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EXAMPLE OF EFFECTIVENESS OF ANALYSIS OF THE GENERALIZED VARIANCE OF TRAITS IN TREES

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An analysis is made of the generalized variance of leaf traits in 39 samples from the populations of three oak species in Dagestan. It was established that the generalized parameters of variance have good differentiating properties during comparison of the populations of both a single and of different species and make possible the analysis of new information associated with the processes of the - adaptation of populations.

Insofar as the diversity in the values of a quantitative trait in natural populations is due to differences in a multitude of genes, the study of the structure of variability and the demonstration of the range of the normal reactions of genotypes with respect to this trait makes it possible to gain a more complete understanding of the genotype as an integral system and to estimate the genetic heterogeneity of natural populations not only in terms of an individual locus but also an aggregate of loci (Glotov, 1983). It is known that it becomes possible to estimate a large sample of genes during study of the several quantitative traits characterizing the various morphofunctional systems of the organism. However, until now there have been no methods for the statistical estimation of the variation of an aggregate of traits.

The classical methods of multivariate analysis (Anderson, 1963) do not permit the computation of the intra- and intergroup components of variance and their comparison, as is done in the case of a single trait. Therefore, the method proposed by Zhivotovskii (1980) for estimating the generalized variance and resolving it into components strikes us as very promising. The method permits the analysis of an aggregate of correlated traits, such that the generalized coefficient of within-class correlation R_w accounts for the mutual dependence of traits. This approach is fundamentally different from the usual tendency to "avoid" correlations by means of various types of transformations and to obtain as a result independent, new traits. In the analysis of generalized variance a new parameter appears, characterizing the degree of agreement between the direction of the correlations within an individual in the limits of a single genotype and between individuals in the population. The need for a consideration of such a problem has been pointed out (Sokal, 1978). Finally, the introduction of the generalized parameters R_w and R_I permits the "shrinkage" of information, the reduction of the number of parameters discussed. This of course does not involve abandonment of the analysis of the variation in separate traits.

The goal of the present paper was to demonstrate the effectiveness of the analysis of generalized variance as exemplified by the study of leaf traits in three oak species in Dagestan.

The materials of herbarium collections of pedunculate oak (*Quercus robur*), eastern oak (*Q. macranthera*), and sessile oak were used in the study (Glotov and Semerikov, 1978) Semerikov and Glotov, 1979, 1980). The taxonomic status of sessile oaks is very difficult (Glotov and Semerikov, 1980; Semerikov, 1986). We consider it as a single complex *Q. sessiliflora*, including the durmast and pubescent oaks, which in spite of a strong intraspecific differentiation do not achieve the rank of "good" species and intergrade into one another by way of several intermediate races.

The material of eight samples each from 10-30 trees of various populations was used for the pedunculate oak; six samples from 13-28 trees for the eastern oak; and 22 samples from

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TABLE 1. Coefficients of Within-Class Correlation for Individual Traits and Generalized Coefficients for Several Samples of Sessile Oak

Sample	Leaf length	Petiole length	Apex length	Leaf width	Dissection	Number of lobes	Aggregate of traits
Vanashimakhi-1	43.0	63.8	17.8	55.3	42.4	3.1	37.9
Vanashimakhi-2	40.8	43.6	0	37.9	9.6 *	52.2 **	45.3
Dylym	18.2	50.3	2.5	6.1	70.4	14.0	44.0
Dubki-1	37.9	39.2	12.0	32.3	69.1	64.6 **	44.3
Ratio of range of variation to mean for 25 samples	1.65	1.36	2.59	1.61	1.25	1.42	0.66

*$P < 0.05$; **$P < 0.01$.

TABLE 2. Average Coefficients of Within-Class Correlation for Individual Traits and Average Generalized Coefficients for Three Oak Species in Dagestan

Species	Leaf length	Petiole length	Apex length	Leaf width	Dissection	Number of lobes	Aggregate of traits
Pedunculate oak	67.9	68.9	38.8	52.9	66.2	70.4	62.6
Eastern oak	21.1	24.9	14.4	40.7	59.1	38.6	37.5
Sessile oak	41.4	47.3	13.1	38.1	63.1	48.1	46.5

25 trees and three samples from 21 trees for the sessile oak. We considered all 25 samples for the sessile oak as independent, although in several cases the samples were made within a single population in different habitats or even in a single habitat in different years. Five leaves were measured from each tree. The following traits were used for the analysis; leaf length, petiole length, the relative length of the apex (to the leaf length), the relative width of the leaf, the dissection (ratio of difference between leaf width across lobes and across the indentations to the width of the lobes), and the relative number of lobes.

The total phenotypic variance in the population with respect to each trait and with respect to the aggregate of the six traits was divided into two components: between trees and within a tree. The coefficient of within-class correlation r_w (ratio of variance between trees to total variance) was calculated for each trait, while the generalized coefficient of within-class correlation R_w and the coefficient of isotropicity R_i were calculated for the aggregate of traits. An approximate estimate of the error in r_w was used:

$$m = \sqrt{\frac{2}{n(n-1)(k-1)}(1-r_w)[1+(n-1)r_w]},$$

where n is the number of leaves per tree (always n = 5) and k is the number of trees in the sample (Zhivotovskii, 1976). The expression for error R_w is more cumbersome, but it can be assumed approximately that it is $\sqrt{l}$ times smaller than the error in r_w, where l is the number of traits (Zhivotovskii, 1984, p. 124), and this is yet another advantage of the analysis of generalized variance.

We shall consider with the example of several samples of the sessile oak the values of the coefficients of within-class correlation for individual traits and the generalized coefficients with respect to the aggregate of all traits (Table 1). The question arises as to in which of the samples is the fraction of variation between trees higher with respect to all traits studied; in other words, which of the samples is more heterogeneous? We shall compare the samples Vanashimakhi 1 and 2. It is apparent that in Vanashimakhi-1 the coefficients of within-class correlation are somewhat higher with respect to the majority of traits; they are significantly higher with respect to dissection ($P < 0.05$) and are appreciably lower only with respect to the number of lobes ($P < 0.01$). Hence there follows the conclusion of the greater heterogeneity of the Vanashimakhi-1 population. However, in reality the difference between the generalized coefficients are statistically insignificant. An analogous situation arises during comparison of the samples Dylym and Dubki-1.

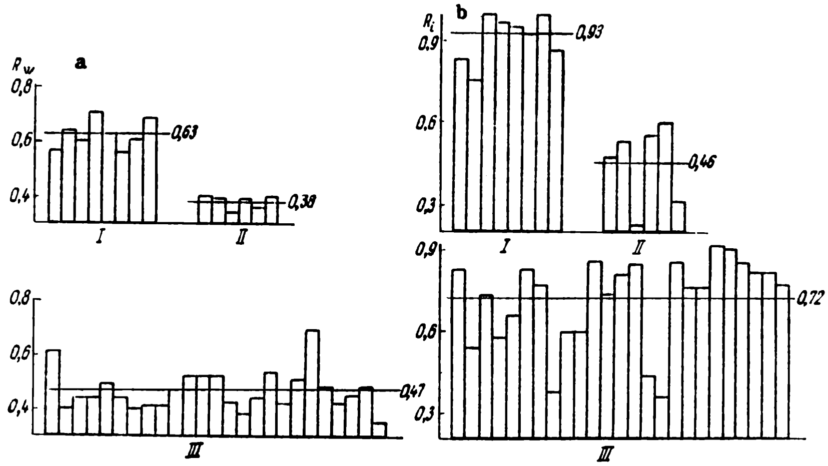

Fig. 1. Generalized coefficients of within-class correlation R_w (a) and coefficients of isotropicity R_i (b) in oak populations in Dagestan. I) *Q. robur*; II) *Q. macranthera*; III) *Q. sessiliflora*.

Table 1 presents the ratio of the range of variation of the coefficients of within-class correlation in 25 samples to the average for all samples. It is apparent that the variation in the coefficients with respect to individual traits is markedly higher than the variation in the generalized coefficients.

We shall now compare the structure of the population variation of all three species of oak. Table 2 presents the average values of the coefficients of within-class correlation for all populations. The pedunculate oak was characterized by a large fraction of variation between trees for five traits of six; the values for leaf dissection in all three species were similar. Sessile oak compared with eastern had larger coefficients with respect to leaf length, petiole length, and the number of lobes but virtually equal values for the apex length and leaf width. The qualitative conclusion would most like run as follows: pedunculate oak was characterized by the greatest fractions of variation between trees in the population, a tendency for larger values of this fraction was observed for sessile oak compared with eastern oak.

Figure 1 shows the generalized coefficients of within-class correlation R_w and the isotropicity R_i for various populations. The generalized fractions of the influence of variation between trees in the overall phenotypic variation have average values of 0.63 for pedunculate oak. 0.47 for sessile oak, and 0.38 for eastern oak. The difference between the values for the pedunculate oak and sessile oak is satisfactorily significant at the 1% level; the other two differences, at the 5% level with the use of the nonparametric Wilcoxon–Mann–Whitney test. The coefficient of isotropicity is close to unity (maximum value) at 0.93 for the pedunculate oak; it is smaller and very variable in different sessile oak populations at 0.72, and is relatively small for the eastern oak at 0.46 (all comparisons give $P < 0.01$).

The substantial interspecific differences in the generalized coefficients of within-class correlation and the coefficients of isotropicity indicate the differing character of the differentiation of populations of the studied species of oak. The pedunculate oak in Dagestan is quite uniform; the differentiation of its populations into groups was only recently sketched (Glotov and Semerikov, 1978), and the variance-correlational variation of the paratypical component in general corresponds to the intrapopulational differentiation. The sessile oak in Dagestan is represented by an elaborate complex of populations, differentiated into four groups at the subspecies rank with morphological transformations of various direction in each group. This is reflected in the values of the generalized coefficients.

The eastern oak in Dagestan is found at the boundary of the distribution range; its populations are extremely scattered and grow under contrasting conditions: in the foothill belt and in alpine Dagestan. Apparently, under these marginal conditions genotypes appear in the eastern oak populations that greatly alter the general plan of leaf morphogenesis. For example, in the populations of the foothill belt, under hot and dry conditions, forms are encountered with large, relatively broad, severely dissected leaves (Semerikov and Glotov, 1979), inconsistent with the general direction of variation, which is characterized, as in other oak species, by an increase in leaf size in the habitat moisture gradient.

Thus, the examples presented show that the analysis of generalized variance has much greater resolving power than the analysis of individual traits and makes it possible to extract more information on the population structure of species on the basis of identical sample data. At the same time a new class of population problems arise, the examination of which remains limited to qualitative considerations. In the oak species studied during decline in the intrapopulational variation the coefficients of isotropicity decline sharply, which is associated with the appearance in the populations of "abnormal" phenotypes with an altered morphogenesis. Apparently, the correlational structure of the paratypic component of the variance is altered during the evolutionary transformations of populations along with the change in the genotypically conditioned variability in traits. The finding and study of populations with a disturbed homeostatic development, characterized by low values of coefficients of isotropicity, permits a more complete understanding of the processes of their adaptation. Therefore, it is very important that further improvement be made in the methods for analyzing the generalized variance in the following directions:

1. Extension of the method to bifactorial and larger hierarchical structures (for example, variation between populations, within a population, in the crown of a tree).

2. Extension of the method to a crossed classification, as a minimum bifactorial. This class of problems is important for characterizing the multitude of norms of reaction of the genotypes in a natural population (Glotov, 1983).

3. The finding of the sample error for the coefficient of isotropicity R_w and the methods of multiple comparisons for R_w and R_i.

LITERATURE CITED

Anderson, T., Introduction to Multimeric Statistical Analysis [Russian translation], Fizmatgiz, Moscow (1963).

Glotov, N. V., "Estimation of genetic heterogeneity of natural populations: quantitative traits," Ékologiya, No. 1, 3-10 (1983).

Glotov, N. V., and Semerikov, L. F., "Variation in pedunculate oak (*Quercus robur*) in Dagestan," in: Problems in Evolutionary and Populational Genetics [in Russian], Dag. Filial Akad. Nauk SSSR, Makhachkala (1978), pp. 78-85.

Semerikov, L. F., Populational Structure of Woody Plants as Exemplified by Oak Species in the European USSR and Caucasia [in Russian], Nauka, Moscow (1986).

Semerikov, L. F., and Glotov, N. V., "Variation in eastern oak (*Quercus macranthera*) in Dagestan," Plant Populations [in Russian], Izd. Lenin. Gos. Univ., Leningrad (1979), pp. 179-189.

Semerikov, L. F., and Glotov, N. V., "Variation of sessile oaks in Dagestan," Ékologiya, No. 4, 23-37 (1980).

Sokal, R. R., "Population differentiation: Something new or more of the same?" in: Ecol. Genet., Interface, New York (1978), pp. 215-239.

Zhivotovskii, L. A., "Analysis of variance," in: Sampling Theory in Plant Populations [in Russian], Nauka, Novosibirsk (1976), pp. 58-69.

Zhivotovskii, L. A., "Measures of population variation in a complex of quantitative traits," Zh. Obshch. Biol., 41, No. 2, 177-191 (1980).

Zhivotovskii, L. A., Integration of Polygenic Systems in Populations [in Russian], Nauka, Moscow (1984).