Tree Improvement in Canada – past, present and future, 2023 and beyond

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ABSTRACT

This paper consolidates the most current information available on tree improvement in Canada and provides a summary of key historical events leading to its development and expansion across the country. The most recent publication on the topic was by Fowler and Morgenstern (1990) compiled over 30 years ago. Since that time, many things have changed and new technologies, such as the increasing use and adoption of genomics, have become part of the tool-box of tree breeders in forestry and natural resource management. This paper provides information on the status of tree improvement programs including their history, objectives, seed production, future outlook and other performance measures by province across Canada.

Key words: breeding objectives, conservation, tree domestication, genetic adaptation in reforestation

RÉSUMÉ

Cet article regroupe les toutes dernières informations disponibles au sujet de l'amélioration génétique des arbres au Canada et constitue un résumé des principaux événements historiques qui ont mené à son développement et son utilisation dans tout le pays. La plus récente publication portant sur ce sujet a été rédigée par Fowler et Morgenstern (1990) il y a plus de 30 ans. Depuis cette date, plusieurs choses ont été modifiées et de nouvelles technologies comme l'accroissement de l'utilisation et l'adoption de la génétique font partie du coffre d'outils des spécialistes en amélioration génétique des arbres et de la gestion des ressources naturelles. Cet article fournit des informations sur les programmes d'amélioration génétique des arbres, notamment leur historique, leurs objectifs, la production de semences, les perspectives et autres mesures de performance pour toutes les provinces du Canada.

Mots-clés : objectifs d'amélioration génétique, conservation, domestication des arbres, adaptation génétique en reboisement

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Introduction

A brief history of tree improvement in Canada

Canada has a long history in tree improvement (TI) dating back to the first decade of the 20th century. This early TI supported settlers on the prairies with trees for protection against wind and sun (Farrar 1969; Schroeder 2023). Beginning in 1901, Norman Mackenzie Ross, Assistant Superintendent of Forestry for Canada, expanded TI in Canada from the new federal Forest Nursery Station in Indian Head, Northwest Territories (Saskatchewan), which was established and providing two million seedlings to settlers by 1905 for shelterbelts and woodlots (Ross 1905). At the time, these shelterbelts consisted primarily of green ash (*Fraxinus pensylvanica* Marsh.) and Manitoba maple (*Acer negundo* L.). The provisioning of shelterbelts across the prairies continued until 2013 with a total distribution of more than 600 million trees (Piwowar *et al.* 2016; Schroeder 2023). Although the federal shelterbelt program was discontinued after 100 years of service, the improved genetic material continues to be available through commercial nurseries.

In eastern Canada, Sir Henri Joly de Lotbinière promoted tree planting in the early 1900s and Quebec's first forest nursery was founded in 1908 in Sainte-Geneviève-de-Berthier by Gustave Clodomir Piché, the first French-Canadian forest engineer. In the 1920s, Ellwood Wilson, R. W. Lyons and G. G. Cosenses recognized the importance of seed sources and established extensive plantations (Lyons 1925; Farrar 1969). Controlled hybridization of aspen began in 1935 by Carl Heimburger at the federal Forest Experiment Station at Petawawa, Ontario. Heimburger recognized that aspen hybrids were more vigorous and more resistant to aspen heart rot (*Phellinus tremulae* (Bondartsev) Bondartsev & P.N. Borisov (1953) (Heimburger 1936).

Tree improvement work experienced a major setback with the beginning of World War II, as scientists were temporarily removed, and funds were cut. Heimburger later moved to the Research Branch of the Ontario Department of Lands and Forests, where he led a major tree improvement program. In 1952, Alan Orr-Ewing developed the first tree-breeding program for coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in British Columbia (Farrar 1969). By the 1960s and early 1970s, all provinces were involved in tree improvement (Carlisle 1970). Until the 1990s, TI was conducted primarily by the federal and provincial governments (Carlisle 1970; Fowler and Morgenstern 1990). In the 1990s, the involvement of the federal government in TI was greatly reduced following a 1995 program review of the Canadian Forest Service (CFS). It was decided that TI and genomics research should rest primarily with the provinces and universities, which coincided with the retirements of CFS scientists including M.A.K. Khalil, Don Fowler, Jerry Klein, Ron Smith, Richard Hunt and followed by the reassignment of locations/roles of others (Peter Hall, Alex Mosseler, Dale Simpson, Yill-Sun Park, Jean Beaulieu, Gaëtan Daoust, Arianne Plourde) (Dale Simpson, pers, comm., March 16, 2017). After 1995, CFS research in forest genetics was moved to the Laurentian Forestry Centre (LFC) in Québec City, Québec, where they now focus on "ecogenomics" (pests/genomics/climate change/adaptation) while the Atlantic Forestry Centre (AFC) in Fredericton, New Brunswick, retained the conservation of forest genetic resources and biodiversity as a focus. The Canadian Wood Fibre Centre (CWFC) was formed in 2006 as a virtual CFS national centre, with a focus on forest productivity. Scientists conducting the CFS and the CWFC's forest tree genetics research currently include Nathalie Isabel, Patrick Lenz and Ian Major in Québec, Funda Ogut in New Brunswick and Miriam Isaac-Renton in British Columbia. Through various combinations of government (provincial and federal) and industry collaboration initiatives, there are 23 species/varieties under some form of TI management across Canada (Tables 1, 2).

Forest management and tree improvement

In Canada, forest management is typically a provincial responsibility, taking place primarily on government-owned Crown forest lands, whereas in the Maritime provinces, New Brunswick (NB), Nova Scotia (NS), Prince Edward Island (PEI) private land management varies from 50%, 65% and 85%, respectively. The annual allowable cut (AAC) on Crown lands is determined by the provinces and reviewed every 5-10 years. As TI activities, in addition to other silvicultural tools, are expected to increase timber yields, an increase in the AAC based on expected future timber yields is known as the allowable cut effect (ACE) (Luckert and Haley 1995) and is an instrument that can be used to increase harvest levels.

Tree improvement is a long-term commitment, particularly given the typically slow-growing tree species which populate the Canadian boreal forests. The goal of TI is to selectively increase the frequency of alleles coding for desirable traits to maximize the economic and social value of planted forests (White *et al.* 2007). In the past, the most desirable TI traits were local adaptation (Langlet 1971), volume and wood quality traits such as stem straightness and self-pruning, and more recently, pest resistance (Table 2). With the increasing pressures from climate change, resistance to abiotic stresses (drought, flooding, cold, heat) are also emerging as traits for improvement. While policies, administrative procedures, and technical approaches in forecasting and regulating wood supply across Canada are fairly consistent, the details of their application vary considerably across each province (Canadian Council of Forest Ministers 2005).

A shift in tree improvement tools

In the past, most TI programs utilized recurrent selection by using selected genotypes as parents in advanced generation testing and selection schemes (Fig. 1). Powerful analytical software using residual maximum likelihood and other techniques (e.g., ASReml and BreedR), have enabled the incorporation of pedigree files and spatial analysis into the evaluation of genetic merit of parents and offspring (forward selections). As a result of these advancements, combined with robust best linear unbiased prediction (BLUPs) of breeding values, it is now possible to analyze large testing programs and conduct meta-analyses across generations and breeding regions (Ukrainetz *et al.* 2018; Cappa *et al.* 2022a).

More recently, molecular techniques and tools from animal and agricultural breeding have been tested and applied in forest genetics (Plomion *et al.* 2011; Beaulieu *et al.* 2022; Cappa *et al.* 2022b). The most promising genomic selection can use genomic-based pedigrees to generate more accurate breeding values while shortening the generation time by reducing the need for at least one generation of progeny test-

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Table 1. Number of breeding programs by species, province and generation (First or Advanced) (data from 2017–2022)

Province	BC		AB		SK		MB		ON		QC		NB		PEI		NS		NL	
Species / Generation	First	Adv.	First	Adv.	First	Adv.	First	Adv.	First	Adv.	First	Adv.	First	Adv.	First	Adv.	First	Adv.	First	Adv.
Abies balsamea (Balsam fir)	–	–	–	–	2	–	–	–	–	–	–	–	1	–	1[a]	–	–	–	–	–
Alnus rubra (Red alder)	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cupressus nootkatensis (Yellow cedar)	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Larix laricina (Tamarack)	–	–	–	–	–	–	–	–	–	–	3	–	1	–	1	–	–	–	–	–
Larix occidentalis (Western larch)	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Larix sibirica[b] (Siberian larch)	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Picea abies[b] (Norway spruce)	–	–	–	–	–	–	–	–	–	–	4	1	1	–	–	–	1	–	–	–
Picea glauca and *Picea spp.* (White spruce/interior)	5	6	9	–	–	–	2***	–	2	2	13	4	2	1	1	–	1	1	1	1
Picea mariana (Black spruce)	–	–	5***	–	–	–	8***	–	–	25	9	7	1	1	1	–	2	1	1	1
Picea rubens (Red spruce)	–	–	–	–	–	–	–	–	–	–	2	–	1	–	1	–	1	1	–	–
Picea sitchensis (Sitka spruce)	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pinus banksiana (Jack pine)	–	–	1	–	–	–	5***	–	–	17	10	6	1	2	–	–	–	–	–	–
Pinus contorta var. *latifolia* (Interior lodgepole pine)	4	4	5	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pinus monticola (Western white pine)	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pinus ponderosa (Ponderosa pine)	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pinus resinosa (Red pine)	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Pinus strobus (Eastern white pine)	–	–	–	–	–	–	–	–	13	–	3	2	1	–	1	–	1	–	–	–
Pinus sylvestris[b] (Scots pine)	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Populus balsamifera (Balsam poplar)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*Populus deltoides***†‡ (Eastern cottonwood)	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–
Populus maximowiczii [b]**†‡ (Japanese poplar)	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–
Populus tremuloides (Trembling aspen)	–	–	2**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*Populus trichocarpa***†‡ (Black cottonwood)	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–
Pseudotsuga menziesii var. *glauca* (Interior Douglas-fir)	4	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pseudotsuga menziesii var. *menziesii* (Coastal Douglas-fir)	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thuja plicata (Western red cedar)	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tsuga heterophylla (Western hemlock)	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

[a]Christmas tree production orchard with 20 families, 480 trees and production target of 100,000 seedlings
[b]non-native to Canada
**no seed orchard
***some programs have orchards for seed production only (not gain)
†vegetative reproduction of improved clones in stoolbed areas
‡parent used for hybrid poplar breeding programs

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Table 2. Objectives, management and productivity of provincial breeding programs/seed orchards (data from 2017–2022)

	BC	AB	SK	MB	ON	QC	NB	NS	NL	PEI
Breeding objectives	**Volume, wood density & quality, leaf blight, deer-browse, blister rust & weevil resistance**	**Volume, form, conservation, weevil resistance**	**Form, volume, height, cold, drought and disease resistance**	**Volume, form, seed production**	**Growth increased rate and maintain diversity**	**Adaptation, wood density then growth, wood quality**	**Volume, form, weevil resistance, Christmas tree production**	**Volume, survival, form, weevil resistance**	**Volume, form, wood density**	**Growth, form, Christmas tree production**
Breeding progam manager (P = provincial Government, F = federal Government, I = Industry, C = cooperative between industry and government)	P, I, C	P, I, C	F	P	–	–	P	P	P	P
Orchard owner (P = provincial Government, F = federal Government, I = Industry, C = cooperative between industry and government)	P, I, C	P, I, C	–	P	–	–	P	P, I	P	P
Range of genetic volume gain at rotation across breeding programs (%)	2–34	0–18.5	–	unknown	–	–	10–20	10–20	10–25	n/a
Range of genetic gain other than volume across breeding programs (%)	2–3 (wood quality)	n/a	–	0	–	–	n/a	4–17	n/a	n/a
Mean & (Range) in effective population size in orchards	20–100	28–151	–	n/a	–	–	n/a	(10.4–377.4)	n/a	n/a
Mean & (Range) in the number of parents/families in orchards	(19–120)	(31–139)	–	(32–430)	–	–	(18–415)	(11–473)	(45–223)	(20–80)
Range of rotation ages across breeding programs (years)	30–80	70–115	–	60–80	–	–	7–80	60–80	40–80	60–100
Range of annual seed production targets across breeding programs (kg)	0.3–460	4.5–56	–	0.7–25.2	–	–	2–47	0–65	n/a	n/a
Range of annual seedling production targets across breeding programs (millions)	187	0.6–17.2	–	0.4–10.1	–	–	0.2–8.6	3.5–12	7–10	0.1–1
Total seed orchard area in 2022 (ha)	**271**	**60.6**	**213**	**69.1**	**552**	**882**	**127.3**	**92**	**18**	**12.3**
Total seed orchard area in 1988 (ha)	**178**	**29**	**41**	**92**	**284**	**1019**	**267**	**77**	**22**	**77**

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Fig. 1. Tree improvement breeding and production cycles (Tree Improvement Cycle 2006 Province of British Columbia ISBN 0-7726-7725-5, https://forestgeneticsbc.ca/resources/information-brochures-and-posters/ downloaded July 11, 2022).

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ing. Therefore, the long timelines typically required for TI in Canada may be significantly reduced in more advanced generations (Fig. 2). These genomic tools, however, are dependent on a solid traditional tree breeding base with well thought-out breeding and progeny test designs and comprehensive phenotyping to inform the genomic models.

From 2001 to the present, genomics research in forestry has been driven largely by Genome Canada (GC) and the associated provincial genome centres, supported by more than $138 M dollars (>$57 M direct GC funds) in research funds (Genome Canada 2022), to develop forest genetic resources in Canada. Much of this work was fundamental in nature due to both the size and complexity of the genomes (Pavy *et al.* 2005) and cost of genomics research. However, applications for TI are now emerging (Cappa *et al.* 2022b). With the 2015 Large Scale Applied Research Project (LSARP) competition through GC, five programs have been funded in forestry ($40.6 M total). The sister program, Genomic Applications Partnership Program (GAPP), is now moving into a new and emerging era of application of this technology and placing it into mainstream TI in Canada. Programs in British Columbia, Alberta and Québec, including interior lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.), Douglas-fir, western red cedar (*Thuja plicata* Donn), white spruce (*Picea glauca* (Moench) Voss), black spruce (*P. mariana* [Mill.] B.S.P.) and Norway spruce (*P. abies* [L.] Karst.) are delving into the potential of genomic selection using genomic estimated breeding values (Beaulieu *et al.* 2014a, 2014b; El-Dien *et al.* 2016; Lenz *et al.* 2017, 2020b; Ratcliffe *et al.* 2015) to determine if the breeding cycle length typically required with traditional tree breeding can be shortened. The pioneering work by Grattapaglia and Resende (2011) brought animal-based models to forestry with the first test cases in *Eucalyptus* (Resende *et al.* 2012a, 2012b). With reference genomes now available for Norway spruce and white spruce (Birol *et al.* 2013; Nystedt *et al.* 2013; Warren *et al.* 2015), analysis of local white spruce populations has been made much more accessible. Pine, however, has had less attention and the current reference genome has its closest relative in Loblolly pine (*Pinus taeda* L.) (Resende *et al.* 2012a), although more recent work at the University of Alberta by Barb Thomas and at Oklahoma State University by Charles Chen will see the publication of an annotated reference genome for interior lodgepole pine in 2024.

Previous constraints on the application of genomic selection in conifers are being overcome with a convergence of quantitative and genomic technologies [Cappa *et al.* (2022b); Beaulieu *et al.* (2014a, 2014b); Grattapaglia *et al.* 2018; Ratcliffe *et al.* (2015, 2017)]. The economic benefits from this technology are expected to increase the rate of return on investments by 16-20 years (Chang *et al.* 2019a; Schreiber and Thomas 2017; Wang *et al.* 2021). Because economics fundamentally drive the success of any TI program, cost reduction with gene sequencing techniques are expected to be used more in the future. Encouraging results have already been shown in Maritime pine (*Pinus pinaster* Ait.) (Bartholomé *et al.* 2016).

With the increasing pressures from both biotic stresses, such as mountain pine beetle and spruce budworm, as well as abiotic stresses, the availability of genomic technologies is likely to be one of only a few options available to tree breeders to ensure resilient and adapted trees are available for future deployment. Genomic technologies also allow breeders to select on more than one or two traits of interest more easily (e.g., Lenz *et al.* 2020b). To take full advantage of enhanced selections, however, there is still the requirement for adaptation testing and testing of materials outside their current ranges, such as with the Assisted Migration Adaptation Trials (AMAT) in British Columbia (O'Neill *et al.* 2017).

Tree improvement in Canada by province

The following is a brief summary of the history and regulation of TI programs by province. Provincial representatives (co-authors of this study) provided information about their provincial TI programs. In cases where no firsthand information was available, we relied on information from reports or personal communications. Furthermore, Tables 1 and 2 provide information about the number of provincial breeding programs as well as their objectives and productivity.

British Columbia

History

Tree Improvement in British Columbia (BC) started in earnest in 1959 with the formation of the Plus Tree Board that brought together industry and provincial researchers. Tree species included coastal Douglas-fir (Alan Orr-Ewing), interior spruce (*Picea engelmannii* x *P. glauca*) (Gyula Kiss), interior lodgepole pine (Mike Carlson), followed by western red and yellow cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) (John Russell), hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Mike Meagher/Charlie Cartwright), interior Douglas-fir and western larch (*Larix occidentalis* Nutt.) (Barry Jaquish). Most TI efforts were conducted at the Cowichan Lake Research Station (coast British Columbia on Vancouver Island) and at the Kalamalka Forestry Centre in Vernon. These species were improved for volume at rotation while John King improved Sitka spruce (*Picea sichensis* (Bong.) Carriere) for white pine weevil (*Pissodes strobi* W.D. Peck) resistance and western white pine (*Pinus monticola* Dougl. ex D. Don) for white pine blister rust (*Cronartium ribicola* J.C. Fisch.) resistance. The weevil resistance programs are considered to be two of the most successful examples of resistance breeding in trees globally.

In early 2000, the Forest Genetics Council (FGC) of BC was created as an advisory body to the province's Chief Forester, representing industry and the province, seed producers, seed users, nurseries and seed dealers. The FGC coordinates funding and provides a framework for policy and sets objectives, assisted by the technical advisory committees (TACs) for coastal and interior breeding programs, seed production and gene conservation. Tree improvement is managed cooperatively between provincial scientists and industry. Selected material is made available to industry for seed orchard establishment with the resulting seed being processed, tested and stored at the province's Tree Seed Centre (TSC) in Surrey, BC. Currently, improved seed is available for all commercial species, including red alder (*Alnus rubra* Bong.). Genetic improvement has resulted in a 20% volume gain, averaged over all species (maximum 35%). Despite high gains from improved hemlock seed (approximately 25%), it

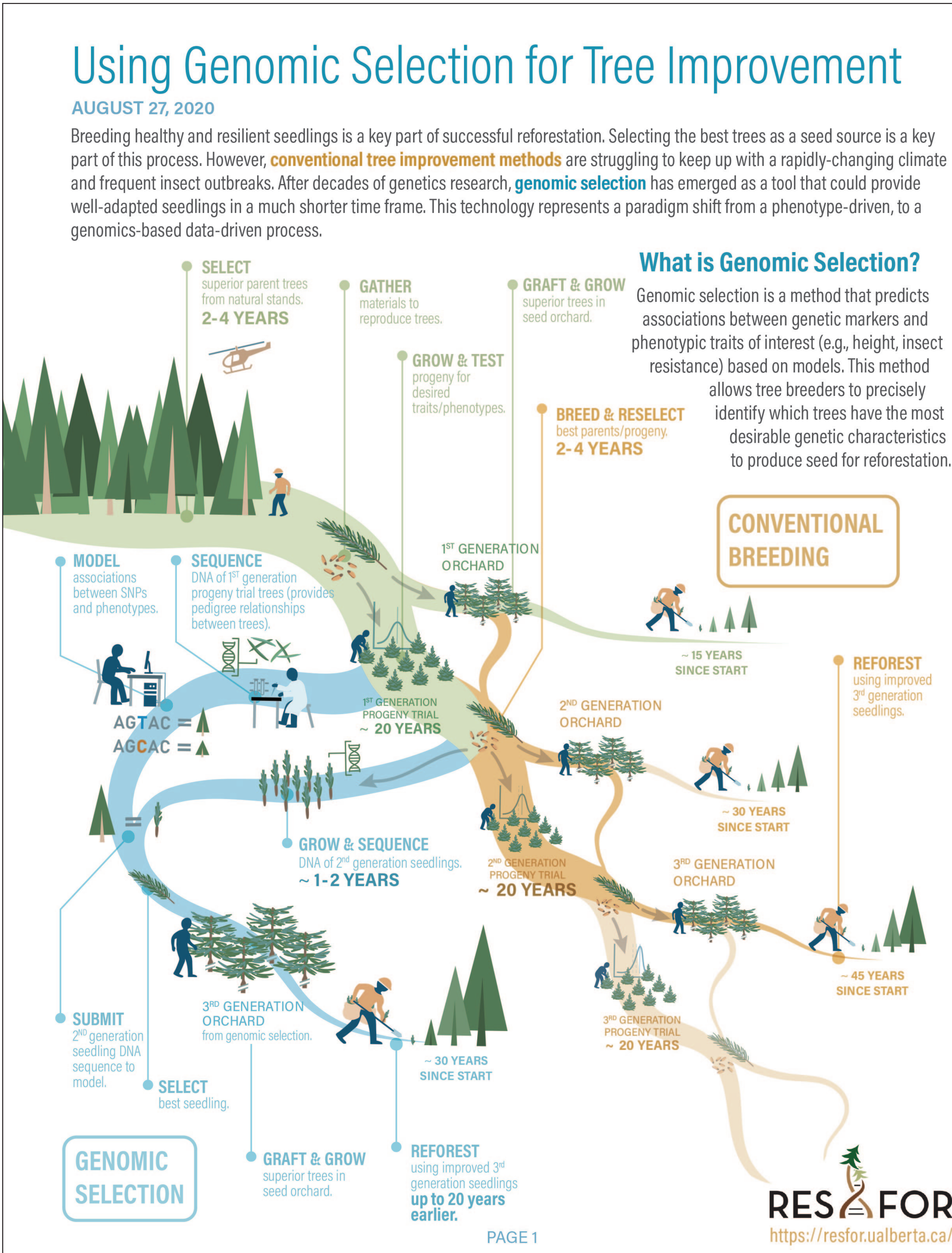

Fig. 2. Page 1 of tree improvement breeding and production cycles comparing traditional methods and incorporation of genomic tools ('Using Genomic Selection for Tree Improvement' August 27, 2020, infographic downloaded from https://resfor.ualberta.ca/ (downloaded July 11, 2022).

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regenerates naturally on forested land and is not widely planted, despite which, orchards are being maintained. Although a black cottonwood (*Populus trichocarpa* Torr. & A. Gray ex. Hook.) collection was made, most testing in poplars is conducted by the forest industry.

Regulation

The rules for using improved seed for reforestation are outlined in BC's Chief Forester's Standards for Seed Use (Nicholls 2018) and include standards to ensure diversity and to regulate Climate-Based Seed Transfer (CBST). As of spring 2022, all crops must be deployed following the CBST system.

Seed deployment

Over 250 million trees are planted annually in BC, over 70% from improved seed. Most of these plantings are lodgepole pine, interior spruce and coastal Douglas-fir. A volume gain of approximately 20% and, in some species, increased resistance to pathogens and pests, has been accomplished.

Economic impact

The volume gains achieved are incorporated into present AAC calculations. The 20% average increase across all species and newly established plantations, represents a large increase to BC's AAC. Plantation maintenance costs are also reduced because they reach 'free-to-grow' status (3 m average height) earlier. As well, smaller seedling containers can be used to grow A-class (improved) seedlings in the nursery. Realized gain trials (RGTs) verify expected genetic gains for several species. Similar gains are anticipated in coastal Douglas-fir, as predicted by genetic analysis of progeny tests (Isaac-Renton *et al.* 2020).

Climate change

Standards for BC's new CBST system came into effect for all commercial tree species in August 2018 and is now fully implemented (Nicholls 2018). The new system differs from the former system because it: 1) is climate-based instead of geography-based; 2) uses a focal zone system instead of a fixed zone system; and 3) uses assisted migration to move seedlots. Eligible seedlots for a given site are those that originate from an ecosystem (Biogeoclimatic Ecosystem Classification Variants (BECvar)) that is generally slightly warmer than the BECvar of the plantation. Each seed orchard is assigned to a single BECvar having the climate most similar to that of the climate mean of the orchard parents (or the "mid-parent climate" in the case of forward selections). Transfers between BECvars are eligible only if the volume forfeiture is less than 5%. Other climate change adaptation strategies include: 1) increased emphasis on disease and pest resistance breeding; and 2) a new species selection system that uses assisted migration. A total of 48 species/seedlot tests, called the Assisted Migration and Adaptation Trials (AMAT), were established by planting 12 test sites over four years, starting in 2009. Test sites cover the area from the Yukon Territory to California and were installed to evaluate the performance, of mainly orchard seedlots, of various species exposed to increasing migration distances (O'Neill *et al.* 2008; Marris 2009). Results from these tests will continue to help refine the CBST limits.

Genetic conservation

For the FGC, genetic conservation of tree species is an important aspect of gene resource management (GRM). Published catalogs of species in parks and protected areas show that most commercial conifers in BC are not threatened and have generally large species distributions and ranges. Progeny tests and other genetic tests are considered *inter-situ* conservation areas and clone banks, and breeding archives are *ex-situ* conservation areas (Yanchuk 2001). Whitebark pine (*Pinus albicaulis* Engelm.) is a species at risk (SAR) (Government of Canada 2012) and is threatened mainly by mountain pine beetle and white pine blister rust but it is also threatened by climate change and fire. The FGC's strategy is to screen families for white pine blister rust resistance and to establish progeny tests for selection.

Genomics

Two genomic selection projects were initiated for coastal Douglas-fir and western red cedar. The genomic selection project for coastal Douglas-fir is a cooperation between the University of British Columbia (UBC) and the province, co-funded by Genome British Columbia, and compares the prediction based on genotypes and phenotypes of a parent population to wood density in progeny populations (Thistlethwaite *et al.* 2017, Fig. 2). Coastal Douglas-fir and lodgepole pine are part of the UBC genomics project involving screening for Swiss needle cast (*Phaeocryptopus gaeumanii* (T. Rohde) Petrak (1938)) in Douglas-fir and *Dothistroma* (Hulbary 1941) in lodgepole pine. A western red cedar genomics project is attempting to select progeny for heartwood rot, a mature-trait, based on parental genotypes and phenotypes.

Genomics studies, and the interior spruce weevil-tolerance work, are being undertaken cooperatively by UBC and the province. Results from genomics projects have not yet been incorporated into the province's operational TI programs.

Research and collaboration

The provincial forest genetics group participates in many collaborations and joint research projects with UBC and other partners (https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/tree-seed/forest-genetics). Given the large number of pedigreed, well maintained, soundly designed and documented progeny and provenance tests, many research projects make use of this tremendous resource. With UBC, LiDAR is now being used by the province to measure tree heights after crown closure in Douglas-fir and interior spruce. Research is also on-going with non-destructive tools to evaluate surrogate wood quality traits (El-Kassaby *et al.* 2011). A provincial/federal co-operative study is underway to assess and screen parents for abiotic stresses.

20-year outlook

The importance of incorporating molecular breeding tools, such as genomic selection, will increase. Tree phenotyping, using tools such as remote sensing (LiDAR, multi-spectral photos) must be refined to get precise individual tree estimates (Du Toit *et al.* 2020). Seed orchards will expand as needed, driven by the new CBST rules, resulting in a need to produce advanced and better adapted selections and progeny. Tree improvement will place more emphasis on resistance/tolerance to pathogens and insects, while continuing to improve wood quality traits. A publication providing a value for 'genetic merit' is forthcoming.

Alberta

History

Tree improvement was initiated in Alberta (AB) by the provincial government at its Alberta Tree Improvement and Seed Centre (ATISC) near Smoky Lake in 1975. The ATISC facility stores all seed to be deployed on Crown land in AB and also maintains seed orchards, clone banks, provenance and progeny trials for various species and programs. The first progeny tests were planted in 1981 and first-generation seed orchards established in 1982. Currently there are 24 breeding programs across five species (Table 1). Genetics plantings have been established in 87 locations across the province with the most advanced programs (20 programs) being lodgepole pine and white spruce. Selection, breeding, testing and production are done by the forest industry, the provincial government or in cooperation between and within sectors (e.g., Huallen Seed Orchard Company, HASOC, Forest Genetics Alberta Association, FGAA).

In the early 1990s, the Western Boreal Aspen Cooperative (WBAC), an industry-led aspen TI program, began selections in the province, grafted a clonal breeding arboretum and methods of clonal propagation were studied. Today, the WBAC is beginning to deploy selections on Crown land and has two approved breeding programs. In the mid-1990s, Alberta-Pacific Forest Industries (Al-Pac), began an intensive poplar and aspen plantation program with a mandate of producing 400 000 m^3 of wood annually on an initial 20-year rotation using hybrid poplars. Breeding efforts were conducted collaboratively with both Saskatchewan and Québec. Although the operational plantation program was terminated in 2014, one of the largest collections of poplars and aspens (natives, hybrids and exotics) (~25 000 genotypes/families), are still maintained at the Al-Pac mill-site.

From 2000 to 2018, the Alberta Forest Genetic Resources Council, including government, industry and academia, advised the minister on current forest genetics issues. In 2011, Tree Improvement Alberta (TIA) was formed to manage a $3M research project titled Tree Species Adaptation Risk Management Project (https://fgrow.ca/publications/tree-species-adaptation-risk-management-project-final-report), and developed terms of reference with a mandate to '*facilitate the delivery of programs or projects related to forest genetics in Alberta*' (https://fgrow.friresearch.ca/program/tree-improvement-alberta-project-team). TIA currently includes 15 industrial members, the provincial government and the University of Alberta, as non-paying members. In 2016, TIA became a 'team' under the Forest Growth Organization of Western Canada (FGrOW 2016).

Regulation

Tree and shrub genetic resources (collection, storage, deployment, production, improvement) in Alberta are regulated through the Alberta Forest Genetic Resource Management and Conservation Standards (FGRMS 2016). The standards were first implemented in 2003 with ~five-year reviews that allow for the incorporation of new procedures, research and enhancements for better management of Alberta's forest resources, including their TI programs.

Seed deployment

In the five-year period from 2015–2019, approximately 106 million trees were planted each year, of which about 50% were white spruce, 44% lodgepole pine, 4% black spruce, 2% jack pine (*Pinus banksiana* Lamb.), and 0.1% trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). Beginning in 2019, approximately 20% of the lodgepole pine, with an increase to 65% of the white spruce deployment, has been from genetically improved seed (Andy Benowicz, personal communication, 2022). In the 2015–2019 period, approximately 95 000 ha of forests were harvested annually by the forest industry. Reforestation is mandatory by law and is the responsibility of the forest management agreement (FMA) holders. All harvested areas are required to be treated within two years of harvesting. A new seed use directive policy implemented in 2016 (AAF 2016) is the first step in active promotion to encourage forest companies, and those undertaking reclamation, to plant improved "Stream 2" seed.

Economic impact

A TI valuation model was developed (Schreiber and Thomas 2017), which shows that TI is a viable option for increasing or maintaining timber supply in Alberta, and that investment in TI is profitable. The model also shows that the area planted is as important as increases in gain. Economic analyses of the value of genomic-assisted TI (Chang *et al.* 2019a) includes a module that links the economics of TI to the provincial growth and yield projection system model (GYPSY; Huang *et al.* 2009). A full review was also conducted by Chang *et al.* (2019b) to assess the economics of TI for planted forests. Galeano *et al.* (2023) conducted an economic comparison of breeding strategies in white spruce.

Climate change

Deployment of climatically adapted seed sources and vegetative propagules is currently regulated and managed through a system of seed zones (90 total in the province), and controlled parentage program (CPP) deployment regions (FGRMS 2016). Given the uncertainty of the impact of climate change on forest health and productivity, the deployed material must be genetically diverse, as specified in the provincial standards (FGRMS 2016). An Alberta climate model was also developed for forest areas not well covered by weather stations (Mbogga *et al.* 2010). The province has recently established new large-scale provenance tests in climatically marginal environments to mitigate the impact of climate change on forests, identifying genotypes with high climatic stress tolerance through genomic tools and testing of non-local species and/or populations (assisted migration). A new climate assisted transfer system for seedlots is also under development with the first meeting between government, industry and TIA held spring 2023.

Genetic conservation

Tree gene conservation in Alberta includes specific standards related to the *in-situ* and *ex-situ* conservation in FGRMS

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(2016). A provincial gene conservation plan for native trees of Alberta was developed in 2009 (ASRD 2009). Seed and clone banking have included plant material as a population conservation effort for Alberta's 28 native tree species and individual trees used in the applied tree breeding programs. Limber pine (*Pinus flexilis* E. James) and whitebark pine are designated as endangered species in Alberta and recovery plans have been prepared for both species (AESRD 2014).

Genomics

Use of genomic technology in TI programs in Alberta has followed-on from the completion of the RES-FOR (2016) Genome Alberta LSARP (Large Scale Applied Research Project) in 2021 (e.g., Cappa *et al.* 2022a, 2022b) and on-going work through the Industrial Research Chair in Tree Improvement held by B.R. Thomas (2014–current) (e.g., Galeano *et al.* 2021, 2023; Schreiber and Thomas 2017). One of the deliverables of the RES-FOR project was development of genomic-estimated breeding values for a number of traits for one lodgepole pine and one white spruce breeding program combined with a selection tool app. The results allow for selection of individuals for the next generation orchards based, not only on improved growth, but also on enhanced wood properties, resistance to pests and diseases, and resilience to climate change (https://resfor.ualberta.ca/).

Research and collaboration

Applied TI research projects have been undertaken by industry and the provincial government separately or in collaboration with the University of Alberta (mainly) and the University of British Columbia. In 2014, the first Industrial Research Chair (IRC) in Tree Improvement with B.R. Thomas (NSERC matching program) was developed at the University of Alberta, financially supported by 10 forest companies and the Government of Alberta and is currently funded until 2025. Considerable funding for TI research has also been supplied through Climate Change Emissions Management (now Emission Reduction Alberta, https://fgrow.ca/project/tree-adaptation-risk-management-project) and FRIAA (the Forest Resources Improvement Association of Alberta).

In 2017 the first realized gain trials (RGT) were established in Alberta with a total of 67 installations of white spruce and lodgepole pine. A combination of wild seed, orchard seed, elite (~10–15 families) or synthetic seedlots were deployed on Crown lands in forest companies' FMA areas. RGT installations continue annually.

20-year outlook

A continued increase in the use of improved seed of lodgepole pine and white spruce (*Picea glauca*) is expected in Alberta, with increases in gain of deployed material, orchard expansions, and second-generation orchard establishment. Work is on-going in the selection for insect, disease and drought resistance, and the establishment of advanced generation progeny tests combined with the installation of large-scale realized gain trials. Development and implementation began in 2022 of a climate-based seed transfer system for wild (Stream 1) and seed orchard (Stream 2) seedlots. The development of the RES-FOR Selection Tool (https://resfor.ualberta.ca/resources/res-for-infographics/), now allows for the integration of genomics-estimated breeding values for two programs. As more TI programs are genotyped, this selection tool will become increasingly important in helping tree breeders and orchard managers determine the best selections for second and third generation orchards. In addition, a new initiative (2024) called BFF-AFIRMS (Best Future Forests-Advanced Genomics and Integrative Resource Management System), is being undertaken at the University of Alberta, and will develop two new (white spruce and lodgepole pine) SNP arrays and a province-wide computing and data centre providing a communal tool and industry-wide enabling platform to facilitate coordinated tree improvement efforts throughout the province by digitizing all genetic resources, enabling landscape resource management decisions, particularly in light of climate change, and increasing the human capacity to adopt and utilize this platform.

Saskatchewan

History

Some of the earliest TI activities in Canada took place on the prairies. Beginning in the late 1880s, the Dominion of Canada's western Experimental Farms at Brandon, Manitoba and Indian Head, Saskatchewan began evaluating tree species for shelterbelts and woodlots (Saunders 1891). Later, after the Dominion Forest Nursery Station was established at Indian Head, TI of tree and shrub species increased significantly under Superintendent Norman Ross (Chief of Tree Planting 1901–1941). A trained forester, Ross understood the importance of evaluating tree performance scientifically (Fig. 3). Soon after setting up the Indian Head nursery, Ross installed experimental plantings of native and non-native tree species. With the initiation of the Prairie Shelterbelt Program in 1901, the Government of Canada provided hardy trees and shrubs to farmers, free of charge, throughout the prairies.

For a century, the Indian Head nursery developed propagation and nursery protocols for more than 50 woody species. By 2013, over 600 million tree seedlings had been distributed for over 51 000 km of shelterbelts (Piwowar *et al.* 2016).

Ross's TI initiatives were continued by succeeding superintendents, John Walker (1942–1958) and Bill Cram (1958–1978) and TI specialists Carl Lindquist (1954–1984)

Fig. 3. Norman Ross at Spruce Wood Reserves in 1908 (photo credit: Agriculture and Agri-Food Canada).

(Schroeder 1994) and Bill Schroeder (1981–2016) (Schroeder 2023). Many species were improved in collaboration with partners in the US Great Plains states. Special attention was given to fast-growing hybrid poplar clones, selected for growth rate, form and resistance to disease and insects and propagated from rooted or unrooted cuttings for distribution to farms. Work on selection of hybrid poplars continues with Raju Soolanayakanahally (2011–present).

Regulation

Seedlings for forest replanting in Saskatchewan come from seed from both TI programs and wild stands. Seed from wild stands, considered to be more genetically diverse, are collected from the seed zone where the seedlings will be planted. Improved seed comes mainly from a seed orchard established by Weyerhaeuser in the 1980s. Crown land forest license holders in Saskatchewan cannot deploy genetically modified seedlings.

Seed deployment

The federal TI programs for shelterbelts, under Agriculture and Agri-Food Canada's (AAFC), concentrated on developing superior seed. The program consisted of: 1) sampling the native range of the species, collecting seed and assessing the range of genetic variation in major traits using provenance trials; 2) selecting superior trees from provenance trials, propagating them vegetatively in a clone bank; 3) crossing superior trees and evaluating their progeny under a variety of site conditions; and 4) roguing the clone banks, leaving only trees whose progeny had the desired traits. These rogued clone banks were used as seed production orchards and seedlings and clones were distributed throughout the Prairie Provinces (Schroeder 1994). For shelterbelt planting, provenance trials, seed orchards and common gardens encompass vast genetic diversity and are used as a seed source.

Commercial forestry species in the provincial Crown land forest includes white spruce, black spruce, jack pine, trembling aspen and balsam fir. White spruce seedlings constitute over 90% of reforestation plantings, over 40% of these seedlings are coming from improved seed.

Economic impact

The social benefits from the Prairie Shelterbelt Program during the period from 1981 to 2001 alone was estimated at over $100 million (Kulshreshtha and Kort 2009). In addition, based on an assumed price of $50 per tonne of carbon, a mature hybrid poplar tree is worth $150–$250 to society. Currently, these values are not internalized in a landowner's decision-making as they do not receive any monetary benefits for planting shelterbelts (Kulshreshtha *et al.* 2018).

Climate change

The *ex-situ* collections of species used in the AAFC shelterbelt program, and the resulting common gardens, have provided opportunities for a variety of studies in population genetics, climatic adaptation, long-term phenology responses of provenances and ecophysiology assessments. In addition, the collections provide foundation stock for basic research and trait-assisted breeding. The climate mitigation potential of shelterbelt species (hybrid poplar (*Populus* spp.), Manitoba maple, Scots pine (*Pinus sylvestris* L.), white spruce, green ash, and caragana (*Caragana arborescens* Lam.)), ranges from 1.78 to 6.54 Mg C km^{-1} yr^{-1} and emphasizes the important role woody perennials can have on the agricultural landscape to mitigate greenhouse gases (Amichev *et al.* 2017).

Genetic conservation

A major component of AAFC's shelterbelt TI program has been the conservation of woody genetic resources which support biodiversity. This included sampling native populations and establishment of common gardens, facilitating access to genetic resources for breeding and the study of genetic diversity. Over 200 genetic trials were established in the prairie region from the early 1960s onward, which included 756 populations and 24 500 individual genotypes. Genera included in the tests are *Pinus*, *Picea*, *Larix*, *Symphoricarpos*, *Acer*, *Quercus*, *Populus*, *Salix*, *Prunus*, *Hippophae*, *Celtis*, *Rosa*, *Crataegus, Shepherdia* and *Fraxinus*. These tests were evaluated every five years (until 2014) for survival, growth, adaptability and pest resistance. Information from the tests was used to recommend new species and/or provide data to support the release of new clones or seed strains. As of 2014, the majority of these were in fair to good condition.

Since 1985, the Siberian larch (*Larix sibirica* Ledeb.) improvement program has introduced and evaluated over 350 new populations in seed source trials at 15 locations in Manitoba, Saskatchewan and Alberta, and developed an improved seed strain, "Lindquist", for agroforestry planting in the Canadian prairies. Provenance tests of Russian seed sources of Scots pine were established in 1962 at the AAFC tree nursery at Indian Head. The "balcania" ecotype from Voronezh, Province of Orel and Smolensk, the "eniseensis' ecotype from Central Siberia and the "altaica" ecotype from southern Siberia were found to be the best adapted to the Canadian prairies. Provenance tests of northern Great Plains seed sources of ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) at Indian Head in 1969, 1984 and 1988 indicated that trees originating from Valentine and Ainsworth, Nebraska and Rosebud, and South Dakota were well adapted to the Canadian prairies. In approximately 1959, vigorous Colorado blue spruce (*Picea pungens* Engelm.) trees were selected from 1911 plantings at Indian Head. The selections were based on blue needle colour and overall vigour.

Tree improvement of green ash was initiated in 1985 when superior trees were selected from native green ash stands in Saskatchewan and Manitoba. These trees were progeny tested and the top genotypes vegetatively propagated and planted in a seed orchard at Indian Head. Since 1947, the hybrid poplar TI program has involved selection and production of new hybrids and maintenance of poplar species and hybrids. The poplar breeding program involved controlled pollination using *P. deltoides* Marsh. var *occidentalis* Rydb., *P. balsamifera*, *P. maximowiczii* A. Henry, *P. nigra* L., *P. laurifolia* Ledeb., *P.×petrowskyana* Schneid., and *P. tristis* Fisch (Fig. 4). Seedlings from the controlled crosses have been planted in clonal trials throughout the prairies and screened mainly for growth rate, but also for adaptation to short summers and growing-season frost, winter hardiness to -50˚C, drought resistance, insect and disease resistance, and optimum form/architecture. In addition, screening for water and nutrient use efficiency and growth responsiveness to increasing atmospheric CO_2 (Soolanayakanahally *et al.* 2009).

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Fig. 4. Bill Cram's breeding program (1947–77) at Indian Head focused on hybrid poplar (photo credit: Agriculture and Agri-Food Canada).

A total of 62 populations were collected along five north-south transects across the natural range of balsam poplar in Canada and Alaska and common gardens exist in Saskatchewan (2006), Québec City (2012), Fairbanks, Alaska (2009), and Burlington, Vermont (2017). A collection of cottonwoods (*P. deltoides* subsp. *deltoides* and subsp. o*ccidentalis*) was initiated in 2008 starting with seven populations from an east-west transect along the South Saskatchewan River from Medicine Hat, Alberta, to Kyle, Saskatchewan, and from riparian populations in Montana, Wyoming, North and South Dakota and eastern cottonwood natural stands in Ontario and Québec. Common gardens were established in 2010 and 2011.

A willow improvement program was also developed and focused mainly on heartleaf willow, *Salix eriocephala* (Michx.) and hungry willow, *S. famelica* (C.R. Ball), both native willows used as parent stock along with other native Canadian species such as pussy willow, *S. discolor* (Muhl.) and sandbar willow, *S. interior* (Nutt.), and introduced species including water willow, *S. dasyclados* (Wimm.) and basket willow, *S. viminalis* (L.) (Murphy *et al.* 2021). The improved willow clones are deployed on marginal land to mitigate salinity and enhance carbon sequestration (Huang *et al.* 2020; Shahariar *et al.* 2021).

Genomics

Genomics research was conducted in collaboration with several university partners on the 62 balsam poplar populations mentioned in the previous section. An LSARP led by UBC, Canadian, and United States researchers studied the extent of genetic variation within and among balsam poplar populations in phenology, ecophysiology and resource-use traits, using single nucleotide polymorphisms (SNPs) (Olson *et al.* 2013). The ability of individuals within a species to adapt to different environments resides in their genetic diversity. This diversity, most commonly manifested as SNPs, can provide clues to the adaptation and population histories that have played a role in a species' evolution and migration northward from glacial retreats. The availability of the black cottonwood sequenced genome (Tuskan *et al.* 2006) made it possible to focus on candidate genes of interest in balsam poplar including phenology, carbon gain, resource use (water and nitrogen), and disease resistance.

Recent efforts include modelling poplar traits using DNA methylation, which can capture tissue-specific epigenetic mechanisms, including total biomass, wood density, soluble lignin and cell wall carbohydrate (Champigny *et al.* 2019). Also investigated were F_1 progenies of an intra-provenance cross (north-north cross at 58ºN) and an inter-provenance cross (north-south cross at 58ºN and 49ºN latitudes) for gene copy number variations (CNVs) using comparative genomic hybridization on arrays of probes targeting gene sequences of balsam poplar. One-to-five gene CNVs were found related to each of the measured adaptive traits and annotated for both biotic and abiotic stress responses (Prunier *et al.* 2018). Overall, findings suggest that gene CNVs typically having higher mutation rates than SNPs, and may in fact represent efficient adaptive variation against fast-evolving pathogens. In addition, making use of the range-wide collection of balsam poplar, Fitzpatrick *et al.* (2021) studied the expected shift in the gene climate association between current and future climates in balsam poplar, allowing quantitative predictions about the degree of expected maladaptation—a metric termed "genomic offset".

Work by Geraldes *et al.* (2015) discovered the sex determining region (SDR) of balsam poplar, pinpointing 13 genes with differentiated X and Y copies. The only SDR gene to show a marked pattern of gender-specific methylation was PbRR9, a member of the two component response regulator gene family involved in cytokinin signalling (Bräutigam *et al.* 2017). Here, work was paired in black cottonwood and balsam poplar, describing one of the smallest sex-determining regions known thus far in complex eukaryotes (~100 kbp) with comprehensive tests for sexual dimorphism, using >1300 individuals from two *Populus* species and assessing 96 non-reproductive functional traits (McKown *et al.* 2017). Unexpectedly, sexual homomorphism was found (no non-reproductive trait differences between the sexes), suggesting that sex is functionally neutral with respect to non-reproductive features that affect poplar survival and fitness (McKown *et al.* 2017).

Another genetic study was conducted from 324 naturally occurring heartleaf willow (*Salix eriocephala* Michx.) accessions from 33 populations sampled across the species' natural range in Canada form Nova Scotia to the Yukon. These samples were analysed using 26 030 polymorphisms to reveal patterns of genetic diversity and population structure. Efforts are on-going to assemble the heartleaf willow genome at AAFC.

Research and collaborations

AAFC's TI program is one of North America's longest continuously run tree breeding programs. Since its outset, and through five generations of tree breeders, breeding partnerships were established with geneticists from Siberia, China, US, Germany, Sweden, Finland, Denmark, United Kingdom, Chile, and across Canada. The poplar breeding program has had strong linkages with the Quebec government's Direction de la Recherche Forestière, MRNF and Alberta-Pacific Forest Industries Inc. near Boyle, Alberta.

20-year outlook

In 2019, the federal government committed to planting two billion trees in natural and urban settings to combat climate change and to address frequent drought episodes and increasing pest and disease pressure. On agriculture landscapes, afforestation programs become relevant under warmer climates with conifers making way for hardwoods (*Acer*, *Quercus*, *Populus*, *Salix*, and *Fraxinus*) in the temperate regions of Canada. Within AAFC, a Climate Change Roadmap under development included a component on the role of trees in future-proofing farming against climate change through agroforestry—the bridge between agriculture and the environment.

Manitoba

History

The Canadian Forest Service of Natural Resources Canada began the first TI program in Manitoba in 1967, leading to the establishment of the family tests and seed orchards in four jack pine breeding zones. Provincial involvement in TI began in the early 1970s with the establishment of local provenance tests of jack pine, white spruce and black spruce. Hybrid poplar trials were established in 1976. A new strategy for the black spruce and white spruce TI programs was developed by the province in the late 1980s. Breeding Zones were established for each of the three major commercial species: jack pine, black spruce and white spruce. The province established the first generation of TI - selecting plus trees, testing their progeny in family tests, and then retaining only the better performing families for seed production and future TI activities. Program costs were kept relatively low through combining testing and seed production functions and converting trials into mass selection seed orchards. The first-generation seedling seed orchards were established with open-pollinated progeny from the plus trees. First-generation clonal seed orchards were established from plus trees which retain the same sexual maturity as the original trees, thereby producing seed much more quickly than orchards established from seedlings. Currently, the province has 29 family test sites, nine orchards, and five mass selection seed orchards. Most orchards have completed their first measurements and roguings (minimum of bottom 25% removed with some orchards rogued to top 50%). Due to the downturn in the forest industry in the last decade, the TI program has had minimal activity in recent years.

Regulation

Manitoba TI programs are not regulated and are cooperative programs between the province's industrial licensees and the province. Louisiana Pacific Canada Ltd. and Tolko Ltd. invested over $2 million into the various programs and seed orchards over the last 25 years.

Seed deployment

Of the over seven million forest seedlings planted annually in Manitoba, the recent deployment consists of approximately 65% (4.55M) unimproved seed and 35% (2.45M) improved seed.

Economic impact

There has been no formal investigation of the economic impact of TI in Manitoba, although a preliminary study has estimated that the 'improved' seed from existing orchards will yield a 5% to 15% increase in volume at rotation.

Climate change

While the Manitoba government may use data from the TI programs for climate change studies, there is no formal strategy linking these two initiatives.

Genetic conservation

A genetic conservation strategy is part of Manitoba's TI programs to ensure the sustainability of its forests. Beyond that, there is no formal conservation strategy being implemented in Manitoba.

Genomics

The province has no plans for implementing the use of genomics technology into the TI programs at this time.

Research and collaborations

An offshoot of the TI programs is an 'assisted migration' trial series in the province. These trials are being conducted in conjunction with the Saskatchewan Research Council and in cooperation with the University of Winnipeg.

20-year outlook

In the near future, the province intends to complete its first generation of progeny trial measurements and to rogue to the top 25% of all orchards. However, as of 2022, due to reductions in government spending and staff shortages, no further TI work is expected at this time.

Ontario

History

Forest genetics and TI work in Ontario was initiated in the 1920s by scientists working for the Canadian Forestry Service at the Petawawa Forest Experiment Station. Efforts by the provincial government were started by the former Department of Lands and Forests in 1946. This early work dealt largely with research aspects of TI and forest genetics. Operational TI started in the 1950s, but the program grew at a relatively slow pace through the 1950s and 1960s. Increasing emphasis was placed on TI during the 1970s. In this period, forest genetics research was conducted by the Ontario Tree Improvement and Forest Biomass Institute (OTIFBI) at Maple, Ontario, then, in the mid-1990s, at the Ontario Forest Research Institute (OFRI) at Sault St. Marie. Major research projects of the time included breeding genetic resistance to white pine blister rust in eastern white pine (*Pinus strobus* L.), which continues under Pengxin Lu; breeding hybrid poplars for biomass and bioenergy, a program which gradually declined and is represented by a few clones archived by OFRI; and establishing tree provenance trials in collaboration with the CFS.

Since 1980, the emphasis has been on TI for commercially important species supporting Ontario's Tree Seed Transfer Policy. Seedling seed orchards were established for both jack pine and black spruce; clonal orchards were established for eastern white pine and white spruce; more effort was devoted to clonal propagation through the rooting of cuttings; and changes were made in the design of seed orchards and genetic tests and in mating designs (OMNR 1987). Large-scale operational TI started in the late 1980s, initiated and funded by the Ontario Ministry of Natural Resources and Forestry (MNRF)

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with support from the forest industry, with a focus mostly on black spruce and jack pine and, to a lesser degree, on white spruce and white pine. Under the assumption of local adaptation, genetic tree breeding zones were delineated following a system of ecological site classification, known as Hills' site regions; as such, each breeding zone required a TI program for each species. TI program designs were guided by the *Tree Improvement Master Plan* (OMNR 1987).

Forest Genetics Ontario (FGO) and three regional genetic associations (the Forest Gene Conservation Association (FGCA) in Southern Region, the Northeast Seed Management Association (NeSMA) in Northeast Region and Superior Woods Tree Improvement Association (SWTIA) in Northwest Region) were incorporated between 1995 and 2000 after the MNRF transferred its forest management responsibilities to sustainable forest license (SFL) holders under Ontario's Crown Forest Sustainability Act. The FGO coordinated the three associations in undertaking operational TI activities with funding from government sources and in-kind contribution from the SFL holders.

New first-generation TI programs were initiated with funding from the Ontario Living Legacy Trust in the early 2000s, filling some TI gaps of earlier years. The FGO was dissolved around 2015 and the three regional genetic associations became responsible for TI and genetic improvement, with the government providing policy and operational support, as well as directed funding from the provincial Forestry Futures Trust. Most of Ontario's TI programs remain in their first generation, with a few programs moving into the second generation in the northwestern region. Seed production areas were also established for some species, including eastern white pine.

Currently, Ontario actively manages 38 first-generation seed orchards. The seed orchards were established using seed from trees with faster growth. The seed orchards in turn provide genetically improved seed for forest renewal to enhance forest productivity. Of those seed orchards, 26 are under active management for black spruce and 14 for jack pine. Since 2011, Ontario has added three first-generation seedling seed orchards (one for black spruce and two for jack pine) and three second-generation clonal seed orchards (two for black spruce and one for jack pine).

Current program delivery

The three regional associations, currently the mainstays of TI in Ontario, are incorporated partnerships that include industry and other aligned organizations, and they deliver the operational portion of Forest Genetic Resource Management (FGRM) in Ontario.

These three associations maintain provincial forest genetic assets for the benefit of Ontario's forests (e.g., seed orchards, tests and genetic tree archives). This independence is supported by a FGRM purpose under the Forestry Futures Trust, which provides operating funds for each association and a small pool of funding that can be applied for each year. The Forestry Futures Trust Committee (FFTC) supports FGRM by administering and reporting on these funds, while advising the associations on their applications.

Regulation

The main policy documents which address TI in Ontario are the *Tree Improvement Master Plan* (OMNR 1987) and its associated *Operational Guidelines for Tree Improvement* (OMNR 1989). However, these policy documents are outdated (e.g., as highlighted in the *Review of the Tree Improvement Master Plan for Ontario*, KBM 2016) and the review concluded that those policies are no longer widely implemented. A review and updates of Ontario's FGRM strategies and policies is expected in the coming years.

Seed deployment

Based on the Ontario MNRF's recent Report on Forest Management 2016 and 2017 (OMNRF 2020a), there were 73 500 000 trees planted for forest regeneration on Crown lands in 2017. Based on Annual Reports of the 2010s, it is estimated that reforestation programs used seed from improved seed orchards for 84 to 87% of black spruce, 67% of white spruce, 46 to 60% of jack pine and 10% of eastern white pine (Elliott, unpublished 2020). Eastern white pine from seed orchards were provided to the Ontario Tree Seed Plant and Forests Ontario for southern-Ontario based orchards (Karen McLaven, personal communication, 2022).

Economic impact

McKenney *et al.* (1992) used modeling and economic analysis to look at Ontario TI programs. They found that the costs of TI programs are far exceeded by improved forest yields, even with small TI gains. However, acceptable methods of valuing genetic gain in forest management planning have not always been applied and new approaches are needed (Ken Elliott, personal communication, 2022).

Climate change

Over the years, Ontario developed several strategies to deal with expected climate change impacts on its forests. Early on, policy gaps were investigated that related specifically to genetic, physical and operational barriers to seed and species movements (OMNR Report 2010). One goal that emerged stressed the importance of increasing the climatic resilience of Ontario's ecosystems (OMNR 2012a) and the enhancement of biodiversity conservation and natural resilience (OMNR 2012b; OMNRF 2017). Some of this has been reconfirmed in the Made-in-Ontario Environment Plan (OMECP 2018) that includes similar policy direction around increasing carbon storage. Climate change is one of many forest management challenges and continues to be considered in policy development.

The *Ontario Tree Seed Transfer Policy* (OMNRF 2020d) addresses the challenge of managing forests in a changing climate. As climate change effects become clearer, the MNRF and forest managers have begun incorporating climate change adaptation actions into forest management. The former Seed Zones of Ontario policy restricted the use of seed within defined seed zone boundaries, however, forest managers need greater flexibility to produce trees that are genetically better adapted to predicted climate scenarios. The updated policy specifies where seed can be collected and used

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and the conditions under which seed may be transferred. A supporting online tool was developed which allows users to find suitable seed and to determine where seed from their areas can be deployed: https://public.tableau.com/app/profile/larlo/viz/SeedSourceOntario/Intro.

The OMNRF is also considering options for enhancing carbon storage in Ontario's Crown forests. *Ontario's Crown Forests: Opportunities to enhance carbon storage?* (OMNRF 2020b). Another document that outlines Ontario's strategies to incorporate climate change action is included in their document, *A Blueprint for Success: Ontario's Forest Sector Strategy* – (OMNRF 2020c). This document includes the following:

- Ontario will continue to advance our understanding of the role of sustainable forest management in climate change adaptation and mitigation.
- We will work with industry to further increase carbon storage in forests and harvested wood products and adapt management practices to enable productive and resilient forests into the future.
- The third theme "Help Ontarians Adapt" within the OMNR (2010) report, outlines the Ministries commitment to "evaluate and adjust policies and legislation to respond to climate change challenges", by investigating "policy gaps related to all natural resources in reference to climate change such as the genetic, physical and management barriers to the movement of species, seed zones, (…) among others".

Genetic conservation

Ontario has a long history of responding to the recovery of species at risk, including tree species such as American chestnut (*Castanea dentata* (Marsh.) Borkh.) and butternut (*Juglans cinerea* L.). Through the efforts of the Canadian Chestnut Council and the Forest Gene Conservation Association, both these species are being bred to encourage tolerance to the blights that have severely impacted their populations. Numerous other tree species also have recovery strategies and conservation.

As part of the legacy of the original TI programs, Ontario has maintained a tree seed archive, field genetic archives, and clone banks of TI stock. Several documents guide this work including *Biodiversity: It's in Our Nature—the Ontario Government Plan to Conserve Biodiversity 2012–2020* (OMNR 2012b) and Ontario Biodiversity Council's (OBC) *Biodiversity Strategy* (OBC 2011) where more broadly MNRF participates and supports the OBC's commitment (http://ontariobiodiversitycouncil.ca/), whereby we commit to "protect, restore and recover Ontario's genetic, species and ecosystem diversity and related ecosystem functions and processes."

Genomics

Genomics is not currently a component of Ontario's TI or conservation programs.

Research and collaborations

The Ontario Forest Research Institute (OFRI) conducts applied forest genetic and TI research to support OMNRFs policy and operational TI programs in collaboration with partners including: the three regional forest genetic associations, Lakehead University, the Canadian Forest Service, the USDA Forest Service and the University of Minnesota. Focus areas include genecology studies of major forest species to support OMNRF's tree seed transfer policy, research on genetic resistance to alien invasive pathogens, TI strategy and data analysis, and vegetative propagation of elite genotypes using rooted cuttings and somatic embryogenesis.

20-year outlook

Ontario continues to review and update forest genetic policy. With the updated seed transfer policy (OMNRF 2020d), climate change is being addressed in terms of both deployment zones and appropriate seedlots.

Québec

History

In Québec, TI activities started in the 1960s under a joint initiative of the federal and provincial governments, Université Laval and the forest industry. They included common garden experiments, introduction of exotic species, and large progeny trials (Desponts *et al.* 2017a). In 1969, Gilles Vallée proposed an ambitious general TI program for Québec (Vallée 1975). The TI programs initiated in the 1970s are still managed by the forestry research branch (DRF) of the Ministère des Ressources naturelles et des Forêts (MRNF). During the 1980s, a large network of first-generation seed orchards was established, accompanied by progeny trials. In all, 83 orchards and 75 tests were installed for black spruce, jack pine, tamarack (eastern larch), European larch (*Larix decidua* Mill.), Japanese larch (*Larix kaempferi* (Lamb.) Carr.), and hybrid larch (e.g., Beaudoin *et al.* 1993). Several provenance trials with exotic species were also established (e.g., lodgepole pine, Scots pine and ponderosa pine; Corriveau and Vallée 1981; Beaudoin 1997). Nineteen arboreta were created with more than 150 exotic and native species. The more advanced and major programs are for white spruce, black spruce, jack pine, Norway spruce, hybrid larch and hybrid poplars (Rainville *et al.* 2003). Selection, breeding, testing, propagation and production are conducted by the Ministry. In some cases, such as for hybrid poplar, part of the testing is conducted in cooperation with industrial partners. The federal Natural Resources Canada's Laurentian Forestry Centre divested to the MRNF its TI responsibilities for white spruce and Norway spruce in 1996 (Beaulieu 1996) and for white pine in 2017. Tree improvement is now solely the MRNF's responsibility. Therefore, other Québec research organizations are involved in other aspects of forest genetics. Following the initial open-pollinated progeny trials and plus-tree selection, the second-generation program involved orchard roguing, selections for breeding, and for clonal seed orchards (e.g., Perron 2010; Desponts and Numainville 2013). Jack pine breeding will focus on open-pollination within the breeding orchards with progeny trials to follow. During the mid-2000s, several progeny trials were established for two white spruce breeding populations and for two black spruce breeding zones. Controlled crosses of superior black spruce parents were used to produce full-sibling crosses. Selected black spruce trees, in initial progeny trials, were cloned and evaluated in two parental clonal tests per breeding zone (Desponts and Numainville 2013; Desponts and DeBlois 2019). From 2007 to 2016, in collaboration with the MRNF's Forest Seed and Seedling Production Branch (DGPSPF), 10 white spruce clonal tests were established to evaluate 1517 clones originating from somatic

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embryogenesis from the 71 best full-sibling families (Wahid *et al.* 2012; Perron and Tremblay 2019). Larch and hybrid poplar breeding programs (Perron 2008) were revised to focus on more vigorous and well adapted taxa and populations: *Larix* x*marchlinsii* (*L. decidua* x *L. kaempferi*), *Populus deltoides* (W. Bartram ex Marshall), *P. trichocarpa* and *P. maximowiczii* (Henry). With climate change, the poplar pathogen *Sphaerulina musiva* (Peck) (Septoria canker, (teleomorph: *Mycosphaerella populorum*)) has expanded into new deployment zones and breeding to improve resistance was implemented (Mottet and Périnet 2010; Otis Prud'homme *et al.* 2023). During this period of TI, activities also began on traits linked to wood quality and insect resistance for Norway spruce (Daoust and Mottet 2006; Mottet *et al.* 2006, 2015). With the advancement of the TI programs, more emphasis is required to improve wood quality traits to meet breeding objectives in more advanced programs (Desponts *et al.* 2017b).

Regulation

Sustainable forest management in Québec relies on ecosystem-based management and integrated, regionalized, resource and land management, to meet these criteria. Reforestation is a mitigation measure used only if required after natural regeneration failures. From 2008 to 2013, reforestation was needed for only 20% of the harvested forest area. Since 2013, the Sustainable Forest Development Act called for the intensification of silviculture practices in specific areas which are particularly well suited for the use of genetically improved material. To ensure sustainable forest management, certification by an independent organization is now required for all forests under management (Québec Official Publisher 2013). Furthermore, in order to increase the economic pull of the Sustainable Forest Development Act, a National Wood Production Strategy (NWPS) was developed. This aims to produce more timber, with the industrially needed traits in public and private forests of the province, with an ambitious target of almost doubling the volume of timber harvested by 2080 (Gouvernement du Québec 2020a).

Seed deployment

Seed orchards, the provincial tree seed centre, and several public nurseries, are managed by the DGPSPF. The first provincial nursery was founded in Berthierville in 1908 where the provincial seed centre was inaugurated in 1928. This facility currently includes a forest seed treatment plant with an annual capacity of 5000 hectolitres of cones and four cold rooms for seed storage. In the early 1980s, the Québec government decided to expand the reforestation program in order to revive the economy. The annual production target was between 250 and 300 million plants and consequently, a large area of seed orchards was established to meet this ambitious goal. At present (2017–2022 average), production of approximately 135 million seedlings is shared among six provincial forest nurseries and 12 private nurseries and comprises approximately black spruce (54%), white spruce (20%), jack pine (17%), tamarack and hybrid larch (2.6%), eastern white pine (1.3%), red spruce (*Picea rubens* Sarg.) (1.1%), red pine (*Pinus resinosa* Sol. ex Ait.) (1.0%), Norway spruce (0.8%), hybrid poplar (0.5%) and other broadleaves (0.8%). The MRNF's genetically improved populations now provide over 85% of the seeds and cuttings used for reforestation in Québec. The remaining 15% that is not serviced by genetically improved trees are for several hardwood species and conifer species in northern forest areas that have not been subject to TI.

Economic impact

In 2019, the GDP for Québec's forest sector was $6 billion, representing 1.6% of the province's GDP (Gouvernement du Québec 2020b), 29% of Canada's GDP for the forest sector and 0.33% of Canada's total GDP (Gouvernement du Québec 2019). The economic activities of more than 250 municipalities depend mainly on the forest sector. Reforestation activities involving 130 million planted seedlings and silvicultural treatments in existing plantations, require an annual investment of approximately $112 million. At an estimated $5–$10 per hectare, the cost of TI is negligible as a component of MRNF operating costs (Martin Perron, personal communication, 2022). This estimate assumes a useful life-span of 30 years for a seed orchard.

Climate change

Adaptation to environmental variability has always been a concern of MRNF TI programs and work began in this area with the development of local deployment territories and establishment of breeding zones (e.g., Beaudoin *et al.* 1993). Climate change has pushed every organization involved in reforestation to pay more attention to adaptation and resilience of forest trees over the entire plantation rotation. Provenance trials that were established before TI activities began have been used to develop seed transfer models for black spruce, white spruce and jack pine (Rainville *et al.* 2014). For white spruce, a small, assisted migration trial of nine sites was implemented from 2013 to 2015 in combination with RGTs. The MRNF has also financially supported many studies linked with climate change that complement on-going breeding and testing activities (see the *Research and collaborations* section below). The MRNF is now putting more emphasis on adaptive traits within the breeding populations. Deployment zones for white spruce and black spruce were revised in 2020 according to 2050 climate prediction transfer models developed by Rainville *et al.* (2014), but only within the limits of the climate variables that were used to build the models, and with a quantification of spring and autumn frost risk (Martin Perron, personal communication, 2022). In addition, development of a SNP traceability system for white pine, which began in 2020 (Godbout *et al.* 2019), will eventually be used to evaluate the pollen dynamic between US and Québec provenances within seed orchards (Mottet and Godbout 2020) and allow for study of the adaptation of these hybrid provenance trees, as an assisted gene flow mitigation strategy.

Genetic conservation

In 2005, following public consultation with various organizations and Indigenous communities, MRNF adopted forest resource protection and development objectives (FPDOs) that were integrated in 2013 into the Sustainable Forest Development Act. The 11 FPDOs include: 1) minimizing the loss of productive forest areas; 2) maintaining a permanent amount of mature and old-growth forests based on regional ecology; and 3) protecting the habitat of threatened or vul-

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nerable species in the forest environment. The responsibility for the conservation of forest genetic resources is shared between MRNF and the Ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs (MELCCFP), with DRF scientific advisors. For deployment populations, breeders are responsible for applying the precautionary principle related to genetic diversity, based on scientific knowledge. For example, after genetic roguing of the MRNF's first-generation seed orchards, hundreds of families and thousands of trees were kept for seed production to preserve diversity (Beaudoin *et al.* 1993). At the same time, for second-generation clonal seed orchards, 60 to 180 selected trees were recommended for each breeding zone according to genetic gains and the estimated seedling requirements for the coming decades (Desponts and Numainville 2013).

Genomics

For over 20 years, MRNF tree breeders have been involved in various Genome Canada and Genome Québec projects such as the recent *FastTRAC* I and II (2015, 2022) and Spruce-Up (2016) projects, both led by the Université Laval in close collaboration with Québec geneticists from NRCan and many other research organizations. These studies have generated many genomic resources and selection tools, mainly for white spruce (e.g., Pavy *et al.* 2017; Lenz *et al.* 2020a; Nadeau *et al.* 2023) but also for black spruce (Lenz *et al.* 2017) and Norway spruce (Lenz *et al.* 2020b). The first direct application of these results within an operational MRNF breeding program was carried out in 2018 as part of the *FastTRAC* I project in which genomic selection was used within the white spruce somatic embryogenesis clone bank containing 3171 lines (Perron *et al.* 2018; Perron and Tremblay 2019). A more recent project (Perron *et al.* 2019) aims to integrate genomic selection at an operational scale in the two most advanced white spruce breeding populations.

Research and collaboration

The MRNF geneticists conduct studies to support their tree breeding activities such as natural regeneration of Norway spruce to support forest certification (Mottet *et al.* 2010, 2021), or quantitative genetic studies to improve estimations of genetic parameters of traits that are costly and logistically hard to measure (Perron *et al.* 2013), or important for breeding objectives (Otis Prud'homme *et al.* 2023). The MRNF's research branch conducts regular surveys and summarizes forest research needs (Gouvernement du Québec 2018) which are used to set internal research priorities and for approval of external projects. Many MRNF forest geneticist collaborations have been undertaken as external projects which covered many genetic subjects with the support of MRNF biological material. Numerous studies concerning genetic parameters and wood properties of poplar hybrids and white spruce were supported financially by MRNF (Pliura *et al.* 2005; Yu *et al.* 2008; Lenz *et al.* 2013). Various black spruce, white spruce and poplar projects, combined the study of genetic variation of important traits for adaptation, resistance to pathogens, and the mitigation of climate change (Beaulieu *et al.* 2004; Feau *et al.* 2010; Prunier *et al.* 2012; Carles *et al.* 2015; Otis-Prud'Homme *et al.* 2018; Benomar *et al.* 2022) have been implemented. Molecular marker projects that support the management of breeding populations, deployment and forest certification were carried out (e.g., Perron *et al.* 2000; Meirmans *et al.* 2014; Godbout *et al.* 2017). Recent support of a large-scale white spruce project led notably to the study of complex traits through phenomics (e.g., D'Odorico *et al.* 2020), information on genetic variation of drought resistance (Depardieu *et al.* 2020, 2021; Laverdière *et al.* 2022), and the economic study of genomic selection (Chamberland *et al.* 2020).

20-year outlook

In 2015, the tree breeding group revised their organization and objectives leading to a new name (Forest Genetics Group, FGG) and identified three areas of focus: improvement, trait adaptation and conservation. The FGG is now planning long-term activities for breeding, adaptation, and conservation of every commercial tree species in Québec. MRNF's new research supporting breeding programs will consider genomics, phenomics, new deployment territories and genetic traceability in order to add rapidity and flexibility to new challenges linked to climate change. For softwood species, the third phase of operational activities (2019–2034) consists of establishing 40 new seed orchards in Québec and covers 615 ha (Gagné *et al.* 2021) for black spruce, eastern white cedar (*Thuja occidentalis* L.), jack pine, Norway spruce, red pine, tamarack, white pine and white spruce. Finally, TI materials, and our knowledge of their adaptation, as well as the expertise of MRNF forest geneticists, will provide the foundation for the implementation of the new National Wood Production Strategy.

New Brunswick
(Government of New Brunswick and J.D. Irving Limited)

History

Genetics research conducted by the CFS began in the mid-1950s. Most of this work consisted of species and provenance trials of native and non-native species. In the mid-1960s work expanded to include *Picea* hybridization to study phylogenetic relationships and *Larix* hybridization to develop sources of more productive breeding material. With the formation of two cooperative TI programs in the mid-1970s (New Brunswick Tree Improvement Council and Nova Scotia Tree Improvement Working Group), research expanded to population and quantitative genetics, seed production, and seed orchard management.

Regulation

The province's Tree Improvement Council (NBTIC) was formed in 1976 as a result of a predicted wood supply shortage (Simpson and Tosh 1997). The CFS took the lead by providing managerial support to the NBTIC, while the New Brunswick Department of Natural Resources (NBDNR) and the provincial government were the core members participating in all aspects of the program. Forest companies participated in the NBTIC program on a voluntary basis. Companies, including J.D. Irving Limited (JDI), selected plus-trees, and established, managed, and measured genetic tests. This informal arrangement served the council well. The NBDNR is responsible for producing genetically improved seed used to grow seedlings for planting on Crown land. JDI with freehold (private) land produces seed for their reforestation programs.

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All NBDNR and JDI seedlings are now derived from seed orchard seed, including white spruce (second generation), black spruce (second generation), red spruce (first generation), Norway spruce (first generation), jack pine (second generation), and eastern white pine (first generation). Second-generation seed orchards began production in 1994 for black spruce and 2013 for white spruce.

Seed deployment

All reforestation in New Brunswick is accomplished with improved seed.

Economic impact

For black spruce, in a replicated realized gain study, 10-year volume was 40% larger for trees from unrogued second-generation seed orchards than for trees from an unimproved source. Similarly, the deployed volume genetic gain from current white spruce orchards can also exceed 40%. The increased growth rates allow for shorter rotations, improved planted stand financial performance, and increased wood supply for the forest products industry, including JDI's sawmills and pulp mills.

Climate change

Climate change is addressed through collaborative research projects (e.g., University of New Brunswick, Canadian Forest Service), maintaining a wide/diverse genetic base in the breeding programs and collaboratively testing across Atlantic Canada. The entire province is considered one breeding zone, encompassing three degrees of latitude and up to several hundred metres in elevation. NBTIC obtained first-generation breeding materials from the State of Maine (US) and the maritime provinces. Depending on performance, some of this material is represented in second-generation breeding populations which helped to broaden the genetic diversity.

Genetic conservation

Genetic conservation occurs naturally, considering the multi-generation clone banks being maintained. The province does not have a gene conservation program for non-commercial species. JDI, however, has established small seed production gene archives for several hardwood species.

Genomics

The NBTIC and JDI are participating in a program led by researchers at Laval University and the Canadian Forest Service's Wood Fibre Centre. Models have been built to predict growth, foliage chemistry for spruce budworm (*Choristoneura fuminerana* [Clem.]) resistance and acoustic velocity (i.e., a surrogate for wood stiffness). White spruce genomic breeding values (GBV) of second-generation selections were used to rogue a JDI seed orchard and to optimize NBTIC breeding using Pedigree Viewer/MateSelect software (Kinghorn and Kinghorn 2020). These GBVs facilitate rapid decision-making and are expected to increase genetic gain per unit time. Additionally, white spruce and Norway spruce genomic models were developed for JDI to screen somatic embryogenesis varieties prior to field testing. Going forward, red spruce genomic models are being developed with these partners and in collaboration with the Nova Scotia Tree Improvement Working Group.

Research and collaborations

The University of New Brunswick had a Chair in Forest Genetics from 1981 to 1993. Many graduate students conducted research that was applicable to the NBTIC program. Numerous undergraduates analyzed family test data for thesis projects, while graduate students conducted research on cone and seed insects, tree growth and development, and pollen management. The University of Moncton has a School of Forestry and for a time, students conducted various projects and participated in field tours of TI activities. Research and cooperation continue on a project-by-project basis as opportunities arise at both universities.

20-year outlook

The NBTIC program has made substantial and continuous progress over the past 45 years. More efficient breeding programs will be conducted in order to capitalize on gains from previous generations and to track pedigrees to maximize outbreeding. Genomic selection has the potential to shorten generation times and to make more efficient selections, particularly as climate change progresses and wood product goals shift. The use of vegetative propagules for reforestation, such as somatic emblings, will continue to have a role for intensively managed, high productivity sites.

In addition, the Atlantic provinces are beginning an exciting new era of collaborative TI. They wish to prepare for climatic change, benefit from economies of scale, and facilitate the exchange of ideas and knowledge and have therefore formed the new Atlantic Tree Improvement Cooperative (AtlanTIC). AtlanTIC officially started in 2020, and initial participants include the four Atlantic provinces, industrial members (JDI, Northern Pulp, Port Hawkesbury Paper, and ForestNB), and the CFS. There are currently no university members although loose collaborations do exist. The participants are organizing and have begun sharing in breeding and testing initiatives. The future is bright with opportunities being pursued, including innovative breeding/testing strategies, accelerated breeding and wide genetic testing.

Prince Edward Island

History and seed deployment

Since 2014, seedling deployment has been approximately 750 000 annually with recent increases to approximately one million seedlings due to funding from the federal government through the Low Carbon Economy Fund.

Overall, approximately 75% of the seedlings deployed are produced in seed orchards which cover 12.3 ha. All seed orchards are first-generation clonal orchards and consist of eastern larch (*Larix laricina* (Du Roi) K. Koch), red spruce, black spruce, white spruce, eastern white pine and a balsam fir orchard used for Christmas tree production. Only the white spruce orchard has been rogued, based on half-sibling polycross tests. PEI is a member of the newly formed AtlanTIC.

Nova Scotia

History

Cooperative TI in Nova Scotia started with the formation of the Nova Scotia Tree Improvement Working Group (NSTIWG) in 1977. Founding members were the Nova Scotia Department of Lands and Forests, the CFS and the three

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major forest companies in the province at the time. Current members are the Department of Lands & Forestry, Northern Pulp Nova Scotia Corp., Port Hawkesbury Paper LP, and JDI Ltd. Don Fowler's CFS Report "*Strategies for the genetic improvement of important tree species in the Maritimes*" (Fowler 1986) was used as a guide for subsequent breeding and deployment programs. In 1980, the province dedicated a 200+ ha block of Crown land for construction of a Tree Breeding Centre. With joint federal and provincial funding, a complex was built with a greenhouse, laboratory, seed storage freezers, workshop and office space dedicated to TI and orchard seed production. In 2000, having progressed to second-generation clonal breeding populations in red spruce, white spruce, and black spruce, and first-generation populations in eastern white pine and Norway spruce, the provincial government scaled back its TI work and closed the Tree Breeding Centre. Measurement of field progeny tests, orchard roguing and unfinished second-generation selection work continued through NSTIWG activities, but active progression to next generation breeding was stopped. However, with the recent release of a provincial forest practices review (Lahey 2018), and plans to adopt a TRIAD (extensive, intensive and conservation areas) approach to Crown land forest management that includes a high production forestry component, there is renewed government interest and support for more active TI work and research which will be organized and managed via the newly formed AtlanTIC.

Regulation

Natural regeneration continues to be the dominant method of reforestation in Nova Scotia, but planting has always been an option for both forestry companies and private landowners who prefer a more intensive management approach. However, it is anticipated that as the province moves forward with TRIAD implementation, use of improved planting stock will be required on Crown land dedicated to high production forestry since production targets will rely on expected TI growth gains. NSTIWG participation is voluntary but guided by a Memorandum of Understanding between working group partners.

Seed deployment

Tree planting in Nova Scotia was just over 8 million annually when NSTIWG was formed in 1977. Between 1981 and 2012, an average of 18 million (range 11 to 31 million) seedlings were planted annually. Planting started to decline in 2013 and is currently at approximately 10 million seedlings. Since 2000, virtually all reforestation stock has been produced from orchard seeds. The Nova Scotia government also sells seedlings produced at the TBC and improved seed to private companies outside of Nova Scotia.

Economic impact

A comprehensive economic impact assessment of TI work has not been conducted in Nova Scotia. However, based on the assumption that juvenile height gain percentages in second generation improved stock are indicative of expected gains at economic maturity, it is estimated that a 20% gain will be realized in red and white spruce volume at rotation which could increase to approximately 25% after further orchard roguing. For black spruce, current expected volume gains are approximately 15% at rotation. Although economic analyses have not been done on the use of improved growing stock to increase yields on a smaller land base, this shift to a TRIAD approach is expected to also contribute to provincial biodiversity and habitat management objectives on non-plantation forest land.

Climate change

Climate change adaptation has not been a consideration in Nova Scotia's provincial TI strategies, although the value of historical provenance testing and datasets for assessment of climatic resilience within the breeding populations is recognized. NSTIWG plans to increase collaboration with research scientists and other TI groups to establish regional trials across a greater range of climate gradients, thereby informing decisions regarding testing, selection, and deployment. The province is also assessing carbon sequestering and climate change adaptation strategies as part of TRIAD and high production forestry implementation.

Genetic conservation

Maintenance of genetic diversity within breeding populations has always been a part of Nova Scotia's tree breeding work and will continue to be in the future. In addition, the province works with the National Tree Seed Centre (Fredericton) to provide wild seed when available and has worked on a tree gene conservation strategy that includes consideration of many species, including eastern white cedar and black ash (*Fraxinus nigra* Marsh.) which are listed as vulnerable and threatened, respectively, in Nova Scotia.

Genomics

Nova Scotia is beginning to look at the potential benefits of incorporating genomic technologies into tree breeding work. The government is a partner with New Brunswick, JDI, Québec, Genome Canada, the CWFC, and Laval University in a funded project called *FastTRAC2*, which will genotype red and black spruce breeding populations in Nova Scotia, New Brunswick and Québec. This three-year project started in 2022 and will allow for accelerated breeding and orchard management using genetic intelligence. This project is expected to provide a SNP-chip, genomic selection models, genomic estimated breeding values and an assessment of introgression in breeding and natural populations.

Research and collaborations

In the early days, NSTIWG regularly collaborated with CFS and the University of New Brunswick's Faculty of Forestry on TI-related projects. More recently, NSTIWG has formed a research partnership with Laval University, the CWFC, Genome Atlantic, and the New Brunswick Tree Improvement Council (NBTIC) to collaborate on genomics projects. NSTIWG also participated in the formation of the AtlanTIC co-operative that brings together the four TI groups in the Atlantic provinces along with industry and other academic partners. The province also has a Research Associate Membership with the North Carolina State University Cooperative Tree Improvement Program (NCSUCTIP).

20-year outlook

With recognized needs related to high production forestry and climate change adaptation, the 20-year outlook for TI in Nova Scotia is very promising. There is renewed interest and

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support for regular program work, applied research, leading-edge genomics research, and regional collaboration. It is also expected that more resources will be made available for gene conservation work as part of a new provincial biodiversity initiative.

Newfoundland and Labrador

History

Tree improvement in Newfoundland and Labrador began in the 1960s with the CFS under the assumption that unimproved native species and local seed sources were inadequate for reforestation. Provenance trials were established to identify suitable exotic species from off-island seed sources. Since then, the provincial Forest Service has largely backed away from the use of exotic species (<5% of all seedlings planted) and has focused its reforestation and TI efforts on native white and black spruce.

A program began to develop six distinct breeding programs representing two seed zones and three native species, black spruce, white spruce and eastern larch. The province was divided into two seed zones: 1) the Northern Peninsula and Labrador Seed Zone; and 2) the Main Island Seed Zone (Fig. 5).

New plus trees were identified throughout Newfoundland and Labrador in the early 1990s. Six first-generation seed orchards were established (three species X two seed zones). These consisted of seedling seed orchards for black spruce and clonal seed orchards for white spruce and eastern larch. Concurrently, testing and breeding began in support of second-generation orchards, which were later established for white and black spruce. Third-generation breeding has begun.

Since the early 1990s, significant “course corrections” were made. The two seed zones were combined for black and white spruce programs with founder plus trees from the Northern Peninsula - Labrador programs being incorporated into the Main Island TI programs. The combined programs will produce reforestation stock for the island of Newfoundland. If Labrador’s minimal reforestation requirements increase, wild local seed will be collected with the option of establishing Labrador-specific orchards from the original Labrador selected plus trees. Additional breeding material was also brought into the black and white spruce programs to maintain a high degree of genetic diversity after roguing. For white spruce, these were incorporated into the second-generation orchard. For black spruce, where the genetic deficit was greatest, a greater number of new founder trees were incorporated into the second-generation breeding program and orchard. However, most of the new selections skipped the second generation and have been incorporated into the third-generation breeding program. The eastern larch programs have been mothballed as it represents a very minor component of the provincial reforestation program (100-200 thousand seedlings per annum) and the first-generation orchards have never produced a successful cone crop. An eastern white pine clonal seed orchard/gene preservation garden was established in 2000. Eastern white pine is an uncommon native species which has been decimated by white pine blister rust. To preserve genetic diversity and to provide for a secure source of seed for reforestation purposes, a clonal orchard established around 2000 consisted of disease-free trees from across the island range of the species.

Regulation

All forestry in Newfoundland and Labrador is managed by the provincial Forest Service.

Seed deployment

Seed deployment consists of 74% black spruce, 17.2% white spruce and the remainder is exotics (5.1%) and other lesser native species (3.6%).

Economic impact

In Newfoundland and Labrador, the TI programs have been delivered at minimal cost and without a stand-alone budget allocation. The program is directed and delivered by operational silviculture program staff. Orchards are established and managed by nursery workers. Two permanent staff and two seasonal staff are responsible for all TI work. These programs have moved ahead methodically and without interruption.

Climate change

Newfoundland and Labrador TI programs have not intentionally incorporated climate change considerations. However, the wide genetic diversity represented in the seed orchards is expected to increase the adaptability of planted forests. The black and white spruce programs also include genetic material originating from off-island. In the case of white spruce, a number of locally tested Ottawa Valley trees have been incorporated. For the black spruce program, a significant amount of genetic material from Ontario, Québec and the Maritimes have been incorporated. This off-island genetic material could well have positive climate change impacts.

Genetic conservation

Efforts associated with conservation are linked to strategies modeled from the Maritime programs while the new AtlanTIC has yet to develop this component of their program.

Genomics

Genomics have not been incorporated into the Newfoundland and Labrador TI programs. To this point, the Newfoundland and Labrador programs have relied exclusively on conventional tree breeding and seedling production techniques. This is, to a large extent, a function of the limited access to academic and government research capacity and support.

Research and collaborations

The provincial Forest Service does not have a forest geneticist on staff and there is no forest genetics capacity at Memorial University or at the local CFS lab. Therefore, since its inception, the Newfoundland and Labrador TI Committee has looked to TI programs and expertise in the Maritimes (in particular NBTIC and CFS-Fredericton), for advice and guidance. Consequently, Newfoundland and Labrador’s TI strategies are modeled on those in the Maritimes.

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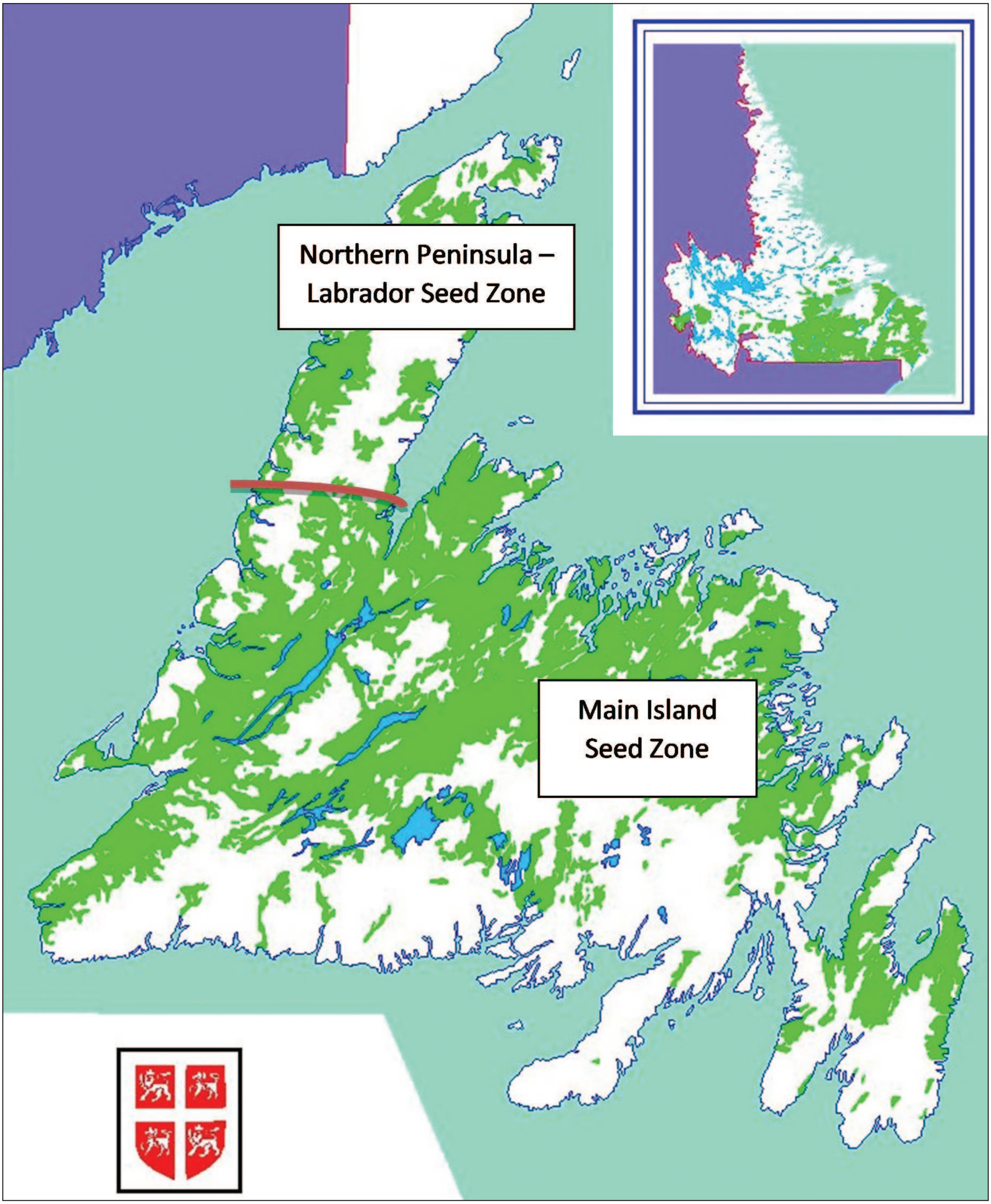

Fig. 5. Delineation of the two seed zones in Labrador and Newfoundland. The red line indicates the break between the northern and southern zones.

20-year outlook

The current TI effort targets the genetic improvement of black and white spruce, the principal reforestation species, which represent more than 90% of all tree seedlings planted. Since its inception, in the mid-1980s, the TI programs have been directed, funded and implemented by the Forest Service of Newfoundland and Labrador, with minimal involvement from industrial forest tenure holders. All tree seedlings planted in the province, regardless of tenure, are produced by the Forest Service and program direction comes from the Provincial TI Committee which is co-chaired by the Manager of the Provincial Tree Nursery and the Supervisor of Silviculture. In addition, Newfoundland and Labrador is now also a member of AtlanTIC.

All black and white spruce reforestation stock comes from rogued first-generation seed orchards. The second-generation black spruce orchard has begun to produce cones and will likely replace the first-generation orchard within the next 5-10 years. Significant yield gains are expected from the rogued first-generation orchards with even greater gains expected from future generations. Polycrosses of orchard selections are underway and all seed orchards will be rogued. Third-generation breeding of black spruce is well underway and also, as of 2018, of white spruce.

A significant gap is the need for RGTs and validated yield gains. Although field testing has shown significant yield gains, they have not been quantified or integrated into wood supply modeling.

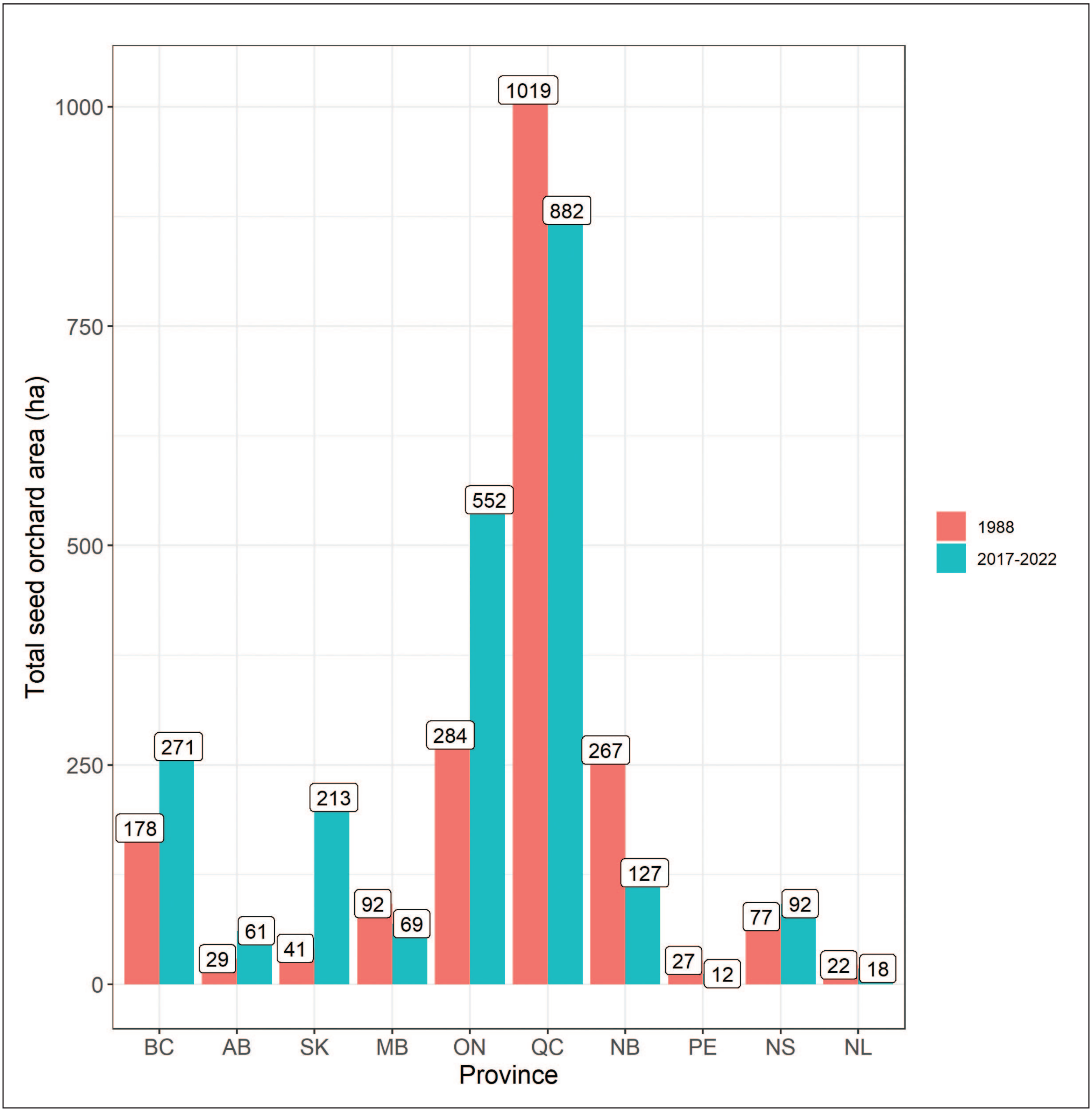

Fig. 6. Total seed orchard area (ha) by province comparing 1988 with 2017 to 2022 values as available.

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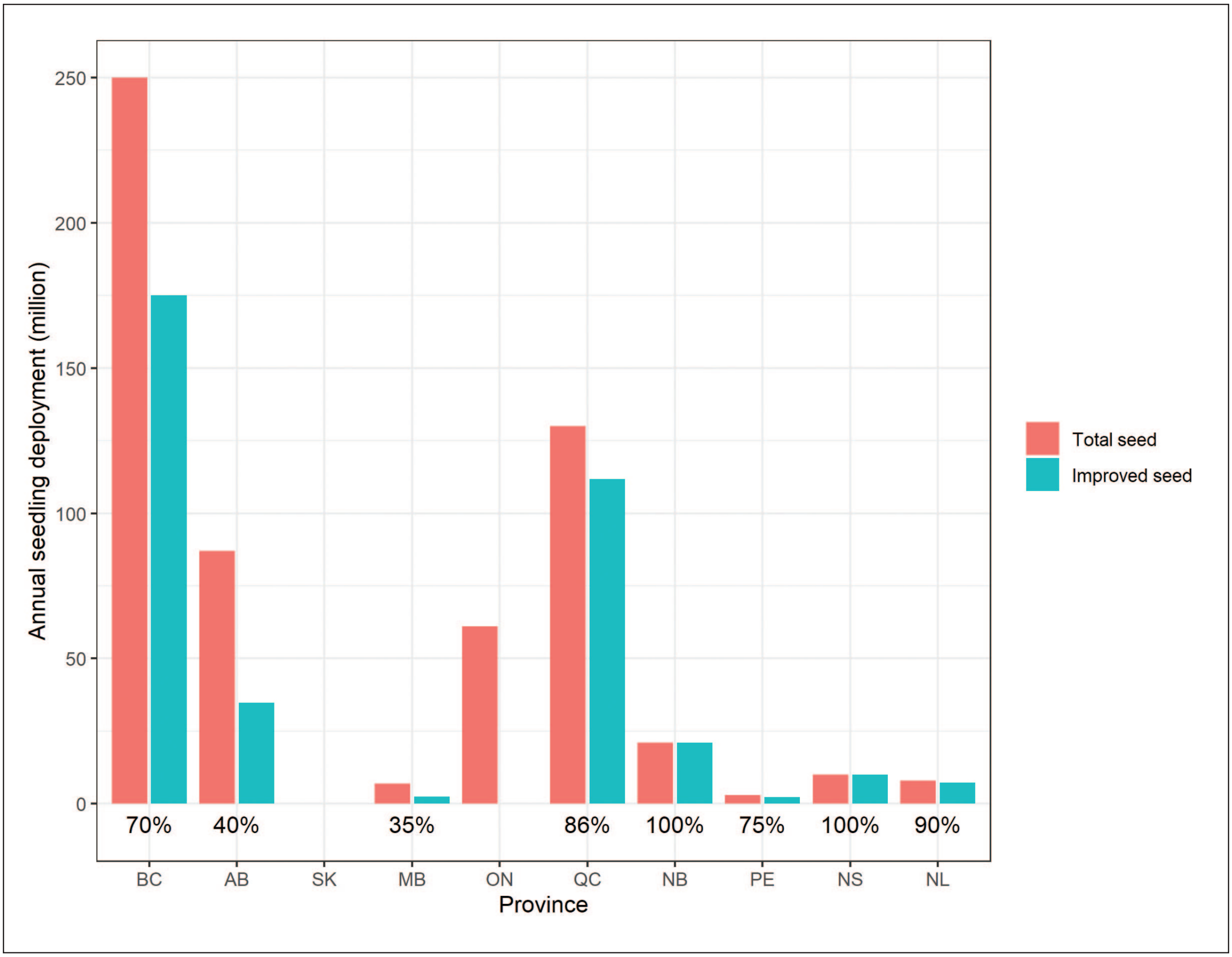

Fig. 7. Total annual seedling deployment, and per cent (%) supplied from seed orchards by province covering the time frame from 2017 to 2022 where available. Note: BC = British Columbia, AB = Alberta, SK = Saskatchewan, MB = Manitoba, ON = Ontario, QC = Quebec, NB = New Brunswick, PE = Prince Edward Island, NS = Nova Scotia, and NL = Newfoundland and Labrador.

Discussion

There is considerable variation in the level of commitment to TI among provinces, including species, generation, area, and objectives (Tables 1, 2). The intensity of programs is not necessarily proportional to the degree to which reforestation relies on seed orchards for their seed supply (e.g., Alberta, Newfoundland and Labrador). Seed production, usage and area planted to seed orchards varies widely across provinces with some data missing for Saskatchewan and Ontario (Figs. 6, 7). Québec has the largest area planted to seed orchards, more than three times that of British Columbia, while Québec's annual deployment is half of British Columbia's. The maritime provinces, despite a lower overall deployment (42 million seedlings), meet 91% of their seed needs from orchards established on 250 ha. In Alberta and British Columbia, where deployment numbers are much greater (337 million seedlings), seed from seed orchards is, on average, meeting only 55% of the deployment needs and the investment in orchard area is 332 ha with the majority of those orchards in British Columbia. Manitoba has a similar area in seed orchards to Alberta (69 vs 61 ha, respectively), although it requires only a fraction of the number of seedlings for reforestation (8%) compared to Alberta. Despite the relatively large seed orchard area, Manitoba meets only 35% of its seed needs through supply from seed orchards.

The introduction of genomics technology into tree breeding has been sporadic and the depth of investment variable. For example, the group working in genomics/genetics at UBC has been very successful at obtaining Genome Canada funding with some labs obtaining > $100 million in funding. Other provinces have not used any genomics technology to advance their programs (e.g., Manitoba, Newfoundland and Labrador). Application of genomic technology is wide-ranging in its utility, from simple genotyping to determining the identity of a family, rebuilding pedigrees, determining pollen contamination levels or more advanced usage such as genomic selection.

A reference genome is available for white spruce (Birol *et al.* 2013) and an annotated reference genome will be available in 2024 for interior lodgepole pine. There are also SNP chips available through Laval University (Bousquet *et al.* 2021) for white spruce, in addition to other technologies more widely available for use such as genotyping-by-sequencing (e.g., Cappa *et al.* 2022b). There is an increasing need for expertise in new and traditional areas of TI including bioinformatics, quantitative genetics, phenomics, proteomics, sociologists, and economists leading to a degree of "precision forestry" and much more rapid advancement of generations. As genotyping, using one method or another, becomes financially feasible, pressures from climate change, and encroaching biotic and abiotic stress increase, selecting for height as a proxy for volume will likely no longer be sufficient to sustain programs or future healthy forests. Recognizing the social perceptions of implementing new technologies and climate-based seed transfers, can also, no longer be overlooked (Findlater *et al.* 2022).

As Canadians, we have a vast resource in our forests, forest industry and research institutions, and despite regional differences and focus, investments span from British Columbia to the Maritimes and across land management boundaries (public *versus* private). The Canadian Forest Genetics Association (https://cfga-acgf.com/), originally established in 1937, has recently invested in a new website, and provides a home to geneticists across Canada and to members with the Tree Seed Working Group.

This paper provides an up-to-date review of the status of TI in Canada, province by province. In preparing this manuscript, we used the previous review, conducted by Fowler and Morgenstern (1990), to highlight the changes that have occurred over the past 30+ years (e.g., see Fig. 6). The future of TI is particularly bright at our coastal boundaries, while all members of this community must be vigilant to preserve our clone banks, breeding orchards and all other forms of genetic resource conservation being conducted either directly or indirectly through our collective efforts across the country. New efforts must be made, to ensure reinvestment in field trials in the face of climate change, to better guide future decisions ensuring adaptation, resilience and the health of our forests and forest-based communities.

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