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Morphological and Genetic Differentiation of Populations of *Rhododendron aureum* Georgi. (Ericaceae) in the Mountains of Southern Siberia and on the Kamchatka Peninsula

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Abstract—A study of morphological traits in the populations of *R. aureum* from Western and Eastern Sayan and Kamchatka has been carried out. The variability of genetic nuclear DNA microsatellite markers (nSSRs) has been studied in the same samples. A total of 15 absolute and relative morphological traits of shoots and leaves, as well as 18 polymorphic microsatellite markers in eight natural populations of *R. aureum,* are observed. It is found that the following parameters are the most variable within species populations: plant size, shoot length, length of the foliated part of shoots, and number of leaves relative to shoot length; relative leaf shape parameters are more stable parameters. The reliable division of populations into three geographical groups on all set of morphological characters is established. One important taxonomic character, the leaf life span, is shown to make a great contribution on the shoot to the division of geographical groups of populations and individual populations. The structure of morphological differentiation of populations is confirmed by the results of the analysis of genetic variability of the same populations of *R.aureum* by nuclear microsatellite markers. The greatest genetic distances from other populations are established for the Kamchatka populations. There is a tendency toward the differentiation of populations within the Altai-Sayan mountain country. The results of the study agree well with the information on geography, ecology, and biology of the species. The study of intra- and interpopulation morphological differentiation of *R. aureum* populations in Siberia is conducted for the first time, following the recently initiated studies on genetic variability of the species in Northern Eurasia.

Keywords: *Rhododendron aureum*, morphological variability, nuclear microsatellite markers, nSSRs, geographic populations

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INTRODUCTION

As is known, rhododendrons are an ancient genus, many representatives of which (including *Rhododendron aureum* Georgi.) belong to tertiary relics and, according to some researchers, are of Holoarctic origin (Aleksandrova, 1975). Eighteen species of rhododendrons grow in Russia, including 11 species in Siberia and the Far East. They are often edificators and subedificators of forest phytocenoses and alpine vegetation. Rhododendrons can grow and develop on the primary products of rock destruction, which increases their importance as soil-fixing plants. However, despite the important role that rhododendrons play in the phytocenoses of mountainous countries, they are still poorly studied.

Golden rhododendron (*Rhododendron aureum*) is one of the key components of the vegetation cover in the mountains of Siberia and the Far East. Its range stretches from Altai to Alaska. The species is included in the Red Books of the Kemerovo and Chita oblasts, the Trans-Baikal Territory (Zabaykalsky krai), and Agin-Buryat Autonomous Okrug. The species is quite widespread in the middle mountains and highlands in the mountains of Southern Siberia (Altai-Sayan mountain country); its western border runs along the Altai. The populations of *R. aureum* are not rare in the Far East, from the southern borders of Russia to Kamchatka, Magadan oblast, and the Chukotka Autonomous Okrug (67°–68° N), including the island of Sakhalin and the Kuril Islands. It also grows in Mongolia, Korea, China, and Japan. *R. aureum* is common in forests on stone fields, in thickets of Siberian dwarf pine, tundra, and is often the dominant or codominant of the shrub layer of coniferous forests. Golden rhododendron performs environment-forming functions in a harsh climate: it maintains the ecological balance of biogeocenosis, forms a specific soil microbiome, and prevents soil erosion (Wang et al., 2017).

Table 1. Characteristics of the *Rhododendron aureum* populations

Populations	Coordinates	Height above sea level
Western Sayan, Mount Polka (Au 1)	52°51′/93°15′	1650
Western Sayan, Mount of Vasili Rogovoy (Au 2)	52°51′/93°16′	1500
Western Sayan, Mount Tushkanchik (Au 3)	52°47′/93°21′	1700
Western Sayan, Kamenny Gorodok (Au 4)	52°53′/92°54′	1400
Western Sayan, Mount Borus (Au 5)	52°47′/91°30′	1450
Eastern Sayan, Mount Obruchev (Au 6)	52°06′/95°58′	1530
Kamchatka, Avacha Volcano (Au 7)	53°15′/158°43′	820
Kamchatka, Mount Vachkazhets (Au 8)	53°04′/157°55′	690

In addition, plants of golden rhododendron contain a number of biochemical components with medicinal properties (Olennikov et al., 2010), which, combined with high decorative properties, is the reason for the increased anthropogenic load on populations, especially those growing near settlements. There is a lack of information about the interpopulation and intrapopulation variability of the characters of golden rhododendron in the literature. However, due to such a wide distribution of the species and its mountain landscape preferences, it is of great interest to study both the morphological and genetic variability of the populations of the species, especially when comparing geographically remote populations of Southern Siberia on the southwestern border of the range and on its northeastern border in Kamchatka. Therefore, the purpose of our work is to study intra- and interpopulation variability of vegetative organs (leaves and shoots) and genetic markers in *R. aureum*.

MATERIALS AND METHODS

The populations of golden rhododendron growing in the Western Sayan (the Kulumys ridge, Au 1, 4; Ergaki ridge, Au 2, 3; Borus ridge, Au 5), on the East Tuva Plateau (Obruchev ridge, Au 6) and on Kamchatka Peninsula (Avachinsky volcano, Au 7, Mount Vachkazhets, Au 8) were studied (Table 1).

In all eight populations, 30 generative individuals were selected to study the morphological variability of *R. aureum* characters at a distance of no closer than 10 m from each other. The following parameters were measured for each plant: the number of leaves on the shoot, pcs; leaf length, mm; leaf width, mm; petiole length, mm; relative leaf length (ratio of width to leaf length); relative petiole length (ratio of petiole length to leaf length); leafiness of the shoot (ratio of the number of leaves to the length of leafy part of the shoot); length of the leafy part of the shoot, mm; leaf life span on the shoot, years; length of annual shoots, mm; height of the shrub, cm, width of the shrub, cm. The length of the shoots was measured in 3-fold and the size of the leaves in 15-fold repetition.

The minimum and maximum values of variance of the character (lim), arithmetic mean (Xav), mean error (m), sample variance (σ), coefficient of variation (Cv), coefficients of asymmetry and excess (As, Ex), and linear correlation coefficient (Rx) were calculated for statistical data processing (Schmidt, 1984). The level of individual variability of characters was determined using the scale of S.A. Mamaev (1973).

The one-way analysis of variance (ANOVA) was used to detect the significance of the differences. The correlation structure of characters was previously studied using correlation analysis (Rostova, 2008). In order to establish the similarity between populations for the entire set of morphological characters, a cluster analysis of the data was carried out using the weighted pair group method with an arithmetic mean, the Euclidean distance was a measure of similarity (Ayvazyan et al., 1974), and discriminant analysis was carried out. Statistical data processing was carried out using Excel and Statistica software packages (Borovikov, 2003).

The silica-gel dried leaves were used for DNA analysis. DNA was isolated according to the standard protocol for plant tissues (STAV method) (Dewey et al., 1996). Eighteen nuclear microsatellite loci developed for *R. aureum* and *R. brachycarpum* were used: RA10, RA20, RA31, RA38, RA65, RA85, RA99, RA114, RA137, RA148, RD4, RD5, RD8, RDE11, RDE12, N8, N73, and N91. (Li et al., 2011; Kwak et al., 2015). The PCR conditions are described in (Li et al., 2011; Kwak et al., 2015). The lengths of the amplified fragments were determined on a Genetic Analyzer 3130 capillary sequencer (Applied Biosystems, United States) in the presence of a molecular-weight size marker of S-450. Electrophoregrams were analyzed using GeneMapper v. 4.0 software. The GenAlEx 6.5 software was used for calculating the parameters of genetic diversity, the Wright fixation index, population differentiation, analysis of the hierarchical structure of variability (AMOVA), PCA analysis of the matrix of genetic distances, and a comparison of genetic and geographical distances using the Mantel test (Peakall and Smouse, 2006).

RESULTS

According to the identification keys, *R. aureum* is an evergreen shrub with creeping stems 20–50 cm tall (rarely higher); the wintering leaves are oblong- or broadly elliptical, obovate, wedge-shaped narrowed to the base, with the edge wrapped down, leathery, dark green and shiny above, somewhat paler beneath. The leaves are 1.5–8 cm long and 0.8–2.5 cm wide. The flowers are collected in 3–5 (8) in umbellate inflorescences; pedicels are reddish-fluffy (Fig. 1). The corolla is light yellow, wide bell-shaped, the calyx lobes are barely noticeable; the capsule is felty–rusty (Poyarkova, 1952; Aleksandrova, 1975; *Opredelitel' rastenii*..., 1979).

As a result of the study, it was found that variability of most of the vegetative characters in populations of golden rhododendron is medium and high (Table 2). Plant sizes are highly variable within populations (the coefficient of individual variability of the height and width of the shrub is 20–46% and 28–59%, respectively), as well as the length of the leafy part and the degree of leafiness of shoots (the coefficient of variability within populations varies within 40–75% and 34–71%, respectively). The variability of individuals by the length of the shoot within populations varies from 27 to 67%. The leaf characters are less variable: the coefficient of variation of the length and width of the leaf and the length of the petiole ranges from 9 to 23%. It should be noted that, among the relative characters of the leaf in *R. aureum,* the coefficient of its shape is the least variable (7–14%); in some populations, the variability of the relative length of the petiole is comparable with the variability of the absolute characteristics of the leaf (10–21%). The leaf life span, which is a taxonomically and ecologically important character for *Rhododendron dahuricum* L. and *Rhododendron ledebourii* Pojark. (Tikhonova, 2019), varied within close limits (9–28%) in *R. aureum*.

Fig. 1. Rhododendron aureum.

A comparison of populations by individual morphological traits showed that the shrub height of the population from Kamchatka (F = 2.82–7.05; p = 0.004–0.00002) and one population from the Western Sayan

Table 2. Average population values and individual limits of variability of some morphological traits of golden rhododendron

Populations	Shrub height, cm	Leaf length, mm	Number of leaves on the shoot, pcs	Relative length of the petiole	Leaf life span, years
Au 1	35 ± 2.42 / 15–59	37.5 ± 0.69 / 12–65	8.6 ± 0.27 / 1–15	0.27 ± 0.009 / 0.02–0.48	2.17 ± 0.06 / 2–3
Au 2	16.8 ± 1.18 / 12–32	36 ± 1.32 / 12–67	9.2 ± 0.48 / 4–18	0.22 ± 0.004 / 0.13–0.38	2.3 ± 0.08 / 1–3
Au 3	27.1 ± 1.45 / 17–48	34.4 ± 1.45 / 12–73	12.3 ± 0.75 / 5–27	0.26 ± 0.006 / 0.14–0.56	2.76 ± 0.061 / 2–3
Au 4	35.7 ± 1.56 / 19–53	44.3 ± 1.38 / 19–76	9 ± 0.7 / 4–18	0.21 ± 0.013 / 0.11–0.32	2.62 ± 0.194 / 1–4
Au 5	37.5 ± 1.32 / 24–68	56.1 ± 1.42 / 25–87	13.8 ± 0.52 / 7–31	0.23 ± 0.005 / 0.14–0.42	2.68 ± 0.083 / 1–4
Au 6	29 ± 1.08 / 20–59	48.8 ± 1.53 / 24–86	12.2 ± 0.53 / 5–21	0.21 ± 0.005 / 0.12–0.35	3.34 ± 0.11 / 2–5
Au 7	30.1 ± 2.51 / 15–62	43.1 ± 1.35 / 17–69	9.4 ± 0.61 / 3–18	0.26 ± 0.005 / 0.07–0.5	2.53 ± 0.093 / 1–4
Au 8	33.8 ± 2.44 / 15–76	35.4 ± 0.98 / 14–73	7.2 ± 0.34 / 3–20	0.27 ± 0.006 / 0.17–0.41	2.11 ± 0.065 / 1–3

Xav ± m is in the numerator, and individual limits are in the denominator. See Table 1 for designations of populations.

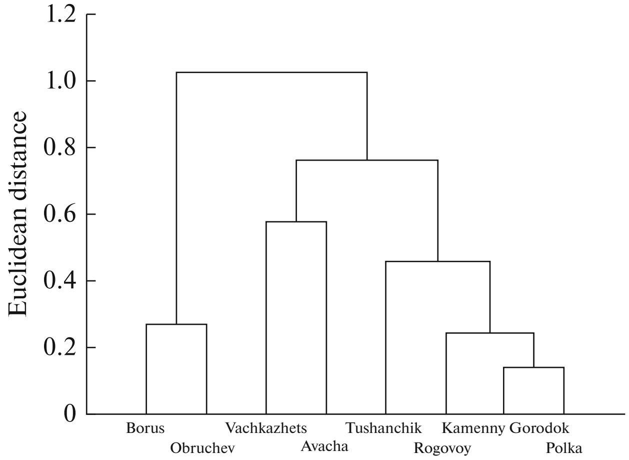

Fig. 2. Dendrogram of the similarity of golden rhododendron populations.

(Mount Polka) (F = 4.02–6.26; p = 0.01–0.00007) significantly differed from the other populations. All populations of *R. aureum* were differentiated in terms of the leaf life span character with a high significance level (F = 2.16–7.11; p = 0.03–0.00001).

In addition, two populations, from the Western Sayan (Mount Polka) and Kamchatka (Mount Vachkazhets), differed from all other populations (F = 2.11–4.16; p = 0.05–0.0003) by the greater relative length of the leaf petiole (Table 2).

The cluster analysis of variability of vegetative characters of golden rhododendron showed a clear division of populations into three clusters: the first and second clusters are separated at a Euclidean distance of 0.78; the first included the four most closely located populations from the Western Sayan (Mount Polka, Mount Rogovoy, Mount Tushkanchik, and Kamenny Gorodok) and the second cluster is formed by two populations from Kamchatka (Fig. 2). The third, the most remote cluster (at a Euclidean distance of 1.12), included populations of golden rhododendron from Obruchev ridge and Borus ridge (in the western part of the Western Sayan).

To clarify the results of cluster analysis, a discriminant analysis was carried out, which makes it possible to identify several discriminating (separating) functions in the variability of a set of characters. It is quite successfully used by botanists in taxonomy (Gasheva, 2006).

As is seen from Table 3, all 12 morphological traits of plants of *R. aureum* significantly participate in the differentiation of populations (F = 2.34–14.14, p < 0.02–0.00000). The total size of the analyzed sample was 223 plants. A large number (6) of significant canonical roots, together explaining 89% of the variability, indicates the effect of many factors on the morphological traits of the compared populations of the species. According to the coefficients for canonical roots (functions), the most important in the differentiation of populations are as follows: root 1, relative coefficients of leaf shape and the number of leaves on the shoot and their lifespan; root 2, absolute leaf size, shoot length, and length of the leafy part of the shoot and other characters (except for the size of the shrub); root 3, absolute and relative length of the petiole and the lifespan of the leaves; root 4, number of leaves on the shoot, shrub width, and the lifespan of the leaves; root 5, shrub height and lifespan of the leaves; and root 6, number of leaves on the shoot, absolute and relative lengths of the petiole, length of the leafy part of the shoot, and lifespan of the leaves. You can see that some characters are involved in several canonical roots and are most correlated with others; they are the life span of the leaves (6 roots), the number of leaves (4 roots), the absolute and relative lengths of the petiole (3–4 roots), the length of the leafy part of the shoot (3 roots), and the shrub size (2 roots).

The second part of Table 3 shows which canonical functions are most significant in the division of particular populations. To visualize the distribution of population samples, a scatter diagram of individuals was constructed on the plane of the first two canonical roots, together explaining 64.7% of the variance of characters (Fig. 3). At the same time, when all the characters were included in the analysis, we got a more distinct division of populations than for several of the most important, from our point of view, diagnostic features. The point clouds were clearly divided into three geographically defined groups of populations. Samples from Kamchatka are differentiated by the first canonical root. The other two groups are separated by the second canonical root: Ergaki ridge and Kulumys ridge and Borus ridge and Obruchev ridge.

Table 4 presents the main indices of genetic variability of populations. In the studied populations of *R. aureum*, rather high values of observed (H_o) and expected (H_e) heterozygosity were found. The Wright fixation index (F) shows the absence of a significant effect of inbreeding on the reproduction of populations. Due to the fact that *R. aureum* reproduces and spreads vegetatively well, the table presents an index of the number of different multilocular genotypes in each sample (N_g). In all populations, the studied loci showed themselves to be highly polymorphic: the proportion of nonrepeatable genotypes is 80–100%. The average values of the main indices for all populations are the average number of alleles per locus N_A = 3.81 and the effective number of alleles per locus N_E = 2.63, and the observed H_o and expected H_e heterozygosity are 0.54. A similar heterozygosity level is also observed in a number of other rhododendron species (Tan et al., 2009; Wang et al., 2013), as well as in endemic populations of *R. aureum* in China, Japan, and Sakhalin (Li et al., 2011; Liu et al., 2012).

According to the results of the hierarchical analysis of molecular variance (AMOVA), most of the genetic variability (62%) of nuclear microsatellite loci is con-

Table 3. Coefficients of characters for canonical variables and of populations for canonical roots

Characters	Canonical roots						F	p
	root 1	root 2	root 3	root 4	root 5	root 6		
Number of leaves	–0.32	0.27	–0.21	0.55	0.06	–0.41	14.14	0
Leaf length	–0.13	0.78	–0.14	0.16	0.07	–0.15	9.45	0
Leaf width	0.27	0.66	0.05	0.24	0.12	–0.15	8.86	0
Petiole length	0.17	0.55	–0.38	0.18	0.02	–0.5	4.52	0.0001
Relative leaf width	0.6	–0.29	0.23	0.16	0.06	–0.25	8.16	0
Relative petiole length	0.37	–0.27	–0.34	0.07	–0.18	–0.35	3.37	0.002
Deciduousness	0.03	–0.27	–0.1	0.02	0.1	0.05	3.39	0.002
Length of leafy part	–0.13	0.42	0.1	0.31	–0.13	–0.29	2.34	0.02
Leaf life span	–0.27	0.27	0.27	0.56	–0.38	–0.27	8.07	0
Length of annual shoot	–0.007	0.38	0.06	0.1	0.08	–0.21	2.6	0.01
Shrub height	0.1	0.1	–0.27	0.12	–0.48	–0.08	6.73	0
Shrub width	0.09	–0.31	–0.15	0.58	–0.07	0.15	9.85	0
Chi-square	90.3	63.6	40.0	24.3	13.5	62.6	–	–
p	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	–	–
Populations	Coefficients for canonical roots							
Polka	0.39	–0.7	–1.16	–1.23	–0.91	–0.38		
Rogovoy	–1.78	–1.1	0.65	–1.01	0.85	0.15		
Tushkanchik	–1.12	–2.18	–0.43	1.34	–0.02	–0.23		
Kamenny Gorodok	–0.14	0.67	1.4	–0.54	0.03	0.41		
Obruchev	–1.42	1.44	1.17	0.44	–0.94	0.1		
Borus	–0.71	2.28	–1.69	0.26	0.56	0.08		
Avacha	2.25	0.59	0.94	0.18	0.47	–0.76		
Vachkazhets	2.47	–0.7	–0.18	0.23	–0.07	0.85		

F is the Fisher criterion; p is the significance.

Table 4. Indices of the genetic diversity of microsatellite loci in samples of *R. aureum*

Populations	N	N_g	N_a	$N_{r(10)}$	N_p	N_e	P_t	H_o	H_e	F
Polka	10	10	3.22	2.79	1	2.23	88.9	0.45	0.46	0.003
Tushkanchik	12	12	3.56	2.86	0	2.35	88.9	0.45	0.48	0.07
Kamenny Gorodok	10	10	3.17	2.8	0	2.27	94.4	0.49	0.51	0.014
Obruchev	14	11	3.61	2.79	1	2.08	94.4	0.45	0.43	–0.03
Avacha	10	10	4.89	3.99	1	3.49	100	0.71	0.67	–0.06
Vachkazhets	7	6	4.44	4.16	2	3.33	100	0.69	0.67	–0.05
On average	10.5 ± 0.18	9.83 ± 0.231	3.81 ± 0.140	3.23 ± 0.165	0.83 ± 0.041	2.63 ± 0.102	94.4 ± 1.71	0.54 ± 0.024	0.54 ± 0.021	0.009 ± 0.025

N is the sample size, N_g is the number of individuals with different genotypes, N_a is the average number of alleles per locus, $N_{r(10)}$ is the average number alleles averaged per a sample of 10 individuals, N_p is the number of unique alleles, N_e is the effective number of alleles per locus, P_t is the proportion of polymorphic loci, H_o the observed heterozygosity, H_e is the expected heterozygosity, and F is the Wright fixation index.

centrated within populations; the differences between the three geographical groups of populations (Western Sayan, Eastern Sayan, Kamchatka) account for 34% of the detected variability. According to the Mantel test (Mantel, 1976), the genetic distance between populations is significantly related to the geographical distance between them: $r = 0.959$ and $p = 0.013$ ($r = 0.684$ and $p = 0.045$, excluding Kamchatka populations).

Genetic distances between populations from Kamchatka and the other populations range within F_{ST} = 0.181–0.223 (D_{Nei} varies from 1.246 to 2.349) and, between populations of Western and Eastern Sayan, F_{ST} = 0.077–0.104 (D_{Nei} varies from 0.201 to 0.534). The F_{ST} distances between populations within regions were 0.025–0.050 (D_{Nei} varies from 0.054 to 0.269).

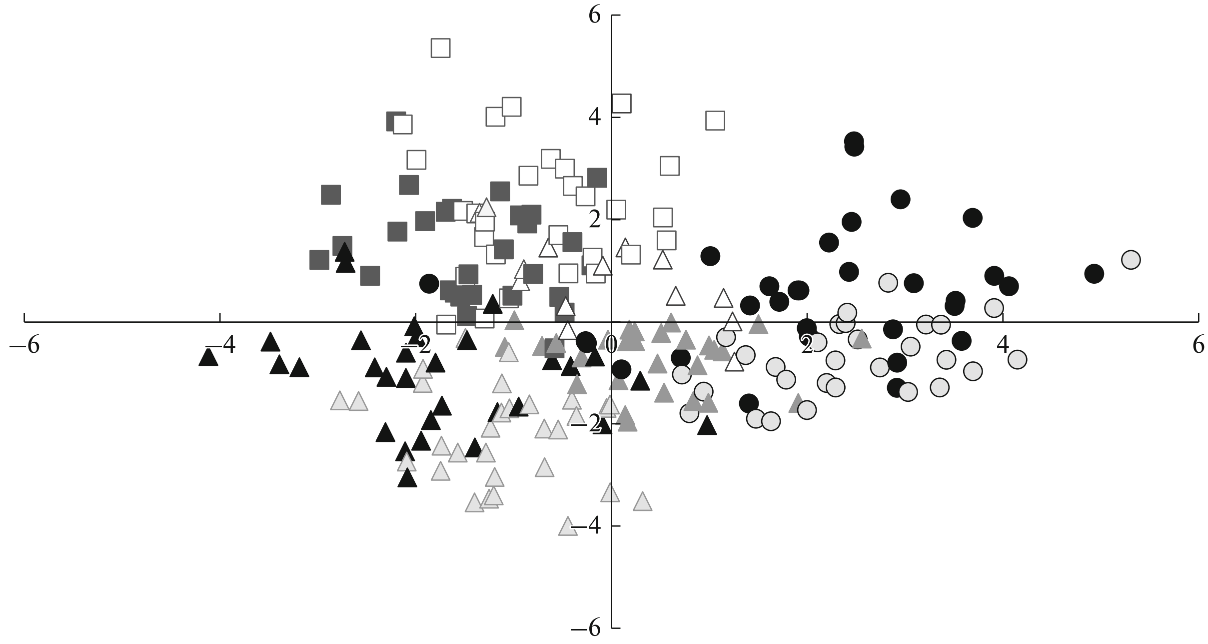

Fig. 3. Scatter diagram. ▵ Mount Polka, ▲ Mount Rogovoy, ▵ Mount Tushkanchik, △ Kamenny Gorodok, □ Borus Ridge, ■ Obruchev Ridge, ● Mount Vachkazhets, and ● Avacha Volcano.

Based on the Nei genetic distances (D_{Nei}), the population structure of the species in the studied part of the range was analyzed by the method of principal coordinates. As can be seen from Fig. 4, the samples from Kamchatka on the plane of the first two principal main coordinates are significantly removed from the rest of the populations of golden rhododendron, and the populations from the Western Sayan (unfortunately, the sample from Borus ridge was not included in the genetic analysis) have a low level of differences; there is a tendency to separate samples from the Eastern Sayan and Obruchev ridge (Tuva). The proportion of the first coordinate is 37% of the variability; that of the second one is 18%.

DISCUSSION

As follows from the above data, the shrub height and the life span of the leaves are the most significant morphological traits in the differentiation of geographically remote populations of *R. aureum*. According to the shrub height, the populations from Kamchatka and one population from the Western Sayan (Mount Polka) differed significantly from the other populations. Moreover, compared to other populations of the Western Sayan, this population grows in the most severe conditions of the mountain tundra on the plateau of Kulumys ridge, where strong winds blow and a low snow cover is formed in winter. All populations of golden rhododendron were differentiated with a high level of confidence according to the leaf life span. Thus, this study confirms the importance of this character in the differentiation of populations and, accordingly, the conditions of their growth not only for *R. ledebourii* (Tikhonova, 2019), but also for *R. aureum,* although the latter winters completely under snow and is a nanophanerophyte, which directly affects the degree of deciduousness (evergreen) plants. Based on the external appearance of *R. aureum,* the features of the leaf structure, and the characteristics of habitats, this is a more heat- and moisture-loving species compared to *R. ledebourii*.

According to the results of a discriminant analysis of all morphological traits, it can be seen that the populations from Borus ridge (Western Sayan) and Obruchev ridge (Eastern Sayan) remote from each other are closer to each other than to other populations of the Western Sayan, possibly due to their proximity to the main waterway (*the Biy-Khem River and Yenisey River*). In general, the results of discriminant analysis complement and specify the characteristics of the population differentiation obtained using the cluster analysis, increasing the values of distances (Mahalanobis) for populations from Kamchatka and confirming the isolation of two groups of populations in the mountains of Southern Siberia.

Thus, the populations from Kamchatka are well differentiated from the populations of the mountains of Southern Siberia by morphological traits, but the differentiation between the populations of the Western and Eastern Sayan is not so distinct. The genetic analysis revealed a clearer differentiation even within the less differentiated Altai-Sayan part of the species range, showing a statistically significant genetic spatial

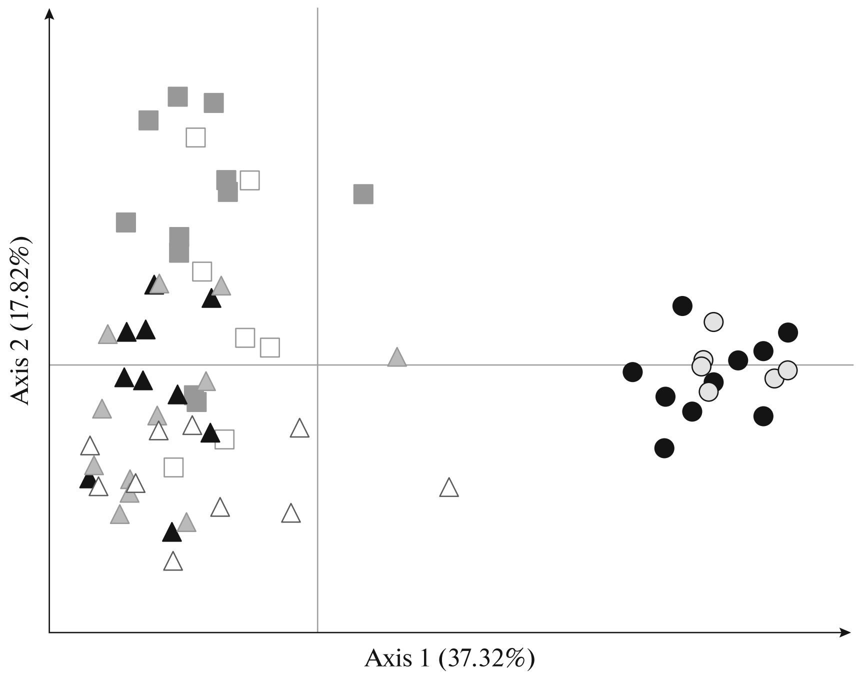

Fig. 4. Ordination of golden rhododendron populations based on genetic distances. ▲ Mount Polka, △ Mount Tushkanchik, △ Kamenny Gorodok, □ Eastern Sayan, ■ Mount Obruchev, ● Mount Vachkazhets, and ● Avacha volcano.

structure. Consequently, the above described population structure of *R. aureum* is confirmed using different research methods.

In addition, in the above results of the genetic analysis, it is necessary to pay attention to the critically low values of the number of migrants per generation in populations (*Nm*): it is 1.01 for all loci and varies from 0.33 to 2.64 in different loci. As is known, the values of $Nm \leq 1$ indicate the absence of gene exchange between populations (Hedrick, 2003). This is also confirmed by rather high inbreeding coefficients relative to the species (F_{IT}), equal on average to 0.238 (0.03–0.40). Low FIS values (0.004) at the same time indicate a sufficiently intensive gene flow within populations and the relative stability of the genetic organization of the species to existence in the conditions of prolonged isolation of populations separated by natural barriers, as well as limited flight capabilities of pollinating insects. Apparently, the threshold values of *Nm* should be species-specific and probably lower for some plant species. In our opinion, this index for species similar to *R. aureum* in their bio-ecological features and biogeography can only be used together with other indices such as the Wright fixation index *F*, H_o, N_A, and N_E and estimates of deviations from the Hardy–Weinberg equilibrium.

CONCLUSIONS

(1) High levels of morphological and genetic variability of individuals within populations were obtained for *R. aureum,* which is consistent with the indices of morphological and genetic variability of other rhododendron species.

(2) The results of the study of the variability of morphological traits of *R. aureum* generally coincide with the results of the analysis of the genetic differentiation of the same populations of golden rhododendron by 18 nuclear microsatellite (nSSR) markers. Consequently, not only genetic markers, but also some morphological traits are promising for large-scale biogeographic studies of this species, such as plant height and leaf lifespan. A discriminant analysis of a set of characters is more informative for this purpose. In this case, a large number of significant canonical roots obtained as a result of multidimensional discriminant analysis, together explaining 89% of the variability of traits, confirms the effect of many factors on the morphological traits of the species populations. We used only vegetative organs of plants for comparison; however, it can be assumed that generative characters can be used to obtain an even more pronounced spatial structure of populations of the species.

(3) According to the results of morphological and genetic analysis, the populations of golden rhododendron are divided into three geographically defined groups: the populations of Kamchatka (1), the populations of the Western Sayan (2), and the populations of the Eastern (Obruchev ridge) and Western Sayan (Borus ridge) (3). Significant genetic distances between geographically remote groups of populations are confirmed, according to the Mantel test, by a significant relationship with the geographical distance between them. The analysis of generalized genetic

indices makes it possible to conclude about an intensive gene flow within populations, but a weak gene flow between most populations, which is explained by their isolation by mountain ranges and pollination by insects.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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