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Original Paper

Genetic determination of elements of the soybean yield structure and combining ability of hybridization components

Oleksandr Mazur[1], Ihor Kupchuk*[1], Oksana Voloshyna[1],
Volodymyr Matviiets[2], Natalia Matviiets[2], Olena Mazur[1]

[1]*Vinnytsia National Agrarian University, Vinnytsia, Ukraine*
[2]*Carpathian State Agricultural Experimental Station of the Institute of Agriculture of the Carpathian region of NAAS, Ivano-Frankivsk, Ukraine*

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The value of soybean varieties in terms of general combining ability (GCA), constants of specific combining ability (SCA) and their variances in terms of productivity elements in two-tester top-cross crossings were determined. Differentiating ability of Hoverla and KyVin testers was revealed. The degree and frequency of positive transgressions in hybrid populations were established.There were established high effects of general combining ability by plant height and height of attachment of lower beans in Sawyer 2-95 variety and KyVin tester; by the number of productive units in Sawyer 2-95 variety and Hoverla tester; by pod number per plant in Sawyer 2-95 and Kyivska 97 and Hoverla tester; by seed number per plant in Kyivska 97 and Medea varieties and Hoverla tester; by 1,000 seed weight in Sawyer 2-95 and Kyivska 97 varieties and Hoverla tester; by seed weight per plant in Medea and Kyivska 97 varieties and Hoverla tester; in terms of yield in Medea variety and Hoverla tester. It was found that additive effects of genes were dominating in genetic control of the traits of plant height, height of attachment of lower beans, number of productive nodes, pod number per plant, seed number per plant, 1,000 seed weight, seed productivity and yield, the share of non-additive effects of the gene interaction was lower, however, it was also reliable. Analysis of dominance indicators revealed combinations of crosses that were distinguished by overdominance of these traits and had significant breeding value: Sawyer 2-95 × Hoverla, Kyivska 97 × Hoverla, Medea × Hoverla.

Keywords: variety, tester, combining ability, variance, overdominance, additive genes, traits

1 Introduction

The most widely-used methods of soybean (*Glycine max*) breeding include mass and individual selection, intraspecific and remote hybridization, experimental mutagenesis and a combination of these methods (Carroll et al., 1985; Riabukha and Kobyzieva, 2010; Kyrychenko, et al., 2016), genetic engineering methods (Babych, et al., 2011; Paziuk et al., 2021), heterosis breeding (Mazur et al., 2021a). The method of synthetic breeding involves a sufficiently large volume of crossings with the involvement of the genetically diverse source material. However, in the initial stages of implementation of the breeding program from a large mass of the breeding material, 60–90% of valuable genotypes is culled out and irretrievably lost (Litun et al., 1980; Poberezhets et al. 2021).

Boroevich (1984) considered selection in the breeding nursery F2 and F3, based on an eye-catching assessment, and on the productivity of plants or components of the crop to be inefficient and unreliable. The main traits for plant selection in the initial stages of breeding are the number of productive nodes, pod number per node and seed number per pod (Shevchenko, 1975), pod number per node, pod number per plant, seed number per pod, and 1,000 seed weight (Xing-Dung, 1958; Palamarchuk and Telekalo, 2018).

Hybridological analysis of productivity elements in F1 hybrid combinations from the crossing of cultivated soybean cultivars and wild forms of Ussuri soybean showed that positive overdominance was detected by the following complex or specific traits: plant height,

***Corresponding author:** Ihor Kupchuk, Vinnytsia National Agrarian University, 3 Sonyachna str., 21008 Vinnytsia, Ukraine; kupchuk.igor@i.ua. ORCID: https://orcid.org/0000-0002-2973-6914

total node number, pod number per plant, seed number per plant, seed weight per plant, and 1,000 seed weight (Babych et al., 2012). Hybridization in soybean breeding is one of the main methods of creating the source material. However, when using this method, breeders have to perform a large number of combinations of crossings and, as a rule, annually study many hybrids. However, successful crossings are quite rare. There are cases when economically valuable varieties did not give practical results when involved in crossings (Mazur et al., 2021b).

The increase in hybridization efficiency is facilitated by the use of parental forms with previously studied high combining ability (CA) in crossbreeding (Litun et al., 2004). Reliable information on the value of certain forms for hybridization is provided by the methods of assessing the general and specific combining ability. In addition, various modifications of diallel analysis are used as well as initially simple pair hybridization between varieties followed by crossing of first-generation hybrids. It is most rational to apply the following order for selection of parent pairs:

1. selection of a group of varieties according to the ecological-geographical principle using local ones well-adapted to given conditions, as well as introduced highly productive forms;
2. distribution of these samples into clusters by genetic divergence;
3. inclusion of valuable varieties from individual clusters in the most suitable for the given conditions crossing scheme to assess the overall combining ability (Litun et al., 2004).

Attention is paid to the assessment of the combining ability of the original forms by the soybean productivity. When splitting hybrids, a significant variability of traits can be observed, the manifestation of which is different from the parental forms. Therefore, according to some researchers, for practical breeding, positive transgressions obtained at the expense of recombinants for various traits are of great importance (Litun et al., 2004).

In order to increase genetic diversity, it is advisable to involve in the selection process not only samples of the cultivated type of plants, but also fasciated forms with a parallel study of the combining ability of soybean samples involved in the selection process to identify genotypes that can provide high heterosis. This will contribute to the detection of highly productive forms in subsequent generations and facilitate the selection of components for hybridization (Mazur et al., 2021b). There can be distinguished general combining ability (GCA) and specific combining ability (SCA). GCA characterizes the average value of the parent components in all hybrid combinations, while SCA refers to individual combinations, when they appear to be worse or better than those expected on the basis of the average value of the varieties studied. Combining ability is determined using special schemes: complete and incomplete diallel and top-cross crossings. For preliminary evaluation of the source material, it is recommended to first use top-crosses (Gorodov, 1986). Specific combining ability of each hybrid combination is determined by the trait value deviation for this combination from the average GCA for two parental forms. GCA is determined by the additive effects of genes, while SCA is determined by the effects of dominant and epistatic interaction of genes (Khotyleva and Tarutina, 1990; Mazur et al., 2019). Analysis of the genetic structure of GCA and SCA suggests that under the absence of epistasis, GCA is determined by the additive and moderately dominant type of gene action, while SCA is determined by overdominance. Under the presence of epistasis, it can be assumed that both types of combining ability contain an epistatic part: GCA includes a medium epistatic effect, and SCA has an epistatic effect associated with individual hybrid combinations (Turbin et al., 1974; Voskresenskaya and Shpota, 1976).

The study of the frequency and degree of transgressions in F2-F4 hybrid generations of soybean show that they depend on the genotype and generation. The degree of transgression is not related to its frequency, the last indicator in the vast majority of hybrid combinations was characterized by a sharp decrease in the third generation compared to the second and its increase in the fourth generation, which must be taken into account in breeding practice (Litun et al., 2004).

2 Material and methods

The research was conducted in conditions of the research field of Vinnytsia National Agrarian University. This area is characterized by gray forest soils of light medium-loamy mechanical composition. The soil has average humus content, high phosphorus supply, and low potassium supply (Kovbasa et al., 2021). Soil acidity is close to neutral. In 2018, in particular April and May, hydrothermal conditions were characterized by insufficient moisture deficiency, especially in April, 14 mm or 39 mm less. Lower precipitation was also observed in May and was 15 mm or 21 mm less compared to the average data. Sufficient rainfall of 186 mm was observed in June, which was 109 mm more compared to the average long-term data. The temperature regime differed little from the average long-term data.

The field research was carried out according to the generally accepted methods (Biliavska et al., 2021). The main method of creating the initial material for soybean breeding was used, namely intraspecific hybridization followed by individual selection among hybrid offspring.

F2 hybrid combinations from intervarietal crossings of soybean varieties of different ecological and geographical origins were studied. There were used top-cross crossings, which made it possible to assess both GCA and SCA – the effects of five varieties: Sawyer 2-95, Ustia, Medea, Kyivska 97 and early Kharkivska, which differed in the level of manifestation of valuable farming characteristics as well as ecological and geographical origin. The trials used a two-test analysis of the combining ability of soybean varieties of hybrid populations of the second generation. Evaluation was carried out by the following traits: "plant height", "height of attachment of lower beans", "number of productive nodes on the main stem", "pod number per plant", "seed number per plant", "seed weight per plant", "1,000 seed weight", "yield". To evaluate the effects of GCA and variance of SCA, crossings were performed according to the full top-cross scheme. Varieties were taken as maternal components, testers as paternal ones. The effects of GCA and variance of SCA were calculated using Excel computer program (Wolf et al., 1980).

The degree of phenotypic dominance was calculated by the formula (Griffing, 1950):

$$hp = \frac{F1 - Mp}{P\max - Mp'} \quad (1)$$

where: *hp* – the degree of dominance; *F*1 – the value of the trait in the hybrid; *Mp* – midparent; *P*max – parent with greatest expression of character

Grouping of the obtained data was performed according to the classification (Beil and Atkins, 1965) (Table 1).

Table 1 Grouping by the degree of phenotypic dominance

Dominance class	Numeric value *hp*
Heterosis (overdominance)	(H >+1)
Partial positive dominance	$+0.5 < hp \leq 1$
Intermediate inheritance	$-0.5 \leq hp \leq 0.5$
Partial negative inheritance	$-1 \leq hp \leq -0.5$
Depression	$hp < -1$

The degree and frequency of transgressions of quantitative characteristics according to the formulas are proposed (Voskresenskaya and Shpota, 1976):

$$Td = \frac{Mg - Mp}{Mp} \times 100\% \quad (2)$$

where: *Td* – transgression degree in *F*2 (%); *Mg* – maximum value of the trait in the hybrid; *Mp* – maximum value of the trait in the best parental form

$$Tf = \frac{A}{B} \times 100\% \quad (3)$$

where: *Tf* – the frequency of transgressions (%); *A* – the number of hybrid plants that predominated the best parental form by the trait; *B* – the number of hybrid plants in the combination analyzed by the trait

3 Results and discussion

Analysis of variance of the data by plant height, attachment of lower beans and elements of the yield structure obtained by crossing these varieties is presented in Table 2 and Table 3. It showed that in this group of varieties there were substantial genotypic differences by these traits. However, highly significant effects of the general and SCA of the studied varieties were established. Significant difference between the variants of GCA and SCA indicated both the importance of additive and non-additive gene action. In addition, it should be noted that the mean square of the GCA for the traits mentioned dominated over the mean square of the SCA, which ranged from 0.7 to 10,617, and those of the SCA from 0.02 to 99.5. GCA/SCA ratio appeared to be high and significant over the years of research.

Therefore, there should be noted the dominance of additive effects of genes in the control system of plant height, height of attachment of lower beans, number of productive nodes, pod number, seed number per plant, seed weight per plant, 1,000 seed weight, and yield. Cognition of the processes and mechanisms of controlling inheritance of useful traits is the most important problem of breeding. The main goal of this issue is to disclose genotypic potential of each parental form and its impact on offspring. Although the role of both partners in hybridization is equivalent, it is important to know whether one of the partners of crossbreeding is in its active or passive form in order to control the inheritance of individual traits (Volkodav, 2001; Mykhailov et al., 2011).

Analysis of the combining ability of varieties by plant height in topcross crossings is shown in Table 4. High reliable GCA effects, which determine high growth of plants, were observed in Sawyer 2-95 (+10.72), Medea (+6.88) and Kyivska 97 (+5.14) varieties. Negative effects of GCA were observed in Ustia (-13.9) and early Kharkivska (-8.84) varieties. KyVin tester provided a high reliable GCA effect (+0.93), and Hoverla tester provided a low one, which must be taken into account when crossing.

Table 2 Analysis of variance of combining ability by plant height, attachment of lower beans and elements of the yield structure

Trait	Source of variation	Sum of squares	Number of degrees of freedom	Mean square	Criterion *F*		
					actual	theoretical	
						0.05	0.01
Plant height	GCA of parental forms	8.8	1	8.8	44	4.21	7.68
	GCA of maternal forms	920	4	230	1150	2.73	4.11
	SCA	25.8	4	6.5	32.5	2.73	4.11
	random deviation	5.5	27	0.2	–	–	–
Height of attachment of lower beans	GCA of parental forms	0.7	1	0.7	100	4.21	7.68
	GCA of maternal forms	8.4	4	2.1	300	2.73	4.11
	SCA	0.13	4	0.03	4.3	2.73	4.11
	random deviation	0.2	27	0.007	–	–	–
Number of productive nodes on the main stem	GCA of parental forms	1.05	1	1.05	105	4.21	7.68
	GCA of maternal forms	24.4	4	6.09	609	2.73	4.11
	SCA	0.09	4	0.02	2.0	2.73	4.11
	random deviation	0.31	27	0.01	–	–	–
Pod number	GCA of parental forms	26.5	1	26.5	220.8	4.21	7.68
	GCA of maternal forms	55.3	4	13.8	115	2.73	4.11
	SCA	9.6	4	2.4	20	2.73	4.11
	random deviation	3.3	27	0.12	–	–	–

Table 3 Analysis of variance of combining ability by the yield structure elements

Trait	Source of variation	Sum of squares	Number of degrees of freedom	Mean square	Criterion *F*		
					actual	theoretical	
						0.05	0.01
Seed number per plant	GCA of parental forms	22.07	1	22.07	105.1	4.21	7.68
	GCA of maternal forms	358.6	4	89.7	427	2.73	4.11
	SCA	3.79	4	0.94	4.47	2.73	4.11
	random deviation	5.6	27	0.21	–	–	–
Seed weight per plant	GCA of parental forms	6.6	1	6.6	132	4.21	7.68
	GCA of maternal forms	42.3	4	10.6	212	2.73	4.11
	SCA	0.56	4	0.14	2.8	2.73	4.11
	random deviation	1.23	27	0.05	–	–	–
1,000 seed weight	GCA of parental forms	107.8	1	107.8	77	4.21	7.68
	GCA of maternal forms	1,692	4	423.0	302.1	2.73	4.11
	SCA	22.7	4	5.7	4.1	2.73	4.11
	random deviation	37	27	1.4	–	–	–
Yield	GCA of parental forms	1,701	1	1,701	243	4.21	7.68
	GCA of maternal forms	42,466.7	4	10,617	1,516.7	2.73	4.11
	SCA	398.1	4	99.5	14.2	2.73	4.11
	random deviation	189	27	7.0	–	–	–

Table 4 Combining ability of soybean varieties by plant height

Varieties	GCA effect of varieties	SCA effect		Constant
		tester 1 Hoverla	tester 2 KyVin	SCA of varieties
Sawyer 2-95	10.72	-1.21	1.21	2.94
Ustia	-13.9	-2.43	2.43	11.89
Medea	6.88	0.38	-0.38	0.30
Kyivska 97	5.14	1.53	-1.53	4.73
Early Kharkivska	-8.84	1.72	-1.72	5.96
GCA effects of testers		-0.93	0.93	–
SCA variance of testers		3.04	3.04	–
LSD 0.05 of GCA in varieties		0.92	–	–
LSD 0.05 of GCA in testers		0.58	–	–

Combination Sawyer 2-95 × KyVin provided high growth due to the high additive action of both the maternal form with the value of GCA effect (+10.72) and the paternal form with the value of GCA effect (+0.93). In addition, this combination provided high effects of non-additive gene interaction (SCA = +1.21).

Higher plant height rates were provided by combinations Medea × Hoverla and Kyivska 97 × Hoverla, which were characterized by high GCA effects of the maternal form (+6.88 and +5.14) and high effects of non-additive gene interaction (SCA = + 0.38 and +1.53), despite a low value of the GCA effect (-0.93) of the tester. It is necessary to note Ustia variety, which had additive effects of genes of short height, but when crossed with KyVin variety, it was characterized by high plant height rates due to high GCA and SCA of the parental form.

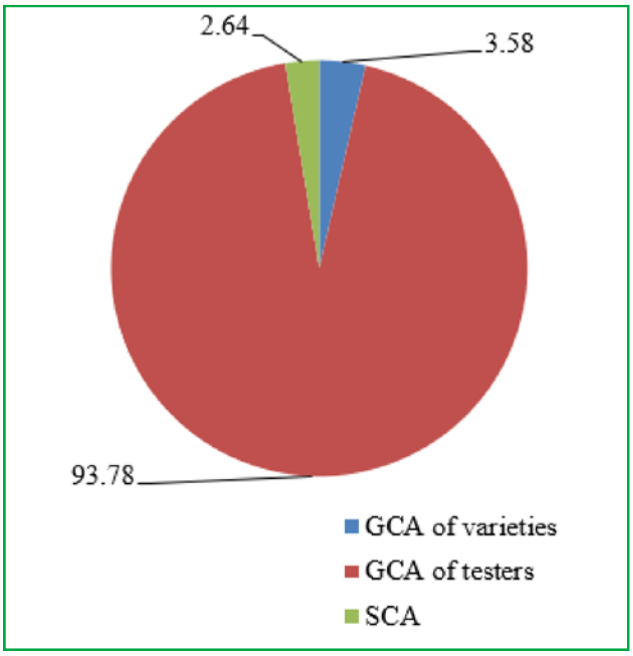

Figure 1 The share of genotypic variability of plant height

When analyzing genotypic variability of plant height, it should be noted that in terms of the trait expression the highest influence was made by the additive effects of variety genes (93.78%), much lower influence was made by the additive effects of tester genes (3.58%), while non-additive effects of gene interaction had the lowest influence (2.64%) (Figure 1).

High reliable GCA effects by the height of attachment of lower beans were observed in Sawyer 2-95 (+1.31) and early Kharkivska (+0.7) varieties (Table 5). Negative GCA effects were observed in Ustia (-0.82) and Kyivska 97 (-1.14) varieties. KyVin tester provided a high reliable GCA effect (+0.27), while Hoverla tester provided a low one, this must be taken into account during crossing. Combination Sawyer 2-95 × KyVin provided high attachment of lower beans due to the high additive action of the maternal form, GCA (+1.31), and the paternal form, GCA (+0.27). This combination also provided high effects of non-additive gene interaction in pair crossing (SCA = +0.18). There should also be noted hybrid combination early Kharkivska × Hoverla having the effects of GCA (+0.7) and SCA (+0.016) in pair crossing with the tester, which indicates the importance of action other than additive genes and non-additive effects in expressing the height of lower beans.

Combinations Medea × Hoverla and Kyivska 97 × Hoverla provided higher rates of attachment of lower beans, which were characterized by negative effects of maternal GCA (-0.05 and -1.14) and high effects of non-additive gene interaction (SCA = + 0.17 and +0.015). Despite a low value of the GCA effect (-0.27) tester, this indicates the importance of influencing the formation of the height of attachment of lower beans, along with the additive interaction of genes and non-additive interaction.

It should be noted that the additive effects of genes of varieties appeared to be more significant compared to

Table 5 Combining ability of soybean varieties by the height of attachment of lower beans

Varieties	GCA effect of varieties	SCA effect		Constant
		tester 1 Hoverla	tester 2 KyVin	
Sawyer 2-95	1.31	-0.18	0.18	0.07
Ustia	-0.82	-0.02	0.02	0.001
Medea	-0.05	0.17	-0.17	0.06
Kyivska 97	-1.14	0.015	-0.015	0.001
Early Kharkivska	0.7	0.016	-0.016	0.001
GCA effects of testers		-0.27	0.27	
SCA variance of testers		0.003	0.003	
$LSD_{0.05}$ of GCA in varieties			0.18	
$LSD_{0.05}$ of GCA in testers			0.11	

Table 6 Combining ability of soybean varieties by the number of productive nodes on the main stem in top-cross crosses

Varieties	GCA effect of varieties	SCA effect		Constant
		tester 1 Hoverla	tester 2 KyVin	
Sawyer 2-95	0.65	0.1	-0.1	0.02
Ustia	-2.72	0.12	-0.12	0.03
Medea	1.2	-0.13	0.13	0.03
Kyivska 97	1.55	-0.02	0.02	0.001
Early Kharkivska	-0.68	-0.07	0.07	0.01
GCA effects of testers		0.32	-0.32	
GCA variance of testers		-0.001	0.001	
$LSD_{0.05}$ of GCA in varieties			0.22	
$LSD_{0.05}$ of GCA in testers			0.13	

testers in the genotypic structure of trait variability, the share of the first one was 74.05%, and the share of the second one was 24.82%, the impact of non-additive effects was 1.12% (Figure 2).

Thus, additive effects of varieties (maternal forms) had a predominant effect on the formation of the height of attachment of lower beans in hybrid combinations, as well as less influence of non-additive effects when crossing them with testers.

The value of varieties was also determined by the number of productive nodes on the main stem in top-cross crosses (Table 6). According to the GCA effects, Kyivska 97 (+1.55), Medea (+1.2) and Sawyer 2-95 (+0.65) were distinguished. Negative effects of GCA were observed in Ustia (-2.72) and early Kharkivska (-0.68) varieties. Hoverla tester provided a high reliable GCA effect (+0.32) and KyVin tester a low one, which should be taken into account when breeding new soybean varieties. Combination Sawyer 2-95 × Hoverla provided a high number of productive nodes due to a high additive action of genes of maternal form, GCA (+0.65) and paternal form, GCA

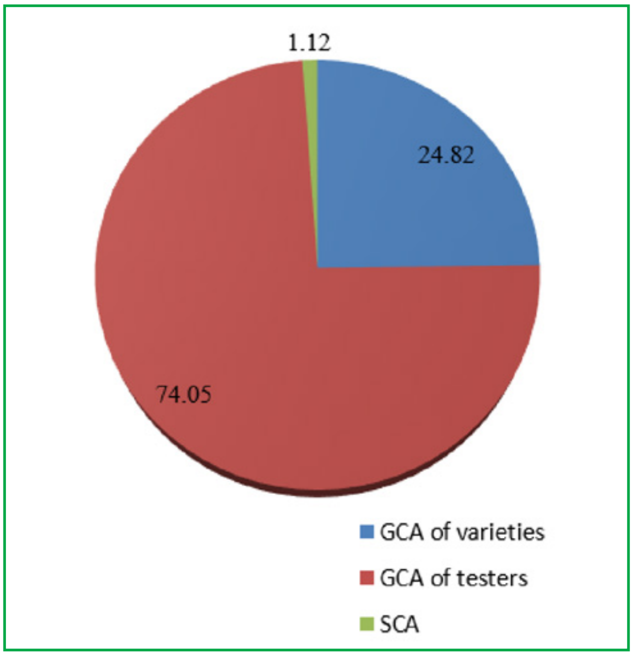

Figure 2 The share of genotypic variability of the height of attachment of lower beans

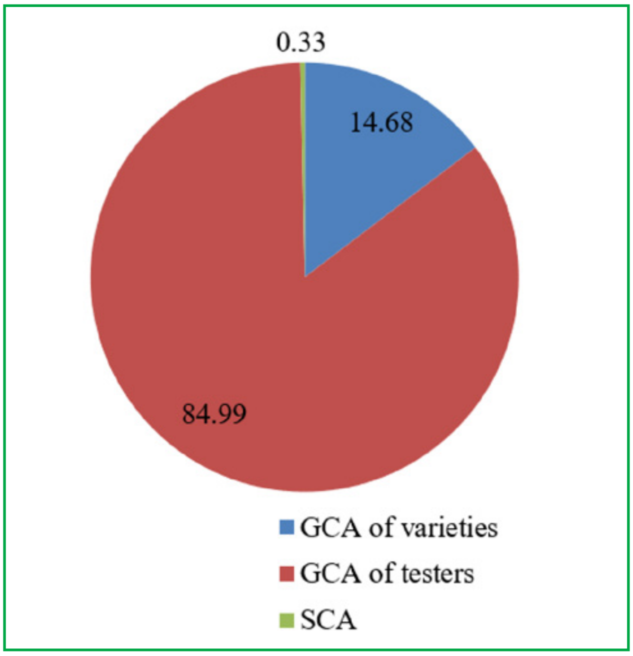

Figure 3 The share of genotypic variability of the number of productive nodes

(+0.32). This combination also provided positive effects of non-additive gene interaction in pair crossing (SCA = 0.1).

Hybrid combinations Medea × KyVin and Kyivska 97 × KyVin, which showed high values of the effects of GCA (+1.2) and (+1.55) of maternal forms, and under pair crossing with KyVin tester, there was achieved an increase in the number of productive stems due to non-additive gene interactions (SCA = + 0.13 and +0.02). Despite negative values of GCA effects of the maternal form (-2.72), hybrid combination Ustia × Hoverla increased the number of productive nodes on the main stem when crossed with Hoverla tester having high GCA effect (+0.32) and non-additive effects of SCA gene interaction (+0.12).

It should be noted that the additive effects of varietal genes were much higher compared to testers in the genotypic structure of variability of productive nodes, and the share of the first one was 84.99%, and the share of the second one was 14.68%, the impact of non-additive effects was 0.33% (Figure 3).

Based on top-cross crossings, it was found that Kyivska 97, Medea and Sawyer 2-95 varieties contain favorable additive genes that control the number of productive nodes on the main stem and should be included in hybridization when creating new soybean varieties. Analysis of the combining ability of soybean varieties by pod number per plant showed that the best one in terms of GCA effects was the variety Kyivska 97 (+3.43), and early Kharkivka appeared to be significantly lower (-3.96) (Table 7).

Hoverla tester provided a high reliable GCA effect (+1.63), and the KyVin tester provided a low one, this must be taken into account when conducting selection. Hybrid combination Sawyer 2-95 × Hoverla provided high SCA effects (+0.47) against the background of the tester with high GCA (+1.63). Combination early Kharkivska × Hoverla provided an increase in pod number per plant due to the high additive action of genes of the parental component GCA (+1.63) and the effects of non-additive interaction of SCA genes (+1.52) in pair crossing. In Ustia × KyVin and Medea × KyVin combinations, the increase in pod number was mainly caused by the effects of non-additive interaction of SCA genes (+1.09) and (+1.02). At the same time, GCA of the maternal forms of these varieties was unreliable and amounted to (0.06) and (0.14).

Analysis of the genotypic variability of pod number showed that the additive interaction of genes of the parental forms (testers) had a leading share (62.06%) in determining this trait (Figure 4).

Table 7 Combining ability of soybean varieties by pod number per plant

Varieties	GCA effect of varieties	SCA effect		Constant
		tester 1 Hoverla	tester 2 KyVin	
Sawyer 2-95	0.33	0.47	-0.47	0.44
Ustia	0.06	-1.09	1.09	2.38
Medea	0.14	-1.02	1.02	2.09
Kyivska 97	3.43	0.12	-0.12	0.03
Early Kharkivska	-3.96	1.52	-1.52	4.63
GCA effects of testers		1.63	-1.63	
SCA variance of testers		0.84	0.84	
$LSD_{0.05}$ of GCA in varieties			0.72	
$LSD_{0.05}$ of GCA in testers			0.46	

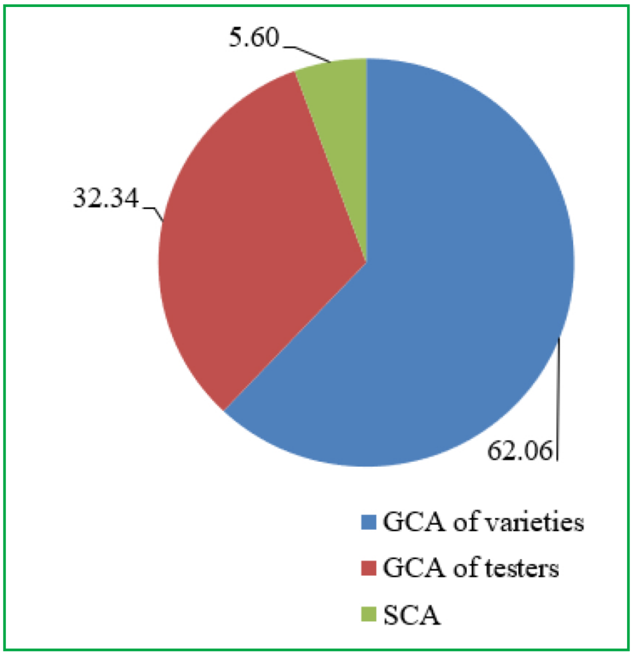

Figure 4 The share of genotypic variability of pod number per plant

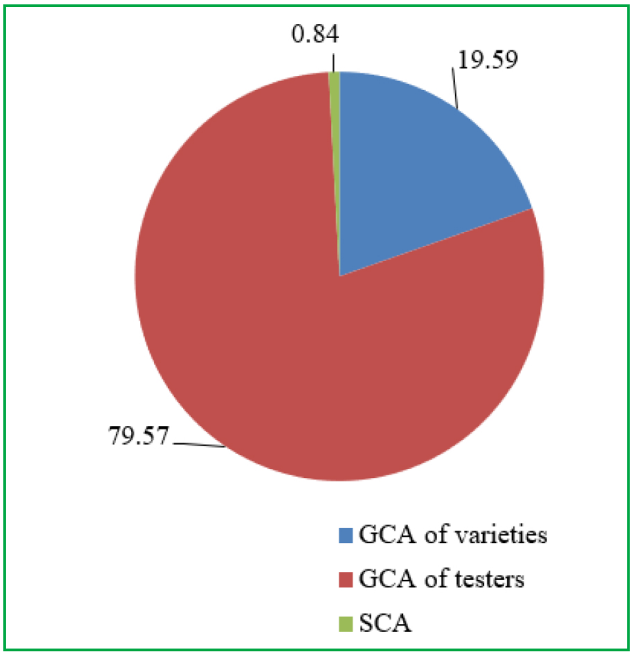

Figure 5 The share of genotypic variability of seed number per plant

The shares of additivity of maternal forms were lower and amounted to 32.34%, and the shares of non-additive interaction of genes were even lower and amounted to 5.6%, respectively, for varieties and testers. High general combining ability by seed number per plant was observed in Kyivska 97 (+ 10.59) and Medea (+1.43) varieties. Low GCA was observed in Sawyer 2-95 (-3.79), Ustia (-1.22) and early Kharkivska (-7.01) varieties (Table 8). Hoverla variety used as a tester provided a high GCA effect (+1.48). Combination Kyivska 97 × Hoverla provided a high seed number per plant due to a high additive action of both the maternal form with the value of GCA effect (+10.59) and the paternal form with the value of GCA effect (+1.48). In addition, the effects of non-additive gene interactions (SCA = +0.21) had an effect on the formation of seed number in this combination. Medea × Hoverla hybrid combination provided high SCA effects (+0.30) against the tester having high GCA (+1.48).

In the structure of the genotypic variability of seed number per plant, a great share was occupied by the additive effects of variety genes – 79.57% (Figure 5). Additive effects of tester genes, which accounted for 19.59%, also had a relatively high share, while non-additive effects of genes accounted for a smaller share in the structure of genotypic variability, namely 0.84%.

Table 9 shows the effects of combining ability of varieties by 1,000 seed weight. GCA effects of varieties differed significantly. High significant GCA effects were observed in the following varieties: Medea (+13.19), Sawyer 2-95

Table 8 Combining ability of soybean varieties by seed number per plant

Varieties	GCA effect of varieties	SCA effect		Constant
		tester 1 Hoverla	tester 2 KyVin	
Sawyer 2-95	-3.79	0.71	-0,71	1.02
Ustia	-1.22	-0.12	0.12	0.028
Medea	1.43	0.30	-0.30	0.184
Kyivska 97	10.59	0.21	-0.21	0.089
Early Kharkivska	-7.01	-1.11	1.11	2.47
GCA effects of testers		1.48	-1.48	
SCA variance of testers		0.295	0.295	
$LSD_{0.05}$ of GCA in varieties			0.93	
$LSD_{0.05}$ of GCA in testers			0.59	

(10.66) and Kyivska 97 (7.47), low GCA effects were observed in early Kharkivska (-18.15) and Ustia (-13.17) varieties.

Hoverla variety with GCA effect of +3.28 appeared to be the best testers. SCA effects of varieties against the background of tester 1 (Hoverla) in the combinations were positive in Kyivska 97 (1.53), Sawyer 2-95 (0.72), Ustia (0.89) and Medea (-2.74) varieties. The additive effects of varietal genes were dominant in the genetic control of 1,000 seed weight – 78.85%, as well as the additive genes of testers – 20.09%, while non-additive effects of gene interaction accounted for only 1.06% (Figure 6). Kyivska 97, Medea and Sawyer 2-95 varieties were characterized by high additive effects by 1,000 seed weight (+ 2.54; + 1.62; + 0,57), while early Kharkivska (-2,88) and Ustia (-1,85) – reliably low (Table 10).

Hoverla variety appeared to be the best tester by seed weight per plant, and its GCA effect was (+0.81). SCA

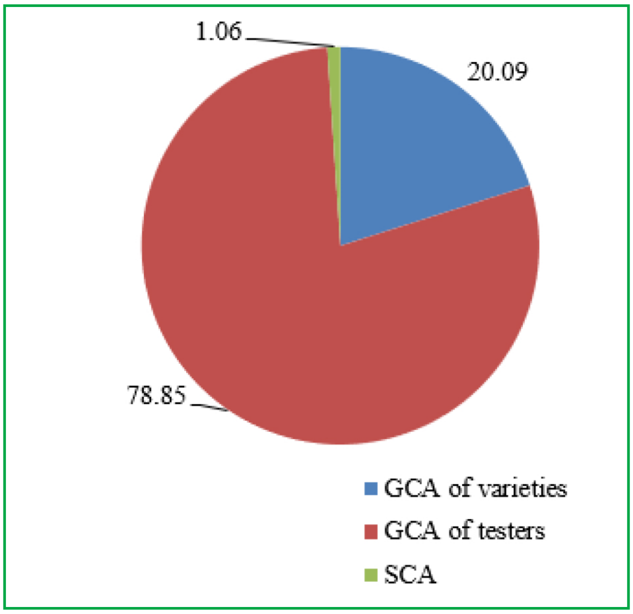

Figure 6 The share of genotypic variability by 1,000 seed weight

Table 9 Combining ability of soybean varieties by 1,000 seed weight in plants

Varieties	GCA effect of varieties	SCA effect		Constant
		tester 1 Hoverla	tester 2 KyVin	
Sawyer 2-95	10.66	0.72	-0.72	1.03
Ustia	-13.17	0.89	-0.89	1.59
Medea	13.19	-2.74	2.74	15.1
Kyivska 97	7.47	1.53	-1.53	4.66
Early Kharkivska	-18.15	-0.39	0.39	0.30
GCA effects of testers		3.28	-3.28	
SCA variance of testers		-0.08	-0.08	
$LSD_{0.05}$ of GCA in varieties			2.39	
$LSD_{0.05}$ of GCA in testers			1.51	

Table 10 Combining ability of soybean varieties by 1,000 seed weight

Varieties	GCA effect of varieties	SCA effect		Constant
		tester 1 Hoverla	tester 2 KyVin	
Sawyer 2-95	0.57	-0.1	0.1	0.022
Ustia	-1.85	-0.11	0.11	0.025
Medea	1.62	0.16	-0.16	0.05
Kyivska 97	2.54	0.36	-0.36	0.27
Early Kharkivska	-2.88	-0.31	0.31	0.19
GCA effects of testers		0.81	-0.81	
SCA variance of testers		0.029	0.029	
LSD0.05 of GCA in varieties			0.44	
LSD0.05 of GCA in testers			0.28	

effects of varieties against the background of tester 1 (Hoverla) in the combinations of Medea and Kyivska 97 were positive (+0.16 and +0.36). Ustia and Sawyer 2-95 varieties in a specific combination with tester 2 (KyVin) had positive SCA (+0.11) and (+0.1). The worst varieties for combining seed weight per plant were Ustia and early Kharkivska (with tester 1 – Hoverla) and Kyivska 97 variety (with tester 2 – KyVin), in which SCA effects were low and amounted to -0.11; -0.31 and -0.36). Early Kharkivska (SCA=+0.31) was well combined with KyVin tester. However, the best tester with high GCA was Hoverla (tester 1), which had a significantly higher effect +0.81.

Analysis of the share of genotypic variability of seed weight per plant indicated the main influence of additive effects of genes (99.2%) (Figure 7).

At the same time, the share of maternal forms accounted for 61.0%, and paternal (testers) – 38.2%. There was observed insufficient effect of non-additive effects of genes – 0.8%.

The analysis of effects of the combining ability of soybean varieties by the yield (Table 11) showed that the highest reliable positive GCA effect was observed in three varieties: Kyivska 97 (+73.6), Medea (+56.71), Sawyer 2-95 (19, 17), while negative GCA effects were observed in early Kharkivska (-97.77) and Ustia (-51.71) varieties. Hoverla tester was the best in terms of yield, its GCA was significantly higher (+13.04). High SCA with tester 2 (KyVin) was observed in early Kharkivska variety (+5.97). In the combination of Medea × Hoverla crosses, in addition to high yields, along with the additive effects of genes of parental components, non-additive effects of the SCA genes (4.21) also contributed to the formation of high yields. It should be noted that hybrid combination Kyivska 97 × KyVin had a crucial role of additive effects of maternal genes (+73.6) and non-additive effects of SCA pair combination genes (+3.90). Similarly, it is necessary to note the combination of Sawyer 2-95 × KyVin, the yield of which was determined by the influence of additive effects of maternal genes (+19.17) and non-additive effects of genes of the pair combination SCA (+4.73).

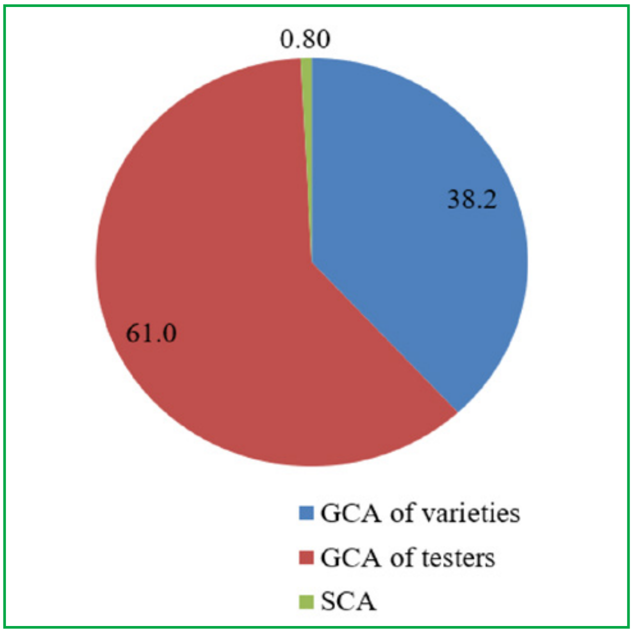

Figure 7 The share of genotypic variability by seed weight per plant

Analysis of the structure of genotypic variability by the plant yield showed that contribution of non-additive effects was insignificant (0.8%), and the share of tester variance was higher, amounting to 13.7%. A great share of genotypic variability of hybrids depended on the additive genes of varieties by 85.5% (Figure 8). Analysis of the structure of genotypic variability by the yield showed that a crucial role in determining the trait was played by the additive effects of genes of varieties and testers,

Table 11 Combining ability of soybean varieties by the plant yield

Varieties	GCA effect of varieties	SCA effect		Constant
		tester 1 Hoverla	tester 2 KyVin	
Sawyer 2-95	19.17	-4.73	4.73	44.76
Ustia	-51.71	10.39	-10.39	215.99
Medea	56.71	4.21	-4.21	35.51
Kyivska 97	73.60	-3.90	3.90	30.47
Early Kharkivska	-97.77	-5.97	5.97	71.32
GCA effects of testers		13.04	-13.04	
SCA variance of testers		40.07	40.07	
$LSD_{0.05}$ GCA in varieties			5.42	
$LSD_{0.05}$ GCA in testers			3.43	

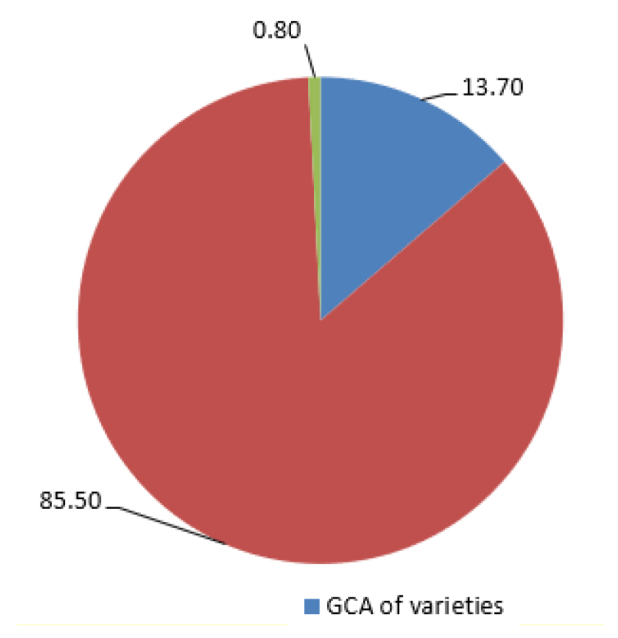

Figure 8 The share of genotypic variability by the yield

which accounted for 85.5 and 13.7%, respectively, and the share of non-additive effects was low (0.8%).

According to the research conducted by Biliavska et al. (2012) at the present stage, soybean breeding is aimed at further reducing the duration of the growing season, increasing the adaptability of varieties, their manufacturability and productivity. Quantitative traits that determine morpho-biological parameters of soybean plants are controlled polygenically, i.e. the contribution of each gene is insignificant, but they affect trait variability. Efficiency of selection in each of the following generations depends on the degree of individual variability (Riabukha, 2009; Biliavska. and Kornieieva 2012). Modern soybean varieties should be characterized by a set of valuable farming features, the main of which include the elements of seed productivity and high technological effectiveness, i.e. suitability for mechanized harvesting. Intraspecific hybridization is the main method of improving existing and creating new varieties, and it makes it possible to obtain a wide range of recombinant forms. Among them, undesirable genotypes are rejected, and the best are selected by special methods and propagated to create new genotypes (Biliavska, 2015). According to Mykhailov et al. (2011), overdominance was the main type of inheritance of such as traits as duration of the growing season, elements of plant structure (height, number of nodes on the main stem, seed weight, pod number, seed number) in most of the hybrids studied. The epistatic effect of interaction of genes that control duration of the growing season, plant height, seed number and seed weight per plant was revealed. No epistatic effects were recorded on the number of nodes on the main stem. The trait "number of nodes on the main stem" was controlled by allelic interaction of genes; the share of dominance of most nodes was 0.65, which indicated the significance of dominance in the control of this feature. When creating new soybean varieties, the main direction of breeding is selection for productivity, so the study of the effectiveness of identification of transgressive forms on the basis of elements of the yield structure is relevant. These traits

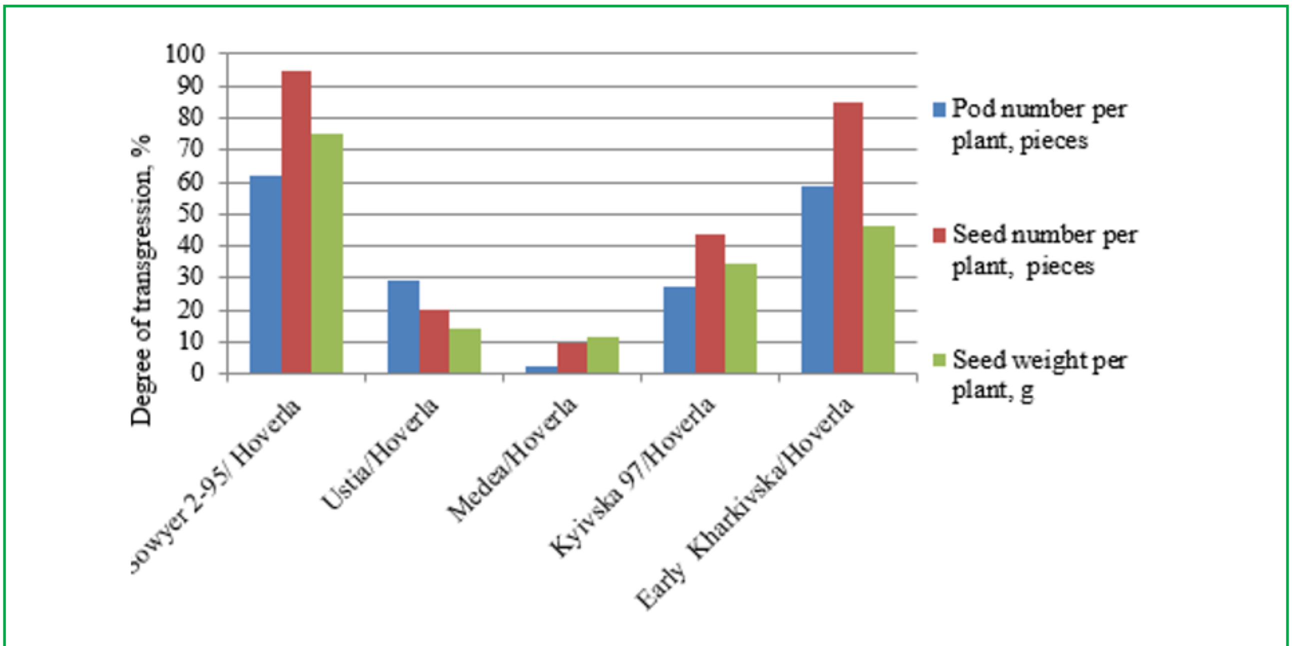

Figure 9 Degree of transgression in hybrid offspring of F 2 soybean

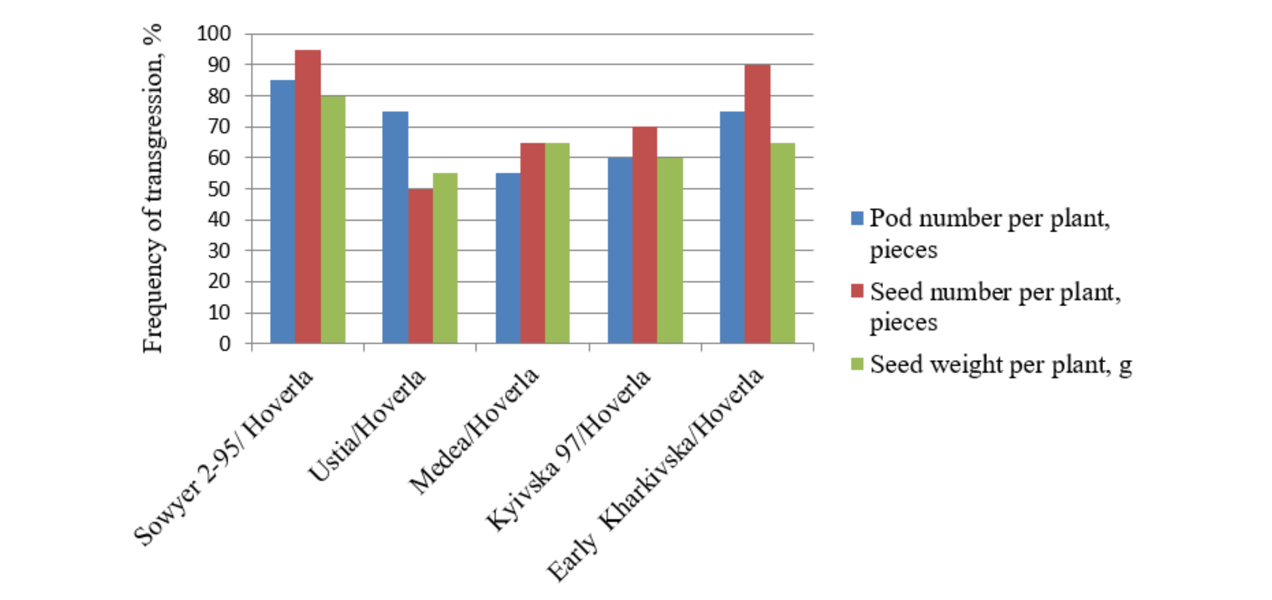

Figure 10 Frequency of transgression in hybrid offspring of F2 soybean

include "pod number" and "seed number per plant", as well as "seed weight per plant". Calculation of the degree of transgression by the elements of the yield structure including: pod number, seed number, seed weight per plant in F2 soybean hybrid populations showed that they varied depending on the hybrid genotype (Figure 9). The highest degree of transgressive forms was found in hybrid combination Sawyer-2-95 × Hoverla, so pod number per plant was 62.2%, seed number was 95% and seed weight per plant was 75.1%. In addition, a high degree of transgressive forms was found in hybrid combination early Kharkivska × Hoverla, thus pod number per plant was 58.6%, seed number was 84.6% and seed weight per plant was 46.0%

Lower degree of transgressive forms was found in hybrid combination Kyivska 97 × Hoverla, so pod number per plant was 27.1%, seed number per plant was 43.6%, and seed weight per plant was 34.4%. It was found that the frequency of transgressive forms of these traits depended on the genotype. Figure 10 shows the frequency of transgressions in hybrid populations that are split.

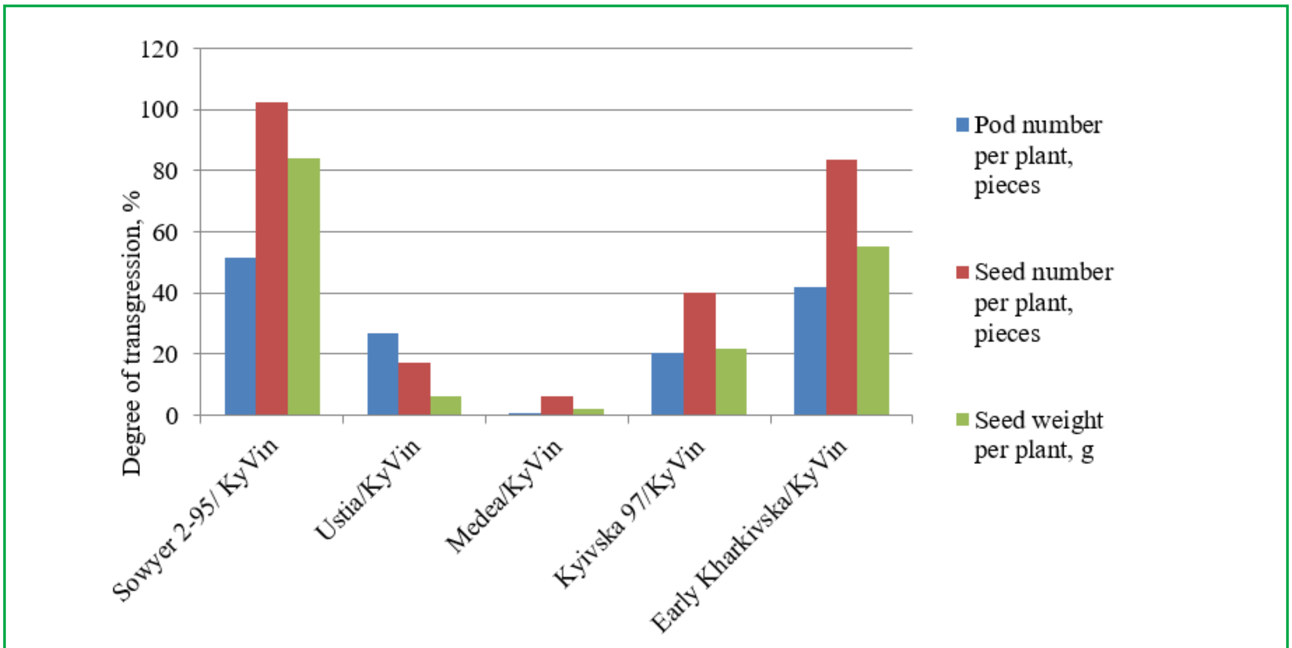

Figure 11 Degree of transgression in hybrid offspring of F 2 soybean

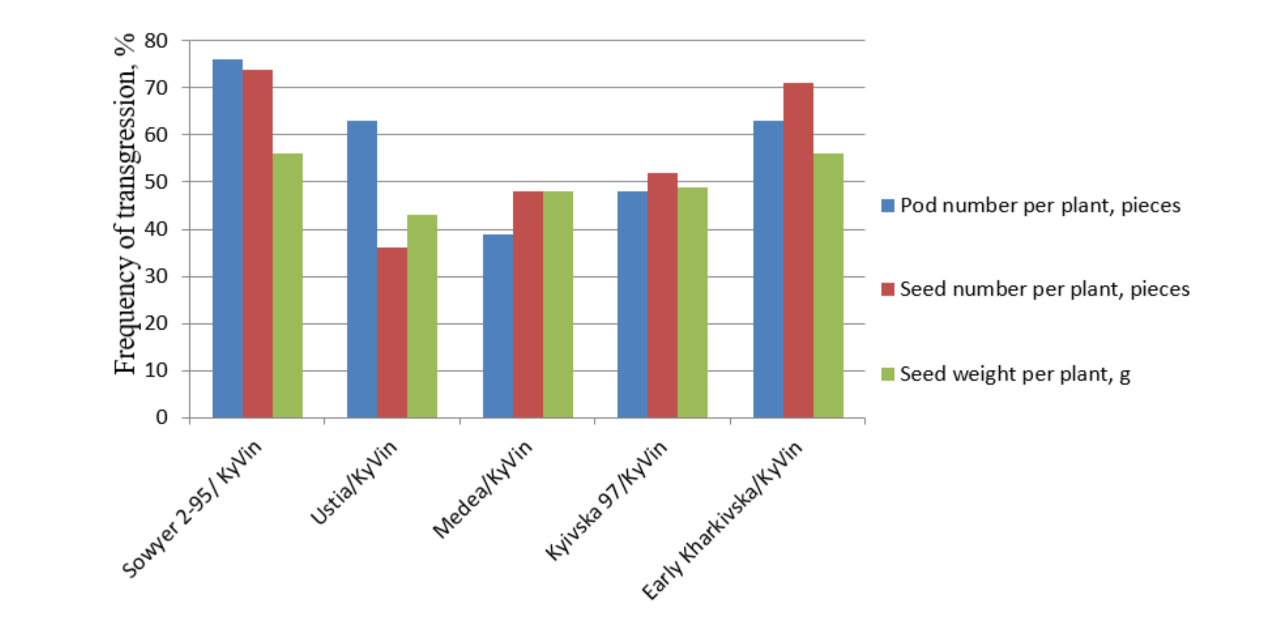

Figure 12 Frequency of transgression in hybrid offspring of F2 soybean

According to the data analysis, high rates of transgression in F2 were observed in two hybrid offspring: Sawyer 2-95 × Hoverla, early Kharkivska × Hoverla. Pod number per plant was 85 and 75%, seed number per plant was 95 and 90%, and seed weight per plant was 80 and 65%.

A high degree of transgressive forms was found in hybrid combination Sawyer-2-95 × KyVin, so pod number per plant was 51.4%, seed number per plant was 102.55%, and seed weight per plant was 84.07% (Figure 11).

A slightly lower degree of transgressive forms was found in hybrid combination early Kharkivska × KyVin, so pod number per plant was 41.87%, seed number was 83.5%, and seed weight per plant was 55.39%.

Lower degree of transgressive forms was found in hybrid combination Kyivska 97 × KyVin, thus pod number per plant was 20.38%, seed number per plant was 40.0%, and seed weight per plant was 21.52%.

Figure 12 shows the frequency of transgressions in two hybrid populations: Sawyer 2-95 × KyVin, early Kharkivska × KyVin, high rates of transgression in F2 were observed. Pod number per plant was 76 and 63%; seed number per plant was 74 and 71%; and seed weight per plant was 56%. The degree of phenotypic dominance is one of the most widely used indicators that characterize the inheritance of traits in Fn. This indicator determines the nature of manifestation of a particular symptom.

Table 12 Distribution of F2 soybean hybrids by the degree of dominance of productivity traits, 2018

Trait	Those having the degree of dominance (%)				
	<-1.0	from -1.0 to -0.5	from -0.5 to +0.5	from +0.5 to +1.0	>+1.0
Plant height	60.0	20.0	20.0	–	–
Height of attachment of lower beans	80.0	–	20.0	–	–
Number of productive nodes	20.0	–	30.0	–	50.0
Pod number per plant	–	–	–	–	100.0
Seed number per plant	–	–	–	–	100.0
Seed number per pod	30		–	20.0	50.0
Seed weight per plant	–	–	–	–	100.0
1,000 seed weight	60.0	–	20.0	10.0	10.0
Yield	10.0	–	40.0	–	50.0
Average by gradations	28.9	2.2	14.4	3.3	51.2
Total	31.2	14.4	54.4		

Having obtained the value of the trait in Fn, the pattern of its inheritance can be qualitatively described.

In 2018, in the nursery for testing hybrids, quantitative traits of yield were determined. The distribution of the nature of manifestation of the degree of dominance in the estimated hybrid combinations Fn by the yield components was undertaken by the whole general set of studied forms. According to the data shown in Table 12, in hybrid combinations the degree of dominance by the studied yield components was at the level of <- 1 to> +1.

According to these traits, positive overdominance predominates (>1.0). Manifestation of gradation effects by the whole set of traits studied was correlated as follows: 51.2% of hybrids had a positive overdominance, 3.3% of hybrids had dominance, 14.4% had an intermediate dominance, 2.2% had a negative dominance, and 28.9% had a negative dominance (depression). The total number

Table 13 The degree of phenotypic dominance and variability of quantitative traits in F2 soybean, 2018

Trait	Parameters	F_2 and parental components of soybean												
		Sowyer 2-95	Sowyer 2-95/ Hoverla	Hoverla	Ustia/Hoverla	Ustia	Medea	Medea/Hoverla	Hoverla	Kyivska 97/Hoverla	Kyivska 97	Early Kharkivska	Early Kharkivska/ Hoverla	Hoverla
Plant height	average	108	80.3	83.6	54.5	77.4	59.4	78.0	83.6	77.5	78.5	60.8	63.7	83.6
	V (%)	12.9	15.7	10.2	14.2	9.5	13.0	13.1	10.2	10.5	8.0	9.0	18.3	10.2
	hp		-1.3		-8.4			0.5		-1.4			-0.7	
Height of attachment of lower beans	average	22.9	9.9	10.5	7.9	9.7	7.5	8.9	10.5	7.6	8.9	11.4	9.5	10.5
	V (%)	22.3	39.2	21.2	17.5	27.0	24.6	18.3	21.2	17.5	21.5	23.6	27.7	21.2
	hp		-1.1		-5.5			-0.1		-2.6			-3.2	
Number of productive nodes	average	18.2	16.2	13.6	12.8	15.5	13.1	16.5	13.6	16.9	15.7	12.8	14.6	13.6
	V (%)	6.1	15.1	12.0	10.1	12.9	6.3	14.1	12.0	9.5	12.0	9.7	16.9	12.0
	hp		0.1		-1.8			12.6		2.1			3.5	
Pod number	average	38.9	63.1	30.5	61.3	47.4	60.2	61.4	30.5	65.9	51.8	37.8	59.9	30.5
	V (%)	33.3	35.9	33.7	27.6	39.5	32.9	32.4	33.7	36.9	31.8	33.7	35.3	33.7
	hp		6.8		2.6			1.1		2.3			7.1	
Seed number per plant	сер.	55.6	123.3	61.9	125.0	104.2	117.1	128.1	61.9	137.2	95.6	64.1	118.3	61.9
	V (%)	34.1	34.2	32.6	31.0	41.2	40.0	31.0	32.6	39.8	35.3	33.8	38.4	32.6
	hp		20.5		2.0			1.4		3.5			50.3	
Seed number per pod	average	1.4	2.0	2.0	2.0	2.2	1.9	2.1	2.0	2.1	1.8	1.7	2.0	2.0
	V (%)	12.1	9.0	8.9	8.8	8.9	10.1	5.7	8.9	10.6	7.0	9.1	18.5	8.9
	hp		1.0		-1.0			2.0		1.2			1.0	
Seed weight per plant	average	8.68	22.2	12.7	19.8	17.4	21.2	23.5	12.7	24.7	18.4	12.4	18.6	12.7
	V (%)	36.5	29.9	33.6	28.0	43.7	35.5	31.9	33.6	40.2	35.6	35.3	46.8	33.6
	hp		5.8		2.0			1.6		3.2			45.2	
1,000 seed weight	average	155.4	184.0	205.1	160.4	164.5	184.3	183.1	205.1	181.6	192.5	193.6	154.1	205.1
	V (%)	6.4	11.2	8.7	8.9	10.1	11.1	6.2	8.7	13.0	14.7	11.9	14.5	8.7
	hp		0.2		-1.2			-1.1		-2.7			-7.8	
Yield	average	386	759	705	704	745	859	806	705	815	787	547	641	705
	V (%)	36.5	24.0	33.6	28.0	40.4	21.6	26.5	33.6	28.6	29.9	33.6	39.7	33.6
	hp		1.3		-1.1			0.3		1.7			0.2	

of effects of positive dominance and overdominance was 54.4%, i.e. half of the hybrids.

The following traits had a positive degree of dominance: seed number per pod, 1,000 seed weight (10.0–20.0%).

Positive dominance was mainly observed by the following traits: pod number per plant, seed number per plant and seed weight per plant (100.0%), as well as the number of productive nodes (50.0%), and seed number per pod (50.0%).

Intermediate inheritance (from -0.5 to +0.5) was observed in 14.4% of hybrids, these indices were reflected in the figures of this series from 20.0 to 40.0% by plant height, height of attachment of lower beans, number of productive nodes, 1,000 seed weight and yield, i.e. by these traits the action of genes was additive. Negative dominance was observed in only 2.2% of hybrids, while negative overdominance was observed in 28.9% of hybrids, namely by plant height, height of attachment of lower beans, 1,000 seed weight, seed number per pod, number of productive nodes and yield from 10.0 to 80.0%.

We also analyzed variability of quantitative traits in the second generation of these hybrids (Table 13). When crossing with the parental form Hoverla, in hybrid combinations there was observed depression as well as partial negative inheritance by plant height and height of attachment of lower beans, except for hybrid combination Medea×Hoverla, where intermediate inheritance was observed by plant height.

By the number of productive nodes in these hybrid combinations, in the vast majority of hybrid combinations there was observed overdominance of the parental form with a higher manifestation of the trait and intermediate inheritance except for hybrid combination Ustia×Hoverla, which revealed depression by this trait.

By pod number plant, seed number per plant and seed weight per plant in all hybrid combinations there was observed inheritance by the type of parental overdominance with higher manifestation of the trait, as well as by seed number per pod and yield, except for hybrid combination Ustia × Hoverla, where negative inheritance and depression were observed. Depression was observed by 1,000 seed weight in these hybrid combinations, except for Sawyer-2-95×Hoverla, where intermediate inheritance was observed.

Depression was observed by plant height and attachment of lower beans, except for combinations Medea×KyVin, where intermediate inheritance was established by both of these traits, and early Kharkivska×KyVin, where partial negative inheritance by plant height was revealed.

4 Conclusions

There were established high GCA effects by plant height in Sawyer 2-95 variety and KyVin tester as well as the height of attachment of lower beans; by the number of productive nodes in Sawyer 2-95 variety and Hoverla tester; pod number per plant in Sawyer 2-95 and Kyivska 97 varieties and Hoverla tester; seed number per plant in Kyivska 97 and Medea varieties and Hoverla tester; 1,000 seed weight in Sawyer 2-95 and Kyivska 97 varieties and Hoverla tester; seed weight per plant in Medea and Kyivska 97 varieties and Hoverla tester; and in terms of yield in Medea variety and Hoverla tester.

It was established that additive effects of genes were dominant in the genetic control of the following traits: plant height, height of attachment of lower beans, number of productive nodes, pod number per plant, seed number per plant, 1,000 seed weight, seed productivity and yield. The share of non-additive effects of the gene interaction was lower, although it was also reliable.

By pod number per plant, seed number per plant and seed weight per plant, in all hybrid combinations there was observed inheritance by the type of overdominance of the parental trait with the highest trait manifestation.

Analysis of the dominance indicators enabled to identify combinations of crosses distinguished by overdominance of these traits and having a significant breeding value: Sawyer 2-95 × Hoverla, Kyivska 97 × Hoverla, Medea × Hoverla.

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