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Ecogeographic Variation in the Generative Organs of Larch in the Russian Far East

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Abstract—Relationships between morphological characters of the generative organs of larch and ecogeographic and climatic factors in the Russian Far East have been analyzed. It has been shown that local ecological factors have an effect on metric morphological characters of cones such as the length, width, and number of seed scales, which are not usually used as diagnostic characters. On the other hand, a major proportion of variation at the regional level in characters regarded as taxonomically significant is accounted for by geographic and climatic factors of the environment.

Keywords: morphology, Far Eastern larches, *Larix*, climate, edaphotope.

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The multiplicity of taxonomic solutions in the systematics of Far Eastern larches (Kolesnikov, 1946; Bobrov, 1972; Dylis, 1981; Koropachinskii and Vstovskaya, 2002; Fu et al., 1999) is explained by the remarkable polymorphism and instability of their morphological characters (Dylis, 1947, 1961, 1981; Bobrov, 1972; Abaimov and Koropachinskii, 1984). As justly noted by Kolesnikov (1946, p. 321), "...in Far Eastern larches, it is difficult to find any morphological characters among those accepted in modern systematics to discriminate between *Larix* species and varieties that would not overlap with the characters of neighboring forms at the limits of their variation ranges. There is hardly any organ or plant part whose size, shape, and structure remain sufficiently stable and constant between individuals..."

In the context of *Larix* systematics, the nature of variation in morphological characters is of special interest. The multitude of approaches to the study of phenotypic variation can be reduced to two main categories. The population genetic approach (Semerikov et al., 1999; Kozyrenko et al., 2004a, 2004b; Vasyutkina et al., 2007; Semerikov and Polezhaeva, 2007; Semerikov et al., 2007) has not yet succeeded in clarifying the situation with taxonomic differentiation of Far Eastern larches. The expected interdependence of population-genetic variation and variation in the morphology of reproductive structures, observed in many conifers (Mamaev, 1973; Muratova, 2004; Putenikhin et al., 2004), proved to be questionable in Far Eastern larch species (Semerikov and Polezhaeva, 2007; Levina et al., 2008). The expansion of geographic genetic research and, in particular, analysis of the geographic distribution of numerous larch morphotypes in relation to ecological and climatic gradients, will hopefully contribute to the development of *Larix* systematics.

In terms of the ecogeographic approach, a major proportion of interspecific phenotypic variation in larches growing in northern Asia can be explained by the effects of environmental factors (Dylis, 1961; Putenikhin and Farukshina, 2004). Since the latitudinal gradient of temperatures in the Russian Far East is combined with the longitudinal gradient of climate continentality, the spectrum of relevant ecogeographic factors in the region is apparently extremely broad, accounting for high variation in the morphological characters of trees. This, in turn, accounts for difficulties in determining the number and volume of larch species growing in this region.

Morphological characters of the generative organs (first of all, macrostrobili) are most often used as diagnostic markers in the systematics of Far Eastern larches. Therefore, this study was aimed at analyzing the relationship between morphological characters of mature female cones and ecogeographic factors under conditions of the Russian Far East. In particular, our purpose was to estimate the contribution of local ecological factors (edaphic and topographic) to variation in the morphological characters of cones within a certain population, on the one hand, and to evaluate the effect of environmental factors acting at the regional level (climatic parameters), on the other hand.

Table 1. Characteristics of larch populations included in the study

Population code	Geographic location	Coordinates of the population geographic center		Elevation above sea level, m
		N	E	
Ku_Kas	The Kuriles, Iturup Island, Kastaka Lake	45°00′38″	147°43′42″	0–30
Ku_Khv	The Kuriles, Iturup Island, Evgeniya Bay, Khvoinyi Creek	45°11′06″	148°13′57″	10–40
Ku_Del	The Kuriles, southern Shikotan Island, Dolphin Bay	43°45′26″	146°36′39″	10
Sa_Gor	Sakhalin, near the village of Gornozavodsk	46°35′34″	141°51′34″	130
Sa_Nysh	Sakhalin, near the village of Nysh	51°32′42″	142°44′50″	70
Sa_Val	Sakhalin, near the village of Val	52°20′46″	143°02′48″	30
Sa_Usp	Sakhalin, between Sladkoe and Uspenskoe lakes	53°27′06″	141°58′01″	5–20
Sa_Shm	Sakhalin, Schmidt Peninsula, between Cape Marii and the Tum' River	54°14′49″	142°24′26″	10–30
Ka_Esso	Kamchatka, near the village of Esso	55°55′28″	158°43′03″	670–820
Ka_Tol	Kamchatka, Mount Tolbachik	55°37′36″	160°14′16″	570
Pr_Kav	Primorye, north of the village of Kavalerovo	44°26′01″	135°14′40″	390–470
Pr_Arz	Primorye, nbetween the Tumanovka and Arzamasovka rivers	44°04′01″	135°06′24″	440–680
Pr_Bar	Primorye, near the village of Barabash-Levada	44°48′36″	131°23′12″	450
Pr_Olg	Primorye, Olga Bay	43°41′24″	135°13′12″	40
Pr_Val	Primorye, Valentin Bay	43°07′12″	134°19′12″	10–200
Pr_She	Primorye, near the village of Shcherbakovka	43°34′48″	134°37′12″	200–600
Pr_Lis	Primorye, the Listvennaya River	43°26′24″	134°40′12″	140
Pr_Ter	Primorye, between the villages of Terney and Kema	45°40′08″	136°46′23″	150–250
Pr_Bik	Primorye, the Bikin River valley	46°37′25″	134°47′26″	100–120
Pr_Im	Primorye, the Iman River valley	45°49′17″	135°15′27″	210
Am_Ek	Amur oblast, near the village of Ekimchan	52°54′40″	131°58′18″	350–630
Am_Bys	Amur oblast, the Byssa River basin	46°37′25″	134°47′26″	270–310
Am_Tal	Amur oblast, near the village of Talakan	50°15′23″	130°11′29″	200
Jew_Bk	Jewish Autonomous Region, the Bastak Nature Reserve	48°58′49″	132°53′31″	150–200

MATERIAL AND METHODS

A total of 24 natural larch populations were included in the study (Table 1). In each population, mature female cones were collected from 3–25 model trees (no less than 20 cones per tree) and analyzed for the following characters: cone length, width, and length-to-width ratio; the numbers of parastichies and seed scales; the angle of scale deflection; the shape of the apical edge (even, serrate, or sinuate), the degree of excurvature, and surface configuration of seed scales (flat or spoon-shaped). The coordinates of each model tree (latitude, longitude, and elevation above sea level) were determined using a GPS receiver.

The material for analyzing the effect of local (topographic and edaphic) factors was collected in populations of Amur oblast, designated Am_Ek, Am_Bys, and Am_Tal (Table 1). In these populations, the data recorded for each model tree additionally included soil moisture and trophic regimes estimated on corresponding ecological scales (Komarova et al., 2003) and topographic parameters of habitat.

Climatic parameters were evaluated with reference to the climatic database (Nakamura et al., 2007, Krestov et al., 2010). The regional climate was described using the following parameters: Kira's (1977) heat and cold indices, total precipitation over the period with monthly average temperatures remaining below zero, the continentality index calculated as the difference between average temperatures of the warmest and coldest months, and the moisture supply index calculated as the ratio of total precipitation over the warm season to potential evapotranspiration estimated according to Thornthwaite (1931). Knowing the precise geographic coordinates of larch populations, we could calculate basic climatic parameters in their habitats with sufficient accuracy.

The relationships between morphological characters of cones and environmental factors (expressed as by categorical variables) were evaluated by means of one-way ANOVA (Hartley, 1967) followed by Tukey's post-hoc test (Winer et al., 1991). Multiple regression analysis was used to estimate the contributions of ecological and geographic factors (expressed as quantitative variables) to the variation of morphological characters (Zar, 1974). Ordination of the populations with respect to variation in the whole set of qualitative and quantitative characters of generative organs was performed by the method of principal component analysis (PCA) (Beals, 1984), with the values of all characters being normalized. The Statistica 8.0 program package (StatSoft, Inc., 2007) was used for statistical data processing.

RESULTS

An analysis of data on populations Am_Ek, Am_Bys, and Am_Tal revealed no statistically significant correlations of any morphological characters of cones with topographic or moisture conditions in their habitats (Fig. 1). Nevertheless, the cone length and the numbers of parastichies and seed scales showed a tendency to decrease with an increase in soil moisture. Statistically significant correlations with soil fertility were recorded for the size of cones (Figs. 1a, 1b) and the number of seed scales (Fig. 1c): cenopopulations growing on medium or rich soils differed from those on very poor soils in having larger cones with a greater number of scales.

The dependence of morphological characters of cones on physiologically relevant climatic factors was estimated by mean of regression analysis. The calculated regression equations show that climatic factors can account for 23% of variation in clone length; 43% of variation in cone width, 38% of variation in cone length-to-width ratio, 49% of variation in the number of seed scales, and 57% of variation in the number of parastichies. The last parameter shows considerable dependence on climatic factors, decreasing with an increase in climate continentality, snow depth, and moisture supply and increasing along with the amount of heat supply during the growing season.

Compared to climatic factors, the coordinates of habitats accounted for a markedly smaller proportion of variation in morphological characters of cones, except for the length-to-width ratio. The value of this important diagnostic parameter proved to decreases at higher latitudes (in the south–north direction) and at lower longitudes (in the east–west direction). On the whole, the level of variation in the morphological characters of cones at the regional level was found to be much higher than at the local level.

An analysis of spatial differentiation of cone samples based on population average values of qualitative characters (Table 2) revealed statistically significant interpopulation differences with respect to all these characters (Fig. 2). Larch populations within subregions of the Kurile Islands, Sakhalin, and Kamchatka were closely similar, and the samples from the Kurile Islands and Kamchatka also showed no significant morphological differences from each other. The Kurile–Kamchatka population group was characterized by the highest values of the cone length-to-width ratio (Table 2). The Sakhalin populations had relatively small, rounded cones with smaller numbers of parastichies and seed scales. Differences from the Kurile–Kamchatka group were revealed only in samples from the southern and northern parts of the island (Sa_Gor, Sa_Nysh, and Sa_Shm). In the case of Kurile populations, they concerned both absolute and relative characters (cone length and the length-to-width ratio), while differences from the Kamchatka

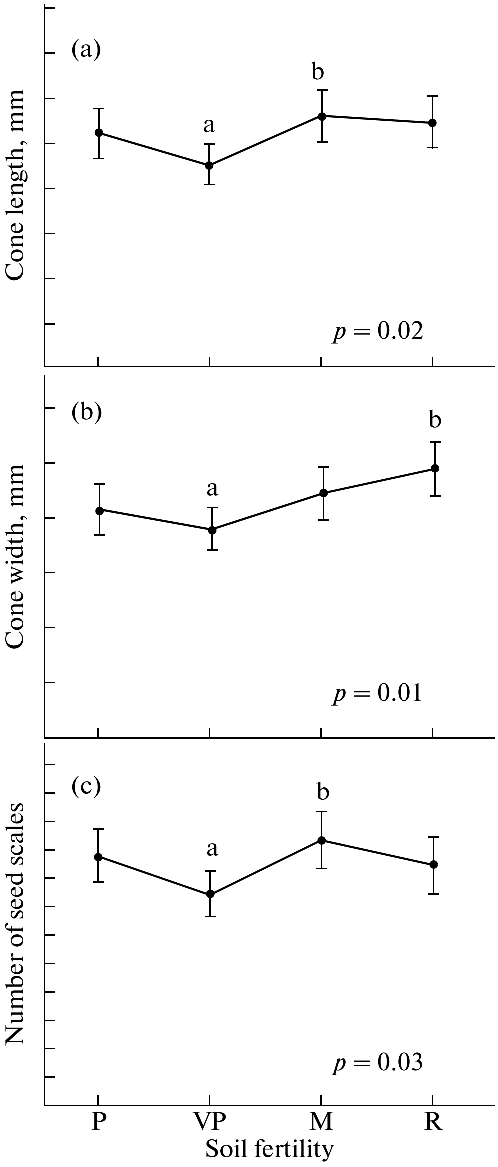

Fig. 1. Variation in morphological characters of larch cones depending on ecological environmental factors. Soil fertility: (P) poor, (VP) very poor, (M) medium, and (R) rich soils. Vertical lines show 95% confidence interval, *p* is statistical probability of error. Different letters above the confidence intervals indicate that differences between the corresponding samples are statistically significant.

Table 2. Quantitative characteristics of generative organs in larch populations

Population code	Cone length, mm	Cone width, mm	Cone length/width	Number of parastichies	Number of seed scales	Scale deflection angle, degrees
Ku_Kas	17.7 ± 1.4	13.3 ± 1.7	1.4 ± 0.1	4.2 ± 0.3	19.9 ± 2.5	29.6 ± 6.2
Ku_Khv	18.7 ± 2.1	13.5 ± 1.8	1.4 ± 0.1	4.4 ± 0.1	21.9 ± 3.6	28.7 ± 4.8
Ku_Del	20.2 ± 1.0	14.3 ± 1.3	1.4 ± 0.1	4.4 ± 0.2	26.2 ± 2.1	36.4 ± 4.5
Sa_Gor	12.0 ± 0.9	12.8 ± 2.0	0.9 ± 0.2	2.8 ± 0.2	15.6 ± 1.4	42.6 ± 16.9
Sa_Nysh	16.0 ± 3.7	15.7 ± 2.7	1.0 ± 0.1	3.9 ± 0.1	18.6 ± 5.2	53.4 ± 6.3
Sa_Val	13.6 ± 1.0	12.0 ± 2.5	1.2 ± 0.3	3.4 ± 0.3	16.1 ± 1.1	35.8 ± 6.8
Sa_Usp	16.8 ± 2.2	12.6 ± 1.6	1.3 ± 0.2	4.0 ± 0.8	19.3 ± 4.1	33.5 ± 5.7
Sa_Shm	13.6 ± 2.2	11.8 ± 1.5	1.2 ± 0.1	3.2 ± 0.6	15.3 ± 3.1	31.7 ± 5.2
Ka_Esso	17.2 ± 1.5	10.8 ± 1.0	1.6 ± 0.1	3.8 ± 0.3	20.7 ± 1.6	25.8 ± 1.2
Ka_Tol	16.5 ± 2.1	11.1 ± 1.4	1.6 ± 0.2	4.0 ± 0.7	19.3 ± 3.0	28.1 ± 1.8
Pr_Kav	17.1 ± 2.8	13.3 ± 2.6	1.3 ± 0.2	4.2 ± 0.5	25.0 ± 3.3	28.9 ± 6.5
Pr_Arz	20.3 ± 1.9	15.8 ± 2.1	1.3 ± 0.2	5.1 ± 0.6	27.2 ± 3.2	32.2 ± 6.2
Pr_Bar	17.9 ± 4.1	15.7 ± 3.4	1.2 ± 0.2	3.9 ± 0.9	20.5 ± 4.8	35.8 ± 9.6
Pr_Olg	18.4 ± 2.3	21.1 ± 1.4	0.9 ± 0.1	7.3 ± 1.0	27.7 ± 3.7	53.4 ± 10.9
Pr_Val	27.6 ± 2.7	24.9 ± 1.7	1.1 ± 0.1	10.4 ± 1.7	41.7 ± 6.1	62.4 ± 16.9
Pr_She	15.4 ± 2.5	18.6 ± 2.8	0.8 ± 0.1	5.4 ± 1.0	20.1 ± 3.4	52.8 ± 7.5
Pr_Lis	21.4 ± 0.5	23.0 ± 0.4	0.9 ± 0.1	7.3 ± 0.8	30.9 ± 1.7	51.8 ± 2.5
Pr_Ter	18.3 ± 0.4	20.3 ± 0.9	0.9 ± 0.1	6.3 ± 0.7	25.6 ± 3.9	52.9 ± 5.9
Pr_Bik	14.1 ± 2.1	13.9 ± 2.7	1.0 ± 0.1	5.4 ± 0.9	15.0 ± 3.3	49.0 ± 8.3
Pr_Im	11.9 ± 0.4	10.4 ± 0.4	1.1 ± 0.1	5.0 ± 0.6	14.9 ± 1.2	61.5 ± 2.2
Am_Ek	15.0 ± 2.3	16.4 ± 1.9	0.9 ± 0.1	6.0 ± 1.1	16.7 ± 2.9	37.6 ± 9.7
Am_Bys	18.2 ± 3.7	22.9 ± 5.4	0.9 ± 0.1	6.6 ± 0.7	18.9 ± 1.4	39.5 ± 8.3
Am_Tal	15.1 ± 1.2	17.3 ± 0.9	0.9 ± 0.1	5.2 ± 0.4	15.7 ± 2.5	44.6 ± 2.5
Jew_Bk	16.8 ± 2.6	18.0 ± 2.8	0.9 ± 0.1	6.2 ± 1.3	16.2 ± 5.6	45.3 ± 8.9

Note: Population average character values with standard deviations are shown. Population codes are deciphered in Table 1.

populations were limited to the length-to-width ratio alone (Fig. 2).

Cones from continental populations differed from insular samples in many morphological parameters (Table 2, Fig. 2). Moreover, certain characters of cones were also found to differ between continental populations. The populations of Amur oblast, Jewish Autonomous Region, and the middle and northern Sikhote Alin, where larch forms continuous forest massifs, are similar in the cone length-to-width ratio and the number of parastichies, whereas the isolated populations of the southern Sikhote Alin are heterogeneous in terms of cone morphology and differ significantly both from each other and from the insular populations. The most significant differences from other samples were revealed in populations growing on the Sea of Japan coast (Pr_Olg and Pr_Val). Moreover, these populations also differed from each other in cone size and the numbers of parastichies and seed scales.

Qualitative characters of seed scales, such as their surface configuration and the pattern and degree of deflection at the edge, also proved to differ between geographic groups of larch populations. In the course of preliminary analysis, we performed ordination of populations with respect to each of these characters to find out which of them makes the greatest contribution to differentiation of populations. On the basis of resulting distributions, the degree of seed scale deflection was identified as such a character, since insular and continental samples differed in this respect. Continental populations, in which seed scale deflection was very rare or absent, formed a fairly compact cluster that also included populations from Shikotan Island and central Sakhalin (Ku_Del, Sa_Val, and Sa_Nysh). Deflected scales in the southern Sakhalin population Sa_Gor were rare. Kurile populations from Iturup Island (Ku_Khv and Ku_Kas) and the northern Sakhalin population Sa_Shm showed the highest variation in this character, and considerable proportions

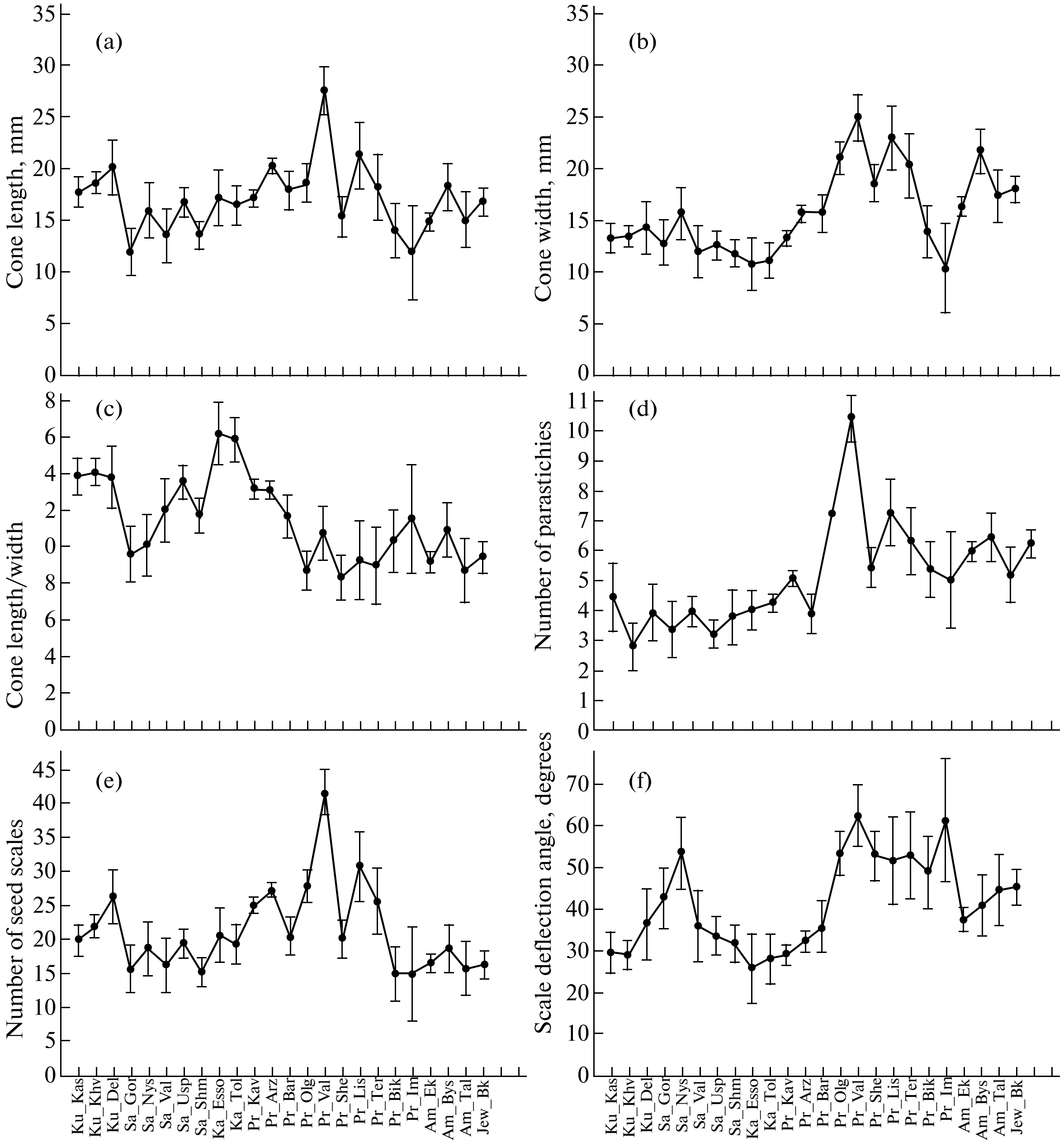

Fig. 2. Variation in morphological characters of cones in larch populations (for population codes, see Table1). Vertical lines show 95% confidence interval.

of cones in these samples had strongly deflected scales (20.4, 9.4, and 17%, respectively). Samples from Kamchatka populations Ka_Esso and Ka_Tolb and the Sakhalin population Sa_Usp contained no such cones but were characterized by fairly high frequencies of cones with moderately deflected scales (23.1, 14.2, and 17%, respectively).

The PCA ordination of populations with respect to the whole set of test characters segregated them into three distinct clusters (Fig. 3). The first cluster comprised populations from the Sea of Japan coast within the boundaries of the traditional *Larix olgensis* range (coastal populations). The second cluster combined continental populations growing in the lower and middle Amur basin, from the northern Sikhote Alin to Amur oblast (continental populations). In addition, it included the population Sa_Nys from central Sakhalin, the area with a continental climate. The third cluster comprised insular and peninsular populations of larch. Three samples from southern Primorye (Pr_Arz, Pr_Kav, and Pr_Bar) also proved to be closer to this rather than to the continental cluster.

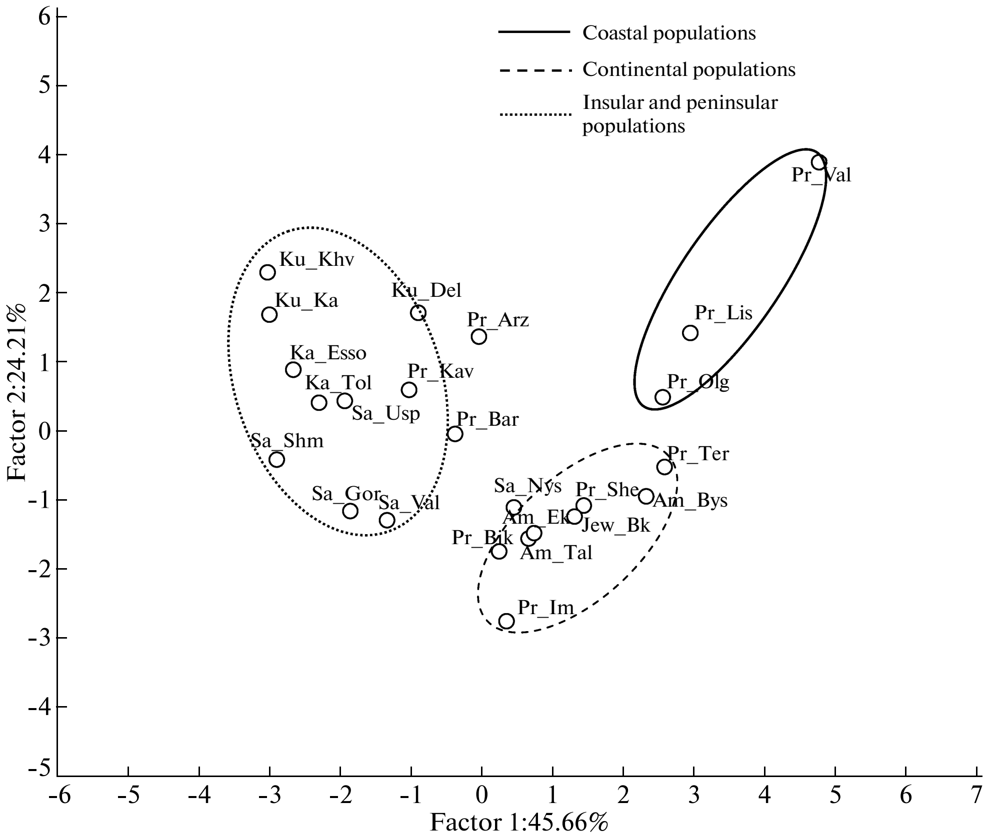

Fig. 3. PCA ordination of larch populations with respect to ten qualitative and quantitative characters of cones (for population codes, see Table 1).

DISCUSSION

The results of this study allow the following conclusions: (1) local ecological factors (edaphotope and topographic features of habitats) have an effect on metric morphological characters of cones such as their length, width, and the number of seed scales, which are not always used as diagnostic parameters; and (2) up to 40–50% of variation in taxonomically relevant characters at the regional level is accounted for by climatic factors, with geographic variables (latitude, longitude, and elevation a.s.l.) accounting for only 15–25%.

The fact that the greater part of morphological characters of macrostrobili show no significant correlation with edaphic and topographic factors confirms the validity of using the generative organs of Far Eastern larches for their taxonomic identification (Kolesnikov, 1946; Dylis, 1961; Koropachinskii and Vstovskaya, 2002). As follows from our data, only metric characters (dimensions of cones) reliably differentiate between cenopopulations of habitats differing in potential productivity within the same genetically uniform population. The characters such as the cone length-to-width ratio, which formally characterizes the shape of the cone and the number of parastichies and is often used in larch systematics, show no dependence on edaphic and topographic factors.

Ecogeographic variation in morphological characters at the regional level is accounted for by a number of factors. According to the results of analysis of geographic and climatic factors, the morphological diversity of larches is not spontaneous but spatially ordered depending on physiologically relevant climatic parameters. As climate continentality increases, the cone size and the numbers of seed scales and parastichies decrease and the angle of scale deflection becomes more acute. In regions where the growing season is warmer, the cones are larger and contain a greater number of seed scales (with the number of parastichies remaining unchanged), and the angle of scale deflection increases. Under conditions of moisture deficiency, the cones become more rounded due mainly to strong deflection of seed scales. Our data allow the conclusion that the observed distribution pattern of cone samples is largely determined by ecological adaptation of larch populations. However, the fact that the complexes of morphological characters are geographically segregated implies that they are controlled genetically. This agrees with data on differences in ecological preferences between larch species, in particular, between the Gmelin larch and the Cajander larch (Koropachinskii and Milyutin, 2006).

Gaining an insight into the role of genetic factors in the morphological diversity of larches is a highly relevant task, but further studies on genetic relationships between larch populations, with the use of molecular genetic markers, are required to accomplish it. However, it can already be assumed that the contribution of ecological factors to the formation of morphological diversity of Far Eastern larches introduces a considerable amount of “”noise” into genetically close populations.

With respect to the set of morphological characters of the generative organs, the studied populations of Far Eastern larches fall into two large groups concentrating either in maritime or in continental regions of Asia. An analysis of phenotypic variation in quantitative and qualitative characters of cones has shown that populations growing in isolation from major massifs of larch forests (on the Kuriles, Sakhalin, and Kamchatka) are less differentiated from each other, compared to continental populations.

Typical of maritime populations are the characters described by Bobrov (1972) and Nedoluzhko (1995) for *Larix kamtschatica* (Rupr.) Carr., the species not recognized in modern taxonomic systems (Koropachinskii, 1989). In this group, larches growing on the southern Kuriles differ from other populations in having large, elongated cones with deflected seed scales sinuate at the edge.

Populations from Olga and Valentin bays (Pr_Olg and Pr_Val) and the bordering area (Pr_Lis) and also populations adjoining the insular group (Pr_Arz and Pr_Kav) markedly differ from other continental populations. All of them grow within the boundaries of the *L. olgensis* A. Henry range, and genetic data on larch populations from this area (Vasyutkina et al., 2007) provide evidence for their high genetic variation and structural heterogeneity. On the basis of Nei’s genetic distances, we classified the populations from Olga Bay (*L. olgensis* locus classicus) and Valentin Bay as *L. olgensis* sensu stricto, while the taxonomic status of other samples was estimated at above the population level. Thus, considerable morphological differentiation of *L. olgensis* populations is in this case concurrent with genetic differentiation, which is a strong argument for recognizing this larch as an individual species (Shishkin, 1933; Kolesnikov, 1946; Bobrov, 1972; Nedoluzhko, 1995).

Populations from the lower and middle parts of the Amur basin, including the Sikhote Alin, are morphologically close to each other and form a compact cluster in different variants of ordination. In Fig. 3, the continental cluster ranges from populations growing in the *L. olgensis* range (Pr_Val, Pr_Lis, and Pr_Olg) to populations classified as *L. cajanderi* (Pr_Bik, Pr_Im, etc.).

These facts suggest that the observed differentiation of populations is apparently determined by the genetic properties of larches growing in this region. However, nonuniformity of climatic and geographic conditions also contributes to their morphological differentiation. A similar pattern of phenotypic variation in the generative organs was also described for Sukachev’s larch (*L. sukaczewii* Dyl.) in the Southern Urals (Putenikhin and Farukshina, 2004).

Thus, a considerable proportion of morphological variation in the generative organs of Far Eastern larches is accounted for by ecogeographic factors. Local ecological conditions have an effect mainly on metric parameters of the cone, whereas regional climatic and geographic factors account for variation in almost all its characters, both quantitative and qualitative. Ecogeographic variation in the morphological characters of cones should be taken into special consideration in population genetic studies aimed at solving current problems in the systematics of Far Eastern larches.

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