

AFORGEN meeting 21. -23. June 2018

Venue: Hotel Kompas, Kranjska Gora, Slovenia

Agenda

Thursday 21. June

9:00 - 9:10	Opening of the meeting and a short presentation of the Slovenian Forestry Institute	Primož Simončič
Session on Botanic and Hybridization		
9:10 - 9:30	Forests and forestry in Slovenia: The mountain forests	<u>Andrej Breznikar</u> , Boris Rantaša, Aleš Poljanec
9:30 - 9:50	Allopoloid hybridization in Sorbus: case study of pink-flowered hybrids	<u>Dušan Gömöry</u> , Ladislav Paule, Juraj Paule, Diana Krajmerová, Veronika Uhrinová
9:50-10:10	Genetic monitoring of hybridogenus populations: an analysis of <i>Abies borisii-regis</i> , a hybrid between <i>Abies alba</i> and the Greek endemic <i>Abies cephalonica</i>	<u>Filippos A Aravanopoulos</u> , Marjana Westergren, Nikos Tourvas, Barbara Fussi, Domen Finžgar, Marko Bajc, Darius Kavaliauskas, Ermioni Malliarou, Fotis Kiourtsis, Hojka Kraigher
10:10-10:30	Ad hoc breeding of firs for Christmas trees in Denmark	<u>Ole Kim Hansen</u> , Jing Xu, Ulrik Bräuner Nielsen
10:30-11:00	Coffee break	
Session on Demographic history and Evolution		
11:00 - 11:20	Demographic and evolutionary history of <i>Abies alba</i> in the Pyrenees	<u>Caroline Scotti-Saintagne</u> , Thomas Boivin, Brigitte Musch, Ivan Scotti, Bruno Fady
11:20 - 11:40	Selection gradients and evolutionary potential in <i>Abies alba</i> and <i>Fagus sylvatica</i> , two emblematic and widely-distributed Alpine trees	<u>Marjana Westergren</u> , Domen Finžgar, Marko Bajc, Hojka Kraigher, Santiago C. González-Martínez
11:40 - 12:00	Demographic and evolutionary history of <i>Pinus nigra</i>	Guia Giovannelli, Caroline Scotti Saintagne, Ivan Scotti, Anne Roig, Ilaria Spanu, Giovanni Giuseppe Vendramin, Frédéric Guibal, <u>Bruno Fady</u>
12:00 - 12:40	Round the table presentation	Everyone without a talk
12:40 - 14:10	Lunch	
Session on Traits and Environment		
14:10-14:30	Carbon storage and water use efficiency in <i>Abies alba</i> seedlings: the effect of genetics and simulated browsing	<u>Alexandra Glauser</u> , Katalin Csillery, Nina Buchmann, Arthur Gessler, Andrea Kupferschmid
14:30 - 14:50	Drought tolerance of silver fir populations across Switzerland and southern France	<u>Katalin Csilléry</u> , Nina Buchmann, Bruno Fady, Felix Gugerli, Otso Ovaskainen, Christoph Sperisen, Alex Widmer

14:50 - 15:10	Environmental drivers of fine scale genetic structure in silver fir populations across the species' distribution range	<u>Enikő Major</u> , Mária Höhn, Camilla Avanzi, Bruno Fady, Katrin Heer, Sascha Liepelt, Lars Opgenoorth, Andrea Piotti, Flaviu Popescu, Dragos Postolache, Giovanni Giuseppe Vendramin, Birgit Ziegenhagen, Katalin Csilléry
15:10 - 15:30	Linking dendroecology and association genetics in forest trees in natural populations	<u>Katrin Heer</u> , David Behringer, Alma Piermattei, Claus Bässler, Bruno Fady, Sascha Liepelt, Andrea Piotti, Giovanni Vendramin, Birgit Ziegenhagen, Ulf Büntgen, Lars Opgenoorth
15:30 - 15:50	A tree phenology and ectomycorrhizal fungal composition correlations - case study on silver fir (<i>Abies alba</i> Mill.)	Tina Unuk, Tijana Martinović, Domen Finžgar, Hojka Kraigher, <u>Tine Grebenc</u>
15:50 - 16:20	Coffee break	
Session on Transcriptomics		
16:20- 16:40	Using transcriptome sequencing and pooled exome capture to study local adaptation of <i>Pinus cembra</i> at the timberline	<u>Christian Rellstab</u> , Benjamin Dauphin, Stefan Zoller, Sabine Brodbeck, Felix Gugerli
16:40 - 17:00	Transcriptome resources of <i>Abies sachalinensis</i> in Hokkaido, Japan	<u>Saneyoshi Ueno</u> , Yukino Nakamura, Masaaki Kobayashi, Shin Terashima, Wataru Ishizuka, Kentaro Uchiyama, Yoshihiko Tsumura, Kentaro Yano, Susumu Goto
17:20 - 17:40	Assembly of complete mitochondrial genome sequences of two <i>Populus</i> species and identification of RNA editing sites	Wolfram Georg Brenner, Malte Mader, Hans Hönicka, Hilke Schroeder, Niels Andreas Müller, Matthias Fladung, <u>Birgit Kersten</u>
17:40 - 18:30	Discussion	

Friday 22. June

Field trip. Departure at 8:30. Arrival back to hotel around 17:00.

Saturday 23. June

9:00-9:15	Update on the Silver fir genome project (SFGP): Elena Mosca & David Neale
9:15-10:30	Discussion on SFGP future steps: Moderated by Berthold Heinze & SFGP SteCom <ul style="list-style-type: none"> • Silver fir controlled crosses: Katalin Csilléry et al. • Options for continuing with SFGP
10:30 - 11:00	Coffee break
11:00 - 12:00	Business meeting & Decision making: Moderated by SFGP SteCom <ul style="list-style-type: none"> • Election of the new steering committee and IUFRO deputies

Session on Botany and Hybridization

Forests and forestry in Slovenia: The mountain forests

Andrej Breznikar, Boris Rantaša, Aleš Poljanec

Slovenian forests are characterized by great variability and by preserved natural structures on different levels. Forestry doctrine and organization are based on close to nature, sustainable and multifunctional principles. Recent natural disasters in Slovenian forests are pointing out a need for adaptation of traditional practices on all fields of forest management, especially in sensitive mountain forests.

Allopolyploid hybridization in *Sorbus*: case study of pink-flowered hybrids

Dušan Gömöry, Ladislav Paule, Juraj Paule, Diana Krajmerová, Veronika Uhrinová

Pink-flowered hybrid species of the genus *Sorbus* comprise bigenomic hybrid species derived from crosses *S. aria* s.l. x *S. chamaemespilus* and trigonomic ones, where *S. aucuparia* was involved as well. Samples from putative maternal species and eight pink-flowered and two white-flowered (*S. aria* x *S. aucuparia*) hybrid species were collected in the Western Carpathians and the Sudetes. Six chloroplast microsatellites were used to infer parentage, whereas nuclear amplified fragment length polymorphism (AFLP) markers were employed for the identification of clones and patterns of genetic variation. Ploidy levels were estimated by flow cytometry.

Genetic data supported hybrid origins proposed based on flower and leaf morphology, and chloroplast DNA revealed recurrent origins (*S. caeruleomontana*, *S. haljamovae*), even from bidirectional hybridization events (*S. zuzanae*). All bigenomic and trigonomic hybrid species (except triploid *S. zuzanae*) were found to be tetraploid. In addition to polyploidy, low genetic variation and the presence of clones within and among populations were observed, suggesting predominantly apomictic reproduction of the hybrid species. Most of the described hybrid species appeared also genetically distinct. The data suggest that multiple hybridization events in the Western-Carpathian *Sorbus* have led to the formation of separate, partially reproductively isolated genetic lineages, which may or may not be discriminated morphologically. Even bidirectional hybridization can produce individuals classified to the same taxon based on phenotype. For some hybrid taxa, hybridization pathways were proposed based on their genetic proximity to parental species and differences in genome sizes.

Genetic monitoring of hybridogenus populations: an analysis of *Abies borisii-regis*, a hybrid between *Abies alba* and the Greek endemic *Abies cephalonica*

Filippos A Aravanopoulos, Marjana Westergren, Nikos Tourvas, Barbara Fussi, Domen Finzgar, Marko Bajc, Darius Kavaliauskas, Ermioni Malliarou, Fotis Kiourtsis, Hojka Kraigher

Abies borisii-regis Mattfeld, is a taxon with a highly debated origin, nevertheless it is currently considered to be a hybrid fir, the result of introgression between silver fir (*Abies alba* Miller) and the endemic Greek

fir (*Abies cephalonica* Loudon). The habitat characteristics and the ecological requirements of the parental species, as well as their anticipated response function to climatic change, are likely to be markedly different. An *Abies borisii-regis* population from Mt. Olympus, Greece is part of a forest genetic monitoring (FGM) assessment that also includes two to *Abies alba* populations from Slovenia and Germany. FGM is the quantification of temporal changes in population genetic variation and structure, which elucidates processes that maintain genetic variation in natural populations, and introduces prognosis, helping to define tools for forest gene conservation, policy and management. FGM is based on the temporal population assessment based on a system of indicators and verifiers. In the present study, 11nSSR loci and one cohort (adult trees) were used. More than half of the private alleles were detected in the Greek *Abies borisii-regis* population, a possible result of its association to the *Abies cephalonica* genome. In the analysis of the adult trees cohort, *Abies borisii-regis* presented higher effective number of alleles, allelic richness and inbreeding coefficient values compared to *Abies alba*, lower observed heterozygosity, while the expected heterozygosity value was intermediate between those of the Slovenian and German silver fir populations. The *Abies borisii-regis* population was the most differentiated as seen from different averaging and multivariate approaches. In the case where interspecific hybridization occurs, a hybridization index can form an important additional verifier for FGM assessment.

Ad hoc breeding of firs for Christmas trees in Denmark

Ole Kim Hansen, Jing Xu, Ulrik Bräuner Nielsen

- Breeding of firs for Christmas trees has been ongoing in Denmark for 25 years.
- Technical developments as well as lack of continuous funding imply that pedigree establishment using DNA markers seems the most realistic way to proceed.

Session on Demographic history and Evolution

Demographic and evolutionary history of *Abies alba* in the Pyrenees

Caroline Scotti-Saintagne, Thomas Boivin, Brigitte Musch, Ivan Scotti, Bruno Fady

Our study is focused on the South Western rear edge of the distribution of *Abies alba* : The Pyrenees mountains. Other Mountains (Massif Central, Southern Alps, Corsica) have been included as outside references.

A total of 1563 individuals has been genotyped at three chloroplast microsatellites (cpSSR) and 10 nuclear microsatellite loci (NuSSR). We observed a gradient of diversity from high genetic diversity in the eastern Pyrenees to low in the west that are explained by the longitude and the seasonality of the precipitation during the mid-Holocene. Clustering analysis reveals the presence of two genetic lineages in the eastern and western parts of the Pyrenees with a hybridization zone in the central part. The

divergence of the Pyrenees lineage from a third Alpine-Corsica-Massif Central lineage took place during the middle quaternary period. The two lineages of the Pyrenees present different demographic histories that could be explained by past climatic and anthropic effects.

Selection gradients and evolutionary potential in *Abies alba* and *Fagus sylvatica*, two emblematic and widely-distributed Alpine trees

Marjana Westergren, Domen Finžgar, Marko Bajc, Hojka Kraigher, Santiago C. González-Martínez

- The distribution of effective reproductive success, a proxy for fitness, was highly skewed in the two species, with lower number of parents contributing to successful regeneration in *F. sylvatica* than in *A. alba*.
- Male selection gradients correlating effective reproductive success and diameter (DBH), a main growth trait, were significant in both *A. alba* and *F. sylvatica*, while female selection gradients were only significant for *A. alba*. Significant selection gradients were also obtained for phenological traits (bud burst) in *Fagus sylvatica* (not tested in *A. alba* yet), both for males and females.
- Preliminary results based on reconstructed pedigrees and relatedness matrices using molecular markers showed significant heritability for bud burst in *F. sylvatica*, once the environmental effects on growth are corrected for ($h^2 \sim 0.178$).
- Positive selection gradients (both species) and significant heritability in the field for bud burst (*F. sylvatica*) suggest evolutionary potential in populations of *A. alba* and *F. sylvatica*. Thus, adaptive responses to selection drivers such as those imposed by climate change are to be expected.

Demographic and evolutionary history of *Pinus nigra*

Guia Giovannelli, Caroline Scotti Saintagne, Ivan Scotti, Anne Roig, Ilaria Spanu, Giovanni Giuseppe Vendramin, Frédéric Guibal, Bruno Fady

Aim of the talk: Fragmentation proceeding over geological times confers wide, biogeographical scale, genetic diversity patterns to species, which are of major significance for adaptation. We describe and model the large scale, spatial genetic structure of the European black pine and we provide a realistic demographic, timed scenario for the patterns observed.

Location of the study: European, North African and Western-Asian countries around the Mediterranean basin.

Taxon: *Pinus nigra* (Arnold), the European black pine, a low elevation mountain conifer widely and patchily distributed in European forests and around the Mediterranean.

Methods: To resolve the contradictory results of previous population genetic and phylogenetic studies, we used a set of different genetic markers, both neutral and potentially adaptive, and either bi-parentally or uni-parentally inherited, and we sampled natural populations across the entire range of the species.

Results and main conclusions: Species with geographically fragmented distribution areas are expected to display strong among-population genetic differentiation and low within-population genetic diversity. *Pinus nigra* displays the opposite genetic patterns which are best explained as resulting from the

relatively recent Holocene fragmentation without genetic bottlenecks, of one ancestral population into seven genetic lineages which we assumed to be the main biogeographical contributors of today's natural forests. Gene flow among lineages is strong and most current populations are admixed, making taxonomic boundary delineation difficult in space.

Session on Traits and Environment

Carbon storage and water use efficiency in *Abies alba* seedlings: the effect of genetics and simulated browsing

Alexandra Glauser, Katalin Csillery, Nina Buchmann, Arthur Gessler, Andrea Kupferschmid

Ungulate browsing severely limits the natural regeneration of silver fir (*Abies alba* Mill.) in European forests. We assessed the morphological and physiological response of four to five year old seedlings to simulated browsing. Seeds were collected from 19 provenances across Switzerland, from three mother trees per site. Seedlings were grown in a common garden experiment in Matzendorf, in the Swiss Jura mountains at 1090m elevation. Five year old seedlings were exposed to two different levels of simulated browsing: light (removal of terminal buds on the terminal shoot) and strong (clipping the terminal and all lateral shoots), and compared to controls (lack of clipping). Growth and morphology were assessed one and two years after clipping. Further, two years after simulated browsing lateral needle tissue was collected from each seedling and used to assess intrinsic water use efficiency ($\delta^{13}\text{C}$), photosynthetic capacity ($\delta^{15}\text{N}$), and sugar/starch content (NSC). We applied linear mixed models, specifically the R-*asreml* implementation of the animal model with clipping treatment and stem diameter as fixed effects and provenance as a random effect to estimate the effect of treatment and the heritability (h^2) and population differentiation (Q_{st}) of each trait. We found that lightly and strongly browsed seedlings had significantly lower height increments in both years following clipping. However, two years after clipping only strongly clipped seedlings had significantly lower biomass than the controls. The strongly clipped seedlings also showed a lower water use efficiency ($\delta^{13}\text{C}$) and higher photosynthetic capacity ($\delta^{15}\text{N}$) than the control and lightly clipped seedlings, suggesting that seedlings were able to recover from light browsing but not from extensive browsing. Heritability was high for all physiology variables (largest h^2 for starch content, 0.30, smallest h^2 for sugar content, 0.15). Morphology and growth traits also had heritability higher than zero, seedling height of 2016 ($h^2=0.16$), biomass ($h^2=0.07$) and seedling height of 2015 ($h^2=0.06$). Population differentiation was the strongest for seedling height in 2015 ($Q_{st}=0.51$) among all variables. Among the physiological variables $\delta^{13}\text{C}$ had the highest population differentiation values ($Q_{st}=0.14$). Comparing estimated population effects for morphology and physiology with downscaled climatic variables, we found that seedlings that originated from warm environments were significantly larger after the stress induced by clipping than seedlings from cold environments. Overall, our results stress the importance of ecological interactions: climate and ungulate herbivory jointly affects recruitment in silver fir seedlings.

Drought tolerance of silver fir populations across Switzerland and southern France

Katalin Csilléry, Nina Buchmann, Bruno Fady, Felix Gugerli, Otso Ovaskainen, Christoph Sperisen, Alex Widmer

Climate change increases the frequency and severity of drought events, altering natural selection acting on forest trees. We studied a notoriously complex trait, drought tolerance, in 19 and 16 autochthonous silver fir populations across Switzerland and Southern France, respectively, combining tools from population and quantitative genetics. For the two regions independently, we estimated drift distances between populations based on 357 single-nucleotide polymorphism (SNP) loci using an admixture F-model. Seedling growth, height and intrinsic water-use efficiency (WUE, in Switzerland) or drought stress response (lack of watering, in France) were measured in common garden experiments. WUE was also measured on adult trees in the seed-source populations using stable isotopes from needle tissue. We

obtained fine spatial scale historical climatic data using statistical downscaling and propose a test to evaluate if selection is driven by climate. Our results indicate strong selection on height and growth driven by temperature, both in Switzerland and France: trees from warm sites grow faster and taller than those from cold sites. The evolution of drought tolerance was strongly correlated with growth both in Switzerland and France: populations that evolved slow growth and small stature also have higher drought tolerance. Our study illustrates the potential of combining different data types and methods to reveal the presence of drought adapted populations.

Environmental drivers of fine-scale spatial genetic structure in silver fir (*Abies alba* Mill.) populations across the species' distribution range

Enikő Major, Mária Höhn, Camilla Avanzi, Bruno Fady, Katrin Heer, Sascha Liepelt, Lars Opgenoorth, Andrea Piotti, Flaviu Popescu, Dragos Postolache, Giovanni Giuseppe Vendramin, Birgit Ziegenhagen, Katalin Csilléry

Many forest tree species exhibit high genetic diversity attributed to the large effective population size and high levels of gene flow. Fine-scale spatial genetic structure (FSGS) is expected to reflect population density and the extent of pollen and seed dispersal. Theory predicts that high population density likely result in a slow decay of kinship due to a high rate of outcrossing, while low population density in the lack or fast decay of kinship as individuals more likely choose selfing for reproductive assurance.

In this study, we explore fine-scale spatial genetic structure (FSGS) patterns in *Abies alba* Mill., along five altitudinal transects from all over the species range. The sampling sites were in the Apennines, the Pyrenees, the South Western Alps, the Southern Carpathians and the Bavarian Forest. Ninety-six to 465 trees were genotyped at 267 single nucleotide polymorphism loci (SNPs) in all plots but the Bavarian site (174 SNP loci). Population genetic diversity indices (H_O , H_E , F_{IS} , F_{ST}) were calculated to characterise the overall genetic structure of populations. FSGS patterns were evaluated through the spatial distribution of pair-wise kinship coefficients using SPAGeDi and R. Our findings show small differences between expected and observed heterozygosity, with no sign of inbreeding or bottleneck effects. Low levels of differentiation were found between low and high elevation sites in all regions, with the highest value in the South Western Alps (0.015) and the lowest in the Apennines (0.001). Significant FSGS was detected in all but the highly isolated Apennine populations. The decay of kinship was the slowest in the Bavarian population, but in all

populations kinship decayed to zero within 100 to 150 meters. Our results support theoretical expectations, as Bavarian populations likely grow until optimum environment conditions and have a high density, while in the southern margins of the species isolated populations most probably have higher selfing rate. Kinship coefficients were correlated with variables from historical climate data and with the quantified data of the species composition.

Linking dendroecology and association genetics in forest trees in natural populations

Katrin Heer, David Behringer, Alma Piermattei, Claus Bässler, Bruno Fady, Sascha Liepelt, Andrea Piotti, Giovanni Vendramin, Birgit Ziegenhagen, Ulf Büntgen, Lars Opgenoorth

Genetic association studies in forest trees would greatly benefit from long-term data on the trees' responses to changing climatic conditions and episodic stress events. Trees harbor these data in their annual growth rings that encode the response of trees in ring width, isotope composition and cell anatomy. However, thus far, genetic and dendroecological data have only too rarely been analyzed together. This can partly be attributed to the different aims of the two disciplines: dendroecology aims at understanding the reaction of trees towards environmental conditions at the stand level, and individual differences are usually discarded as noise. In contrast, association studies require individual-based data to address the relationship of genotypic and phenotypic variation. For a joint analysis of dendroecological and genetic data in natural populations, we need measures that describe the response of individual trees and take into account the microclimatic differences as well as differences among populations. In a study on silver fir (*Abies alba*) we exemplify such an approach by exploring the genetic basis of the response to episodic stress in surviving trees during the forest dieback of the 1970s and 1980s in Central Europe. We defined dendrophenotypes that characterize tree variability in resistance, resilience and recovery during this period. A joint analysis of these dendrophenotypes and SNPs in 103 candidate genes identified 15 genes that were associated with the dendrophenotypes, including genes linked to photosynthesis and drought stress. We show that phenotypic time-series data archived in tree-rings can be a powerful resource for genetic association studies that permits accounting for environmental variation both at the stand and individual tree level.

A tree phenology and ectomycorrhizal fungal composition correlations - case study on silver fir (*Abies alba* Mill.)

Tina Unuk, Tijana Martinović, Domen Finžgar, Hojka Kraigher, Tine Grebenc

- Interactions between aboveground and belowground components of terrestrial ecosystems are highly important in driving ecosystem processes.
- Ectomycorrhiza from a natural uneven aged *Abies alba* stand showed statistically significant differences in fungal communities of silver fir between groups of early and late flushing saplings.
- Among adult trees there was no statistically significant differences in ectomycorrhizal communities, although there were insignificant differences in alpha diversity as well as in fungal composition between early flushing and late flushing adult trees.
- *Abies alba* inoculation seedlings experiment confirmed the effect of provenance of seedlings on the mycorrhization success and selection (share) of specific types of ectomycorrhizal fungi under a one-year controlled inoculation process.

Session on Transcriptomics

Using transcriptome sequencing and pooled exome capture to study local adaptation of *Pinus cembra* at the timberline

Christian Rellstab, Benjamin Dauphin, Stefan Zoller, Sabine Brodbeck, Felix Gugerli

- Assembly of the transcriptome
- Differential gene expression
- Identification and removal of paralogous genes
- Exome capture in wild populations, including the closely related species *P. sibirica*
- Effect of paralogous genes on assessing the neutral genetic structure and adaptive genetic variation

Transcriptome resources of *Abies sachalinensis* in Hokkaido, Japan

Saneyoshi Ueno, Yukino Nakamura, Masaaki Kobayash, Shin Terashima, Wataru Ishizuka, Kentaro Uchiyama, Yoshihiko Tsumura, Kentaro Yano, Susumu Goto

Todo-matsu (*Abies sachalinensis*) is one of the most important forestry species in Hokkaido, inhabiting widely from near sea level to the alpine zone. To understand the adaptation to the habitat and identify relevant genes of the species, RNA-Seq data were collected from male and female, leaf and bark tissues, totaling 34.7 Gb, which were assembled and clustered into 158,542 transcripts from 69,618 loci. These transcripts covered 95.6 % of conserved eukaryotic genes. Annotations with various databases identified 134,190 (84.6 %) of transcripts with at least one hit. When transcripts were queried against congeneric *A. alba* proteome, 114,038 (71.9 %) of *A. sachalinensis* transcripts had candidate homologues. Simple sequence repeats (SSR) and single nucleotide variants (SNV) were screened, resulting in 28,944 and 80,758 candidates respectively. Digital expression analysis was carried out with RSEM (RNA-Seq by Expectation-Maximization) and identified candidate transcripts that were expressed specifically in each tissue. All results from these analyses were loaded onto a relational database TodoFirGene, which provides an interface for various queries and homology search, and can be accessed at the following URL: <http://plantomics.mind.meiji.ac.jp/todomatsu/>. This database hosts not only the *A. sachalinensis* transcriptome but also links to the proteomes of 13 other species, allowing a comparative genomic study of plant species.

Assembly of complete mitochondrial genome sequences of two *Populus* species and identification of RNA editing sites

Wolfram Georg Brenner, Malte Mader, Hans Hönicka, Hilke Schroeder, Niels Andreas Müller, Matthias Fladung, Birgit Kersten

- The complete mitochondrial genome sequences of *Populus tremula* and *P. alba* were assembled based on NGS data from total DNA.

- Combining *P. tremula* genomic data with newly generated and publicly available RNAseq datasets, we so far identified more than 300 RNA editing events (C to U changes) in the CDS of 26 out of 33 protein-coding transcripts annotated.
- Most of the editing events were identified at position 1 or 2 of the codons, usually altering the encoded amino acid; that might be important in restoring genetic information at the mRNA level.
- The highest density of RNA editing sites was observed in *ccmC* transcripts (50.5 sites per kilobase of coding sequence; 38 sites).
- Most of the RNA editing sites identified in *P. tremula* are highly conserved in *P. alba* and *P. trichocarpa*.