



## GENE ACTION FOR KERNEL WEIGHT PER PLANT IN SPRING BARLEY

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### ABSTRACT

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The breeding and genetic peculiarities for kernel weight per plant in spring barley varieties of different origin (Ukraine, Western European countries, and Canada), purposes of usage (forage, malting, food) and botanical varieties (covered and naked, awned and awnless) under conditions of Ukrainian Forest-Steppe were revealed. In the diallel crossing scheme with only elite malting barley varieties accordance with the additive-dominant system and overdominance in loci were found. The manifestation of kernel weight per plant was reliably increased by the dominant effects. Accordingly to the indicator of the degree of phenotypic dominance, parameters of genetic variation, graphical regression analysis, effects of GCA and constants of SCA in the hybrid populations will be effective final selection for high kernel weight per plant in later generations, when dominant alleles become homozygous. When different botanical varieties were involved in crosses much more complex gene action for the trait manifestation with strong epistasis and multidirectional dominance were determined. Thus, it is theoretically possible to select plants with high productivity on recessive or dominant basis. The negative aspect is that it will require further extensive evaluation of the splitting generations. Awned spring barley varieties Datcha and MIP Myroslav, as well as awnless variety Kozyr can be used as an effective genetic source for involvement in crossings aimed to improving the kernel weight per plant. Naked spring barley varieties require more breeding improvement in plant productivity compare to covered ones.

**Contribution/Originality:** The paper contributes to further development of studies devoted to evaluation of gene action for yield-related traits in spring barley, as well as identification of new genetic sources for plant improvement. For the first time breeding and genetic peculiarities for kernel weight per plant in spring barley varieties of different origin, purposes of usage and botanical affiliation under condition of the central part of Ukrainian Forest-Steppe were revealed.

## 1. INTRODUCTION

Barley (*Hordeum vulgare* L.) is worldwide important agricultural crop. The main purposes of barley usage and, accordingly, the breeding aims are feed, malting and food. Each of these purposes has specific requirements for the grain quality, which for the malting industry is directly opposite to feed and (or) food usage (Bleidere & Gaile, 2012; Fang, Zhang, & Xue, 2019; Rani et al., 2021). The most suitable for malting are covered barley varieties. Naked barley is promising source for functional nutrition of human and high-quality feed of animal. Awnless barley varieties have practical value for dual-purpose use (grain and straw) in animal feeding. Breeding programs for all purposes of barley usage are carried out in many countries and in particular in Ukraine (Assefa, Girmay,

Alemayehu, & Lakew, 2021; Hernandez, Meints, & Hayes, 2020; Hudzenko et al., 2020; Laidig, Piepho, Rentel, Drobek, & Meyer, 2017). However, most of created barley varieties require further breeding improvement, especially which belong to naked and awnless botanical varieties. Nevertheless of the purpose of usage or botanical differences the commercial barley varieties should combine of high yield performance with a set of economically valuable and adaptive traits (Hudzenko et al., 2021). Barley grain yield is a product of the productivity of individual plants (kernel weight per plant) and their number per unit area. Plant productivity is a complex quantitative trait, which level of manifestation is determined by the action of many different genes and it is largely modified by environmental conditions (Hu, Barmeier, & Schmidhalter, 2021; Rodrigues, Minella, & Costenaro, 2020; Russu, Porumb, Mureşanu, & Tritean, 2019; Swati, Tiwari, Jaiswal, Kumar, & Goel, 2018; Vasilescu, Petcu, & Sîrbu, 2020; Xu et al., 2018). These aspects significantly complicate the effective evaluation and selection promising strains in the breeding process.

Despite of the unprecedented development of molecular and genetic approaches, including whole-genome prediction (Li et al., 2016; Philipp et al., 2016; Thorwarth et al., 2017) determination of parameters of genetic variation and combining ability based on statistical analysis of phenotypic manifestation of traits remain effective in practical plant breeding (Potla, Bornare, Prasad, Prasad, & Madakemohekar, 2013; Singh, Prasad, Kuduka, Kailash, & Prasad, 2017; Zhang, Lv, Lv, Guo, & Xu, 2015). The information from systemic crosses is valuable not only for cross-pollinated crops. It is confirmed by the data from numerous of recent publications which report about the evaluation of gene action for different traits in wheat (Ahmad et al., 2020; Kamara et al., 2021; Kandil, Sharief, & Gomaa, 2016; Ljubičić et al., 2017; Mohamed, 2019; Mwadingeni, Shimelis, & Tsilo, 2018) and in barley (Kumari, Vishwakarma, & Singh, 2020; Mansour & Moustafa, 2016; Vashchenko & Shevchenko, 2021; Zymogliad et al., 2021). However, research papers devoted to the assessment of parameters of genetic variation and combining ability for yield-related traits in barley are significantly differ in the revealed peculiarities of gene action mode (Bargougui, 2016; Eshghi & Akhundova, 2009; Jalata, Mekbib, Lakew, & Ahmed, 2019; Madić, Kuburović, & Paunović, 2000; Patial, Pal, & Kumar, 2016; Shendy, 2015). In our opinion, it can be due to the different parental components involved in crossings and the contrasting environmental conditions of the study. Thereby, all above mentioned show the relevance to establish breeding and genetic peculiarities for main yield-related traits in barley varieties of different aims of usage under particular environmental conditions of breeding efforts.

Thus, the purpose of our study is to reveal gene action for kernel weight per plant in spring barley varieties of different purposes of usage, as well as to identify effective genetic sources to improve the trait under conditions of the central part of Ukrainian Forest-Steppe.

## 2. MATERIALS AND METHODS

The peculiarities of gene action for kernel weight per plant in  $F_1$  of spring barley were evaluated in two complete ( $6 \times 6$ ) diallel crossing schemes at the V. M. Remeslo Myronivka Institute of Wheat of NAAS of Ukraine (MIW). Into the Scheme I we included elite Ukrainian (MIP Tytul and Avhur) and Western European (Datcha, Quench, Gladys, and Beatrix) malting spring barley varieties. Into the Scheme II we involved awnless covered barley varieties Kozyr and Vitrazh created at the Plant Production Institute named after V. Ya. Yuriev of NAAS of Ukraine, naked barley varieties Condor and CDC Rattan from Canada, as well as awned feed barley variety MIP Myroslav developed at MIW and malting barley variety Sebastian from Denmark. Thus, the studied varieties differed in the purpose of usage, geographical origin and botanical affiliation. Plants of the parent components and  $F_1$  were sown in three randomized replications. Distance between plants in row was 5 cm, and between rows was 15 cm. Structural analysis of the bundle material (no less than 25 plants) was performed from each replication.

For more reliable and informative characterization of barley varieties and their progeny for kernel weight per plant in terms of inheritance, parameters of genetic variation and combining ability we conducted statistical analyses of experimental data from 2019 and 2020 growing seasons. The main difference between two growing

seasons in weather conditions consisted in significantly lower average monthly air temperature in May 2020 (+12.8 ° C) compared to 2019 (+17.3 ° C). In this term May 2020 was also significantly different from an average long-term value (+16.2 ° C). Along with that, the monthly amount of precipitation (91.6 mm) in May 2020 significantly exceeded value of 2019 (50.9 mm), as well as average long-term amount (56.4 mm). The average monthly temperature in June exceeded the average long-term value (+19.5 ° C) both in 2019 (+22.6 ° C) and in 2020 (+21.7 ° C). It should be noted that the amount of precipitation in June, on the contrary, in 2019 (86.8 mm) was close to average long-term values (82.7 mm), and in 2020 it was significantly lower (57.1 mm).

The degree of phenotypic dominance in F<sub>1</sub> was calculated according to well-known method (Beil & Atkins, 1965). The combining ability and parameters of genetic variation were determined according to the manual (Fedin, Silis, & Smiryaev, 1980) based on original works (Griffing, 1956a; Griffing, 1956b; Hayman, 1954; Hayman, 1957; Hayman, 1958; Hayman, 1960). Computer programs Microsoft Excel 2010 and Statistica 12 were used for calculations.

### 3. RESULTS AND DISCUSSION

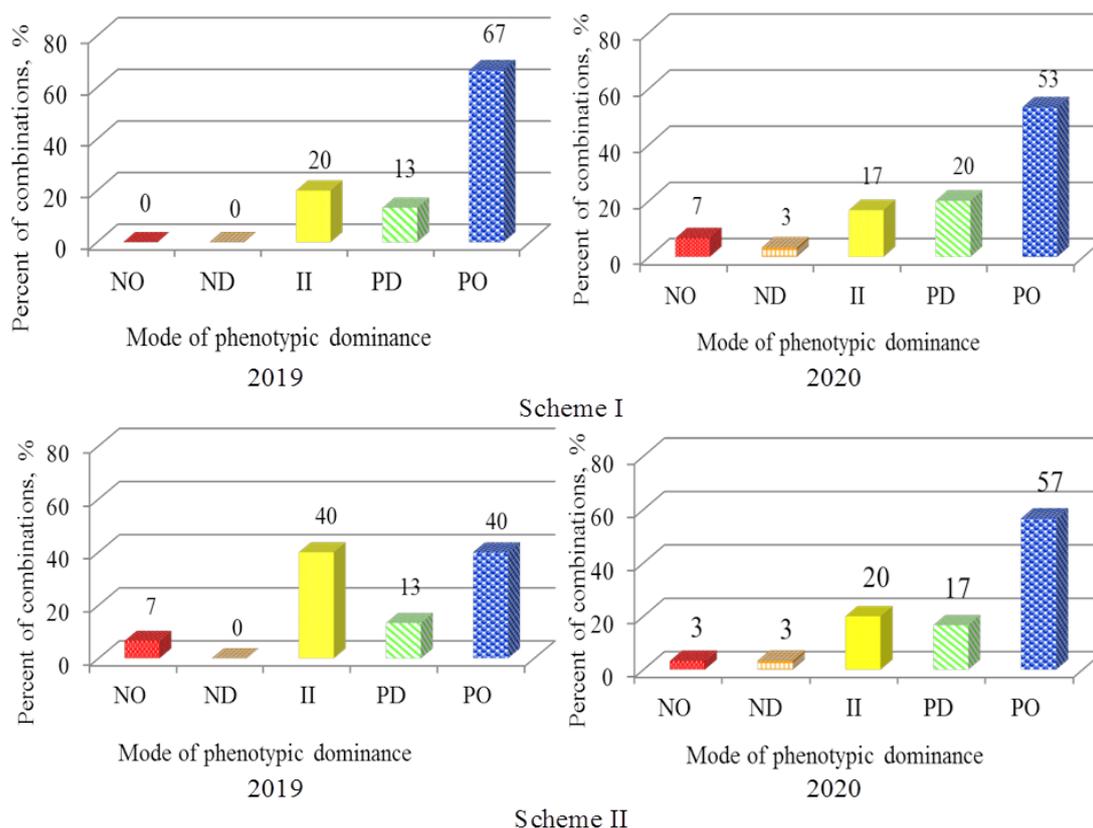
Table 1 shows the manifestation of kernel weight per plant in spring barley varieties involved in crosses (P) and average value for all hybrids (F<sub>1</sub>) created with particular parent component. In the Scheme I, the highest level of manifestation of kernel weight per plant for two years was observed in the variety Datcha, and the lowest level was detected in the variety Avhur. In the Scheme II, the superior plant productivity performance has the variety Kozyr, and the poorest performance has the variety Sebastian.

**Table 1.** Level of manifestation of kernel weight per plant in spring barley varieties and F<sub>1</sub> created by crossing with them, g per plant.

Variety	2019		2020		Mean	
	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>
<b>Scheme I</b>						
MIP Tytul	4.581	6.013	6.105	6.395	5.343	6.204
Beatrix	5.402	5.887	5.733	6.714	5.568	6.301
Datcha	6.636	6.324	7.503	7.435	7.070	6.880
Quench	5.260	5.886	6.188	6.563	5.724	6.225
Gladys	4.378	5.754	5.138	6.283	4.758	6.019
Avhur	5.012	6.042	5.517	6.608	5.265	6.325
Mean	5.211	5.984	6.031	6.666	5.621	6.325
LSD <sub>0.5</sub>	0.315	0.428	0.498	0.445	0.407	0.442
<b>Scheme II</b>						
Kozyr	4.984	5.499	7.331	7.546	6.157	6.525
Condor	4.040	4.819	4.935	7.490	4.485	6.155
Vitrazh	4.819	4.748	6.713	6.441	5.765	5.594
Sebastian	3.675	5.046	3.618	5.533	3.648	5.288
MIP Myroslav	4.791	6.069	6.504	7.476	5.646	6.775
CDC Rattan	3.088	4.233	4.732	6.631	3.909	5.432
Mean	4.233	5.069	5.639	6.853	4.937	5.960
LSD <sub>0.5</sub>	0.338	0.461	0.248	0.314	0.296	0.388

**Note:** P – is for level of trait manifestation in particular parent component; F<sub>1</sub> – is for average level of trait manifestation for all hybrids created with involving particular parent component.

The patterns of distribution of crossing combinations according to the indicator of degree of phenotypic dominance showed the prevalence of positive overdominance in both crossing schemes in both years Figure 1. Along with that, it should be noted the variability in the percent of combinations with the particular mode of the inheritance in different crossing schemes in different years. Parameters of genetic variation showed that in both crossing schemes in both years the effects of dominance (H<sub>1</sub> i H<sub>2</sub>) were superior over the additive ones (D) Table 2.



**Figure 1.** Distribution of crossing combinations in F<sub>1</sub> of spring barley according to the indicator of degree of phenotypic dominance for kernel weight per plant.

**Note:** NO – is for negative overdominance, ND – is for negative dominance, II – is for intermediate inheritance, PD – is for positive dominance, PO – is for positive overdominance.

**Table 2.** Parameters of genetic variation for kernel weight per plant in F<sub>1</sub> of spring barley.

Parameters of genetic variation	Scheme I		Scheme II	
	2019	2020	2019	2020
D	0.595	0.661	0.526	1.955
H <sub>1</sub>	0.933	0.917	2.464	4.934
H <sub>2</sub>	0.844	0.819	1.860	3.910
F	0.385	-0.091	-0.440	0.155
$\sqrt{H_1/D}$	1.567	1.178	4.679	2.524
$(\sqrt{4DH_1} + F)/(\sqrt{4DH_1} - F)$	1.696	0.889	0.676	1.495
H <sub>2</sub> /4H <sub>1</sub>	0.226	0.223	0.189	0.198
$r[(W_r + V_r)_I; x_i]$	-0.781 ± 0.312	-0.885 ± 0.233	-0.097 ± 0.498	0.343 ± 0.470
F <sub>1</sub> -P	0.773	0.636	0.836	1.214

**Note:** D – is for additive effects, H<sub>1</sub> i H<sub>2</sub> – is for effects of dominance, F – is for the indicator of relative distribution frequency of dominant and recessive alleles,  $\sqrt{H_1/D}$  – for the average degree of dominance in loci,  $(\sqrt{4DH_1} + F)/(\sqrt{4DH_1} - F)$  – is for the ratio of the total quantity of dominant and recessive alleles, H<sub>2</sub>/4H<sub>1</sub> – for average measure of alleles in loci,  $r[(W_r + V_r)_I; x_i]$  – is for the indicator of direction of dominance, F<sub>1</sub>-P – is for the indicator of mode of dominance.

Therefore, in all cases, the indicator  $\sqrt{H_1/D}$  revealed the overdominance in loci. The parameters of the relative frequency of distribution of dominant and recessive alleles (F) and the ratio of the total quantity of dominant and recessive alleles  $(\sqrt{4DH_1} + F)/(\sqrt{4DH_1} - F)$  indicated the prevalence of dominant effects over recessive in the Scheme I in 2019 and in the Scheme II in 2020. Accordingly, in Scheme I in 2020, as well as in the Scheme II in 2019, recessive effects were superior over dominant ones. An uneven distribution of dominant and recessive effects was found for all variants of the experiment (H<sub>2</sub>/4H<sub>1</sub> ≠ 0.250). Especially strong asymmetry was detected in the Scheme II. In both crossing schemes in both years the F<sub>1</sub>-P index had positive value. Therefore, it indicated that the

average manifestation level of kernel weight per plant in hybrids was higher than in parent components. That is, the dominance was aimed at increasing the trait. In the Scheme I, the significant negative value of the coefficient of correlation between the sum of covariance and the sum of variance and the mean of the trait ( $r[(Wr + Vr); x_i]$ ) indicated that in both years the dominance was unidirectional and due to dominant effects.

In the Scheme II in both years the coefficient of correlation ( $r[(Wr + Vr); x_i]$ ) was not reliable. Therefore, the indicator pointed on the presence in population the recessive effects that lower the trait manifestation and recessive effects that increase the trait manifestation, as well as dominant effects that increase the trait manifestation and dominant effects that lower the trait manifestation. Thus, in the Scheme II, the dominance was multidirectional and the selection to increase the trait can be carried out on dominant or recessive basis. To some extent, this may be due to the more diverse parental components involved in crossings. In turn, it will require further extensive evaluation of the splitting generations.

Graphical analysis (Hayman's graphs) of the regression of covariance ( $Wr$ ) on the variance ( $Vr$ ) confirmed and complemented the information revealed with parameters of genetic variation Figure 2. The coefficient of regression in the Scheme I in 2019 was  $b = 0.767$ , and in 2020 it was  $b = 1.011$ . Therefore, we can note that in barley varieties involved in the Scheme I the manifestation of kernel weight per plant was mainly determined by the additive-dominant system. In the Scheme II the coefficient of regression in 2019 was  $b = 0.415$ , and in 2020 it was  $b = 0.115$ . That is, in the Scheme II in both years was detected non-allelic interaction (epistasis). It was very strong in 2020. The epistasis is clearly noticeable on Hayman's graphs because of the slope of the regression line.

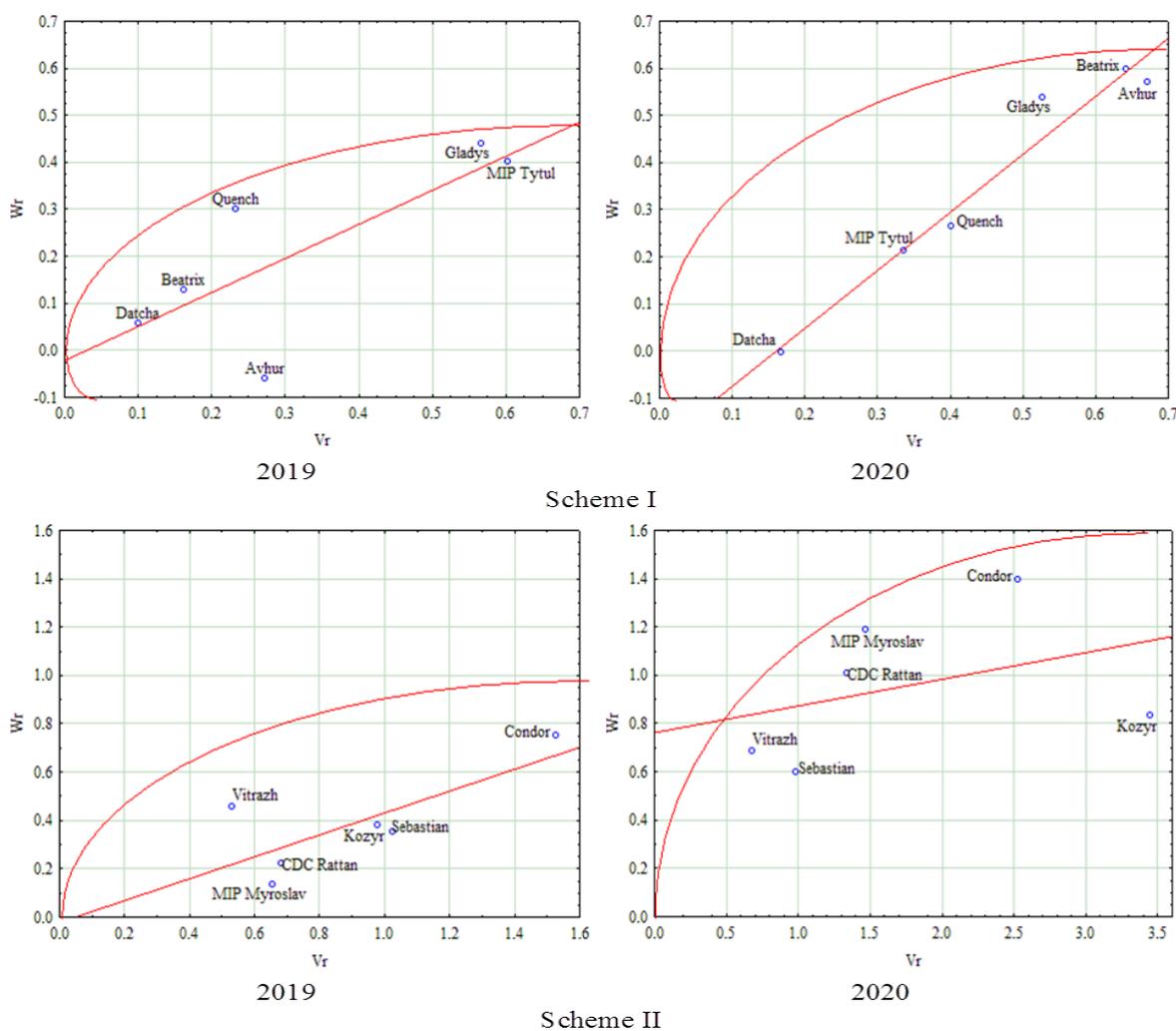


Figure 2. Graphs of regression  $Wr / Vr$  for kernel weight per plant in  $F_1$  of spring barley.

If the additive-dominant model is consistent, Hayman's graphs make it possible to visually characterize the parental components for the relative ratio of dominant and recessive effects. In particular, in the Scheme I the variety Datcha was located in the dominant zone in both years. Accordingly, this variety is characterized with a prevalence of dominant effects over recessive. All other varieties in the Scheme I showed significant changes in their location relative to regression line in different years. In the Scheme II it was revealed the huge variability for all varieties in different years in the relative ratio of dominant and recessive effects. The results obtained may be associated with a strong influence of epistasis.

Characteristics of genotypes involved in both crossing schemes by the effects of general combining ability (GCA) are given in Table 3. The parental components with high and relatively stable effects of GCA under different growing conditions are the most desirable in plant breeding. In the Scheme I significantly high effects of GCA (reliable ( $LSD_{0.05}$ ) predomination over zero) in both years were observed only for the spring barley variety Datcha. In the Scheme II high effects of GCA in both years were found for varieties Kozyr and MIP Myroslav. In the variety Condor effects of GCA varied from very low in 2019 to high in 2020. For the other spring barley varieties low effects of GSA in both years or variation of effects of GSA from low to average level were revealed.

**Table 3.** Effects of general combining ability (GCA) for kernel weight per plant in  $F_1$  of spring barley.

Scheme I			Scheme II		
Variety	Effects of GCA		Variety	Effects of GCA	
	2019	2020		2019	2020
MIP Tytul	0.036	-0.340	Kozyr	0.537	0.867
Beatrix	-0.122	0.060	Condor	-0.312	0.797
Datcha	0.425	0.961	Vitrazh	-0.401	-0.515
Quench	-0.123	-0.129	Sebastian	-0.029	-1.650
Gladys	-0.288	-0.480	MIP Myroslav	1.250	0.779
Avhur	0.072	-0.073	CDC Rattan	-1.045	-0.277
$LSD_{0.05} (g_i)$	0.168	0.163	$LSD_{0.05} (g_i)$	0.179	0.209
$LSD_{0.05} (g_i-g_j)$	0.260	0.253	$LSD_{0.05} (g_i-g_j)$	0.277	0.323

In the Scheme I, significantly high constants of specific combining ability (SCA) in both years were observed only in the crossing combination Avhur / MIP Tytul Table 4. Positive in both years, but reliable only in one year were constants of SCA in the crossing combinations Beatrix / MIP Tytul, Quench / Beatrix, Gladys / Datcha, and Avhur / Gladys.

**Table 4.** Specific combining ability for kernel weight per plant in  $F_1$  of spring barley (Scheme I).

Variety	Year	Variety				
		MIP Tytul	Beatrix	Datcha	Quench	Gladys
Beatrix	2019	0.252				
	2020	0.549				
Datcha	2019	0.026	-0.137			
	2020	-0.308	-0.016			
Quench	2019	-0.327	0.271	0.278		
	2020	-0.476	0.471	-0.117		
Gladys	2019	-0.376	-0.243	0.334	-0.078	
	2020	-0.084	-0.410	0.123	0.269	
Avhur	2019	0.425	-0.143	-0.501	-0.144	0.363
	2020	0.321	-0.593	0.318	-0.147	0.102

Note: 2019:  $LSD_{0.05} = 0.284$ , 2020:  $LSD_{0.05} = 0.267$ .

In the Scheme II, the constants of SCA constants were consistently high only in the crossing combination Condor / Kozyr Table 5. In the crossing combinations CDC Rattan / Vitrazh and CDC Rattan / Sebastian constants of SCA were positive in both years, but reliable only in 2019.

Table 5. Specific combining ability for kernel weight per plant in F<sub>1</sub> of spring barley (Scheme II).

Variety	Year	Variety				
		Kozyr	Condor	Vitrazh	Sebastian	MIP Myroslav
Condor	2019	0.795				
	2020	1.181				
Vitrazh	2019	0.009	0.003			
	2020	-0.877	-0.302			
Sebastian	2019	-0.090	-0.767	-0.186		
	2020	-1.077	0.237	0.372		
MIP Myroslav	2019	-0.100	0.331	-0.055	0.060	
	2020	1.093	-1.290	0.368	0.293	
CDC Rattan	2019	-0.613	-0.362	0.228	0.983	-0.236
	2020	-0.321	0.173	0.438	0.175	-0.465

Note: 2019: LSD<sub>05</sub> = 0.303, 2020: LSD<sub>05</sub> = 0.354.

Thus, our results of an in-depth evaluation of gene action for kernel weight per plant in F<sub>1</sub> of spring barley by the indicator of degree of phenotypic dominance, parameters of genetic variation, regression analysis, effects of GCA and constants SCA showed that the maximal of the trait improvement could be achieved in crossing with spring barley awned varieties Datcha and MIP Myroslav, and awnless variety Kozyr. As it was expected, we established that naked spring barley varieties require more breeding improvement in plant productivity compare to covered ones.

#### 4. CONCLUSION

In the present study we revealed gene action for kernel weight per plant in spring barley varieties of different origin (Ukraine, Canada, Denmark, and Germany), purposes of usage (feed, malting, and food) and botanical affiliation (covered and naked, awned and awnless). The obtained features allow breeder optimally choose of the parental components for crossing and to carry out targeted selection for improving kernel weight per plant in the conditions of the Ukrainian Forest-Steppe. We established significant differences in the gene action for kernel weight per plant among the varieties involved in crossings. In the crossing scheme with only elite malting barley varieties (Scheme I) accordance with the additive-dominant system and overdominance in loci were revealed. The manifestation of kernel weight per plant was reliable increased by the dominant effects. We found the much more complex gene action when different botanical varieties were involved in crosses (Scheme II). In this crossing scheme the strong epistasis and multidirectional dominance were determined. Thus, according to the indicator of the degree of phenotypic dominance, parameters of genetic variation, graphical regression analysis, effects of GCA and constants of SCA in hybrid populations from the Scheme I the final selection for high kernel weight per plant will be effective in later generations, when dominant alleles become homozygous. In the Scheme II it is theoretically possible to select plants with high productivity on both recessive and dominant basis, but with taking into account non-allelic interaction. This greatly complicates the planning of selection. Awned spring barley varieties Datcha and MIP Myroslav, as well as awnless variety Kozyr can be used as effective genetic sources for improvement of plant productivity. However, only the spring barley variety Datcha is characterized by a significant quantity of dominant effects that reliable increase manifestation of the trait. In spring barley varieties MIP Myroslav and Kozyr, genetic control of the kernel weight per plant is more complex.

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**Competing Interests:** The authors declare that they have no competing interests.

**Authors' Contributions:** All authors contributed equally to the conception and design of the study.

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