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TO THE EXPERIMENTAL CONFIRMATION OF THE HYPOTHESIS ABOUT AN ECO-GENETIC NATURE OF THE PHENOMENON GENOTYPE × ENVIRONMENT INTERACTION FOR WOODY PLANTS

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Abstract

The hypothesis of the eco-genetic nature of the phenomenon genotype × environment interaction (GEI) was developed by Russian scientists in 1984 after discovering an epigenetic phenomenon, the change in the spectra of genes that determine the same quantitative trait in annual crops with a change in the limiting factor. Perennial fruit trees are ideal objects for studying mechanisms of genotype × environment interaction. Genetic diversity within a fruit tree variety is practically zero as the trees are genetically homogeneous clones due to grafting, plants in a commercial garden are of the same age because of simultaneous planting, and they have the same soil area of nutrition, that is, there is no superposition of genetic and environmental competition. Annual growth in thickness of trunk and branches is very informative, and the pattern of a tree's annual growth rings records information about growth conditions, above all weather conditions, for many years. We studied apple (*Malus domestica* Borkh.) and apricot (*Prunus armeniaca* L.) varieties of northern and southern origin which possess different tolerance to weather stressors. To reveal alterations in the spectra of genes determining an increase in the thickness of a tree trunk and branches, we compared annual rings in the commercially grown trees of different adaptiveness which undergone the action of various limiting weather factors changing over a long period, particularly the effects of dry and hot years in contrast to the wet and cool years. It was revealed that wet and cold weather caused a bigger increase in branch thickness in the northern-originated apple variety Krasa Severa from Ekaterinburg with better genetic and physiological systems for cold resistance, whereas dry and hot weather similarly affected the southern-originated variety Bahorn from Uzbekistan. Pubescence of leaves and cuticle thickness which contribute to drought resistance cannot contribute to an increase in cold resistance. Hence, a change in the incremental thickness grades suggests a change in the set of component traits, and, therefore, the sets of genes that determine these traits, with a change in the limiting factors of the environment. Thus, due to the choice of the varieties of different origin and adaptability and the years with contrasting limiting environmental factors, we succeeded to discover the facts that were predicted by the hypothesis of the nature of the genotype × environment interaction phenomenon.

Keywords: nature of genotype × environment interaction, fruit crops, adaptability, change of gene spectra

In 1984, a group of executives of the cooperative programme DIAS (Genetics of production character of summer wheats of Western Siberia) discovered a new epigenetic phenomenon — changing the set of products of genes determining the same polygenic character. It has been established that productivity and yield are determined by changing sets and number of gene products at the change of the environmental limiting factors]1].

The concept of genotype × environment interaction (GEI) in a narrow sense appeared at the start of ecological tests of pre-varieties and varieties. The phenomenon of changing productivity ranks in a set of varieties was identified, when they were tested in different years in the same geographical location, or in the same year, but in different locations. The GEI phenomenon appears if there are at least two genotypes, and it is expressed in the change of their ranks on production characters at least in two environments [3, 4]. If in one econiche the ranks of four varieties in terms of productivity are 1, 2, 3, 4, and in the other 1, 2, 3, 4, then GEI is equal to zero. If in one environment the ranks are 1, 2, 3, 4, and in the other 4, 1, 3, 2, then GEI is present. When the same genotype is studied in different environments (comfortable and uncomfortable), then GEI phenomenon cannot be observed, because only non-heritable changes of characters (modifications) will appear [5]. Y.N. Sinskaya [6], and later S.G. Inge-Vechtomov [7] noted that the deficit of knowledge about the nature of modifications remains a significant problem in genetics. The mechanisms of modifications are being studied intensely now [8-12], but there is no complete understanding of their nature so far. GEI is a more complex phenomenon than modification and, possibly, this is why there was not any hypothesis on GEI nature until the end of the 20th century either in classical genetics (Mendelism), or in biometrics and modern molecular genetics.

At the beginning of the 20th century, K. Pierson [13] formulated a rigorous definition for GEI phenomenon and suggested a rank correlation coefficient for its measurement. Later R.A. Fisher [14] created two-way analysis of variance for a more rigorous quantitative estimate of GEI effects. Now, there are different statistical methods for quantitative determination of GEI effects [15-20]. However, their estimate in different environments without understanding of the nature (mechanisms) of this phenomenon does not allow building a system of forecasts for values and shifts of GEI effects, which does not allow predicting productivity ranks and yields of a specific variety in different geographical locations.

The hypothesis of the GEI nature evolved from the theory of ecological and genetic organisation of polygenic characters (TEGOPC) was formulated as follows: "Mechanism of GEI effects is the change of set of gene products available in cells of varieties and determining the production character at the change of the environment lim factor". The hypothesis was checked on the character "transpiration rate" (TR) in two groups of varieties of summer wheat: group I with large, closely placed stoma on leaves and thick, dense cuticle, and group II with small, widely-spaced stoma and thin, spongious cuticle. The morning TR was more intense in group I varieties, the day (cuticular) TR was more intense in group II. In the morning, the TR differences between groups of varieties were determined by genetic systems checking the size and spacing of stoma on the leave, at noon — by wax synthesis genes determining the cuticle thickness and density. Herewith, the TR ranks of groups changed, i.e. the GEI effect appeared. Its mechanism is evident: the change of sets of gene products determining the TR character [22].

When solving the vertical inheritance problems, one should select objects with short onthogenesis period (drosophila, arabidopsis, coliform bacterium). To decrypt the GEI phenomenon mechanisms (the problem of "heritable implementation"), due to absolute lack of knowledge of the paths from GEI to a particular gene [23], we selected an ideal, as we deem, object (perennial fruit plants) and an ideal character (the thickness of annual wood increment in the required year).

The perennial fruit plants have some advantages for research into GEI mechanisms. They propagate by graftage, i.e. each variety is a clone, inside which the genetic diversity on character determination is actually equal to zero. The orchards of perennial fruit trees are planted simultaneously with same-age plantlets, i.e. all the trees are the same age. The trees are planted equispaced, they have equal growing spaces (there is no genetic and environmental competition). To increase the yields, several varieties are planted in the orchard, so that intercross would occur due to pollen of different genotypes; it precludes any diminishing of yield due to self-fertilization. Many varieties of fruit trees have been created all over the world (from northern to southern), so one can always find varieties different in terms of adaptability in the same orchard. The character "annual growth ring area" in the required year (on the trunk or branch saw cut) enables estimating the averaged quality of growth conditions in each year for a long-term period. This character logs information about integral conditions of the year, which is thus preserved for the whole life of the tree.

In this paper, the hypothesis of ecological and genetic nature of GEI phenomenon is experimentally checked for the first time on an ideal object, the varieties of perennial fruit crops.

The objective of the research was decryption of epigenetic nature of "genotype × environment interaction" (GEI) by experimental verification of the GEI nature hypothesis.

Techniques. The research was carried out in K.A. Timiryazev Experimental Production Farm (the Krasnodar Territory, Ust-Labinsk city), Tsentralnoye Experimental Production Farm CJSC, FSBSI North Caucasian Federal Scientific Centre for Horticulture, Grape Culture, Wine-Making and Plodovod LLC (Krasnodar city). It included the study of varieties with different degree of adaptability depending on their origin: apple tree varieties (*Malus domestica* Borkh.) Bakhorn from Uzbekistan and Krasa Severa from Yekaterinburg (Tsentralnoye Experimental Production Farm CJSC), apricot variety (*Prunus armeniaca* L.) New Jersey from USA and local variety Krasoschyokii (K.A. Timiryazev Experimental Production Farm LLC, Plodovod LLC).

The annual wood thickness increment rank change was analyzed in three surfaces from three trees according to methodology of G.N. Terenko [20]. The thickness was measured on cores extracted from the main branches or on branch saw cuts using a drill. In the weather database the years with different combination of temperature and humidity regime were selected (humid and cold; dry and hot), that is those, in which the annual increment thickness ranks change and GEI phenomenon manifestation were expected. The average growth ring width and the ring area were measured for the required year.

During statistical data processing, the average values of the annual growth ring width or area (M) and errors of mean (±SEM) were calculated.

Results. The hypothesis postulates that the GEI nature is the change of gene products determining the same character at change of the environment limiting factor [21, 22, 25]. In a dry hot year, the annual wood increment thickness shall be greater in a southern drought resistant variety, because it carries the best genetic and physiological systems of drought and heat resistance formed by natural and artificial selection over the years of the variety breeding in dry hot zone. In a humid and cold year, the annual growth thickness shall be greater in a variety created in a moderate or northern zone and having better cold-resistant systems.

The obtained data confirmed validity of the formulated hypothesis (Table 1, 2). In a humid and cols year, the annual branch thickness increment shall be greater in the northern apple tree variety Krasa Severa, in a dry and hot year — in southern variety Bakhorn.

Since such component characters contributing into the drought resistance enhancement as pubescence of leaves and cuticle thickness cannot contribute into the cold resistance in principle, it means that the change of ranks on the annual wood growth thickness indicates to the change of the set of adaptability component characters and the gene products sets determining these characters at the change of the environment lim factor.

1. The annual primary branch grown thickness in two apple tree varieties (*M*±SEM, orchard planted in 2007, rootstock M 9, Tsentralnoye Experimental Production Farm CJSC, Krasnodar city)

Variety	Origin	Average annual growth ring thickness, mm		Annual growth ring area, mm^2	
		2011 (HC)	2012 (DH)	2011 (HC)	2012 (DH)
Bakhorn (n = 9)	Uzbekistan	0.78±0.19	0.95±0.18[a]	1.91±0.09	2.83±0.07
Krasa Severa (n = 9)	Sverdlovsk	1.50±0.46	0.75±0.12[a]	7.07±0.22	1.77±0.11

N o t e. HC — humid and cold year, DH — dry and hot year. Statistically significant at significance level 5%. Between the variants marked with letter ([a]) there are no statistically significant differences at p = 0.05.

2. The annual primary branch grown thickness in two apricot tree varieties (*M*± SEM, orchards planted in 2006, rootstock: cultivar plantlets, wild apricots)

Variety	Annual growth ring area, mm^2		
	2007	2010	2014
	P l o d o v o d LLC (Krasnodar city)		
New Jersey (n = 9)	27.45±0.77	196.37±0.98	341.12±7.00
Krasnoschyokiy (n = 9)	23.12±0.84	119.94±0.88	428.50±1.42
	K.A. T i m i r y a z e v E x p e r i m e n t a l P r o d u c t i o n F a r m L L C (Ust-Labinsk city))		
New Jersey (n = 9)	29.00±2.53	185.00±3.81	697.34±4.72
Krasnoschyokii (n = 9)	13.52±0.13	73.30±0.34	498.40±1.12

N o t e. VDH — very dry and hot yea; LDH — less dry and hot year, WI — winter icing (there was no icing in K.A. Timiryazev Experimental Production Farm LLC in 2014).

Summer 2007 in Krasnodar city and Ust-Labinsk city was very hot and dry, summer 2010 was characterized also by high air temperatures on the background of long-term moderate drought. Herewith, conditions in Ust-Labinsk city were significantly severer in terms of water availability and increased temperature regime in summer vegetation period.

The annual growth ring areas in both inspected apricot species appeared to be much greater in 2010, which means more comfortable growth conditions (see Table 2). The significant differences in the annual growth ring areas of primary branches of Krasnoschyokii variety trees in 2007 and 2010 were caused by the variety's response in yield, which in this case ensured a more intense growth of young apricot trees.

In 2014 from January 22 until 24, an abnormal weather phenomenon was observed in Krasnodar city – ice rain (precipitation in the form of a rain at air temperature 0 or –1...–2 °C). It resulted in gradual icing of trees, which remained in such a state for 2 days. The icing caused significant damages of vegetative organs and reproductive buds of all fruit cultures (especially apricots) and, consequently, inhibition of growth. There was no such a phenomenon in Ust-Labinsk city. In Ust-Labinsk city, the variety New Jersey exceeded the variety Krasnoschyokii in terms of the annual growth thickness in all three years, and lim factor "ice rain" in Krasnodar city resulted in the change of ranks of varieties, i.e. to expressed manifestation of GEI phenomenon (see Table 2).

Thus, by means of selecting the years contrast in terms of lim factors from the weather data bank and by selecting varieties different in terms of origin and adaptability, it became possible to discover the facts, which were predicted by the hypothesis of "genotype × environment interaction" (GEI) nature. The experimentally validated hypothesis of the nature (mechanisms) of GEI phenomenon allows forecasting GEI phenomena in a new environment, if typical behavior of lim factors is known for it. Knowing the geographical locations of origin of the varieties used for the experiment and the main lim factors in such locations and comparing them to typical behavior of lim factors in the new environment where we want to introduce our varieties, one can forecast the varieties' ranks on yields before carrying out of the experimental introduction. It opens perspectives of a new approach to selection of varieties introduced into other zones and allows assessing specific genetic drawbacks of each variety for their subsequent elimination using selection methods for the complete compliance of each new variety with typical lim factors of the growing zone.

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