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POPULATION AND PHENETIC STRUCTURE OF LAUREL POPLAR *Populus laurifolia* Ledeb. IN THE TOM RIVER BASIN

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In the basin of Tom River (Russia) the distribution of laurel poplar *Populus laurifolia* Ledeb. populations is fragmentary due to its ecological requirements and to the anthropogenic transformation of the territory. Adaptability of *P. laurifolia* to well-aerated gravel-boulder alluvium results in its narrow ecological niche, confining it to grow mostly in the multi-stream areas of mountain rivers. Current distribution of poplar stands in the Tom River basin, their primary location near islands and tributary mouths are largely determined by human economic activity in the 20th century. At present the relative sustainability of these poplar stands under anthropogenic transformations in the region is ensured by their low accessibility. The natural dynamics of poplar stands is influenced by massive invasion of alien plant species into the indigenous floodplain plant communities. Spatial differentiation of *P. laurifolia* populations according to their composition takes place in the area. The grey-bark form with rounded wedge-shaped leaf blade base is common in the up-stream areas, while in the tributary basin and mid-stream areas the white-bark form with a heart-shaped leaf blade base is common as well. Combined analyses of quantitative and qualitative traits and phenotype frequencies also confirmed population differentiation according to their composition. The mid-stream laurel poplar stands display greater phenotype diversity and a higher proportion of inter-population differences in phenotype composition. The latter trait did not differ significantly among the up-stream populations with low differentiation. It was suggested that the current population structure in the Tom River basin area developed as a result of the original populations' fragmentation due to the combined effect of neotectonics, valley glaciation in the Kuznetsk Alatau Mountains and anthropogenic influence.

Keywords: *Populus, populations, morphological attributes, phenotypes, glaciation, refugium, Kemerovo Oblast, Russia.*

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INTRODUCTION

The most important components of floodplain plant communities are the species of poplars *Populus* L. genus, playing the leading role in primary succession and regulating streambed dynamics. To obtain valid estimates of the ecosystem functions and services of the region one needs to know the poplar population structure and sustainability. Also, poplar trees are of high economic importance due to their rapid growth, ecological flexibility and easy vegetative proliferation (Bakulin, 2005; Tsarev et al., 2016). However, the assortment of poplar species used in our economy, especially in Siberia with its poor natural dendroflora, does not meet current economic requirements. Increasing areas of disturbed land in need of recultivation and global climate changes make us intensify poplar coenoses and enhance their sustainability. The aim can be achieved by preserving their genetic resources and controlling the rational use of the plants. Therefore, the studies of phenotypic variability of poplar populations are indispensable for forest tree breeding and sustaining.

As it was shown earlier (DeWoody et al., 2015; Guet et al., 2015), leaf morphological characteristics together with chloroplast haplotypes play an important role in assessing historical differentiation of floodplain poplar species, since these characteristics do not correlate with contemporary climatic conditions and only slightly reflect adaptive differences. Morphological features only reflect the occurrence of potential refugium as well as species recolonization in Pleistocene and Holocene. Therefore, investigating phenotypic variability is an important tool for the study of current spatial differentiation of poplar populations.

In the Tom River floodplain along its up- and mid-stream sections, i. e. in the area we examined, the following poplar species grow: the black poplar *P. nigra* L., the laurel poplar *P. laurifolia* Ledeb., their natural hybrid *P.* × *jrtyschensis* C. Y. Yang and aspen *P. tremula* L. (Klimov, 2007). In the floodplain area below the city of Novokuznetsk one may find the white poplar *P. alba* L. and grey poplar *Populus* × *canescens* (Aiton) Sm. The Siberian poplar *P.* × *sibirica* G. V. Krylov et G. V. Grig. ex A. K. Skvortsov occasionally occurs near cities and settlements.

The laurel poplar is a mountain valley species, growing in the river floodplains in the Altay-Khangay-Sayan Mountain area (Maskaev, 1987; Bakulin, 2004). Systematically the species belongs to the *Tacamahaca* Mill. section, i. e. balsamic poplars (Eckenwalder, 1996; Poplars…, 2014).

Similarly to the poplar genus itself, the time and site of the group emergence remains unclear. According to some researchers (Collinson, 1992; Wang et al., 2014; Du et al., 2015; Liu et al., 2017), poplars emerged in Eocene in the North America, from where they inhabited Eurasia via intercontinental land bridges, existing then. At the same time, the investigation of numerous leaf fossils, found on the territory of the former Soviet Union and China, evidenced somewhat earlier emergence of the genus at the beginning of Paleocene (Ilinskaya, 2003; Iskopaemye tsvetkovye rasteniya…, 2005; Liang et al., 2016). The sites near the Amur River and the ones close to the southern areas are likely to be the areas where poplar genus emerged.

So far any fossilized laurel poplar residues have not been found. However, the most ancient poplar species in Asia *P. kamaevae* Iljinskaja sp. nov., known to have existed since low Paleocene, in its leaf morphology is very similar to the contemporary laurel-leaved poplars as laurel polar and densely leaved poplar *P. talassica* Kom. (Ilinskaya, 2003). The poplar of Iljinskaja *P. iljinskajae* Akhmet. sp. nov., dating back to the upper Eocene, is considered as a possible ancestor of laurel polar (Iskopaemye tsvetkovye rasteniya…, 2005). Yet other researchers believe that laurel poplar emerged in Neogene at the border between humid and arid locations in the Altay-Khangay-Sayan Mountain area.

At present, the area occupied by laurel polar is seriously fragmented. To a certain extent this fragmentation results from its ecological requirements and adaptation to floodplains in the mountainous regions. To a certain extent, due to that laurel poplar forests’ formation took place in early Neo-Pleistocene 500–600 thousand years ago and widely spread in mid Neo-Pleistocene (Maskaev, 1987), certain tectonic processes of alpine orogenesis might have facilitated a segregation of the area.

As our earlier studies in the Tom river basin showed, the distribution of laurel polar is also fragmentary. In the up-stream region from the mouth of the Balyksu River to the mouth of the Bol’shoy Kazyr River (Khakassiya) the species does not grow. More down the Tom River to the mouth of the Teba River (Kemerovo region) one can see sparse bush plants. On the islands and along the banks reproductively mature laurel poplar stands can be observed from the mouth of the Belsu River to the mouth of the Usa River, whereas further down the Tom River the poplar stands are strongly dominated by black poplar, and laurel polar trees, which are quite sparse. In the mid-stream area only one population on the gravel-boulder alluvium was found near Erunakovo settlement.

The laurel polar stands are also common in the basins of the right mountain tributaries of the Tom River, e. g. Verkhnyaya and Srednyaya Ters’ Rivers. The laurel poplar is predominating in the poplar stands of the area, reaching as high as 500 m above the sea level along the slopes of the Kuznetsk Alatau Mountains.

During the field studies carried out in 2015–2017 we examined various forms of laurel polar in the basin of the Tom River. We identified the tree habitus, bark colour, leaf blade shape, the hairiness of leaves and stems (Proshkin, Klimov, 2017*b*; Klimov, Proshkin, 2017*a*). The studies showed heterogeneity of form composition in the populations of the basin area. The grey-bark form with the rounded wedge-shaped base was found to be common in the up-stream area.

The white-bark form with the heart-shaped base of leaf blades can be observed beside the grey-bark poplar form in the mid-stream floodplains. In the poplar stands along the right tributaries the white form was found to dominate the population along the Verkhnyaya Ters' River (63.0 % of all the trees), and, albeit less abundant (33.0 %), it was found in the Karlyk River populations (Abashevo District). In the mid-stream Tom River area the form can be found in the Erunakovo population (17.0 %). The absence of the white-bark form in the upper Tom River basin enables us to regard it as a local phenotype, confirming spatial differentiation of laurel polar populations within the basin.

The aim of the present study was to identify the current structure of the laurel poplar populations in the basin of the Tom River. To reach the aim, we 1) revealed the degree of phenotypic diversity by analyzing endogenous, individual and inter-population variability of the trees, including qualitative traits (phenes); 2) studied tree form structure; and 3) considered in detail the causality of the observed spatial differentiation of the laurel poplar populations.

MATERIALS AND METHODS

The study was carried out in five laurel poplar natural populations in the Tom River floodplain and three natural populations in the Tom tributaries' floodplains, within southern part of Kemerovo Oblast, Russia (Fig. 1).

The population structure of the floodplain poplar species is known to be significantly influenced by the anthropogenic factor (Macaya-Sanz et al., 2012; Variability…, 2014; Proshkin, Klimov, 2017*c*). The studied region has been quite involved in economy, with the rivers experiencing much pressure in the 20th century. Therefore, we also discussed some issues of river use and estimated direct and indirect impact of anthropogenic activity on poplar populations.

To study the variability of morphological traits we collected herbarium material on each study site from 30 mature trees from the southern side mid-crown. From each individual tree 15 well developed non-damaged leaves were collected only from the middle part of the shorter branches (Proshkin, Klimov, 2017*d*). Overall 3600 leaves were sampled from 240 poplar trees.

The following morphological traits were recorded for each leaf.

The main traits: L – blade length, mm; D – maximal blade width, mm; P – petiole length, mm; A – the distance between the widest part of the leaf blade and leaf base, mm.

The derivative traits: P/L – ratio between petiole length and blade length; D/L – ratio between the maximal blade width and blade length; A/L – ratio between the distance from the widest part of the leaf blade to its base and blade length.

The main morphometric traits were measured using Zeiss Axio Vision software version 4.8.2 (ZEISS, 2018). Graphs and statistical analysis were made using Excel and IBM SPSS Statistics 23.0

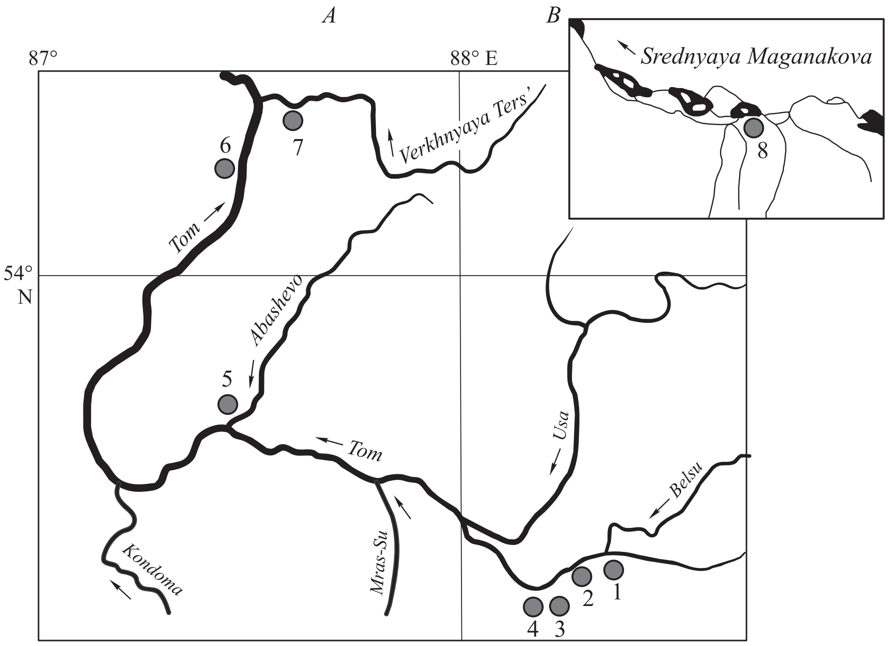

Fig. 1. Geographic location of the studied populations. *A* – the area of the up- and mid-stream Tom River basin; *B* – part of the Srednyaya Maganakova River basin. Poplar populations: 1 – Belsu; 2 – Studeny Ples; 3 – Vorony; 4 – Maizas; 5 – Karlyk; 6 – Erunakovo; 7 – Verkhnyaya Ters'; 8 – Srednyaya Maganakova.

software (IBM…, 2018). The variability values were estimated using the empirical scale proposed by S. A. Mamaev (1973).

To analyze qualitative values as morphological markers of the intraspecies structure we chose the characteristics of branches and leaves. For each individual tree studied we determined the branch morphotypes, as well as the shape of leaf blades, their top and base.

The laurel poplar branch morphotypes were determined by analyzing leaf and branch hairiness: *1Pl* – naked branches and leaf blades, petioles with scarce short hairs; *2Pl* – branches and leaves with scarce long hairs; *3Pl* – branches and leaves with dense short hairs (Klimov, Proshkin, 2017*b*).

Since terminology used by different researchers to describe leaf characteristics may often drastically differ, to describe morphology and determine leaf blade shape we applied the terms proposed by A. A. Fedorov et al. (1956), that were established according to *A*/*L* ratio. We used the following ranges: triangular (< 0.25), egg-shaped triangular (0.25–0.35), egg-shaped (0.35–0.45), elliptical (0.45–0.65) and reversed egg-shaped ones (> 0.65).

A combination of qualitative morphological traits was used to assign a certain phenotype to an individual tree.

The variability of the studied traits was analyzed statistically at three hierarchical levels of the obtained data array, i. e. individual tree (endogenous variability), study site (individual variability) and between study sites (inter-population variability). To describe the data sets we used arithmetical means ($\bar{x}$) and their standard errors (s. e. m.), maximal and minimal values, standard deviations (s. d.) and coefficients of variation (*CV*, %). We applied ANOVA to show if the differences in morphometric traits were statistically significant, with the threshold of $p < 0.001$ being a critical one (Glass, Stanley, 1976).

To estimate intra- and inter-population variability we applied hierarchical cluster analysis making use of Euclid distances as a measure of similarity and χ^2 criterion and integral indicators proposed by other researchers (Zhivotovskiy, 1991; Putenikhin et al., 2004; Boronnikova et al., 2009). Diversity of qualitative traits, satisfying criteria for «phene», was analyzed according to the method recommended by Vidyakin (2004).

Any study of a species population structure implies discriminating between local populations (Timofeev-Resovsky et al., 1973; Yablokov, 1987; Semerikov, 1992). The most detailed method to discriminate between areal groupings of woody plants using the morphological and phenotypical markers was proposed by A. I. Vidyakin et al. (2014, 2015). However, since the studies of floodplain poplar species have not been performed, we regard any representative set that differs significantly from its neighbour populations as a population.

RESULTS AND DISCUSSION

Anthropogenic transformation of laurel poplar stands. The studied area of the Tom River and some of its tributaries' basins was seriously disturbed in the 20th century by the economic activity. In particular, a strong impact can be seen in the Kondoma River valley, where poplar stands were practically destroyed (Proshkin, Klimov, 2017*a*). The right tributaries' basins were less affected due to a more complex relief, low feasibility of establishing settlements and hard access.

The black poplar stands of the Ob River basin had been severely damaged by clear cutting to make fishing net floats (Bakulin, 2007). The Tom River basin stands were also used for the purpose. From our communication with the indigenous people inhabiting the areas along the Verkhnyaya and Srednyaya Ters' Rivers, the residents do no discriminate between the *P. nigra* and the *P. laurifolia* poplars, regarding them as one tree species and calling either a poplar or a black poplar and confirming cutting laurel poplars for fishing net floats in the past.Obviously, the residents also did not differentiate between poplar forms. Our observations also showed no difference between the white-bark and the grey-bark poplar forms in their bark thickness, reaching 8 cm in both forms. Thus form- and species-discriminating poplar cutting may be considered as given up. The cutting was primarily made in easily accessible sites as they required less time and energy for cutting.

Scattered timber rafting, widespread in the past, was very likely to affect poplar forests of the region. Major forest cutting in the south of Kemerovo Oblast began at the end of the 1940s with the activities of the South-Kuzbas Prisoners' Labour Camp by the order of the USSR Ministry of Domestic Affairs (the so called Yuzhkuzbaslag), that dealt with forest cutting (Ryabova, 2016). Both major and smaller rivers of the region were used for timber rafting. This activity led to river melioration and renovation, clearing streambeds, cutting bank bushes and tree stands, constructing log walls to protect low banks, islands, channels and bays. Scattered timber rafting had been practiced till the 1990s.

Thus regional poplar stands were greatly disturbed by such cutting activity. Young stands were stubbed out almost everywhere to clear river banks, while mature trees were used to construct booms. This, however, t served to protect poplar stands on islands and small river mouths and thus determined the areas occupied by poplar stands. The plants to be sustained were the most resilient individuals capable of vegetative proliferation.

The location of the majority of the studied laurel poplar stands is in the Tom River basin on islands, and, as a consequence, their relatively impeded accessibility currently ensure their sustainability under anthropogenic changes in the region. Nonetheless, increasing pressure on the floodplain areas, especially within the Novokuznetsk agglomeration, can significantly enhance further fragmentation of this species area, bringing with it genetic transformation of poplar populations.

Currently natural dynamics of poplar forests is strongly influenced by an indirect force, such as mass invasion of sugar maple *Acer negundo* L. and red ash *Fraxinus pennsylvanica* Marshall into indigenous floodplain communities in the Novokuznetsk environments. These invasive species are the so called ecosystems transformers, seriously changing the outline of aboriginal communities, disrupting succession links and hampering proliferation of aboriginal species (Chernaya Kniga…, 2016). Poplars are pioneer plants, playing vital role in natural successions; therefore the degradation of their populations can result in an irreparable destruction of sensitive floodplain ecosystems (Floate et al., 2016).

Yet the greatest threat for the local poplar species, including laurel polar, is posed by spontaneous hybridization, taking place in the region between laurel polar and widely spread poplar cultivar the Siberian poplar *P.* × *sibirica* (Proshkin, Klimov, 2017*d*). Close contact between the latter stand and aboriginal species populations may be fraught with potential invasion of exotic genes into natural gene pools, thus threatening their preservation due to weakening or even disrupting natural adaptation mechanisms.

All these factors call for detailed investigation of contemporary spatial differentiation of poplar populations and genetic variability of native poplar species populations. As noted above, we revealed spatial differentiation of populations while studying the diversity of laurel poplar forms. The next step in our studies is to analyze quantitative traits.

Variability of quantitative traits. Variability of quantitative traits in laurel poplar populations was shown to be moderate or increased (Table 1).

Individual variability was 1.5–2.0 times higher as compared to the endogenic one, both for individual traits and combined coefficients. In the upstream Tom River populations the expected variation coefficient was lower than observed, with surplus phenotypic variability being quite common (2.3–33.6 %). The mid-stream populations, though, were found to lack in variability (7.3–22.5 %.). One-factor ANOVA of quantitative traits between population subsets confirmed their difference for some traits, namely *D*, *D*/*L* and *A*/*L*. The last two traits showed low or very low variation rates. It should be noted that *D*/*L* trait reflects the pres-

Table 1. Variability of qualitative traits of laurel poplar leaves in the Tom River basin as estimated by aggregate indicators of variation

Population	Code	Indicator			
		CV_{en}	CV_0	CV_e	F_{cv}
		%			
Up-stream					
Belsu	Be	14.590	21.540	21.010	–0.025
Studeny Ples	SP	11.860	24.440	18.280	–0.336
Vorony	Vo	12.670	19.540	19.090	–0.023
Maizas	Ma	9.610	18.080	16.030	–0.127
Mid-stream and tributaries					
Karlyk	Kr	9.440	13.750	15.860	+0.133
Erunakovo	Ye	9.240	12.130	15.660	+0.225
Verkhnyaya Ters’	VT	10.010	15.220	16.430	+0.073
Srednyya Maganakova	SM	11.350	15.440	17.770	+0.131

Note. CV_{en} – averaged coefficient of endogenic variation; CV_0 – observed coefficient of individual variation calculated directly for each population; CV_e – theoretical (expected) coefficient of individual variation; F_{cv} – index of intra-population variation.

ence or absence of white-bark forms in populations (Proshkin, Klimov, 2017*d*). The forms did not differ significantly in *A*/*L* value, but, since the trait results from the leaf blade shape, all the studied populations differ in it. Thus we may conclude that the analysis of quantitative traits shows some difference between the studied subsets in respect to form composition and *D*/*L* trait should be considered as the key one. This was also confirmed by ANOVA performed on the datasets, with the white-bark forms were excluded. As a result, the grey-bark trees of the studied population groupings did not differ significantly in any of the traits examined. In our opinion, this result confirms the local character of the white-bark phenotype, with their presence in the populations along tributaries determining spatial variation of laurel poplar populations within the Tom River basin.

It should be noted that phenetic studies of black poplar populations carried out by J. Guet et al. (2015) and J. DeWoody et al. (2015) to assess their differentiation also used quantitative traits. The low adaptation of the latter to contemporary climatic conditions, according to J. Guet et al. (2015), is determined by the slow influence of natural selection on the quantitative traits due to the polygenetic control and pleiothropy.

Variability of the qualitative traits. At the endogenic level laurel poplar was found to lack variability in three of the examined qualitative traits, namely the tree top shape, the base of the leaf blade and the branch morphotype. Short branches always have pointed leaf tops. The leaf blade base within the studied area was shown to discriminate between the white- and gray-bark poplar forms (Proshkin, Klimov, 2017*d*). All distinct morphotypes were found in all the studied populations, but their ratios differed as a rule, with one morphotype predominating (Klimov, Proshkin, 2017*b*). Overall, the studied area is dominated by specimens with branches and leaves covered with long hairs.

Laurel poplar in the studied area is characterized by egg-shaped triangular, egg-shaped and elliptic leaf blades. An individual tree can have several forms simultaneously, although one of the forms drastically prevails. Elliptic leaf blades can be found on one or several trees growing within a study site. In most of the studied poplar stands, egg-shaped leaves are most widely spread (50.0–70.0 %). Although the leaf blade shape does not meet all the criteria allowing it to be a considered a proper phene, and, in particular, the alternativity criterion; if a data set is sufficiently large, the leaf blade shape is an important indicator of specific variability in poplar qualitative traits.

The rate of intra-population diversity in laurel poplar qualitative traits within the Tom River basin in significantly higher than the inter-population rate, which contributed only 21.5 % to the total variance (Table 2).

The up-stream populations differed mostly in the leaf blade shape, whereas the mid-stream populations were found to differ in branch morphotypes. The moderate rate of phenotypic diversity within mid-stream populations were shown to be higher than those in the up-stream populations, most likely due to the increased number of leaf blade base morphotypes (Table 3).

Multivariate cluster analysis performed to compare the populations for the entire set of qualitative traits confirmed the population differentiation observed in tree form composition (Fig. 2).

The dendrogram shows two main populations groupings: the first one consisting of the up-stream laurel poplar populations, and the second one consisting of the mid-stream populations.

Table 2. Intra- and inter-population phenotypic diversity of laurel poplar in the up- and mid-stream Tom River basin (Shannon's index)

Trait*	Up-stream populations (Be, SP, Vo, Ma)**				Up-stream populations (Ye, Kr, VT, SM)**				Entire basin populations			
	H	H_p	F_p	F_{ip}	H	H_p	F_p	F_{ip}	H	H_p	F_p	F_{ip}
LBS	1.302	1.168	0.897	0.103	1.095	1.061	0.968	0.032	1.223	1.114	0.910	0.090
LBBS	0.000	0.000	0.000	0.000	0.836	0.809	0.967	0.033	0.836	0.404	0.483	0.517
LBTS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
BM	1.344	1.219	0.907	0.093	1.537	1.287	0.837	0.163	1.467	1.253	0.854	0.146
Mean	0.661	0.596	0.902	0.098	0.867	0.789	0.910	0.090	0.881	0.692	0.785	0.215

Note. * *LBS* – leaf blade shape; *LBBS* – leaf blade base shape; *LBTS* – leaf blade top shape; *BM* – branch morphotype; ** – see Note to Table 1; H – diversity index for the entire data set; H_p – mean value of the diversity index for population data sets; F_p – diversity index for subsets within populations; F_{ip} – inter-population diversity index.

Table 3. Intra-population phenotypic diversity in qualitative traits

Indicator	Populations*							
	Be	SP	Vo	Ma	Ye	Kr	VT	SM
μ	26.152	25.897	27.604	28.291	30.415	29.880	30.980	30.514
S_μ	3.977	3.930	4.247	4.374	4.659	4.560	4.764	4.677
H_0**	0.550	0.545	0.624	0.668	0.763	0.613	0.827	0.791

Note. * – see Table 1 for code explanation; μ – Zhivotovskiy (1991) intra-population diversity index; S_μ – error of μ; H_0** – averaged Shannon's index of the population diversity.

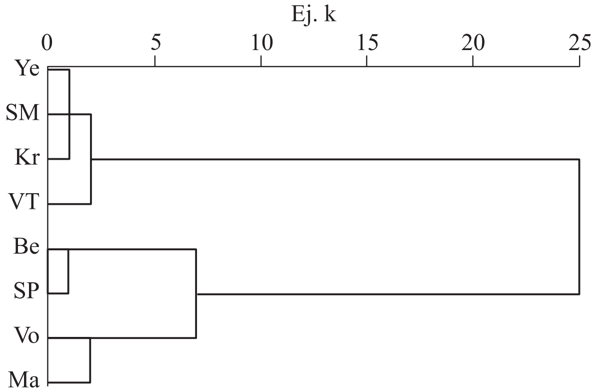

Fig. 2. Similarity dendrogram for laurel poplar population in qualitative traits: Be – Belsu; SP – Studeny Ples; Vo – Vorony; Ma – Maizas; Kr – Karlyk; Ye – Erunakovo; VT – Verkhnyaya Ters'; SM – Srednyaya Maganakova.

The combination of all the laurel poplar qualitative traits within the studied basin allowed to distinguish 15 phenotypes, of which only 5 were common for both groups of populations. Most common are grey-bark forms with rounded wedge-shaped leaf blade base, pointed blade top and with scarce long hairs on branches and leaves (22.3 % of the set).

Pairwise comparison of all the subsets using χ^2 and Zhivotovskiy (1991) (*I*) criteria revealed the extent of differences between the populations and confirmed the presence of distinctive groups located in different areas of the Tom River basin (Table 4).

In poplar stands located mid-stream and along the tributaries, the observed intra-population diversity was accompanied by increasing inter-population differences, reaching 20 % in phenotype combinations (Table 5).

Spatial differentiation of laurel poplar populations. Earlier it was shown that spatial differentiation of poplar genus populations was governed by historical processes, mainly in Pleistocene and Holocene (Keller et al., 2010; Macaya-Sanz et al., 2012; Liang et al., 2016; Meirmans et al., 2017; Fan et al., 2018). The domineering phenomena at the time were drastic climate fluctuations with alternating glacial and inter-glacial periods, generally resulting in drastic changes of environmental conditions.

The contemporary population structure of many poplar species, as well as that of other woody plants, is determined by the location of glacial and interglacial refugium and the routes of further colonization (Keller et al., 2010; Gavin et al., 2014; Fan et al., 2018). Refugium is an area-sustaining environment favorable for long-term survival of a population (Tzedakis et al., 2013).

Table 4. Pairwise comparison of the data sets for phenotype frequency. The Zhivotovskiy (1991) identity criterion (*I*) is shown above the diagonal, and χ^2 criterion is shown above it

Populations***	Be	SP	Vo	Ma	Kr	Ye	VT	SM
BE		11.760	3.960	22.920	18.480	12.960	47.400**	27.840*
SP	11.190		15.160	13.200	27.840*	21.120	48.960**	34.800**
Vo	3.490	14.350		22.920	24.600*	8.400	45.360**	32.640**
Ma	20.470	11.900	20.580		32.400**	23.520	34.440**	15.600
Kr	15.830	24.660*	23.060	37.290**		17.640	35.160**	31.800**
Ye	12.610	19.820	8.210	21.700	19.020		32.640**	28.080*
VT	46.910**	46.610**	44.870**	34.310**	37.330**	32.170**		23.520
SM	27.830*	31.280**	28.320*	15.110	29.660**	25.340*	22.470	

Note. * – 0.05; ** – 0.01; *** – see Table 1 for codes.

Table 5. Indices of intra-, group- and inter-population diversity of phenotypes

Populations*	μ	S_{μ}	H	S_h	H_0
Be	4.490	0.276	0.102	0.055	2.211
SP	4.862	0.429	0.189	0.071	2.707
Vo	3.383	0.146	0.041	0.036	2.152
Ma	5.326	0.345	0.112	0.057	2.689
Kr	5.336	0.343	0.110	0.057	2.438
Ye	5.745	0.220	0.042	0.036	2.785
VT	6.786	0.220	0.030	0.031	2.843
SM	5.683	0.245	0.520	0.040	2.724
Population groups					
US	4.804	0.593	0.313	0.042	–
MS	10.923	0.313	0.089	0.025	–
B	12.068	1.086	0.195	0.025	–

Populations*	$H_{см}$	H_p	F_p	F_{ip}
Population groups				
US	2.731	2.440	0.893	0.106
MS	3.373	2.697	0.799	0.200
B	3.310	2.568	0.775	0.224

Note. * – see Table 1 for code explanation, US – up-stream areas, MS – mid stream areas, B – entire basin; H_0 – Shannon's diversity index; $H_{см}$ – diversity index for the entire data set; H_p – mean value of the diversity index for population data sets; F_p – diversity index for the subsets within populations; F_{ip} – inter-population diversity index; μ – Zhivotovskiy (1991) intra-population diversity index, S_{μ} – error of μ; *h* – the share of rare morphs; S_h – error of *h*.

According to D. Macaya-Sanz et al. (2012), bioecological characteristics of the floodplain poplar species and their narrow focus on certain habitat conditions were the factors ensuring in the past their best adaptation to drastic climate changes. Even now the development of the stands does not depend on macroclimatic conditions, being mostly governed by the streambed dynamics (Zhang et al., 2016; Proshkin, Klimov, 2017*c*). River valleys are considered to be the best areas to buffer the effect of climate fluctuations due to warmer and more humid conditions, which make them good sites for refugium emergence (Medail, Diadema, 2009; Nieto Feliner, 2011). High vegetative proliferation also facilitates poplar survival in critical environments (Katenin, 1980). At the same time, narrow specialization enhances isolation of their populations. However, gene flow over mid-range distances enables them to effectively overcome the threat of genetic drift and subsequent inbreeding (Macaya-Sanz et al., 2012). We also believe that strict dioecious nature of poplars plays an important role in the process.

Next, the processes of environmental changes on the studied area in Neo-Pleistocene and Holecene will be considered. According to Yu. M. Maskaev (1987), the wide spread of laurel poplar stand formations over the territory of the Altay-Hangay-Sayan Mountain area took place in mid Neo-Pleistocene. Then the studied area underwent lifting of the Kuznetsk and Salair Ridges and some parts of the Gornaya Shoriya. The major hypsometric slope of the Kuznetsk hollow plain in the north resulted in a closure of the up-stream river flow within the boundaries of the Yurginsky highlands, Krapivinsky dome and Central mulda. The process resulted in the development of a singular water body called the pra-Tom River (Fayner, 1969) flowing to the north. The lifting of the Kuznetsk Alatau Mountains in the Neo-Pleistocene led to the formation of a hydrological network of 80–120 m (Nekratova et al., 1991).

Temperature decline taking place 28–19 thousand years ago during the Selitkan (Sartan–Valdai) glacial period was the main climatic change in Pleistocene. The Gornaya Shoriya territory can be regarded as a classic refugium, having never experienced the glaciation effect (Novák et al., 2014). However, there is little paleographic evidence to support this idea. M. M. Adamenko et al. (2017) demonstrated that Pleistocene glaciation was quite large and: «at least all the mid-highland areas without loess-like loam cover can be regarded as the territory of the former mountain glaciation».

The reconstruction of the late-Pleistocene–Holocene glaciation was carried out by M. M. Adamenko et al. (2015). Based on scar relief analysis, glacier valleys and moraine deposit geomorphology, the authors described morphology and dynamics of glaciations. They confirmed repeated glaciation over the Tigertysh Ridge (the highest point of the Kuznetsk Alatau). It was also shown that during the maximum of the last Pleistocene glaciation epoch, the glaciation of the Tigertysh Ridge was of the vast mountain-valley character. The resultant moraine complexes are quite pronounced, covered by loess and located in the valleys of the major rivers, i. e. the Belsu River and the Kasyra River at the absolute altitudes of 720–850 m a. s. l.

The time of glaciers' development and their rapid onset agrees with the decline in air temperatures in the Early Dryas, while the offset of the valley glaciers coincides with the Holocene start. Moreover, the Pleistocene–Holocene transition witnessed alternating warming and freezing periods (Adamenko et al., 2015).

The mountain-valley character of the Kuznetsk Alatau glaciation, in our opinion, gave an impetus to the development of poplar refugium in the region. This assumption is corroborated by the studies of the regional forest flora which was shown to be quite conservative, without any catastrophic changes in Pleistocene, which helped to preserve mountain forest species (Nekratova, 2005).

The data obtained in this study suggest the presence in the examined area of two sites that can be regarded as laurel poplar refugium. The first site is the Verkhnyaya Ters' River basin with the highest concentration of white-bark trees. High extent of the preservation is proved by significant diversity and relatively balanced allochthonous and autochthonous processes (Sheremetova, 2015).

The second site that we propose to consider a refugium embraces the Tom River floodplain area from the Belsu River mouth to that of the Usa River one. The presence of a major snake's head fritillary *Fritillaria meleagris* L. population there (Krasnaya Kniga…, 2012) along with the islets of the Siberian lime tree *Tilia sibirica* Bayer (Amelin, Blyakharchuk, 2016) is witnessing high extent of flora preservation in the area.

Different forms of laurel poplar could have emerged as early as in its primary dispersal. Thus contemporary population structure in the Tom River basin could have developed as a result of initial population fragmentation under the combined influence of neotectonics and mountain-valley glaciation of the Kuznetsk Alatau Mountains.

The white-bark forms of laurel poplar were found not only in the Tom River basin, but also in the populations in the south of the Tyva Republic (Koropachinskiy, 2016). Although the distance separating these populations from those in the present study exceeds 1000 km along a straight line. However taking into consideration the mountain relief this same distance would exceed several thousand kilometers. The light-coloured bark forms were observed in the southernmost Tyva areas, although they are absent in more humid forest sites (Koropachinskiy, 2016). On the contrary, in the Tom River basin such poplar forms can be seen in the most humid areas on the west macroslope of the Kuznetsk Alatau Mountains. However, as we have noted above, floodplain poplars are tolerant to macroclimatic conditions. We assume that the absence of the white-bark forms in the other parts of laurel poplar area is due to the fact that the site was poorly studied.

The preservation of such forms in tributary basins during glaciers' development must be brought about by that the glaciers did not reach their mid- and lower stream areas. Mountain relief, winding streambeds, humid climate and laurel poplar ecological specialization must have ensured its preservation. Moreover, currently laurel poplar stands along the right mountain tributaries are located mostly in the inter-mountain hollows where the valley somewhat widens, and hence the floodplain is more developed, while the river splits into several streams. The combination of all the factors, in our opinion, ensured maximal preservation of poplar genetic diversity.

In contrast, the laurel poplar populations in the upstream of Tom River area, being geographically closer to the major glaciation centre in the Tigertysh Ridge, underwent more drastic demographic shocks due to Neo-Pleistocene climatic fluctuations and, possibly, alpine orogenesis. The observed low variability in the combination of qualitative traits and phenotype frequency, along with low inter-population variability, confirm a great decrease of their population in the past, i. e. imply the idea of the «bottleneck» stage in their development.

One should take into account that the long history of laurel poplar growth in the studied area and preservation of its population diversity in refugium during the crucial periods in Pleistocene and Holocene periods is also confirmed by f other poplar forms along with the white- and grey-bark forms discussed above. In particular, in mid-stream areas green-bark forms can also be found (Proshkin, Klimov, 2017*b*). Near Atamanovo settlement we found a large-leaf form with 160 mm of the minimal and 200 mm of the maximal values of leaf blade length on short branches, while corresponding general values for the trees in the region are 80–130 mm. In the up-stream floodplain one can see the tree form with dense column-shaped, almost pyramidal crown, the latter being well presented in the Maizas population.

To conclude, we would like to emphasize that although the studies of phenetic and qualitative traits variability provide important initial information about the spatial population structure of a species and the history of its dispersal in Holocene (Vidyakin et al., 2014, 2015), more detailed studies with molecular-genetic markers should be carried out to validate the suggested hypotheses. These studies will be the next stage of our research.

CONCLUSION

The distribution of laurel poplar in the Tom River basin was found to be fragmentary due to both ecological requirements and anthropogenic transformation of the territory; besides, spatial differentiation of its populations was also observed. Spatial differentiation of poplar species was governed by historical processes, mainly in Pleistocene and Holocene. The results obtained allow to suggest in the examined area the presence of the two sites that can be considered as refugium for laurel poplar. The first site is the Verkhnyaya Ters' River basin, with the highest frequency of the white-bark forms observed. The second site embraces the area of the Tom River floodplain between the mouths of the Belsu and the Usa Rivers. The studied laurel poplar forms could have emerged in their primary dispersal. Apparently, the contemporary poplar population structure in the Tom River basin could have developed due to fragmentation of the initial populations under the combined influence of neotectonics and mountain-valley glaciation of the Kuznetsk Alatau Mountains.

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ПОПУЛЯЦИОННО-ФЕНЕТИЧЕСКАЯ СТРУКТУРА ТОПОЛЯ ЛАВРОЛИСТНОГО *Populus laurifolia* Ledeb. В БАССЕЙНЕ РЕКИ ТОМИ

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В бассейне р. Томи распространение тополя лавролистного *Populus laurifolia* Ledeb. носит фрагментарный характер, что связано как с его экологическими требованиями, так и с антропогенной трансформацией территории. Адаптивность тополя лавролистного к хорошо аэрируемому гравийно-валунному аллювию приводит к тому, что он отличается узкой экологической амплитудой и встречается на многорукавных участках горных рек. Современное распространение топольников в бассейне Томи, их приуроченность к островам, устьям притоков в значительной степени обусловлены хозяйственной деятельностью человека в XX в. В настоящее время относительная труднодоступность избавляет их от антропогенной трансформации в регионе. На естественную динамику топольников оказывает воздействие массовое внедрение в коренные пойменные сообщества инвазионных видов. В бассейне Томи наблюдается пространственная дифференциация популяций тополя лавролистного по формовому составу. В насаждениях верхнего течения распространена серокорая форма, у которой листовые пластинки отличаются округленно-клиновидным основанием. В популяциях бассейнов притоков и в среднем течении Томи наряду с ней встречается белокорая форма с сердцевидным основанием листовых пластинок. Комплексный анализ количественных и качественных признаков встречаемости фенотипов также подтверждает дифференциацию популяций по формовому составу. При этом в насаждениях среднего течения наблюдаются увеличение фенотипического разнообразия и усиление доли межпопуляционных отличий по составу фенотипов. В верхнем течении популяции достоверно не отличаются по последнему признаку и степень их дифференцировки низкая. Выдвинута гипотеза, что современная популяционная структура в бассейне сформировалась в результате фрагментации исходных популяций при комплексном воздействии неотектоники и горно-долинного оледенения Кузнецкого Алатау, а также антропогенного воздействия.

Ключевые слова: *Populus, популяции, морфологические признаки, фенотипы, оледенение, рефугиум, Кемеровская область, Россия.*