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THE STATE OF GENE POOL OF THE BASIC FOREST-FORMING SPECIES OF THE WHITE SEA WATERSHED (ON THE EXAMPLE OF A *PICEA* × *FENNICA* (REGEL) KOM. AND *PINUS SYLVESTRIS* L.)

© **Ilinov[1], B.V. Raevsky[2], O.V. Chirva[2]**

[1] Forest Research Institute of the Karelian Research Centre of the Russian Academy of Sciences, Petrozavodsk, Russia;
[2] Karelian Research Centre of the Russian Academy of Science, Petrozavodsk, Russia

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❀ **Background.** The genetic diversity of forest tree species populations is a key factor contributing to their resistance against negative effects of human activity, and the global climate change. The aim of the present study was to evaluate the state of gene pools of the main forest-forming species in the White Sea watershed. **Materials and methods.** Five populations of Norway spruce and seven populations of Scotch pine have been selected within the Arctic zone of the European part of Russia (the western part of the White Sea watershed), along with two boundary ones located near the northern borders of the abovementioned species areas. The analysis of the spruce samples had been performed using five nuclear SSR loci, while for the pine samples it was four. DNA fragments were separated on a sequencer CEQ 8000. The main criteria of the genetic diversity ($A_{99\%}$, H_o, H_e) and F-statistics were calculated. **Results.** The marginal spruce populations were characterized by the largest magnitude of the genetic diversity ($H_o = 0.46$; $H_e = 0.47$) and isolation ($F_{ST} = 0.33$) compared to other populations of the same species. The differences were statistically significant. All pine populations studied demonstrated a higher level of genetic diversity ($H_o = 0.50$, $H_e = 0.63$) compared to spruce populations. The differences between the boundary and in-area populations were not statistically reliable ($F_{ST} = 0.04$). **Conclusion.** Our investigation revealed a sufficiently high level of spruce and pine northern populations' genetic diversity making them able to withstand expected negative effects of anthropogenic activity and global climate change.

❀ **Keywords:** *Pinus sylvestris* L.; *Picea* × *fennica* (Regel) Kom.; marginal populations; microsatellite loci; genetic diversity.

СОСТОЯНИЕ ГЕНОФОНДОВ ОСНОВНЫХ ЛЕСООБРАЗУЮЩИХ ВИДОВ ВОДОСБОРА БЕЛОГО МОРЯ (НА ПРИМЕРЕ *PICEA* × *FENNICA* (REGEL) KOM. И *PINUS SYLVESTRIS* L.)

© **А.А. Ильинов[1], Б.В. Раевский[2], О.В. Чирва[2]**

[1] Федеральное государственное бюджетное учреждение науки «Карельский научный центр Российской академии наук», Институт леса, Петрозаводск, Республика Карелия;
[2] Федеральное государственное бюджетное учреждение науки Федеральный исследовательский центр «Карельский научный центр Российской академии наук», Петрозаводск, Республика Карелия

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❀ С использованием ядерных микросателлитных локусов дана оценка состояния генофондов ели финской и сосны обыкновенной в западной части водосбора Белого моря. Северотаежные популяции ели финской характеризовались средними ($H_o = 0{,}20$, $H_e = 0{,}27$), а периферические — максимальными значениями параметров генетического разнообразия ($H_o = 0{,}46$, $H_e = 0{,}47$), различия между этими двумя группами популяций были статистически достоверными. Анализ F-статистик выявил уникальность генетической структуры периферических популяций ели, с чем может быть связан высокий уровень их генетической обособленности ($F_{ST} = 0{,}33$). Все исследованные популяции сосны обыкновенной отличались более высоким по сравнению с елью финской уровнем генетического разнообразия ($H_o = 0{,}50$, $H_e = 0{,}63$), причем различия между периферическими и остальными популяциями были статистически недостоверными. Результаты анализа F-статистик популяций сосны свидетельствуют об однородно-

сти генофонда вида в регионе. Выявленный уровень генетического полиморфизма популяций сосны обыкновенной и ели финской в западной части водосбора Белого моря свидетельствует, что при принятии мер по сохранению и поддержанию генетических ресурсов этих видов (мониторинг состояния, содействие естественному возобновлению, создание лесных культур и т. п.) будут обеспечены необходимые условия для минимизации отрицательных последствий антропогенного воздействия и глобального изменения климата.

❀ **Ключевые слова:** *Pinus sylvestris* L.; *Picea* × *fennica* (Regel) Kom.; периферические популяции; микросателлитные локусы; генетическое разнообразие.

INTRODUCTION

According to the definition of the Intergovernmental Group of Experts, the Arctic is one of the regions most vulnerable to global climate change [1]. The natural complexes of the Arctic, characterized by extreme climatic and geophysical conditions, are especially vulnerable and unstable to external influences and have a reduced ability for restoration and self-purification [2]. The White Sea, including the catchment basin, is critical for the study and development of the Arctic resources, because it is represented by a relatively small, semi-enclosed water source, so complex fundamental and applied research can be easily conducted in the area compared with other seas of the Arctic [3].

The catchment basin of the White Sea occupies most of the Arctic zone of the European North of Russia, including the territories of the Murmansk and Arkhangelsk regions, as well as the Republic of Karelia. They belong to the first group of territories directly adjacent to the sea and have a significant impact on its ecosystem [4]. The territories are represented by two natural zones, tundra and taiga, which are the main forests of the northern taiga subzone. The relevance of the conservation of the biological diversity of terrestrial ecosystems in this region is governed by the diversity and multiplicity of ecosystem services that humans receive from them. In particular, boreal forests occupy most of the territory and perform functions that are critical at all levels (local, regional, and global). The ecosystem functions of forests, such as fishing, hunting, leisure, spiritual activities, and economic opportunities, are critical to local people. Globally, boreal forests represent one of the most important regulators of the planet's climate through the energy and water exchange. They also store an enormous amount of biogenic carbon, which is as large as that supplied by rainforests. The contribution of forests and afforestation to the solution of present issues, such as reducing risks from anthropogenic impacts and global climate change, in ensuring sustainable development of the region under study, partly depends on the presence of a rich interspecific and intraspecific diversity of tree species. Forest ecosystems remain the main refuge for biodiversity conservation. An important component of this contribution is genetic diversity, which is biodiversity at the intraspecific level of the main forest-forming species. Genetic diversity ensures the survival, adaptation, and development of tree forest species under changing environmental conditions. It also maintains the vitality of forests and provides resilience to stresses such as pests and diseases [5]. In addition, maintaining a high level of genetic diversity is necessary for breeding programs to create adapted varieties of clones or secure useful traits. Preserving the genetic potential of forest tree species, especially in a highly vulnerable region such as the Arctic, is vital as it represents a unique and irreplaceable resource for the future.

The study aimed to assess the current state of gene pools of the main forest-forming species of the White Sea catchment basin and predict the impact of anthropogenic factors on them, including global climate change.

MATERIALS AND METHODS OF RESEARCH

The objects of the study were the populations of Finnish spruce (*Picea* × *fennica*) and Scotch pine (*Pinus sylvestris*) located in the northern taiga subzone, as well as two peripheral populations of pine and spruce growing at the northern margin of the distribution area of these species in the transitional forest–tundra zone (Fig. 1 and Table 1). When selecting objects for research based on a complex of forest indicators, the category of forest biogeocenosis (plantation) was determined.

Dendrocenoses resulting from natural processes, after certain natural catastrophic events of varying intensity and which did not experience a strong anthropogenic impact, belonged to the category of "indigenous low disturbance." The presence of traces of selective felling of low intensity in this case was considered acceptable. Forest stands formed after total anthropogenic disturbance (clear felling) due to preliminary and subsequent natural regeneration were characterized as "secondary forest stand".

Permanent sample plots (PSP, Fig. 1) were established in natural pine forests and spruce forests within the western part of the White Sea catchment basin (northern taiga subzone of Karelia and Murmansk oblast). Table 1 presents the characteristics of the populations.

To analyze the genetic structure of the populations, samples of needles or wood (cores) were obtained from 30 model trees at each PTP. Spruce and pine genomic DNA samples were isolated using a standard kit (QIAGEN). Microsatellite analysis of

Table 1

Characteristics of of *P. sylvestris* and *P.* x *fennica* populations investigated

Populations	Location of population	Geographical coordinates (degrees N/W)	Forest category	Stand age, years
P. x *fennica*				
Pasvik_E1	M*, Pechenga district	69.27669/29.40130	Climax virgin	>180
Murmansk_E2	M, Kolsky District	68.87333/33.24000	Secondary	>100
Paanajarvi_E3	K**, Loukhsky District	66.30634/30.44258	Climax virgin	>200
Paanajarvi_E4	K, Loukhsky District	66.30093/30.45887	Climax virgin	>200
Kivakka_E5	K, Loukhsky District	66.20677/30.53473	Climax virgin	>140
Kivakka_E6	K, Loukhsky District	66.20574/30.53897	Not defined (mountain tundra)	>100
Pongoma_E7	K, Loukhsky District	65.33901/34.40335	Climax virgin	>120
Pongoma_E8	K, Kemsky District	65.35168/34.36869	Climax virgin	>140
Pezhostrov_E9	K, Kemsky District	65.33981/34.47903	Climax virgin	>160
P. sylvestris				
Pasvik_C1	M, Pechenga District	68.99571/28.98872	Climax virgin	>140
Murmansk_C2	M, Kola District	68.89139/33.33194	Secondary	>80
Alakurtti_C3	M, Kandalakshsky District	66.95278/29.61083	Climax virgin	>180
Gridino_C4	K, Kemsky District	65.96686/34.65734	Climax virgin	>180
Pyaozero_C5	K, Loukhsky District	65.94450/31.08857	Climax virgin	>140
Voynitsa_C6	K, Kalevalsky District	65.15505/30.19625	Climax virgin	>120
Maslozero_C7	K, Medvezhyegorsky District	63.52453/32.78677	Climax virgin	>240

Note. * M – Murmansk region; ** K – Republic of Karelia.

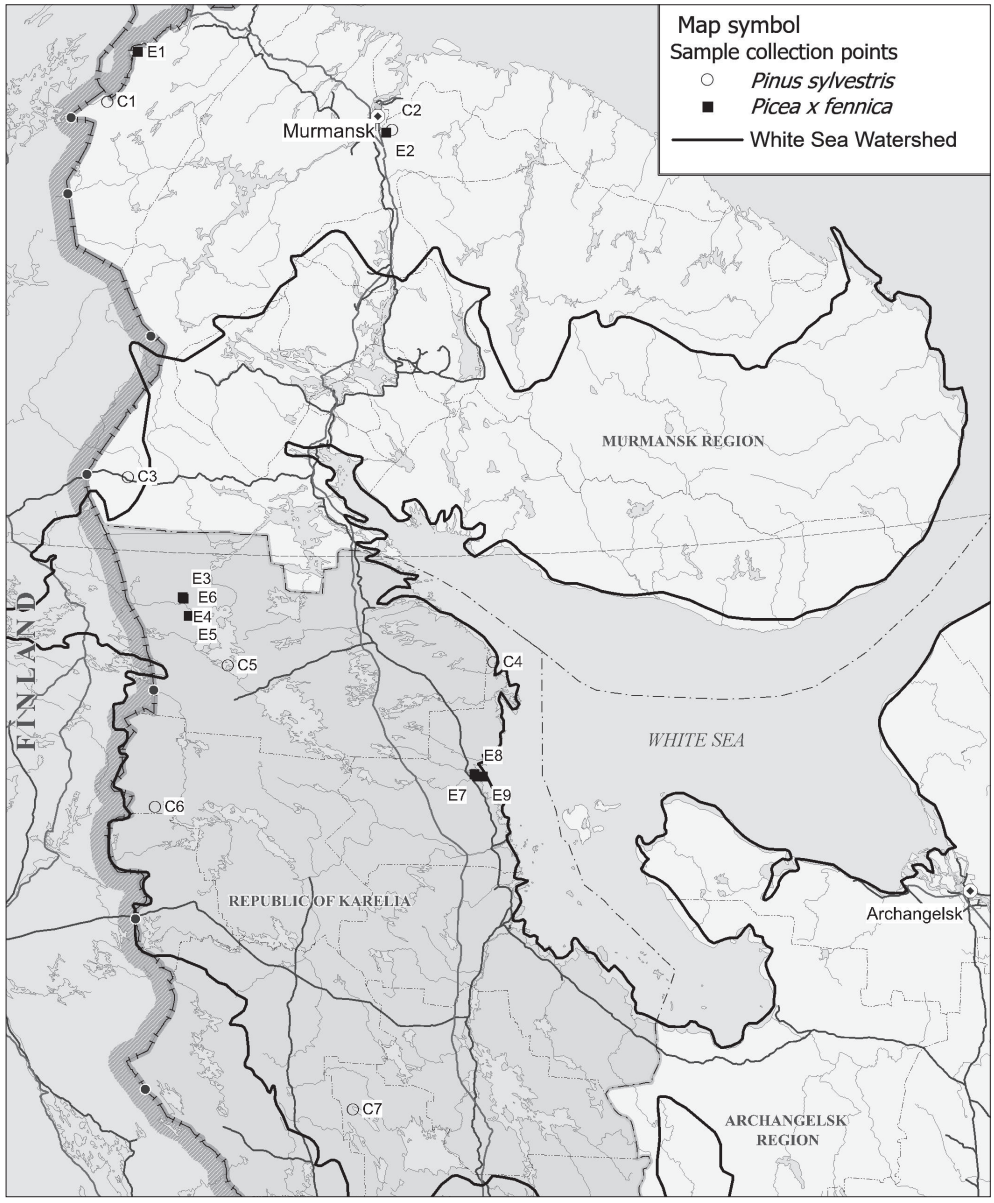

Fig. 1. Schematic map of locations of *P. sylvestris* and *P.* x *fennica* sample collection points in Karelia. Point names are given in accordance to Table 1

Finnish spruce was performed at five nuclear loci, namely, UAPgTG25, UAPgAG105, UAPgAG150, EATC2C06, and EATC2C10 [6, 7]. For the analysis of Scotch pine populations, four loci were selected: PtTX2123, PtTX2146, SPAC11,8, and SPAC12,5 [8, 9]. The characteristics of microsatellite primers used for DNA amplification are presented in Table 2. For the polymerase chain reaction, 26 μl of the reaction mixture (50 ng of DNA of the test samples, 100 pM primer, and 5 μl of a kit with Taq DNA polymerase) was used. Amplification conditions included denaturation for 30 s at 94 °C, annealing for 30 s at 53 °C–62 °C (depending on the primer used), polymerization for 40 s at 72 °C; 35 cycles; and completion of fragments for 6 min at 72 °C. Amplification was performed on a MaxyGene Gradient (QIAGEN) tool. Separation and determination of DNA fragments were carried out using a capillary electrophoresis system on a CEQ 8000 device (Beckman Coulter).

Average number of alleles per locus, average effective number of alleles, observed and expected heterozygosities, inbreeding coefficient (Wright fixation index), unbiased-genetic-distance measures [10] and Wright's F_{IT}, F_{IS} and F_{ST} statis-

Table 2

Parameters of microsatellite primers used to analyzing populations pine and spruce

Locus	Motif	Annealing temperature, *t*, °C	Number of alleles	Size of fragment, bp
P. x *fennica*				
UAPgTG25	$(TG)_{27}$	62	8	100–116
UAPgAG150	$(AG)_{11}$	54	4	160–166
UAPgAG105	$(AG)_{19}$	56	8	144–158
EATC2C06	$(CAT)_{7}$	58	10	136–166
EATC1C10	$(GA)_{8}$	53	4	150–159
P. sylvestris				
Spac11,8	$(TG)_{16}$	55	13	132–160
Spac12,5	$(GT)_{20}(GA)_{10}$	54	29	129–199
PtTX2123	$(AGC)_{8}$	57	3	192–201
PtTX2146	$(GAG)_{5}...(GAG)_{8}CGG(GAG)_{7}CGG(GAG)_{4}$	57	13	180–249

tics were calculated with the GenAlEx 6.5 program [11]. Dendrograms of the similarity between pine and spruce populations were constructed using the POPTREE program [12].

RESULTS

Finnish spruce. Analysis of the genetic structure of the Finnish spruce populations showed that all the microsatellite loci used were polymorphic. A total of 34 alleles were identified (Table 3).

The northern taiga populations of Pongoma_E7, Pongoma_E8, and the island Pezhostrov_E9 were monomorphic at the UAPsTG25 locus, the Pongoma_E8 population was also monomorphic at the EATC2C06 locus, and Kivakka_E6 was monomorphic at the UAPgAG105 locus. Almost all spruce populations of the western catchment basin of the White Sea were characterized by the same total number of alleles (16), with the exception of spruce growing on the top of a mountain under mountain tundra conditions (Kivakka_E6) and characterized by their minimum number (12). The peripheral populations of Pasvik_E1 and Murmansk_E2, located at the northern margin of the species habitat, were characterized by the maximum number of alleles detected (18 and 17, respectively). Thus, the studied spruce populations differed both in allelic composition and in the ratio of alleles, with the maximum number revealed in the marginal populations.

The results of the analysis of genetic diversity (including allelic) of Finnish spruce populations are presented in Table 4. In terms of allelic diversity parameters, peripheral populations were generally superior to northern taiga ones ($A_{99\%}$ = 3.500 and 3.029, $A_{95\%}$ = 2.835 and 2.336, and n_e = 1.995 and 1.619, respectively). The observed heterozygosity H_o varied in the northern taiga populations of spruce from 0.127 (Pongoma_E8) to 0.300 (Paanajarvi_E3 and Kivakka_E6), averaging 0.204. According to the level of expected heterozygosity H_e, the minimum value was revealed for Pongom_E7 (0.221), and the maximum value was found for Pongom_E8 (0.310), with an average of 0.266. The Murmansk populations Pasvik_E1 and Murmansk_E2 were also characterized by the maximum values of the parameters of genetic variability, and the difference between them and the northern taiga populations of spruce in terms of expected and observed heterozygosity was statistically significant (Table 4). Positive values of the Wright fixation index were revealed for all spruce populations, with the exception of Pasvik_E1 and Kivakka_E6; for the populations of Kivakka_E5,

Table 3

Genetic structure of *P.* x *fennica* populations, expressed in frequency of occurrence of alleles

Locus	Allele	Populations								
		E1*	E2	E3	E4	E5	E6	E7	E8	E9
Sample size		19	20	30	31	29	10	30	30	30
UAPgTG25	100	0.000	0.000	0.050	0.016	0.000	0.000	0.000	0.000	0.000
	102	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	104	0.026	0.000	0.950	0.952	0.845	0.900	1.000	1.000	1.000
	106	0.605	0.875	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	110	0.000	0.000	0.000	0.000	0.000	0.050	0.000	0.000	0.000
	112	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
	114	0.079	0.000	0.000	0.016	0.138	0.050	0.000	0.000	0.000
	116	0.289	0.075	0.000	0.016	0.000	0.000	0.000	0.000	0.000
UAPgAG105	160	0.711	0.525	0.867	0.984	0.983	1.000	0.983	0.967	0.917
	162	0.000	0.050	0.067	0.016	0.000	0.000	0.017	0.000	0.000
	164	0.289	0.325	0.067	0.000	0.017	0.000	0.000	0.033	0.083
	166	0.000	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000
UAPgAG150	144	0.000	0.000	0.733	0.581	0.552	0.850	0.800	0.300	0.317
	146	0.868	0.650	0.067	0.048	0.034	0.050	0.017	0.017	0.083
	148	0.053	0.350	0.033	0.226	0.241	0.000	0.033	0.000	0.217
	150	0.026	0.000	0.000	0.000	0.103	0.000	0.000	0.083	0.033
	152	0.000	0.000	0.083	0.000	0.000	0.000	0.000	0.350	0.117
	154	0.026	0.000	0.083	0.000	0.000	0.000	0.000	0.150	0.000
	156	0.026	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	158	0.000	0.000	0.000	0.145	0.069	0.100	0.150	0.100	0.233
EATC2C06	136	0.000	0.000	0.133	0.065	0.138	0.000	0.100	0.000	0.017
	139	0.079	0.325	0.733	0.839	0.724	0.950	0.800	1.000	0.933
	142	0.684	0.450	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	145	0.158	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	148	0.000	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	151	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017
	154	0.053	0.000	0.000	0.000	0.034	0.050	0.017	0.000	0.033
	157	0.000	0.050	0.133	0.081	0.103	0.000	0.067	0.000	0.000
	160	0.026	0.050	0.000	0.016	0.000	0.000	0.017	0.000	0.000
	166	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000
EATC1C10	150	0.500	0.500	0.833	0.903	0.983	0.450	0.767	0.200	0.783
	153	0.500	0.500	0.133	0.097	0.017	0.000	0.050	0.300	0.150
	156	0.000	0.000	0.033	0.000	0.000	0.150	0.050	0.200	0.067
	159	0.000	0.000	0.000	0.000	0.000	0.400	0.133	0.300	0.000

Note. * Designation of populations in accordance with Fig. 1.

Table 4

Indices of genetic diversity in *P.* x *fennica* populations

Populations	*n*	$A_{99\,\%}$	$A_{95\,\%}$	n_e	H_o	H_e	*F*
Marginal populations							
Pasvik_E1	19	3.600 ± 0.678	2.600 ± 0.400	1.839 ± 0.152	0.495 ± 0.134	0.439 ± 0.054	−0.126 ± 0.237
Murmansk_E2	20	3.400 ± 0.748	3.200 ± 0.583	2.151 ± 0.307	0.420 ± 0.169	0.493 ± 0.077	0.109 ± 0.337
Mean		3.500 ± 0.477	2.835 ± 0.367	1.995 ± 0.170	0.457 ± 0.102*	0.466 ± 0.045**	−0.008 ± 0.198
North taiga populations							
Paanayarvi_E3	30	3.200 ± 0.490	2.800 ± 0.374	1.472 ± 0.131	0.300 ± 0.072	0.298 ± 0.064	0.004 ± 0.081
Paanayarvi _E4	31	3.200 ± 0.490	2.000 ± 0.447	1.436 ± 0.256	0.200 ± 0.067	0.235 ± 0.098	0.045 ± 0.069
Kivakka_E5	29	3.200 ± 0.583	2.200 ± 0.583	1.574 ± 0.300	0.152 ± 0.053	0.280 ± 0.115	0.258 ± 0.128*
Kivakka _E6	10	2.400 ± 0.400	2.400 ± 0.400	1.458 ± 0.291	0.300 ± 0.158	0.232 ± 0.105	−0.182 ± 0.085
Pongoma _E7	30	3.200 ± 0.735	2.200 ± 0.583	1.341 ± 0.134	0.187 ± 0.076	0.221 ± 0.084	0.102 ± 0.129
Pongoma _E8	30	2.800 ± 0.970	2.400 ± 0.872	2.176 ± 0.706	0.127 ± 0.095	0.310 ± 0.177	0.402 ± 0.213***
Pezhostrov _E9	30	3.200 ± 0.860	2.400 ± 0.748	1.873 ± 0.658	0.160 ± 0.096	0.283 ± 0.136	0.379 ± 0.176***
Mean		3.029 ± 0.237	2.336 ± 0.254	1.619 ± 0.150	0.204 ± 0.034	0.266 ± 0.040	0.131 ± 0.053
All populations							
Mean		3.133 ± 0.212	2.433 ± 0.216	1.702 ± 0.124	0.260 ± 0.038	0.310 ± 0.035	0.096 ± 0.061

Note. *n* – number of trees studied; *A* – average number of alleles per locus; $A_{95\,\%}$ – average number of common alleles per locus; n_e – effective number of alleles per locus; H_o and H_e – observed and expected heterozygosity, respectively (*, ** – statistical significance at $p = 0.05$; 0.01 between marginal populations and other ones); *F* – inbreeding coefficien (*, *** statistical significance at $p = 0.05$; 0.001 between observed and the expected heterozygosity).

Pongoma_E8, and Pezhostrov_E9, the differences were statistically significant [13], which indicated a deficiency of heterozygotes in these populations.

In general, the studied populations of Finnish spruce were characterized by a low level of genetic diversity at microsatellite loci, although it exceeded that at allozyme loci [14].

Analysis using Wright's *F* statistics (Table 5), calculated to characterize subdivisions and assess the level of differentiation between the studied populations within the groups, revealed low F_{st} values (0.051 and 0.102 for peripheral and northern taiga populations, respectively). The average F_{st} value for all populations was 0.33. This ratio indicated an extremely high level of genetic differentiation between peripheral and other populations.

The results of the analysis of the interpopulation differentiation of Finnish spruce in the western part of the White Sea catchment basin were clearly represented as a similarity dendrogram constructed using the UPGMA method based on the Nei genetic distance matrix (Fig. 2). All populations were divided into two groups, namely, northern taiga Karelian and peripheral Murmansk ones. Within these groups, the level of differentiation was relatively low ($D_N = 0.11$ and 0.09 for the Karelian and Murmansk populations, respectively). At the same time, the level of differentiation between the northern taiga and peripheral spruce populations was almost an order of magnitude higher ($D_N = 0.99$). The statistical significance of combining marginal and northern taiga populations into separate groups was confirmed by high

Table 5

Values of Wright's *F*-statistics values for *Picea* x *fennica* populations

Loci	*F*-statistics		
	F_{IS}	F_{IT}	F_{ST}
Marginal populations			
UAPgTG25	0.264	0.321	0.077
UAPgAG105	0.097	0.118	0.023
UAPgAG150	0.622	0.656	0.090
EATC2C06	0.296	0.340	0.063
EATC1C10	−1.000	−1.000	0.000
$M \pm m$	0.056 ± 0.277	0.087 ± 0.285	0.051 ± 0.017
North taiga populations			
UAPgTG25	0.111	0.166	0.061
UAPgAG105	0.220	0.253	0.042
UAPgAG150	0.261	0.353	0.125
EATC2C06	0.090	0.147	0.062
EATC1C10	0.322	0.471	0.219
$M \pm m$	0.201 ± 0.044	0.278 ± 0.060	0.102 ± 0.032
All populations			
$M \pm m$	0.156 ± 0.058	0.432 ± 0.088	0.334 ± 0.078

Note. F_{IS} – inbreeding coefficient of individuals relating to sub-populations; F_{IT} – inbreeding coefficient of individuals relating to a total species population; F_{ST} – inbreeding coefficient of sub-populations relating to a total species population.

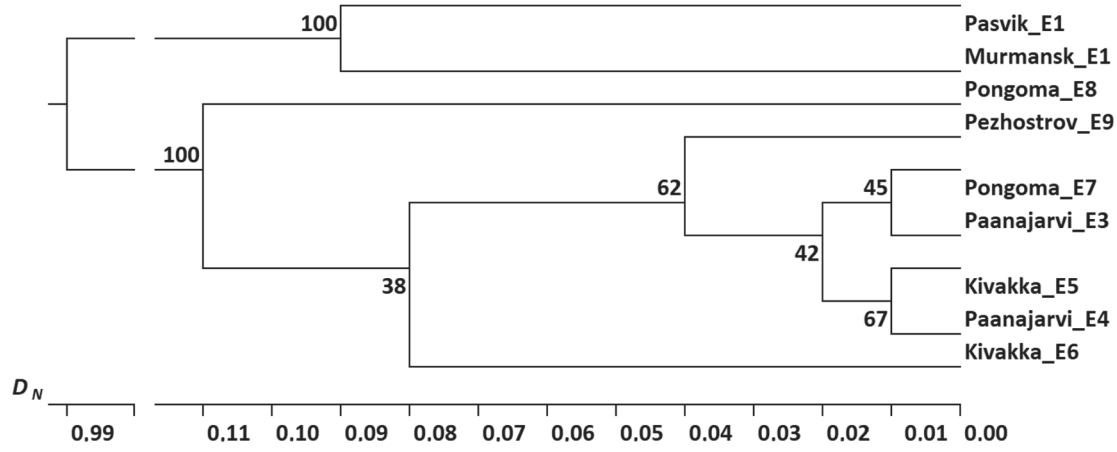

Fig. 2. Dendrogram of the similarity of Karelian populations of *P.* x *fennica* according to the Nei genetic distance (D_N); bootstrap probabilities BP (%) are indicated in the nodes of the dendrogram

bootstrap probabilities (*BP* = 100%) [15], indicating the genetic isolation of marginal (peripheral) spruce populations.

Scotch pine. Amplification of four pine microsatellite loci from seven natural populations enabled 60 alleles to be identified (Table 6). The minimum number of alleles identified was found in the populations from the Murmansk region, namely, Pasvik_C1 (peripheral) and Alakurtti_C3 (northern taiga) (30 alleles in each), while the maximum (40)

Table 6

Genetic structure of populations of *P. sylvestris*, expressed in the frequency of occurrence of alleles

Locus	Allele	Populations						
		C1	C2	C3	C4	C5	C6	C7
Sample size		20	21	13	30	30	29	29
PtTX2123	192	0.125	0.048	0.077	0.217	0.250	0.069	0.155
	195	0.875	0.952	0.885	0.783	0.750	0.931	0.845
	201	0.000	0.000	0.038	0.000	0.000	0.000	0.000
PtTX2146	180	0.000	0.024	0.000	0.017	0.000	0.000	0.000
	183	0.175	0.143	0.231	0.200	0.233	0.224	0.190
	186	0.000	0.000	0.000	0.000	0.000	0.017	0.000
	195	0.125	0.167	0.231	0.133	0.183	0.121	0.172
	201	0.000	0.000	0.000	0.017	0.000	0.000	0.000
	204	0.025	0.024	0.077	0.100	0.017	0.034	0.000
	213	0.000	0.000	0.000	0.000	0.000	0.000	0.017
	219	0.000	0.000	0.000	0.000	0.000	0.000	0.017
	222	0.425	0.452	0.269	0.383	0.500	0.500	0.500
	228	0.150	0.048	0.115	0.067	0.017	0.086	0.052
	237	0.025	0.095	0.000	0.017	0.000	0.000	0.000
	243	0.075	0.048	0.038	0.000	0.000	0.017	0.017
	249	0.000	0.000	0.038	0.067	0.050	0.000	0.034
Spac11.8	132	0.000	0.024	0.000	0.067	0.000	0.103	0.017
	134	0.150	0.024	0.077	0.133	0.133	0.017	0.155
	136	0.500	0.452	0.346	0.433	0.450	0.362	0.655
	138	0.225	0.333	0.423	0.267	0.283	0.207	0.121
	140	0.000	0.000	0.038	0.000	0.017	0.052	0.000
	142	0.025	0.071	0.000	0.017	0.033	0.000	0.017
	144	0.000	0.048	0.038	0.000	0.017	0.121	0.017
	146	0.050	0.000	0.000	0.033	0.000	0.000	0.000
	148	0.000	0.000	0.000	0.017	0.033	0.103	0.000
	150	0.000	0.000	0.000	0.033	0.033	0.034	0.000
	154	0.000	0.000	0.077	0.000	0.000	0.000	0.017
	158	0.050	0.024	0.000	0.000	0.000	0.000	0.000
	160	0.000	0.024	0.000	0.000	0.000	0.000	0.000

Table 6 (continued)

Locus	Allele	Populations						
		C1	C2	C3	C4	C5	C6	C7
Spac12.5	129	0.000	0.000	0.000	0.000	0.033	0.000	0.017
	131	0.000	0.000	0.000	0.000	0.033	0.000	0.034
	133	0.000	0.000	0.000	0.000	0.033	0.034	0.103
	135	0.000	0.000	0.000	0.050	0.017	0.000	0.017
	137	0.000	0.000	0.000	0.000	0.033	0.000	0.000
	141	0.000	0.000	0.038	0.000	0.017	0.000	0.000
	143	0.000	0.000	0.000	0.000	0.017	0.000	0.000
	145	0.000	0.024	0.038	0.000	0.000	0.000	0.000
	147	0.300	0.119	0.038	0.117	0.050	0.034	0.000
	149	0.200	0.024	0.192	0.083	0.100	0.034	0.069
	151	0.075	0.190	0.000	0.083	0.017	0.052	0.034
	153	0.025	0.095	0.000	0.050	0.000	0.069	0.034
	155	0.000	0.048	0.000	0.067	0.183	0.121	0.086
	157	0.025	0.024	0.038	0.033	0.050	0.086	0.069
	159	0.050	0.095	0.192	0.117	0.017	0.155	0.017
	161	0.025	0.048	0.038	0.117	0.167	0.017	0.052
	163	0.050	0.071	0.000	0.033	0.033	0.052	0.086
	165	0.100	0.095	0.115	0.033	0.000	0.052	0.069
	167	0.000	0.024	0.000	0.033	0.000	0.017	0.052
	169	0.025	0.024	0.115	0.000	0.033	0.052	0.052
	171	0.050	0.000	0.038	0.083	0.017	0.069	0.052
	173	0.000	0.000	0.038	0.000	0.033	0.000	0.017
	175	0.050	0.000	0.000	0.000	0.000	0.034	0.000
	177	0.000	0.095	0.115	0.067	0.050	0.034	0.052
	179	0.000	0.000	0.000	0.000	0.000	0.052	0.034
	181	0.000	0.000	0.000	0.033	0.033	0.017	0.000
	183	0.025	0.024	0.000	0.000	0.033	0.017	0.000
	189	0.000	0.000	0.000	0.000	0.000	0.000	0.034
	199	0.000	0.000	0.000	0.000	0.000	0.000	0.017

was in the northern taiga Maslozero_C7. Analysis of the main parameters of genetic diversity, including allelic (Table 7), revealed that all Scotch pine populations were characterized by their high values. The northern taiga populations demonstrated a higher level of genetic diversity than the peripheral taiga populations, with the exception of the observed heterozygosity H_o. However, no statistically significant differences were found in the level of genetic variability in the peripheral and northern taiga populations of Scotch pine, which indicated a high degree of homogeneity of the gene pool of the species in the western part of the White Sea catchment basin and its sufficient representation in the marginal Scotch pine populations.

Similar to the case of the Finnish spruce, the Scotch pine populations showed a higher level of expected heterozygosity H_e compared with the observed heterozygosity H_o. However, the difference was statistically significant only in Pyaozero_C5, indicating a deficiency of heterozygotes in this population. In general, the studied populations

Table 7

Indices of genetic diversity in *P. sylvestris* populations

Populations	*n*	$A_{99\,\%}$	$A_{95\,\%}$	N_e	H_o	H_e	*F*
Marginal populations							
Pasvik _C1	21	7.000 ± 2.273	3.500 ± 0.645	3.654 ± 1.077	0.512 ± 0.46	0.616 ± 0.140	0.110 ± 0.107
Murmansk _C2	20	8.000 ± 2.449	5.000 ± 1.472	4.367 ± 1.807	0.513 ± 0.164	0.600 ± 0.175	0.126 ± 0.162
Mean		7.500 ± 1.558	4.230 ± 0.833	4.010 ± 0.983	0.512 ± 0.102	0.608 ± 0.104	0.118 ± 0.090
North taiga populations							
Alakurtti _C3	13	7.000 ± 1.871	4.000±0.707	4.368 ± 1.441	0.558 ± 0.167	0.643 ± 0.149	0.107 ± 0.151
Gridino _C4	30	8.500 ± 2.661	5.500 ± 1.708	5.455 ± 2.372	0.542 ± 0.132	0.688 ± 0.124	0.179 ± 0.162
Pyaozero _C5	30	9.250 ± 4.110	3.750 ± 0.854	4.715 ± 2.140	0.417 ± 0.135	0.660 ± 0.110	0.333 ± 0.207*
Voynitsa _C6	29	9.000 ± 3.582	5.500 ± 1.708	5.512 ± 2.643	0.474 ± 0.158	0.629 ± 0.174	0.164 ± 0.186
Maslozero _C7	29	9.500 ± 4.052	5.000 ± 2.041	5.774 ± 3.590	0.491 ± 0.114	0.603 ± 0.142	0.156 ± 0.110
Mean		8.650 ± 1.354	4.840 ± 0.756	5.165 ± 1.015	0.496 ± 0.058	0.644 ± 0.057	0.188 ± 0.068
All populations							
Mean		8.321 ± 1.054	4.695 ± 0.602	4.835 ± 0.774	0.501 ± 0.049	0.634 ± 0.049	0.168 ± 0.055

Note. * The difference between observed and expected heterozygosity is significant at $p < 0{,}05$.

Table 8

Values of Wright's *F*-statistics values for *P. sylvestris* populations

Loci	*F*-статистики		
	F_{IS}	F_{IT}	F_{ST}
PtTX2123	0.003	0.044	0.041
PtTX2146	−0.091	−0.070	0.019
Spac11.8	0.570	0.586	0.037
Spac12.5	0.233	0.264	0.041
$M \pm m$	0.179 ± 0.147	0.206 ± 0.144	0.035 ± 0.005

of *Pinus sylvestris* are characterized by a higher level of genetic diversity revealed by microsatellite analysis compared with the data obtained using isozyme analysis for populations from this part of the Scotch pine habitat area [16].

The results of the analysis of subdivision and interpopulation differentiation by using Wright's *F* statistics are presented in Table 8. The loci PtTX2123 and PtTX2146, in contrast to Spac11.8 and Spac12.5, were characterized by the minimum values of F_{is} and F_{it}.

The F_{st} coefficient, an indicator of subdivision of populations, varied from 0.019 for PtTX2146 to 0.041 for Spac12.5 and PtTX2123, with an average of 0.035. Thus, most of the total genetic variance (96.5%) found based on the study of microsatellite loci accounted for the variability within pine populations. The results of the analysis indicated a low level of interpopulation differentiation of Scotch pine in the studied part of the habitat area and the homogeneity of the gene pool of the species in the western part of the White Sea catchment basin.

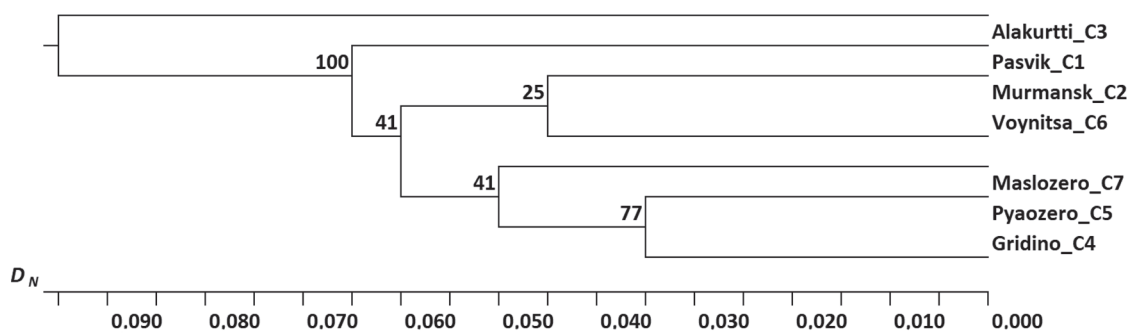

Fig. 3. Dendrogram of the similarity of the Karelian populations of *P. sylvestris* by the Nei genetic distance (D_N); bootstrap probabilities BP (%) are indicated in the nodes of the dendrogram

These results were confirmed by the similarity dendrogram constructed using the UPGMA method based on the Nei genetic distance matrix (Fig. 3). The main group ($D_N = 0.04–0.07$) included with a significant probability ($BP = 100\%$) all populations of Scotch pine, both peripheral and northern taiga, with the exception of Alakutti_C3, whose genetic distance from the rest of the populations turned out to be maximum ($D_N = 0.09$). One of the reasons for the relatively high genetic isolation of this population may be the small sample size ($n = 13$).

DISCUSSION

Thus, the data obtained on the state of the gene pool of the main forest-forming species, Scotch pine and Finnish spruce in the western part of the White Sea watershed, indicated a higher level of genetic diversity (including allelic) in the studied pine and spruce populations at microsatellite loci compared with these and other coniferous species with the use of isozymes [14, 16–19]. Moreover, the data on the genetic diversity of various pine and spruce species obtained using microsatellite markers indicated higher genetic variability compared with the populations of Scotch pine and Finnish spruce in the western part of the White Sea catchment basin [20–23]. Such level of genetic variability of populations in the studied part of the pine and spruce range at nuclear microsatellite loci can be attributed to several reasons. One of them is the relatively recent (less than 10,000 years ago) dissemination in the postglacial period of the species under consideration in the Arctic zone of the European part of Russia. Another reason may be the peculiarities of the distribution of the genetic diversity of the loci selected among the studied populations of these species.

In the investigated part of the habitat area, a deficiency of heterozygotes was revealed in some populations of both *Pinus sylvestris* and *Picea* × *fennica* (Regel) Kom. This phenomenon is not uncommon for populations of coniferous species [19, 24]. Many publications have noted that such a deficiency is a normal component of the genetic structure of coniferous populations and can be caused by inbreeding due to partial self-pollination, the Wahlund effect, the closely related crossing in the presence of a family spatial structure of forest stands, the presence of null alleles, and other reasons [25–29].

Peripheral populations of both pine (Pasvik_S1, Murmansk_C2) and spruce (Pasvik_E1, Murmansk_E2) growing on the northern border of the habitat areas did not reveal a decrease in genetic diversity in comparison with the northern taiga populations of these species. By contrast, the peripheral spruce populations were characterized by higher values of genetic diversity (including allelic) compared with the northern taiga ones. To date, there is no unified opinion on the level of genetic polymorphism that should be in peripheral (marginal, boundary) populations located on the border of the range. Previous studies confirmed [30, 31] that the level of genetic variability is maximum in the optimum zone and decreases toward the periphery of the species distribution area. However, the results of some studies [32, 33] recorded similar levels of genetic diversity between marginal and central populations.

In recent years, a new hypothesis has emerged, according to which the spatial distribution of the genetic diversity of populations of most species of the boreal zone, including coniferous trees, is mainly due to climatic changes that occurred in the Quaternary period [34]. Peripheral populations located on the northern border of the habitat, which are developing new territories suitable for growth and reproduction due to global warming, may be more adapted to changing conditions than populations on the opposite southern border of the habitat [35].

In our case, considering the data on the increase in the average annual temperature, which occurs especially rapidly in the Arctic zone [36], the high level of genetic variability in peripheral populations may be due to the displacement of the border of the ranges of Scotch pine and Finnish spruce further to the north. This phenomenon is due to more favorable conditions emerging in this territory, as well as the history of the postglacial dissemination of these species mentioned above.

Particular interest in the problem of the state and conservation of genetic resources of boreal tree species is determined by the currently recorded and predicted future influence of global climate change on their genetic diversity [37]. According to studies on this issue, a record-breaking rapid increase in the average annual temperature over the past 100 years has been revealed [38].

Yu.N. Kondrasheva et al. [39] believe that a global increase in the concentration of carbon dioxide in the Earth's atmosphere will create favorable conditions for the growth, development, and process of photosynthesis of higher plants. Thus, biomass buildup in forests may occur. However, an increase in the surface air temperature may be accompanied with an increase in the frequency of droughts and hot periods, a decrease in precipitation, a violation of the soil hydrological regime, an increase in the frequency of forest fires, and other events unfavorable for plants [40].

Some scientists believe that predicted temperature changes may lead to a shift in the boundaries of climatic zones to the north [39, 41]. Even insignificant temperature fluctuations in the current century have caused changes in the distribution areas of certain species [42]. However, these changes occur slowly. For tree species, the average rate of the habitat displacement is several tens of kilometers per century [41]. Thus, the shift in vegetation zones will lag behind climatic changes. There is also a delay in the response of forest ecosystems to climatic changes, which can range from tens to hundreds of years [41].

Notably, climatic changes strongly affect the species adapted to certain habitats. Such species are often characterized by a lower level of genetic diversity than species occupying an area with a wide range of ecological conditions [43]. At the same time, forest ecosystems, including such widespread species as *Pinus sylvestris* and *Picea abies* (including *P. obovata* and hybrid spruce *P.* x *fennica*), have large tolerance ranges that enable them to tolerate adverse environmental influences. The above-described negative consequences of global climate change are related to the southern boundaries of the ranges of boreal species, whereas warming at the northern margin of distribution contributes to an improvement in growing conditions, an increase in seed productivity, an increase in the effective number of peripheral populations, and an increase in genetic diversity.

Nevertheless, to minimize the possible negative consequences of global climate change (violation of the hydrological regime, pests, and diseases, etc.) on forest ecosystems, including on the state of genetic resources of the main forest-forming species, the response reactions of ecosystems to the climatic changes observed must be monitored. This primarily concerns such vulnerable natural systems as the northern taiga forests of the Arctic zone, including pine and spruce forests of the White Sea catchment basin.

As discussed above, the populations of species characterized by a low level of genetic diversity and a sharp decrease in effective abundance have high vulnerability, which can lead to inbreeding (i.e., crossing between closely related trees, resulting in a decrease in the viability of offspring) and local extinction of forest stands. Consequently, one of the main measures to minimize the negative consequences of both anthropogenic impact and climate change on forest ecosystems should

be the maintenance of the genetic potential of forest-forming species and the required effective size of their populations by promoting natural renewal and the creation of forest crops. This largely concerns the studied populations of Finnish spruce, which are characterized by great vulnerability due to the average level of their genetic diversity and a high degree of interpopulation differentiation.

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❀ Authors and affiliations

Aleksey A. Ilinov – PhD, Senior Researcher. Forest Research Institute of the Karelian Research Centre of the Russian Academy of Sciences, Petrozavodsk, Russia. SPIN: 2850-3404. E-mail: ialexa33@yandex.ru.

❀ Информация об авторах

Алексей Алексеевич Ильинов — канд. с.-х. наук, старший научный сотрудник, отдел комплексных научных исследований. ИЛ КарНЦ РАН, Петрозаводск. SPIN: 2850-3404. E-mail: ialexa33@yandex.ru.

❀ Authors and affiliations

Boris V. Raevsky – Doctor of Science, Senior Researcher, Department of Multidisciplinary Scientific Research. Karelian Research Centre of the Russian Academy of Science, Petrozavodsk, Russia. SPIN: 2136-7785. E-mail: borisraevsky@gmail.com.

Olga V. Chirva – Junior Researcher, Department of Multidisciplinary Scientific Research. Karelian Research Centre of the Russian Academy of Sciences. Petrozavodsk, Russia. SPIN: 4755-2713. E-mail: tchirva.olga@yandex.ru.

❀ Информация об авторах

Борис Владимирович Раевский — д-р с.-х. наук, старший научный сотрудник, отдел комплексных научных исследований. ФГБУН ФИЦ КарНЦ РАН, Петрозаводск. SPIN: 2136-7785. E-mail: borisraevsky@gmail.com.

Ольга Владимировна Чирва — отдел комплексных научных исследований. ФГБУН ФИЦ КарНЦ РАН, Петрозаводск. SPIN: 4755-2713. E-mail: tchirva.olga@yandex.ru.