

ISSN 1029-8940 (Print)

ISSN 2524-230X (Online)

UDC 575.174.015.3+58.009+582.394

<https://doi.org/10.29235/1029-8940-2025-70-3-207-215>

Received 21.01.2025

Natallia U. Hudnaya<sup>1</sup>, Aliaksandr M. Mialik<sup>1</sup>, Tatsiana G. Kulahina<sup>1</sup>,  
 Dam Ngoc Anh Luu<sup>2</sup>, Vladimir V. Titok<sup>1</sup>

<sup>1</sup>Central Botanical Garden of the National Academy of Sciences of Belarus, Minsk, Republic of Belarus<sup>2</sup>Vietnam National Museum of Nature of the Vietnam Academy of Science and Technology, Vietnam

## GENETIC STRUCTURE OF POPULATIONS OF THE NATIVE SPECIES *SALVINIA NATANS* L. PROGRESSING IN BELARUS

**Annotation.** The article presents the results of a study on the genetic diversity and structure of seven populations of *Salvinia natans* L. in Belarus, in both the natural (Pinsk, Mukhavets, Strelsk, and Rogachev) and progressing (Kamenets, Krivoshin, and Shchara) parts of the range. Using molecular iPBS markers, the study found that the natural populations of Pinsk and Mukhavets populations have the highest level of genetic diversity, and the island population of Kamenets is characterized by genetic impoverishment. Low rates of genetic diversity are also characteristic of other populations located in island localities (Krivoshin, Shchara) and on the northern (Rogachev) border of the *Salvinia natans* L. range. The study revealed that the level of interpopulation variability was lower than intrapopulation variability (22 and 78 %, respectively). The PhiPT value of 0.22 indicates significant genetic differences among the populations. For the studied species, the gene flow level is 0.80, which is an average value and is probably due to the specificity of reproduction of this species as a spore plant. Analysis of genetic distances showed that the lowest Nei distance (0.11) was observed between the Pinsk and Shchara populations, and the highest (0.21) between the Strelsk and Krivoshin populations. This is generally consistent with their geographic location. The ward.D2 analysis, based on Nei's distance matrix, confirms these results and demonstrates that the studied populations are divided into two main clusters, corresponding to their location in the Pripyat and Zapadny Bug river basins. The obtained experimental data show that, given global warming, the range of *Salvinia natans* L. will continue to expand northward. However, the probability of expansive properties of this species in newly developed territories remains low due to the insignificant genetic diversity of border populations and a fairly low level of gene flow between them.

**Keywords:** protected plants, aquatic macrophytes, molecular iPBS markers, genetic diversity of populations

**For citation:** Hudnaya N. U., Mialik A. M., Kulahina T. G., Luu D. N. A., Titok V. V. Genetic structure of populations of the native species *Salvinia natans* L. progressing in Belarus. *Vesti Natsyonal'nai akademii nauk Belarusi. Seriya biyagichnykh nauk* = *Proceedings of the National Academy of Sciences of Belarus. Biological series*, 2025, vol. 70, no. 3, pp. 207–215 (in Russian). <https://doi.org/10.29235/1029-8940-2025-70-3-207-215>

Н. В. Гудная<sup>1</sup>, А. Н. Мялик<sup>1</sup>, Т. Г. Кулагина<sup>1</sup>, Д. Н. А. Луу<sup>2</sup>, В. В. Титок<sup>1</sup>

<sup>1</sup>Центральный ботанический сад Национальной академии наук Беларуси, Минск, Республика Беларусь<sup>2</sup>Вьетнамский национальный музей природы Вьетнамской академии наук и технологий, Вьетнам

## ГЕНЕТИЧЕСКАЯ СТРУКТУРА ПОПУЛЯЦИЙ ПРОГРЕССИРУЮЩЕГО В БЕЛАРУСИ АБОРИГЕННОГО ВИДА *SALVINIA NATANS* L.

**Аннотация.** В статье представлены результаты изучения генетического разнообразия и структуры 7 популяций *Salvinia natans* L. на территории Беларуси в естественной (Пинск, Рогачёв, Мухавец, Стрельск) и прогрессирующей (Каменец, Кривошин, Щара) частях ареала. Благодаря использованию молекулярных iPBS маркеров было установлено, что естественные популяции Пинск и Мухавец обладают наивысшим уровнем генетического разнообразия, а островная популяция Каменец характеризуется генетической обедненностью. Достаточно низкие показатели генетического разнообразия свойственны и другим популяциям, расположенным в островных локалитетах (Кривошин, Щара) и на северной (Рогачёв) границе ареала *Salvinia natans* L. Установлено, что уровень межпопуляционной изменчивости оказался ниже, чем внутривидовой (22 и 78 % соответственно). Значение PhiPT = 0,22 указывает на то, что генетически популяции различаются значительно. Для исследуемого вида уровень потока генов равен 0,80, что является средним показателем и обусловлено, вероятно, спецификой размножения данного вида как спорового растения. Анализ генетических расстояний показал, что наименьшее значение расстояния Нея (0,11) наблюдалось между популяциями Пинск и Щара, а наибольшее (0,21) – между популяциями Стрельск и Кривошин, что в целом согласуется с их географическим положением. Результаты анализа ward.D2, основанного на данных матрицы расстояний Нея, также подтверждают эти данные и демонстрируют подразделение изученных популяций на два основных кластера, соответствующих их расположению в бассейнах рек Припять и Западный Буг. Полученные экспериментальные данные показывают, что с учетом потепления климата продолжится расширение ареала *Salvinia natans* L.

в северном направлении. Однако вероятность проявления данным видом агрессивных свойств на новоосвоенных территориях остается пока невысокой в связи с незначительным генетическим разнообразием краевых популяций и достаточно низким уровнем потока генов между ними.

**Ключевые слова:** охраняемые растения, водные макрофиты, iPBS маркеры, генетическое разнообразие популяций

**Для цитирования:** Генетическая структура популяций прогрессирующего в Беларуси аборигенного вида *Salvinia natans* L. / Н. В. Гудная, А. Н. Мялик, Т. Г. Кулагина [и др.] // Весці Нацыянальнай акадэміі навук Беларусі. Серыя біялагічных навук. – 2025. – Т. 70, № 3. – С. 207–215. <https://doi.org/10.29235/1029-8940-2025-70-3-207-215>

**Introduction.** Because of natural climate changes and the consequences of the complex impact of anthropogenic factors, the distribution and population size of individual plant species change, which leads to the dynamics of their ranges. While stenotopic species with a narrow ecological amplitude demonstrate a decrease in numbers and a reduction in range, some species (including those native to a given area) can expand their distribution area, exhibit expansive properties, which can also have negative consequences.

Such species, in the understanding of N. Kozlovskaya [1], are among the progressive ones that are deliberately not classified as adventitious flora. Their ranges are located near the studied territory and tend to progressively expand, advancing both naturally and with the assistance of anthropogenic factors.

The category of non-synanthropic progressive species should include that part of progressive species whose dispersal occurs naturally as a result of the dispersion of diaspores and their establishment in new places. The advancement of this group of species can be carried out both through disturbed plant communities created under the influence of natural factors (fires, floods, avalanches and mudflows) and through natural phytocenoses. The dispersal of these non-synanthropic progressive species is characterized, as a rule, by low rates, locality of the initial sites of introduction and their small distance from the original areas [2].

One of the progressive native species in the flora of wetlands of Belarus is *Salvinia natans* L. – floating salvinia, included in the Red Book of the Republic of Belarus (IV category of protection) and in Appendix I of the Bern Convention. The limiting factors for this species are the destruction of floodplain lakes because of hydromelioration and water pollution by industrial waste. However, at present, due to global warming, the range of this species is expanding in the northern direction.

Previously, *S. natans* was known only within the Belarusian Polesie in the basins of the Pripyat, Dnieper, Sozh and Zapadnyj Bug rivers, where it was noted mainly in the valleys of these rivers – backwaters, oxbow lakes. In recent years, a clear trend has emerged to increase the number of known habitats of this species both in the valleys of the rivers noted above and in new localities, which, taking into account the growth of the total population, will allow us to classify this species as progressive or expansive. In the field season of 2023–2024, an ecological-coenotic study of *S. natans* populations was carried out both within the natural range and in new island habitats. According to our own research data and literary references, new habitats of *S. natans* have been identified in the Shchara River basin (a tributary of the Neman) [3], Lesnaya (a tributary of the Zapadnyj Bug), and in the territory of the Pukhovichy Plain [4], which indicates an expansion of the species' range to the north and its expansion into the Neman River basin, where this taxon was previously absent.

The above shows a high probability of further dispersal of *S. natans*, which, given the ability of this species to form monospecific thickets and displace other hydrophytes from aquatic ecosystems, requires timely preventive measures to prevent possible negative consequences. This determines the relevance and purpose of the work – based on the study of the genetic diversity and population structure of *S. natans* in the natural and progressive part of the range, to assess the adaptive potential of this species and to predict possible negative consequences of the expansion of its range for wetland ecosystems in the central and northern parts of Belarus.

**Objects and methods of research.** *Salvinia natans* L. (floating salvinia) is a heat-loving, aquatic, free-floating annual fern from the Salviniaceae family. Plants usually range in size from 3 to 7 cm, but in favorable years in some reservoirs the stems can reach 10–12 cm or more. The leaves are arranged in whorls of three, two of which are ovoid in shape and are on the surface of the water, while the third is underwater and dissected into filiform lobes. At the base of the underwater leaves are clusters of 4–8 spherical sori (Fig. 1).



Fig. 1. General appearance of *Salvinia natans* L. and the consequences of its expansion

The plants overwinter as macrospores immersed in the bottom soil, some of which germinate with the onset of spring, while the rest form a “spore bank” and germinate the following year, which insures the species against extinction in the event of a sharp change in habitat conditions. *S. natans* prefers small, well-warmed stagnant bodies of water (continental and floodplain lakes, river backwaters), from where it can enter rivers, where it is usually found in the coastal zone.

To assess the possible negative consequences of the expansion of *S. natans*, studies were carried out on the natural (Brest, Pinsk, districts of the Brest region, Mozyr district of the Gomel region) and evolutionary (Lyakhovich, Ivatsevichi and Kamenets districts of the Brest region) parts of the range, where material for molecular genetic research was collected (Fig. 2).

Seven populations of *S. natans* were studied, the detailed characteristics of which are given in Table 1. Five samples were collected from the populations of Kamenets (Km), Krivoshin (Kr), Pinsk (Pn), Shchara (Sch) and Mukhavets (Mh), and four samples were collected from the populations of Strelsk (St) and Rogachev (Rg). Parts of the leaves were pre-washed in distilled water and then dried in silica gel. In each studied population, a floristic description of the phytocenosis, an assessment of the number and vitality of plants, as well as the collection of voucher herbarium samples and documentation of populations on the inaturalist.org platform were also carried out.

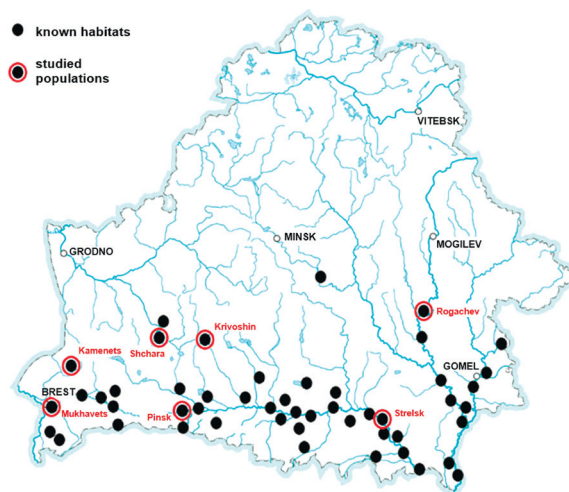


Fig. 2. Location of the studied populations of *Salvinia natans* L.

Table 1. Characteristics of model populations of *Salvinia natans* L.

Population	Location	Coordinates	Phytocenosis, occurrence	Author of the collection and date	Documentation
Kamenets (Km)	Brest region, Kamenets district, village Novitskovichi, 1.2 km to the east	52.445204, 23.865521	Near the pond shore, among macrophytes, rarely	Mialik A. M., Tretyakov D., 29.09.2023	<a href="https://www.inaturalist.org/observations/185454989">https://www.inaturalist.org/observations/185454989</a> , herbarium MSKH
Krivoshin (Kr)	Brest region, Lyakhovichsky district, village Krivoshin, 1.5 km to the southeast, Repikhovo park	52.855865, 26.144998	Near the pond shore, very often	Mialik A. M., Vabishchevich M., 31.08.2023	<a href="https://www.inaturalist.org/observations/181073471">https://www.inaturalist.org/observations/181073471</a> , herbarium MSKH
Pinsk (Pn)	Brest region, Pinsk district, Pinsk city, southern outskirts, Pina river	52.116828, 26.120350	Near the shore among macrophytes, often	Mialik A. M., 22.09.2023	<a href="https://www.inaturalist.org/observations/184405446">https://www.inaturalist.org/observations/184405446</a> , herbarium MSKH

The end Table 1

Population	Location	Coordinates	Phytocenosis, occurrence	Author of the collection and date	Documentation
Shchara (Sch)	Brest region, Ivatsevichi district, village Chemely, 1.4 km to the east, Shchara river	52.789325, 25.557824	In the river backwater among, macrophytes, often	Mialik A. M., Vabishchevich M., 31.08.2023	<a href="https://www.inaturalist.org/observations/181073171">https://www.inaturalist.org/observations/181073171</a> , herbarium MSKH
Mukhavets (Mh)	Brest region, Brest district, Brest city, central beach, Mukhavets river	52.079203, 23.702991	by the river bank, very often	Mialik A. M., Kulinka E. M., 11.09.2024	<a href="https://www.inaturalist.org/observations/241275872">https://www.inaturalist.org/observations/241275872</a> , herbarium MSKH
Strelsk (St)	Gomel region, Mozyr district, village Strelsk, eastern outskirts, Pripyat river	51.957780, 29.424520	by the river bank, occasionally	Mialik A. M., Kulinka E. M., Kulahina T. G., 05.09.2024	<a href="https://www.inaturalist.org/observations/240007585">https://www.inaturalist.org/observations/240007585</a> , herbarium MSKH
Rogachev (Rg)	Gomel region, Rogachev district, village Luchin, 1 km to the east, Dnieper river	53.003830, 30.029682	an oxbow lake, among macrophytes, not infrequently	Mialik A., Kulinka E. M., Kulahina T. G., 04.09.2024	<a href="https://www.inaturalist.org/observations/240005638">https://www.inaturalist.org/observations/240005638</a> , herbarium MSKH

DNA was isolated using the DNA-Extran-3 reagent kit (Synthol, Russia). The study used 30 iPBS primers [5] (Table 2). PCR was performed in 25 µl of the reaction mixture containing 25 ng of DNA, 5 µl of the ready-made ScreenMix PCR mixture (Eurogen, Russia), 1 mM of primer for 12–13 bp primers or 0.6 mM for 18 bp primers, and water.

Table 2. Primers used in the study

Primer	Optimum annealing temperature Ta, °C	Sequence (5'–3')
2074	49.6	GCTCTGATACCA
2389	50.0	ACATCCTTCCCA
2373	51.0	GAAGTTGCTCCGATGCCA
2277	52.0	GGCGATGATACCA
2376	52.0	TAGATGGCACCA
2375	52.5	TCGCATCAACCA
2377	53.0	ACGAAGGGACCA
2378	53.0	GGTCCTCATCCA
2383	53.0	GCATGGCCTCCA
2374	53.5	CCCAGCAAACCA
2095	53.7	GCTCGGATACCA
2083	54.6	CTTCTAGCGCCA
2237	55.0	CCCCTACCTGGCGTGCCA
2239	55.0	ACCTAGGCTCGGATGCCA
2272	55.0	GGCTCAGATGCCA
2077	55.1	CTCACGATGCCA
2232	55.4	AGAGAGGCTCGGATACCA
2390	56.4	GCAACAACCCCA
2273	56.5	GCTCATCATGCCA
2394	56.5	GAGCCTAGGCCA
2220	57.0	ACCTGGCTCATGATGCCA
2242	57.0	GCCCCATGGTGGGCGCCA
2076	59.2	GCTCCGATGCCA
2271	60.0	GGCTCGGATGCCA
2415	61.0	CATCGTAGGTGGGCGCCA
2078	62.8	GCGGAGTCGCCA
2080	63.3	CAGACGGCGCCA
2081	65.0	GCAACGGCGCCA
2270	65.0	ACCTGGCGTGCCA
2079	65.2	AGGTGGGCGCCA



The PCR program consisted of: 1 cycle at 95 °C for 5 min; 38 cycles at 95 °C for 15 s, annealing was carried out at a temperature of 49.6–65.2 °C (depending on the primer) for 60 s, elongation at 68 °C for 90 s. The final elongation was carried out at 72 °C for 8 min. Amplification was carried out in a C1000 Touch Thermal Cycler programmable thermostat (MJ Research Inc., Bio-Rad Laboratories, USA). Electrophoresis was carried out at 65 V for 5 hours in 2 % agarose gel. Ethidium bromide was used to stain the gel for 30 min and visualized using the UV Imager Gel Doc XR+ system (Bio-Rad, USA).

PyElph 1.4 software was used to construct binary matrices based on electrophoresis images. All DNA fragments that could be accurately recognized were considered as single dominant loci. The presence or absence of fragments was designated as “1” or “0”, respectively. The resulting data in the form of a binary matrix were processed using PopGene 1.31 software to calculate the following parameters: the proportion of polymorphic loci (P), the effective (Ne) and observed numbers of alleles (Na), Shannon information index (I), Nei's gen diversity (He), total gene diversity (Ht), gene diversity in populations (Hs), genetic differentiation coefficient ( $G_{ST} = [H_t - H_s] / H_t$ ), and gene flow among populations (Nm). The GenALEX 6.5 software package for MS Excel was used to calculate the polymorphism information content (PIC), average genetic distance, analysis of molecular variance (AMOVA), and principal coordinate analysis (PCoA). The Stats package for R was used to construct the dendrogram using the ward.D2 method.

To assess the genetic diversity of *S. natans*, two primers were selected – 2383 and 2078, since they allowed obtaining clear DNA fragments with polymorphic loci. The PCR results using marker 2383 are presented in Fig. 3.

As a result of gradient PCR, the optimal annealing temperatures of the selected primers were established and are presented in Table 3.

Table 3. Optimal primer annealing temperatures after optimization

Primer	Optimum annealing temperature $T_a$ , °C	Sequence (5'-3')
2383	51.4	GCATGGCCTCCA
2078	59.6	GCGGAGTCGCCA

For the selected iPBS markers, parameters such as the number of polymorphic loci, their proportion and the polymorphism information content (PIC) were established (Table 4).

Table 4. Characteristics of selected iPBS markers

Primer	Number of loci	Number of polymorphic loci	Proportion of polymorphic loci, %	Polymorphism information content (PIC)
2383	37	28	74.68	0,22
2078	40	37	92.50	0,30

For the primers used, 37 and 40 loci were obtained, of which 28 and 37, respectively, were polymorphic. The average proportion of polymorphic loci for two primers was 83.58 %. The obtained values of the polymorphism information content (PIC) are quite high, which allows using these markers for further research.

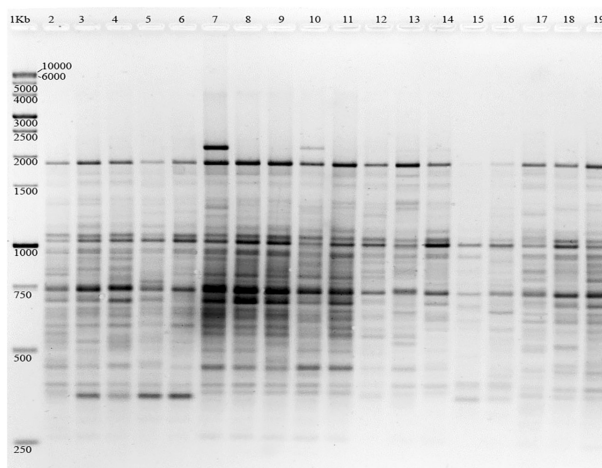


Fig. 3. PCR results using 2383 iPBS primer for the populations of Kamenets (lanes 2–6), Krivoshin (lanes 7–11), Pinsk (lanes 12–16), and Shchara (lanes 17–19). Lane 1 – 1 Kb molecular weight marker

**Results and its discussion.** As a result of the conducted research it was established that the model populations of *S. natans* Pinsk and Mukhavets have the highest proportion of polymorphic loci – 51.95 and 53.25 %, respectively (Table 5). The obtained values of Na, Ne, He, I are also higher in these populations compared to the others (1.52, 1.37, 0.21, 0.30 in the Pinsk population and 1.53, 1.36, 0.20, 0.30 in the Mukhavets population). Consequently, these populations have the highest level of genetic diversity and, accordingly, have a higher adaptive potential. The obtained data are consistent with the number of plants in the noted populations, as well as their location within the natural part of the range of *S. natans*.

Table 5. Parameters of genetic diversity of the studied populations of *Salvinia natans* L.

Parameter	Population							Common to populations
	Km	Kr	Pn	Sch	Mh	St	Rg	
Proportion of polymorphic loci, %	31.17	38.96	51.95	36.36	53.25	45.45	40.26	83.12
Na	1.31 ± 0.05	1.39 ± 0.06	1.52 ± 0.06	1.36 ± 0.06	1.53 ± 0.06	1.46 ± 0.06	1.40 ± 0.06	1.83 ± 0.04
Ne	1.21 ± 0.04	1.27 ± 0.04	1.37 ± 0.05	1.26 ± 0.04	1.36 ± 0.05	1.28 ± 0.04	1.27 ± 0.04	1.45 ± 0.04
He	0.12 ± 0.02	0.15 ± 0.02	0.21 ± 0.03	0.15 ± 0.02	0.20 ± 0.02	0.16 ± 0.02	0.15 ± 0.02	0.26 ± 0.02
I	0.17 ± 0.03	0.22 ± 0.03	0.30 ± 0.05	0.21 ± 0.03	0.30 ± 0.03	0.25 ± 0.03	0.23 ± 0.03	0.40 ± 0.03
Ht	–							0.27 ± 0.004
Hs	–							0.16 ± 0.002
Gst	–							0.38
Nm	–							0.80

The lowest level of genetic diversity indicators is found in the Kamenets population, where Na, Ne, He, I are 1.31, 1.21, 0.12, 0.17, respectively. Other studied populations located in island localities (Krivoshin, Shchara) or on the northern (Rogachev) border of the *S. natans* range are also characterized by low indicators of genetic diversity.

For all loci of the studied populations of *S. natans*, the following were calculated: Na, Ne, He, I and the proportion of polymorphic loci, which amounted to 1.83, 1.45, 0.26, 0.40 and 83.12 %. The analysis of the population genetic structure showed that most of the genetic diversity is concentrated within the populations, since the level of genetic differentiation (Gst) among them was 0.38. The gene flow between populations of this species is 0.80, which is an average indicator [6]. At the same time, the obtained value indicates a fairly low level of gene exchange between individual populations, which is probably due to the specificity of reproduction of the species itself as a spore plant. Since this indicator was less than one, then according to the “theory of evolution with shifting equilibrium” [7], this indicates a violation of gene exchange between populations of *S. natans* in the territory of Belarus.

The AMOVA results confirm the previously obtained Gst value, namely, that the established level of interpopulation variability was lower than that of intrapopulation variability (22 and 78 %, respectively). The PhiPT value of 0.22 indicates that the populations differ significantly genetically, since the PhiPT value is >0.2 [8]. The difference between individuals in the populations was statistically significant with a P value of <0.01 (Table 6).

Table 6. AMOVA results for *Salvinia natans* L. populations

Source of variability	Number of degrees of freedom (df)	Sum of squares (SS)	Mean square (MS)	Dispersion	PhiPT	Share in variation
General	32	329.70	–	10.58	0.219*	–
Between populations	6	114.90	19.15	2.31		0.22
Within populations	26	214.80	8.26	8.26		0.78

Note. \* – differences are significant at a significance level of  $P < 0.01$ .

The compiled matrix of pairwise genetic similarities and Nei distances (Table 7) demonstrates the differences between the studied populations of *S. natans* located in different parts of the species range within Belarus.

Table 7. Matrix of pairwise genetic similarities (above the diagonal) and Nei distances (below the diagonal)

Популяцыя	Km	Kr	Pn	Sch	Mh	St	Rg
Km	—	0.87	0.84	0.85	0.88	0.83	0.86
Kr	0.14	—	0.86	0.87	0.85	0.81	0.82
Pn	0.17	0.15	—	0.90	0.87	0.88	0.83
Sch	0.16	0.14	0.11	—	0.88	0.86	0.87
Mh	0.13	0.16	0.14	0.13	—	0.88	0.85
St	0.18	0.21	0.13	0.15	0.13	—	0.84
Rg	0.15	0.19	0.19	0.13	0.16	0.17	—

The presented data show that the lowest value of the Nei genetic distance (0.11) was observed between the Pinsk and Shchara populations, and the highest (0.21) between the Strelsk and Krivoshin populations, which is generally consistent with their geographic location. The results of the ward.D2 analysis (Fig. 4), based on the Nei distance matrix data, also confirm these data and demonstrate the division of the studied populations into two main clusters.

Using PCoA analysis, it was found that the first three components of the principal coordinates account for 30.64 % of the total variation (Fig. 5). The points marking individual samples from the Pinsk and Shchara populations are close to each other, indicating their high genetic similarity, as well as between the Kamenets and Mukhavets populations.

Assessing the genetic relationship of the studied populations of *S. natans* based on the above data, the following can be noted: populations located in the Pripyat River basin (Pinsk and Strelsk) in the zone of the natural range are characterized by the greatest genetic relationship, which is quite logical given their position within the same watercourse. The closest to them is the Shchara population, located in an island locality on the northern periphery of the *S. natans* range. Thus, as a result of the studies, it was experimentally confirmed that the progressive spread of this species to the Neman River basin occurred from the Pripyat basin, probably with the participation of migrating waterfowl. A separate cluster also includes populations from the Zapadnyj Bug River basin – Mukhavets and Kamenets. The maximum degree

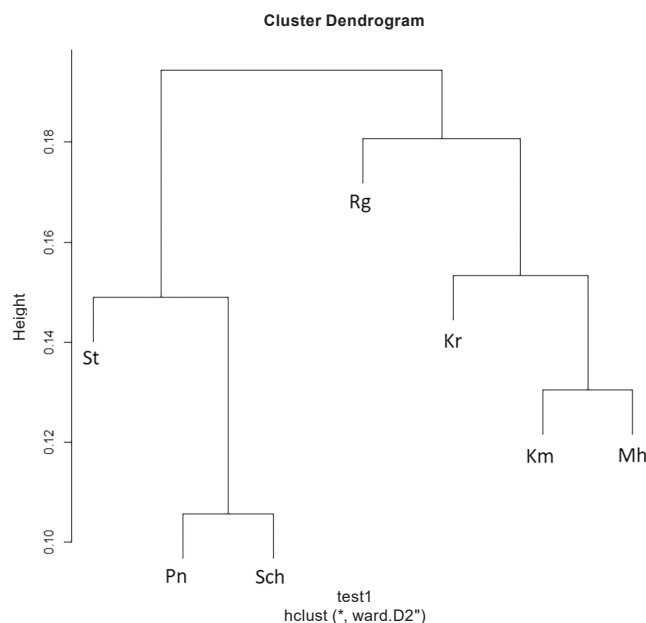


Fig. 4. Dendrogram based on Nei's genetic distance showing the relationship between the studied populations of *Salvinia natans* L.

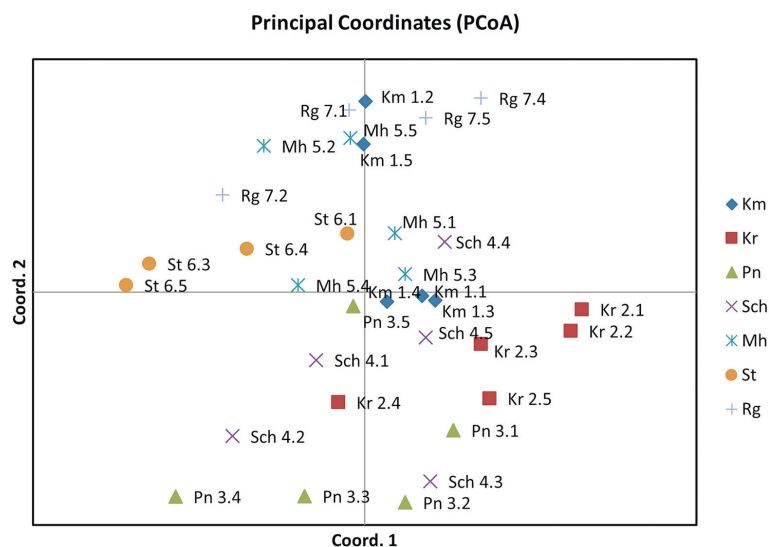


Fig. 5. Distribution of the studied populations of *Salvinia natans* L. on the first two principal coordinates (PCoA)

of genetic relationship was also revealed between them, in connection with which the genesis of the Kamenets population from the progressive part of the *S. natans* range was established. According to the constructed dendrogram (Fig. 4), this cluster contains another population (Krivoshin) from the progressive part of the range within the Neman basin, where waterfowl also probably brought the *S. natans* diaspores. At the same time, the PCoA analysis data show its high genetic relationship with the Shchara and Pinsk populations, which is more logical given their close geographical location.

Similar features are noted for the Rogachev population located in the Dnieper basin in eastern Belarus. According to the dendrogram constructed on the basis of the Nei genetic distance, it is closer to the *S. natans* populations from the Zapadnyj Bug basin, which is inconsistent with their geographical location, but can be explained by the introduction by waterfowl. The latter is indirectly confirmed by its location within an isolated oxbow lake. At the same time, the PCoA analysis data demonstrate some similarity with the more closely located Strelsk population.

Considering *S. natans* as a progressive species with expansive properties, it is possible to note the low genetic diversity of the marginal populations and, accordingly, their insignificant adaptive potential. The genetic impoverishment of the marginal populations of this species in the territory of Belarus has already been noted earlier [9]. Similar patterns of loss of genetic diversity have been noted for the closely related species *S. minima* Baker during its expansion from the east to the west of the USA [10].

The obtained experimental data indicate that, given the global warming, the range of *S. natans* will continue to expand northward. However, the probability of the expansive properties of this species in newly developed territories remains low due to the insignificant genetic diversity of the marginal populations and the rather low level of gene flow between them.

**Conclusion.** As a result of the conducted studies using molecular iPBS markers, an assessment of the genetic heterogeneity and relatedness of populations of the progressive native species *S. natans* in the natural and expanding parts of the range was made. It was found that the populations in the natural part of the range (Pinsk and Mukhavets) have the highest level of genetic diversity, while the marginal (Rogachev) and island progressive (Kamenets, Krivoshin) populations are characterized by genetic impoverishment. An assessment of the population structure showed that *S. natans* is dominated by intrapopulation variability (78 %). The level of gene flow for the studied species is 0.80, which indicates the genetic isolation of individual populations.

Data on the genetic relationship of *S. natans* populations in the natural part of the range show their unification into 2 separate clusters according to the location in the Pripyat and Zapadnyj Bug basins. The revealed genesis of progressive populations, showing the simultaneous penetration of *S. natans* into the Neman basin from the Pripyat and Zapadnyj Bug river basins, confirms the characteristic feature Zapadnyj of representatives of hydrophilic flora – the ability to migrate with the help of waterfowl.



In general, the obtained data show the genetic impoverishment of populations in the northern peripheral part of the range, which is associated with the low probability of this species exhibiting expansive properties in newly developed territories.

**Conflict of interest.** The authors declare no conflict of interest.

**Acknowledgments.** The work was carried out with the financial support of the Belarusian Republican Foundation for Fundamental research (grant BRFFI-VANT 2023, No. B23V-005, QTB01.03/23-24).

## References

1. Kozlovskaya, N. V. *Flora of Belarus, patterns of its formation, scientific basis for use and protection*. Minsk, Nauka i tekhnika Publ., 1978. 128 p. (in Russian).
2. Agafonova L. A. Progressive species and their position in the structure of the adventive element of flora. *Voprosy obshchei botaniki: traditsii i perspektivy: materialy Mezhdunarodnoi nauchnoi konferentsii, posvyashchennoi 200-letiyu Kazanskoi botanicheskoi shkoly (23–27 yanvarya 2006 goda)* [General Botany Issues: Traditions and Prospects: Proceedings of the International Scientific Conference Dedicated to the 200<sup>th</sup> Anniversary of the Kazan Botanical School (January 23–27, 2006)]. Kazan, 2006, pt. 2, pp. 134–136 (in Russian).
3. Myalik A. N., Kruchonok A. V., Gulis A. L. New floristic finding of rare and protected native species in Belarus. *Izvestiya Gomel'skogo gosudarstvennogo universiteta imeni F. Skoriny* [News of the Gomel State University named after F. Skorina]. Natural sciences, 2021, vol. 126, no. 3, pp. 48–54 (in Russian).
4. Savitskaya, K. L. Flora structure of the Pukhovichy plain waterbodies and waterflows. *Botanika (issledovaniya)* [Botany (research)], 2024, no. 53, pp. 28–37 (in Russian).
5. Kalendar R., Antonius K., Smýkal P., Schulman A. H. IPBS: a universal method for DNA fingerprinting and retro-transposon isolation. *Theoretical and Applied Genetics*, 2010, vol. 121, no. 8, pp. 1419–1430. <https://doi.org/10.1007/s00122-010-1398-2>
6. Wright S. *Evolution and the genetic of population, variability within and among natural populations. Vol. 4*. Chicago, University of Chicago Press, 1978. 580 p.
7. Wright, S. Random Drift and Shifting Balance Theory of Evolution. *Mathematical topics in population genetics. Vol. 1*. Berlin, 1970, pp. 1–31. [https://doi.org/10.1007/978-3-642-46244-3\\_1](https://doi.org/10.1007/978-3-642-46244-3_1)
8. Resmi L., Nair A. R., Nair A. S. Population genetic structure and diversity analysis of South Indian banana cultivars. *Journal of Plant Breeding and Crop Science*, 2016, vol. 8, no. 1, pp. 1–12. <https://doi.org/10.5897/JPCS2015.0519>
9. Yukhimuk A. N., Dzhus M. A., Vlasov B. P., Vlasova A. B. Population genetic resource of a rare species of aquaflore of Belarus *Salvinia natans* L. *Manitoryng i atsenka stanu raslinnaga svetu: materyyaly IV Mizhnarodnai navukovai kanferentsyi (Minsk – Braslaŭ, 30 verasnya–4 kастрыchnika 2013 goda)* [Monitoring and assessment of the state of the flora: materials of the IV International Scientific Conference (Minsk – Braslav, September 30–October 4, 2013)]. Minsk, 2013, pp. 353–355 (in Russian).
10. Rove C. A., Hauber D. P., Wolf P. G. Genomic Variation of Introduced *Salvinia minima* in Southeastern United States. *Aquatic Botany*, 2018, vol. 151, pp. 38–42. <https://doi.org/10.1016/j.aquabot.2018.07.011>

## Information about the authors

*Natallia U. Hudnaya* – Researcher. Central Botanical Garden of the National Academy of Sciences of Belarus (2v, Surganov Str., 220012, Minsk, Republic of Belarus). E-mail: N.Samakhvalava@cbg.org.by

*Aliaksandr M. Mialik* – Ph. D. (Biol.), Assistant Professor, Head of the Sector. Central Botanical Garden of the National Academy of Sciences of Belarus (2v, Surganov Str., 220012, Minsk, Republic of Belarus). E-mail: aleksandr-myalik@yandex.ru

*Tatsiana G. Kulahina* – Researcher. Central Botanical Garden of the National Academy of Sciences of Belarus (2v, Surganov Str., 220012, Minsk, Republic of Belarus). E-mail: T.Shlapakova@cbg.org.by

*Dam Ngoc Anh Luu* – D. Sc. (Philos.), Head of the Department. Vietnam National Museum of Nature of the Vietnam Academy of Science and Technology (18, Hoang Quoc Viet Str., Cau Giay, Hano). E-mail: ngocanh@vnmn.vast.vn

*Vladimir V. Titok* – Corresponding Member, D. Sc. (Biol.), Assistant Professor, Chief Researcher. Central Botanical Garden of the National Academy of Sciences of Belarus (2v, Surganov Str., 220012, Minsk, Republic of Belarus). E-mail: V.Titok@cbg.org.by

## Информация об авторах

*Гудная Наталья Владимировна* – науч. сотрудник. Центральный ботанический сад НАН Беларуси (ул. Сурганова, 2в, 220012, г. Минск, Республика Беларусь). E-mail: N.Samakhvalava@cbg.org.by

*Мялик Александр Николаевич* – канд. биол. наук, доцент, заведующий сектором. Центральный ботанический сад НАН Беларуси (ул. Сурганова, 2в, 220012, г. Минск, Республика Беларусь). E-mail: aleksandr-myalik@yandex.ru

*Кулагина Татьяна Геннадьевна* – научный сотрудник. Центральный ботанический сад НАН Беларуси (ул. Сурганова, 2в, 220012, г. Минск, Республика Беларусь). E-mail: T.Shlapakova@cbg.org.by

*Луу Дам Нгок Ань* – доктор философии, заведующий отделом. Вьетнамский национальный музей природы Вьетнамской академии наук и технологий (18, Hoang Quoc Viet Str., Cau Giay, Hano). E-mail: ngocanh@vnmn.vast.vn

*Титок Владимир Владимирович* – член-корреспондент, д-р биол. наук, доцент, гл. науч. сотрудник. Центральный ботанический сад НАН Беларуси (ул. Сурганова, 2в, 220012, г. Минск, Республика Беларусь). E-mail: V.Titok@cbg.org.by