single gene in the host interact with the products of a virulence (or avirulent) gene in the pest. It is well known that in the 1970s the large scale destruction of maize in the U.S. corn belt by southern leaf blight was due to a susceptible cytoplasmic male sterility gene. While this was not a classic single gene susceptibility of a nuclear gene, it is a good example of the failure of mono-, single, or major genes. Many other examples are also present in the literature, but these type of losses due to transient VR systems are now what we refer to as the "worst-case scenario" (WCS). This term is important for later points I will make.

Recently, analysis of the vertical resistance system has been carried out by Frank (1994, 1996) in terms of a "matching allele" or the more general "gene-for-gene" model. The former is the true allele matching system between parasite and host, and the latter is the more common expectation that some parasite alleles cannot successfully attack with a corresponding resistant allele in the host, but others cannot be matched by any host allele. Parker (1996) reviewed Frank's work and suggested that most of the plant breeding literature shows that the gene-for-gene system is prevalent. Although it may exist, there is little proof the matching-alleles system is common. The implications for these two systems, for the sake of our discussion, is that on an evolutionary scale it may have large effects on potential virulence in the parasite population (Frank 1991, 1996). Its evolutionary importance is not trivial as it is being invoked as one of the key factors in explaining the evolution of sex (Clay and Kover 1996; Lively 1996), as well as resurrecting interest in the "Red Queen" hypothesis (Rosenzweig 1996).

Mutation of avirulence to virulence genes can occur by several mechanisms which then removes the plant's ability to recognize the pathogen, so the plant requires a mutation to a new function and not a mutation to a loss of function (Hammond-Kosack and Jones 1995). These models suggest that extreme competition to overcome current resistance exists at several levels, and with the matching-allele system largely being rare, pests have many alleles segregating which are currently virulent to resistant genes.

There is very little reason to believe that gene-for-gene resistances are not common in trees. The realization that they will be difficult to find, and that they have not, for some time now, been attractive resistances for crop breeders (Russell 1978), sends an important message to tree breeders. However, we should not ignore them if they show themselves as elegantly as they have in the sugar pine - blister rust pathosystem (Kinloch *et al.* 1970). In this classic but rare form - major gene resistance (MGR) - they could still be very useful and likely used more effectively than they have been in past crops (Person *et al.* 1982). It is likely that most of the major genes we will be able to detect will be non-race specific (NR), as described by Simmonds (1991), as single-genotype isolates, screening of the disease or insect will be rarely done. NR is assumed to be major-gene resistance that provides resistance to several, if not all, virulent genes segregating in the pest population.

There is a plethora of other labels for HR which are expected to be based on more than one-gene (e.g., stable, oligogenic, polygenic, durable, weak, minor, complex, etc.), but still very little is known about the underlying genetics of HR. The only way to truly understand how individual genes involved in HR contribute to resistance, would be to create isogenic lines where we can isolate single genes, and then look for specific expression in different genetic backgrounds. When this type of work has been done, it has shown that resistance is expressed differently in different genetic backgrounds and defeated genes can still resist (Nelson 1982). The economics, the outcrossing nature of most forest trees, and the generation length will likely make this impossible to do and we will simply have to accept the fact that we will be working in the "genetic dark" for many of our pest resistance problems. Fortunately, this approach, although being less than desirable, has been successful in other breeding programs, such as for Hessian fly resistance (Painter 1968). However, biotype evolution has continued in this pest therefore development of resistance is continually needed (Ratcliffe *et al.* 1996).

A more recent synthesis of the genetics of HR has been provided by Simmonds (1991), which suggests that this resistance is pathotype non-specific, is "durable" over time, has several components, applies to all crop-pathogen systems, and depends upon genetic analysis for critical demonstration. Person *et al.* (1982) added another important criteria not mentioned by Simmonds (1991); that of the relative ranking of resistance remains constant. This criteria is important because a given genotype expresses resistance at the same relative level across environments or years and is therefore the most practical kind of durability.

Quantitative genetic studies in forestry that examine pest resistance generally report a normal distribution of breeding values. This is likely due to the many pest virulence interactions with resistances, and our rather arbitrary scoring of defense response is simply not able to provide statistical clarity of the underlying genetics. A further mistake is then made by claiming that the gene action of this resistance is largely additive because we detect large and significant family components of variance. Recall that at the CTIA conference in Victoria, B.C. in 1995, Barker (1995)(who referenced the early work of Lush (1945)) pointed out as an example that for a two locus epistasis (where two alleles at a locus were at gene frequencies of 0.5), genetic variances would be partitioned as 4/7 additive, 2/7 dominance and 1/7 epistatic. The discussions of whether resistance is additive or non-additive, at least from statistical analyses, is no longer providing much guidance. The point here is as Nelson (1982) summarized; expression of all resistance can be described as a continuum and in the end there are simply genes that confer pest resistance.

For tree breeders two issues appear evident: 1) it will be rare that we will ever have any real clarity with any resistances we work with, at least in our generation, but we will get to read about them in tomatoes, wheat and Hessian flies (with a few exceptions, such as the MGR in white pine to blister rust), and 2) nevertheless we should try to categorize various resistance traits as to some general physiological basis and develop hierarchical "lines of defense" among various putative resistances, and to be on the safe side, assume that they are controlled by very few genes (and perhaps even assume monogenic inheritance).

Moreover, many of the resistances we claim to be horizontal may not be resistances *per se* as much as evolutionary responses to wounding events. These types of "passive" resistance mechanisms are not directed co-evolved resistances to biochemical signals from a pest (referred to as "active"). This will be discussed further in the example of weevil resistance in spruce, but this leads me to believe that a good number of resistance options not previously considered or even available to breeders of crop species are available to tree breeders.

## THE MECHANISMS IN BREEDING

With that light review of resistance mechanisms behind us, I would like to put forward three genetic issues that I believe now underlie the basis of developing and deploying resistant material in forestry.

### Is Genetic Uniformity The Problem?

Past "mistakes" made in agriculture immediately raise the issue of large scale loss to pests, which is usually blamed directly on the reduction of genetic diversity. Averaged over many years, however, the losses are not large but unfortunately spectacular, costly, and disruptive to crop markets when they occur. In forestry, spectacular losses can also occur (e.g., dutch elm disease, chestnut blight, white pine blister rust), but losses of plantation forests would not instill great confidence in the public's perception of tree breeding. However, minor incipient losses may be tolerable and are a fact of simple forest stand development.

Plant breeding objectives, particularly in the early years, concentrated on both yield and uniformity of the crop. High yields were only possible by using a handful of the best producing genotypes, so genetic diversity was also low. This approach with maize led to the development of inbreeding systems followed by hybrid matings for commercial seed productions. However, this system was not solely developed because of some unique genetic system of maize (Duvick 1996); seed growers had exclusive control of the production of the hybrid seed. It is important to note that diversity can be lowered in the selection process without having extremely high uniformity, as was desired in maize.

The basis for this argument is obvious in a very simple one locus, two allele system; let's say **A** and **a**, where the gene frequency of **A=a**. In a hybrid situation all genotypes are **A|a**, and if **A** is dominant susceptible, all plants die. If **a** is recessive susceptible, then all plants live and the breeder was lucky. In the other approach, where genotypic frequencies are allowed to vary (with recombination working in the production population [e.g., seed orchards]), the genotypic frequencies in this example follow Hardy-Weinberg ratios and we have either ¾ or ¼ of the plantation dying. Economics aside from these two loss scenarios, the gene frequencies are the same, yet we have a fair portion of the crop surviving in both situations.

This idea is further supported by disease problems in animals, as they certainly have not received the same level of scientific, public, and media hype that is commonly associated with losses in crops. Disease problems in domestic animals are certainly real, and one only has to look at intense inbreeding examples, such as with domestic dogs, to see the types of problems very narrow breeds can have. Inbreeding will occur in any improvement system and can be shown to be beneficial to purging some types of genetic load (Fu *et al.*, 1997). Nevertheless, inbreeding depression always remains a problem, because semi-deleterious alleles are difficult to purge and exist across many loci. But this is not directly caused by a reduction in genetic diversity or extreme genotypic uniformity.

It is likely that basic biological and physiological differences between host-pest interactions in animals and plants have led to the differences between plant and animal pest resistance biology (for example, plants lack a circulatory system and antibodies and individual plant cells must defend themselves). However, more recent evidence suggests that some necrotic resistance reactions can trigger a "systematic acquired resistance" that can be expressed throughout the plant (Ecker 1995; Hunt and Ryals 1996). Even more important may be the fact that gene frequencies are the managed unit in animal breeding, rather than genotypic frequencies, which tend to be more the case in crop species. This difference is the fundamental reason why forestry may have an advantage; we have the opportunity to manage both gene and genotypic frequencies, similar to animal breeders, but in an environmental context more similar to that which plant breeders consider.

### What Are The Target Sets Of Genes?

The next concept that should be considered is that there are two "sets" of gene systems that must be considered over and above the uniformity issue. The first is the gene set(s) for resistance traits under selection (i.e., some currently known pest). As mentioned earlier, this may be difficult if not impossible to know but knowledge about disease resistance genes is increasing, and we are likely dealing with a rather small number of loci, probably less than 10 in many cases (Simmonds 1991). This set of genes in the production population will require construction of genotypes and deployment of these genotypes in a manner to insure evolutionary pressures on the pests are not large. I will discuss this in the deployment section later.

The second set of genes are those in what we could refer to as the "background genotype." In other words, these are loci that may be relevant to some currently unknown pest. They are unselected loci that will vary by the processes of sampling errors or drift and are the basis for the early work on risk to a plantation to some future pest by Libby (1982) and now others (Bishir and Roberds 1995). This set of genes, although playing themselves out in genotypes, are largely dependent upon the gene frequencies that are present in the deployed populations.

There could be, of course, overlap in these two gene systems. We can never be sure of how we are affecting changes in the phenotype by selecting on traits that are affected by many loci, which could be pleiotropic or linked, or how genetic drift plays out in the final tally after selection.

### What Are The Genetic Correlations?

A major problem breeders face is that it is rare we only have one trait we wish to improve (e.g., both growth and disease resistance). Genetic correlations are almost always something to contend with, and it is important to consider these if they can be measured with some precision. For some species, like western white pine, where we are only considering resistance to *Cronartium ribicola*, there are also genetic correlations among the resistance mechanisms (Yanchuk *et al.* 1994). So, we need to be concerned about both pest resistance trait correlations and pest resistance and other traits.

The two causes of genetic correlations are pleiotropic effects of genes and linkage disequilibrium (LD) among genes. The first, pleiotropy, is caused by a gene affecting more than one trait, therefore it is more difficult to "break" a correlation of this type, if not impossible. One hopes there are several alleles in the population and that one or two of them can confer positive economic attributes in both traits. Linkage is due to different loci which affect the same trait being physically in close linkage, or the linkage is observed in a statistical sense because of drift; i.e., selection causing statistical LD (Bulmer 1985).

These two factors are important because they lie at the heart of the controversy surrounding the issue of a cost of resistance. In other words, do products of genes that provide resistance have a cost to plant growth? Costs of resistance (or virulence) appear necessary in some situations to provide long-term durability of resistance (Gould 1994; Marshall 1989; Trenbath 1984). Bergelson and Purrington (1996) recently examined the literature on this important topic and found that costs of resistance were least often present with herbivorous species and more often with crop species rather than in wild plants. Furthermore, they suggested that many examples of costs of resistance appeared to be due to linkage rather than pleiotropic effects. This should be good news for tree breeders, as correlations caused by LD have better possibilities of being broken down by recombination and progress in both traits should be possible. However, the degree of linkage will be important and, unfortunately, it appears resistance genes appear in clusters in the plant genome (Hammond-Kosack and Jones 1995).

## MOLECULAR BREEDING

### Marker Assisted Selection

Vanderplank (1968) suggested that in the presence of VR genes, it would be difficult to select for HR. In other words, there is a tendency for minor resistance alleles to be eliminated by selection for resistance in the host population in the presence of major alleles. This idea became known as the *vertifolia* effect, after the famous German potato variety *vertifolia* that had very little resistance once two VR genes were defeated by a new virulent race. There has been some controversy on how real this phenomenon is but it has recently been re-analyzed by Cox (1995). He showed that the vertifolia effect is present, but tending to occur only when there is negative pleiotropic effects and increased greatly with linkage between major and minor resistance genes. Unfortunately, as previously mentioned, resistance genes can be in groups making physical linkage a problem, which would exasberate the vertifolia effect (Cox 1995).

How could molecular markers be used to overcome, or at least offset this effect? Since major genes show dominance or epistasis, Cox (1995) suggested that all individuals with more than one major allele linked to a marker be discarded (or better yet, put aside), and the remaining offspring be tested for minor gene resistance. If several quantitative resistance loci (QRL) have good markers, individuals carrying any of the desirable combinations (if combinations are desirable) can be retained (Young 1996). Of course, markers for major gene resistances will have little practical value if it is cheaper to simply screen the population with the pest themselves.

### Transgenics

The cost-benefit economics of transgenic trees in Canada requires careful scrutiny. It will contribute important scientific knowledge and development of the technology will continue with or without the input of traditional tree breeders. With continued success of transgenic agricultural crops, the financial and political spillover into forestry will continue to attract this technology (Raffa 1989).

The primary contribution transgenics will have in forestry is that it may be one of the few, if not the only method of rapidly incorporating important genes (which will have to be at low frequencies in our breeding populations) into unrelated but high breeding value genetic backgrounds for other traits. Conventional backcrossing techniques are not possible in most forest tree species, but costs and timeframes of transgenics technology must be considered and may in fact be prohibitive. Full development of this technology is several years away, and even in maize, transgenic plants for traits other than those affected by single genes is 5-15 years in the future. In specific situations, it may be able to provide us a means of accessing important pest resistant genes and even allow for pyramiding genes (i.e., putting in major genes into good HR resistance genotypes). The process will be slow as stability of the transgenes needs to be demonstrated. Although a few of the large U.S. seed companies already have "stable transgenic" plants, the ecological impacts of such a technology have not been considered to date. This is exemplified by the cross-resistance already developed to Bt multiple toxins (McGaughey 1994), and this issue is something we need to consider as well. However, it is a question of how to use these genes (the technology almost becomes irrelevant, other than the economics of it), which I will address next.

## DEPLOYMENT STRATEGIES FOR IMPROVED PEST RESISTANCE MATERIAL

The question of how to best deploy resistant material has been around now for a couple of decades. The basic questions that most research has attempted to address fall into the categories of how to construct mixtures of resistance genes within plants, among plants, and the type of resistance (minor or major genes) in these mixes. Single resistance gene deployment schemes in forestry are no longer worthy of much discussion, even though some have stood up well in some agriculture crops, the risks are simply too high in forestry in the face of the large body of knowledge that has accumulated over the last 20 years.

### The Use Of Major Gene Resistances

However measured or defined, these should be resistances that segregate out in the typical 1:3, 1:1, or 3:1 ratios in half or full-sib family arrays. The segregations similar to that reported by Kinlock *et al.* (1970) for major gene resistance (MGR) in sugar pine to blister rust, and by Vanderkamp (1991) in scots pine to western gall rust, are these kinds of genes we hope to find in this category. As indicated earlier, these will most likely be NR.

MGR resistances should be useful, but as we have already seen, they will likely cause us some inefficiencies in selecting for more complex resistances. We also know that they can be quickly overcome, as is the case for the MGR resistance in sugar pine in forestry (Kinloch and Comstock 1981). Person *et al.* (1982) suggested that there are both practical and theoretical investigations to support the view that major genes could be used more efficiently than they have been in the past. If possible, it may be best if they can be used as the "last line of defense," rather than the first.

### Finding And Using Minor Resistances (or HR)

Without observing 3:1, 1:1 or 1:3 segregations in various family arrays, we can assume that many complex gene-for-gene resistances are present. Some may be VR but most others will be a host of complex physiological responses triggered by the entrance of the pest in or onto the tree; this is by definition polygenic or HR. By simply selecting families or clones on criteria such as less attack or less damage, we could be well on our way to providing a mixture of various VR and HR's. These could bring us very successful levels of durable field resistance, as previously mentioned for Hessian fly resistance. "Cross and hope for the best," is not being suggested as the final approach but all pointers indicate that a general recurrent strategy should create quite a mix of resistances. The two basic problems with this "select and pray" approach are: 1) the vertifolia effect, and 2) not knowing if there is only one resistance mechanism controlled by one or a very small number of genes.

### Genetic Diversity In The Background Genotype

From Libby (1982) and Bishir and Roberds (1995) we now know that only a handful of unrelated genotypes (clones) are needed to minimize risk to a plantation from the WCS described earlier. The numbers vary quite a bit, depending upon assumptions and scenarios, but the common consensus appears to be settling in around 5-30 (clones). These numbers should translate in a straightforward manner, if Hardy-Weinberg equilibrium is invoked, to effective population size (Ne) estimates. In other words, for a single locus, two-allele system the number of clones modeled in Bishir and Roberds (1995) should be represented by an Ne statistic, relevant to a seed orchard crop. So a 30 clone or parent seed orchard would be similar to 30 unrelated clones used for deployment. This is indeed good news as these numbers are quite workable in terms of breeding and developing production populations. It is, of course, easy to develop scenarios that will violate these numbers and cause a higher level of risk in plantations, but there seems to be little to be gained by doing so, particularly at the larger landscape level.

## Genetic Diversity In Resistance To Target Pests

It is a general view now that it may be best to develop approach's that allow for some losses to pests, but within acceptable economic limits. Staying away from immunity breeding is critical, as we know that single or even multiple VR or NR resistance systems will quickly succumb to the pest. However, we should not be afraid to use VR/NR resistance systems, if found, (e.g., major gene resistance in sugar pine to blister rust), as they can be useful for a period of time. They have been successful for some types of more immobile pathogens (e.g., soil-borne pathogens like root rots may be relevant here), and as a small proportion of the deployed population. So, it seems, we need to develop our selection strategies to 1) screen our parents for any disease resistance and broadly categorize the resistance, and 2) develop some mixture strategies for deployment in space and time, to guard against biotype evolution.

## Deployment On The Landscape

This is of course the most important aspect of resistance breeding, although it has nothing to do with breeding *per se*. This is the ecological arena where we face the pest for the second time. (The first time is when we see the pest operating in the forest at a level causing considerable economic damage.) But we know something about the pest and several deployment issues need to be considered.

First, we have very long rotation ages and we know the pests we typically encounter will have many "genetic cracks" at us. So a strategy to minimize the potential for co-evolution in the pest is critical. How is this best accomplished? Gould (1986a, b) and Trenbeth (1984)(summarized by Wilhoit (1992)) have provided some guidance on these questions. The results, as expected, are quite complex and depend upon the genetic details of the host-pest system, such as recessive or dominance virulence, recessive or dominance resistance, gene frequencies, and epistasis. In general, mixed deployment provided more durability and durability was increased with the planting of susceptible varieties (e.g., 25% susceptible). For two resistance factors in the host (independent of specific gene action) and two corresponding virulence genes in the insect, pyramiding resistances worked well with susceptible varieties planted, but this was only the most effective deployment scheme with recessive virulence and negative epistasis. (Sequential deployment of resistances with forest trees does not seem to be a reasonable option, due to the long rotation ages of trees.) Marshall (1989) examined several more scenarios, ranging from overlapping resistant gene sets, to a fully susceptible component in a multiline mixture. He concluded that the inclusion of susceptible varieties is beneficial but may need to be as high as 30 to 40% of the crop to ensure the survival of non-virulent races. Caprio (1994) reported that the inclusion of non-Bt transgenic resistant plants (11%) lengthened the durability of the resistance, but unmanaged refugia strategies were the most effective. Further to this, Ives (1996) and Alstad and Andow (1996) have both commented on the concept of using "trap crops," to slow the evolution of resistance to the *cry* proteins, but an economic decision needs to be made on what level of damage can be tolerated in these non-resistant "attractive refugia." The size of these blocks then becomes an important issue, however, in *Brassica*, size of blocks had little affect on density of herbivorous insects (Grez and Gonzalez 1995). While mixtures of resistance factors along with susceptible material in some form (in a mixture or as a refugia) appear to be the best solution so far (Gould 1991), it is possible in some situations for mixtures to hasten insect resistance (Mallet and Porter 1992). In summary, the genetic details of the host-pest populations dynamics are extremely important to the end result, and may be at a level where we could never fully understand specific situations, but complexity of the resistance(s) appears to be the common link that provides some level of durability.

Second, while we may have single-gene resistances that we can use, they should be considered only temporary protection and should not be used exclusively if they inhibit our ability to rely on the tree's more complex ability to tolerate losses. Trees have evolved many mechanisms to protect themselves over their long lives and many are basic wound response resistances that may serve to reduce or repair physical damage. It is stand performance and economic return that we hope to attain with resistance breeding and not individual tree immunity. In fact, there is a disadvantage in seeking a level of resistance greater than necessary when other restraints are added in a pest management system (van Edam 1991).

Third, and related to the fact that we do not require immunity, we can sacrifice a fair percent of our crop. Natural stand processes can remove up to 50% of our planted trees through basic competition effects. For instance, we plant somewhere between 700-1500 trees per hectare, and only expect to harvest 300-700 trees at rotation. We consider thinning many times. This gives us a flexibility not available to most other plant breeders. While losses up to 50% may be on the extreme side, if totally inflicted by a pest, we are in the position of setting some acceptable level of loss, as in the models of Libby (1982) and others. Discounting refugia, as it does not seem appropriate to establish plantations for complete destruction, we may be faced with having to develop "refugia" within our plantations.

Fourth, natural parasites can have profound effects on the pest's population demographics and it may be important to know if under certain population sizes or conditions natural pest parasites can effectively neutralize the pest to acceptable loss levels. This has been shown for the gall rust-lodgepole pine pathosystem (Vanderkamp and Blenis 1996). Furthermore, there appears to be a beneficial interaction as a higher percentage mortality of pest occurs on resistant than susceptible varieties in the presence of natural enemies (van Edam 1991).

Fifth, Namkoong (1994) has proposed that offensive tactics (relevant to insect pests), be considered instead of strict defensive tactics. With some ability to breed the pest in artificial settings, tactics to introduce a fertility enhancing gene with a conditional lethal (e.g., cold susceptibility) could exert enormous control over the insect's population growth, in local settings. We, therefore, control the genetics of the pest and effectively disarm the insect. Consideration for operational feasibility is important, but with tactics such as this, resistance breeding in the host may not even be necessary.

## AN EXAMPLE STRATEGY: RESISTANCE AGAINST WHITE PINE WEEVIL OF SPRUCE IN B.C.

Several years ago, we identified that substantial levels of resistance to the terminal weevil are present in both interior and Sitka spruce in B.C. (Kiss and Yanchuk 1991; Ying 1991). This has been well documented in other publications (e.g., Alfaro *et. al.* 1996a, b) as well as a general framework in the context of an integrated pest management strategy (Alfaro *et al.* 1995). In B.C., we are considering most of the issues addressed above with an added option of the use of resistant clones through the advent of operational somatic embryogenesis.

However, most of the interest to-date has been in research activities for identifying more genotypes which are resistant and the basis of this resistance (e.g., Alfaro *et al.* 1996a, b; Sahota *et al.* 1994; Thomlin and Borden 1994). While the genetics of the resistance mechanisms we believe might be working is currently unknown, several broad morphological and physiological response types could be implicated and some guesses (at least for know) could be made as to the kind of resistance that may be present (i.e., NR or HR).

### Chemical Attraction

It is evident that some resistant trees repel weevils after some initial attempts at feeding/ovipositing. The basis for this is not well known, but it is clear that several host terpenes at higher concentrations can act as feeding deterrents (Alfaro and Borden 1985). This resistance, however, could be overcome in a limited choice situation as caged weevils seem to feed on putatively resistant and susceptible trees equally (Sahota, *et al.* 1994). Major gene inheritance of monoterpenes has been well established (e.g., Squillace 1971), so chemical attraction/deterrence differences among trees could be considered along the lines of NR.

### Constitutive Resin Canals

Constitutive or preformed resin represents the first line of chemio-mechanical defense of many conifers to stem-invading insects. Variation in preformed cortical resin canals, mainly in phloem tissues, and chemical composition of constitutive resin is present, has been related to resistance in some spruce clones (Thomlin and Borden 1994). If chemical attraction/deterrence, as mentioned above in "1," is positively correlated with the weevils detection of an overwhelming resin duct structure in the bark tissue, then the utility of mechanism "1" might be is lessened.

### Induced (Traumatic) Resin Response

This second line of resistance is characterized by varying levels of resinosis from the development of traumatic resin canals in the most recently formed secondary xylem tissues in the leader. It has been described recently by Alfaro *et al.* (1996b), who categorized resin canal response into six levels. The induced resin canal characteristic, we expect, would be controlled by more than one gene and could be placed in our HR arsenal. However, recent evidence from molecular genetics shows that even large structural changes to a plant can reside with allelism at one locus (e.g., Doebley *et al.* 1997, for apical dominance in maize). Although this may simply be variation in wounding response, it is not known how the six levels of wound response are related to allelochemical changes in the resin acids. Formation of these defensive structures could be considered costly, but the results suggest the costs are not manifested in reduced growth rates (Kiss and Yanchuk 1991; King *et al.* 1997).

### Chemical Response In Resins

In addition to the increase in resin producing cells in xylem and phloem tissue, there may be increases in the major components of the resins themselves (Chencilet 1987; Raffa and Smalley 1995). These can be different than those produced with aseptic wounding alone. Properties of chemicals within tree resin complexes differ in response to levels of wounding or attack (van Buijtenen and Santamour 1972). Not surprisingly, the definitive chemicals associated with resistance(s) at this level have been elusive (Manville *et al.* 1994), but it is clear, variation is present to work with. Inheritance of major chemicals in resins could be expected to be similar as in Squillace (1971), but these require specific study. However, if they are inherited in MGR fashion, they could represent more valuable NR resistances and be considered second or third line defenses, as suggested by Person *et al.* (1982) as more appropriate.

### Tree Recovery

Although we fully expect damage in a percentage of our improved material, it appears that some families have the ability to recover from damaged or successfully attacked trees better than others. Recovery appears to occur as lateral branches quickly turn up and take over as the main leader the same year as the attack, or the following year. The degree of recovery is of course on a quantitative scale, but clearly genotypes capable of fast recovery could play an important role in minimizing plantation damage. We have not yet determined heritabilities for this trait, but will do so in a set of trials in 1998.

These five mechanisms could provide us with three broad *resistance types*. If we take a conservative approach for the time being, and assume that mechanism(s) 1 and 2 (Type I) are the same or highly genetically correlated, and the same with mechanism(s) 3 and 4 (Type II), and 5 is independent of the other two (Type III), then this leaves us with three "mechanism types" to consider in deployment for the time being. Genetic correlations between these three mechanism types are important, presenting another level of uncertainty to us at this time. Once a greater understanding of the specific host-pest interaction leading to resistance in these three resistance types is developed, new approaches will have to be considered.

*Breeding And Production Of "Resistance Types"* Identification of all three resistance types in parents undergoing testing is occurring in both Sitka and interior spruce populations and will be expanded over the next few years. In Sitka spruce the main trait for improvement will be weevil resistance, whereas in interior spruce weevil resistance and growth are receiving more attention.

Open pollinated seed orchards composed of these putatively resistant parents will likely provide us with a range of resistance types (i.e., susceptible, VR, NR and HR). In spruce, we have the capability of producing rooted cuttings from elite full-sib families, and "somatic seedlings" from somatic embryogenesis (SE)(but costs are quite high at this time for SE trees in relation to rooted cuttings). So "pure" blocks or mixes of type I, II and III resistances could be at our disposal rather soon. SE trees offer the added benefit of being clonal, and specific mechanisms could be identified and kept intact. Currently, a 1 000 clone test of interior spruce is underway (from a base of about 40 resistant parents), with the objective of selecting approximately 50 operational clones. Specific resistance studies will obviously be carried out on these clones.

*Deployment: An Example For Interior Spruce* With this complex of resistant types available to us now and in the near future, how do we best deploy these improved populations in operational settings? The main objectives will be to reduce damage on spruce to a level which is economically acceptable, and ensure very little evolutionary pressure is put on the weevil populations. The most desirable approach would be to first consider site hazard rating, as it makes little sense to plant resistant material on sites where little weevil damage is expected. Some information is present on hazard rating and seems to depend largely on the number of growing degree days present for full weevil development. For interior spruce, this suggest sites under 1 050 m of elevation are in a higher hazard classification (Spittlehouse *et al.* 1994).

One could argue that seed from an open-pollinated orchard of ~30 of the most resistant parents should produce all possible combinations of susceptible to pyramided resistances, and this in itself could be a very durable system. As well, these numbers (in the order of 5-30) of parents provide low levels of risk to the WCS mentioned earlier. So is any further analysis necessary and can we simply operate along the same lines as we do for most other traits? Probably not, at least not in the long-term. The two points mentioned previously, cross resistance being developed to Bt toxins and mixtures of resistance types can in fact speed the evolution of resistance in the pests, are cause for concern. This requires us to move to deployment of better known genotypes for various resistances, with some understanding of the genetics of the resistance mechanisms. The continual search for populations of genotypes with adequate diversity, high breeding values for economic traits and various "durable" resistance mechanisms will not be an easy task, but essential in order to sustain the long-term progress of tree improvement.

## CONCLUSIONS AND SUMMARY

The discovery of genetic resistances, and examining the genetic basis of this resistance, to an exotic or endemic pest known to cause economic levels of damage is exciting. However, it needs to be honestly tempered with practical solutions that are ecologically and genetically cost effective. With what we currently know about breeding for pest resistance, from crops, animals and trees, trees present us with some remaining questions:

1) *Do we need to breed for resistance, or are there some other strategies that we can use?* Although genetic alternatives are attractive and successful, well planned silvicultural techniques may be a more practical approach to dealing with pest problems. Each individual situation needs to be carefully analyzed.

2) *If breeding is required, what level of resistance do we actually need? Is a little enough?* It seems that susceptible individuals may be important to retard biotype evolution, and normal forest stand processes give us flexibility to "lose" individual trees. The proportion of trees required for a commercially viable stand should be determined and planned for with both known and unknown pest threats.

3) *If a little resistance is enough, could NR type systems in diverse ecological settings provide adequate protection and not cause high levels of biotype evolution in the pest?* The durability of more simply inherited resistances could be longer in forestry than in agricultural settings, but they fail eventually and likely in a time frame too short to protect most forest stands during establishment periods (e.g., sugar pine and MGR to blister rust). However, as "stage two" level resistances they may be more important and increase durability greatly. We should consider HR and NR as our only real "pyramiding" option available to us.

4) *If high levels of resistance are required, are we likely to apply evolutionary pressure on the pest?* It now seems clear that in order to attain durable levels of resistance HR systems should be considered, particularly as the first line of defense. It would be useful to show the interrelationships of resistance types III and IV as soon as possible. If they can be found, mixtures of resistance should be used as we still do not know enough about the demographics of the parasite we are likely to face. Enough work has been done in other species, subject to less generation lag in resistance breeding, to show that a variety of mechanisms must be used. This is not new, but the advent of molecular information has shown there may be ways around the classical problems in pest resistance breeding (e.g., the vertifolia effect).

5) *Are there any options available to us for resistance to the terminal weevil of spruces in the short-term?* For weevil resistance in spruces in B.C., a two phase approach seems viable at this time. For lower hazard sites, open-pollinated seed orchard seed from putatively resistant parents could offer cost-effective and durable resistance. For higher hazard sites, a mixture of the three resistant types with approximately 10-20% susceptible mixed in, appears to be an good first approximation at cost-effective and durable resistance in an ecologically tricky situation. In any event, we may have a 10-year window to articulate

this pathosystem, as it is likely we will not be able to deploy large enough volumes of resistant material to put extremely large pressure on the pest.

Pest resistance continues to be an important, if not the most important, trait in tree breeding. While yields in crop plants have steadily improved, much of this is due to pest resistance improvement in concert with growth improvements. The continued expenditures in pest resistance breeding in agriculture clearly point to the fact that they are essential traits to consider in breeding. While many of our tree species under genetic improvement do not have significant pest problems, pest problems do appear, as history has shown us time and time again.

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# PROGRESS TOWARDS DETECTING AND VERIFYING QTLs FOR WOOD PROPERTY TRAITS IN LOBLOLLY PINE AND ADAPTIVE TRAITS IN DOUGLAS-FIR

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## INTRODUCTION

Quantitatively inherited traits in forestry are normally assessed in terms of variance components and heritabilities. Although very useful for breeding applications, the molecular basis of quantitative inheritance cannot be ascertained from statistical parameters. Quantitative trait locus (QTL) mapping is a relatively new technique for determining the number, effects, and modes of gene action of complex traits. The fundamental approach to QTL mapping is to measure phenotypes (quantitative traits) and genotypes (usually molecular markers) on all members of a segregating population, and then associate phenotype with genotype to estimate QTL numbers and effects. If the molecular markers are positioned onto genetic maps, then the genomic location of the QTL can also be estimated. The earliest successful demonstrations of QTL mapping were achieved in agricultural crops such as maize and tomato where backcross and F2 populations were used to identify yield and fruit quality QTLs, respectively (Edwards *et al.* 1987; Paterson *et al.* 1988). QTL mapping has since been applied to nearly all agronomic crops and more recently to forest trees.

QTL mapping in forest trees presents some unique challenges as compared to most crops including: 1) the lack of inbred lines and BC and F2 populations, 2) long generation times, and 3) the practical difficulties of assessing traits of interest in trees (i.e. establishing and maintaining large field tests and measuring traits such as volume growth and wood properties). As a result, most QTL mapping experiments to date have been practiced on existing crosses with relatively small sample sizes. Nevertheless, these early QTL detection experiments, with their low power and precision, have demonstrated that QTLs can be detected and mapped in forest trees for growth and form, wood quality, disease resistance, adaptive, and reproductive traits (Groover *et al.* 1994; Bradshaw and Stettler 1995; Grattapaglia *et al.* 1995, 1996; Plomion *et al.* 1996; Bryne *et al.* 1997a, b; Aitken *et al.* 1997). QTLs detected in each of these studies should be treated as putative until verified by independent tests. Verification tests are in progress for many of the studies listed above. We will report here on our progress towards detecting and verifying QTLs for wood quality traits in loblolly pine and adaptive traits in Douglas-fir.

## DETECTION OF WOOD PROPERTY QTLs IN LOBLOLLY PINE

We are interested in identifying QTLs for both wood quality and wood chemistry traits in loblolly pine. The trait of initial and greatest interest is wood specific gravity. Groover *et al.* (1994) mapped five QTLs in a single three-generation pedigree of 177 progeny using the single-factor ANOVA method. The five QTLs accounted for 23% of the total phenotypic variance. Knott *et al.* (1997) repeated the analysis but this time used an all-marker, interval mapping procedure. This approach is expected to have greater power for detection of QTLs and provide more precise estimates of effects. A more complete genetic map was used in the analysis by Knott *et al.* (1997) which accounts for why several new QTLs were detected. However, some of the QTLs previously detected by Groover *et al.* (1994) were not detected, likely due to the higher significance threshold used in the Knott *et al.* (1997) study.

More recently we have initiated studies to identify component trait QTLs for wood specific gravity. Traits included are: earlywood specific gravity, latewood specific gravity, percent earlywood and latewood, and microfibril angle. Wood specific gravity was measured by x-ray densitometry in these studies which provides estimates for individual rings. Additional QTLs, specifically for earlywood specific gravity and latewood specific gravity, were detected in these analyses which were not detected following the analyses using oven dry weight, green volume measures of entire cores.

We are also attempting to determine if QTLs can be detected for wood chemistry components. We have used molecular beam mass spectrometry to estimate the relative proportion of lignin, cellulose, and hemicellulose in earlywood and latewood samples from members of our mapping population. Considerable variation exists within a single full-sib family for these wood chemistry components. We have mapped three QTLs for percent lignin which in total account for approximately 20% of the total phenotypic variance. Because the lignin biosynthetic pathway has been fully characterized it should be possible to identify candidate genes for these QTLs. We are currently mapping genes coding for enzymes in the lignin biosynthetic pathway (PAL, CAD, etc.) in hopes of identifying such candidate genes.

## DETECTION OF ADAPTIVE TRAIT QTLs IN DOUGLAS-FIR

Douglas-fir has a very broad geographic range and grows across diverse and heterogeneous environments. For these reasons, an understanding of the genetic control and breeding for adaptive traits has always been of interest in this species. We are using QTL mapping to estimate the numbers and effects of genes controlling a suite of adaptive traits. Our initial studies have focused on bud phenology and cold-hardiness. As in our loblolly pine experiments, we are using a three-generation pedigree for QTL mapping. In addition, we have clonally replicated each of the 250 progeny of the cross. Cloning provides better estimates of phenotypic values and also allows for estimating QTL x environment interactions and destructive sampling. We have established two replicated field tests with the clones for estimating adaptive trait QTLs.

Terminal and lateral bud flush in each of three years (1995-97) was measured by determining the proportion of ramets within a clone that flushed on a single day. The day chosen for assessment was when approximately half of the clones had flushed. As many as sixteen QTLs for terminal or lateral bud flush have been identified and mapped to twelve different linkage groups. Many of the QTLs are for both terminal and lateral bud flush, suggesting that some of the same genes control these two traits. The effects of the bud flush QTLs were generally quite small, less than 5.0% of the phenotypic variance each. Estimates of these effects may increase in time as the genetic tests mature and establishment effects decrease. Nevertheless, these effects are much less than those reported for QTLs of various traits in other experiments, including spring bud flush in hybrid poplar (Bradshaw and Stettler 1995). However, effects have most likely been significantly overestimated in all published reports due to the small size of mapping populations. The effects estimated for spring bud flush in the current study may be closer to the true effects of QTLs due to the larger mapping population and the clonal replication used in this study.

Another adaptive trait of interest in Douglas-fir is cold-hardiness. Spring and fall cold-hardiness were evaluated using methods described by Aitken and Adams (1996). Briefly, branch tips were sampled from three ramets of each clone and were subjected to low temperature freezing treatments. Freeze damage was evaluated visually on needles, stems, and buds and scored on a scale of 1-10. As many as 14 QTLs, mapping to 8 linkage groups, for spring cold-hardiness were identified whereas only five QTLs, mapping to five linkage groups, were identified for fall cold-hardiness. In only three cases were the same QTLs detected in more than one tissue type, thus it remains unclear whether the same genes are responding in all tissue types or whether it is just not possible to detect the same QTL from all tissue types due to the error and imprecision in QTL detection or error in phenotypic assessment of cold-hardiness. One interesting observation from these results was that four QTLs for bud flush and four QTLs for spring cold-hardiness mapped to the same genomic locations, suggesting a pleiotropic effect of these QTLs. This result is not surprising in that the genetic correlations between these traits are known to be very high.

## VERIFICATION EXPERIMENTS

Our QTL mapping experiments to date in both loblolly pine and Douglas-fir have been conducted with mapping populations of modest size and in a very limited number of genetic backgrounds. Although we have used very high significance thresholds for estimating QTLs to avoid Type I errors, we still consider all QTLs as putative until verified in an independent experiment. A verification experiment has been established for loblolly pine and a similar verification experiment for Douglas-fir is planned. In loblolly pine, 500 new progeny for each of our mapping populations have been planted in single family block plantations at a test site in North Carolina. These trees completed their fifth growing season in 1997. In 1998, increment cores will be taken for wood quality and wood chemistry assessment to verify QTLs previously detected for these traits. In addition, these trees will be measured for an array of growth, form, and phenology traits and QTL analyses will be conducted for these traits as well. It is our hope that these experiments will provide sufficient power and precision such that QTLs can be estimated with real statistical confidence.

We are also planning a verification experiment for Douglas-fir. Five-hundred new progeny have been established from the original mapping population (Jermstad *et al.* 1994). These progeny will be cloned in early 1998. Clones will be grown under experimental treatment conditions in an attempt to identify QTLs responding to different environmental stimuli in affecting the timing of bud flush and the timing of bud set. For example, clones will be grown under two levels of winter chill and three levels of spring heat sum to identify bud flush QTLs responding to these different stimuli. Likewise, clones will be grown under two levels of photoperiod and three levels of moisture stress to identify bud set QTLs responding to these stimuli. Following these experiments, the clones will be evaluated for cold-hardiness traits to more accurately estimate and verify QTLs for these traits as well.

## SUMMARY AND FUTURE PROSPECTS

QTL mapping experiments conducted in our lab and others around the world have shown that QTLs can be detected for many traits of economic importance in forest trees but verification is still needed for accurate detection and estimation of effects. Estimation in additional genetic backgrounds will also be needed, such as that derived from diallel mating designs. At this point it should be possible to accurately evaluate the potential for marker-assisted breeding or selection (MAB/MAS) in forest trees. Where clonal deployment is possible, such as in poplar and radiata pine, MAS/MAB should be economical to apply. Even without direct application to MAB/MAS, QTL detection in forestry is justified based on the improved understanding of quantitative inheritance it can provide. Knowledge of the numbers and effects QTLs, pleiotropic QTLs, and epistatic interactions of QTLs controlling economic traits will certainly have impacts on designing breeding and testing strategies in conventional breeding programs.

An emerging new opportunity for identifying the genes which control complex traits will come from the gene sequencing projects that have been initiated in the United States, New Zealand, and Europe. DNA sequences are being determined for tens of thousands of expressed genes, known as expressed sequenced tags (ESTs), from tissues such as xylem, phloem, leaves and needles, roots, reproductive structures, and more. There are EST projects for radiata pine, loblolly pine, poplar, Norway spruce, and probably several more. Once DNA sequences are known then gene identities can often be determined by database comparisons. The ESTs can also be positioned onto existing genetic maps and if there is phenotypic data for the mapping population, then it is possible to associate allelic variation of ESTs with phenotypic values, just as is done with QTLs. For example, we are mapping ESTs from loblolly pine xylem to our genetic maps for which we have wood quality and wood chemistry data on the members of the mapping population. We hope to be able to identify candidate genes for wood properties in this way and also estimate the effects of allelic substitutions at the candidate genes on the phenotypic value of the quantitative traits. Clearly, there are many genes which determine complex traits and it will be difficult to identify all ESTs for genes controlling a trait. But it is likely that some genes will be identified in this way and once done, these ESTs will make for very useful markers for MAB/MAS and other types of diagnostic screening. The methods of modern genomic science that have been developed largely as a result of the human genome project are just beginning to be applied to forestry, but in time will contribute significantly to our understanding of the genetics of quantitative trait variation in trees.

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# FUTURE DIRECTIONS AND CONTRIBUTIONS TO SUSTAINABLE DEVELOPMENT

# TREE IMPROVEMENT: AN INDUSTRIAL PERSPECTIVE OF CHALLENGES AND OPPORTUNITIES

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## INTRODUCTION

Organized tree improvement programs for native species began across Canada in the 1970's (Hall, 1979), following the introduction of large scale reforestation programs. In many areas, cooperative models were followed involving government agencies, universities, and industry. In this respect, the general goals of industrial tree improvement programs are similar to those of, for instance, provincial efforts; however, there are some differences in perspectives. I am sure there is a wide range of industrial perspectives towards tree improvement in Canada which I can't address but I can provide an overview of the J.D. Irving, Limited (JDI) point of view.

By way of background, J.D. Irving, Limited is a diversified, family-owned forest products company headquartered in Saint John, New Brunswick. The company operates 11 sawmills and 5 pulp and paper facilities and has forest management responsibilities for 2 million ha of land in New Brunswick, Nova Scotia, and the State of Maine. Half of these lands are part of provincial Crown Licenses in New Brunswick and the other half are privately owned by the company. JDI has had a progressive reforestation program since the late 1950's and in 1997 celebrated 40 years of planting trees. Approximately 15-16 million trees are planted on Freehold lands and 8-12 million are planted on Crown land. Another important component of the company's silviculture program is pre-commercial spacing of naturally regenerating areas. This work has been ongoing since the early 1980's and in the last three years between 10 000 and 20 000 ha have been treated annually, including softwood, mixed wood, and hardwood stand types.

The company began working on tree improvement in 1978, shortly after the formation of the New Brunswick Tree Improvement Council (NBTIC) and work intensified greatly in 1980. In 1989, JDI joined the Nova Scotia Tree Improvement Working Group (NSTIWG) with the acquisition of additional lands in that province. Less formal cooperative tree improvement efforts have also been made in Maine. The species of concern initially were black spruce, white spruce , jack pine and tamarack. Subsequently, Norway spruce, red spruce, and most recently, white pine were included. Seedling seed orchard establishment for jack pine and black spruce began in 1979 with clonal orchard establishment beginning in 1983. Seed production began in the latter half of the 1980's and by the early 1990's, all seed used for reforestation stock for the initial species was coming from seed orchards. Second generation seed is now becoming available for black spruce and jack pine.

In the following sections, the role of tree improvement, including the future challenges and directions, will be described from the JDI perspective.

## WHAT IS THE IMPORTANCE OF TREE IMPROVEMENT?

The company has long believed in the importance of increasing forest growth to allow the greatest sustainable allowable annual cut (AAC) while maintaining or enhancing other elements of sustainable forest management including environmental quality and biodiversity. The organizing committee of the Canadian Tree Improvement Association meeting posed the question: "Do we need tree improvement programs to increase forest productivity for competing in local and foreign markets?". The answer to this question is ABSOLUTELY! The demand for forest products is gradually increasing in New Brunswick. In the period from 1984-1994, on average, 16% more wood was harvested than in the 10 previous years (source - Timber Utilization Surveys). At the same time, the percentage of land with a primary management goal other than wood production (but not necessarily excluding some form of harvesting) is increasing. Approximately 25% of forest land managed by JDI has a non-timber primary management objective including riparian zones, wildlife management areas, unique sites, and others. This places increasing emphasis on areas where intensive forest management is applied and tree improvement is one of the tools to increase productivity on these areas.

Productivity of plantations compared to the natural forest is evident in plantations established in the Blackbrook district in northern New Brunswick in the 1960's. Because the company is focussed strongly on solid wood products, considerable effort has been expended on developing commercial thinning strategies. At present, commercial thinning is conducted on 1 500 ha per year of 20-30 year old plantations in Black Brook. Approximately 40% of the volume is removed by modified thinning from below (Brunsdon and Pelletier 1995). At present, 20% of the softwood harvest in this district is from plantations and this will increase dramatically when second commercial thinning begins. The current thinking is that most plantations in this district will receive at least one thinning and plantations on better sites will receive as many as three thinnings with the final removal occurring at an age of 60 - 70 years. The oldest tree improvement test plantings are reaching the age where productivity can be compared to plantations established from unimproved seed. In an initial effort to look at this, 15 year growth data from a 2 ha open-pollinated NBTIC black spruce family test in Blackbrook was used in the managed stand growth model used in New Brunswick to project stand growth over time. Four similarly aged operational black spruce plantations, grown on similar sites, were also evaluated and modelled. The family test growth curve and the average of the four operational plantation growth curves are plotted in Figure 1. The first thinning of black spruce plantations in Blackbrook is around 25 years. The family test will be operable approximately two years earlier than comparable operational plantations. This is only an initial effort and we need to use every opportunity for comparison to derive appropriate growth curves for plantations from improved seed. Realized gain tests planted by NBTIC members in the early 1990's and other demonstration plantings established by the company will be used to refine forest growth projections for determination of sustainable AAC. The increased growth of genetically improved stock may also have important economic impacts at the establishment end of the reforestation cycle as well as at the harvest end. The use of improved stock may reduce the need for competition control treatments. This is one of the recognized benefits of the use of improved Sitka spruce cuttings in the United Kingdom (Lee, pers. comm.).

Improvement of quality traits should not be ignored. For some species such as jack pine and tamarack, improvements in stem straightness and branching characteristics in the first generation of tree improvement have been dramatic. In our company's experience, form improvements in jack pine were the first noticeable impacts of tree improvement on reforestation stock. Field observations were verified in five-year assessments of jack pine realized gain tests established by NBTIC in 1991. An unrogued first generation orchard source was 24% straighter than unimproved sources based on a 1-6 subjective scale (NBTIC 1996).

## WHAT TRAITS SHOULD WE BREED FOR?

Other questions posed by the organizing committee were "Should we develop breeding programs for specific products?" and "What traits should we breed for in priority?". With JDI being a diversified forest products company, the answer to the first question is probably 'no'. Flexibility with respect to product goals is crucial considering the long-term nature of investment in plantations as well as the cyclical nature of forest products markets. Who can say what the most profitable mix of products will be 50 years from now? As with most tree improvement programs, volume production will remain a major focus of effort. Quality traits, such as stem straightness and branch size may be important, especially for species where longer rotations, including multiple thinning, are implemented for production of large, high value logs.

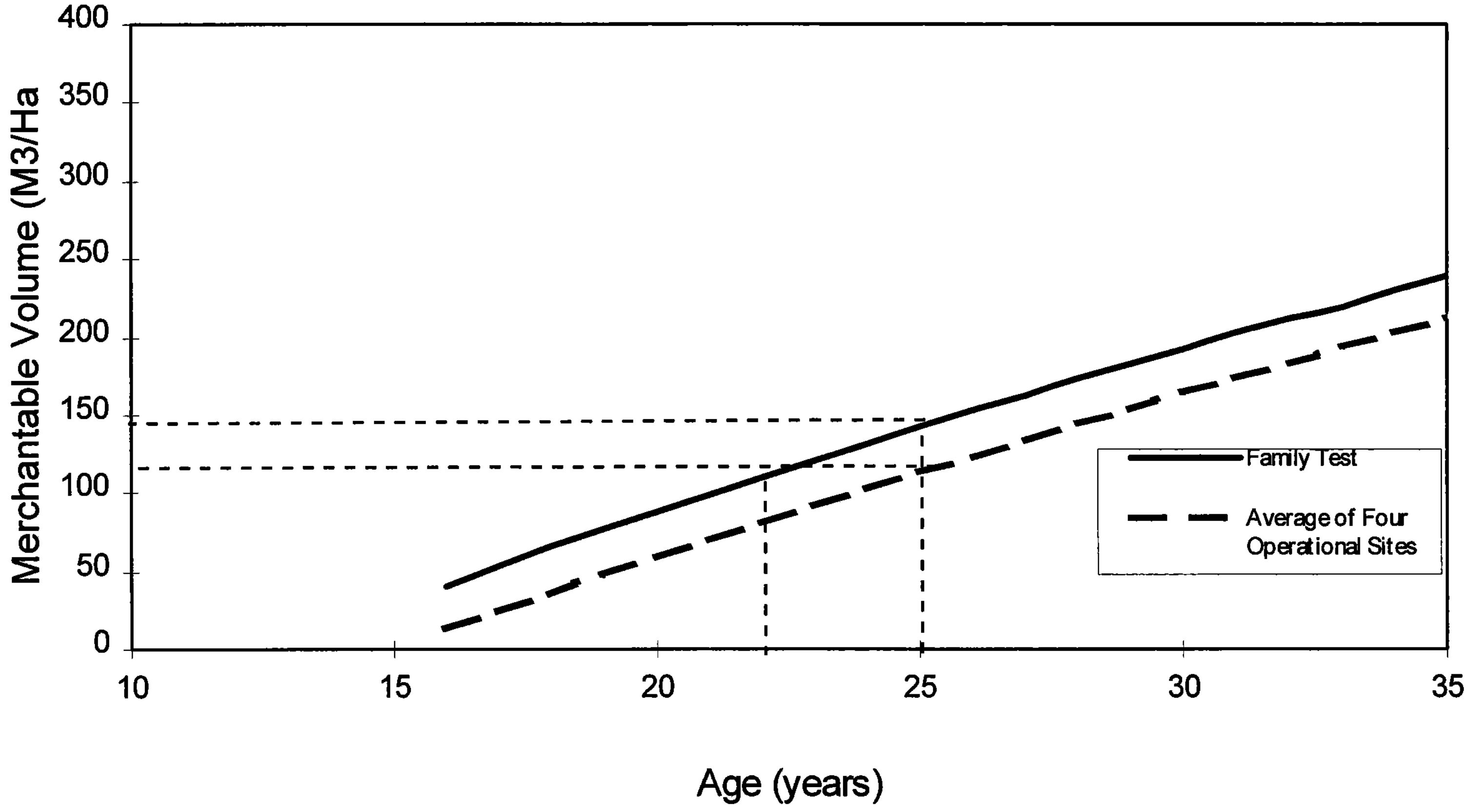

Figure 1. Projected volume in a black spruce family test at Black Brook compared to operational plantations.

Wood properties will also be considered in breeding programs. The trait that we know most about is relative density and for a number of our species, such as, black spruce (Zhang and Morgenstern, 1995), white spruce (Corriveau *et al.*, 1991) and Norway spruce (Hylen, 1997) adverse genetic correlations are documented. Consideration of this trait in breeding programs will likely involve restriction selection indices where density is not allowed to fall below threshold levels. At present, I don't think we have the knowledge to assess the likelihood of other wood properties being incorporated in our breeding or production programs.

Insect and disease resistance breeding is an area which will become more important for some species in the JDI tree improvement program. White pine and Norway spruce are two high value species which are seriously affected by the white pine weevil. Resistance to this pest has been shown to be heritable in Sitka and interior spruces in British Columbia ( King *et al.* 1997) and there is evidence that this is also the case in Norway spruce (Nieman and Boyle 1989). Putatively resistant Norway spruce selections have been observed in New Brunswick and flower induction techniques are being used so that breeding and testing may be conducted. White pine tree improvement is in the very early stages with JDI and along with weevil resistance or tolerance, susceptibility to white pine blister rust will be investigated. Spruce budworm is the most serious forest insect pest in the Maritimes. Strategies employed by JDI to combat this pest include species selection in plantation establishment and during pre-commercial spacing of natural regeneration to favour spruce species over balsam fir. The spruce budworm tends to have less impact on spruce (varying by species) than fir. Maintenance of vigorous stand conditions through commercial thinning should also increase the tolerance of stands to defoliation. Population levels of the budworm are currently at the low point of a cycle which has historically been approximately 20 years. When infestations return, genetic tests will have developed to the stage where they will be affected by this pest and assessment of pest tolerance can be undertaken, particularly for those species more susceptible to damage such as white spruce. Genetic variation in susceptibility of white spruce to a number of less economically important pests such as spruce budmoths, adelgids and midges has already been demonstrated (Quiring *et al.* 1991; Teerling 1997).

Other traits related to adaptiveness may also become important in JDI tree improvement programs, particularly as new genetic information becomes available and operational production and deployment systems become more sophisticated through family bulking or clonal production. In some areas where the company conducts forest management, the planting of white spruce and Norway spruce is restricted because of damage from late spring frosts. Selection of late flushing clones of Norway spruce in Finland has been undertaken where similar problems occur (Napola 1992). This approach could also be adopted in the Maritimes.

## NEW DIRECTIONS AND CHALLENGES

Tree improvement programs have progressed through assembling of breeding populations, establishment of seed orchards, and first generation breeding and testing for most of the commercially important conifer species utilized by JDI. We are rapidly entering a transition period where we can utilize the information that we have all worked very hard to obtain to make more significant impacts on the value of the plantations that we establish. At the same time, longer term decisions are being made related to management of genetic diversity which will set the course for future populations. Issues important in the JDI tree improvement effort are: 1) delivery of genetic gain, 2) use of biotechnology, and 3) genetic diversity. These will be discussed in the following sections.

### Delivery of Genetic Gain

To date, considerable effort has been made to increase orchard productivity and currently genetic roguing is being conducted as rapidly as field test results permit. These activities are geared towards ensuring that the investment in tree improvement translates into increased forest productivity and value. In early phases of tree improvement, seed orchards were managed as a unit and planting stock derived from these orchards will realize some percentage of the potential genetic gain. Figure 2 (from Adams and Tosh 1998) illustrates the necessity for looking beyond bulk orchard production in a white spruce seed orchard. Breeding values of 38

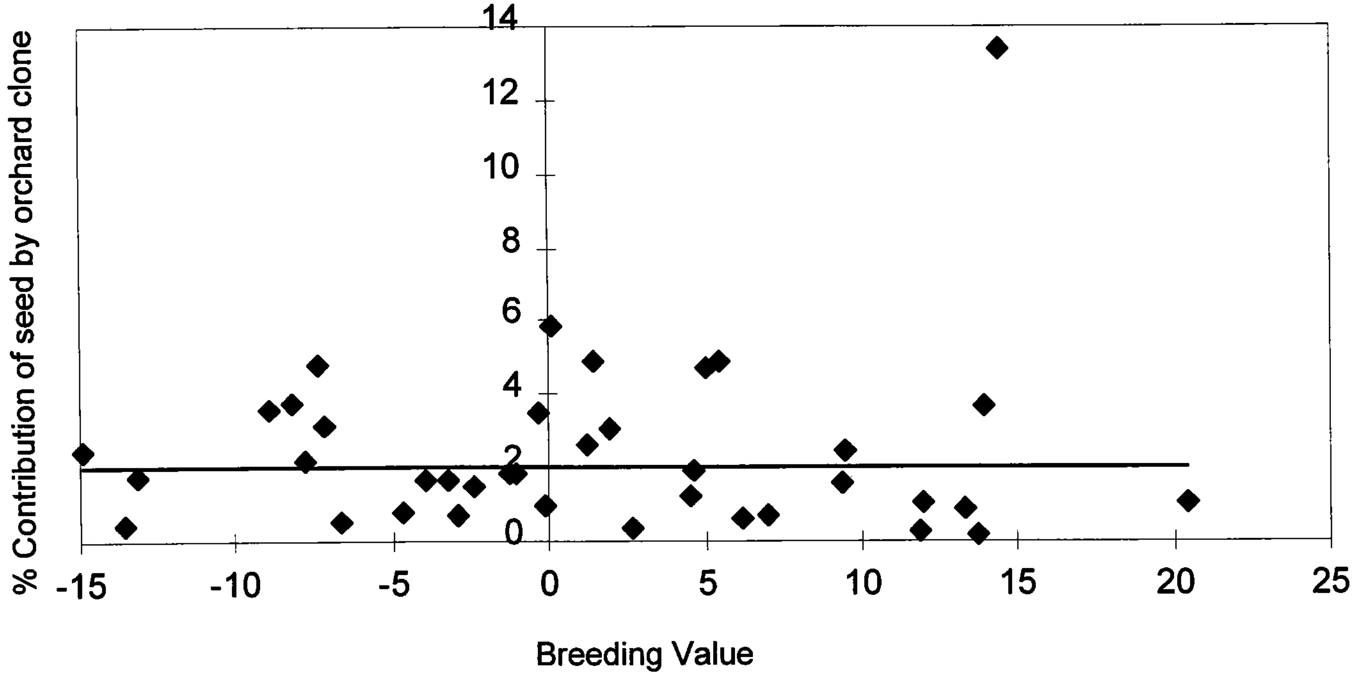

Figure 2. Breeding value of white spruce clones versus contribution to orchard mix in a J.D. Irving, Limited seed orchard. The axis at the 2% level indicates balanced contribution. Points above the line are over contributing clones and those below are under contributors. (from Adams and Tosh 1998)

clones in a JDI orchard were plotted against the percent seed contribution of each clone to the orchard mix.

A total of 50 clones were represented in the orchard block where seed production by clone was studied. If the clones contributed equally, each would produce 2% of the seed in the mix. Clones over this threshold were classed as over-contributors and those under were classed as under-contributors. There was no significant correlation between breeding value and seed production; however, of the ten clones with the highest breeding value, seven were under-represented in the seed orchard mix. Techniques such as flower induction and vegetative propagation or alternative seed orchard designs may now be used along with genetic test information to achieve greater gains in production populations.

JDI has developed a clonal production system based on controlled pollination in a breeding hall, clone bank or seed orchard, followed by potted hedge establishment and vegetative bulking by rooted cuttings. This work began in 1993 using crosses among second generation black spruce selections and has now been expanded to include Norway spruce and white spruce. For the past two years, we have been striking 1 million cuttings per year and production will expand in 1998. Twenty to 30 crosses are made annually per species, so each year new genetic test information may be incorporated to continually increase genetic gain. Hedge stock plants are identified by family so adjustment of mixes is also possible by culling past years' hedges. At present, most of the rooted cuttings are planted as bulk mixtures although trial plantings of family blocks have been established. Besides the flexibility for adjusting the genetic composition of reforestation stock, scale-up periods are reduced compared to traditional seed orchards. This has been evident in the parallel development of the 7 ha second generation orchard of black spruce established by JDI. The establishment of the production populations for both seed orchard and controlled pollination/vegetative bulking projects began with grafting in 1989. By the end of 1997, over two million rooted cuttings were produced compared to approximately 250,000 orchard seedlings.

Controlled pollination and vegetative bulking will be a valuable production method for introducing stock with specialized trait combinations such as rapid growth, insect and disease resistance, particular wood properties, or adaptive traits. In spite of all the advantages, development of efficient production systems is critical. Production costs of rooted cuttings are significantly higher than seedlings and there are logistical problems with increased labour required and the relatively narrow time window for cutting production. JDI has spent considerable time in improving cost and plant quality, however, it remains a challenge to scale up rooted cutting production to a higher proportion of total nursery production.

Another aspect related to realizing the potential genetic gain from tree improvement at the forest level is the allocation of improved stock. This aspect is discussed in detail by Talbert (1993). Planting stock of the highest genetic quality will always be scarce and the overall cost effectiveness of the tree improvement program will be greatest when the best quality stock is planted on the best sites for that species. Field experience of foresters charged with the task of land management across the districts in combination with geographic information systems (GIS) are important factors. In New Brunswick, new information such as forest soils maps (Colpitts *et al.*, 1995) will also help in the decision making process. As we develop more precise methods to deliver genetic gain, continual refinement to the allocation of improved stock will have a large impact on overall effectiveness of the JDI tree improvement program.

## Biotechnology

There are a number of research areas in the biotechnology arena which have the long-term potential to make significant impacts to JDI on genetic improvement of reforestation stock. The area which has progressed the furthest is somatic embryogenesis (SE). JDI has been involved in SE since 1991 (Adams *et al.* 1994) and efforts are geared toward using this method for clonal storage using cryopreservation during the lengthy clonal testing period. Loss of juvenility is a well-known impediment to implementing clonal forestry in many tree species (Kleinschmit *et al.* 1993). JDI is presently hedging approximately 250 SE derived clones (which have also been cryostored) from over 30 full-sib second generation black spruce families. Rooted cuttings will be produced in 1998 for clonal test establishment. Additional clones will be tested in a stepwise fashion over the next five years and efforts have been expanded to include Norway Spruce and white spruce. Figure 3

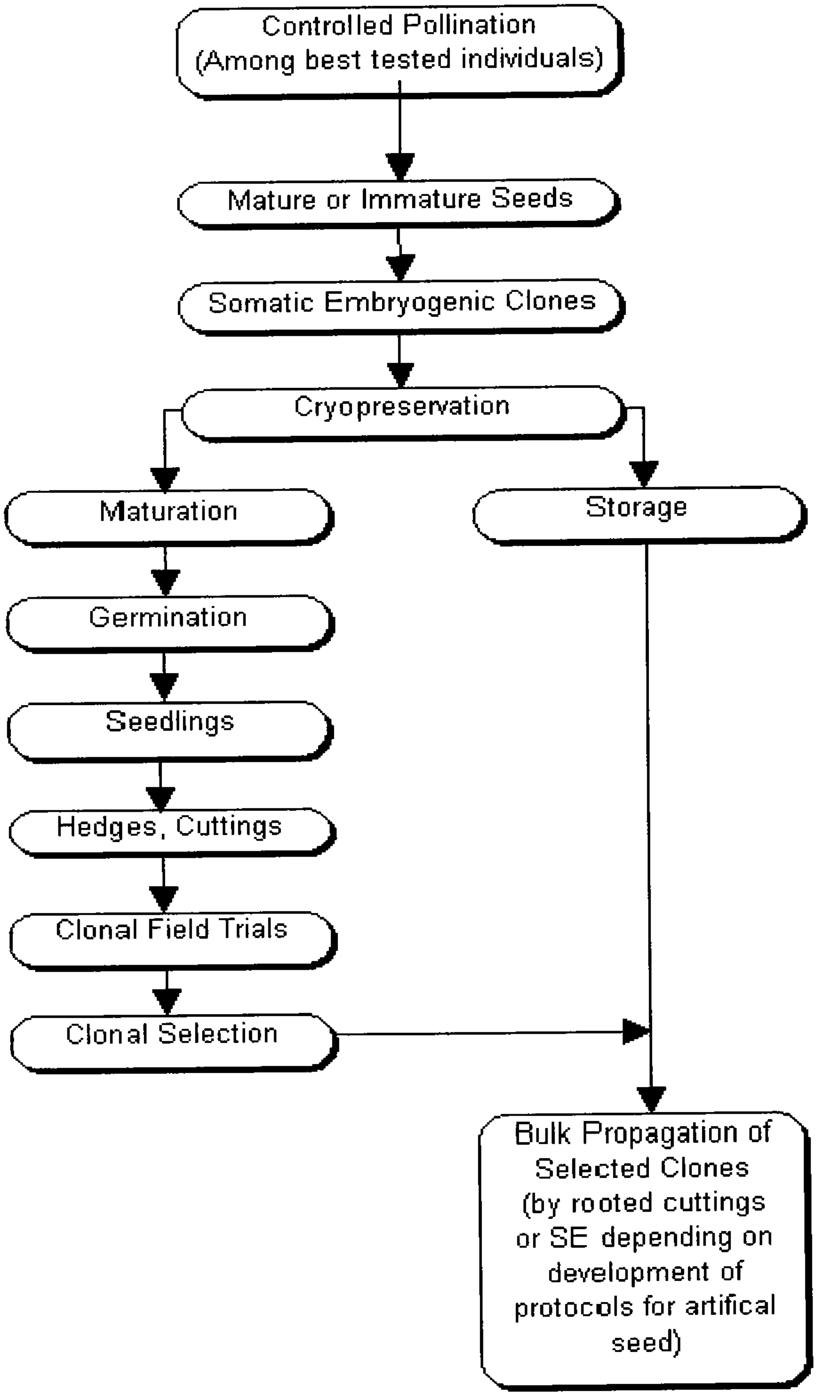

Figure 3. Flowchart for the integration of somatic embryogenesis into a commercial clonal testing program.

illustrates how SE is likely to be integrated into a JDI operational clonal production program.

Other areas of biotechnology such as genetic engineering and marker-aided selection are recognized as having significant potential, however, the time frame for practical application is much longer. JDI is quite interested in the potential of genetic engineering for pest resistance to insects such as the spruce budworm and white pine weevil, although it is well-recognized that these tools must be developed within the context of broader integrated pest management frameworks. Similarly, marker-aided selection may also find a place in selection programs, particularly for screening of production clones and for within-family selection in breeding programs. JDI is participating peripherally in a project conducted by Unversité Laval, Canadian Forest Service, Forintek Canada, and Ministère des Ressources Naturelles du Québec investigating genetic markers for wood density in white spruce and black spruce.

### Genetic Diversity

This is an area where our industrial perspective will be similar to that of most tree breeding programs. Genetic diversity of the main commercial reforestation species will be managed through regional cooperatives in the Maritimes. A strategy based on the development of sublines is being implemented for most species as we move into the second generation. The target for second generation populations is 400 selections in each breeding zone, split into 20-tree breeding groups (Fowler 1986), although this will probably vary slightly by species. The development of diverse multiple populations as described by Namkoong (1997) within species will be important from a conservation standpoint as well as for the provision of production populations. As we learn more about the patterns of genetic variation for adaptive as well as economically important traits, we will be in a very good position to develop specialized sublines which will provide greater flexibility to respond to future conditions. Currently, there are independent tree breeding programs for a number of species in each of the Maritime provinces. Fowler (1986) recommended that the Maritime provinces be treated as overlapping breeding zones. This is already providing some of the population diversity in the Maritime region as described by Namkoong (1997). Though the regional populations may remain independent, there is a strong case to be made for species to be tested, at least at some level, across regions.

Genetic diversity will need to be addressed at the production as well as breeding population level as we become more sophisticated in allocating genetic materials as described previously. Most genetically improved stock produced in the Maritimes today is allocated by bulk mixtures from orchards containing typically 40-100+ unrelated parents. Some trials have been initiated by JDI where half-sib seedlings or full-sib cuttings have been planted as mosaics of family blocks. If these deployment methods become more prevalent, guidelines for genetic diversity will need to be developed at the landscape level. Trials were initiated in 1997 which will evaluate clonal mixtures of black spruce compared with small mono-clonal blocks.

Efforts towards gene conservation of minor tree species are also being considered and this is an area where industry may play a role. Over the past few years, there have been demands for planting stock of several less common species such as the ashes and red oak for various environmental planting projects. Local seed sources are often difficult to obtain and of questionable quality. We are working towards the establishment of a few small, low-intensity seed production areas for several hardwood species. Collections are being made across a number of stands for each species and seedlings will be produced when three or four good stands can be represented. This work is at the initial stages and would benefit from a multi-agency approach.

## CONCLUSIONS

J.D. Irving, Limited has made a strong commitment to tree improvement in the past 18 years. In the next 20 years, this investment will begin to pay dividends in the same manner that initial reforestation efforts are paying off today. Maintaining flexibility to respond to changing market or environmental conditions will be an important ingredient of breeding and production strategies. A major focus of the company's tree improvement efforts will be to utilize the potential genetic gain as efficiently as possible in operational stock production. Efforts will continue to integrate new technologies such as somatic embryogenesis and as new biotechnological tools become available, they should be tested for potential application. Maintaining broad genetic diversity must be considered essential to ensure that we provide future selection opportunities.

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# TREE IMPROVEMENT IN SUSTAINABLE FORESTRY: AN ECOLOGICAL VIEW

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## SUMMARY

The productivity of forest ecosystems increases to some peak after disturbance and then gradually declines; in contrast, forest biodiversity tends to increase steadily after disturbance. These contrary trends pose a challenge for forest management: maximizing the yield of forest products at a site calls for harvesting at intervals antagonistic to the preservation of site biodiversity. This contradiction can only be resolved by management at the landscape scale, that is by dedicating some part of the landscape primarily to the preservation of biodiversity and other parts to the production of forest products. At one extreme are extensive forest reserves outside of harvest where natural processes can sustain biodiversity in perpetuity. At the other extreme are plantation forests where biodiversity is not among the management goals. Natural forests managed for sustainable yields of forest products and reasonable levels of biodiversity comprise the third element in a landscape scale strategy for sustainable forestry.

The major contributions of tree improvement programs in this tripartite strategy of sustainable forestry lie in providing better stock for plantation forestry. The greater the production of forest products per unit land area in plantations, the easier it will be to meet societal demands for forest products without compromising the preservation of biodiversity. Plantation yields can replace forest products now harvested from natural forests, which lets greater amounts of land be set aside in forest reserves and allows commercial forests to be harvested less intensively. Especially in light of the ongoing global change, there is no better means to preserve biodiversity than setting aside large tracts of forest land where natural ecological and evolutionary processes can operate with little or no human interference. Biodiversity sacrificed on a relatively small proportion of the land base, including marginal agricultural lands, thus allows the preservation of a higher level of biodiversity on forest lands as a whole. Plantation forests also offer an effective means of mitigating the rising levels of atmospheric carbon dioxide that contribute to global climate change. Furthermore, the domestication of trees suited to the more uniform and relatively favorable environmental regimes associated with plantation culture can proceed more quickly and effectively than programs directed at stock for reforestation of harvested forests. Finally, the introduction of improved stock into extensively managed forests runs the risk of eroding the genetic diversity of local tree populations. All these considerations suggest that concentrating tree improvement on the production of plantation stock will yield the best returns not only for production of forest products but also for the preservation of forest biodiversity.

## INTRODUCTION

The practice and profession of forestry is undergoing a period of reassessment and restructuring in the face of widening public concern about management of our natural resources. The collapse of fisheries and the cutting of a fast dwindling supply of old growth timber have accelerated public awareness of the limits on the ability of natural ecosystems to supply the goods and services on which human society depends. Scientists must come to grips not only with the challenges imposed by society's growing demand for resources, but also with a social and regulatory environment that is increasingly complicated. This paper is a contribution toward meeting these challenges, in particular considering how tree improvement programs might contribute to a successful strategy for sustainable use of our forests. I begin by sketching out an ecological view on sustainable forestry in a world affected by global change, and then turn to some specific questions about the future roles for tree improvement.

## AN ECOLOGICAL VIEW OF SUSTAINABLE FORESTRY

Forestry has had a tradition of sustainability throughout this century, but in large part that tradition focussed on sustaining the timber resource: "wise use" of previously unharvested forests that would carry the industry through to the time when replanted stock would yield a steady annual harvest from managed forests (Carrow 1997). In this traditional view, value is placed on maximizing the rate of growth for high quality timber in stands established after harvest, hence reducing the time to the next economically viable harvest at the site. In support of this goal, tree breeders have focussed on selecting lines that can provide planting stock with rapid growth and good form across a wide range of environmental conditions (Zobel 1984). Given an emphasis on timber yield and the nature of temporal changes in the productivity of forest ecosystems, this approach only makes sense. Once annual wood production per unit land area begins to decline, an economic analysis calls for harvesting and replanting to maximize timber yields over time and space in the managed landscape. From an ecological viewpoint, there is a problem with this narrow economic analysis of managing timber yields – value is not assigned to a critically important parameter in the analysis of sustainability: biodiversity.

In the past decade, there has been a worldwide focus on biodiversity and Canadian foresters have not stood apart from this discussion (Namkoong 1991; Boyle 1991, 1996; Riley 1995; Kimmins 1997a, b; Carrow 1997). There is an emerging consensus that the preservation of biodiversity is an essential element in achieving the sustainable use of natural ecosystems (Harding and McCullum 1993; Taylor 1994; Mooney *et al.* 1996; Christenson *et al.* 1996; Ehrlich 1996). The Convention on Biological Diversity agreed to at the United Nations Conference on Environment and Development in Rio de Janeiro in June 1992 commits governments to promoting "the conservation of biodiversity [and] the sustainable use of its components". There has been much discussion of just what biodiversity and sustainability actually mean in practice (Grayson 1995; Szaro and Johnston 1996; Christenson *et al.* 1996; Ehrlich 1996; Kimmins 1997a,b), and in this context it is useful to note the formal definitions in this international Convention itself:

> "Biological diversity" means the variability among living organisms from all sources including, *inter alia*, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems
>
> "Sustainable use" means the use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining its potential to meet the needs and aspirations of present and future generations.

Under the 1992 Convention on Biodiversity, we also are committed specifically (Article 8) to various measures that bear directly on forest management and in turn on future strategies for tree improvement: 1) establish a system of protected areas or areas where special measures need to be taken to conserve biological diversity, 2) regulate or manage biological resources important for the conservation of biological diversity whether within or outside protected areas, with a view to ensuring their conservation and sustainable use, 3) promote the protection of ecosystems, natural habitats and the maintenance of viable populations of species in natural surroundings, 4) promote environmentally sound and sustainable development in areas adjacent to protected areas with a view to furthering protection of these areas, 5) rehabilitate and restore degraded ecosystems and promote the recovery of threatened species, and 6) prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species.

Internationally, attainment of these objectives is being advanced through the cooperative efforts of the Intergovernmental Panel on Biodiversity and the Intergovernmental Panel on Sustainable Forestry. There is a rapidly evolving body of international initiatives and regulations (Grayson 1995). In Canada each province has pursued these goals, to greater or lesser degrees in consonance with the federal government's Canadian Biodiversity Strategy. There is also an increasingly wide public interest in the management of our forests (Blouin and Comeau 1993; Harding & McCullum 1993; Taylor 1994; Parfitt and Zimmermann 1994; Pendleton 1997), and an associated development of certification procedures for sustainability (Armson 1996; Ozanne and Vlosky 1996). It is clear enough that the practice of forestry must now include sustaining not only timber resources but also the biodiversity of forest lands (Christenson *et al.* 1996). We need only ask, how do we translate these general commitments into a practical prescription for management of Canadian forests and what are the implications of that prescription for tree improvement?

To an ecologist, one point where traditional forest management is shifted by these commitments to sustaining biodiversity becomes immediately clear: forest systems that have passed the phase of peak productivity and therefore are overdue for harvest, in the traditional analysis, in fact hold increasing value as reservoirs of biodiversity. In any forest ecosystem, there will be species associated with its early development after disturbance but others that only enter the system after a time (Norse 1990; Peterken 1996; Davis 1996). There are species found only in more mature forest stands and others found only in younger, early successional stands (Halpern and Spies 1995; Timoney and Robinson 1996; Noon and McKelvey 1996). Recovery of local biodiversity after disturbance can take years, even centuries (Foster *et al.* 1996). If we too drastically alter the natural balance of young and old stands in any forest type on the landscape, we run the risk of losing species or impoverishing the genetic diversity of species. If we convert too much of our forested land to young stands, we increase the risk of establishing alien species, which tend to invade disturbed sites (Binggeli 1996; Reichard and Hamilton 1997). These points have not been unrecognized by foresters. Witness recent discussions of new harvest methods designed to help maintain site biodiversity (Bamsey 1995; Cantin and Potvin 1996; Lieffers *et al.* 1996; Bergeron and Harvey 1997) and the development of landscape scale management plans including reserves (Pojar *et al.* 1994; Fenger 1996; Delong and Tanner 1996).

From an ecological viewpoint (Christenson *et al.* 1996), the nature of biodiversity in forests and our international commitments suggest a tripartite strategy for the management of Canadian forest lands:

1) *Setting aside a larger fraction of our forest lands as reserves outside of commercial exploitation in perpetuity.* Only about 2% of our forests are protected as parks and reserves, compared to 16% in Russia (Dixon *et al.* 1994; Colwell *et al.* 1997). About 57% of our forests are deemed suitable for commercial use, and 29% are under exploitation and management now (Carrow 1997). This preponderance of unexploited forests is unusual (Lamas and Fries 1995) and gives us opportunities denied to most other countries, opportunities that some may consider radical or unrealistic. We would do well to set aside a significant part of the commercial forest lands and the large part of the 43% forest land now classed as noncommercial moved across into reserves. These reserve systems should represent every major forest type at different stages of present development (not only "old growth"), and each reserve should be large enough and appropriately situated (watershed integrity, buffer zones, roadless tracts) to sustain its natural biodiversity and function over time. These reserves should be left largely unmanaged and only little used for low impact recreation and scientific research. This expanded, extensive system of forest reserves would provide our primary reservoirs for the preservation of genetic and species diversity over the coming centuries.

2) *Continued exploitation of some part of the natural forest lands that are being commercially harvested and managed now, but using strategies of harvest and reforestation to promote sustainable timber yields and reasonable levels of biodiversity.* New silvicultural strategies are being developed that respect the ecological diversity of different forest types and that show promise for sustaining biodiversity (Bamsey 1995; Cantin and Potvin 1996; Bergeron and Harvey 1997).

3) *Augmentation of industrial forest lands through afforestation of marginal agricultural lands and increased use of fiber and wood products from plantations.* Less than 1% of Canadian forest lands are in plantations, compared to almost 4% in Russia and over 2% worldwide (Dixon *et al.* 1994). Increased use of plantation forestry in Canada could relieve pressures on harvest of natural forest and allow their better management for sustainability of biodiversity (Gladstone and Ledig 1990). Indeed, assuming no change in societal demnds for forest products, we can only ethically set aside more land in forest reserves if the consequent shortfall in our production of forest products can be offset by increased yields in plantations. Otherwise we will only satisfy societal demands for forest products by increased exploitation of natural forests elsewhere, quite probably with adverse consequences for global biodiversity (Libby 1995).

This tripartite strategy for managing our forest resources is essentially conservative, but that is its strength, not a weakness. Natural ecosystems are richly complex and only partly understood. If we wish to leave these systems resilient and in good shape for future generations, it behooves us to be cautious in their exploitation, not to push them to their limits. Human history in the long settled European landscape offers far too many examples of systems degraded in their productivity and biodiversity by overexploitation the last few millenia. Here in Canada we are stewards of a forested landscape that is still extensively wild, and this wilderness is at the root of the cultural identities of all North Americans. The majority of the populace may now be urban, but our values draw on the experience of living on a vast and little populated continent. We are stewards of wilderness, and wilderness is worth preserving for our own grandchildren and more generally for the world. Many Canadians share that sentiment from personal conviction if not from scientific assessment (Blouin and Comeau 1993; Harding and McCullum 1993; Taylor 1994; Parfitt and Zimmermann 1994; Cantin and Potvin 1996; Pendleton 1997).

## CONTRIBUTIONS OF TREE IMPROVEMENT IN SUSTAINABLE FORESTRY

The organizers of this symposium invited an ecological view of how tree improvement might contribute to sustainable development, and more particularly requested consideration of two specific questions: 1) Can tree improvement help in resolving the global warming issue? and 2) Should we use genetically improved material to regenerate natural ecosystems, or only for industrial plantations? These questions may seem somewhat unrelated, but their answers are in fact directly linked and interdependent elements in the tripartite strategy for sustainable forestry. Effective and much expanded plantation forestry, perhaps the most novel element of the tripartite strategy, also is central in the answers to both these questions about strategies for tree improvement.

### Can Tree Improvement Help in Resolving the Global Warming Issue?

To answer this question, we must begin by considering the ways that forestry practice might contribute to mitigation of greenhouse gas emissions – it is in that framework that tree breeders would have to play a role. Contemporary scientific opinion, summarized in the 1995 Assessment Report by the Intergovernmental Panel on Climate Change (IPCC), recognizes two basic mitigation strategies open to forestry (Watson *et al.* 1996, Chapter 24):

1) *STORAGE: the more carbon tied up in forests and forest products, the less carbon dioxide is in the free atmosphere to act as a greenhouse gas.*

> Store carbon by reducing the loss of existing forests to harvest, deforestation and other anthropogenic disturbances; and/or
>
> Store carbon by augmenting the pool of forest-stored carbon through afforestation and reforestation, as well as through use of cultural practices that increase the amount of carbon stored in an area of forested land.

2) *SUBSTITUTION: the more forest biomass that can be cycled through biofuels and wood-derived synthetic products, the less fossil fuel need come out of deep storage pools into the active global carbon cycle.*

Assuming a system of forest management on the lines outlined above, how can tree improvement aid and abet these different mitigation strategies? There are two complementary approaches to increasing the pool of carbon stored in forests: 1) reducing the loss of existing forests to harvest, deforestation, and other anthropogenic disturbances, and 2) augmenting the pool of forest-stored carbon by afforestation and reforestation as well as through use of cultural practices that increase the amount of carbon stored in an area of forested land.

In terms of augmenting storage, breeders have little or no direct role in management of wild forests, BUT they can relieve the pressures on wild forests by creating stock for effective plantations and/or replanting material that will grow more rapidly (store carbon more quickly) than wild stock (Gladstone and Ledig 1990; Wright *et al.* 1992; Barker *et al.* 1995; Maclaren 1996). New Zealand has adopted this strategy for sustainability. The 23% of its land surface in natural forests is set aside for conservation and commercial forestry occurs only on another 4.8% of the land surface in plantations, mostly *Pinus radiata* (Clapp 1995; Maclaren 1996). Plantations are playing an increasing role in forestry worldwide to the advantage of timber resources and carbon sequestration (Sedjo 1996; Winjum and Schroeder 1997). Tree breeders can play a direct and significant role by breeding stock for afforestation or reforestation of degraded or agriculturally marginal sites – trees can store more carbon on these marginal lands than herb or shrub-dominated ecosystems (Sampson and Hair 1992; Watson *et al.* 1996). Species can be bred for production of biomass energy or biochemical products in intensively managed plantations (Sedjo 1996; Winjum and Schroeder 1997).

### Should We Use Genetically Improved Material to Regenerate Natural Ecosystems, or Only for Industrial Plantations?

There are two considerations in answering this question, both suggesting that tree improvement should favor development of improved stock primarily for industrial plantations. On the one hand, planting improved stock into natural forests imposes some risk of disrupting patterns of genetic diversity in these natural populations. Tree improvement programs strive to retain the full range of genetic diversity in natural populations through both *in situ* and *ex situ* collections, but fully achieving this goal is difficult (Riggs 1990; El-Kassaby 1992; Yang and Yeh 1992). Furthermore, the selection procedures and criteria used in tree improvement favor only a subset of the genetic diversity in natural populations, potentially to the disadvantage of specialized adaptations to particular sites and unusual environmental conditions (Friedman and Foster 1997; Libby *et al.* 1997). Planting of improved stock in natural forests can introduce novel genes to a population already reduced in genetic diversity through harvest (Buchert *et al.* 1997), which may further erode adaptation to local conditions. It therefore seems preferable ecologically that natural forests that are harvested should be regenerated with local seed or by advance regeneration. Little is gained and some level of local adaptation may be lost by planting improved stock to regenerate natural forests. Let improved stock be restricted to plantations and urban forests where reduced and selected levels of genetic diversity are the norm and the potential gains of domestication are greatest (Zsuffa *et al.* 1996; Winjum and Schroeder 1997; Lambeth and McCullough 1997; Libby *et al.* 1997). This is the second, and perhaps strongest, argument in favor of restricting the planting of genetically novel stock to plantations: trees can then be selected more effectively for performance in the favorable resource regimes typical of plantation systems. The breeder's strategy can essentially focus on domestication of wild or hybrid lines with a greater probability of rapid gains in productivity, hence better advantages in terms of sustainable forestry and preservation of biodiversity on the landscape as a whole. *Eucalyptus*, *Larix*, *Pinus*, and *Populus* all show promise as domestic tree crops with *Populus* perhaps the best current example of these advantages in northern forests (Stettler *et al.* 1996; Bisoffi and Gullberg 1996; Zsuffa *et al.* 1996).

## TREE IMPROVEMENT FOR AN UNCERTAIN FUTURE

Whatever reductions we may achieve in greenhouse gases over the next few decades, it is clear we will still live in a different climatic regime later in the 21st Century (Houghton *et al.* 1996; Watson *et al.* 1996). The scientific consensus on this has taken hold even if there is still considerable uncertainty about the details in time and space. There will be substantial changes in our forests both naturally and through our interventions, changes that will feed back on the climate system itself (Apps and Price 1996; Breymeyer *et al.* 1996). We need to consider whether the preceding analysis and recommendations are likely to hold up in the face of ongoing global change. To do so we need to think about our forests not on the time scale of decades or centuries involved in stand development, but rather on the time scale of millenia.

Consider the forest cover of the northern hemisphere 18 000 years ago (Watson *et al.* 1996); different models generate somewhat different detail, but the broad patterns are consistent and useful for our discussion. The boreal species that now constitute our commercial forest base were restricted to a very small land area well to the south, or stranded on isolated mountain peaks in the west. Over the course of the 10-12 000 years since the ice really began to retreat from the Canadian landscape, the forests we know today have built up through dispersal from glacial refugia (Ritchie 1987; Delcourt and Delcourt 1991; Gordon 1996). This revegetation of the landscape has not occurred or been sustained in a stable unchanging climate, but rather in the face of interannual variation set against a backdrop of longer term cyclic trends (Houghton *et al.* 1996). The plants and animals in our forest ecosystems have had to deal with variable and changing climate in the past, and to some degree must have been selected for survival in the face of these long term natural cycles. Now these forests are facing a far more rapid set of changes in climate and resource availability.

The future landscape is likely to be much altered and poses many interesting challenges for forest tree improvement. The climatic regimes favoring different forest types are shifted northward (Watson *et al.* 1996), but the soils on which these new forests grow will be those developed under postglacial regimes. Will grasslands really grow on the podzolic soils of former boreal forest just because the climate has become favorable? It certainly seems unlikely that we can convert these new northern grasslands to traditional agricultural crops, but perhaps we should look to developing trees for plantations in these regions as climate change proceeds? Can the deciduous habit attain dominance in a climatically favorable, but edaphically impoverished region? Theory suggests that this combination will favor needle-leaf evergeens more like the present southern pines – should we look to breeding such new stock? We have no answers to such questions now, but they are worth thinking about seriously.

Whatever the answers to such questions, it seems likely that the tripartite strategy for sustainable forestry holds the best promise for protecting both forest productivity and biodiversity into a somewhat uncertain future. Many of the reserves we set aside now will be much altered as climate change proceeds, but let them be. If we have appropriately laid out the reserves on the landscape, they will be sufficiently connected to allow species to migrate in the face of climate change. They will have preserved genetic diversity that may allow some *in situ* adaptation to the changing conditions. These reserves will continue to harbor material that we can tap for tree improvement programs. They will serve as scientific benchmarks for the ongoing global change. That's why it is so important to set aside these reserves now – without the full range of biodiversity to draw on, we may not be able to engineer our way out of the changes we have set in motion. Our best hope is to preserve the materials that we need to devise ways to meet the challenges of this much altered global system. To discover or create the trees we need to sustain the flow of forest products that society requires, we will need to draw on the full range of genetic and species diversity. The best way to do that is to immediately set aside from commercial exploitation or management fairly large tracts of wild land. The present Canadian Biodiversity Strategy calls for 12% of our land base in reserves, which would indeed be a significant improvement – but setting aside something on the order of 40% of our forest lands in reserves, 40% in managed natural forests, and 20% in highly productive plantations would be an even better investment in our future. Such large tracts of forest can be removed from harvest only if the productivity of plantations is high enough to offset the reduction in harvests from forest lands. That is likely only if marginal agricultural lands are shifted to use as forest plantations and if tree improvement is focussed on maximizing productivity in plantations instead of survival and growth in stock for reforestation.

As scientists we are trained to provide precise answers to particular questions, no less anywhere than in tree improvement with all its emphasis on quantitative genetics. In the light of what seems to be happening in the natural world right now, it would do us all well to hear the admonition of John Tukey (1962) on dealing with uncertainty: "Far better an approximate answer to the right question, which is often vague, than the exact answer to the wrong question, which can always be made precise". In other words, let's not let earlier pre-occupation with the management for sustained timber yield block a creative re-assessment of goals for tree improvement that is focussed on the balance between managing both timber and biodiversity. Breeding trees in the light of only ever more precise definition and improvements linked only to growth and yield on lands managed for their annual allowable cut will miss the point. We really need to recast and redirect tree improvement goals so that they also serve the needs of preserving biodiversity. That calls for a focus on plantation forestry.

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# L'AMÉLIORATION GÉNÉTIQUE :
# OUTIL DE DÉVELOPPEMENT DURABLE À PRIVILÉGIER

**Gilles Vallée**

Ce sujet sera abordé dans le contexte du Québec où le secteur forestier a atteint un stade de développement économique et social qui risque d'être limité dans son expansion compte tenu de différentes contraintes que j'énoncerai plus loin.

## LA SITUATION ACTUELLE DU REBOISEMENT

Lorsque j'ai commencé en 1968 mes travaux de recherche et développement en amélioration génétique des arbres, le premier manuel que j'ai lu s'intitulait *Aspect génétique de l'amélioration des arbres* de Jonathan W. Wright publié en 1963. Dans cet ouvrage, Wright écrit « qu'une bonne sylviculture fait autant qu'une sélection génétique dans un peuplement régénéré naturellement. S'il pratique une sylviculture intensive, le forestier conserve à l'occasion des éclaircies successives les meilleurs arbres tout comme le sélectionneur garde les meilleurs arbres comme porte-graines. C'est pourquoi le sélectionneur sera plus utile en encourageant le forestier à pratiquer une sylviculture intensive qu'en se substituant à lui ». Dans le même chapitre, Wright écrit que « la sélection pour la vitesse de croissance peut être plus intéressante pour des espèces destinées à être plantées sur des bandes nettoyées (cultivées) que pour des espèces destinées à être mises en place, sans préparation préalable (du site), au milieu de la végétation naturelle existante ». Je reviendrai sur cette dernière citation.

Dans *Introduction to forest genetics* du même auteur publié en 1976, Wright écrit dans la préface que « les forestiers autrefois se fiaient surtout sur la régénération naturelle ; maintenant ils trouvent souvent plus expéditif de planter immédiatement après la récolte. En effet, dans plusieurs régions la foresterie est synonyme de culture de plantation » (traduction libre de l'anglais). Dans les années 1970, c'était l'époque où au Québec comme ailleurs dans le monde, le reboisement était considéré comme une activité écologique et avait le vent dans les voiles. Par ricochet, l'amélioration génétique des arbres avait les faveurs des gestionnaires forestiers, de l'industrie et des gouvernements du Québec et du Canada. De grandes superficies étaient reboisées après la récolte de la forêt naturelle et après, bien sûr, une préparation sommaire des sols (scarifiage). Des plants les moins coûteux et non améliorés étaient mis en terre et on appliquait des phytocides pour dégager les arbres plantés.

Les opérations d'établissement des plantations étaient généralement faites sur la base du coût minimum pour chacune des opérations sans trop de considération de l'impact d'une opération sur la suivante et aussi sur la production et la période de rotation des plantations.

Après quelques années dans ce type de fonctionnement, force fût de constater que nos plantations imitaient la régénération naturelle et qu'il valait peut-être mieux mettre l'accent sur la protection de la régénération naturelle et des sols lors de la récolte des arbres, faire le regarnis de la régénération naturelle pour augmenter le *stocking* et faire de l'éclaircie précommerciale dans les jeunes peuplements. D'ailleurs, quelques études faites dans les régénérations naturelles ainsi traitées montrent que la production attendue est comparable à celle des plantations conventionnelles dans le cas de l'épinette blanche, de l'épinette noire et du pin gris. C'est d'ailleurs une hypothèse de production retenue dans le manuel d'aménagement forestier du ministère des Ressources naturelles du Québec.

Le reboisement effectué actuellement au Québec, qui est d'environ 150 millions de plants par année, est donc fortement concurrencé par une sylviculture intensive des forêts naturelles, d'autant que celles-ci peuvent produire plus de bois immédiatement par l'application d'éclaircies commerciales à tous les peuplements traitables actuellement ou qui le deviendront. Donc plutôt que de faire des reboisements qui imitent la forêt naturelle, mieux vaut appliquer une bonne sylviculture à la forêt naturelle.

Cependant, la sylviculture intensive des peuplements naturels au Québec a ses limitations, comme par exemple l'éloignement d'une grande proportion de la forêt commerciale des bassins de main-d'oeuvre nécessaire à la réalisation des traitements sylvicoles, la structure d'âge des peuplements, la composition des peuplements (mélange d'espèces), etc. Il faut donc élaborer d'autres approches pour assurer un développement social et économique durable du secteur forestier québécois. La culture intensive d'arbres en plantation ne serait-elle pas une approche à mettre de l'avant, comme l'a suggéré Wright (1963) ?

## LA SITUATION DU DÉVELOPPEMENT DURABLE DU SECTEUR FORESTIER

Quelle est actuellement au Québec la situation du développement durable du secteur forestier ? Pour moi, le développement durable du secteur forestier signifie son expansion dans l'avenir et non seulement le maintien des activités économiques et sociales au niveau actuel.

Le tableau 1 fournit quelques statistiques sur la possibilité annuelle de récolte de bois par rapport aux attributions des volumes de bois en forêt publique et à l'utilisation des bois en forêt privée.

Tableau 1. Possibilité annuelle de récolte de bois ( en millions de $m^3$) dans les forêts du Québec, comparée aux attributions de bois en forêt publique et à la récolte en forêt privée [1]

| | **Forêt publique** | | **Forêt privée** | | **Total** | |
|---|---|---|---|---|---|---|
| | **Possibilité** | **Attribution** | **Possibilité** | **Bois récolté** | **Possibilité** | **Attribution plus bois récolté** |
| Résineux | 31,5 | 27,3 | 5,1 | 4,1 | 36,6 | 31,4 |
| Peupliers | 3,9 | 2,8 | 2,2 | 4,9 | 6,1 | 11,2 |
| Autres feuilles | 7,9 | 3,5 | 5,4 | | 13,3 | |
| Total | 43,3 | 33,6 | 12,7 | 9,0 | 56,0 | 42,6 |

[1] Extrait de : *Ressource et industrie forestières, portrait statistique*, édition 1996. Ministère des Ressources naturelles du Québec, Gouvernement du Québec.

Pour bien interpréter ces données, il faut tenir compte de la récolte économiquement rentable des volumes de bois disponibles et de l'inaccessibilité de certains volumes de bois liée à la situation géographique et topographique ou du mélange d'espèces.

Ainsi l'écart de 5,2 millions de mètres cubes entre la possibilité et la récolte annuelle des bois résineux diminue très significativement lorsque l'on tient compte des contraintes mentionnées précédemment, auxquelles il faut ajouter des réserves de bois nécessaires pour compenser les pertes inévitables par le feu, les épidémies d'insectes et des catastrophes climatiques. C'est ainsi que l'on considère qu'il n'y a pratiquement pas de disponibilité en bois résineux au Québec pour approvisionner de nouvelles usines. D'ailleurs, déjà certaines régions du Québec souffrent d'une pénurie de bois résineux qui s'est traduite par une diminution des approvisionnements des usines durant les dix dernières années.

La disponibilité en bois feuillu est plus élevée que pour les résineux, soit 8,2 millions de mètres cubes. Cependant, une forte proportion de cette disponibilité est constituée de bois de trituration pour lequel les marchés de transformation sont très limités, particulièrement dans le cas des feuillus à bois dur. Par contre, il y a un déficit important entre l'offre et la demande en bois feuillu de qualité sciage et déroulage. Actuellement, des usines de transformation du Québec importent du bois de cette qualité des États-Unis et d'autres pays.

Quelle est l'importance sociale et économique du secteur forestier - filière du bois ? En 1995-1996, la filière bois du secteur forestier contribuait pour 19,3 % des exportations et 3,1 % du produit intérieur brut du Québec, fournissant 15,3 % de la masse salariale et 13,8 % des emplois directs du secteur manufacturier du Québec. Il y a au Québec 62 usines de pâtes, papiers et cartons, 1 032 usines de sciage et 1 825 autres usines transformatrices de bois. Environ 250 municipalités dépendent directement de la récolte et de la transformation du bois, qui engendrent près de 200 000 emplois.

Ces statistiques démontrent l'importance cruciale pour la société québécoise du secteur forestier - filière bois, auquel il faut ajouter la contribution des autres ressources forestières comme le tourisme, la chasse et la pêche, etc. La forêt et la production de bois sont des vocations naturelles du Québec dont la forêt couvre 757 900 km$^2$, ce qui représente 2 % des forêts mondiales pour une population québécoise de 6,9 millions d'habitants.

D'autres contraintes plus récentes viennent ou viendront de plus en plus diminuer la disponibilité des bois et donc la possibilité de production de bois des forêts naturelles et, par conséquent, le développement durable du secteur forestier (filière bois) :
1) L'aménagement intégré des ressources du milieu forestier, la diversité biologique ainsi que les règlements et normes d'intervention en forêt imposent que lors de la récolte, des bandes riveraines, des aires de confinement pour le gibier et des milieux de vie de certaines espèces soient laissées intactes ou coupées en éclaircie. Ces superficies sont autant de forêts soustraites totalement ou partiellement à la production de bois.
2) Les pressions internationales se font de plus en plus pressantes auprès des gouvernements pour la création de réserves écologiques intégrales. Une norme de 12 % des superficies forestières mises en réserve écologique est proposée en Europe mais pour des grands pays forestiers comme le Canada, les États-Unis et d'autres, cette norme pourrait être plus élevée, surtout si l'on considère la faible intensité de sylviculture pratiquée. Au Québec par exemple, en augmentant l'intensité de sylviculture des forêts près des lieux habités, il serait probablement possible de produire tout le bois nécessaire aux usines de transformation en place et même plus, d'où la possibilité de laisser plus de superficies de forêt en réserve écologique intégrale pour le patrimoine international.
3) Aussi, quelles seront les contraintes imposées à la production de bois des forêts naturelles lorsque l'on connaîtra en partie le fonctionnement des écosystèmes forestiers pour faire par la suite un aménagement durable des ressources du milieu forestier, obtenir la certification CSA et répondre à la norme IS0 14000 pour harmoniser la gestion de l'environnement à l'échelle internationale ?

## UNE DES SOLUTIONS: LA CULTURE INTENSIVE D'ARBRES

Toutes ces contraintes que je viens d'énoncer et d'autres qui s'ajouteront dans les prochaines années, m'amène à la conclusion que l'aménagement et la sylviculture de la forêt naturelle peuvent permettre une augmentation de la production de bois pour supporter le développement durable du secteur forestier, mais cette option risque d'atteindre à moyen terme ses limites tant biologique qu'économique. D'ailleurs, cette récolte se compare dans une certaine mesure à la cueillette des fruits et des racines des plantes que faisaient les hommes préhistoriques pour se nourrir avant qu'ils développent l'agriculture. Je crois que le temps est venu de penser en terme de « culture intensive d'arbres sur des superficies de terre réservées à la production de bois ou de biomasse ligneuse », semblable aux superficies de terre qui sont réservées et aménagées pour les productions agricoles.

C'est dans les conditions de culture intensive d'arbres que l'amélioration génétique des arbres va devenir un outil puissant à privilégier pour contribuer et assurer le développement durable du secteur forestier, comme d'ailleurs l'amélioration génétique des plantes dont l'humain se nourrit a trouvé son plein épanouissement avec l'intensification des cultures agricoles. Dans ces conditions, les arbres améliorés pourront pleinement exprimer tout leur potentiel de production et donc le maximum du potentiel des gains génétiques pour lesquels ils ont été sélectionnés. De plus, comme c'est le cas actuellement, les risques de dissémination des gènes des lignées améliorées seront réduits vu que les plantations ne seront plus dispersées ici et là à travers la forêt naturelle.

Mais les stratégies d'amélioration actuellement retenues répondent-elles adéquatement aux besoins d'une culture intensive des arbres?

Je dirais « oui » pour les espèces d'arbres faciles à bouturer, mises en terre sous forme de clones comme les peupliers hybrides, les eucalyptus, etc. mais j'en doute pour les espèces dont les variétés améliorées proviennent de vergers à graines comme la majorité des espèces résineuses (épinette, pin, mélèze) difficiles à multiplier par bouturage à faible coût. Pour ces espèces, les stratégies se préoccupent d'avoir une base génétique large avec des sous-populations afin de poursuivre à long terme le processus d'amélioration génétique et de s'assurer d'une bonne diversité génétique. Ces stratégies sont très valables et nécessaires pour le long terme et pour ne pas aboutir à un cul-de-sac. Cependant, elles ne recherchent pas nécessairement à court terme les gains génétiques maximums que la culture intensive d'arbres exige pour s'épanouir.

Ainsi, certains types de travaux d'amélioration génétique des arbres ne se font pas parce qu'ils ne font pas partie des étapes d'amélioration à long terme, même s'ils peuvent donner à court terme des informations pour développer des variétés améliorées à forts gains génétiques. Au Québec par exemple, certains vergers à graines de 1<sup>re</sup> génération produisent plus de graines que les besoins mais avec un gain génétique amoindri pour la croissance à cause des objectifs de production en graines préalablement prévus et pour conserver une diversité génétique. Ne pourrait-on pas dans ces vergers faire une récolte sélective sur les arbres-mères donnant des descendances hautement productives ?

Je citerai ici le cas des vergers à graines clonaux d'épinette blanche du Québec. Une recherche a débuté en 1996 pour identifier les clones produisant les meilleures descendances, de façon à pouvoir recommander une récolte sélective de cônes en fonction du gain en croissance désiré. Compte tenu des connaissances sur la variation de croissance entre les familles d'épinette blanche provenant d'arbres sélectionnés en forêt naturelle et du nombre de clones en verger soit ± 200, on estime qu'en sélectionnant 25 % des clones par verger on obtiendra entre 20 à 30 % de gains en croissance en produisant toutes les graines nécessaires pour 25 M de plants[1], car les arbres de ces vergers auront atteint dans 5 à 10 ans leur pleine maturité sexuelle et leur pleine production en cônes (arbre de ± 10 mètres).

Mais on peut obtenir plus de ces travaux, en réalisant une sélection plus intense des clones qui donneront des descendances avec des gains en croissance de plus de 30 % peut-être et en visant une densité plus élevée du bois pour contrer la forte proportion de bois juvénile chez les arbres cultivés. Les ramets de ces clones pourraient subir des traitements culturaux et d'induction florale de façon à produire suffisamment de graines pour réaliser des plantations intensivement cultivées. Les vergers à graines de 1<sup>re</sup> génération sont pleinement productifs ; pourquoi ne pas exploiter et rentabiliser cette infrastructure au maximum ? Certains diront : attention à la diversité génétique ! Je pense que dans ces plantations cultivées intensivement sur de courtes ou moyennes rotations, la diversité génétique n'est pas aussi nécessaire que dans les plantations conventionnelles avec des rotations de 80 à 100 ans ; à titre d'exemple, pensons aux plantations clonales de peupliers hybrides, de saules, d'eucalyptus, etc. qui, malgré les grandes superficies qu'elles occupent, ne subissent pas de catastrophe pathologique ou entomologique lorsque les clones plantés sont bien adaptés aux stations et aux climats pour lesquels ils ont été sélectionnés.

La mise au point d'une technique de pollinisation massale laisse entrevoir des gains génétiques encore plus importants en permettant la production de masse de semences de croisements biparentaux spécifiques ou interspécifiques produisant des familles sélectionnées pour leur forte croissance et la qualité de leur bois. Dans le programme d'amélioration génétique des espèces résineuses en cours de réalisation au Québec par le ministère des Ressources naturelles, les stratégies d'amélioration comprennent la mise au point de variétés multifamiliales dans le but d'obtenir le maximum de gains pour la production et la qualité du bois. Parallèlement, un projet de recherche est en cours pour mettre au point une technologie peu coûteuse de production massale de semences de croisements biparentaux.

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[1] Vallée, G. et J. Beaulieu, 1995. *Options pour obtenir des gains génétiques supplémentaires pour la croissance : Sélection des meilleurs clones des vergers à graines clonaux de 1<sup>re</sup> génération d'épinette blanche*. Rapport interne n° 407. Ministère des Ressources naturelles, Direction de la recherche forestière.

Dans le cas de l'épinette noire, des tests précoces de descendances biparentales obtenues de croisements entre des arbres sélectionnés des meilleures provenances et descendances connues montrent qu'il est possible d'obtenir des gains de 56 $m^3$/ha à l'âge de 35 ans par rapport à des provenances témoins (communication de Michel Villeneuve). Ce résultat a été obtenu avec un nombre restreint de croisements utilisant des géniteurs n'ayant subi qu'une étape de sélection. Quels gains obtiendra-t-on par des croisements entre les meilleurs arbres des meilleures familles sélectionnées à partir de ces croisements ? Il faut noter aussi que ces résultats ont été obtenus dans des conditions de culture intensive (sol labouré, désherbé et fertilisé).

Parlant de culture intensive d'arbres, a-t-on toute la technologie pour mettre en place des systèmes de production adaptés aux espèces recherchées par l'industrie au Québec ?

Comme c'est le cas pour les plantes agricoles, il serait important que parallèlement à l'amélioration génétique, on mène des recherches et du développement sur la culture intensive des arbres. Parmi les avenues à explorer, des recherches plus importantes devraient être faites sur des modèles économiques et sur le recyclage des biomasses polluantes, comme les boues d'épuration des eaux usées, les boues primaires et secondaires des usines de pâtes et papiers, les lisiers, etc., afin d'accroître la fertilité des sols. Ce recyclage aurait un effet bénéfique environnemental qui s'ajouterait à celui sur la réduction du gaz carbonique de l'air, grâce à une fixation accrue liée à la croissance accélérée des arbres cultivés.

## EXEMPLES D'IMPACTS DE L'AMÉLIORATION GÉNÉTIQUE DES ARBRES SUR LA PRODUCTION DE BOIS

Le tableau 2 montre les gains de production obtenus avec les quatre meilleures familles d'épinette noire sélectionnées parmi 200 familles testées (informations fournies par Michel Villeneuve). On prévoit un gain en volume marchand de 43 % à l'âge de 35 ans. Pour fin de démonstration, je prendrai un gain de 30 % que j'appliquerai à l'ensemble des plantations de 150 millions de plants résineux faites au Québec. On notera que l'épinette noire et l'épinette blanche constituent près de 70 % des reboisements faits au Québec et sont moins productives que les autres espèces résineuses plantées comme les pins, les mélèzes et l'épinette de Norvège. La superficie occupée par 150 millions de plants mis en terre à 2 000 plants/ha (espacement 2,0 x 2,5 m) représente 75 000 ha. Au Québec, les plantations d'épinettes blanche et noire produisent en moyenne environ 125 $m^3$/ha en volume marchand sur une période de 35 ans. Si on obtient un gain génétique de 30 %, c'est environ 38 $m^3$/ha produit en plus. À ce gain génétique, il faut ajouter ceux de la mise en terre de plants de meilleures qualités, d'une culture plus intensive du sol et d'une fertilisation à l'âge de 10 ans. J'estime à plus de 30 % ces gains d'après les résultats d'essais[2] effectués au Québec. On peut donc s'attendre d'obtenir une production d'au moins 200 $m^3$/ha en volume marchand à l'âge de 35 ans.

Avec ces gains, la production totale de 75 000 ha plantés annuellement serait de 15,0 millions de $m^3$, ce qui correspond à près de la moitié de la consommation annuelle de l'industrie en bois résineux, qui est de ± 31,4 millions de $m^3$. Il faut noter qu'à l'âge de 35 ans les arbres auraient en moyenne un diamètre valable pour le sciage.

Si le programme de reboisement du Québec revenait aux objectifs de 1983 soit 300 millions de plants/année ou 150 000 ha/année, c'est 30,0 millions de $m^3$ de bois qui pourraient être produits à partir de plantations, ce qui est presque la consommation des usines en 1995.

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[2] Plusieurs essais de fertilisation de plantations âgées de 10 ans donnent des gains de production de plus de 20 % d'après des publications de Gilles Sheedy de la Direction de la recherche forestière du MRNQ. La plantation de plants de fortes dimensions (hauteur de 50 cm et plus) d'épinette permet de raccourcir les rotations de 3 à 5 ans.

Tableau 2. Gains en production obtenus avec les quatre meilleures familles d'épinette noire sélectionnées parmi 200[5] pour un espacement de 2,00 x 2,50 m, soit 1 975 arbres/ha

| **Âge** | **I.Q.S.** m | **HM** m | **DHPM** cm | **VM** $m^3$/ha | **Gain VM** $m^3$/ha |
|---|---|---|---|---|---|
| 40 | 10,0/50 ans[1] | 8,1 | 6,5 | 29 | 56 93 |
| 40 | 14,0/50 ans[2] | 11,4 | 10,0 | 92 | |
| 35 | 8,5/25 ans[3] | 13,6 | 15,7 | 129 | |
| 35 | 11,0/25 ans[4] | 17,6 | 21,9 | 185 | |

[1] Peuplement naturel, indice de qualité de station moyen selon Carpentier *et al.* 1993.

[2] Peuplement naturel, indice de qualité de station la meilleure selon Carpentier *et al.* 1993.

[3] Indice de qualité de station moyen pour les plantations d'épinette noire au Québec selon Prégent *et al.* 1996.

[4] Indice de qualité de station des quatre meilleures familles présentant un gain de croissance en hauteur de 34,7 % à l'âge de six ans par rapport à des provenances locales. IQS = 8,5 m x 1,3 = 11,05.

[5] Informations et données fournies par Michel Villeneuve et Guildo Gagnon du Service de l'amélioration des arbres.

Mais que représentent 150 000 ha de reboisement au Québec par rapport à la superficie totale des terrains forestiers ? Cette superficie représente 0,20 % des 75,8 millions d'hectares des forêts du Québec. Sur une rotation de 35 ans, c'est 7,0 % des 75,8 millions d'hectares qui serait en plantation, soit 5,3 millions d'hectares. À titre de comparaison, la superficie totale des terres agricoles au Québec est de 3,5 millions[3] d'hectares. Ces terres agricoles sont des écosystèmes plus artificiels que des plantations d'arbres, car la forêt est l'écosystème naturel correspondant au climat du Québec.

Dans cet exemple d'impact, j'ai utilisé des rotations de 35 ans mais la culture intensive d'autres essences comme les mélèzes hybrides pourraient produire des volumes de bois équivalent aux plantations d'épinettes sur une période de moins de 30 ans, comme le montrent les résultats présentés au tableau 3, obtenus sans qu'une amélioration génétique importante ait été faite et sans culture intensive. Il y a aussi les peupliers hybrides dont les clones recommandés pour différentes régions du Québec produisent de 8 à 10 $m^3$ par hectare par année sur des rotations de 10 à 25 ans selon la qualité des sols et la longueur de la saison de végétation. Cette production représente de trois à quatre fois plus que celle des tremblaies naturelles (voir tableau 4).

En conclusion, l'amélioration génétique des arbres deviendra un outil de développement durable à privilégier, lorsqu'une culture intensive des arbres en plantation sera pratiquée dans le but de favoriser une expansion du secteur forestier. Cette approche permettra d'augmenter la quantité de bois disponible pour créer de nouvelles usines et donc des emplois et, par conséquent, amener un développement social et économique durable des régions rurales et forestières du Québec. Ce faisant, les gains génétiques obtenus par l'amélioration des arbres seront pleinement réalisés et la production de quelques millions d'hectares de terrains forestiers pourrait passer à plus de 5,0 $m^3$/ha·a selon les espèces cultivées par rapport à ± 1,5 $m^3$ en moyenne pour la forêt naturelle.

Je crois que l'époque des reboisements éparpillés imitant plus ou moins la forêt naturelle est révolue, à cause des contraintes environnementales qui s'appliqueront à la forêt naturelle. Il est maintenant temps au Québec de concentrer les reboisements dans des zones réservées à la ligniculture où les plantations d'arbres

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[3] Source : *Profil des exploitations agricoles, édition 1995.* Gouvernement du Québec, ministère de l'Agriculture, des Pêcheries et de l'Alimentation, Direction de l'analyse et de l'information économique.

génétiquement améliorés seront cultivées intensivement.

Tableau 3. Indice de qualité de station (IQS) et volume marchand à 30 ans d'une variété de mélèze hybride (MEH), comparée aux mélèzes d'Europe (MEU) et du Japon (MEJ) dans des tests établis en 1977. Espacement 2 x 2 m

| Arboretums | MEH | | | MEJ | | MEU | |
|---|---|---|---|---|---|---|---|
| | IQS | VM | | IQS | VM | IQS | VM |
| | | m$^3$/ha | %G | | m$^3$/ha | | m$^3$/ha |
| Bonaventure | 15,8 | 204 | 10 | 15,0 | 185 | 11,9 | 123 |
| Dablon | 15,1 | 188 | 22 | 13,5 | 154 | 10,8 | 103 |
| Villeroy | 17,0 | 233 | 8 | 16,3 | 216 | 13,0 | 144 |
| Mastigouche | 13,4 | 152 | 13 | 12,5 | 135 | 8,3 | 63 |
| Matapédia | 14,6 | 177 | 31 | 12,5 | 135 | 10,0 | 89 |
| Verchères | 19,1 | 287 | 14 | 17,8 | 252 | 12,9 | 142 |
| Moyenne | 15,7 | 205 | 14 | 14,6 | 180 | 11,2 | 111 |

MEH : hybride danois, verger à graines FP 211 SORO 1, Christiansminde.
MEJ et MEU : provenances témoins, Joliette, utilisées dans le reboisement des années 70.
IQS : Hauteur à l'âge de 25 ans.
%G : Par rapport au VM du MEJ.
Origine des données : Ante Stipanicic

Tableau 4. Exemple de production obtenue dans des tests clonaux pour des clones recommandés de peupliers hybrides

| **N° clone** | **Endroit** | **Espacement initial m** | **Taux de survie du test %** | **Âge du test an** | **Hauteur moyenne m** | **DHP[2] moyen mm** | **VM[2] m$^3$/ha** | **AAM[2] m$^3$/ha/an** |
|---|---|---|---|---|---|---|---|---|
| Q22 | Populetum Matane[1] | 3,0 x 3,0 | 92 | 20 | 19,5 | 223 | 284 | 14,2 |
| Q1062 | Populetum Matane[1] | 2,4 x 3,0 | 44 | 20 | 19,2 | 294 | 278 | 13,9 |
| Q3374 | Normandin[1] | 2,0 x 3,0 | 79 | 7 | 9,4 | 126 | 36 | 5,1 |
| Q3230 | Saint-Hugues[1] | 2,4 x 3,0 | 49 | 10 | 14,4 | 218 | 132 | 13,2 |

[1] Populetum de Matane : région écologique 5c.
Normandin : région écologique 6a.
Saint-Hugues : région écologique 2b.

[2] DHP : Diamètre à 1,3 m du sol.
VM : Volume marchand.
AAM : Accroissement annuel moyen en volume marchand.

# BIOTECHNOLOGY AND MOLECULAR POPULATION GENETICS

# RESTORATION OF LONGLEAF PINE (*Pinus palustris* Mill.) IN THE SOUTHEASTERN USA: THE GENETIC RESOURCE

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Restoration of the longleaf pine ecosystem will necessarily require a great deal of planting (or perhaps direct seeding) of longleaf pine. Choosing the proper seed source will be essential to ensure long-term success of restoration plantings.

Seed were collected from 26 geographic sources of longleaf pine, 16 of which were located in provenance test plantings of the Southwide Southern Pine Seed Source Study (SSPSSS). Seed was also collected from three seed orchards and an old-growth stand. A total of 618 individual trees were genotyped at 24 isozyme loci.

The mean number of alleles per locus ranged from 1.5 to 2.27, the percentage of polymorphic loci ranged from 41 to 81, and mean heterozygosity ranged from 0.069 to 0.144. These values average lower than diversity indices found in a similar loblolly pine study. Diversity indices of the seed orchard sources were similar to those in the provenance test sources and the old-growth stand. F statistics indicate very little inbreeding overall (mean $F_{IS} = 0.002$) and low differentiation among populations (mean $F_{ST} = 0.038$). Volume per acre and height data at 25 years from the SSPSSS were compared to diversity indices. There was a positive relationship between volume and all three diversity indices. Longleaf pine appears to have less allozyme variability than loblolly pine, but there is a geographic pattern to the variability which may be useful in defining seed zones. Allozymes also appear to be useful in determining whether or not certain populations are inbred, and therefore less likely to form healthy, vigorous stands.

# HYBRIDIZATION AND INTROGRESSION IN WHITE AND ENGELMANN SPRUCES

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White spruce (*Picea glauca* (Moench) Voss) and Engelmann spruce (*Picea engelmannii* Parry) are important economically and ecologically in Western North America. These sister species form a mosaic hybrid zone in Alberta and B.C. To assess the magnitude of interspecific exchange of genes, we used the RAPD technique to analyze five natural populations of white spruce and four populations of Engelmann spruce from outside the sympatric zone and seven populations that appeared to contain hybrid swarms. A small number of markers was found to be specific to either white spruce or engelmann spruce. A radiolabeled probe made from one of these RAPD species-specific fragments used in Southern blots of the amplified products gave a quantitative difference rather than qualitative between these two species. The hybrid nature is estimated by the frequency of co-segregation of diagnostic markers each specific for a different species and the data indicate the existence of bidirectional gene flow from the sympatric zone. The extent and evolutionary significance of interspecific introgression and implications for conservation of genetic resources were discussed in the context of sustainable development.

# MICROSATELLITE DNA VARIATION AND GENETIC STRUCTURE OF OLD-GROWTH EASTERN WHITE PINE (*Pinus Strobus*) POPULATIONS IN ONTARIO

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Microsatellite DNA variation was examined at seven loci in a complete census of 222 old-growth (~250 years) eastern white pine (*Pinus strobus*) trees from two nearby populations (A and B) in Ontario. Six of the seven microsatellite DNA loci were polymorphic in both populations. Two to 17 alleles were observed at a polymorphic locus. Fifty alleles were detected in population A and 47 in population B at seven loci, with a total of 55 alleles in both populations. Forty-three to 54% of these alleles were rare at 5% criteria and 17% to 20% rare at 1% criteria. Significant heterogeneity in allele frequencies was observed over the two populations. Although these populations were only a few km apart, each of them had unique alleles. The average number of alleles per locus was 7.1, and 6.8, the average observed heterozygosity was 0.45, and 0.46, and the average expected heterozygosity was 0.48, and 0.49, respectively, in population A and B. Most of the genetic variability resided within populations, with only 1.5% genetic differentiation between the populations. The results were compared with those obtained from allozyme analysis of the same populations, and implications for gene conservation were discussed.

# CONSTRUCTION OF HIGH DENSITY GENOMIC MAP AND IDENTIFICATION OF QTLs FOR WESTERN GALL RUST RESISTANCE IN ALBERTA LODGEPOLE PINE

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We report on the construction of a high density genomic map and the identification of three quantitative trait loci (QTLs) that confer resistance to western gall rust *(Endocronartium harknessii)* in Alberta lodgepole pine *(Pinus contorta* var. *latifolia)*. Genomic DNAs from haploid megagametophytes of a half-sib family with large phenotypic variance in resistance to western gall rust (WGR) were amplified with 840 random decamer oligonucleotide primers by the polymerase chain reaction. One hundred and ten decamer oligonucleotide primers were segregating and they generated 245 sharp and reproducible Random Amplified Polymorphic DNA (RAPD) markers. Each megagametophyte was obtained by removal from the extending cotyledonary needles from germinating seedlings prior to natural abscission. The seedlings were inoculated separately with two WGR fungal isolates sampled in Alberta and Manitoba and evaluated for WGR resistance. Two hundred of 245 RAPDs were mapped onto 16 linkage groups covering a distance of 3663.2 cM. Two putative QTLs each accounted for 32% of the total phenotypic variance in resistance to WGR fungal isolates from Alberta. A third putative QTL accounted for 23% of the total phenotypic variance in resistance to WGR fungal isolates from Manitoba.

# BIOTECHNOLOGY OF ECTOMYCORRHIZAL FUNGI IN TREE IMPROVEMENT

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Biotechnology of ectomycorrhizal inoculation is being assessed for conifer growth and/or biological control of fungal root pathogens. In this study, five spruce and pine species were tested with 14 ectomycorrhizal strains in a fully randomized factorial design. After 18 weeks, shoot height, root collar diameter, and shoot dry weight were collected. Reverse-hplc was used to quantify fungal biomass in ectomycorrhizas by ergosterol assay. PCR-based markers for ectomycorrhizal DNA fingerprinting were developed. These markers will then be used for monitoring the persistence of introduced selected beneficial ectomycorrhizal strains by inoculation in forest nurseries as well as in the field. Fungal metabolites showing antagonistic effects against fungal root pathogens are also being isolated and characterized. From our results, it appears that the inoculation of tree seedlings in nurseries with specific ectomycorrhizal fungi, ecologically adapted to the planting site, would improve field performance and increase plantation productivity. Moreover, the inoculation of genetically improved plant stocks will likely maximise the benefits of the whole process of tree improvement for sustainable development.

# IMPROVED ROOTING ABILITY, ROOT-CULTURE PERFORMANCE AND STEM-GROWTH MODIFICATIONS IN *rol*-Gene-TRANSGENIC ASPEN PLANTS

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A novel and highly efficient wild-type *A. rhizogenes*-mediated transformation and regeneration procedure was developed for aspen (*Populus tremula*). Specific phenotypical changes were related to *rol*-gene expression in the transformed plants. Analyzed transgenic clones exhibited extensive root formation, with a larger root surface area and root mass relative to control (non-transformed) plants. Adventitious root formation in stem cuttings of transgenic plants showed very rapid kinetics, requiring a much shorter culture time: 4 to 12, days as compared to about 30 days for the control. Transgenic plants maintained 100% rooting throughout the year, whereas control plants had a year-round average of 90%, with considerably reduced rooting during the winter. Enhanced breakdown of apical dominance in several transgenic plants resulted in the development and elongation of up to four axillary buds per explant, in contrast to the single-shoot pattern of control plants. These transgenic plants also exhibited a higher cumulative stem length and enhanced growth rate, resulting in a higher stem-production index in several clones. Liquid-culture technique was developed for mass propagation and root production. Roots of two different transgenic lines were cultured in liquid media, in the presence of different growth regulators. Control (non-transformed) roots cultured in a hormone-free medium showed the highest number of regenerated shoots but the lowest root biomass, relative to the transgenic lines. The addition of hormones to the culture media resulted in increased shoot regeneration in control and transgenic lines. However, in the presence of BA or NAA, transgenic lines developed a higher number of shoots and root biomass as compared to the control (non-transformed) plants, resulting in a higher shoot-production index in the former. We suggest that specific poplar-tree traits can be improved through *rol* genetic transformation and selection of the desired plants.

# THE PARADOX OF GENETIC ENGINEERING IN TREES

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Genetic Engineering offers prospects for genetic improvement in forest trees at an accelerated pace. A major concern regarding gene transfer in trees, or for that matter in plants and animals, is how to regulate or direct where an alien gene, or its copies, would be integrated in the genome. A second concern is the stability and expression of transgenes themselves, or host endogenes, on a short-term and long-term basis. A third concern is the containment of the transgenic pollen. Although several heterologous model promoters have been tested for the expression of transgenes in a number of annual plant species, very little is known about their expressive control in woody perennials. Transgene expression seems to be variable and less stable in the model plant species tested. Transgene inactivation has been observed in annual plants in the form of position effects, gene silencing, and cosuppression. This might suggest that it is hard to predict if transgenes would be stably expressed in annual crops, or in forest trees with extended vegetative phases ranging from one to several decades. A number of questions present themselves that are relevant to the stability and expression of transgenes in long-lived forest trees. In addition, is it possible that tissue culture itself might contribute to genetic variation (somaclonal variation) of the transgenic plants? Or is it that the observable variation is solely due to the transgene inactivation? And finally, would genetic engineering, in reality, provide a means for achieving forest tree improvement at an accelerated rate for sustainable development? In order to guarantee stable expression of transgenes, it would be necessary to subject transgenic trees to time-consuming selection and hybridization programs before they are ready for commercial exploitation. In this presentation, available experimental data in transgenic plants, including those from our lab were discussed, and theoretical arguments on the integration, stability, and expression of transgenes in woody plants were presented.

# PHYSIOLOGICAL GENETICS
# AND PEST RESISTANCE

# INFLUENCE OF MATERNAL ENVIRONMENTS ON FROST TOLERANCE OF *Picea glauca* PROGENIES

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In order to evaluate the influence of maternal environment on the cold tolerance of *Picea glauca* (Moench) Voss progenies, full-sib families were obtained from the same controlled crosses done on container-grown grafts placed in a greenhouse and on field-grown grafts. Crosses in the greenhouse were done in January 1993 (20/15EC d/n; 16 h photoperiod). These grafts (1-2 m tall) were flower-induced in June 1992 and also received a heat treatment (28/30EC d/n; June 30 to July 30). Controlled crosses on field-grown grafts (3-7 m tall) were done in May 1992 and 1994 at a breeding orchard. They were flower-induced the preceding June. Seedlings of 5 similar crosses done in both environments (greenhouse and field) were produced and frost tolerance of needles was measured at the end of September and October 1996. Families grown from greenhouse crosses were less frost tolerant than families grown from field crosses. The experiment will continue to evaluate if the difference in frost hardiness decreases with age.

# AUXIN SCREENING OF *Pinus banksiana* Lamb. SEEDLINGS FOR PURPOSES OF EARLY SELECTION

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A monoclonal antibody against indol-3-ylacetic acid (IAA, auxin) was produced and an enzyme-linked immunosorbent assay (ELISA) for measurement of IAA levels was developed. Using combined gas-chromatography-mass spectrometry, the IAA-ELISA method was confirmed to give accurate and precise estimates of endogenous IAA content in the cambium of jack pine *(Pinus banksiana)*.

Three half-sib families of jack pine of known height growth potential (weak, intermediate, strong) were selected for investigation. Using IAA-ELISA, 3-month-old greenhouse-grown seedlings (10-30 cm tall, 2-6 mm root collar diameter) of the three families were analyzed for their auxin content. A direct correlation was found between height growth potential and cambial IAA, with the weak family having mean IAA content < 100 ng $g^{-1}_{fw}$ and the strong family having > 150 ng $g^{-1}_{fw}$.

Pole-sized specimens, 18 years old and 9-11 m in height, of the same three half-sib families also were investigated for their cambial IAA content. Again, the shortest trees (weak family) yielded the lowest mean IAA content (600 ng $g^{-1}_{fw}$). However, the family of intermediate height yielded a mean IAA content higher than that of the tallest family (1300 ng $g^{-1}_{fw}$ and 1100 ng $g^{-1}_{fw}$, respectively). The family of intermediate height-growth potential nevertheless exhibited the strongest rate of diameter growth (hence, more taper); thus, the higher IAA content in the intermediate family is in agreement with current physiological understanding of IAA promotion of diameter growth.

[1] PhD dissertation, funded jointly by NSERC and J.D. Irving, Limited (NRC/IRAP program).

# GENETIC VARIATION FOR WESTERN GALL RUST RESISTANCE IN HIGH ELEVATION LODGEPOLE PINE IN ALBERTA:
## A COMPARATIVE ASSESSMENT ACROSS TWO SITES

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The expression of genetic variation for resistance of lodgepole pine (*Pinus contorta* var. *latifolia*) to western gall rust (WGR) (*Endocronarium harknessii*) was studied at two geo-climatically different environments, Norris and Redrock, Alberta. A total of 454 half-sib families of superior trees, found mostly in high elevation natural stands in west central Alberta, were out-planted in 1990 at both sites. A modified randomized complete block design was used with 19 sets of 24 families each planted in 10 replications and three single-tree non-contiguous plots. The trials were measured at age 6 for incidence (presence and absence of galls) and severity [0 (no WGR symptoms) to 6 (maximum infection)]. Height, survival, and climatic injury were also assessed. Survival at both sites was very similar (85-87%). Mean family height at Redrock was almost 10 cm higher (60.5 cm) than that at Norris (51.0 cm). In contrast, mean family WGR incidence was 25% at Norris but only 1.6% at Redrock. A similar site difference was also observed for WGR severity. Accordingly, estimates of family and individual heritabilities for both incidence and severity varied substantially across the two sites. The possible causes of differentiated expression of genetic variation for WGR resistance at the two sites was discussed.

# CLONAL VARIATION IN NORWAY SPRUCE (*Picea abies* (L.) Karst.) RESISTANCE TO WHITE PINE WEEVIL (*Pissodes strobi* (Peck)

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An effective technique to control the white pine weevil is lacking. Integrating tree resistance into an IPM approach could be a key strategy in reducing the weevil impact. This study reflects the initial steps toward developing resistant trees suitable for Quebec conditions. In a clone bank, 67 clones represented by 2 ramets in 2 replications were used. On the terminal leader of each of these ramets, 3 female and 3 male weevils were caged during June and July in 1994 and 1996. Each year, the leaders were harvested before emergence of the new generation of adults and brought to the laboratory for observation of emergence. Leaders were kept individually in cardboard cylinders to allow the emergence of the insects, which were counted and weighed alive. Thereafter, characteristics related to insect behavior were noted (number of oviposition and feeding cavities, damage length) as well as some characteristics of the leaders (bark thickness, length).

Results demonstrated that the number of insects was significantly different per clone and per year. However, a significant interaction between year and clone was observed. Similar results were observed with insect weight, which was used as an indicator of its biological performance. Clones that produced the lowest number of insects per leader during both years were selected.

# GENETIC AND ENVIRONMENTAL DYNAMICS OF AN ARTIFICIAL INFESTATION OF A SITKA SPRUCE PLANTATION WITH THE WHITE PINE WEEVIL

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The impact of the white pine weevil (*Pissodes strobi* Peck) on young spruce plantations is of major concern to the British Columbia forest industry. Sitka spruce is especially susceptible and is so severely damaged that it has all but ceased to exist as one of our important commercial species. Annual planting of Sitka spruce has been reduced from 10 million to less than a million (mainly on the Queen Charlotte Islands) because of the severe damage (B.C. Ministry of Forests annual reports 1988-89, 1993-94, and current sowing).

Genetic resistance to the attack of white pine weevil has been noted at provenance (Ying and Ebata 1994), family (Kiss and Yanchuk 1991; Alfaro and Ying 1990; King *et al.* 1996) and clonal levels (Ying 1991; King 1994). Research into this genetic resistance, which can be quite marked (Ying 1991; Kiss *et al.* 1994), has uncovered some putative resistance mechanisms (Alfaro 1995; Alfaro *et al.* 1996a; Sahota *et al.* 1994; Tomlin and Borden 1994). We are unsure at this time how many mechanisms of resistance might be involved, how they might work and interact with each other, and how they are inherited.

Selecting and breeding for this weevil resistance is one of the major efforts we are making for Sitka spruce. We currently have around 250 OP families and over 300 clones in trials. A fast method of assessing these trials by artificial infestation has proven very successful. Three weevils were placed at the base of each tree in the first 10 replicates of a Sitka spruce progeny trial. Two years have elapsed since the infestation and attack rates in these first 10 reps are heavy at about 70%. The infestation is moving through the plantation like a wave. The original hypothesis that provenances from the dry Douglas-fir zone is supported although there is definitely a hot spot of resistance around East-Central Vancouver Island. The nature of the geographic distribution of the weevil resistance indicates some very large genetic effects.

# FIELD TESTING AND GENETIC GAINS

# MAXIMIZING A BREEDING GOAL THAT CONSIDERS BOTH GAIN AND DIVERSITY

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Breeders would like to minimize relatedness in selected populations, to conserve genetic diversity, while achieving as much gain as possible. The degree of relatedness within a population can be described as the *average coancestry* for all possible relationships, including selfs, and is the probability that two genes sampled from the population gene pool are identical by descent. We propose incorporating average coancestry in a selection criterion for the value of a set of genotypes: $B_\omega = \bar{g}_\omega - c\,\bar{\theta}_\omega$ where $B_\omega$ is the criterion, which we call the "benefit"; $\omega$ is the set of considered genotypes; $\bar{g}_\omega$ is the average of the breeding values of $\omega$; $c$ is a constant; and $\bar{\theta}_\omega$ is the average coancestry of $\omega$. The goal of breeding is defined as selecting the set of individuals $\omega$ which maximizes $B_\omega$. An iterative search algorithm for *coancestry-adjusted selection* was developed to find this maximum. Simulation was used to compare this technique with the more conventional method of restricting the number of selected progeny per parent. Coancestry-adjusted selection never produced less benefit than the conventional method and usually produced substantially more, and is thus a more efficient way to achieve gain while maintaining diversity.

# FIELD PERFORMANCE OF *Raivola* SIBERIAN LARCH AT TWO ECOLOGICALLY DIVERSE SITES IN ALBERTA

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Siberian larch (*Larix siberica*) is considered to be a promising exotic species for reforestation in Alberta. Forestry testing of the species in the province was started in the early 1970's. We report results of 17-year field testing of the species at two ecologically diverse sites. Site 1 (HRA) is located in northern Alberta (59E08' N latitude and 370 m elevation) in the boreal mixedwood wetland eco-subregion. It is characterized by silty clay soils with mesic to wet microsites. Site 2 (PRFN) is located in central Alberta (54E 04' N latitude and 610 m elevation) in an area of transition between boreal forests to the north and aspen parklands to the south. The site occupies rapidly drained sandy loam to loamy sand soils with uniform microsites. The two trials were assessed for survival, height, dbh, tree vigor, stem straightness, and climatic and pest damage. Large differences were found between plantings for survival, height, and dbh. The best performance was realized at the PRFN site where mean survival, mean height, and dbh were 94%, 8.0 m, and 14.7 cm respectively. Corresponding values for HRA were 78%, 5.8 m, and 8.1 cm respectively. Site effects on the performance of Siberian larch and its comparative performance to traditional reforestation species in Alberta were discussed.

# GENETIC INVESTIGATION OPPORTUNITIES AT PETAWAWA

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Starting in the 1920's, scientists created, studied, and monitored over 300 hundred genetic experiments at the Petawawa Research Forest. Meticulous documentation of pedigree records and measurement data has always been the norm. Studies related to transport of seed sources for planting, the effects of climate change, early growth and yield prediction, and breeding to evaluate growth performance and resistance to pests can be found. Questions concerning current interests, for example; genetic biodiversity in forest ecosystems with opportunities for *in situ* gene conservation of endangered populations, species and genotypes; demographic studies of major native conifers can be further addressed, among others, using the existing experiments.

During 1996 and 1997, an evaluation of each experiment was conducted to identify a nucleus of first class genetic materials. It is intended that these resources will be managed and protected in support of research activities and investigations. To this end, it is essential that the investigative forestry community be made aware of this elite resource and of the opportunities to further studies in current research themes.

# TREE SEED WORKING GROUP

# WORKSHOP

The papers were published in full in the March/April 1998 issue of

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# FROM FLOWERING TO ARTIFICIAL POLLINATION IN LARCH FOR BREEDING AND SEED ORCHARD PRODUCTION

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In larches, breeding and production of improved seeds in seed orchards are difficult because of the particular reproductive biology of these species. This paper presents original technological developments, particularly from CEMAGREF in France, in the field of flowering induction, mechanized pollen harvesting, controlled crosses for breeding, and supplemental mass pollination in seed orchards. Problems related to pollen drying and testing are also discussed briefly.

# CONTROLLED MASS POLLINATION IN LOBLOLLY PINE TO INCREASE GENETIC GAINS

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Controlled mass pollination (CMP) is one way to increase the genetic gains from traditional wind-pollinated seed orchards. Methodology is under development by several forestry companies in the southern USA. Costs of CMP depend on the efficient installation, pollination, and removal of inexpensive paper bags. Even in pilot-scale studies these costs seem reasonable. Net present values from CMP in a sample of 67 loblolly pine *Pinus taeda* L. seed orchards in the Western Gulf Forest Tree Improvement Program are conservatively expected to average $ 108 (US) per acre of plantation established with seedlings from CMP among the best 6 parents in each of 5 breeding regions and $ 154 (US) per acre for CMP among the best pair of parents in each breeding region.

# THE STATUS AND POTENTIAL OF USING CONTROLLED PARENTAGE IN OPERATIONAL REFORESTATION IN NEW BRUNSWICK

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Tree improvement programs began in New Brunswick in the 1970's and by the early 1990's, most seed used in reforestation programs originated from seed orchards. Initial research, such as fertilizer trials and other flower induction methods, focussed on increasing seed orchard yields. Trials have also been established to investigate parental contribution to seed orchard production. As the New Brunswick Tree Improvement Council (NBTIC) breeding programs advance into the second generation, two approaches have been developed to capture genetic gain more efficiently. The use of controlled breeding and vegetative multiplication of black spruce has been used operationally by J.D. Irving, Limited and a jack pine meadow orchard has been established by the NB Department of Natural Resources and Energy. This paper presents an overview of these programs and the future challenges of using controlled parentage in operational reforestation stock production.

# POSTERS

# EFFECTS OF FLORAL INDUCTION TREATMENTS ON THE GENETIC CONSTITUTION OF ALLOZYME VARIANTS IN NORWAY SPRUCE (*Picea abies (L.) Karst.*)

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The production of genetically improved material in a seed orchard can be optimized when all the genotypes contribute equally to the seed crop. Hormone treatment in Norway spruce, in synchrony with favorable climatic conditions, has been very effective in increasing the proportion of genotypes supplying male and female gametes and raising the level of production of almost every clone (Daoust, 1996). In the summer of 1993, clones of Norway spruce were induced to flower by a gibberellin ($A_{4/7}$) injection on field-grown grafts and by a combined treatment of gibberellin ($A_{4/7}$), heat stress, and root pruning on container-grown grafts in the greenhouse. The following year, we investigated crop production and noticed that the cones obtained from the induced material in the greenhouse were significantly smaller than those from the controls in the field, with fewer scales per cone and reduced seed weight. In the field, cone length only was significantly affected by flower induction treatments. Furthermore, we conducted a segregation analysis to evaluate the possible impact on transmission of alleles to the offspring produced using flower induction treatments. Sixty megagametophytes from nine clones were genotyped for each of three conditions: induced and control in the field and induced in the greenhouse. Results from thirteen enzymatic loci show that no distortion was observed. Hence, there is no reason to believe that the flower induction treatment, as applied, will have an impact on the genetic quality of seeds in Norway spruce.

Daoust, G. 1996. Flower induction in conifers : a tool to increase genetic diversity in reforestation. *in* Proc. 14th North. Am. For. Bio. Wkshp., Forest Management Impacts on Ecosystems Processes, Université Laval, Ste-Foy,.

# RÉSULTATS À 5 ANS DES TESTS DE DESCENDANCES D'ÉPINETTE DE NORVÈGE DE LA ZONE D'AMÉLIORATION DES APPALACHES

# (5-YEAR RESULTS OF NORWAY SPRUCE PROGENY TESTS IN THE APPALACHIAN BREEDING ZONE)

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En 1989, le Québec a été subdivisé provisoirement en trois zones d'amélioration pour l'épinette de Norvège (*Picea abies* [L.] Karst.) et chacune de ces zones a été assortie de recommandations de provenances. Afin de vérifier ces recommandations et d'élargir la base génétique de la population d'amélioration, une étude regroupant plus de 250 descendances uniparentales et 3 provenances témoins (Smith, Proulx et Istebna) a été mise sur pied. Les descendances représentent des provenances recommandées, des plantations commerciales, et des provenances polonaises. En 1992, un test a été établi dans chacun des trois domaines écologiques de la zone d'amélioration des Appalaches.

Après 5 ans de croissance, des interactions ont été trouvées tant chez les descendances que chez les provenances pour les trois domaines écologiques testés. Toutefois les provenances les plus productives démontrent une grande stabilité phénotypique. Il s'agit de deux provenances recommandées Auce et Suwalki, de la provenance polonaise, Istebna, qui fut également utilisée comme témoin et de deux provenances commerciales Gould et Proulx-Duchesnay qui offrent une supériorité en hauteur à 5 ans de 3,5 % sur les témoins. Pour ce qui est des 10 meilleures descendances offrant une grande stabilité, elles présentent une supériorité en hauteur de 10,5 % sur les témoins. Bien que des changements dans le classement soient probables jusqu'à l'âge de 10 ans, ces premiers résultats semblent très prometteurs et laissent entrevoir des gains de croissance appréciables.

# GENETIC VARIATION IN ADAPTIVE AND QUANTITATIVE ATTRIBUTES OF MOUNTAIN HEMLOCK (*Tsuga mertensiana* Bong.) IN BRITISH COLUMBIA

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Patterns of genetic variation in adaptive and quantitative attributes in mountain hemlock (*Tsuga mertensiana* Bong.) seedlings, from British Columbia were examined at the population (provenance) and family levels. The population and family levels were represented by twelve provenances and ten families from one location, respectively. The adaptive attributes were: photosynthesis (A), transpiration (E), intercellular to ambient $CO_2$ concentration ratio (Ci/Ca), mesophyll conductance (gm), stomatal conductance (gs), and water use efficiency (WUE). The quantitative traits included: height (H), stem diameter (CAL), root dry weight (RDW), shoot dry weight (SDW), and harvest index (Hi). Univariate and multivariate analyses of the studied attributes revealed significant differences at the population and family levels. Although the populations differed significantly in all traits, a relatively small portion (5-15%) of the total variation was attributed to among populations. Due to the observed large withi- population variation, no trend between the studied traits and geography was discovered based on individual seedlings. However, significant geographical trends were found for some characteristics using population means. No appreciable relationship was detected between the quantitative and adaptive attributes. Within-population analyses produced high narrow sense heritabilities for the majority of the attributes. The observed high within-population variation and strong genetic control over the studied attributes present an opportunity for genetic improvement. On the other hand, the detected significant differences among populations represent a challenge for gene conservation efforts.

# DIVERSITÉ GÉNÉTIQUE À L'INTÉRIEUR ET ENTRE LES POPULATIONS D'IF DU CANADA (*Taxus canadensis* Marsh.)

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L'if du Canada est une essence forestière ayant un port généralement rampant à tiges multiples et ne dépassant pas deux mètres de hauteur dans les formes les plus dressées. On le retrouve principalement dans les forêts décidues et mixtes de l'est des États-Unis et du Canada à partir du sud-est du Manitoba. Jusqu'à récemment, on ne lui trouvait aucune utilité économique. La situation a toutefois changé avec la découverte de taxanes, le paclitaxel, contenues dans ses tissus foliaires. Ce produit est actuellement utilisé pour le traitement de certaines tumeurs cancéreuses et les pressions de récolte vont aller en croissant.

Contrairement à l'if de l'Ouest (*Taxus brevifolia* Nutt.), peu d'études ont été réalisées à ce jour sur la génétique de l'if du Canada. Il est donc primordial de connaître les niveaux de base de diversité génétique existant dans les populations naturelles avant que des effets anthropiques ne viennent les modifier, et de recueillir l'information nécessaire à la mise en place de mesures de conservation.

Dans la présente étude, six populations naturelles du Québec ont été échantillonnées. Des semences ont été récoltées sur 30 arbres dans chaque population et la diversité génétique sera étudiée à l'aide de marqueurs alloenzymatiques. Les résultats préliminaires seront présentés et discutés.

# DIVERSITÉ ET STRUCTURE GÉNÉTIQUE DES POPULATIONS DE NAYER CENDRÉ (*Juglans cinerea* L.)

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Le noyer cendré colonise le nord-est des États-Unis et le sud-est du Canada, principalement au Québec et en Ontario. Depuis quelques années, les populations de noyer cendré localisées aux États-Unis dépérissent dramatiquement à tel point que cette essence est maintenant considérée comme étant en danger d'extinction dans plusieurs états. Elles sont l'objet d'attaques par une souche virulente d'un champignon pathogène (*Sirococcus clavigignenti-juglandacearum*) induisant la maladie appelée chancre du noyer cendré. La première épidémie d'importance a été rapportée en 1967 dans le Wisconsin et la maladie se déplace depuis vers le nord pour atteindre les forêts canadiennes. La maladie a été rapportée pour la première fois au début des années 90 au Canada.

Les objectifs du présent projet sont de quantifier le niveau de diversité génétique dans les populations naturelles encore non affectées ou faiblement affectées et d'en déterminer la structure. Des populations seront également échantillonnées en régions fortement affectées pour obtenir une première estimation des effets du pathogène sur la diversité génétique de cette essence. Les études seront menées à l'aide de marqueurs isoenzymatiques. Les résultats préliminaires seront présentés et discutés.

# WHITE PINE (*Pinus strobus* L.) AND ALDER (*Alnus incana*) MIXED PLANTATION: ESTIMATES OF GENETIC PARAMETERS FOR JUVENILE GROWTH AND BRANCH TRAITS

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Genetic parameters for 15 juvenile growth and branch traits in eastern white pine were estimated using data from a provenance/progeny test. In 1989, five-year-old white pine seedlings were planted alternately with alder seedlings. This mixed plantation was used as a silvicultural method for decreasing the risk of weevil damage. Spacing was 1.5 m within rows and 2.0 m between rows. A subset of five provenances, each represented by five families, was used in this study. The experimental design was a randomized complete block, with each family randomly assigned within each block and represented by a 4-tree row plot. Heritabilities of growth traits at 10 years of age were generally weak. However, for height growth they are similar to estimates already reported for white pine families growing in cut-strips within hardwood stands. Branch angle for the older whorls was under moderate genetic control while for younger ones it was much more affected by environmental conditions. Heritability of branch length was close to zero for each whorl except for the first one. Competition may have prevented the white pine genotypes from expressing their full potential and affected the estimates of genetic control on crown traits observed. However, only estimates from a pure white pine genetic test will permit the evaluation of its effects.

# LES PLANTATIONS D'ARBRES À CROISSANCE RAPIDE: LEUR IMPACT DANS NOTRE ENVIRONNEMENT?

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En raison de la rareté grandissante des ressources disponibles pour approvisionner leurs usines, des industries forestières veulent mettre à profit les nombreuses connaissances acquises et établir des plantations d'arbres à croissance rapide (mélèze, peuplier, etc.). Quels seront les impacts environnementaux de l'introduction d'une telle approche sylvicole? Le projet vise à regrouper toute l'information disponible pour faire l'évaluation environnementale d'une ligniculture sur de courtes rotations. Toute personne ayant connaissance d'informations permettant d'évaluer les répercussions possibles de la ligniculture sur les composantes biophysiques, fauniques et végétales des territoires concernés ainsi que les répercussions potentielles d'une telle approche sur les plans social et économique est invitée à nous en faire part.

Une évaluation préliminaire nous indique qu'il pourrait être financièrement intéressant de remplacer des sources d'approvisionnement éloignées par des bois provenant de plantations d'arbres à croissance rapide àtablies près des usines. Cette évaluation environnementale se veut une contribution à l'émergence de la ligniculture, en regroupant les éléments de connaissance et d'aide à la décision sur les plans techniques, socio-économiques et environnementaux. Il s'agit d'informations essentielles en prévision des diverses problématiques susceptibles de survenir avec la mise en application d'une telle orientation.

# APTITUDE AU SÉCHAGE DU BOIS D'ÉPINETTE BLANCHE DE PLANTATION ÉVALUÉE À PARTIR D'UN ESSAI DE PROVENANCES

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Il est bien connu que le bois de plantation possède des propriétés physico-mécaniques et une aptitude à la transformation très différentes du bois de forêt naturelle. La forte proportion de bois juvénile, le fort taux d'accroissement, la plus grande fréquence de noeuds et de fil dévié et d'autres caractéristiques peuvent changer radicalement les propriétés d'utilisation d'une espèce donnée. La thèse de Herzig (1991) a clairement démontré que les propriétés physico-mécaniques de l'épinette blanche de plantation sont plus faibles que celles du bois d'épinette de forêt naturelle et également plus variables. On peut facilement présumer que l'impact de ces propriétés sur l'aptitude du bois de cette espèce au séchage risque d'être très important. Les essais de séchage sont effectués selon deux procédés soit : le séchage à moyenne température et le séchage à haute température. Pour chaque procédé trois fournées de séchage sont effectuées. Chaque fournée est constituée de 156 colombages, dont 150 prélevés à partir de 25 provenances d'épinette de plantation (25 provenance x 1 arbre x 2 billes x 3 colombages) et le reste d'épinette de forêt naturelle. Les principaux paramètres d'évaluation de l'aptitude au séchage sont : les teneurs en humidité finales et leur distribution, le gauchissement, le retrait, les fentes et gerces, l'exudation de résine, les gradients de teneur en humidité dans l'épaisseur et les contraintes résiduelles. Finalement l'effet de provenance est étudié à partir de ces résultats. Dans le cadre de ce congrès les résultats des premières fournées seront présentés.

Herzig, L. 1991. Évaluation du module d'Young de bois d'épinette par méthode ultrasonore sur carotte de sondage. Thèse de maîtrise, Département des sciences du bois, Université Laval. 341p.

# ALTERING NURSERY ENVIRONMENTAL CONDITIONS: PRECONDITIONING WHITE SPRUCE SEEDLINGS TO TOLERATE LOW RELATIVE HUMIDITIES

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Methods of increasing spruce planting stock quality through altering nursery cultural practices is currently under investigation. Changing nursery growing environments to reflect more realistic field conditions (lower relative humidities (RH)) during the shoot elongation phases of tree growth, may precondition seedlings to tolerate high vapor pressure deficits after planting. White spruce seeds from one seed source were germinated and grown in growth chambers under standard nursery conditions, except during the early and exponential growth phases, where seedlings were allocated to one of three treatments: 30, 50 or 80% RH. After hardening off, the seedlings were placed in cold storage for 12 weeks. Results indicate that seedlings from the 80% treatment had the highest height and root collar diameter, followed by the 50%, then the 30% treatment. Significant differences in needle length, internodal distance and number of lateral shoots/buds between treatments were found. When seedlings were flushed under low RH (stressed) vs high RH (unstressed) conditions (in general) the 30% seedlings were found to flush earlier, and in greater proportions than either the 50 or 80% treatments. It is concluded that seedlings reared under low RH alter their morphology to adapt to high vapor pressure deficits, while concurrent changes in physiology allow higher flushing rates in the low RH vs. the high RH preconditioned seedlings.

# THE SEARCH FOR MARKERS ASSOCIATED WITH SE INITIATION IN *Picea glauca* (Moench) Voss

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A previous study by Park *et al.* (1993) showed that initiation of somatic embryogenesis (SE) in white spruce was under strong additive genetic control ($h^2 = 0.73$), especially when stored mature zygotic embryos were used as a source of explants. Based on these results, we initiated a project to better understand SE initiation and go beyond its genetic dissection in order to find markers associated with this trait. To do so, 60 female trees, which had been polycrossed with a mix of pollen from 20 trees, were characterized for their embryogenic capacity. Mature zygotic embryos were used as a source of explants since the initiation of embryogenic tissue with this type of material is likely to be under stronger genetic control than with immature material. The initiation rates were found to vary from near 0% to 60% among trees and were at best weakly correlated with germination rates of zygotic embryos from the corresponding seedlots. Consequently, six trees were selected from different classes of initiation rates and controlled crosses were performed among them (complete diallel). In parallel, we have begun developing single-tree genomic maps for two of the selected trees using RAPD markers.

# CODOMINANT PCR-BASED MARKERS OF BLACK SPRUCE GENES

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We have designed PCR primers that reveal codominant polymorphisms of expressed genes in black spruce. We sequenced 50 arbitrarily selected black spruce cDNA clones and constructed opposing primers (one in the 3'-UTR, the other in the coding region) for each cDNA. These primers were then used in amplifications of haploid and diploid black spruce DNAs originating from 22 provenances scattered across the species range. Codominant markers of 15 loci were resolved on standard agarose gels, but null alleles were also evident at three of these loci. Up to 5 alleles were detected per locus. Differences in the sizes of alleles ranged from 1 bp to about 180 bp and DNA sequencing revealed that most, but not all of the insertions/deletions were in noncoding regions. Allelic segregation among megagametophytes of heterozygous trees did not deviate significantly from the expected 1:1 ratio. If only the 12 polymorphic loci for which we have no evidence of null alleles (i.e., the loci likely to be most useful in population studies) are considered, our rangewide sample of 22 trees had an average observed heterozygosity of 0.26 and an average of 2.8 alleles per locus.

# N.B.T.I.C.: 20 YEARS TOGETHER AND 10 YEARS OF BREEDING

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The New Brunswick Tree Improvement Council recently celebrated its twenty year anniversary. Industry and government, as well as the universities, have co-operated to achieve genetic improvement of four native species: black spruce (*Picea mariana* (Mill.) B.S.P.)), white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.) and tamarack (*Larix laricina* (Du Roi) K. Koch). The landmark for the N.B. Dept. of Natural Resources and Energy (D.N.R.E.) is ten years of tree breeding. Techniques have been refined and skills improved over the years as staff has become familiar with the biology of the four species in the program. In the last ten years, D.N.R.E. has bagged almost 200 000 females using close to 8 700 bags equalling almost 2 500 crosses. This effort has resulted in roguing of 1st generation white spruce and tamarack clonal seed orchards, testing of 2nd generation black spruce and jack pine selections, and producing material for 2nd generation white spruce selections as well as 3rd generation black spruce and jack pine selections. Since 1990, D.N.R.E. has grown only improved stock for its reforestation efforts and is harvesting second generation seed from its black spruce and jack pine orchards. Pollen handling techniques have also improved over the years and there is currently close to 3 kg of viable pollen in storage.

# CONE SIZE AND CLONES INFLUENCE EGG LAY AND SURVIVAL OF CONE MAGGOTS IN WHITE SPRUCE

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The cone maggot (*Strobilomyia neanthracina* Michelsen) is the most damaging insect pest of white spruce *(Picea glauca* (Moench) Voss.) seeds in Canada and is capable of destroying entire seed crops. Because the cone maggot larva is restricted to a single cone for its development, the female cone fly should lay eggs in cones that provide her progeny with a good probability of survival. We tested the predictions that oviposition, larval survival, and pupal weight of the cone fly were positively related to size of white spruce cones and that larval survival was limiting in smaller cones.

The number of cone maggot eggs laid per cone was positively related to cone size and varied significantly among clones. The proportion of seeds eaten per cone was negatively related to cone length, suggesting that larval resources were limited in smaller cones. Larval survival and pupal weight were positively related to cone size. Because the maggots target the largest cones that contain more and larger seed than smaller cones, their impact on seed production is greater than if oviposition is random. If the cone maggots clonal preferences are consistent from year-to-year, the contribution of "magggot-preferred" genotypes to the seedlot may be less than expected.

# HYBRID LARCH: A CONCRETE EXAMPLE OF FORESTRY GENETICS RESULTS OBTAINED WITH HYBRID LARCH (*Larix x eurolepis* Henry) IN SOME 15-YEAR-OLD TESTS

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In Quebec, three species of the *Larix* genus are currently used for reforestation: European larch, Japanese larch, and tamarack. However, the *L x eurolepis* hybrids are less frequently used due to a shortage of good quality seed. On the other hand, crossing European and Japanese larches often demonstrates the phenomenon of heterosis (hybrid vigor), and hybrids can give spectacular results when planted on appropriate sites. In 1972, a provenance-progeny trial was set up by Mark Holst (Petawawa National Forestry Institute, experiment No. 378) with the collaboration of the Quebec Ministry of Natural Resources. Hence, 42 seedlots representing three larch species (European, Japanese and hybrid) were sown in 1973. Field trials were established in 1977 and 1978 in seven arboretums in the Great Lakes-St. Lawrence forest region, with each arboretum representing a different forest association. Results from the three most complete tests (Bonaventure, Villeroy, and Verchères arboretums) showed that 15 years after planting, the hybrids were, on average, superior to pure species. The mean dominant height in the three tests was 12.0 m, compared with 10.2 m for the controls (European larch and Japanese larch, the two species currently used in reforestation). However, there is considerable variation among hybrid larch in terms of the seed sources used. Fisher's multiple comparison method (LSD) shows significant differences among the seedlots for mean height and DBH. The best seed source (seed orchard F.H.211, Sorø 1, Denmark) attained a mean dominant height of 12.8 m. With the help of yield tables (Bolghari and Bertrand 1984), the data allow us to forecast a total yield of 245 $m^3$/ha at age 35 for hybrids in general, and 270 $m^3$/ha for the F.H.211 seed orchard. The expected yield from the control seedlots is about 188 $m^3$/ha. Depending on site conditions, the total projected volume at age 35 for seedlot F.H.211 varies between 357 $m^3$/ha in the Verchères arboretum (forest association: sugar maple/hickory and sugar maple/basswood) and 197 $m^3$/ha in the Mastigouche arboretum (forest association: sugar maple/yellow birch/beech). For the controls, production varies between 250 $m^3$/ha and 133 $m^3$/ha, respectively, for the two arboretums.

This study proves that larch can surpass all softwood species used in reforestation programs in Quebec due to its productivity on sites for which it is adapted. Its rapid juvenile height growth allows it to quickly outgrow the competing vegetation. On the other hand, the variability of traits between different families shows the necessity for systematic and well-planned genetic improvement work to search for new and better performing larch varieties.

Bolghari, H.A.; Bertrand, V. 1984. Tables préliminaires de production des principales essences résineuses plantées dans la partie centrale du sud du Québec. Ministères des Ressources naturelles du Québec. Mémoire de recherche forestière n° 79.

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# PHOTOS

Les étudiants invités ont reçu en cadeau une copie dédicacée du nouveau livre de Kris Morgenstern «Geographic Variation in Forest Trees» / The sponsored students received an inscribed copy of Kris Morgenstern's new book "Geographic Variation in Forest Trees." De gauche à droite/*From left to right* : Yijun Xu (University of New Brunswick), Kris Morgenstern, Frédéric Poirier (Université de Moncton), Sauphie Senneville (Université Laval), Andy Benowicz (University of British Columbia), Christina Idziak (University of Toronto), Daniel Rouillard (Lakehead University), Michel Villeneuve.

La dernière Cène... Encore des places pour le banquet?/*The Last Supper... Any more tickets for the banquet?* (Pierre Bélanger, François Larochelle, André Rainville, Michel Villeneuve)

Un volontaire pour organiser la conférence de 2002? Ah! Enfin... Apportez encore du vin!!!/*A volunteer to take charge of the 2002 meeting? Ah! Finally... Bring more wine!!!* (Michel Villeneuve, Jean Beaulieu, Om Rajora, Jean Bousquet)

Une scène du cocktail au Cercle de la Garnison/*Scene from the cocktail party at the Garrison Club*

Çà sent bon! Si seulement Kris pouvait arrêter de parler.../*It smells good! If Kris could only stop talking...* (Al Gordon, Kris Morgenstern)

Ante Stipanicic : «C'est bien la PREMIÈRE fois que je peux prendre le micro quand Gilles est dans la salle!/*It's the first time EVER that I can have the microphone when Gilles is in the same room!*»

Gilles Vallée: «Voyez, j'ai encore réussi à l'éclipser !/*See, I've managed to take the spotlight again !*»