Genetics, Breeding, Improvement and Conservation of *Pinus strobus* in Canada

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Abstract—The aim of this paper is to present an overview of the research work carried out in eastern Canada over the last 50 years to increase knowledge of the genetics of eastern white pine (*Pinus strobus* L.), the most majestic conifer of eastern Canada. The intent of the paper is also to describe the accomplishments achieved in breeding and tree improvement by a number of private and public sector organizations from different eastern Canadian provinces as well as the activities that are currently underway. Ontario's program, which has been cancelled but which comprised the production of interspecific hybrids from rust-resistant species such as Himalayan white pine (*P. wallichiana* A.B.Jackson), is briefly described. Results of recent studies of population structure of eastern and western North American blister rust (*Cronartium ribicola* J.C. Fisher) are reported. Estimated genetic gain for height 10 years after plantation from a network of three provenance-progeny tests established in Quebec is presented with the origin of the most promising progenies. Other related subjects such as white pine weevil, flower induction, somatic embryogenesis and seed orchard production are discussed. Finally, work presently being carried out for *in situ* and *ex situ* conservation of genetic resources of eastern white pine in eastern Canada are summarized.

Key words: eastern white pine, *Pinus strobus*, genetics, interspecific hybrids, blister rust.

Introduction

Eastern white pine (*Pinus strobus* L.) is the most majestic of all the conifer species growing in eastern Canada. It has a very broad tolerance range and is found on a wide variety of soils ranging from well-drained sands and rocky ridges through sphagnum bogs (Farrar 1995). In Canada, eastern white pine's natural range is limited mainly to the southeast, and extends from eastern Manitoba all the way to Newfoundland (fig. 1). This species is characteristic of Canada's Great Lakes and St. Lawrence Forest Region, where fire plays a primary role in the establishment of extensive stands of eastern white pine (Whitney 1986).

Eastern white pine was overharvested for many decades, owing to the huge size of the mature trees and their prized wood qualities. By the end of the 19th century, the extensive resources of this species had been irremediably decimated in all of eastern Canada, from Ontario to Newfoundland. The subsequent introduction of an exotic pathogen—white pine blister rust (*Cronartium ribicola* J. C. Fisher)—caused major losses in areas that had been naturally and artificially regenerated. Today, with the exception of some zones of white pine in southeastern Ontario and southwestern Quebec, there are only scattered remnants of the beautiful natural stands that once covered eastern Canada. In Quebec, for the year 1998, nearly 90 percent of the volume of wood harvested out of the eastern white pine annual allowable cut of 730,000 m^3 came from the southwestern part of the province (Bouillon 1998).

During the past century, the efforts devoted to reforestation of this species have varied considerably both spatially and temporally. The virulence of pests like blister rust and the white pine weevil (*Pissodes strobi* Peck) are largely to blame for the failures and cutbacks that have occurred in reforestation programs. At present, white pine makes up just a little over 1 percent of the total number of conifer seedlings planted in eastern Canada yearly. Scattered distribution of the species at the landscape level, fire

Figure 1—Natural range of eastern white pine (Wendel and Clay 1990).

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suppression, competition from other plants and blister rust have affected natural regeneration and have dramatically reduced the presence of the species in the landscape. In some regions such as Anticosti Island, browsing from white tail deer prevents development of advance regeneration. To put harvested stands back into production, forest companies currently rely mainly on silvicultural practices designed to mimic natural disturbances that favour eastern white pine natural regeneration.

Over the past 50 years, a number of private and public sector organizations have made great efforts to learn more about the genetics of this species, establishing breeding programs and increasing knowledge of the most damaging pests. This document provides an overview of the results obtained to date and describes briefly the activities that are currently underway in eastern Canada.

Population Genetics

Population genetics studies help us to understand genetic changes occurring within and among populations. Knowledge obtained can be used to devise breeding strategies adapted to the species life history traits. During the last decade, studies of eastern white pine population genetics were carried out using isozymes as well as DNA markers. Results of these studies showed that there was a high level of genetic diversity in this species, and that about 95 percent of it is located within populations. Population differentiation was reported to be about 2 percent on average for populations sampled in Quebec (Beaulieu and Simon 1994, Isabel and others 1999) while it was about 6 percent for populations located in Ontario and Newfoundland (Rajora and others 1998). This low level of population differentiation means that gene flow is extensive. It was also shown that eastern white pine is a predominantly outcrossing species with a very low selfing rate as reported in a study of its mating system in two populations (Beaulieu and Simon 1995). Finally, while it was shown that the level of genetic diversity in this species is relatively high, a loss of genetic diversity was made clear in the St. Lawrence Lowlands and it is believed to be caused by highgrading that was practiced during the last century (Beaulieu and Simon 1994).

Provenance Testing

Provenance testing of eastern white pine started as early as the 1950s in Ontario, but these first trials were inconclusive and did not include a good representation of provenances (Zsuffa 1985). The first comprehensive information on genetic variation in eastern white pine was derived from a range-wide provenance test initiated by the U.S. Department of Agriculture in 1955. Two out of the 15 provenance tests established were located in southern Ontario (Ganaraska and Turkey Point; fig. 2) and included 12 out of 31 provenances tested in the range-wide study. However, only three provenances of eastern Canada (Ontario, Quebec

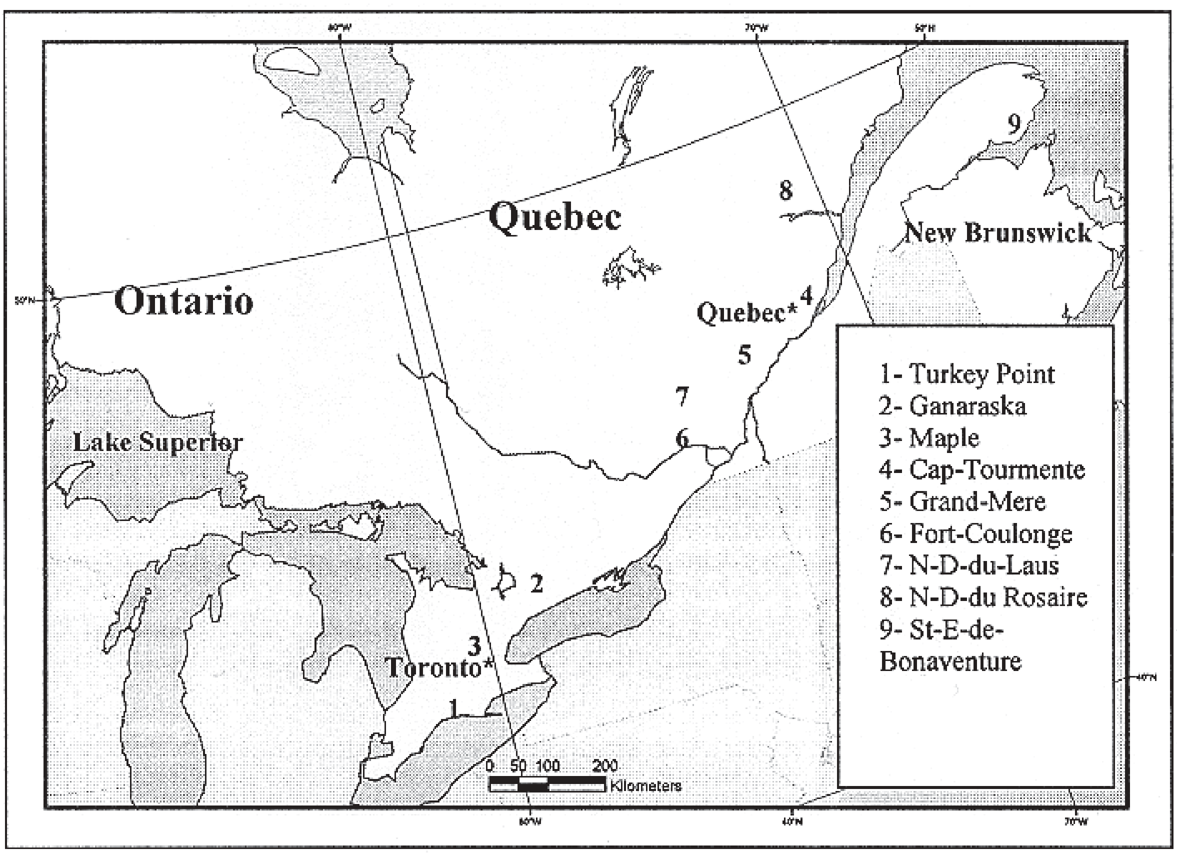

Figure 2—Location of some collections and some provenance-progeny tests in Ontario and Quebec.

and Nova Scotia) were represented. Results observed in these two tests located in southeastern Ontario were reported for 7-year (Fowler and Heimburger 1969) and 28-year (Abubaker and Zsuffa 1991) morphological and growth traits. Significant differences among provenances were found for each of the 12 morphological and growth characters studied. Variation in some characters was more significant than for others. The fastest growing provenances (Pennsylvania, Maine, New York in the U.S.A. and Nova Scotia in Canada) had fewer forked trees, wider branch angles and finer branch diameters and were all from the Atlantic coast. On a broader perspective for provenance testing carried out in North America, Wright and others (1979) demonstrated that trees from the southern Appalachian mountains grew the fastest in the eastern United States and eastern Canada.

The number of provenances originating from Quebec and Ontario tested in the range-wide provenance trial was too small to provide the basic information needed for the breeding program initiated in the 1970s in Quebec (Corriveau and Lamontagne 1977). Hence, a series of three provenance-progeny tests was established in Quebec in 1988. Over 250 open-pollinated progenies belonging to 67 provenances coming from eastern Canada and the eastern United States were tested. Four- and ten-year height data were analyzed by Beaulieu and others (1996) and Li and others (1996). It was shown that there is an extensive variation in eastern white pine and that much of this variation is located within progenies and provenances. Significant differences among provenances and among progenies within provenances were disclosed. Furthermore, the estimates of heritability at the family level were moderate (10-year) to high (4-year), suggesting that tree breeding would be successful. Culling the worst progenies in the nursery could be effective without negatively impacting the expected genetic gain. Nine out of the 10 best provenances identified at 10 years of age were from outside Quebec. Four of them were from the Atlantic coast and the five others were from the Great Lakes region (Ontario in Canada and Minnesota and Michigan in the U.S.A.).

Blister Rust

Introduced in the early 20th century into North America on eastern white pine seedlings imported from Germany, white pine blister rust is now considered to be the most prevalent disease of eastern white pine in eastern Canada. In general, disease incidence increases from west to east and is related to total rainfall and the decrease in mean July and August temperatures. Populations growing on coastal areas are particularly affected by the disease. In Newfoundland, for instance, all the trees in some young plantations, with some as young as 6 years old, were killed by the rust (pers. comm. J. Bérubé 2001). In other provinces, such as Quebec, areas where eastern white pine is particularly susceptible to the rust have been mapped (Lavallée 1986), and ecological characteristics of plantation sites that reduce the risk of infection have been identified (Lavallée 1991). Plantations established in partial shade are generally less severely affected than those established in open fields (Boulet 1998).

Recently, Et-touil and others (1999) studied the genetic structure of nine populations of blister rust in eastern Canada. They found that most of the total gene diversity ($H_T = 0.386$) was present within populations ($H_w = 0.370$), resulting in a low level of genetic differentiation among populations ($F_{st} = 0.062$). No statistically significant genetic differences either among provinces or among regions were revealed. The eastern Canadian provinces are considered to make up one large white pine blister rust epidemiological unit. Furthermore, gene flow between the populations is high and trees tested in this unit could be infected by inoculum travelling hundreds of kilometres.

Comparing eastern Canadian blister rust populations with western ones, Hamelin and others (2000) found that the populations clustered into two distinct clades, one from the east and one from the west. Furthermore, the genetic differentiation was very high ($F_{st} = 44$ percent). Results of this study suggest the presence of a barrier to gene flow between blister rust populations from eastern and western North America but that there may be zones in central North America where the two populations can bridge. It will be important to determine if the genetic differences between eastern and western populations could also be translated into differences in adaptation, virulence, or any other traits having a high impact in terms of this host-pathogen pathosystem.

White Pine Weevil

The white pine weevil (*Pissodes strobi* Peck) is the native insect that has the greatest impact on the quality of white pine trees growing in plantations. Studies conducted on this insect and its relationship with the species have focussed primarily on management techniques (Stiell and Berry 1985) and on the environmental variables of plantation sites (Lavallée 1992, Lavallée and others 1996) with the goal of reducing tree susceptibility and the consequences of infestation. In eastern Canada, few genetic studies have been carried out on family or individual resistance to the weevil but it was demonstrated by Ledig and Smith (1981) that there is genetic variation for weevil resistance in eastern white pine. With regard to the susceptibility of different provenances, Abubaker and Zsuffa (1991) showed that there was a significant difference among the 12 North American seed sources tested at two locations in Ontario. However, the variance that could be attributed to the provenances accounted for only 11.5 percent of total variance. Although it is possible to select specific phenotypes (narrow crown, slender leader and resin flow) for their resistance to the weevil, this phenotypical resistance appears to vary widely and even disappear depending on the environment and the conditions at the plantation site (Zsuffa 1985). In 1996, a farm-field test comprising 14 open-pollinated families with some putatively resistant families was established at the Valcartier Forest Station in Quebec and will make it possible in the near future to study family variation for resistance to the weevil (pers. comm. R. Lavallée 2001).

Breeding and Improvement

History and Present Status in Ontario

The first breeding program for eastern white pine in eastern Canada was initiated in Ontario by C. Heimburger in 1946. The main goal of this program, which was a major effort for that time, was to develop varieties resistant to white pine blister rust. The program included selection in natural stands and the propagation of white pines free of symptoms of the disease, as well as the production of interspecific hybrids from rust-resistant species such as Himalayan white pine (*P. wallichiana* A.B.Jackson (syn. *P. griffithii* McClelland). For the eastern white pine, any significant resistance expressed after blister rust inoculation was particularly notable in the progenies coming from healthy parents. Zufa (1971) found that the percentage of diseased trees in progenies of both healthy and diseased parents was similar and very high. No major genes for resistance were found.

A great deal of effort was put into developing hybrids. At the Maple Research Station (fig. 2) , 17 soft pine species were tested and the breeding effort resulted in about 100 hybrids (table 1). The program was successful, resulting in the development of rust-resistant interspecific hybrids (Zsuffa 1981). Most notable were the eastern and Himalayan white pine hybrids, because of their superior growth, high level of resistance to blister rust and ability to transmit these characteristics to future generations (Heimburger 1972, Zsuffa 1976). However, selections of resistant material based

Table 1—List of the interspecific five-needle pine hybrids produced by the Ontario Ministry of Natural Resources and maintained in research archives by the Ontario Forest Research Institute.

armandii x albicaulis	*peuce x (strobus x peuce)*
ayacahuite x strobus	*(peuce x strobus) x (peuce x strobus)*
cembra x armandii	*pumila x strobus*
cembra x albicaulis	*pumila x (wallichiana x strobus)*
cembra x strobus	*strobus x albicaulis*
flexilis x wallichiana	*strobus x (flexilis x wallichiana)*
koraiensis x albicaulis	*(strobus x wallichiana) x (wallichiana x strobus)*
koraiensis x lambertiana	*(strobus x wallichiana) x (wallichiana x strobus) (P. Schwerinii)*
lambertiana x koraiensis	*strobus x (wallichiana x strobus)*
monticola x ayacahuite	*strobus x wallichiana*
*monticola x (wallichiana** x strobus (P. Schwerinii))*	*strobus x monticola*
monticola x parviflora	*strobus x parviflora*
(monticola x parviflora) x strobus	*(strobus x parviflora) x peuce*
(monticola x parviflora) x (wallichiana x strobus)	*(strobus x parviflora) x strobus*
(monticola x parviflora) x pentaphylla	*(strobus x parviflora) x (strobus x parviflora)*
monticola x pentaphylla	*strobus x pentaphylla*
monticola x peuce	*strobus x peuce*
(monticola x peuce) x (wallichiana x strobus)	*(strobus x peuce) x wallichiana*
monticola x strobus	*(strobus x peuce) x peuce*
parviflora (glaucous)*	*(strobus x peuce) x monticola*
parviflora (glaucous) x (strobus x parviflora)*	*(strobus x peuce) x (peuce x strobus)*
parviflora glauca	*strobus x (peuce x strobus)*
parviflora glauca x strobus	*strobus x (strobus x parviflora)*
parviflora x albicaulis	*wallichiana x albicaulis*
parviflora x wallichiana	*wallichiana x ayacahuite (P. Holfordiana) x parviflora*
parviflora x strobus	*wallichiana x (wallichiana x parviflora)*
parviflora x (strobus x parviflora)	*wallichiana x lambertiana*
(parviflora x strobus) x strobus	*wallichiana x (wallichiana x strobus)*
(parviflora x strobus) x (strobus x parviflora)	*wallichiana x (wallichiana x strobus) (P. Schwerinii)*
pentaphylla x peuce	*wallichiana x strobus*
pentaphylla x (strobus x parviflora)	*wallichiana x koraiensis*
peuce x (flexilis x wallichiana)	*wallichiana x parviflora*
peuce x (wallichiana x strobus)	*(wallichiana x parviflora) x (wallichiana x parviflora)*
peuce x flexilis	*wallichiana x pentaphylla*
peuce x wallichiana	*wallichiana x peuce*
peuce x (monticola x parviflora)	*wallichiana x strobus (P. Schwerinii) x wallichiana*
peuce x parviflora	*wallichiana x strobus (P. Schwerinii) x (wallichiana x strobus)*
peuce x pentaphylla	*wallichiana x strobus (P. Schwerinii) x peuce*
peuce x (peuce x strobus)	*(wallichiana x strobus) x (wallichiana x parviflora)*
peuce x strobus	*(wallichiana x strobus) x (wallichiana x strobus)*
(peuce x strobus (wind) x (peuce x strobus)*	*(wallichiana x strobus) x (wallichiana x strobus) (P. Schwerinii)*
(peuce x strobus (wind) x strobus*	*(wallichiana x strobus) x pentaphylla*
peuce x (strobus x wallichiana)	*(wallichiana x strobus) x strobus*
(peuce x strobus) x (flexilis x wallichiana)	*wallichiana x strobus (P. Schwerinii)*

* Recognition of this name uncertain.
** Syn*. P. griffithii McClelland*
Source: Personal communication from B. Sinclair, Ontario Forest Research Institute, 2001.

on the results of this program were never made and included in operational seed orchards (Cherry and others 2000). In a study using eight *P. wallichiana* x *P. strobus* clones, Zsuffa (1975) found moderate broad sense heritability values for tree heights (0.62) and diameters (0.45) and moderately high broad sense heritability values for branch lengths (0.76) and branch angles (0.71).

Although significant efforts were also made to develop varieties resistant to the white pine weevil, they were mainly unsuccessful, particularly the hybrids of such promising species as *Pinus peuce* Griseb. and *Pinus monticola* Doug. The *P. monticola* hybrids were poorly adapted to climatic conditions in Ontario while the resistance of several *P. peuce* hybrids broke down (Zsuffa 1985). In the mid-1980s, the financial resources allocated to the production and the selection of interspecific hybrids and to the development of blister rust resistant eastern white pine were reduced and finally the program ended. The most promising material (pure or hybrid species) produced in this program was established on six different sites in Ontario and comprised, at the beginning, more than 4500 trees. The Ontario Forest Research Institute (OFRI) is conserving these research archives. The status of these collections is however presently unknown and there is a high probability that most of the trees are dead due to several factors including lack of cold hardiness (pers. comm. B. Sinclair 2001).

In the late 1970s, an intensive plus-tree selection program was launched by the Ontario Ministry of Natural Resources (OMNR) in all the major white pine regions to meet the needs of an expanding reforestation program. By the late 1980s, the province had developed eight breeding populations and an extensive network of seed orchards, comprising 18 orchards covering over 130 hectares. However, few seeds were collected from the selections and, therefore, no progeny tests were carried out (Cherry and others 2000). Despite warnings by Zsuffa (1985) that only continued efforts would allow full benefits to be derived from all the work done to date, significant budget cuts in the mid-1990s stripped breeding programs to their bare bones. The white pine breeding program and the development of seed orchards were put on hold. Unfortunately, to all intents and purposes, no improved seed has been obtained from the orchards for reforestation. All the seeds being used in the current reforestation program were collected in natural stands during logging operations (pers. comm. D. Joyce 2001).

In the mid-1990s, a genecology study of eastern white pine that sampled the current Ontario natural range of eastern white pine east of Lake Superior was initiated by the OMNR. Genetic tests were set up and preliminary results were used to establish a breeding zone for the 'North Bay' tree improvement program. Growth variation among populations was significant and showed a clinal pattern along environment gradients; southern populations generally grew faster than the northern ones (pers. comm. P. Lu 2001). Now there is a renewed interest in Ontario for research on eastern white pine resistance to blister rust and progeny testing of the genotypes present in the seed orchards (Cherry and others 2000). P. Lu has recently proposed a study of genetic resistance to blister rust (pers. comm. D. Joyce 2001). To meet some forest management objectives, the forest company Tembec Inc. has also recently reactivated a genetic improvement program for eastern white pine in the North Bay area. Open-pollinated families collected on 265 clones present in the regional seed orchard were recently sown. The company plans to carry out progeny tests in 2002.

History and Present Status in Quebec

In the late 1970s, an eastern white pine breeding program was initiated for Quebec by Corriveau and Lamontagne (1977), under which genetically improved varieties would be created by selecting and hybridizing superior genotypes for growth, shape and resistance to white pine blister rust and white pine weevil. Although a 1995 program review recommended this area of activity be transferred to the provincial government, the program has remained headed by the Canadian Forest Service (CFS). The ministère des Ressources naturelles du Québec (MRNQ) has not been able to take it over due to limited human and financial resources. Progress and accomplishments of the breeding program were reported by Daoust and Beaulieu (1999).

From 1976 to 1986, over 150 selections were made to create the first-generation breeding population in Quebec. Selections were propagated by grafting and grown in a breeding orchard at the Cap-Tourmente National Wildlife Area east of Quebec City (fig. 2). Beginning in 1992, large crops of seed and pollen cones allowed the production of full-sib families; in addition, a 6 x 6 diallel was created for a study on genetic variation in the capacity of somatic embryogenesis initiation. Several experimental designs to evaluate general and specific combining ability were developed in the last few years and are now in production at the Valcartier Forest Station or are in their first post-planting year. Seeds produced in breeding orchards that are not needed for the breeding program are collected by the MRNQ for its reforestation program. In the 1980s, plus-tree selections made in natural stands by the MRNQ as well as selections formerly made for the breeding program were used to establish a network of six seed orchards for producing more than 3 million seedlings yearly. Significant seed production has begun in two out of the six orchards. However, cones were heavily damaged by a white pine cone beetle (*Conophthorus coniperda* (Schwartz). Insect populations will have to be monitored and controlled. Use of pheromones to control this insect seems to be promising. A research project is in progress at the Institut National de Recherche Scientifique (INRS) - Institut Armand-Frappier (pers. comm. R. Trudel 2001).

Since the inception of the breeding program, seeds were collected in more than 100 eastern white pine natural populations in Quebec for *ex situ* conservation and genecological studies. Seed lots from neighbouring provinces and states have also been obtained from a number of collaborators. In 1986, the first phase of a genecology study involving 300 progenies derived from 160 populations was established on three different sites in Quebec (Fort-Coulonge, Notre-Dame-du-Rosaire, Saint-Elzéar-de-Bonaventure; fig. 2). These tests were set up in cut strips under a partial canopy of tolerant hardwoods, a plantation management technique recommended to reduce risks of infestation by the white pine weevil. Despite an initially high survival rate (+ 80 percent after 6 years) and intensive stand tending, it became clear that little valuable information about genetic variation in juvenile growth could be obtained from these tests because blister rust was ravaging the plants, as was significant browsing damage from hares. At Saint-Elzéar-de-Bonaventure, the most eastern site, the survival rate was only 46 percent 11 years after planting and half of the survivors were rust infected; no progeny with more than 50 percent of unaffected seedlings was found. Only 14 percent of the progenies tested showed a proportion between 30-43 percent of unaffected seedlings.

Fortunately for this first phase, growth and phenological traits measured during production in the greenhouse (1 year) and nursery (3 years) made it possible to study the genetic structure and patterns of variation of white pine populations in Quebec (Li and others 1997). Data were also used to delineate preliminary seed zones following a method proposed by Campbell (1986), which estimates relative risks in transferring seed sources. Principal component analysis (PCA) was used to take into account all the traits at the same time. Analysis of variance made it possible to show that provenances were significantly different for each of these traits as well as for the PCA scores. In examining the patterns of variation, it was clear that even though south-eastern provenances flushed later, they had superior growth mainly because they set their buds later. Seed source transfer for eastern white pine in southwestern Quebec is now controlled through estimates of relative risks obtained from mathematical models that were developed.

In 1988, another series of three other genecological tests was established (Grand-Mère, Notre-Dame-du-Laus, Notre-Dame-du Rosaire; fig. 2) under a partial canopy of mature pioneer species. These tests included 250 progenies representing 67 provenances. Although intensive stand tending was done from the beginning, the average survival rate for each test 12 years after planting ranged from 53 percent to 69 percent. The main pest affecting tree survival in the tests was blister rust. Genetic variation in juvenile growth was analyzed using these tests and the main conclusions were reported by Beaulieu and others (1996). Provenances and progenies were shown to be phenotypically stable over the three environments. Breeding values were estimated using best linear predictions (BLP) and estimates of genetic gain for height, 10 years after plantation, were obtained for the best 50 progenies. Hence, a 14 percent (9-29 percent) genetic gain is expected for height growth 12 years after planting. For each progeny, three elite trees were chosen and propagated by grafting to create a breeding population. Out of the 50 progenies selected, 22 are from Quebec, 6 from Ontario, 10 from Vermont, 5 from Michigan and 7 from other U.S. states.

During the 1990s, several other provenance-progeny tests comprising a smaller number of progenies were established to improve the distribution of experimental blocks in the province. One of these is located in Béarn in the Témiscamingue region and was carried out in co-operation with Tembec Inc. These tests will supplement the information obtained to date and be used for estimating the number of progenies required to accurately evaluate the value of a provenance.

Up to now, little work has been done to select material resistant to blister rust in eastern white pine. This is mainly because breeders considered that the genetic variability in blister rust resistance in eastern white pine is too low to expect substantial gains through intra-specific selection and breeding. So, most of the work has been directed toward transferring blister rust resistance found in other species to the eastern white pine. It is for this purpose that the most interesting exotic material, identified in Ontario's former program, was included in the breeding program. Thus, 6, 12 and 22 genotypes of *P. wallichiana*, *P. koraiensis* and *P. peuce*, respectively, were obtained from the collection gathered by the OFRI at the Maple Research Station and put together with genotypes making up our eastern white pine breeding population. Seeds obtained from these clones as well as those from interspecific crosses were sown in 2000 and transplanted in the nursery at the Valcartier Forest Station in 2001. Exotics and hybrids will eventually be evaluated for growth, form and resistance.

History and Present Status in the Atlantic Provinces

As mentioned earlier in this document, mortality caused by blister rust infection in natural stands or in plantations is more severe as we move east and closer to the maritime climate. For example, in Newfoundland mortality can reach 30 percent in natural stands and even 100 percent in plantations (pers. comm. J. Bérubé 2001). So, the plus-tree selection program carried out in the Atlantic provinces has always considered blister rust as the main concern and all the trees selected were free of symptoms of the disease at the time of selection.

At present, there is no tree breeding program for eastern white pine in New Brunswick that is headed by the government. However, J.D. Irving. Inc., a forest company, recently initiated a breeding program by establishing a seed orchard including plus-trees selected in New Brunswick and others obtained via collaborators from neighbouring provinces such as Quebec.

Nova Scotia has a breeding program underway for eastern white pine. A clonal seed orchard, made up of 58 locally selected genotypes, was set up in 1981. In 1998, it produced over 26 kg of seed, which exceeds the requirements of the province's reforestation program for the species.

In Prince Edward Island, there is currently no genetic improvement program underway and none is planned in the short term since over 90 percent of forest lands are privately owned. However, first-generation seed orchards were established at the end of the 1980s by the provincial government. Cones have been collected on a regular basis since the mid-1990s (2.7 kg of seeds in 1996).

Although Newfoundland has no active breeding program for the species at this time, interest in eastern white pine is growing. A seed orchard, made up of 200 clones from plus-trees free of symptoms of blister rust selected in natural populations on the island, was established between 1998 and 2000. The orchard will ensure a supply of high-quality seed while allowing the *ex situ* conservation of genetic diversity of the island (English and Linehan 2000).

Progress reports about eastern white pine breeding and improvement are regularly produced and published by the active members of the Canadian Tree Improvement Association in their biennial proceedings. A description of the eastern white pine seed orchards in place in the eastern Canadian provinces is presented in table 2.

Table 2—Description of the eastern white pine seed orchards in the eastern Canadian provinces.

Province	No. of seed orchards	No. of clones	Year of establishment	Breeding generation	Area (ha)	Seed production
Ontario	18	2500	Late 80s	First	130	No
Quebec	7	700	1981-91	First	33.3	Yes
	1	140	1999	Second	1	No
New Brunswick	1	—	1998	First	—	No
Prince Edward Island	2	70	1988-90	First	2.8	Yes
	1	—	1995-97	—	—	No
Nova Scotia	1	58	1981	First	2.1	Yes
Newfoundland	1	200	2002	First	2.0	No

Flower Induction

In the late 1980s, studies on flower induction in eastern white pine were undertaken in Ontario and Quebec. In Ontario, flower induction trials carried out on 3-5-year-old potted grafts revealed that spraying $GA_{4/7}$ at concentrations of 250 and 500 mg /L were effective in promoting pollen- and seed-cone production. Significant increases in pollen-cone production were obtained when applications were made during the period of rapid terminal shoot elongation whereas applications made about one month after completion of the terminal shoot elongation were the best for favouring seed-cone production (Ho and Schnekenburger 1992). Similar results were also obtained at the Valcartier Forest Station, Quebec, between 1990 and 1992, where some trials including root pruning, spray application of $GA_{4/7}$ and heat stress were carried out on 1.5-m to 2-m high potted grafts. Despite high clonal variation, some ramets produced over 200 seed cones and over 500 pollen strobili (Daoust and Beaulieu 1999). For field-grown grafts, Ho and Eng (1995) found that $GA_{4/7}$ injection made during the period of shoot elongation also promoted pollen- and seed-cone production.

Somatic Embryogenesis (SE)

Significant progress has been achieved in this research field at the CFS since the first study was carried out in 1990. Garin and others (1998) investigated the somatic embryogenic process using immature and mature zygotic embryos of eastern white pine originating from 13 open-pollinated seed families sampled in the breeding population maintained at the Cap-Tourmente National Wildlife Area. From the immature zygotic embryos, embryogenic tissues were obtained for 12 out of the 13 families with initiation rates varying from 2.6 percent to 23 percent. Mature somatic embryos were produced for 30 out of 52 cell lines and plants were regenerated. Embryogenic tissues were also obtained from mature zygotic embryos and embryogenic cell lines developed for 5 out of the 13 families tested with a maximum initiation rate of 2.7 percent. Plants were produced from four cell lines. Those produced from immature as well as from mature zygotic embryos are presently under evaluation at the Valcartier Forest Station. After the success obtained in SE, it was decided to make a complete 6 x 6 diallel with maternal trees whose seed families had high, intermediate and low initiation rates. This diallel will make it possible to determine the genetic components and their effects on SE initiation.

Recently, the optimal concentration of plant growth regulator to be put into the culture medium was found. It made it possible to increase the SE initiation rate in eastern white pine from approximately 20 percent to 53 percent (Klimaszewska and others 2001). This study also demonstrated that a low level of plant growth regulator in the medium used for initiation and proliferation consistently produced a high number of somatic embryos. The different concentrations of plant growth regulator tested allowed somatic embryos to convert to plants at an overall frequency of 76 percent. An estimated narrow-sense heritability for somatic embryogenesis initiation (h^2) of 0.25 was found and indicates that selection of responsive families can be done. According to the authors, with these improved protocols, application of eastern white pine somatic embryogenesis in commercial clonal forestry is feasible as an alternative to traditional breeding for reforestation purposes.

Conservation

In eastern Canada, eastern white pine is not considered as a local species at risk or as an endangered species at present. The Ancient Forest Exploration & Research group from Ontario estimated that less than 2 percent of our old-growth white pine forests remain world-wide, making them an endangered ecosystem type (Quinby 2000). After a report prepared by the White Pine Working Group of Newfoundland, describing the deplorable situation of the species in the province, the government issued a moratorium on domestic and commercial cutting licences in 1998. The province's policy is underpinned by a reforestation program and precise guidelines on precommercial thinning operations. A genetic diversity selection and conservation program was launched on the island in 1999 and a 2-ha seed orchard was established.

Presently on crown lands, where harvesting is carried out, forest companies are required to regenerate the species naturally or artifically and must also comply with the sustainable management principles that are enforced in the various provinces. In Ontario, for example, the Ministry of Natural Resources put out a silviculture guide partly designed for white pine stands in 1998 (OMNR 1998) and developed a conservation strategy for old-growth pine forest ecosystems (OMNR 2001). However, it seems that in all the conservation programs in place in eastern Canada, not enough resources are allocated to study the impact of blister rust on the long-term survival of the species.

In situ conservation of the species is also being carried out in existing parks and reserves in eastern Canada (Boyle 1992). This protection may be complete as is the case in national parks or it may be partial, as in some provincial parks. In the latter case, logging activities can take place but they are subject to certain restrictions designed to ensure natural regeneration of harvested species among other things. In Ontario, following the recommendations of the Temagami Comprehensive Planning Council, the government decided in 1996 to protect 11 old-growth red and eastern white pine stands ranging from 100 to 9,000 ha in the Temagami region (Quinby 2000). In Quebec, the most representative ecosystems are protected by a network of ecological reserves. Other stands, identified as exceptional forest ecosystems, will be protected in the near future by a recently adopted law (pers. comm. N. Villeneuve 2001).

In Mauricie National Park, Quebec, a master plan has been drawn up for the ecological rehabilitation of white pine (Quenneville and others 1998). Tests involving prescribed burning were conducted but proved to be inconclusive since they did not coincide with a good cone crop year. In eastern Quebec, work is also in progress to establish a white pine restoration program. In spring 2001, for instance, the Lower St. Lawrence Model Forest collaborated on the establishment, within its territory, of two open-pollinated progeny tests that will be used to estimate the breeding values of the trees making up the first-generation breeding population built up by the CFS. In Ontario, the OMNR has begun to develop restoration goals for white pine ecosystems along the northern edge of its range and a task force has been mandated to develop principles, criteria and management guidelines for ensuring the long-term persistence of old-growth forest in unprotected areas. The task force will use white pine as a test case (pers. comm. D. Joyce 2001).

Ex situ conservation activities include all the experimental plots used for breeding programs, such as provenance tests, progeny tests, breeding orchards and clonal archives. Similarly, the regional seed orchards put in place by provincial governments and forestry companies are excellent tools for conserving genetic resources. These orchards, which are made up of locally selected genotypes, represent a broad sample of the genetic diversity that is present in eastern white pine in eastern Canada. The different provincial reforestation programs, which are carried out using local seed sources most of the time, also help to conserve genetic diversity at the regional level.

Another valuable *ex situ* conservation approach is the maintenance of seed banks such as the one that the CFS maintains at its National Tree Seed Centre in Fredericton (Simpson and Daigle 1998) and at the Laurentian Forestry Centre in Quebec City. The seedlots in these collections provide a very good sampling of the genetic diversity of eastern white pine populations in northeastern North America.

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