

QUANTITATIVE ANALYSIS OF THE EFFECT OF GENOTYPE AND ENVIRONMENT IN FOREST TREE POPULATIONS

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SELOSTE:

GENOTYYPIN JA YMPÄRISTÖN VAIKUTUKSEN KVANTITATIIVINEN ANALYYSI METSÄPUUPOPULAATIOISSA

In the development of the theoretical basis for plant and animal breeding it is important to note the regularities of the variability of characteristics in natural and experimental populations. Research on this problem is not only of purely academic interest (e.g. the study of many aspects of the evolutionary process), but it also has its practical implications (e.g. the establishment of the principles of practical breeding). It is precisely this fact that explains the great interest of the plant-growers of different fields in the study of intra- and interpopulation variability of species. Considerable interest in this problem is also shown by forestry scientists, who are developing the scientific basis for the improvement of the productivity and qualitative composition of forests on the principles of genetics and breeding.

Perhaps the main, and most complicated, problem in the understanding of the laws of intrapopulation variability of the species of woody forest plants is the study of the structure of their populations. The population structures may be characterized by a number of parameters. If we speak about the variability of alternative characteristics, the parameters are as fol-

lows: frequencies of separate genes and genotypes, inbreeding coefficient, (homozygosity coefficient), the realization degree of the highest possible variability in a given locus. Considerably more complicated is the study of the population structures by their quantitative characteristics, which at the same time are of the greatest importance in the breeding for improved productivity. It is generally clear that the intrapopulation variability of quantitative characteristics appears as a result of environmental and genetic factors, but to determine the relative weight of these factors in every concrete case is not as easy as it first seems. Several mathematical models have been developed for this purpose, but all these models should be taken as an approximate approach to the formal analysis of the structure of populations by characteristics due to their very complicated nature.

Up to the present day in many countries an enormous amount of facts about intraspecific variability of forest trees has been accumulated. This material is of undeniable value in understanding the course of evolution of different species and genera and is relevant to practical breeding. At the same time, forest genetics is still lagging

behind in the study of the structure of populations. The research so far completed, at best throws light on the frequency of different possible phenotypes, which very roughly characterizes the genetic structure of populations in the true sense of the word. A. I. IROŠNIKOV (1970) is completely correct in that the classification and description of the numerous intraspecific forms of many species does not give us a complete picture of the structure of populations. The goal of the research into the structure of populations is to study the frequency distribution of homozygotes and heterozygotes in a randomly crossing population, the relations in the distribution of concentrations of different genes and genotypes (SEREBROVSKIJ 1970). From this point of view, the populations of the bulk of the species of forest trees are almost unstudied, though the current requirements of practical breeding urgently call for such research.

The populations of cross-pollinating plants, i.e. the overwhelming majority of the species of trees and shrubs, are heterogeneous by their genotype. At present, the analysis of their structure cannot be imagined without widespread use of mathematical methods. Mathematical research in the field of populations and population genetics made by G. HALDANE (1924), R. FISHER (1930) and S. WRIGHT (1949) has gained the recognition of geneticists all over the world. Unfortunately, in forest genetics the methods of mathematical analysis of the structure of populations have not yet gained proper attention. S. SOKOLOVSKIJ (1931) has worked on this problem in a study of the frequency distribution of phenotypes varying by the colour of seeds and wings in populations of Scots pine. The research proves that there are two homozygote variations in these populations (with dark or light colour of wings and seeds) and that the distribution of their frequency in populations is balanced, i.e. it follows the theoretical distribution ensuing from the Hardy-Weinberg law. V. A. DRAGAVCEV (1962) has studied the quantitative relation of phenotypes varying by the colour of seeds in a population of *Haloxylon*. The results show that the empirical frequency distribution of phenotypes does not differ from the theoretical distribution. A. TEICH (1970) has studied

the phenomenon of serotification in populations of *Pinus banksiana* and *Pinus contorta* and has stated that this characteristic is genetically controlled and is governed by two allelomorphs of one gene, but the frequency distribution of the genotypes, which vary by the degree of the opening of cones, follows the Hardy-Weinberg law. A number of studies of this problem has been published by the present author (PETROV 1967, 1970, PETROV and VIDJAEV 1970). These investigations show that the frequency distribution of phenotypes by the form of crown in populations of some species of *Populus* and by the degree of the pubescence of shoots in a population of *Acer negundo* also do not differ from the theoretical distribution.

The application of the Hardy-Weinberg law in the analysis of population structures is necessary because the analysis of the distribution of allelomorphs in panmictic populations shows mechanisms leading to a regular distribution of genotypes by pairs of allelomorphs in combinations with some pairs of allelomorphs and in the case of splitting by series of allelomorphs (DUBININ and GLEMBOTSKIJ 1967). According to N. V. TIMOFEEV-RESOVSKIJ et al. (1969) the importance of the Hardy-Weinberg law is that when proceeding from the discrete character of genetic material it proves that there cannot be any genetic variation in the gene pool of populations without leaving some kind of trace. The practical importance of similar research lies in the fact that a conformity between empirical and theoretical frequencies of genotypes allows us to state the probability of the frequency in populations of useful mutations in homozygote and heterozygote positions, which is necessary for choosing the most effective method of breeding. However, it is necessary to stress the fact that this kind of compliance must in no case be understood to be absolute, to say nothing about far-going conclusions. S. A. MAMAEV (1973) correctly notes that the analysis of the frequencies of phenotypes in populations sometimes leads to simplified ideas about the genetic structure of populations of woody plants. N. V. TIMOFEEV-RESOVSKIJ et al. (1973) have noticed that to discover in a population the relationship $p^2 : 2pq : q^2$

between the frequencies of phenotypes by no means proves that the population is in genetic balance regarding this characteristic and that the characteristic is controlled by an autosomal diallel gene, i.e. that it is inherited monogenically, since the real character of the inheritance of characteristics can only be proved by genetic analysis of certain crossing combinations. As the above mentioned authors have shown it very often happens that a simultaneous existence in population of two or more alleles is explained by a delicate balance of pressures, in different directions, by natural selection. Therefore the Hardy-Weinberg law can be widely applied only as a rough estimate of the frequency of homozygotes and heterozygotes in real populations, or it may characterize particular borderline conditions.

N. I. Vavilov has pointed out that «Widespread attention must be paid to the genetic problem of quantitative characteristics in the coming years. Until now, genetics has mainly dealt with the inheritance of qualitative characteristics». These words of a prominent scientist have not lost their relevance in our time, especially when concerning forest trees. The absolute majority of the so called productive characteristics (such as height and diameter of trunk, size of fruits and seeds, resin yield and pulp yield of wood) are of a quantitative nature. Breeding work with quantitative characteristics is greatly complicated by the facts that, 1) the number of genes controlling the development of such characteristics is usually very large and in many cases they cannot be exactly counted, 2) genes can be in interaction with each other (allelic and nonallelic interaction), 3) the development of the quantitative characteristics is strongly influenced by the environmental conditions. Therefore, the study of the structure of populations by their quantitative characteristics, in contrast with the search for particular genes, has a wider task: to establish the relevance of the hereditary differences of the individuals of a population. A further task is to identify the differences caused by diverse growth conditions and how these are reflected in the level of general (total) phenotypic variability of the quantitative characteristic under study in a given population.

The first necessary phase in the organization of such research is the detailed study of the endogenous (metameric) variability of given characteristics. Metameric variability is manifested in all those cases where the same characteristic appears in different parts of the crown and has therefore developed under different conditions of water-supply, nutrition, supply of light etc. The majority of alternative characteristics are characterized by the smallest metameric variability, whereby the metameric coefficient of variation in a certain age range practically equals nil. Low metameric variability also characterizes some quantitative characteristics, basically those of the regenerative organs. Many quantitative characteristics of the vegetative organs are characterized by a considerably higher level of metameric variability. Different forest tree species have more or less equal levels of metameric variability in different characteristic. This indicates the lack of the specificity of species at the level of metameric variability of characteristics, not only in conifers (MAMAIEV 1973), but in woody plants in general.

Different characteristics in the metamers of the crown are to some extent in close correlation with each other. On this context we have to make a clear distinction between two categories of correlations: correlations of the characteristics of the same organ, and correlations of the characteristics of different organs. Correlations in the first category are usually the highest. From among the characteristics of the same organ, the highest correlation occurs between the unstable or almost unstable quantitative characteristics. On the other hand, characteristics stable in metamers usually do not correlate with unstable characteristics, or the correlation is only weak.

The degree of linkage of the same characteristics in the metamers of the crown of different trees, which are members of a population, can vary across a considerable range. As such, this fact may be of great importance in practical breeding, since it appears that by artificial selection it is possible not only to synthesize new correlative relations, but also to break or to a considerable extent weaken old ones.

Relative independence (autonomy) of characteristics from variations in external factors and the levels of their correlation in metamers are closely connected with each other. Stabilization of a characteristic is reached as a result of the formation in ontogenesis of complicated correlative relations which maintain its development within certain limits (KAMŠILOV 1939).

These were, then, the results of the quantitative analysis of the metameric variability of the characteristics of woody forest plants. The levels of the intrapopulation variability of characteristics are related to a number of factors, closely interacting with each other, including the level of the hereditary heterogeneity of population, variation of ecological conditions, ecological interactions between individuals within a population, their age structure etc. Variability of quantitative characteristics in both vegetative and generative organs appears in populations at all possible levels, and these levels of variability, especially concerning the characteristics of generative organs, are clearly species specific. In many cases, the levels of intrapopulation variability of the same characteristics are higher than the levels of their metameric variability. This is explained by the fact in the metamers of separate individuals variability in characteristics is mainly caused by the diversity of external and internal factors of non-hereditary character. Some extra variability caused by the genotypic differences of the individual members of the population also appears in the population.

Correlations between unstable characteristics, which are to be found in metameric formations, considerably weaken at the population level, or are totally broken when correlation coefficients are calculated in one square of the correlation matrix. However, more infrequent cases may also occur, when the values of intrapopulation correlation coefficients in comparison with the metameric ones not only do not decrease but even increase. An explanation of these facts has been proposed by Ju. A. FILIPŠENKO (1968), who has shown on the basis of the study of the variability of quantitative characteristics with soft wheats that, influenced by the genetic differences in genotypes making up a population, all

kinds of correlations may be established depending on their direction within biotypes and within the population itself.

All the above mentioned facts pertain to the analysis of phenotypic variability of characteristics. N. I. VAVILOV (1935) has said that «research of phenotypes is the first approach, which must be followed by genetic research». For the purposes of practical breeding only those characteristics which are determined by genetic factors are of interest. Each characteristic develops as a result of the interaction of genotype and environment. Therefore it is not only important to establish the genetic nature of a given characteristic, but it is also necessary to indicate the degree of the participation of genetic and environmental factors in its manifestation.

Research into the genotypic and genetic variability of characteristics, for which repeatability and broad or narrow sense heritability serve as estimates (LUSH 1945), is made in many countries of the world. As a result quite a large amount of material concerning the magnitude of the heritability of many characteristics of plants and animals has been accumulated. Research into the heritability of woody plants characteristics are essentially in the primary stage. To some extent this may be explained by insufficient elaboration of the theoretical aspects of the problem, by cumbersome methods for determining heritability and also by specific difficulties in the research of the object itself — populations of woody plants.

One of the most important, economically valuable characteristic of woody plants is the shoot growth. Shoot growth belongs to a group of very unstable characteristics varying to a great extent from year to year. Research has shown that the genotypic influence on the phenotypic variability of shoot growth in 6–25 year old stands of Scots pine in northern Kazakhstan (PETROV 1965) is not a suitable basis for carrying out in these stands an effective mass selection of the best phenotypes (values of repeatability equalled $r_w = 0.200 - 0.280$). It must be noted, however, that along with the age development of the stands, a tendency towards an increase in

the significance of this index for genotypic variation was observed.

According to N. A. PLOHINSKIJ (1973), the study of the repeatability of characteristics is of great practical and theoretical importance for estimating the effectiveness of selection. However, the methodological difficulty of such work lies in the impossibility of separating paratypic changes, i.e. changes created by the variations of the environment during ontogenesis, from the changes due to age. Unfortunately, a reliable method for the separation of paratypic and age variability has so far not been found. In making related research, therefore, we have to operate with approximate estimates of the genotypic influence on the phenotypic variability of quantitative characteristics in ontogenesis. The level of genotypic variability of a characteristic in population can be more objectively estimated by heritability.

Decomposition of the total phenotypic variance into different components (genotypic and environmental variance), which is essential for determining broad sense heritability (h^2), was carried out in our experiments by some methods well-known in the literature.

1. Standard method. This method was initially applied by S. WRIGHT (1920) in a study of the variability of pigmentation in guinea pigs. The utilization of this method for indicating the degree of genotypic variability of the energy of shoot growth in model populations of poplars consisting of different clones showed that in populations of different genotypic composition this variability is very uneven ($h^2 = 0.185 - 0.574$). V. Ja. DIŠLER and I. D. RAŠAL (1973) noted that the above mentioned method gives considerable over-estimates of heritability in comparison with other methods, thereby it has to be used with great caution and only for a rough estimation of heritability. The utilization of this method is strictly limited by two conditions: i) the plant groups compared are under strictly identical conditions (which in practice cannot be achieved), ii) the genotypes of the groups compared react analogously upon the conditions of the environment (in reality, this condition is also unattainable).

2) The method of background characteristics. This method was suggested by V. A. DRAGAVCEV (DRAGAVCEV 1962, GINZBURG and DRAGAVCEV 1970). The method has been used for the estimation of the genetic variability of the energy of shoot growth in an eleven-year old population of Scots pine, which turned out to be very weak ($h^2 = 0.159$).

3) The variance analysis method. The method of analysis of variance, suggested by the English scientist R. Fisher, is the basis of many mathematical and statistical methods used in genetic research and is also used for the partitioning of total phenotypic variance into different components. The utilization of this method for the analysis of phenotypic variability of the stem height in a model population consisting of 17 clones of *Populus* showed that the genetic nature of the energy of shoot growth in this population is high enough ($h^2 = 0.455$) in order to use it as an effective selection criterion of the fastest growing clones.

4. Shrikhande's method. The method has been developed by the Indian scientist V. SHRIKHANDE (1957). The results of the application of this method to the estimation of genotypic variability of the height of woody plants led to the conclusion that it gives considerable over-estimates for the heritability of this characteristic. According to P. F. ROKITSKIJ et al. (1977) the premises of Shrikhande's method are insufficiently grounded genetically and, therefore, its utilization is methodologically unfounded. Recently, S. P. MARTYNOV (1978) has suggested a two step corrective test for Shrikhande's method, which makes it possible to test its conditions in practical situations. The conditions referred to are: 1) a significant correlation between intergroup and intragroup variances at different standard deviations; 2) a linear relationship between the logarithms of intergroup variances and group sizes.

Above we have examined the genotypic variability of the energy of shoot growth estimated by broad sense heritability. As we know, broad sense heritability includes all genetic effects (additive effects of genes, dominance and epistasis), i.e. it characterizes the highest limit of genetic vari-

ability of a characteristic in the population. However, of greatest value in the study of the variability of quantitative characteristics in the populations of species propagated by seeds, is the determination of narrow sense heritability, since the basic reason for the effective selection by phenotype is only the additive action of genes, ensuring a correlation in the parent-progeny system.

In the literature, information on this topic is very contradictory. According to ROHMEDEK (1961 a) a 25-year research on seedling progenies of pine, spruce and oak has shown that the utilization of the seed of the fastest-grown individuals does not increase the productivity of the following generation. In another work (1961 b) he puts it still more clearly: since the genetic differences of trees are covered up by the influence of the environmental conditions on their growth, mass selection based on the phenotype without a progeny test cannot be regarded as a breeding measure. A number of other researchers (LÜCKE 1963, SAHAROV 1969, PUGACH 1970, FARMER 1970, CAMPBELL and others 1972), also emphasize the very low correlation between the phenotypic values of the height of parent trees and that of their progeny. This material shows that additive factors are significantly involved in the genetic control of the energy of shoot growth of forest trees. However, in the literature there are alternative views (HALEY 1960, EHRENBURG 1966, DAVYDOVA and others 1970), which point out that the growth energy of parental plus trees is to a considerable extent inherited by their seedling progeny, i.e. the additive effect of genes in the manifestation of vigour is large enough.

The experimental results obtained by the present author (PETROV 1975) in research concerning inheritance of the height of mother trees by their half-sibs in *Quercus robur*, *Betula pendula* and some species of *Populus* showed that at least at the juvenile phase (1-4 years) the growth energy of mother trees is very weakly manifested in the progeny (narrow sense heritability $h^2 = 0.012 - 0.342$). On the basis of research into the separate effects of female and male parent trees on the genetic variability of characteristics in a two-year old progeny of *Betula pendula* (full-sibs), it was

concluded that in the population studied the effect of male parents on the growth of the progeny is slightly stronger ($h_s^2 = 0.327$) than the effect of female parents ($h_d^2 = 0.26$). As a whole the additive effect of genes controlling shoot growth was quite small in this population, which is in accordance with the material mentioned earlier. Mass selection (selection by phenotype) becomes ineffective in these cases and there is a need to employ other methods that are more complicated (individual selection, selection by general and specific combining ability, utilization of selection indices etc). One of these methods was considered by the present author to be promising (PETROV 1975 b) during experiments included in research concerning the combining ability of parents in the above-mentioned population of *Betula*. As a result, a pair of parental individuals were selected by their specific combining ability, the crossing of which has brought about a strong heterotic effect.

A practical aspect of great interest is the influence of the growing conditions on the level of the heritability of characteristics. This question is still under discussion in the literature. According to the most widespread opinion (PLOHINSKIJ 1964, VATTI and others 1966, genetic heterogeneity of populations occurs more distinctly in optimal conditions for growth and development, i.e. the values of heritability are higher. Other researchers (JOHANSSON 1953, SINSKAJA 1963, DRAGAVCEV and OSTRIKOVA 1966) consider that genetic differences among individual members of a population do not manifest themselves less distinctly in poor conditions than in good ones.

To study this question, an experiment was made in order to find out the effect of moisture and soil fertility on the level of genotypic differences of plants concerning the energy of shoot growth. A clinal population model consisting of five different clones of *Populus*, each clone being represented by 30 plants, was grown in a plot with a gradient with respect to soil moisture and the humus content in the root layer. Analysis of the experimental material showed that the heritability of the height of plants during the whole period of vegetation was considerably higher in the

best conditions ($h^2 = 0.345 - 0.754$) than in dry conditions ($h^2 = 0.125 - 0.318$).

Summarizing the material presented in this report and also the many references to literature allows some general propositions concerning the heritability of characteristics in the populations of forest trees to be made:

1. Heritability does not characterize the genotypic variation of characteristics in general, it does so only in a specific population and under specific conditions. In different populations the value of heritability of one and the same characteristic may vary within broad limits.

2. The value of heritability of any quantitative characteristic does not remain unchanged in a given population, but may vary during the process of ontogenesis.

3. There is an inverse relationship between the value of heritability and the diversity of the growth conditions of a population. A high value of heritability in a progeny under relatively uniform conditions indicates a considerable genotypic variability of the parental individuals regarding the studied characteristic. A high index of heritability in a very diverse environment indicates a stability of the characteristic with respect to the varying conditions of the environment.

4. In uniform environmental conditions the value of heritability is increased regardless of the constancy of genotypic or genetic variances. In uniform but unfavourable growth conditions many genes which contribute to a high breeding value of the individual, have no effect, as a result of which genotypic variation, especially that of growth energy, decreases and so does the value of heritability.

5. In well established small populations, owing to a considerable fixation of genes, the heritability of characteristics is usually much lower than in large populations.

6. The theory of heritability requires further elaboration both as a whole and in details which concern the populations of forest trees.

In conclusion, it is necessary to have a brief look at the results of the analyses of the phenotypic and genotypic correlations of quantitative characteristics. Correlative relations of characteristics are widely used in breeding practice. However, most of this

type of research is devoted to the study of phenotypic correlations only. However, of great significance in breeding work are genotypic and genetic correlations, on the basis of which it is possible to predict how breeding for one characteristic may affect another. The importance of such research can be shown by the following example. In breeding for shoot growth energy in forest trees, one question remains open: is thick-branchiness, which, as we know, decreases the technical quality of wood, genetically connected with shoot growth energy? Observations made in a population of Scots pine have allowed us to state that the average value of the metameric correlation coefficient (paratypic correlation) between the amount of shoot growth in leader shoots and the amount of diameter growth of the corresponding side shoots equals $r_e = 0.936$, i.e. within the limits of the crown, branch thickness is functionally dependent on the shoot growth energy of the leader shoot. This correlation is only somewhat weaker at the population level (the coefficient of phenotypic correlation equalled $r_{ph} = 0.811$). Heritability of the shoot growth energy in leader shoots was $h^2 = 0.142$ and that of the diameter growth of side shoots $h^2 = 0.044$. According to FALCONER (1964) low values of heritability indicate that phenotypic correlation is mainly determined by paratypic correlation, i.e. by the correlation that arises from a common effect of the environmental factors on both of the characteristics. Therefore, we can assert that selection for shoot growth energy in the studied population of Scots pine did not lead to a genetic deterioration of the progeny as far as branch thickness was concerned. On the other hand, selection of fastgrowing individuals with thin branches becomes ineffective in such a population. This conclusion confirms the opinion of LANGNER (1958) concerning the difficulty of combining such characteristics as rapid growth and thin-branchiness.

These are some of the results of the quantitative analysis of the effect of the main factors (heritability and environment) in populations of forest trees. We can hope that a broad use of the methods of this analysis, notable for their strictness

and conceptual power, will raise forest genetics and forest tree breeding to a new, higher stage of development, from an art of individual originators to science, which

in the end will contribute to the genetic improvement of forests, and increase their productivity and quality.

SELOSTE:

GENOTYYPIN JA YMPÄRISTÖN VAIKUTUKSEN KVANTITATIIVINEN ANALYYSI METSÄPUUPOPULAATIOISSA

Aluksi todetaan, että perintötekijäin ja ympäristön vaikutusten tuntemisella on suuri merkitys niin tutkimukselle kuin käytännön metsänjalostuksellekin. Tärkein tutkimusaihe on populaatiokeräminen, erityisesti kvantitatiivisten ominaisuuksien muuntelu populaatioissa. Luokkamuuntelua osoitavissa ominaisuuksissa on todettu Hardy-Weinbergin mukaisia jakautumia, mutta yhdessä sukupolvessa todettu tilanne ei vielä todista genettistä tasapainotilaa. Kvantitatiivisten ominaisuuksien suhteen ongelma on vielä vaikeampi ratkaista. Ensiksi tarvitaan yksilön sisäisen vaihtelun (metameria) yksityiskohtainen selvitys. Sama ominaisuus voi ilmetä saman puun eri osissa eri asteisena. Korrelaatio saman ominaisuuden ilmenemismuodoissa puun eri osien välillä voi saman populaation yksilöissä olla erilainen. Useimmissa tapauksissa yksilöiden välinen vaihtelu populaatioissa

on todettu suuremmaksi kuin yksilöiden sisäinen (metameerinen) vaihtelu. Todettu fenotyyppinen muuntelu täytyy jakaa geneettiseen ja ei-geneettiseen komponenttiin.

Metsäpuiden kohdalla tämä työ on vasta alkua. Tähän mennessä kehitetyt teoreettiset mallit ja laskentamenetelmät heritabiliteetin määrittämistä varten eivät metsäpuiden kohdalla ole tyydyttäviä. Kirjallisuudesta poimitujen esimerkkien avulla osoitetaan, että pituuskasvulle saadut heritabiliteettiarvot ovat kovin vaihtelevia, usein jopa miinusmerkkisiä. Kirjoittajan omasta aineistostaan laskemat heritabiliteettiarvot ovat myös alhaisia. Eri kvantitatiivisten ominaisuuksien väliset geneettiset korrelaatiot ovat myös tärkeitä, jotta voitaisiin arvioida, miten yhden ominaisuuden jalostaminen vaikuttaa muihin ominaisuuksiin.