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PLANT GENETICS

Genetic Variability and Differentiation in the Larch Populations within the Range of *Larix olgensis* A. Henry in Primorye

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Abstract—The level of within- and among-population variation of larch inhabiting the range of *Larix olgensis* A. Henry in Primorye was estimated on the basis of 440 RAPD loci identified by means of 12 random primers. In ten populations examined, the proportion of polymorphic loci was 35–60%, the average expected heterozygosity varied from 0.1340 to 0.2169, and the average gene flow estimate was 1.38. According to Fisher's test for heterogeneity, the pairwise differences of the fragment frequencies between the populations were statistically significant. The subdivision index G_{ST} = 0.2663 indicated that the interpopulation variation component accounted for approximately 27% of the total variation. Coefficients of Nei's genetic distance between the populations varied from 0.0137 to 0.0934. Most of the samples with high support clustered according to the geographic positions relative to one another within the range. These results suggest that the populations examined are characterized by high genetic variation, like the larch populations of Siberia and the Russian Far East studied earlier, but, in contrast to the latter, exhibit higher among-population variability.

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INTRODUCTION

According to various literature sources, several larch species—*Larix lubarskii* Sukacz., *L. komarovii* Kolesn., *L. amurensis* Kolesn., *L. ochotensis* Kolesn., *L. maritime* Sukacz., *L. olgensis* A. Henry [1–3] occur on the territory of Primorye. According to a number of authors, of all these species, only Olga Bay larch *L. olgensis* does not have a hybrid origin, whereas the remaining forms may be assigned to a complex that resulted from introgressive hybridization [4, 5]. Hybridization leads to high variability of morphological traits and to controversial views in taxonomy of larches from Primorye.

Larix olgensis is among the most ancient larches. This species is a Pliocene relict [6] listed in the Red Book of the Russian Federation [7]. In the Russian Far East, it occupies a small area in the southeastern Primorye stretching along the coast of the Sea of Japan and eastern slopes of Sikhote-Alin' [1]. As the competitive ability of *L. olgensis* is lower than that of other forest species, including hybrid larches, the former occurs in small isolated patches [1], which creates the risk of its extinction.

Since *L. olgensis* is a putative parent of a number of hybrid complexes of larches from the south of the Russian Far East, which arose in Pleistocene–Holocene [8], it seems important to study genetic variation and the population structure of this species using molecular DNA markers, which permit, in contrast to allozyme analysis, to examine variation of both coding and noncoding DNA regions. One of such methods used in population genetics of conifers is DNA amplification by primers with random nucleotide sequences (random amplified polymorphic DNA, RAPD) [9–15]. Using the RAPD method, genetic variability of larches from various geographic regions of Siberia and the Russian Far East and their genetic relationships were evaluated [9, 10].

The aim of this study was studying genetic variability and establishing genetic relationships among the natural larch populations within the range of *L. olgensis* in Primorye based on RAPD marker analysis.

MATERIALS AND METHODS

In our study, we used needles of nine to twelve trees from each of the ten samples examined (Fig. 1). The samples are described in Table 1. Genomic DNA was isolated from 300–500 mg of fresh needles following the protocol from [11] with slight modifications.

Polymerase chain reaction was run in a thermal cycler UNO II 48 (Biometra, Germany) with decamer random primers (Operon Technologies, United States; SibEnzyme, Novosibirsk), using the reaction mixture and temperature conditions described in [16]. The control probe contained the total amplification mixture without DNA. Each reaction was run in two to four replicates. The amplification products were fractionated by electrophoresis in 1.4% agarose gel in the presence of ethidium bromide and photographed in UV light. To assess size of the fragments (amplicons), *Eco*RI + *Hin*dIII restriction fragments of phage lambda DNA (Fermentas, Lithuania) were used as molecular mass markers.

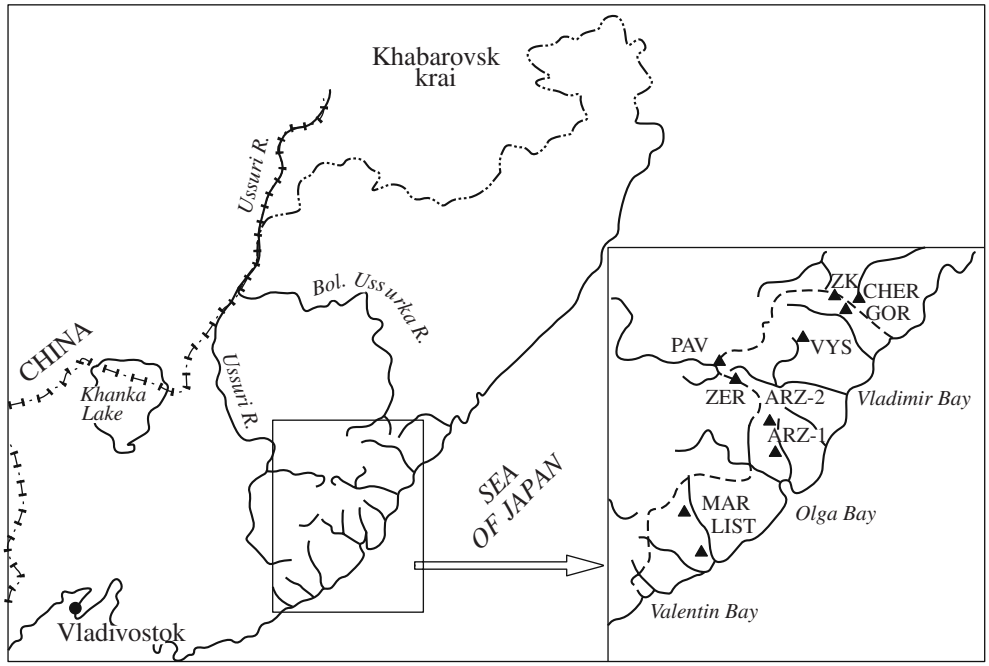

Fig. 1. Sampling localities of larch within the area of *L. olgensis* in Primorye. The species range was described by Gukov [1].

Only distinct and reproducible fragments were scored in electrophoregram analysis. Different band intensity in amplicons of the same size was not taken into account.

The RAPD patterns of the samples examined were represented as binary matrices, in which the presence and the absence of the identical fragments in the pattern was denoted 1 and 0, respectively.

To calculate the proportion of polymorphic loci at 95% (P_{95}) and 99% (P_{99}) levels, mean expected heterozygosity H_e, estimate population differentiation by means of Fisher's test and Nei's genetic distances D_N, and construct dendrograms of genetic relationships between the samples on the basis of matrices of D_N values by means of pair-group cluster analysis (UPGMA), the TFPGA software package was used [17]. The mean number of alleles per locus *A,* mean sample gene diver-

Table 1. Larch samples studied

Sample	Geographic location	Coordinates		Number of trees in the sample	Species composition of the stand*
		N	E		
ARZ-1	Middle flow of Arzamazovka R.	43°59′810″	135°10′563″	9	4Ca 3Pm 1Ph 2 Lo
ARZ-2	Source of Arzamazovka R.	44°02′965″	135°11′648″	11	6Lo 1Bp 1Qm 1Be
MAR	Middle flow of Margaritovka R.	43°35′901″	134°35′999″	10	3Lo 3Ps 2Bp 2Ah
ZK	Zmeinyi Klyuch (tributary of Bol'shaya Ussurka R.)	44°42′161″	135°39′076″	11	8Lo 1Pa 1Bp
ZER	Source of Zerkal'naya R.	44°16′930″	134°53′591″	10	7Lo 1Bp 1Pk 1Pa
VYS	Source of Vysokogorskaya R.	44°29′126″	135°23′506″	11	6Lo 2Pk 1Pa 1Bp + Bd
PAV	Upper Pavlovka R. (tributary of Ussuri R.)	44°17′340″	134°52′052″	10	5Lo 5Bp
LIST	Middle flow of Listvennaya R. (tributary of Margaritovka R.)	43°26′450″	134°39′450″	12	6Lo 3Bp 1Am + Ul
GOR	Gorbusha R. (tributary of Rudnaya R.)	44°39′514″	135°39′505″	9	7Lo 2Bp 1Pt
CHER	Source of Cheremukhovaya R. (tributary of Dzhigitovka R.)	44°41′692″	135°45′134″	9	7Lo 2Bp 1Pa

* Ca, *Chosenia arbutifolia*; Pm, *Populus maximoviczii*; Ph, *Phellodendron amurense*; Lo, *Larix olgensis*; Bp, *Betula platyphylla*; Qm, *Quercus mongolica*; Be, *Betula ermanii*; Bd, *Betula dahurica*; Ps, *Pinus syvestris* (culture); Ah, *Alnus hirsute*; Pa, *Picea ajanensis*; Pk, *Pinus koraiensis*; Am, *Acer mono*; Ul, *Ulmus laciniata*; Pt, *Populus tremola*.

Table 2. Primers used in this study

Primer	Nucleotide sequence (5' > 3')	LIST	MAR	ARZ-1	ARZ-2	ZER	PAV	VYS	RUD	CHER	ZK	Total number of loci scored
OPA-01	CAGGCCCTTC	14/22	12/15	11/14	13/18	7/14	11/17	9/19	6/10	7/12	10/16	27
OPA-04	AATCGGGCTG	38/39	24/25	32/33	33/34	25/27	21/22	24/28	31/32	39/40	31/32	60
OPA-07	GAAACGGGTG	40/42	10/11	31/31	34/36	26/28	29/30	28/28	31/33	30/32	24/27	59
OPA-09	GGGTAACGCC	19/22	13/15	16/19	17/19	15/19	17/19	16/18	13/15	20/20	13/17	37
OPA-11	CAATCGCCGT	22/26	20/21	19/20	17/18	17/19	21/23	19/21	28/30	27/29	20/22	42
OPA-12	TCGGCGATAG	15/17	20/22	11/15	9/13	15/18	18/21	17/20	13/16	17/19	10/13	30
OPA-19	CAAACGTCGG	23/23	9/12	14/14	14/15	18/20	15/17	18/19	13/15	11/13	21/23	31
OPA-20	GTTGCGATCC	27/29	17/20	18/20	20/22	22/24	24/26	15/18	21/21	21/21	17/21	34
OPB-07	GGTGACGCAG	28/28	20/22	26/27	28/30	20/24	23/26	13/18	31/31	26/26	17/18	43
OPB-10	CTGCTGGGAC	19/21	13/17	12/15	14/18	11/16	13/17	12/16	11/13	15/17	15/19	25
OPB-11	GTAGACCCGT	16/17	8/10	9/10	10/12	14/16	13/14	12/15	15/17	15/18	8/9	23
OPC-02	GTGAGGCGTC	17/20	9/11	12/14	13/15	16/18	15/18	16/18	14/17	14/18	16/18	29
Total		278/306	175/201	211/232	222/250	206/243	220/250	199/238	227/250	242/265	202/235	440

Note: Numerator, the number of polymorphic loci; denominator, the number of loci scored for each sample.

sity H_S, total gene diversity in the total sample H_T, population subdivision index G_{ST}, gene flow Nm, mean intragroup similarity S_{pop} were computed using the POPGENE software package [18]. The dendrogram of genetic relationships between individual representatives with bootstrap support of branching order (1000 replications) was constructed using the TREECON software package [19].

RESULTS AND DISCUSSION

RAPD analysis of the samples using 12 random primers effective in PCR with larch DNA [20] yielded 440 amplicons, 433 of which (98%) were polymorphic. Seven monomorphic loci were common for all samples. The number of RAPD fragments scored varied from 23 to 60 depending on the primer (Table 2). The samples examined differed in the frequencies of RAPD loci; some amplicons were sample-specific.

Main parameters of genetic variation for each of the samples examined are listed in Table 3. The proportion of polymorphic loci at the 95% criterion in individual samples varied from 35 to 60% and in six samples coincides with the proportion of polymorphic loci at the 99% criterion. However, in four samples (ARZ-2, LIST, VYS, ZK), the P_{99} value increased, which may be explained by the presence of rare loci not taken into account in P_{95} calculation in these samples. The LIST sample exhibited the highest values of A, H_e, P_{95}, and P_{99}. The MAR population, which is closest to population LIST (Fig. 1), showed the lowest values of A, H_e, and P_{95}. The mean intragroup similarity, which measures genetic similarity between the trees in a sample, varied from 0.5618 to 0.6768 (Table 3). Samples CHER and GOR, located at the northern border of the area examined, showed the maximum within-sample differentiation; the genetic distances between trees in these samples were on average 44%. In all of the populations studied, S_{pop} estimates were lower than those in Siberian and Far Eastern larch species [9], which apparently reflects complex microevolutionary processes in the Primorye populations.

In general, the estimates of genetic variability of larches inhabiting the *L. olgensis* range, presented in Table 3, are comparable to those inferred from RAPD markers for populations of *L. sibirica* (P_{95} = 45%, A = 1.54, H_e = 0.1698) and *L. gmelinii* (P_{95} = 32%, A = 1.32, H_e = 0.1373) [21], and for a number of larch populations from Primorye [10].

Fisher's test showed that differences in the fragment number between most populations were significant. However, in four pairs (ARZ-1 and ARZ-2, PAV and ZER, VYS and ZER, GOR and CHER), the differences were not significant, which may be explained by small geographic distances between the members of each pair.

The mean sample gene diversity, total gene diversity in the total sample, and the total diversity among the larch samples were on average 0.1500 ± 0.0101, 0.2044 ± 0.0205, and 0.0544, respectively. Hence, the within-population variation component accounts for most of the gene diversity, which is generally character-

Table 3. Main parameters of genetic variability in the samples

Sample	A	H_e	P_{95}, %	P_{99}, %	S_{pop}
ARZ-1	1.4841	0.1684	48.41	48.41	0.5961
ARZ-2	1.5068	0.1626	41.59	50.68	0.5998
MAR	1.3955	0.1231	39.55	39.55	0.6321
ZK	1.4614	0.1340	34.55	46.14	0.6435
ZER	1.4727	0.1573	47.27	47.27	0.6768
VYS	1.4591	0.1505	37.73	45.91	0.6597
PAV	1.5023	0.1593	50.23	50.23	0.6287
LIST	1.6523	0.2169	59.77	65.23	0.6040
GOR	1.5227	0.1733	52.27	52.27	0.5731
CHER	1.5614	0.1751	56.14	56.14	0.5618

Note: A, the mean number of alleles per locus; H_e, mean expected heterozygosity at all loci; P_{95}, the proportion of polymorphic loci at the 95% criterion; P_{99}, the proportion of polymorphic loci at the 99% criterion; S_{pop}, mean intragroup similarity.

istic of conifers [9, 10, 22–24]. The G_{ST} value for the samples studied was 0.2663, which shows that about 27% of the variation is explained by the interpopulation component. Subdivision estimates inferred from RAPD data on other Primorye larch populations were as high (G_{ST} = 27.69%) [10], while in populations of *L. sibirica* and *L. gmelinii* this estimate was 11% for each of the species [9, 10, 21]. In their review, Nybom and Bartish [25] have shown that, in spite of differences in the absolute values of the intrapopulation variation estimates, the G_{ST} values based on allozyme analysis and RAPD, were close, which permits to compare them. For instance, interpopulation differences obtained with allozyme markers were 8.2% in *L. sibirica*, 2.0–3.8% in *L. laricina*, 4.0–5.1% in *L. decidua,* 8.6% in *L. occidentalis* [26], and 3.8% in *L. gmelinii* [27]. Based on their analysis of literature data, Krutovskii et al. [22] estimated the average G_{ST} value for 22 coniferous species equal to 0.059. Thus, the populations examined, which are characterized by high values of interpopulation differentiation (G_{ST} = 26.63%), are highly differentiated, which is probably explained by patchy distribution of larch on the examined area.

The mean gene flow between the populations, computed from the subdivision index, was 1.38 migrants per generation, which is lower than the corresponding estimates for *L. sibirica* and *L. gmelinii* (2.6 and 2.5, respectively) [28] and similar to the *Nm* value of 1.3057, which was estimated for populations of various larch species from Primorye [10].

Nei's genetic distances D_N between the populations examined are listed in Table 4. Differences in the distances between the populations are fairly high. The CHER–GOR pair was closest genetically (D_N = 0.0137); according to our data, this pair was also characterized by the highest gene flow value (*Nm* = 7.8). The most genetically distant were population pairs VYS–CHER (D_N = 0.0934) and ZK–GOR (D_N = 0.0876). The mean D_N value averaged over all samples was 0.0638, which is comparable with the mean genetic distance between Eurasian larch species based on allozyme data (D_N = 0.0590) [23]. For larch populations from Primorye that were studied earlier, the mean D_N was even higher (0.0809) [10].

From the genetic distances, a dendrogram reflecting the genetic relationships among the larch populations studied was constructed (Fig. 2). The samples grouped into two major clusters, the first of which included samples GOR and CHER, and the second, the remaining samples, which, in their turn, formed two large groups. One group consisted of the samples from the central part of the area examined (except ZK), the other, of the samples from the northwestern part of the area (except LIST). In general, all samples clustered pairwise with high bootstrap support, which is in agreement with their mutual positions within the area (Fig. 1).

The fact that samples GOR and CHER formed a separate cluster may be explained by their extreme northern position within the area, where, according to literature data, Ohkhotsk larch occurs [1]. Clustering of ZK with MAR is of interest. It would seem that the location of sample ZK near GOR and CHER implies their genetic similarity, but the former sample is actually positioned on another watershed where it is likely to be affected by Komarov larch [1]. The genetic exchange between the members of the GOR–CHER–ZK is low (gene flow 1.9), whereas *Nm* between GOR and CHER is 7.8 migrants per generation.

In general, our results suggest that the genetic diversity of the larch populations inhabiting different parts of the *L. olgensis* range in Primorye is rather high (P_{95} = 34.55–59.77%, A = 1.3955–1.6523, H_e = 0.1231–0.2169) and similar to that characterizing of other widespread larch species. However, in contrast to these species, the

Table 4. Nei's genetic distances between the samples studied

Sample	ARZ-1	ARZ-2	MAR	ZK	ZER	VYS	PAV	LIST	GOR
ARZ-2	0.0291								
MAR	0.0484	0.0546							
ZK	0.0591	0.0607	0.0442						
ZER	0.0557	0.0717	0.0810	0.0848					
VYS	0.0527	0.0675	0.0756	0.0853	0.0375				
PAV	0.0459	0.0629	0.0656	0.0772	0.0293	0.0451			
LIST	0.0559	0.0609	0.0689	0.0768	0.0618	0.0600	0.0583		
GOR	0.0539	0.0629	0.0838	0.0876	0.0717	0.0799	0.0541	0.0704	
CHER	0.0657	0.0669	0.0792	0.0848	0.0864	0.0934	0.0633	0.0765	0.0137

genetic differentiation of the samples examined is far higher: G_{ST} = 0.2663, mean D_N = 0.0638, Nm = 1.38, which is probably explained by their fragmented distribution caused by contrasting landscape and climate.

According to calculations by Krutovsky based on allozyme analysis [22], populations, races, subspecies, and species of conifers show genetic distances D_N of respectively 0.007–0.013, 0.029, 0.036, and 0.185. In particular, intraspecies coefficients of genetic distance were 0.008–0.025, while between Eurasian larch species they varied in the range of 0.007–0.171 [23]. According to RAPD data, the mean interpopulation distance for *L. sibirica* was 0.0353 and varied from 0.0361 to 0.1802 for different taxa of larches from Siberia and the Russian Far East [9]. Thus, in larches estimates of intra- and interspecies distances inferred from RAPD and allozyme data are close. Taking into account allozyme data [22], this suggests that most of the samples from the Olga Bay larch range have a rank higher than that of population. It may well be that the samples studied here do not belong to populations of Olga Bay larch, but to higher-rank taxa different from this species. In this connection, it seems interesting and promising to study population genetic parameters of the samples collected at the site of description of *L. olgensis* A. Henry near Olga Bay in Primorye.

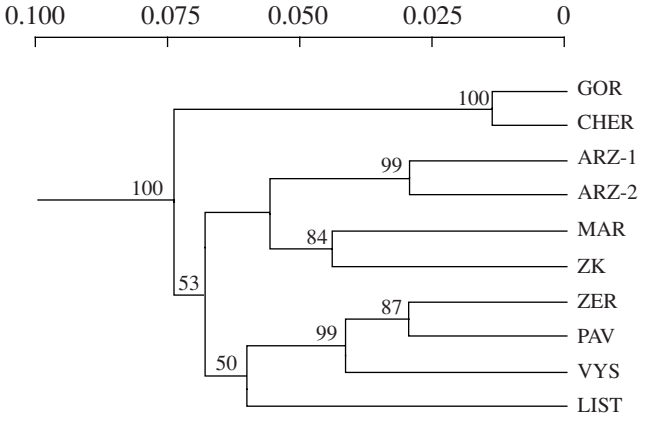

Fig. 2. UPGMA dendrogram of the genetic relationships among the samples. Numerals indicate cluster validity (bootstrap indices).

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