

**PROCEEDINGS OF THE THIRTY-SECOND MEETING
OF THE
CANADIAN FOREST GENETICS ASSOCIATION**

PART 1 Minutes and Members' Reports
PART 2 Symposium

**Forest Genetics & Tree Improvement:
New Knowledge, Challenges &
Strategies**



**Génétique forestière & amélioration des
arbres : nouvelles connaissances, défis
& stratégies**

**COMPTES RENDUS DU TRENTE-DEUXIÈME CONGRÈS
DE
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**ADVANCES IN SPRUCE GENOMICS, QUANTITATIVE GENETICS AND
POPULATION GENETICS AT THE CANADIAN FOREST SERVICE,
CANADIAN WOOD FIBRE CENTRE, QUEBEC REGION**

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This report summarizes the progress made by the Canadian Forest Service (CFS) - Canadian Wood Fibre Centre (CWFC) in forest genetics, genomics, molecular ecology, and biodiversity for the 2008–2011 period. Our research activities were mainly focused on spruce. This work was made possible through grants obtained from the NRCan–Forest Industry Long-Term Competitiveness Strategy; the CFS–Genomics R&D Initiative; and through our participation in the *Arborea* project (J. Mackay and J. Bousquet, Univ. Laval), a major initiative funded by Genome Canada and Genome Quebec to develop molecular breeding in softwood trees. We also continued investing considerable time and effort in population genetics studies of forest tree species as part of our participation in the research activities of the Canada Research Chair in Forest and Environmental Genomics (Tier I), via a Natural Sciences and Engineering Research Council (NSERC) strategic grant for the development of a Phylogeographic Atlas of Canadian Conifer Tree Species (J. Bousquet and J. Beaulieu), as well as a grant from the Ministère du Développement économique, de l'Innovation et de l'Exportation du Québec (MDEIE) to foster collaboration with Mexico (D. Khasa, J. Bousquet, and J. Beaulieu). Other research activities on the genetics of the white spruce root system were also conducted in collaboration with Hank Margolis of Univ. Laval and Mohammed Lamhamedi of the Ministère des ressources naturelles et de la faune (MRNF), with funding received from the Fonds québécois de la recherche sur la nature et les technologies (FQRNT).

Research accomplishments were made possible thanks to the generous contribution of dedicated staff and collaborators who deserve our recognition. They are: Michèle Bernier-Cardou, Pamela Cheers, Éric Dussault, Philippe Labrie, Audrey Lachance, Isabelle Lamarre, Patrick Laplante, Daniel Plourde, Esther Pouliot, and several summer students.

SPRUCE GENOMICS

During the last three years, grants were obtained from the CFS–Genomics Research & Development Initiative (GRDI) and the NRCan–Forest Industry Long-Term Competitiveness Strategy to carry out association studies of wood traits, both in white spruce and black spruce. These grants were also used as co-funding for research activities of the *Arborea* project, a major initiative funded by Genome Canada and Genome Quebec to develop molecular breeding in softwood trees and co-led by J. Mackay and J. Bousquet (Univ. Laval).

A first discovery population of 495 white spruce (*Picea glauca*) was assembled along with a validation population consisting of 200 trees. Increment cores were collected from these trees and phenotypic values for a variety of wood traits and properties were assessed at FPinnovations–Paprican’s facilities in Vancouver, British Columbia. Hence, radial profiles of over 25 wood physical properties were obtained for each of the 695 trees. An Oligo Pool All array including 1536 single nucleotide polymorphisms (SNPs) harboured by 625 candidate genes for wood formation was built and the discovery population was genotyped using the Illumina GoldenGate genotyping assay. Candidate genes were either selected based on expression profiling studies and literature reports or were detected *in silico* from the gene sequences. Association studies are underway and the first gene variants associated with wood traits in white spruce have been identified. Data analysis made it possible to find between 8 and 21 SNPs that were significantly associated ($P \leq 0.01$) with each of the earlywood, latewood, and total wood traits. After controlling for multiple testing ($Q \leq 0.10$), 13 SNPs were still significant across as many genes belonging to different families, each accounting for 3% to 5% of the phenotypic variance in 10 wood characters (Beaulieu et al. 2011). When analyzed simultaneously, the cumulative effect of multiple significant SNPs for the same trait could explain a higher proportion of the total phenotypic variation (e.g., 9.7%, 8.7%, and 11.1% for average ring width in latewood, cell wall thickness in early wood, and percentage of earlywood, respectively). The SNPs that were found significant in the first association study are being tested in collaboration with Y.S. Park (CFS) using a 14-year-old clonal test established in New Brunswick.

The white spruce discovery population was expanded from 495 to 1700 trees and wood physical traits of the additional trees were also assessed by FPinnovations using the SilviScan technology. Thanks to our collaboration with *Arborea* and funding from Genome Canada and Genome Québec, the large discovery population could be genotyped using the Illumina Infinium iSelect genotyping bead chip. Hence, over 6700 high-quality SNPs were available for new association studies. Preliminary results of single-locus analysis show that a total of over 100 SNPs were found associated with wood traits, each explaining between 1% and 5% of the phenotypic variation in these wood traits. Analyses were also carried out with the subset of SNPs found significantly associated at $P \leq 0.05$ with a given wood trait using the Bayesian hierarchical model (BAMD). Hence, for wood density, a subset of 47 SNPs with effects significantly different from zero was delineated, which could explain close to 40% of the variation. These results show that Bayesian multilocus approaches are promising for the identification of groups of markers that could be used for the selection of trees with desirable wood attributes. A manuscript is in preparation to report the results of these new analyses, which were presented at the “Genomics-based Breeding in Forest Trees Symposium” held in Davis, California, in June 2011.

Efforts were also made to develop molecular breeding for wood traits in black spruce (*Picea mariana*). Wood physical properties of a discovery population of 400 samples were assessed by FPinnovations using the SilviScan technology. The population was assembled from a progeny test in New Brunswick with the collaboration of the New Brunswick Tree Improvement Council (Kathy Tosh). The search for SNPs in gene sequences amplified using primer pairs developed for white spruce was achieved for over 1500 contigs using white spruce cDNA sequences available through our partnership with *Arborea* and funding previously obtained from FQRNT with J. Bousquet for black spruce marker development. The development of an Oligo Pool All (OPA) array to genotype the discovery population was completed and association studies were carried out using multi-SNP Bayesian hierarchical models to identify gene variants that have the potential to be used as selection tools. We have begun testing markers to rank a Newfoundland and Labrador black spruce breeding population for wood traits.

In collaboration with *Arborea* (J. Bousquet) and the financial support of FQRNT, outlier detection methods were used to scan the black spruce genome for gene SNPs involved in adaptation to variation in temperature and precipitation. This scan involved close to 600 SNPs from over 300 genes. Using two detection approaches, a total of 26 SNPs from 25 genes distributed among 11 of the 12 linkage groups were detected as outliers with F_{ST} values as high as 0.078. Several genes carrying outlier SNPs belonged to gene families previously found to harbour outlier SNPs in white spruce. The functional annotations of these genes and regression of SNP frequencies on climatic variables supported their involvement in adaptive processes. Results were published in *Molecular Ecology* (Prunier et al. 2011).

A Laboratory Information Management System (LIMS), supported by a relational database (TreeSNPs), was developed for SNP discovery in our genomics projects in collaboration with *Arborea* researchers (Clément et al. 2010). Its functions include bulk data submission, reporting of candidate gene selection, cDNA and PCR primer sequences, amplification success and resequencing results, and export of tables (CSV format) for downstream analysis. The system, source code, and documentation are available for download at <http://treesnpspub.arborea.ulaval.ca:3000/download>. A second database (PhenoTree) was developed and it characterizes each tree in our discovery and validation populations by its pedigree,

growth environment, and phenotype. Phenotypic data include tree morphological data (dbh, height, crown dimensions, branching), wood chemical determinations, and physical properties.

QUANTITATIVE GENETICS

Quantitative Genetics of Wood Properties

In collaboration with J. Mackay (*Arborea*), we investigated the genetic control of wood physical properties in white spruce as a function of cambial age (up to 16 years at DBH) to improve juvenile wood attributes of this species. Increment cores were taken from 375 trees randomly selected from 25 open-pollinated families in a provenance-progeny test established on three sites. High-resolution pith-to-bark profiles were obtained for microfibril angle (MFA), wood stiffness, wood density, tracheid diameter, cell wall thickness, fibre coarseness, and specific fibre surface using the SilviScan technology. The heritability estimates obtained indicate that genetic control of cell anatomy traits and wood density increases with cambial age, whereas the genetic control of MFA and wood stiffness remains relatively low across growth rings. Significant genetic gains could be expected in tree improvement programs for wood density, radial tracheid diameter, cell wall thickness, and specific fibre surface. Genetic and phenotypic correlations between wood traits along the cores from pith to bark were also estimated. Results show that most correlations become stronger in magnitude in rings closer to the bark. An exception to this rule was found between MFA and wood stiffness, where correlations were strongly negative from the pith to the bark. Age-age correlations for different wood traits were found to be high and possible gains from early selection were estimated to be good in ring 8 and older for most traits. MFA was the trait with the strongest potential for selection as early as ring 4, but a detrimental correlation with wood density may represent a drawback of this juvenile selection approach. Results were published in two scientific papers (Lenz et al. 2010, 2011).

Other Quantitative Genetics Studies

In collaboration with H.A. Margolis (Univ. Laval) and with funding from FQRNT, the genetic variation and control of seed and germination characteristics were investigated, as well as the extent to which they influence the early growth of 75 open-pollinated white spruce families. Seed characteristics studies included 1000-seed weight, length, width, area, and volume whereas germination ones included germination capacity, peak value, and germination value. Seedlings were also produced and measured at the end of the first and second growing seasons. Significant variation due to families was found for all the traits, with the between-family variation explaining 23% to 98% of total variation in the various seed traits. Family differences at the seed stage could explain up to 33% of root dry weight at the first-year seedling stage and 12% of shoot dry weight at the second-year seedling stage (Carles et al. 2009).

Genetic variation in rooting characteristics of white spruce cuttings harvested from 2-year-old stock plants of the same 75 open-pollinated families was also explored. Growth, root system architecture, and gas exchange of the cuttings during the rooting phase and the two subsequent growing seasons were evaluated. Root initiation as well as root development during the two following years were found to be under strong genetic control. Strong positive correlations between plant root and aboveground traits at the end of years 2 and 3 suggest that an indirect selection for families producing cuttings with heavier root dry masses could be based on aboveground traits. Results were published in the Canadian Journal of Forest Research (Gravel-Grenier et al. 2011).

Quantitative genetics studies were also carried out with collaborators on one Mexican and one African tree species. For the first study, 13 *Pinus patula* populations were sampled in the state of Oaxaca, Mexico, along an altitudinal gradient (2400 m to 4000 m). Seedlings were grown in tree pots in two environments: in a shade house located in Ixtlán de Juárez and in a greenhouse followed by a shade house in Quebec City. Total seedling height was measured at 6 months of age in both locations. Results indicate that the populations differed significantly and that there was no significant genotype x environment interaction. The population found at 2650 m was the tallest. These results suggest the presence of a weak altitudinal pattern of variation in seedling height. This research was carried out by Professor Cuauhtémoc Sáenz-Romero during his sabbatical stay in Quebec City (Sáenz-Romero et al. 2011). We also determined whether *Allanblackia floribunda*, a forest tree species growing in Africa and valued for the fat extracted from its seeds, could be genetically improved for fruit/seed production. Seventeen to forty fruits from each of 70 trees distributed among four sites in Cameroon were sampled. Fat was extracted from the seeds and

the stearic and oleic acid contents of the fat were estimated. Highly significant ($P < 0.0001$) between- and within-tree variation characterized the fruit and seed traits. Stearic and oleic percentages in seed fat ranged from 44% to 66% and from 25 and 48% per tree, respectively. Moderate repeatabilities were estimated for fruit traits and mean seed mass. Moderate positive relationships were also found between stearic and oleic acid percentages. Results of the study were published (Atangana et al. 2011) and show that there is a potential for breeding *Allanblackia floribunda* for stearic and oleic acid contents in seed fat.

POPULATION GENETICS

Phylogeography

During the 2008–2011 period, we continued investing time and energy in the development of knowledge in phylogeography of North American conifer species. Studies were carried out in collaboration with Jean Bousquet's (Univ. Laval) team and support from NSERC, and results were published in various scientific journals. Besides completing an invited review on the phylogeography of North American trees (Jaramillo-Correa et al. 2009), the first study aimed to determine whether the phylogeographic structure of jack pine (*Pinus banksiana*) populations in eastern Canada was supporting the existence of a coastal glacial refugium in mid-latitudes. One maternally inherited mitochondrial DNA (mtDNA) minisatellite marker and four paternally inherited chloroplast DNA (cpDNA) microsatellite markers were used to assess the range-wide geographical structure of jack pine populations. A total of 1240 trees was sampled from 83 populations. Fifteen mitotypes and fifty chlorotypes were found. Results show that populations from the Maritimes present a unique mtDNA background characterized by very low diversity and the preponderance of a distinctive mitotype. The distribution of cpDNA diversity was not spatially structured, although three chlorotypes were restricted to the east. Based on the patterns observed, we concluded that populations from the Maritimes region likely derive from a genetically depauperated north-coastal refugium (Godbout et al. 2010).

In a second study, we also focused our interest on eastern North America. Our objective was to determine whether genetic diversity in eastern hemlock (*Tsuga canadensis*) is uniformly distributed or structured; this information is relevant to help guide conservation efforts. A total of 892 individuals from 60 populations representative of the entire natural range was sampled and genotyped at seven polymorphic cpDNA markers. Sixteen chlorotypes were identified. Among-population differentiation was low ($G_{ST} = 0.02$). Moreover, the distribution of chlorotypes did not show a strong geographical pattern. A spatial Bayesian approach made it possible to reveal two distinct groups of populations, with the southern Appalachian populations harbouring greater population differentiation and conserving relatively high allelic richness. In an article published in the Canadian Journal of Forest Research (Lemieux et al. 2011), we concluded, based on the patterns observed, that the southern part of the eastern hemlock range should be considered high priority for *ex situ* conservation.

In a range-wide population genetics study of black spruce (Gérardi et al. 2010), we compared transcontinental chloroplast and mitochondrial DNA population structures in order to identify putative ancestral and new cytoplasmic genome assemblages. A total of 597 trees was sampled in 32 populations, three of them being from Alaska. Trees were genotyped for four mtDNA polymorphic markers resulting in 10 mitotypes and five cpDNA regions generating 93 different chlorotypes. Mean within-population diversity and allelic richness for cpDNA markers were 0.80 and 4.21, respectively, and diminished westward. Population differentiation estimates were $G_{ST} = 0.104$ and $G_{ST} = 0.645$ for cpDNA and mtDNA, respectively. At least three genetically distinct cpDNA lineages partially congruent with those inferred from mtDNA data could be delineated. Patterns observed in Alaska suggest that black spruce could have survived the last glacial maximum there. Results also suggest the occurrence of extensive pollen gene flow between ancestral lineages that preferentially occurred west to east, while seed-mediated gene flow was geographically restricted.

With the financial support from MDEIE and in collaboration with J. Bousquet and D.P. Khalsa (Univ. Laval), Douglas-fir (*Pseudotsuga menziesii*) was also the subject of a range-wide phylogeography study and results were published in Tree Genetics & Genomes (Wei et al. 2011). This study was also a mandate from the North American Forest Commission of the FAO. Two organelle DNA markers with contrasting modes of inheritance were genotyped for 613 trees from 44 populations covering all of the species' natural range, from Mexico to Canada. Two mitotypes and 42 chlorotypes were recovered in this survey. Significant subdivision was observed in both genomes, which is an indication that seed and pollen gene flows were restricted. Three distinct cpDNA lineages were delineated, corresponding to the Pacific Coast, the Rocky Mountains, and Mexico. The northern populations were characterized by a high level of genetic

diversity, indicating a large zone of contact between coastal and Rocky Mountains lineages. A possible northern refugium was also inferred from the data collected. The Mexican lineage, which appeared to originate from the Rockies lineage, was characterized by the lowest genetic diversity but the highest population differentiation. Our results emphasize the pressing need for conservation of Mexican Douglas-fir.

Mating Patterns in a Breeding Orchard

A study was carried out to test the predictive value of biological and ecological variables on male fertility patterns in a white spruce breeding orchard using genetic markers and a full-likelihood Bayesian paternity analysis. The orchard located at the Cap Tourmente Wildlife Reserve contains 104 clones from 36 provenances, with up to 10 ramets per clone. Each individual ramet was assessed visually for the number of male strobili produced over a 2-year period. Moreover, five seedlots were collected from each of two designated mother clones in the orchard. A random sample of seed from lots collected during both years was sown and grown in a greenhouse. A total of 522 surviving offspring were genotyped along with the 104 clones from the orchard at nine sequence tagged sites (STS) and two microsatellite loci. Results of the analyses (Doerksen et al. 2011) showed that distance alone was predictive of siring success, whereas fecundity and a provenance indicator variable captured additional – but not all – remaining variation. Using additional non-genetic measures to predict siring success increased individual probabilities of paternity over a genetic-only model. Not all successful males were consistently successful over the years. Overall rate of selfing was 14% in the surviving (56% – 63%) seedlings. For 6% of the sampled progeny, breeding orchard fathers could not be assigned. These results highlight the need to be cautious when open-pollinated seedlots are collected in breeding orchards for reforestation needs.

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