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ПОСТГЕНОМНЫЕ ТЕХНОЛОГИИ В ПРАКТИЧЕСКОМ ЛЕСНОМ ХОЗЯЙСТВЕ: РАЗРАБОТКА ПОЛНОГЕНОМНЫХ МАРКЕРОВ ДЛЯ ИДЕНТИФИКАЦИИ ПРОИСХОЖДЕНИЯ ДРЕВЕСИНЫ И ДРУГИХ ЗАДАЧ

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Данные о последовательности генома, которые были недавно получены для нескольких основных видов хвойных, вносят значительный вклад в развитие лесной генетики и программ улучшения и защиты деревьев. Они позволяют идентифицировать и аннотировать гены и другие функциональные элементы (короткие РНК, факторы транскрипции, регуляторные элементы и т. д.) и выявить генетические системы, которые контролируют адаптацию и устойчивость к болезням. Их можно использовать для разработки высокоинформативных генетических маркеров, которые можно использовать в популяционно-генетических исследованиях для создания популяционно-генетических баз данных, необходимых для борьбы с незаконной рубкой и торговлей древесиной. Геномные данные очень необходимы для разработки полногеномных генетических маркеров для изучения связи генетической изменчивости (SNP, аллели, гаплотипы и генотипы) с факторами окружающей среды, адаптивными признаками и фенотипами, а также для лучшего понимания генетического контроля селекционных и экономически важных признаков. Они также могут быть использованы для разработки полногеномных генетических маркеров, применяемых в геномной селекции для получения более адаптированных, устойчивых к стрессу и к изменению климата деревьев с желаемыми качественными экологическими и экономическими характеристиками. Наконец, знание полной нуклеотидной последовательности генома позволяет интегрировать протеомику, транскриптомику и метаболомику и обеспечивает референсные геномы для ресеквенирования. В этом кратком обзоре мы хотели бы представить также одно из многих практических применений генетики и геномики в лесном хозяйстве – разработку высокополиморфных и информативных молекулярно-генетических маркеров для нескольких очень важных хвойных видов бореальных лесов Евразии, лиственницы сибирской (*Larix sibirica* Ledeb.), сибирской кедровой сосны (*Pinus sibirica* Du Tour) и сосны обыкновенной (*Pinus*

sylvestris L.) на основе полногеномных данных, полученных в рамках проекта «Геномные исследования основных бореальных лесообразующих хвойных видов и их наиболее опасных патогенов в Российской Федерации», финансируемого Правительством Российской Федерации (грант № 14.Y26.31.0004).

Ключевые слова: генетическое разнообразие, геном, *Larix sibirica*

POSTGENOMIC TECHNOLOGIES IN PRACTICAL FORESTRY: DEVELOPMENT OF GENOME-WIDE MARKERS FOR TIMBER ORIGIN IDENTIFICATION AND OTHER APPLICATIONS

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Abstract

The forest genetics, tree improvement and protection can greatly benefit from complete genome sequence data made recently available for several major conifer species. They allow to identify and annotate genes, other functional elements (sRNA, transcription factors, regulatory elements, etc.) and genetic networks that control adaptation and disease resistance. They can be used to develop highly informative genetic markers that can be used in population genetic studies to create database of barcodes for individual populations to fight illegal timber harvest and trade. They are very much needed for development of genome-wide genetic markers for association studies for linking genetic variation (SNPs, alleles, haplotypes, and genotypes) with environmental factors, adaptive traits and phenotypes for better understanding genetic control of agronomically and economically important traits. They can be also used to develop genome-wide genetic markers for genomic-assisted selection to breed for better adapted, stress resistant and climate change resilient trees with desirable quality ecological and economic traits. Finally, whole genome sequences allow to integrate proteomics, transcriptomics and metabolomics and provide reference genomes for resequencing. In this brief summary we would like to present one of many practical applications of genetics and genomics in forestry– development of highly polymorphic and informative molecular genetic markers for several very important boreal forest species in Eurasia, Siberian larch (*Larix sibirica* Ledeb.), Siberian stone pine (*Pinus sibirica* Du Tour) and Scots pine (*Pinus sylvestris* L.), based on the whole genome data obtained in the “Genomics of the Key Boreal Forest Conifer Species and Their Major Phytopathogens in the Russian Federation” project funded by the Government of the Russian Federation (grant no. 14.Y26.31.0004).

Keywords: genetic diversity, genome, *Larix sibirica*, microsatellite markers, NGS, *Pinus sibirica*, *Pinus sylvestris*, Siberian larch, Siberian stone pine, Scots pine, whole genome sequencing

Introduction

The whole genome sequence data are the foundation for subsequent studies of evolutionary, biochemical and physiological processes in the sequenced organisms. Deep knowledge of the genome structure including the fine exon-intron gene structure, repeated sequences and intergenic sites help us better understand the mechanisms of gene regulation and expression, as well as the genome evolution. The whole genomic data become more available recently, including conifer species, and are widely used now to develop new DNA markers, such as single nucleotide polymorphisms (SNPs) and microsatellite loci or simple sequence repeats (SSRs) that can be used in population genetic analysis and for solving practical forestry problems, for example, to identify the origin of wood and planting material, for certification and identification of clones.

The development of molecular genetic markers for the main forest-forming tree species are extremely important and needed for solving problems of forestry, reforestation and afforestation. To solve these problems, estimates of the level of genetic variability, data on the population structure and differentiation, and effective methods of genetic identification of the wood and plant material origin are required.

Among the available genetic markers, nuclear microsatellite loci can be used to address these problems and are most fully meet requirements for reliable and convenient genetic markers. They are characterized by high specificity, reproducibility, codominance, multiple alleles, high heterozygosity and, moreover, do not require sophisticated equipment for analysis.

For example, Siberian larch (*Larix sibirica* Ledeb.) is one of the main forest-forming conifer species in Siberia, such species-specific markers have not been developed till recently. Siberian larch grows in the forest zone of the east and northeast of the European part of Russia, the Urals, Western and Eastern Siberia. Its area stretches from tundra (71°N latitude) on the north to the southern latitudes of Altai and Sayan (46° N) on the south. On the territory of the Russian Federation, larch forests occupy 263 million hectares, about 40% of the forest area of the country (769.8 million hectares). Previously, markers based on nuclear microsatellite loci developed for other species of this genus were used to analyze the population-genetic variation of *L. sibirica* [1-3]. With the help of these markers, genetic diversity and differentiation were studied in several populations of this species [4, 5]. However, a small number of markers was used in these studies due to poor PCR amplification and the presence of a large number of “null alleles” for many non-species-specific markers.

Siberian stone pine, *Pinus sibirica* Du Tour and Scots pine (*Pinus sylvestris* L.) are also among the most economically and environmentally important forest-forming species of conifers in Eurasia. To study these forests a large number of highly polymorphic molecular genetic markers, such as microsatellite loci, are also required that were unavailable for Siberian stone pine till recently.

Prior to the new high-throughput next generation sequencing (NGS) methods, discovery of microsatellite loci and development of microsatellite markers were very time consuming and laborious. The recently developed draft assemblies of the Siberian larch, Siberian stone pine and Scots pine genomes sequenced using the NGS methods in the Laboratory of Forest Genomics of the Siberian Federal University [6-8], it has become possible to develop species-specific microsatellite primers for these species.

Materials and methods

The draft genome assemblies presented in Table 1 allowed us to identify a large number of microsatellite loci in the Siberian larch and Siberian stone pine genomes and to develop species-specific PCR primers for their amplification and genotyping. The primers were designed using contigs containing short simple sequence tandem repeats.

To develop new highly informative microsatellite genetic markers for Siberian larch and Siberian stone pine using their whole genome assemblies a computer search for microsatellite loci with high repetitive simple motifs was done in the genomic DNA sequences, oligonucleotide primers were developed, synthesized and tested for the selected loci.

Table 1

Whole-genome sequencing data used to develop microsatellite markers in Siberian larch (*Larix sibirica*) and Siberian stone pine (*Pinus sibirica*) and mitochondrial markers in Scots pine (*Pinus sylvestris*)

Genome assembly	Total number of sequence reads, mln	N50, bp	Longest, bp	Total assembly length, Gbp
Larix sibirica				
Contigs	12.4	1074	128642	7.99
Scaffolds	11.33	6443	354326	12.34
Pinus sibirica				
Contigs	10.75	948	105599	7.01
Scaffolds	9.45	6920	110935	13.56
Pinus sylvestris				
Contigs	15.22	488	75010	6.748
Scaffolds	14.79	654	105091	7.807

A preliminary estimate of allelic diversity was made on two test samples of a Siberian larch population collected in the Republic of Khakassia (Russian Federation) and several Siberian stone pine populations [9, 10].

The most promising markers were selected, and multiplex genotyping panels were designed for Siberian larch and tested for fragment analysis using the ABI 3130xl Genetic Analyzer with capillary electrophoresis [10].

The sequencing of the Siberian larch genome was done with 93X coverage using the Illumina HiSeq 2000 platform. To select high quality reads and to remove adapter dimers the raw reads were filtered using MUSKET [11] and Trimmomatic [12]. A draft assembly was generated using the CLC Assembly Cell assembler (https://www.qiagen-bioinformatics.com). The obtained assembly contained 12.4 million contigs with a total length of ~8 Gbp. This assembly was searched for contigs containing microsatellite loci using the GMATo program [13]. The preliminary analysis showed that microsatellite loci with tri-, tetra- and pentanucleotide motifs were much less variable in larch than the loci with dinucleotide motifs. Therefore, from all microsatellite loci found, only loci with dinucleotide motifs repeated at least 20 times were selected for the PCR primer design. Primers for the selected microsatellite loci were designed using the WebSat online service [14]. As a result, 59 primers pairs were designed and tested. Needle samples collected from 100 individual Siberian larch trees in 2014 in two populations (50 trees per population) in the Republic of Khakassia were used in this study [10]. The one population is located in the Shirinsky District of Khakassia near the Shira-Berenjak highway (larch forest with pine on a gentle slope), another – near the Efremkino Village (larch on a steep slope and at its foot).

Similar search for microsatellite loci were done using the Siberian stone pine 32X genome coverage assembly [9]. The designed primers were first tested on DNA samples of four P. sibirica trees to select successful primers that generate amplification product and to optimize the PCR conditions. The selected primers were then tested on eight specimens from the same population in order to detect polymorphisms. Variability of the loci that were monomorphic in this sample was tested further in nine individuals from nine geographically distant populations representing different regions of the Siberian stone pine area. The final testing of the polymorphic loci was performed using 10-12 specimens per each of several populations.

To develop mitochondrial DNA markers in Scots pine contigs from its partial genome assembly were mapped to the mitochondrial DNA (mtDNA) contigs of Norway spruce (*Picea abies* (L.) Karst.) and loblolly pine (*Pinus taeda* L.) to identify homologous mitochondrial fragments of Scots pine. Then, they were resequenced in a sample of the Scots pine trees of European, Siberian, Mongolian and Caucasian origin in order to develop mtDNA markers. Flanking non-

coding regions of some mitochondrial genes were also investigated and resequenced [15].

Results and discussion

***Larix sibirica* SSRs**

Among 59 primer pairs selected in the first test 20 produced no product, 12 had non-specific amplification and 27 stably amplified supposedly a single-locus PCR product that could be well-genotyped on gels. After the first selection, the forward primer in each of the 27 pairs was labelled either by "blue" (FAM) or "green" (HEX) fluorescent dyes for further testing on the ABI PRISM 3730 sequencer. The labelled oligonucleotide primers were synthesized by Sigma (Germany). The trial PCR multiplexes consisting of two or three primer pairs were made taking into account the size of the PCR fragments. Multiplexing was done at the PCR reaction stage by combining two or three different primer pairs in the same PCR reaction and adjusting the total volume by reducing the water portion accordingly. The obtained PCR amplification product was necessarily diluted 50–100 times before electrophoresis. The testing of polymorphic loci at this stage was carried out using 8–16 samples from each of the two populations. After this testing on a capillary sequencer, additional 9 pairs of primers had to be excluded due to poor or non-specific amplification, and supposedly a large number of null alleles.

***Pinus sibirica* SSRs**

Based on the testing of primers for 70 microsatellite loci with tri-, tetra- or pentanucleotide repeats, 18 most promising, reliable and polymorphic loci were selected that can be used further as molecular genetic markers in population genetic studies of Siberian stone pine [9].

***Pinus sylvestris* mitochondrial DNA markers**

Five SNPs and a single minisatellite locus were identified [15]. Caucasian samples differed from the rest by three SNPs. Two SNPs have been linked to an early described marker in the first intron of the *nad7* gene, and all together revealed three haplotypes in European populations. No variable SNPs were found in the Siberian and Mongolian populations. The minisatellite locus contained 41 alleles across European, Siberian, and Mongolian populations, but, this locus demonstrated a weak population differentiation (F_{ST} = 0.058), probably due to its high mutation rate.

These new markers were further used in the Scots pine population and phylogeographic studies [16]. Three mitochondrial DNA markers were genotyped in 90 populations of Scots pine located from Eastern Europe to Eastern Siberia. The geographic distribution of seven mitotypes demonstrated the split between western and eastern populations approximately along the 38th meridian. Genetic diversity in the western part was significantly higher than in the eastern one. Five mitotypes were western- and one eastern-specific. One mitotype was common in both regions, but in the eastern part it occurred only in the South Urals and adjacent areas. The geographic structure in the mitotype distribution supports a hypothesis of post-glacial recolonization of the studied territory from the European and Ural refugia.

Conclusions

The whole genome sequencing data provided rich material for developing highly polymorphic molecular genetic markers that were efficiently used for genotyping of natural and artificial populations of Siberian stone pine, Siberian larch and Scots pine, Newly developed markers will allow us obtaining reliable quantitative estimates of the parameters of their genetic structure, such as within and between population allelic and genetic diversity, genetic subdivision and differentiation at different hierarchical levels, inbreeding, gene flow, etc.

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