



GENETIC VARIABILITY AND INHERITANCE PATTERN OF YIELD COMPONENTS THROUGH DIALLEL ANALYSIS IN SPRING WHEAT

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SUMMARY

Wheat is the third most important staple crop in the world, hence, its sustainable production remained the primary focus due to increasing global consumption. This study aims to determine the genetic potential of spring soft wheat (*Triticum aestivum* L.) F₂ populations for yield traits. Six wheat genotypes were used for diallel reciprocal crossing and a total of 12 hybrids in comparison to parental genotypes were studied from 2015 to 2018 at the Institute of Genetics and Plant Experimental Biology, Academy of Sciences, Tashkent, Uzbekistan. In parental genotypes, the average spikelets per spike were similar, however, the highest index per spike was recorded in cultivars Bardosh (56.8±1.02), Unumli Bugdoy (57.9±1.05), and Sayhun(56.3±0.79). The F₂ populations were recorded with the highest number of spikelets per spike and shifted to the right side by 2-3 classes compared to the parental genotypes. The appearance of right-sided regression and identified genotypes with higher 1000-grain weight was observed in the populations of cultivar Bardosh. Populations with higher indices (3.5 to 4.4) than parental genotypes were observed in the cross Bardosh × Unumli Bugdoy (21.7%). The range of variability for 1000-grain weight in the cultivars Kroshka and Bardosh belonged to 2nd class, and cultivars Kayraktash, Unumli Bugdoy, Saykhun, and K-5076 belonged to 3rd class. Populations with 1000-grain weight ranged from 44.0 g to 47.9 g, with a percentage estimate of 63.3% for cultivar Kroshka, and 76.7% for Kayroktosh. In the second generation, the variability range was distributed into eight classes. Larger grains were observed in the hybrids of cultivar Kayroktash. Hybridological analysis of the inheritance of quantitative traits exhibited that the grains per spike were mainly inherited according to the type of dominance of the best parent with a high trait index. The grain number and grain weight per spike were inherited by overdominance type of gene action in the characterized F₁ populations.

Keywords: Bread wheat, quantitative traits, yield, transgressive variability, reciprocal combination

Key findings: Wheat (*Triticum aestivum* L.) spike is an important morpho-functional complex structure, that various combinations and expression of the structural elements manage significant variability in wheat productivity. The selection of the genotypes with high rates is justified by the wheat cultivars' high potential in terms of the grain number and grain weight per spike, the role of dominant genes in the phenotypic manifestation of these traits, and their preservation in subsequent generations. Thus, the possibility of using this indicator as a genetic marker when evolving new cultivars through breeding.

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INTRODUCTION

Grain yield is a complex trait that resulted from the interaction of various yield components and the influence of environmental factors in wheat (*Triticum aestivum* L.) (Donmez et al., 2001; Ma et al., 2004; Fallahi et al., 2008; Tembo, 2021). Given the polygenic nature of its inheritance and the influence of environmental factors, it is difficult to increase wheat productivity through traditional breeding (especially in early generations) (Novoselovic et al., 2004). An increase in grain yield is fundamentally based on an enhancement and improvement in yield components i.e., plant height, productive stems per unit area, spike length, and the number of grains and grain weight per spike in wheat (Harasim et al., 2016; Abdel-Lateif and Hewedy, 2018; Attyaf et al., 2019). All these yield components are genetically determined (Reynolds et al., 2007) and the genetic control of yield components can be well established in diallel crosses of *Triticum aestivum* L. (Gupta et al., 1988; Knežević and Kraljević-Balalić, 1993; Menon and Sharma, 1994). Such type of inheritance and the effects of genes mainly depend upon the parental genotypes used for diallel crossing. For this reason, the choice of wheat parental cultivars for the breeding program is very important (Joshi et al., 2002; Gorjanović and Kraljević-Balalić, 2004).

The quantitative traits of plant productivity are determined by polymeric genes and are characterized by a wide range of variability under the influence of environmental conditions. Therefore, it is important to know how the economically valuable traits of the parental genotypes are inherited in wheat hybrids (Singh et al., 2012; Baloch et al., 2016). The effectiveness of breeding programs is largely determined by the knowledge of the character of inheritance of quantitative traits associated with the productivity of an individual wheat plant (Ljubcic et al., 2017). Wheat landraces with high adaptability are of greater practical significance due to the wider genetic basis thus, can provide valuable traits for breeding (Lopes et al., 2015; Baboev et al., 2017). By analyzing the cross combinations of the cultivars of different ecological origins, the rare valuable combinations of traits can be found (Dinglasan et al., 2018).

The complete genetic information on the variability of quantitative traits in wheat cultivars can be obtained by using the diallel crosses (Ljubcic et al., 2015; Baloch et al., 2016). Diallel crossing scheme is one of the most effective methods to get data on the character of the inheritance of selectable traits, for it allows to obtain significant information about the genetic control of the investigated elements in the original parental genotypes, coming from the analysis of a relatively small number of first-generation plants, (Joshi et al., 2004; Reynolds et al., 2007; Rigatti et al., 2018). The manifestation of inheritance and interaction of genes during hybridization depends on the genotypes, environments, and genotype by environments interactions (Nehe et al., 2019). Therefore, the information obtained in the area for which the cultivar is being created is of exceptional importance for improving the efficiency of breeding work.

In common wheat, the inheritance of plant height, tiller productivity, 1000-grain weight, and grain weight per plant that occurs according to the overdominance and the absence of an epistatic effect on these traits has been observed (Ljubcic et al., 2016). This work provides an assessment of quantitative traits that determine grain yield and their phenotypic manifestation, taking into account the influence of polymeric genes. The study aimed to determine the characteristics of inheritance and variability of quantitative traits that determine grain yield when crossing geographically distant parental genotypes of the common wheat.

MATERIALS AND METHODS

Wheat hybrid material and design

For diallel reciprocal crossing, the six bread wheat (*Triticum aestivum* L.) genotypes with different geographic origins were used i.e., cultivar Kroshka (widely cultivated in Uzbekistan since 2000), cultivar Bardosh (selection made from breeding material of the CIMMYT, Mexico), local cultivars Sayhun, Unumli Bugdoy, K-5076, and the landrace Kayroktosh. The field studies were done from 2015 to 2018 on grey clay soil at the Institute of Genetics and Plant Experimental Biology,

Academy of Sciences, Tashkent Region, Uzbekistan. A total of 12 hybrid combinations, derived from the involvement of six parental genotypes, were studied. The seeds of F₁ hybrids were sown manually in the hybrid nursery in two rows with one meter length, and F₂ populations in four rows with five meter length. Parental cultivars were used as standard checks and were planted on the two sides of each hybrid. All the experiments were performed with three replications.

Yield component analysis

For the analysis of productivity traits, 30 spikes were selected from parental genotypes, and 160 were randomly selected from hybrid populations. The analyses were performed on traits such as spikelets per spike, grain weight per spike, and 1000-grain weight following the method by Beil and Atkins (1967). Descriptive statistical analysis of data of yield components was carried out in an excel sheet. It summarizes several hybrid plants, the standard deviation of traits, variance, including heritability evaluation.

RESULTS

Uzbekistan is significantly exposed to the threat of climate change. Annual air temperature from the beginning of observations up to date shows that warming trends are evident in all the climatic zones, and the rate of temperature increase is significantly higher than the average rate observed on a

global scale. Weather conditions noted during the years of research (2015-2018) showed that 2016 was the warmest and driest year, where the month of February was the driest, with only 5-6 mm of rainfall during said month. Meanwhile 64 mm was considered the normal rainfall in 2017 and 2018, and the mean monthly rainfall was closer to the multi-year average monthly rainfall.

The analysis of the quantitative traits that determine the grain yield in soft wheat cultivars and their F₁ and F₂ diallel populations from different geographic origins and planted under the same conditions in triplicate, revealed significant differences for three yield traits i.e., spikelets per spike, grain weight per spike, and 1000-kernel weight.

Hybridological analysis of the inheritance of quantitative traits showed that the grains per spike were mainly inherited according to the type of dominance of the best parent in a cross with a high trait index; the grain weight and grains per spike were managed by the overdominance type of gene action in the F₁ populations. In the K-5076 × Bardosh combination, the parental genotypes which significantly differed in the value of the trait, the dominance degree was $h_p = 0.7$, which indicates inheritance is bias towards the best parent (Table 1). In the analysis of variance, series of grain traits in F₂ populations were divided into eight classes (Figure 1), and grain weight was divided into seven classes (Table 2) with the same distance, the range of variability dependent on the segregation of genotypes, and the right-sided transgression observed in all reciprocal diallel hybrids.

Table 1. The degree of dominance for various traits in F₁ hybrid combinations.

F ₁ populations	Grains spike ⁻¹	Grain weight spike ⁻¹	1000-grain weight
Kroshka × Unumli Bugdoy	4.9	11.3	55.5
Unumli Bugdoy × Kroshka	5.0	7.7	20.0
Kroshka × Sayhun	29.2	21.0	-2.2
Sayhun × Kroshka	35.2	23.0	1.0
Bardosh × Unumli Bugdoy	14.9	62.0	2.3
Unumli Bugdoy × Bardosh	23.4	98.0	4.1
Bardosh × Kayroktosh	10.8	6.8	0.1
Kayroktosh × Bardosh	10.2	6.8	0.7
Unumli Bugdoy × K-5076	3.8	3.8	3.1
K-5076 × Unumli Bugdoy	3.6	3.2	2.6
Sayhun × Kayroktosh	3.2	2.3	-0.4
Kayroktosh × Sayhun	23.2	11.6	0.9
Bardosh × K-5076	0.8	2.0	3.0
K-5076 × Bardosh	0.3	0.7	0.9

Table 2. Inheritance and variability of grain weight per spike in F₂ populations.

Parental cultivars & F ₂ populations	N*	Grain weight per spike (g) / Plants (%)							x±Sx	V%	h ²
		1.5-1.9	2.0-2.4	2.5-2.9	3.0-3.4	3.5-3.9	4.0-4.4	4.5-4.9			
Parental genotypes											
Kroshka	30		30.0	53.3	16.7				2.60±0.06	9.9	
Bardosh	30		10.0	60.0	30.0				2.78±0.06	10.3	
Unumli Bugdoy	30		33.3	33.3	33.3				2.72±0.06	11.6	
Sayhun	30		10.0	60.0	30.0				2.74±0.05	8.6	
Kayroktosh	30		66.7	33.3					2.38±0.05	10.1	
K-5076	30		76.7	23.3					2.22±0.04	8.8	
F₂ Populations											
Kroshka × Unumli Bugdoy	160	6.9	28.8	39.4	18.8	4.4	1.9		2.63±0.04	19.0	0.62
Unumli Bugdoy × Kroshka	160	7.5	20.6	29.4	25.0	14.4	3.1		2.82±0.05	21.3	0.74
Kroshka × Sayhun	160	5.0	25.6	43.8	15.0	8.8	1.9		2.68±0.04	18.6	0.74
Sayhun × Kroshka	160	2.5	35.6	35.6	18.8	5.0	2.5		2.65±0.04	19.0	0.62
Bardosh × Unumli Bugdoy	160	3.1	6.3	18.8	40.6	21.9	8.1	1.3	3.17±0.05	17.9	0.68
Unumli Bugdoy × Bardosh	160	3.8	15.6	44.4	21.9	10.6	3.1	0.6	2.83±0.04	19.2	0.68
Bardosh × Kayroktosh	160	6.3	25.6	35.6	20.6	10.6	1.3		2.76±0.04	18.8	0.6
Kayroktosh × Bardosh	160	5.0	34.4	36.3	21.9	2.5			2.62±0.04	16.5	0.5
Unumli Bugdoy × K-5076	160	1.3	9.4	30.6	35.6	20.6	1.9	0.6	3.05±0.04	16.2	0.63
K-5076 × Unumli Bugdoy	160	1.3	15.0	33.8	30.6	12.5	6.8		2.98±0.05	18.8	0.65
Sayhun × Kayroktosh	160	1.3	28.8	35.6	19.4	11.9	2.5	0.6	2.78±0.05	20.0	0.78
Kayroktosh × Sayhun	160		15.6	30.6	32.5	16.3	3.8	1.3	3.03±0.05	18.5	0.76

* Number of plants

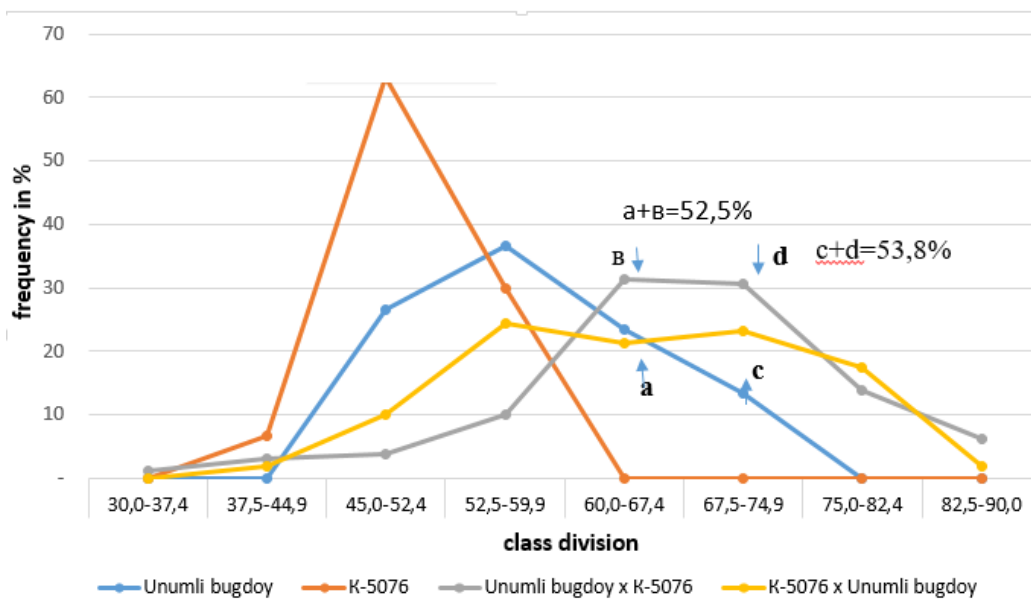


Figure 1. Transgressive variability of the grains per spike.

The range of variability for the grains per spike in the parental genotypes, in general, took three to four classes. The cultivars, Kayroktosh and K-5076, have same grains per spike, and 53.3% to 63.3% of plants had 45.0 to 52.4 grains. In cultivars Sayhun and Kroshka, 50% of the investigated plants had 52.5 to 59.9 grains per spike. In the cultivar Bardosh, 46.7% of plants, and Unumli Bugdoy, 36.7% of plants had 52.5 to 59.9 grains per spike. Significantly, the percentage of plants that had the highest grains per spike (67.5 to 74.9) were 3.3% and 13.3%, respectively. In the cultivars, the average indicators for grains per spike were close to each other, ranging from 45 to 75 grains per spike. The highest rates were in the cultivars Bardosh at 56.8 ± 1.02 pieces, Unumli Bugdoy at 57.9 ± 1.05 pieces, and Sayhun at 56.3 ± 0.79 pieces.

An increase in the range of variability for the grains per spike in F_2 populations was noted and the appearance of genotypes with a higher grain number and a shift to the right side by 2-3 classes in comparison with the parental cultivars were observed. In the reciprocal hybrids of cultivars, Unumli Bugdoy and K-5076, 52.5% of the plants have 60.6 to 67.4 grains per spike, 53.8% of plants have 67.5 to 74.9 grains spike⁻¹, while the average values for the said trait were 66.3 ± 0.83 and 64.4 ± 0.83 grains, respectively, which were the highest among all the F_2 populations (Figure 1). It has also been proven that in cross combinations of cultivars Unumli Bugdoy and K-5076, the grains per spike were transmitted to subsequent hybrid generations with an increase in the proportion of additive effects of dominant genes, which suggests the breeding value of these hybrid populations.

By analyzing the range of variability for grain weight per spike, it was observed that in the investigated cultivars the average values were within the range of 2.22 to 2.78 g and the range of variability corresponds to classes 2-3 (Table 2). The highest rates were observed in the cultivars Bardosh and Sayhun (2.78 ± 0.06 g and 2.74 ± 0.05 g, respectively). In cultivars Kayroktosh and K-5076, 66.7% to 76.7% of plants ranged from 2.0 to 2.4 g for grain weight per spike and were placed within the class.

In cultivars Bardosh, Unumli Bugdoy and Sayhun, 30% of plants, and in cultivar Kroshka, 16.7% of plants had a grain weight per spike of more than 3.0 g. In cultivars Bardosh and Sayhun, 60% of plants while in cultivar Kroshka 53.3% of plants obtained 2.5 to 2.9 g grain weight per spike. In cultivars Kroshka, Sayhun and K-5076, the coefficient of

variation for the said trait was low (8.6% to 9.9%), while in other cultivars it was higher than 10% which indicates the average variability of the trait.

In reciprocal hybrids obtained with the involvement of the cultivar Kroshka, the left- and right-sided transgressions were observed. The negative transgression in hybrids manifested itself with a shift on one class to the left. With the involvement of the cultivar Kroshka in diallel hybrids, in 21.9% of plants, the grain weight per spike ranged from 1.5 to 1.9 g. In reciprocal hybrids of cultivars Kroshka and Unumli Bugdoy (39.4% and 29.4% of plants), and cultivars Kroshka and Sayhun (43.8% and 35.6% of plants) showed 2.5 to 2.9 g grain weight per spike.

The emergence of right-sided transgression and the formation of genotypes with a high grain weight per spike was observed in hybrids with the involvement of cultivar Bardosh. Plants with a higher grain weight per spike (3.5 to 4.4 g) than those of the parental genotypes occur in hybrids Bardosh \times Unumli Bugdoy (21.8% of plants), Unumli Bugdoy \times Bardosh and Bardosh \times Kayroktosh with the same value (10.6% of plants), and Kayroktosh \times Bardosh (2.5% of plants).

Results further revealed that the average grain weight per spike in F_2 populations of the Unumli Bugdoy \times K-5076 combination was 3.05 ± 0.04 g, while in its reciprocal cross K-5076 \times Unumli Bugdoy, 2.98 ± 0.05 g. In this reciprocal combination, the percentage of plants with a higher grain weight per spike (compared to the parental forms) was 42.4%, the heritability coefficient was equal to 0.63. The genotypes selection with high rates is justified by the high potentialities of the cultivar Unumli Bugdoy in terms of grains per spike and grain weight per spike, the role of dominant genes in the phenotypic manifestation of these traits, and their preservation in subsequent generations. This strengthens the possibility of using this indicator as a genetic marker while developing new wheat cultivars through breeding.

According to the analysis of the 1000-grain weight, which provide the productivity of geographically distant wheat genotypes with high rates, it was revealed that the variability for the said trait was ranging from 32 to 65 g and correspond to class eight. In cultivars Kroshka and Bardosh, the range of variability occupy class 2, cultivars Kayroktosh, Unumli Bugdoy, Sayhun, and K-5076 were in class 3. In cultivar Kroshka 63.3% of plants, in cultivar Kayroktosh (76.7%), while in cultivar K-5076

(53.3%) the 1000-grain weight s ranged from 44.0 to 47.9 g. In 70% of plants for cultivar Bardosh, 43.3% of plants for cultivar Unumli Bugdoy, and 63.4% of plants for cultivar Sayhun, the 1000-grain weight ranged from 48.0 to 51.9 g.

In the backcross hybrid of the cultivar Unumli Bugdoy with Bardosh, 36.9% of the plants have a 1000-grain weight that ranged from 40.0 to 44.0 g, while in the reciprocal hybrid of this cultivar with K-5076 for 1000-grain weight the plants percentages were 17.5% and 21.9%, respectively. In hybrid Kayroktosh × Sayhun, 34,4% of plants belong to the class with a value of 1000-grain weight at 48 to 52 g. The reciprocal hybrids derived with the involvement of different landraces were found more productive than their parental genotypes with different ratios ranging from

8.1% to 21.9%. In hybrid K-5076 × Unumli Bugdoy, the average 1000-grain weight was 45.8±0.34 g, while in the hybrid Kayroktosh × Sayhun, the said value was 48.0±0.36 g. In reciprocal hybrids (derived with the involvement of the cultivar Kayroktosh), the 1000-grain weight was more than 60 g in 1.3% of their plants. The high range of variability for 1000-grain weight in these reciprocal hybrids indicates the possibility of isolating plants with large and full-fledged grains (Figure 2).

In the reciprocal hybrid Sayhun × Kayroktosh, values for the highest heritability coefficients regarding the number of spikelets per spike ($h^2 = 0.73$ and $h^2 = 0.85$), grain weight per spike ($h^2 = 0.78$ and $h^2 = 0.76$) and 1000 grain weight ($h^2 = 0.81$ and $h^2 = 0.78$) in combination with right-sided positive transgressive forms were noted (Table 3).

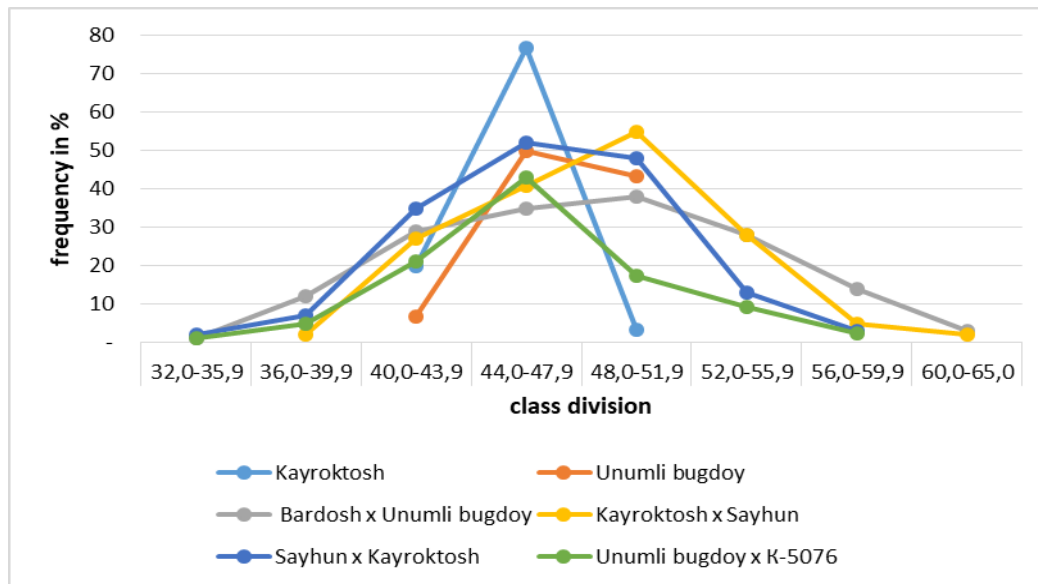


Figure 2. Transgressive variability of the 1000-grain weight.

Table 3. Heritability index and variability of yield components in wheat.

F ₂ Populations	Spikelets per spike		Grain weight per spike		1000-grain weight	
	V%	h ²	V%	h ²	V%	h ²
Kroshka × Unumli Bugdoy	19.6	0.67	19.0	0.62	9.4	0.69
Unumli Bugdoy × Kroshka	19.4	0.64	21.3	0.74	9.1	0.67
Kroshka × Sayhun	16.5	0.72	18.6	0.74	9.9	0.82
Sayhun × Kroshka	17.5	0.71	19.0	0.62	8.6	0.78
Bardosh × Unumli Bugdoy	16.8	0.59	17.9	0.68	12.1	0.89
Unumli Bugdoy × Bardosh	16.1	0.57	19.2	0.68	8.4	0.65
Bardosh × Kayroktosh	16.7	0.58	18.8	0.60	8.3	0.61
Kayroktosh × Bardosh	15.2	0.54	16.5	0.50	9.2	0.80
Unumli Bugdoy × K-5076	15.5	0.65	16.2	0.63	9.5	0.76
K-5076 × Unumli Bugdoy	15.9	0.57	18.8	0.65	9.2	0.78
Sayhun × Kayroktosh	16.9	0.73	20.0	0.78	9.4	0.81
Kayroktosh × Sayhun	18.2	0.85	18.5	0.76	9.3	0.78

DISCUSSION

Genetic parameters like mean performance, variance, heritability, genetic gain, and correlation coefficient are helpful tools to evaluate the genetic potential of a particular wheat genotype and also to determine the effectiveness of breeding a particular trait in a genotype under the existing environment (Salim *et al.*, 2003). Heritability studies guide plant breeders to predict the interaction of genes in succeeding generations and thus, provide a key component of traits for a successful breeding program. Improving quantitative traits through hybridization is the most efficient way to select desirable traits in advanced segregating populations of *Triticum aestivum* L. (Singh and Yunus, 1988).

Environmental conditions have a slight impact on the wheat grain size which is the most accessible structural trait for the individual selection in segregating populations. As noted by Chowdhry *et al.* (2002) in their previous work, the 1000 kernel weight is characterized by high values of the heritability coefficient and is controlled by the overdominance type of gene action, while spike length was regulated by partial dominance with additive gene action and spikelets per spike was under the control of partial dominance in wheat. Consequently, the 1000-grain weight is an important trait in the breeding program for wheat productivity.

Hybridological analysis of the inheritance of quantitative traits showed that the grains per spike were mainly inherited from the type of dominance of the best parent with a high trait index. The traits grain number and grain weight per spike in all characterized F₁ populations were inherited and managed by the overdominance type of gene action. The higher grains per spike is an important trait which directly linked with grain yield in wheat. Variability distribution of the grains per spike in parental genotypes generally occupied 3-4 classes. In the second generation of the hybrid Unumli Bugdoy × Bardosh, grains per spike varied from 52.5 to 59.0. However, few outliers plants had 67.5 to 74.9 grains per spike.

The present results were also inconsistent with past findings of different researchers who reported that grains per spike augment grain yield in wheat crops (Sakuma and Schnurbusch, 2020). Moderate heritability with high genetic advance was estimated for flag leaf area, tillers per plant, spike length, and grains per spike in wheat (Chowdhry *et al.*, 1997). Similarly, high heritability and genetic

gain for grain yield and grains per spike were also recorded by Ozkan *et al.* (1997) and Salim *et al.* (2003), respectively in wheat.

Wheat yield is a complex trait consisting of three main components i.e., the spikes per area, grains per spike, and 1000-kernel weight. Among them, the 1000-kernel weight has relatively high heritability which is a quantitative trait (Alexander *et al.*, 1984). As one of the key components of grain yield, the 1000-grain weight was mainly influenced by grain size and grain filling (Simmonds *et al.*, 2014). Although these components are susceptible to environmental conditions, their inheritance was relatively stable compared with the total yield of wheat. Therefore, 1000-grain weight and its related traits are often used in the genetic analysis of wheat grain yield. According to 1000-grain weight analysis, providing the productivity of geographically distant genotypes with high rates, it was revealed that the variability range of the trait indicators ranged from 32 to 65 g and was distributed into eight classes. The selection of more productive populations as compared to the parental genotypes with high genotype rates is observed in all the reciprocal hybrids with the participation of the ancient local cultivars.

Grain size is less influenced by environmental conditions and is essentially one of the most accessible structural features for individual selection in early generations of the splitting hybrids. The 1000-grain weight was characterized by high values of the coefficient of heritability and is controlled in most cases by dominance and overdominance type of gene action, and hence, is of great interest in breeding for wheat productivity. The present study proposed to identify the valuable genotypes with a high heredity coefficient and the occurrence of right-sided positive transgressive type by the grain number and weight per spike, as well as, by the 1000-grain weight during hybridization of geographically distant parental genotypes.

CONCLUSIONS

The genetic analysis showed that inheritance of the investigated traits was controlled by the polymeric genes — in the recessive state of these genes, genotypes with lower indices than the parental genotypes occurs, and in their dominant state, the genotypes with the highest indices appear; in the heterozygous state of genes and within the framework of their additive influence, segregation occurs into

intermediate classes. Positive transgression in terms of the grains per spike in F₂ generation revealed the appearance of populations with more densely spaced spikelets in the spike as compared to the parental genotypes. A higher coefficient of variation for grain number and weight per spike was observed as compared to the parental genotypes. This phenomenon is important in wheat breeding and allows to increase productivity due to grain number and weight per spike, without increasing the plant density.

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