ISSN 0096-7807

Vol. 11, No. 4, July-August, 1980

March, 1981

SJECAH 11(4) 197-254 (1980)

THE SOVIET JOURNAL OF

ECOLOGY

ЭКОЛОГИЯ/ÉKOLOGIYA

TRANSLATED FROM RUSSIAN

CONSULTANTS BUREAU, NEW YORK

VARIABILITY OF SESSILE OAKS IN DAGESTAN

L. F. Semerikov and N. V. Glotov

UDC 581.52+581.154+633.872.1

A study was made of the variability of morphological traits of leaves which discriminate between sessile and pubescent oaks, and between their subspecies in Dagestan. It was shown that variability of taxonomically important traits is of a continuous nature and is closely connected with gradients of ecological conditions. It was found that in Dagestan both species form a single system whose core is the Georgian subspecies of sessile oak.

The first indications of the establishment of sessile oaks in Dagestan were made by Ya. S. Medvedev (1908, 1919). In his opinion, in Dagestan is distributed mostly *Quercus sessiliflora* Salisb. and its numerous varieties and forms, including: *Q. iberica* Stev.; f. *typica* Med., identical with the west European sessile oak; f. *mannifera* Boiss., identical with the golden oak (*Q. hypochrisa* Stev.) described by Ch. Steven (1857) from Eastern Transcaucasus; f. *pinnatipartita* Medw., which possesses dense but rapidly shed pubescence. At the same time, Ya. S. Medvedev (1908) pointed out that *Q. pubescens* Willd. was growing in Dagestan, which he identified with the south-European pubescent oak, and cited *Q. crispata* Stev. as a form of pubescent oak described by Ch. Steven (1857) from Crimea.

Yu. N. Voronov (1930) and V. P. Maleev (1935, 1936) regarded as indubitable that the following species grew in Dagestan: *Q. iberica* Stev., *Q. petraea* Liebl. (*Q. sessiliflora* Salisb., f. *typica* Medw.); *Q. hypochrysa* Stev.; *Q. pubescens* Willd. (*Q. sessiliflora* Salisb., f. *pinnatipartita* Medw.).

The species independence of the enumerated taxons was subsequently recognized by most botanists, and only the species status of the golden oak was open to question (Sosnovskii, 1943; Grossgeim, 1945; Bandin, 1952, 1954; Mitikashvili, 1961). Moreover, for southern Dages-

Institute of Plant and Animal Ecology, Ural Scientific Center, Academy of Sciences of the USSR. Translated from Ékologiya, No. 4, pp. 25-37, July-August, 1980. Original article submitted October 31, 1979.

0096-7807/80/1104-0213$07.50

tan and western Azerbaidzhan, probably under the influence of the ideas of O. Schwarz (1937), yet more species, *Q. anatolica* (Schwarz) Sosn. ex Bandin was described (Sosnovskii, 1943; Bandin, 1952, 1954).

According to the ideas of D. I. Krasil'nikov (1962, 1963), in Dagestan and in adjoining regions of eastern Transcaucasia and Precaucasia grow two species of sessile oaks: durmast oak (*Q. petraea* Liebl.) with its standard form (ssp. *petraea* Krassiln.) and Georgian form [ssp. *iberica* (Stev.) Krassiln.], and pubescent oak (*Q. pubescens* Willd.) with the standard subspecies (ssp. *pubescens* Krassiln.) and the curly form [ssp. *crispata* (Stev.) Krassiln.]. Yu. L. Menitskii (1971) considers that the following oaks grow in Dagestan: durmast oak with the subspecies Georgian and Medvedev's [*Q. petraea* Liebl., ssp. *medwediewii* (Camus) Menits.-*Q. pubescens* Willd. ssp. *pubescens* Krassiln.], and pubescent oak, identical with the south European pubescent oak (*Q. pubescens* Willd. ssp. *pubescens* Menits.) equal in volume to the curly subspecies of D. I. Krasilnikov and to the standard subspecies of pubescent oak [*Q. lanuginosa* (Lam.), ssp. *lanuginosa* Schwarz], O. Schwarz (Schwarz, 1937).

Taxonomic arrangement of sessile oaks by D. I. Krasil'nikov and Yu. L. Menitskii had no great effect on subsequent notions; in characterizing sessile oaks, geobotanists and silviculturists continue (probably by tradition) to adhere to the opinions of V. P. Maleev (1935, 1936) and A. A. Grossgeim (1945) concerning the nomenclature of these species as reflected in the "Flora of the USSR" and "Flora of the Caucasus" (Chilikina and Schiffers, 1962; L'vov, 1964; Ostapenko, 1968; Gulisashvili et al., 1975).

A short digression into the systematics shows its complexity and unsolved problems and also indicates the high variability of sessile oaks in Dagestan and the need for the detailed investigation of the population structure.

MATERIAL AND METHODS OF INVESTIGATION*

The basic massifs of forests in Dagestan, formed by sessile oaks, are concentrated in its foothills at elevations from 200-500 to 1100 m above sea level, starting from the foremost ridges turned towards the maritime lowland, to the slopes of high ridges bordering on the inner mountainous Dagestan. The total area of forests amounts to about 170 thousand ha. These are situated in an intermittent strip from the southeast to the northwest and do not form a solid forest belt, alternating with associations of meadow, steppe, and mountain xerophytic vegetation (Chilikina and Shiffers, 1962). A similar geobotanical and typological characterization of oak forests with domination of sessile oaks is recorded by P. L. L'vov (1964) and B. F. Ostapenko (1968).

In the past, piedmont oak forests occupied considerably larger areas, possibly covering totally the foothills of Dagestan (L'vov, 1964); at present, they are largely destroyed, and numerous surviving sections are transformed into coppice woods and shibliaks under the effect of constant uncontrolled selective fellings and pasturage of livestock.

To characterize population variability of the species and subspecies of sessile oaks, we have conducted population collections on 30 test areas arranged according to conventional methods. Moreover, we have attempted to include all basic massifs and to characterize the entire spectrum of conditions of growth of these species in Dagestan.

In collecting and analyzing the material, great difficulties were at once encountered in distinguishing not only the subspecies but also the species of oaks. Therefore, to identify the trees on trial areas, a qualitative analysis of variability was carried out. We have used basic taxonomic traits which discriminate between the form of pubescent oaks (Krasil'nikov, 1962; Menitskii, 1971). The traits were studied in two grades: Values of traits peculiar to sessile oak were marked by capital letters, and those peculiar to pubescent oak, by lower-case letters.

A. Leaves large, 8-14 cm long.

a) Leaves less than 8 cm long.

B. Lobes short, obtuse, often (in Georgian subspecies) almost triangular, represent

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*We wish to thank I. E. Benenson for mathematical assistance and M. M. Magomedmirzaev for help in organizing the expedition through Dagestan and discussion of the results of the study.

less than]/3 of the width of the half-blade; secondary serration absent or developed only on larger lobes in the middle part of the blade.

b) Lobes long, more than 1/3 width of the half-blade, containing secondary serration.

C. Intermediate veins absent, or located only at leaf base; first-order veins are almost parallel.

c) Intermediate veins numerous, distributed over the entire leaf blade; veins of the first and second order form a rough irregular network.

D. Number of lobes amounts to 7 pairs or more.

d) Less than 7 pairs of lobes.

E. Pubescence of leaves imperceptible to the naked eye.

e) Pubescence of leaves very well expressed. Frequently one-year-old shoots are pubescent.

K. Flat leaf blade.

k) Leaves curly on edges.

Therefore, the "morphotype" of sessile oak is marked ABCDEK; the morphotype of pubescent oak is marked abcdek. Altogether $2^6 = 64$ "forms" can be recognized purely qualitatively, and every tree on the test areas can be classed as belonging to one of these forms. Using the 64-place table, the frequency of the forms and their quantity on the test areas can be evaluated.

For quantitative estimation of variability, between 11 and 84 trees on the test areas were used. From each tree five to six shoots were taken, and five leaves from each shoot were measured for all eight traits; four traits, i.e., shape of the lobe, curliness of the leaf, and pubescence of leaves and of shoots, were assessed qualitatively for the tree as a whole. For each tree, and then for the test area, the mean values of measurable traits and the frequency of qualitative traits were calculated.

The study of the population structure of sessile oaks was conducted by comparing the samples simultaneously for the complex of traits and by using multivariate estimatiions of differences between the samples. Matrices were obtained of 30×30 Makhalanobis intervals (D^2) and mean divergence (J) between the samples, and methods of standard analysis were applied (Anderson, 1958; Kul'bak, 1967; Pao, 1968; Menitskii, 1971; Blackith and Reyment, 1971).

Standard analysis makes it possible to reduce the interval of traits to intervals of lesser dimensionality by finding standard axes. In our material the first two standard vectors represent 74%, and the first three, 88% of all variability. This makes it possible to represent the studied samples on a plane formed by two first standard vectors without significant distortion of Makhalanobis intervals, for direct examination of the population structure of sessile oak.

Assessment of the structure of variability for all studied traits was made with the use of three-factor hierarchic dispersion analysis (Glotov et al., 1975). In the hierarchic scheme, on the upper level, were studied the differences between groups of populations (factor A), separated with the help of standard analysis, and then differences between populations (factor B), and interpopulation heterogeneity (factor C). On the lower level was shown the variability in the crown of trees (factor E). By expanding the values of mean squares, dispersion which depended on the effect of the studied factors was obtained, and the proportion of these factors' influence on the structure of trait variability was calculated.

For estimation of the degree of genotypic conditionality of variability of traits, an analysis was made of the semisiblings for two populations: at Dubki (test area 8) situated in the belt of the lower foothills, and at Manasaul (test area 11) in the high foothills. The seedlings were grown in the Botanical Garden of the Institute of Plant and Animal Ecology of the Ural Scientific Center of the Academy of Sciences of the USSR from acorns arising in free pollination, gathered separately from each tree. From the Dubki population, 22 trees were taken; from the Manasaul population, 17 trees. From each tree 50-200 seedlings were grown.

TABLE 1. Distribution of "Forms" of Trees on the Test Plot 11 (Manasaul)

AbC	*ABC*	*Abc*	*abc*	*abC*	*aBC*	*ABc*	*aBc*	
1	0	0	0	0	0	0	0	*Dek*
1	5	2	0	0	0	2	1	*DeK*
0	0	0	0	0	0	0	0	*dek*
0	0	0	0	0	0	0	0	*deK*
5	34	3	0	1	6	2	2	*DEK*
0	2	0	0	0	1	0	0	*dEK*
0	1	0	0	0	0	0	0	*dEk*
1	7	0	0	0	0	0	0	*DEk*

TABLE 2. Distribution of "Forms" of Trees on Test Plot 8 (Dubki)

AbC	*ABC*	*Abc*	*abc*	*abC*	*aBC*	*ABc*	*aBc*	
2	0	2	0	0	0	0	0	*Dek*
7	2	0	0	0	0	0	0	*DeK*
0	0	1	0	0	0	0	0	*dek*
6	0	0	0	1	1	0	0	*deK*
8	15	2	0	0	2	1	0	*DEK*
3	0	1	0	0	0	0	0	*dEk*
10	1	0	0	1	0	0	0	*dEK*
1	2	2	0	0	0	1	0	*DEk*

TABLE 3. Distribution of "Forms" of Trees on Test Plot 14 (Talgi)

AbC	*ABC*	*Abc*	*abc*	*abC*	*aBC*	*ABc*	*aBc*	
0	1	3	1	0	0	1	1	*Dek*
2	4	2	2	3	0	1	2	*DeK*
2	2	5	5	4	3	2	1	*dek*
8	6	4	3	5	4	2	1	*deK*
0	6	3	0	0	2	1	1	*DEK*
1	0	0	1	0	0	0	0	*dEk*
1	0	0	0	0	0	0	1	*dEK*
0	0	0	0	0	0	0	0	*DEk*

RESULTS OF INVESTIGATION AND DISCUSSION

Qualitative estimation of variability indicates that on the trial plots 5, 6, 11, 17-20, 22, 23, and 30, marked out in the belt of high foothills, 60-90% of the trees approach the morphological type of the Georgian subspecies of sessile oak; the remainder deviate toward the pubescent oak. Altogether 5 to 15 forms were distinguished. As an example, Table 1 shows the distribution of trees on test plot 11 (Manasaul).

On test plots 1-4, 7, 8, and 16 marked out in the belt of low foothills at elevations from 500 to 800 m above sea level, in drier and warmer biotopes, the number of forms increases to 30, for instance, in test plot 8 (Table 2).

Although on the above test plots large-leaved forms dominate, they have at times a very peculiar morphological appearance. The traits of the Georgian subspecies of sessile and of pubescent oaks are combined in diverse combinations (Fig. 1).

A still larger variability have the trees on test plots 9, 13-15, and 24-29 situated at the seaside ridges in the driest conditions of growth. In this connection, test plot 14 is representative, situated near the settlement Talgi; here, 40 forms are distinguished (Table 3). On the plot area of 1-2 ha, trees both with large and with small leaves of various shapes are encountered with approximately the same frequency. Trees were found whose leaves had as many as 12 pairs of lobes and, at the same time, leaves were found whose margins were almost entire. Occasionally, individuals are found with small ovate leaves and short lobes directed forward, whose ends are attenuated into a very short point, resembling oaks of the *Gallifera* subspecies (Spach.) Guerke (Fig. 2).

Trees of different morphological appearance encounterd on the same test plot, at a distance not exceeding 100 m between them, belong to the same interbreeding assembly: Observations have indicated that there are no observable phenological and ecological differences between them. Therefore, the test plots can be regarded as samples of corresponding populations, and the mean values of variability traits can be calculated (Tables 4 and 5).

Collections of herbarium material from most of the test plots were conducted in August-September 1975, and on plots 13 and 27, after a very wet spring for Dagestan, 1976. Moreover,

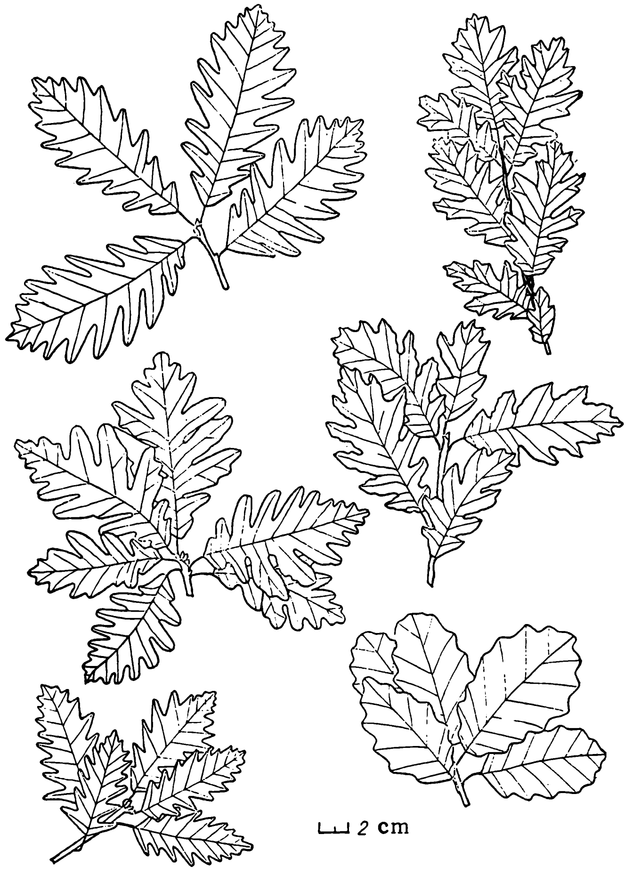

Fig. 1. Herbarium samples from test plots 8 and 11.

test plot 13 was laid out in direct proximity of plot 14, and plot 27 in proximity to plot 25. Tables 4 and 5 show that they differ little from each other; therefore, the pairs of test plots 13-14 and 25-27 can be regarded as samples of the same populations.

Test plots 7, 8 (settlement Dubki), 10, 11, 12 (village Manasaul), 17, 18 (Gubden), 19, 20 (vill. Vanashimakhi), 21, 22 (vill. Alkhadzhikent), 28, 29 (vill. Magaramkent) were laid out in adjacent forest regions, but on opposite slopes of river valleys and ridges. Differences in mean values and frequencies of traits, and confinement to orographically and lithologically different territories, compel us to suppose that the enumerated test plots, despite their spatial closeness, represent samples of different populations.

Spatially distant test plots undoubtedly belong to different populations, although some of them, for instance the 5th and 30th, are similar in mean values and frequencies of traits. Therefore, for brevity's sake, we shall henceforth refer to the test plots as populations.

Quantitative analysis (Tables 4 and 5) as well as qualitative analysis single out, on the one hand, populations 9, 13-14, 15, 25-27, and 26 with smallest leaves and most developed traits of xeromorphism, and on the other, populations 5, 10, 11, 19-23, and 30 with large leaves and more mesophilic habit. The remaining populations have intermediate character of traits. This is in accordance with the results of the standard analysis.

On the planes of the first and second standard vectors, the populations form one fairly disperse cluster (Fig. 3). The first standard vector "expands" this cluster into three groups. On the left side stand out populations 9, 13-14, 15, 25-27, and 26 which can be ascribed to the curly subspecies of pubescent oak; on the right are populations 5, 10, 11, and 19-23 approaching, by the appearance of their leaves, the Georgian subspecies of sessile oak; in the center are located populations with intermediate values of traits.

The second standard vector separates the intermediate populations into two groups. The first of these contains populations 1, 2, 3, 4, 7, 8, 12, and 16 which are characterized by relatively large leaves, their deep slits, and development of secondary serration. By their

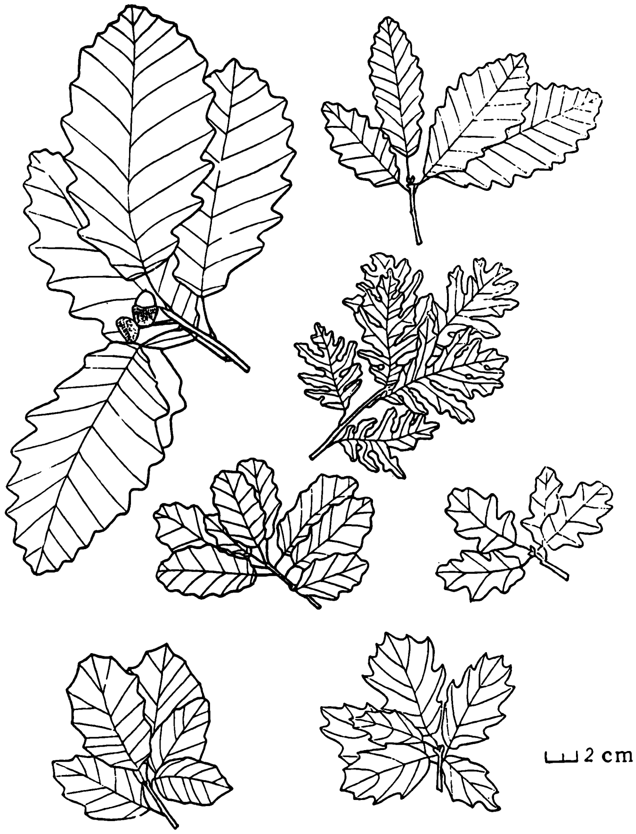

Fig. 2. Herbarium samples from test plot 14.

morphological appearance, the populations of that group can be related to the typical subspecies of pubescent oak. The second group includes populations 6, 17, 18, 24, 28, and 29 which by a complex of traits belong to the intermediate position between the curly subspecies of pubescent oak and Georgian subspecies of sessile oak.

Application of the hierarchic variance analysis reveals the structure of variability of traits in groups of populations separated by means of standard analysis (Table 6). Differences between the groups of populations are highly reliable in a majority of the studied traits ($p < 0.01$-0.001) with the exception of the tangents of the angle of divergence of the lateral veins. By relative contribution to the total variability, the differences between the groups of populations exceed, as a rule, the differences between the populations. Although differences between populations within the groups are of high reliability ($p < 0.001$), they are closer to one another than those from different groups. This indicates the correctness of separation of the groups of populations.

Highly reliable differences between trees ($p < 0.001$) constitute about one-third of total variability and are, apparently, of complex ecological-genetical nature. Estimation of variability within the tree crown (factor E) makes it possible, however, to take into account the paratypical (environmental in the narrow sense) component and subtract it from the total variability. Therefore, we are of the opinion that the difference between trees of the same population and of different populations are, to a great extent, determined genotypically.

This confirms the results of the analysis of home-grown seedlings for their leaf characters, raised from acorns gathered from the populations Dubki (8) and Manasaul (11). These are presented in Table 6 in the form of fractions of variability of the traits of seedling leaves, which are determined by differences between the parent trees.

For the population 8, low or unreliable fractions of the effects of parent trees are characteristic; only the shapes of lobes and leaf pubescence have high estimations of heritability. In population 11, the fractions of the influence of parent trees are considerably higher and approximate to estimations of intrapopulation variability (factor C, Table 6); while the heritability of the shape of lobes and of pubescence is unreliable. It is likely that genetical heterogeneity of this population is, by and large, higher. However, the phe-

TABLE 4. Mean Values of Traits of Leaves of Sessile Oaks in Dagestan

No. of sample	n	Length of leaf, mm	Length of petiole, mm	Relative length of apex, %	Relative width of leaf, %	Slitting, %	No. of lobes	Tangent of angles of veins, x10	Secondary serration
1	12	105,1	13,1	37,8	57,9	51,1	15,4	9,2	3,73
2	30	98,6	15,6	42,7	62,1	52,8	16,4	13,3	4,72
3	27	101,8	12,4	44,1	60,5	51,9	15,1	12,3	3,44
4	15	101,9	12,7	40,2	61,6	52,3	15,6	12,9	4,57
5	45	103,6	14,5	40,5	60,4	62,3	16,2	10,5	1,50
6	12	87,4	13,9	45,7	61,4	62,2	15,2	11,6	1,27
7	39	95,0	14,8	49,4	62,2	47,2	14,9	12,6	3,95
8	49	90,0	14,2	48,3	62,1	38,4	13,2	13,1	3,49
9	32	75,8	9,1	47,2	58,2	59,0	12,8	11,9	0,63
10	30	111,6	15,7	45,7	61,7	58,0	17,0	11,9	4,83
11	21	127,2	17,5	44,5	63,0	67,1	18,4	13,2	3,91
12	48	103,7	14,8	43,2	61,2	54,4	14,8	10,3	3,57
13	21	73,2	8,5	41,7	60,5	56,4	12,9	12,0	1,14
14	84	83,0	11,9	45,9	62,3	54,6	12,5	10,9	1,50
15	15	83,4	12,7	46,2	63,7	50,7	14,4	13,2	2,03
16	32	99,2	12,7	36,8	53,3	38,8	16,2	8,6	3,90
17	25	93,6	13,9	37,2	57,5	61,2	16,5	7,8	0,16
18	33	90,3	13,2	40,2	54,5	51,7	15,8	9,8	1,09
19	33	108,3	18,2	41,8	64,0	64,3	17,4	11,9	1,65
20	32	112,2	17,4	40,8	63,9	67,9	19,0	11,9	2,11
21	31	104,1	16,2	43,3	59,8	61,8	15,1	9,3	0,99
22	26	109,3	16,1	49,2	57,5	38,4	15,1	11,9	0,62
23	32	106,4	15,2	41,0	60,4	69,3	19,0	11,5	1,27
24	43	86,9	12,2	42,6	61,9	63,9	16,2	13,3	1,70
25	24	50,1	4,2	42,5	60,7	59,9	12,5	12,4	1,31
26	25	52,1	3,8	45,3	60,2	61,4	12,7	9,7	2,29
27	11	57,6	5,8	38,6	64,5	63,5	11,5	11,6	0,26
28	43	88,9	14,1	42,4	59,6	58,3	13,9	8,5	1,66
29	41	102,6	15,6	37,4	54,7	63,7	15,4	8,6	1,52
30	21	96,2	13,4	46,8	63,7	66,4	16,5	12,8	1,60

TABLE 5. Frequencies of Qualitative Traits of Sessile Oaks in Dagestan, %

No. of sample	n	Shape of lobe	Curliness	Pubescence of leaves: stellate	flocculent	velvety	Pubescence of shoots
1	12	7,8	0,0	0,0	84,5	15,5	15,5
2	30	20,0	30,0	10,0	86,7	3,3	33,3
3	27	48,2	11,1	7,4	92,6	0,0	3,7
4	15	0,0	0,0	13,3	80,0	6,7	6,7
5	45	20,0	35,6	100,0	0,0	0,0	0,0
6	12	25,0	8,3	100,0	0,0	0,0	0,0
7	39	7,7	0,0	30,8	64,1	5,1	5,1
8	49	0,0	2,0	20,4	63,3	16,3	26,6
9	32	71,8	25,0	40,6	0,0	59,4	40,6
10	30	3,3	3,3	31,0	65,5	3,5	13,8
11	21	9,5	14,3	95,3	0,0	4,7	4,7
12	48	0,0	39,6	20,8	79,2	0,0	0,0
13	21	28,6	33,4	42,8	0,0	57,2	57,2
14	84	79,8	36,9	14,3	0,0	85,7	78,6
15	15	26,7	33,3	46,7	0,0	53,3	53,3
16	32	12,5	65,6	37,5	62,5	0,0	0,0
17	25	16,0	56,0	72,0	0,0	28,0	8,0
18	33	39,4	30,3	97,0	0,0	3,0	0,0
19	33	3,0	3,0	100,0	0,0	0,0	0,0
20	32	6,3	12,5	90,6	0,0	9,4	3,1
21	31	6,4	96,8	67,8	0,0	32.2	6,4
22	26	11,5	11,5	73,1	0,0	26,9	11,5
23	32	18,8	0,0	100,0	0,0	0,0	0,0
24	43	32,6	41,8	37,2	0,0	62,8	46,5
25	24	20,8	12,5	0,0	0,0	100,0	100,0
26	25	52,0	100,0	20,0	0,0	80,0	72,0
27	11	36,3	81,8	0,0	0,0	100,0	100,0
28	43	37,2	72,0	30,2	0,0	69,8	53.5
29	41	34,2	90,2	17,1	0,0	82,9	68,4
30	21	14,3	4,8	85,6	0,0	14,4	4,8

notypic variability of the 8th population, as already mentioned (see Tables 1 and 2), is substantially higher than that of the manasaulian population; probably, a considerable part of phenotypical variability in population Dubki is determined by modifications.

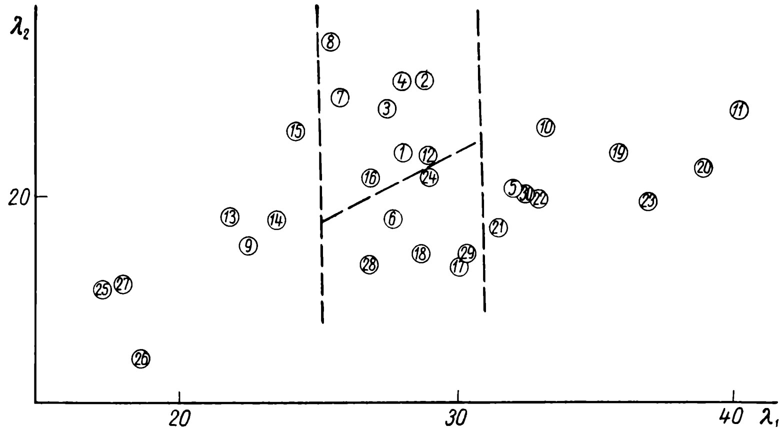

Fig. 3. Distribution of the population of sessile oaks of Dagestan on the plane of the two first standard vectors.

Of particular interest is the nature of inheritance of leaf pubescence which is subdivided into four types: 1) scattered pubescence with straight, stellate, and reduced hairs, characteristic for the typical subspecies of sessile oak; 2) scattered or dense pubescence of stellate 3-6 radial hairs 50-100 μ long, characteristic for the Georgian subspecies of sessile oak; 3) dense, velvety-to-the-touch pubescence of straight stellate hairs 300-500 μ long, characteristic for the curly subspecies of pubescent oak; 4) pubescence dense, felt-like, easily rubbed off in fingers, matted into lumps and shed at the end of vegetative growth,

TABLE 6. Structure of Variability of Traits of Leaves of Sessile Oaks in Dagestan, % (length of petiole and tangent in home-grown seedlings not estimated in analysis)

Factors	Length of leaf	Length of petiole	Relative length of apex	Relative width of leaf	Slitting of leaf	No. of lobes
A. Differences between groups of populations	35,9‡	26,1‡	19,0‡	31,9‡	37,7‡	23,3 ‡
B. Differ. between populations	11,3‡	13,1‡	22,7‡	11,7‡	9,1 ‡	8,7 ‡
C. Intrapopulation variability	23,1‡	33,1‡	21,7‡	25,6‡	34,4 ‡	30,4 ‡
E. Variability in tree crown	29,7	27,7	36,6	30,8	18,5	37,6
Differences between seedlings from parents at Dubki (8)	14,4‡	—	—	3,5*	—	18,8 ‡
at Manasaul (11)	22,4‡	—	21,1‡	10,3‡	31,3‡	25,3 ‡
Factors	**Tangent**	**Secondary lobes**	**Shape of leaf**	**Curliness**	**Pubescence of leaves**	**Pubescence of shoots**
A. Differences between groups of populations	2,4	8,4†	29,4‡	10,9*	34,1 ‡	37,4‡
B. Differ. between populations	29,6‡	11,3‡	8,2‡	29,8‡	16,8 ‡	12,6 ‡
C. Intrapopulation variability	29,5‡	48,9‡	62,4	59,3	49,1	50,0
E. Variability in tree crown	38,5	31,4	—	—	—	—
Differences between seedlings from parents at Dubki (8)	—	4,2‡	41,3‡	6,8‡	54,9 ‡	—
at Manasaul (11)	—	16,2‡	—	27,2‡	—	

*p<0.05.
†p<0.01.
‡p<0.001.

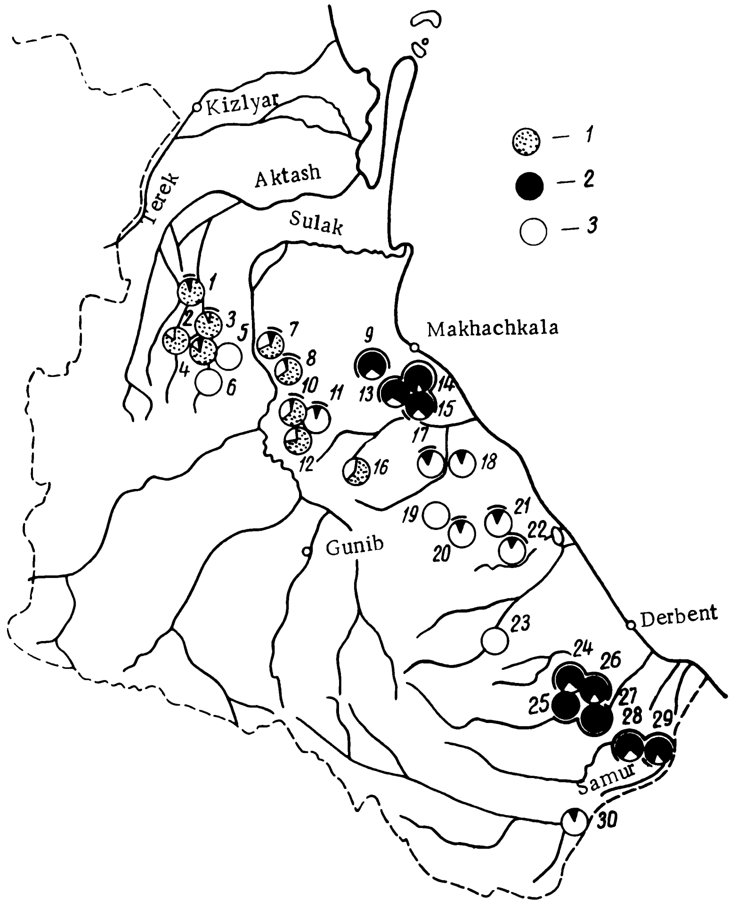

Fig. 4. Distribution of frequencies of pubescence of leaves and shoots in populations of sessile oaks in Dagestan: 1) felty pubescence; 2) dense velvety pubescence; 3) thin stellate pubescence. The length of the outer arc corresponds to the frequency of pubescence of shoots.

formed by stellate, strongly curled hair up to 1 mm long, characteristic for the typical subspecies of pubescent oak.

Trees with the first kind of leaf pubescence are very rare on Dagestan territory. In the progeny of trees with fine stellate pubescence, two classes of seedling appear. Seedlings with the parental type of leaf pubescence predominate; occasionally, seedlings with dense velvety pubescence are encountered. For the progeny of trees having dense velvety pubescence on the leaves, three classes of seedlings are characteristic: with pubescence of parental type; with fine stellate pubescence; and with dense felty pubescence. In the progeny of trees with dense felty pubescence, also three classes of seedlings are found: with pubescence of parental type (predominant); with velvety pubescence, and less frequently are encountered seedlings having leaf pubescence characteristic for the standard subspecies of durmast oak.

We have still insufficient data for accurate genetical interpretation of that trait which discriminates the species of sessile oaks in taxonomy; however, we believe that pubescence is this trait, a fairly simply inheritable characteristic which in the species and subspecies of sessile oaks is of the same nature.

In Fig. 4 is presented the geographical distribution of frequencies of pubescence of leaves and shoots on sessile oaks in Dagestan. Attention is drawn to the sloping nature of variability of pubescence types: Frequency of velvety leaf pubescence increases with the gradient of aridity of biotopes, from the high to the low foothills; felty pubescence predominates in the north of Dagestan. Similarly, in the gradient of ecological conditions the other qualitative traits vary (see Table 5).

The "behavior" of measured traits can be estimated from the results of standard analysis (Fig. 3). Coordinates of populations by the first standard vector are very closely connected with the gradient of aridity of the habitat and the elevation above sea level. In the gradient of ecological conditions from relatively moist and cool biotopes in the belt of high foothills to the driest and warmest in the belt of low foothills, particularly on the frontal ridges, there is gradual replacement of trees with morphological appearance of Georgia subspecies of durmast oak by trees with developed traits of xeromorphism, approaching the morphological appearance of pubescent oak.

Differentiation of populations by the second standard vector is closely connected with the nature of soils. In the northern part of Dagestan, under conditions of widely distributed limestones (the Limestone Dagestan) on calcareous soils are formed populations with predominant traits of the typical subspecies of pubescent oak; in the south, in Schistous Dagestan, on siliceous soils are formed populations with predominant traits of the Georgian and the curly subspecies.

The existence of transitory genetical polymorphism in types of pubescence, and correlation of other taxonomically important and obviously genotypically determined traits, with gradients of ecological conditions, compels us to assume that the differentiation of populations of sessile oaks is the result of natural selection. This does not contradict most of the facts concerning the leading role of natural selection and differentiation of plant populations which can be quite significant in contrasting ecological conditions even despite the strong pressure of migrations.

Therefore, the species and subspecies of sessile oaks in Dagestan represent a single population system. The nucleus of this system is the Georgian subspecies of sessile oak — it contains most strongly expressed ancestral traits and is among the lines of the oldest representatives of sessile oaks. On the maritime ridges of Dagestan, the Georgian subspecies is the direct predecessor of the curly subspecies of pubescent oak. In the north of Dagestan, the curly subspecies, in turn, interlaces with the typical subspecies of pubescent oak.

The mentioned subspecies were separated as a result of differentiation of population of the Georgian subspecies on the peculiar, "analyzing," background which is constituted by the territory of Dagestan. Numerous researchers (Grossgeim, 1936; Magomedmirzaev, 1975, and others) have drawn attention to the peculiar nature of this region as the arena of vigorous microevolutionary processes.

CONCLUSION

The sessile oaks of Dagestan constitute a single population system. The traits of sessile and pubescent oaks, and of their subspecies, are combined in various combinations, so that their identification is difficult. With the help of standard analysis of populations of sessile oaks, it was possible to separate them into four groups: populations of the belt of high foothills, by their morphological appearance and leaf pubescence corresponding to the Georgian subspecies of sessile oak; populations of leading ridges and uplands of the belt of low foothills, belonging to the curly subspecies of pubescent oak; a group of populations of the belt of low foothills with values of traits intermediate between these two taxons; and, finally, on the north of Dagestan stands apart the group of populations approximating to the typical subspecies of pubescent oak.

The study of the structure of variability of traits and the analysis of home-grown seed crops have shown that the intra- and interpopulation variability of leaf traits is determined genotypically. Particularly clearly is manifested the genetic nature of leaf pubescence. Variability of traits is closely correlated, on the one hand, with the gradient of dryness of the biotopes from high to low foothills, and on the other, with calcareous or siliceous types of soil.

This allows us to assume that differentiation of populations of sessile oaks in Dagestan is determined by natural selection. Typical and curly subspecies of pubescent oak and Georgian subspecies of sessile oak appear to be formed by selection of ecological races of a single community complex, understood in the wide sense, of sessile oak.

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