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THE MODELS FOR ESTIMATION OF A COMBINING ABILITY OF VARIETIES AND ROOTSTOCKS TO FORECAST YIELDING IN APPLE TREES

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Abstract

Vegetative reproduction of the best varieties of fruit crops by grafting on clonal rootstocks provides uniform trees, early onset of fruiting, it allows to create dense plantings. In order to identify rootstock, which gives maximum crop yield of the grafted varieties, a large number of expensive tests of cultivar-rootstock combinations, lasting dozens of years, are carried out, and the results of such empirical selection were reported in numerous publications. Therefore, so far there is no theory or methods of forecasting yields for trees grafted on indicators of variety and rootstocks. To increase efficiency of such searches and to lower expenses and time for their carrying out, there is the only possible way based on theoretical researches targeted to development of the principles of prediction of signs of grafted trees according to characteristics of varieties and rootstocks. Our researches summarized herein, are curried out to clarify the features of use of the principles and mathematical models of biometrical genetics for knowledge of communications in a system «grafted components—grafted plant». The implementation of this program started with studying possible applications of the formulas for calculation of the combinational ability of varieties and rootstocks as measures of their influence on the quantitative signs of the resulting combinations. The data on yielding in 28 such combinations (4 grades of apple, namely Jonathan, Golden Delicious, Idared, and Korah, and 7 rootstock, 1-48-1, 1-47-55, 1-48-46, M2, M3, M4 and M7), averaged up for 21 years fruiting, were used as the experimental material. It is established that the genotypes of varieties differ on both the productivity averaged for all rootstocks and the degree of dependence of this sign from the rootstocks. Besides, the rootstocks unequally differentiate varieties according to phenotypic manifestation of productivity. The widely used method and mathematical models for an assessment of combining ability of the parental lines of F_1 hybrids can be successfully applied to estimate the influence of common and specific combining ability of the varieties and rootstocks on crop yield in grafted trees. It is based on the fact that in variation of the total combining ability of grafting components the general combining ability (GCA) as a function of additive genes, similar to that observed in the parental forms of hybrids, is relatively prevalent. When formulas of biometrical genetics are used, the calculations show that the general combining ability (GCA) of grafting components is 6.4 times more than their specific combining ability (SCA). It caused high efficiency of the forecasts on productivity of grafted trees based on the GCA of varieties and rootstocks. The high coefficient of correlation between the actual and predicted estimates of productivity has been noted (r = 0.930). Close correlation between the predicted on the GCA and actual estimates of productivity of the variety—rootstock combinations shows the high degree of integration of grafting components in the manifestation of quantitative sings of a grafted tree. The preliminary analysis revealed the possibility for further improving accuracy of such forecasts due to separating the linear component from the dispersions of the specific combinational ability (SCA) estimates.

Keywords: models, variety, rootstock, combining ability, the forecast yield.

«Manage means to foresee»
Catherine II the Great
«To foresee means to manage»
Blaise Pascal

Modern industrial gardening is based on vegetative propagation of the best varieties of fruit trees grafted on clonal rootstocks (1, 2). This ensures uniformity of trees, compact planting and early onset of fruiting. The influence of rootstocks on yields is also important. Thus, due to favorable rootstocks the apple and pear yields increased 1.5-2.0 times (3-6).

To find the rootstock contributing to the maximum yield of the grafted cultivar, the expensive and long termed empirical investigations must be conducted using numerous combinations. The only way to intensify and accelerate the search is to develop the principles and models for predicting traits of grafted plants basing on characteristics of the grafted varieties and the rootstocks (7-9).

First attempts were made long ago. F. Kobel' (10) wrote that the causes of unequal effects of different rootstocks are difficult for elucidation, and the question is remains poorly studied. N.P. Krenke, a foremost authority in plant transplantation, stated the impossibility to select rootstocks basing on theoretical approach (11). Afterward, J. Shmadlak (1), with respect to complicated mutual effects between grafted varieties and rootstocks made a conclusion about little knowledge of their relationships. In next period the problem still remained unsolved. In numerous publications the results of empiric selection were most reported, so, nowadays, there is neither theoretical background, nor practical recommendation on forecasting yields in grafted plants on the base of characteristics of varieties and rootstocks.

Investigation and long practical experience show that the yield in grafted trees is influenced by both variety and rootstock genotypes. Thus, the study of their interaction should be based on the principles of genetics. The peculiarities of mutual effects in different combinations were being studied for long time (12-14), but these investigations have been undertaken to elucidate the inheritance of modification in one of the component caused by other component in the combination. As far as it had been found out no inheritance, and the modification were termed temporary, so the forecasting modifications due to grafting has been considered irrelevant for genetics (13). Nevertheless, it should be noted that these modifications are temporary in sense of occurring until one of grafting component affects the other component but not transferring by seed progeny. Moreover, S.Ya. Kraevoi (14) reported the modifications in the grafted variety are adequate to a specificity of the rootstock genotypes. In industrial gardening a specific effect of rootstock genotype on grafted fruit crop variety traits is extremely imported, being a genetic background for forecasting most effective combinations. Though high yield in the best of such combinations is a temporary modification in a genetic sense, it is the constant parameter for gardeners since they use only grafted plantations and do not propagate plants via seeds.

For studying modifications caused by mutual effect of grafted varieties and rootstocks, the samples with different qualitative traits should be used. S.Ya. Krevoi showed (14) that in tomato plants after grafting tobacco or datura plants, the nicotine or atropine were synthesized instead of solanine, and a potato variety used as a cion induced tuber formation in a wild species, the *Demissum*. But for practical gardening the quantitative polygenic traits, i.e. yield value, adaptability, etc., are most important (15). Variability of these traits is the subject of biometrical genetics, but even in a fundamental monograph of K. Mather and J. Jinks (16) the problems of grafting was not raised. According to their opinion, the correlations are mainly due to gene linage but not the pleiotropy. Though such a reaction of the variety to rootstocks can not been explained by gene linkage, the principles and mathematical models of biometrical genetics should be used to study an interaction between the grafting components, mostly formulas for estimation of combining ability of the variety and the rootstock because the combining ability reflects the extent of their impact on qualitative traits in a pair combination.

In trees, long time from seedling to flowering and fruiting restricts the reconnaissance crosses in genetic study of parental forms and selection of prospective donors for breeding (17). Despite that, these experiments are conducted to study the structure of genotypic dispersions (18-20) and to estimate general and specific combining ability of crossed components (21-23). But the scientists who studied the inheritance of variability of polygenic traits in fruit crops did not try to use the principle and models of biometrical genetics when examined the effect of varieties and rootstocks on yields and other properties of grafted plants. There was even no attempt to use the formulas for calculation of combining ability at crosses to estimate the combining ability at grafting, though the grafted plant is a holistic organism (1, 2, 11, 12), in some way similar to that of F_1 plant containing hereditary factors of gametes of both parents.

We aimed to study the efficacy of mathematical models of biometrical genetics under estimation of general and specific combining ability in cions and rootstocks used for forecasting yield production in the grafting combinations, and also to elucidate the extent of integration of grafting component into the traits of grafted plants.

Technique. Four tested apple varieties, i.e. Jonathan, Golden Delicious, Idared and Korah, are winter ripening with branched spreading crown shape. Each variety was grafted on 7 rootstocks, the 1-48-1, 1-47-55, 1-48-46, M2, M3, M4 и M7 (Zonal Research Institute of Orcharding and Viniculture; the garden was planted in 1977). The rootstocks were mostly middle-height, except a semidwarf M7. M2, M3, M4 and M7 were originated from Great Britain, and 1-48-1, 1-47-55, 1-48-46 were selected in Zonal Research Institute of Orcharding and Viniculture.

For all tested combinations the same scheme for planting (7×5 m) was applied and the same agrotechnologies and protection methods were used. The weather was mostly typical for the region, but different stressors also occurred.

Yield (x_{ik}) of *i-th* variety on *k-th* rootstock was averaged for 21 year fruiting to minimize random errors under estimation.

Indicators of combining ability of grafting components and forecasted yield of grafted trees were calculated using the formulas of biometrical genetics (24-26). The results were subjected to correlation and regression analyses on the entire data set and by stratified sampling. To determine the reliability of correlation between forecasted and actual yield the calculated correlation coefficients were compared with their critical values at different levels of significance with respect to degrees of freedom.

Results. Fruit yield, as an integrated index of adaptability and productivity of perennial fruit plants, reflected the effects of weather stressors.

1. Average yields (x_{ik}, centner/ha) **in different grafted combinations of apple trees** (OPKh «Tsentral'noe», Krasnodar, 1982-2002)

Variety	Rootstock							Average, $x_{i\cdot}$
	1-48-1	1-47-55	1-48-46	M2	M3	M4	M7	
Jonahtan	129,3	122,7	173,1	169,2	158,8	195,2	146,7	156,4
Golden Delocopus	187,4	202,9	204,4	213,9	202,0	211,3	187,4	201,3
Idared	196,4	186,7	232,7	203,6	187,5	217,4	185,3	201,4
Korah	189,9	166,5	235,0	232,5	234,5	241,6	212,2	216,0
Average, $x_{\cdot k}$	175,8	169,7	211,3	204,8	195,7	216,4	182,9	$x_{\cdot\cdot}$ = 193,8

Comments. $x_{i\cdot}$ — average value for individual variety on each rootstocks, $x_{\cdot k}$ — average value for each variety on indicidual rootstock, $x_{\cdot\cdot}$ — average value over all combinations.

Our tests revealed significant differences in yield production between the combinations, from x_{ik} = 122.7 centner/ha in Jonathan grafted on 1-47-55 to x_{ik} = 241.6 centner/ha in Korah on M4 (Table 1). General variability appeared to be influenced by the cions rather the than by rootstocks. A specific effect of individual variety and rootstocks was also found out. For instance, the 1-47-55 and M4 rootstocks were the best and the weakest differentiators, respectively, the differences between maximum and minimum actual yields were 80.2 and 46.4 centner/ha, respectively. Among the varieties, the reaction to rootstock genotype was the highest in Jonathan varieties and the lowest in Golden Delicious, the same differences were 72.5 and 26.5 centner/ha, respectively. Unexpected capabilities of the rootstocks to differentiate the grafted varieties and different response of the varieties to rootstock specificity allow to suggest different combining ability of the tested grafting components.

To estimate the traits of parents via their hybrids, two parameters, i.e. general combining ability and specific combining ability, are proposed in biometrical genetics (24). As V.K. Savchenko described (25), general combining ability (GCA) means an average genotypic value of a parental line in hybridization, and specific combining ability (CCA) reflects the frequency of better or worse combinations than those predicted from an average quality of crossed lines. There is a basic mathematical model for estimation of a combining ability, and its modification was proposed by L.V. Khotyleva and LA. Tarutina (26) for full diallel crosses:

$$x_{ik} = x.. + g_i + g_k + S_{ik} + r_{ik} + e_{ik}, \qquad [1]$$

with x_{ik} as the value of each hybrid from crossing *i*-th and *k*-th parents; x.. as an average value for the hybrids of all used combinations; g_i as GCA effect of *i*-th parent; g_k as GCA of *k*-th parent; S_{ik} as SCA effect of *i*-th and *k*-th parents; r_{ik} as a reciprocal effect; e_{ik} as random deviations for each hybrid.

Diallel analysis allows to elucidate structure of inherited variability for qualitative traits in plants subject to number of requirements, but these limitations are not essential under estimation of a combining ability, thus making this approach widely applicable (26). It also allows to suggest this method and mathematical modeling to be applied with a view to calculation of the combining ability in the variety and rootstock genotypes from yield values in their combinations.

Using the equation [1], it should be noted that the reciprocal grafting is meaningless, thus, r_{ik} should be excluded. Since the data in Table 1 are averaged for 21 years, e_{ik} random deviations are of the minimum, allowing their conditional neglecting to simplify calculations. Then the following formula could be used to analyze the combining ability in t he grafted combinations:

$$x_{ik} = x.. + g_i + g_k + S_{ik}, \qquad [2]$$

g_i being the GCA_i effect of the variety and g_k being the GCA_k effect of the rootstock. For g_i and g_k the data from Table 1 and the formulas are used:

$$g_i = x_{i}. - x.., \qquad [3]$$

$$g_k = x._{k} - x.., \qquad [4]$$

meaning the GCA_i effect of *i*-th variety is equal to its average yield on all rootstocks minus an average yield of all tested combinations. Similar calculations should be also carried out for GCA_k of each *k*-th rootstock.

2. GCA effects of apple tree varieties (g_i, centner/ha) **and rootstocks** (g_k, centner/ha)**, and the forecasted yields** ($\widehat{x}_{ik}$, centner/ha) **in their combinations** (OPKh «Tsentral'noe», Krasnodar, 1982-2002)

Variety	Rootstocks							g_i
	1-48-1	1-47-55	1-48-46	M2	M3	M4	M7	
Jonathan	138,4	132,3	173,9	167,4	158,3	179,0	145,5	–37,4
Golden Delicious	183,3	177,2	218,8	212,3	203,2	223,9	190,4	7,5
Idared	183,4	177,3	218,9	212,4	203,3	224,0	190,5	7,6
Korah	198,0	191,9	233,5	227,0	217,9	238,6	205,1	22,5
g_k	–18,0	–24,1	17,5	11,0	1,9	22,6	–10,9	

To elucidate whether the mathematical methods and models commonly used for estimation of combining ability in F_1 parents are applicable at grafting, and to verify the possibility for forecasting yield in the grafted trees from GCA and SCA of the variety and the rootstock, it is necessary to carry out the calculations and estimate correlations between the forecasted and actual values. According to experimental data (see Table 1), we calculated g_i and g_k for each variety and rootstock (Table 2).

Different formulas are used to calculate the yield in grafted trees from GNA together with SCA generated deviations. Contribution of g_i and g_k effects to GCA based yield x_{ik} could be calculated as

$$\widehat{x}_{ik} = x.. + g_i + g_k, \quad [5]$$

or

$$\widehat{x}_{ik} = x_i. + g_k, \quad [6]$$

as far as from [3] $x_i. = g_i + x..$.

Formula [6] shows that the yield generated by GCAs of *i*-th variety and *k*-th rootstock without SCA effects could be denoted as an average yield $x_i.$ of the *i*-th variety adjusted for g_k as a GCA_k effect of *k*-th rootstock. In fact, the $\widehat{x}_{ik}$ values calculated from [5] and [6] are the same (see Table 2).

Comparing $\widehat{x}_{ik}$ (see Table 2) to x_{ik} (see Table. 1), reliability could be estimated for forecasting yield in a variety-to-rootstock combination from the GCA effects of its components. The correlation was high ($r = 0.930$) exceeding 0.1 % significance level, with determination coefficient $Cd = 86.5$ %. This indicates a relatively high efficiency of these forecasts, which allow to use only the most promising combinations of grafted varieties and rootstocks, without analyzing combination with reliably low predictive yields. According to assessment of the significance of combining ability of genotypes for breeding, P.F. Rokitskii wrote (24) that these methods were first used on corn, but also are applicable on other plants or animals due to being much more informative if compared to empiric analysis of crossed race, lines, or animal breeds. For forecasting yields under grafting, the importance of this method is as much higher, as the tree testing is longer then annual crop F_1 testing.

Data in the Tables 1 and 2 indicate that no forecasted value was accurately the same as the actual value, though in 7 of 28 forecasts the deviations were less then 2 centner/ha (e.g. Jonathan on 1-48-46, M2, M3 and M7 rootstocks, Golden Delicious on M2 and M3, and Korah on 1-48-46). An explanation arises when comparing [2] and [5]. Thus, the forecast, if estimated on GCA for the variety and rootstocks (see Table 2), ignores effects S_{ik} of their interaction, i.e. the SCA (22). S_{ik} is calculated as

$$S_{ik} = x_{ik} + x.. - x_i. - x._k; \quad [7]$$

data for these calculations are taken from Table 1 and the results are presented in Table 3.

3. Effects of specific combining ability (S_{ik}, centner/ha) **in variety and rootstock combinations in apple trees** (OPKh «Tsentral'noe», Krasnodar, 1982-2002)

Variety	Rootstock						
	1-48-1	1-47-55	1-48-46	M2	M3	M4	M7
Jonatha	–9,1	–9,6	–0,8	1,8	0,5	16,2	1,2
Golden Delicious	4,1	25,7	–14,4	1,6	–1,2	–12,6	–3,0
Idared	13,0	9,4	13,8	–8,8	–15,8	–6,6	–5,2
Korah	–8,1	–25,4	1,5	5,5	16,6	3,0	7,1

The same as at estimation of SCA in parents of F_1, the characteristic feature of grafted varieties and rootstock SCAs is that the sum of these effects is equal to zero for each variety and for columns in the table, the deviations due to rounding being less than 0±1) (see Table 3):

$$(\sum_k S_{ik} = 0).$$

When comparing the SCAs (see Table 3), an average effects due to interaction of Jonathan with rootstocks were found to be minimal, the 1-47-55 affects the varieties most significantly, and the effects of M2 and M7 were minimal. We failed to reveal clearer patterns of S_{ik} variability fro all the data from Table 3. Only in Jonathan and Korah a trend was observed of S_{ik} increase as x_{ik} rises.

In general, for the entire dataset (see Tables 1 and 3) the correlation between x_{ik} to S_{ik} was although significant at the 5% level, but low (r = 0,368 at Cd = 13,5 %). It means yield forecasting in grafted trees basing on SCAs, as the effects of variety and rootstock interaction, in unreliable. In this connection it should be noted that in biometrical genetics an interaction means the deviation from additivity. In our case the $\widehat{x}_{ik}$ values in Table 2 were calculated for an additive contribution of the components. Withal their values could be calculated not only by [7], but also as:

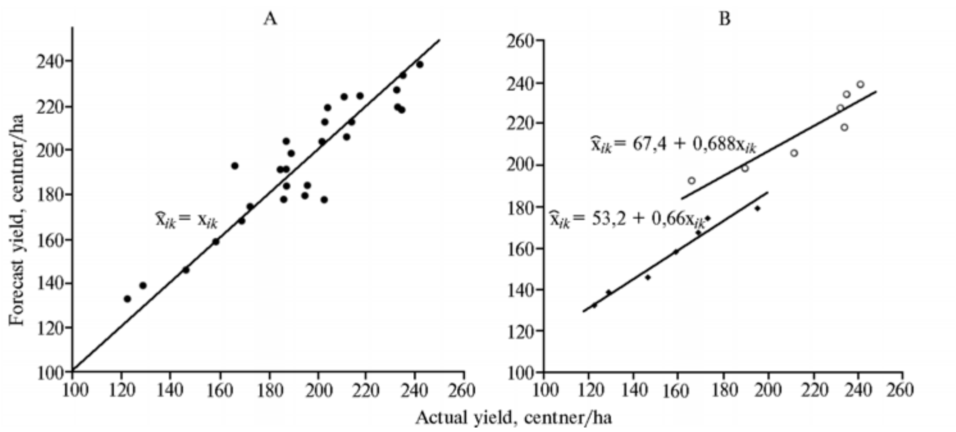
$$S_{ik} = x_{ik} - \widehat{x}_{ik}, \qquad [8]$$

since an interaction hereby implies a nonadditivity. Hereinabove, there was Cd = 86.5 % shown for the yield variations in grafted trees predicted from GCAs of the variety and the rootstock, and Cd = 13.5 % due to unpredictable effects of their SCAs, thus the predictable variation for the entire set of studied combinations being 6.4 times higher comparing to unpredictable.

Obtained results indicate that the further improvement of yield forecasting in grafted trees requires the in-depth analysis of this trait variation caused by the unpredictable effects of SCSs of the components by means of both biological and statistical approaches. Of biological traits, the morphophysiological features of varieties, rootstocks and grafted trees with different SCA effects should be investigated. At statistical analysis a dispersion of the variety and rootstock interaction should be separated into the predictable linear and unpredictable nonlinear components.

Some bases for underestimating S_{ik} values in individual combinations of i-th varieties and k-th rootstocks could already be seen from data of Tables 1 and 2. So far as the same averaged g_i values for i-th variety were used in calculation, the differences of $\widehat{x}_{ik}$ between any two varieties were the same for all rootstocks. Accordingly, a specific response of i-th variety to the rootstock was not considered. For instance, in Golden Delicious and Idared the average yield values $x_{i\cdot}$, as well as g_i, differed by 0.1 centner/ha, resulting in the same difference of 0.1 centner/ha between their $\widehat{x}_{ik}$. In Korah and Jonathan, the differences between average $x_{i\cdot}$ values and also between forecasted $\widehat{x}_{ik}$ values were identical and equal to 59.6 centner/ha. Because of this calculation method, k-th rootstock contributed the same g_k value to x_{ik}, predicted from GCA, therefore, for example, the differences of $\widehat{x}_{ik}$ values for each variety on 1-48-1 and 1-47-55 were the same and equal to 6.1 centner/ha. As a result of such estimation of $\widehat{x}_{ik}$ on GCAs of k-th and i-th components, the forecasts are overestimated in low-yielding combinations, and underestimated in high-yielding combinations, leading to an overestimation of variety and rootstock SCAs and less effective prediction. This disparity could be assessed by regression (Fig.) of plotted $\widehat{x}_{ik}$ on x_{ik} from Tables 1 and 2 .

According to [3], [4] and [5] used for calculation of $\widehat{x}_{ik}$ from OCAs of the variety and the rootstock, a regression coefficient (b) for $\widehat{x}_{ik}$ on x_{ik} should be equal 1, so the drown line should cross the axes at 0. It means that in case the actual yield is higher than an average $x_{\cdot\cdot}$ by 1 centner/ha, the forecasted yield value should also increase by 1 centner/ha on average with a regression line defined by $\widehat{x}_{ik} = x_{ik}$. The line on a graph (see Fig., A) fits the plotted points quite enough. Obviously, not all of the points fall on the line due to calculated GCA effects of grafting components, and these deviations reflect both SCAs impact and the differences between actual and forecast estimations.



A forecast yield calculated from general combining ability of the grafting components ($\hat{x}_{ik}$, centner/ha)**, the actual yield** (x_{ik}, centner/ha) **summarized for all grafted apple trees (Jonathan, Golden Delicious, Idared and Korah) (●)** (A)**, and those for Jonathan (♦) or Korah** (○) **varieties** (B) (OPKh «Tsentral'noe», Krasnodar, 1982-2002).

On the left (see Fig., A), all the points for 28 combinations of four varieties on 7 rootstocks are visualized as a single aggregate group, while two groups can be seen if each individual variety on different rootstocks is analyzed (see Fig., B). Particularly, for Jonathan and Korah there were free terms in $\hat{x}_{ik}$ on x_{ik} regression equations, and the regression coefficients decreased to b = 0,674 on average resulting in $^2/_3$ centner/ha increase of forecast yield predicted from GCAs, when the actual yield increased by 1 centner/ha. It is due to smaller differences between forecast yield estimations calculated as [3], [4] and [5]. Similar system errors cause the point deviations from $\hat{x}_{ik} = x_{ik}$ line (see Fig., A) and SCAs overestimation, and decrease efficacy of yield prediction from GCAs of grafting components. Therefore, the improved models free from these limitations allow us to forecast yield of grafted trees more accurate. Basing on them, a new method and formulas could be allowed to separate SCA effect into two components, the predictable linear and unpredictable non-linear.

In existing manuals on GCA and SCA assessment in F_1 parents (22-24) the system errors that arise at SCA calculations and yield prediction for the hybrids from GCA of the parents, are not considered. Moreover, there is no attempt to divide SCA effects into linear and non-linear. An estimation of combining ability of the parental plants is empirical in itself and based on numerous crosses and tests (25-27). L.V. Khotyleva and L.A. Tarutina ascertain all these complications being a result of poor understanding the genetic basis of a combining ability (26). The same is the reason of poor understanding whether an entire organism of grafted tree is functionally similar to F_1 hybrid. However, rather high accuracy of yield forecast from GCAs of the variety and the rootstocks shows a significant integration of the traits at grafting.

So, genotypes of apple varieties differ on both the productivity averaged for all rootstocks and the degree of dependence of this sign from the rootstocks. Besides, the rootstocks unequally differentiate varieties according to phenotypic manifestation of productivity. This variability leads to yield variations in grafting combinations from 122.7 to 241.6 centner/ha observed in the course of 21 year examination. parental lines of F_1 hybrids can be successfully applied to estimate the influence of common and specific combining ability of the varieties and rootstocks on crop yield in grafted trees. It is based on the fact that in variation of the total combining ability of grafting components the general combining ability (GCA) as a function of additive genes, similar to that observed in the parental forms of hybrids, is relatively prevalent. When formulas of biometrical genetics are used, the calculations show that the general combining ability (GCA) of grafting components is 6.4 times more than their specific combining ability (SCA). It caused high efficiency of the forecasts on productivity of grafted trees based on the GCA of varieties and rootstocks. The high coefficient of correlation between the actual and predicted estimates of productivity has been noted (r = 0.930). Close correlation between the predicted on the GCA and actual estimates of productivity of the variety—rootstock combinations shows the high degree of integration of grafting components in the manifestation of quantitative sings of a grafted tree. The preliminary analysis revealed the possibility for further improving accuracy of such forecasts due to separating the linear component from the dispersions of the specific combinational ability (SCA) estimates.

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