

NOVEL TRANSGRESSIVE SEGREGATION IN BREAD WHEAT

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Key words: *Triticum aestivum* L., *Transgressive segregation*, *Genetic variability*, *Correlations*.

Due to the world's population is expected to reach approximately 9 billion by the year 2050, food security has become an outstanding challenge to reach zero hunger and keep world peace. To meet the food demands of the growing world's population, grain production of major food crops must be doubled by 2050 (Semenov and Stratonovitch, 2013; Tilman *et al.*, 2011 and FAO, 2009).

Wheat is one of the vital food grain crops and is the most widely adapted cereal crops worldwide (FAO, 2016). Over 35% of the global human population depends on wheat as a staple food crop and accounts for 20% of the calories consumed by humans (Kim *et al.*, 2017). Improving grain yield of wheat is the main goal in wheat breeding programs (Guo *et al.*, 2018; Kim *et al.*, 2017). Grain yield and its components are complex traits and controlled by multiple quantitative trait loci (QTLs) and modified by environmental conditions. Grain yield of wheat is determined by spikes per unit area, grains per spike and grain weight (Zhou *et al.*, 2017).

An important strategy to improve grain yield potential of wheat is the utilization of transgressive segregation phenomenon. Many workers defined transgressive segregation as a fraction of individuals that exceed parental values in negative or positive direction in segregating hybrid populations (Grant, 1975; de Vicente & Tanksley, 1993; Rieseberg *et al.*, 1999; Mackay *et al.*, 2020). Rieseberg *et al.*, (1999) demonstrated that transgressive segregation occurs when phenotypic trait values in hybrid populations fall outside the range of the parents. They added that transgressive segregation demonstrates how hybridization can produce novel phenotypes and enable adaptation to new ecological niches, found new lineages and plays a significant and creative role in evolution. Moreover, they pointed out that transgressive segregation is distinct from heterosis because it manifests predominantly in the F₂ and later generations. Transgressive segregations were observed in plant and animal segregating hybrid populations. At least one transgressive character was reported in 155 reviewed studies and 44% out of 1229 examined

characters were transgressive (Rieseberg *et al.*, 2003).

Observations on transgressive segregations in segregating hybrid populations of wheat were previously reported (Yadav *et al.*, 1998; Yadav *et al.*, 1992 and Smith, 1966). Goulet *et al.*, (2017) reported that Grant, (1975) credits Nilsson-Ehle, (1911) with one of the earliest explicit proposals of the transgressive segregation phenomenon in wheat (*Triticum aestivum* L.).

The phenomenon of transgressive segregation was exploited for improving yield in wheat (Yadav *et al.*, 1998) and in barley (Vega and Frey, 1980) and for developing resistant wheat genotypes to leaf rust (Broers and Jacobs, 1989 and Yadav *et al.*, 1992). Recently, Guindon *et al.*, (2018) studied the transgressive segregations observed in F₂ and F₃ generations from a cross between two pea varieties. They observed high frequency of transgressive segregations in F₃ for number of pods (15.5%) and number of seeds (13.6%). Raval *et al.*, (2018) studied the transgressive segregation in desi chickpea. Number of branches per plant, days to flowering and days to maturity, number of pods per plant and seed yield per plant recorded greater number of transgressive segregants. Shreya *et al.*, (2017) evaluated four crosses of groundnut. They selected transgressive segregations for total biomass, harvest index, shoot weight, root weight, shelling out-turn, mature pod weight and kernel weight per plant. Koseoglu *et al.*, (2017) identified transgressive segregations in reciprocal inter-

specific crosses between *C. arietinum* and *C. reticulatum* Ladiz. Mao *et al.*, (2011) observed transgressive segregation for kilo-gram weight in a recombinant inbred line population of rice derived from the cross between an indica variety, Teqing, and a wide compatible japonica variety, 02428.

The present study was undertaken on a hybrid population between wheat mutant line 10 (WM10) and Gemmeiza 9 cultivar of bread wheat. Moreover, a selected transgressive segregation from F₂ was field evaluated in the F₃ generation for number of spikelets/spike, number of kernels/spike, number of kernels/spikelet, number of fertile spikes/plant, 1000 kernel weight (g) and grain yield/plant (g). The aims of this study were to: (1) create new genetic variation, (2) phenotypic evaluation of F₂ and F₃ segregated populations and (3) estimate interrelationships between all possible pairs of studied traits to help in selection for transgressed traits in the current transgressive hybrid population.

MATERIALS AND METHODS

Plant materials

Wheat mutant line 10 (WM10) and Gemmeiza 9 cultivar were crossed and used as parents in the present study. The WM10 (parent 1) was developed by the wheat breeding program of the Atomic Energy Authority, Anshas, Egypt (Al-Bakry, 2004). It was selected in the second mutated generation (M₂) resulting from irradiation of the wheat variety Sids1

with 300 Gray (30 Krad) of gamma rays in 2001/2002. Gemmeiza 9 cultivar (parent 2) was released by Wheat Research Section, Field Crops Research Institute, Agricultural Research Center (ARC), Giza, Egypt.

Population development

Each experiment in this investigation was conducted in a randomized complete block design at the experimental farm of Plant Research Department, Nuclear Research Center, Egypt. To develop F_1 seeds, Gemmeiza 9 (P_2) was grown on 1st of November 2016, while WM 10 (P_1) was grown on 21st and 28th of November to match each other during flowering and crossed during February and March 2017. To develop F_1 plants, F_1 seeds were grown during winter season 2017/2018. To generate F_2 population, F_2 seeds were grown during winter season 2018/2019. This experiment consisted of three replications; each replication included two rows for each of P_1 and P_2 , and ten rows for F_2 plants. Individual grains were planted in 2.0-meter rows. Each row included 20 plants spaced 10 cm apart and rows were spaced 30 cm apart in plots. To generate F_3 population, single seeds of F_2 -selected transgressive segregant were grown during winter season 2019/2020. This experiment consisted of three replications; each replication included two rows for each of P_1 and P_2 , and ten rows for F_3 plants. Individual grains were planted in 2.0-meter rows. Each row included 20 plants spaced

10 cm apart and rows were spaced 30 cm apart in plots.

Data collection

On an individual plant basis, data were collected from each replication on 10 healthy, vigorous and guarded plants of WM 10 (P_1), Gemmeiza 9 (P_2) and 270 plants of F_2 and 135 plants of F_3 populations, on the following traits: number of spikelets/spike, number of kernels/spike, number of kernels/spikelet, number of fertile spikes/plant, 1000-kernel weight (g) and grain yield/plant (g).

Estimation of heterosis

Heterosis was estimated over the better parent, it is referred to as heterobeltiosis. It is worked out as outlined by Singh and Narayanan, (2000), using the following formula:

$$\text{Heterobeltiosis} = [(\bar{F}_1 - \overline{BP})/\overline{BP}] \times 100$$

Where, \overline{BP} is the mean trait value of the better parent.

\bar{F}_1 is the mean trait value of the F_1 generation.

Estimation of inbreeding depression

Inbreeding depression was estimated as follows:

$$\text{Inbreeding depression} = [(\bar{F}_1 - \bar{F}_2)/\bar{F}_1] \times 100$$

Where, \bar{F}_1 and \bar{F}_2 are the mean values of F_1 and F_2 progeny, respectively, of the given trait.

Estimation of phenotypic (PCV) and genotypic (GCV) coefficients of variation

In F₃ generation, phenotypic (PCV) and genotypic (GCV) coefficients of variation were calculated for the studied characters as described by Burton, (1952).

Estimation of simple correlations

The simple correlations (r) between all possible pairs of studied transgressed characters in F₃ population were estimated as outlined by Snedecor and Cochran, (1967), and Singh and Narayanan, (2000).

RESULTS AND DISCUSSION

Heterosis and inbreeding depression

Means of parental, F₁, heterobeltiosis and inbreeding depression estimates in the hybrid population WM10×Gemmeiza9 of bread wheat for number of spikelets/spike, number of kernels/spike, number of kernels/spikelet, number of fertile spikes/plant, 1000-kernel weight and grain yield/plant are presented in Table (1).

All the studied traits showed positive heterobeltiosis, except for number of spikelets/spike and number of kernels/spikelet which showed negative heterobeltiosis values. The highest heterobeltiosis value was exhibited in grain yield/plant (82.76%) followed by fertile spikes/plant (26.83%); while, the

lowest heterobeltiosis estimate was shown by number of kernels/spike (0.06%). The highest heterobeltiosis estimate shown by grain yield was accompanied by high heterobeltiosis for number of spikes/plant (26.83%), 1000-kernel weight (3.81%) and number of kernels/spike (0.06%).

Estimates of inbreeding depression (%) in F₂ hybrid population WM10×Gemmeiza9 of bread wheat for number of spikelets/spike and related traits are presented in Table (1). All studied traits showed inbreeding depression, except for number of kernels/spikelet which showed negative inbreeding depression value (- 1.62%). The highest inbreeding depression was exhibited by grain yield/plant (37.43%) followed by number of fertile spikes/plant (30.19%) and 1000-kernel weight (7.40%); while, the lowest inbreeding depression was shown by number of kernels/spike (0.01%).

The high estimates of heterobeltiosis for grain yield/plant, number of spikes/plant and 1000-kernel weight were followed by inbreeding depression. These results indicate the presence of non-additive gene action (dominance and epistasis) controlling these characters. Mean performance for number of spikelets/ spike, number of kernels/spike and number of kernels/spikelet are nearly the same in F₁ and F₂, this revealed the presence of

additive gene action controlling these traits.

Parental and F₂ means

Means of P₁, P₂, F₂ and ranges for number of spikelets/spike, number of kernels/spike, number of kernels/ spikelet, number of fertile spikes/plant, 1000-kernel weight and grain yield/plant are presented in Table (2).

Gemmeiza9 cultivar was higher yielding, had more fertile spikes/plant, and had a greater number of spikelets/spike, while mutant line 10 (WM10) had a greater number of kernels/spike, number of kernels/spikelet and 1000-kernel weight.

Compared to the original parents, F₂ generation was higher yielding and had a greater number of kernels/spike than the parental lines; while the F₂ values for number of fertile spikes/plant, number of spikelets/spike, and 1000-kernel weight tend to the mean values of the best parent. Wide ranges of minimum and maximum values for all the studied traits in F₂ generation were exhibited. The maximum values for all characteristics was higher than that of the best parent.

Phenotypic evaluation of the F₂ generation

Frequency distributions for number of spikelets/spike, number of kernels/spike, number of kernels/ spikelets, number of fertile spikes/plant, 1000-kernel weight and grain yield/plant

in the F₂ generation are displayed in Fig. (1).

In general, all the studied traits showed continuous variation and polygenic segregation patterns. Number of spikelets/spike, number of kernels/spike, number of kernels/ spikelets and 1000-kernel weight showed normal distribution, whereas, grain yield/plant and number of spikes/plant departed from normality.

Transgressive segregations in F₂

Considerable bi-directional transgressive segregations were observed for number of spikelets/spike and related traits (Fig. 1). This bi-directional transgressive segregations suggest that both parents contributed increasing alleles to these traits. An exceptional transgressive segregation exceeded its parental phenotypic values in positive direction for number of spikelets/spike was selected from F₂ generation (Fig. 2). This transgressive segregation has 38 spikelets/spike. The original parents i.e. WM10 and Gemmeiza 9, have 21.90 and 23.90 spikelets/spike, respectively. This novel transgressive segregation has an increased percentage of number of spikelets/spike 73.51% and 58.99%, respectively, as compared to WM10 and Gemmeiza 9. This novel transgressive segregation has 125.8 kernels/spike, 10 spikes/plant and 61.98 g for grain yield/plant, however, it has 3.31 kernels/spikelet and 49.27 g for 1000-kernel weight. It is worthy to note that, Mujeeb-Kazi and Villareal, (2002) demonstrated that the terminal wheat spike

is made up of 10-30 spikelets in the CIMMYT wheat germplasm.

Phenotypic evaluation of the transgressive segregation progeny in F₃

Means of P₁, P₂, progeny of the transgressive segregation in F₃ and ranges for number of spikelets/spike, number of kernels/spike, number of kernels/spikelet, number of fertile spikes/plant, 1000-kernel weight and grain yield/plant are presented in Table (3).

Compared to the original parents, F₃ generation had a greater number of spikelets/spike, more number of kernels/spike, number of fertile spikes/plant, and higher grain yielding. The F₃ population had a maximum 38 spikelets/spike, 194.5 kernels/spike, 6.1 kernels/spikelet, 19.0 fertile spikes/plant, 64.72 g for 1000-kernel weight and 115.11 g for grain yield/plant.

Frequency distributions for number of spikelets/spike, number of kernels/spike, number of kernels/spikelets, number of fertile spikes/plant, 1000-kernel weight and grain yield/plant in the F₃ generation are displayed in Fig. (3). All the studied traits showed continuous variation.

Coefficients of variability in F₃ generation

Relative values of genotypic (GCV), phenotypic (PCV) and environmental (ECV) coefficients of

variation estimated in F₃ generations are presented in Table (4). Genotypic and phenotypic coefficients of variation exhibited considerable high estimates for grain yield/plant, number of kernels/spike, number of fertile spikes/plant, 1000-kernel weight and number of spikelets/spike. Number of kernels/spikelet had low relative values of genotypic (GCV) and phenotypic (PCV) coefficients of variation.

Segregation in F₃ population

Number and percentage (%) of parental and transgressive segregants for number of spikelets/spike, number of kernels/spike, number of kernels/spikelet, number of fertile spikes/plant, 1000-kernel weight and grain yield/plant, scored in F₃ hybrid population of the cross WM 10 × Gemmeiza 9 are presented in Table (5). Number of spikelets/spike, number of kernels/spike, and grain yield/plant had the highest percentages of transgressive segregations i.e., 79.26, 77.04 and 80.74%, respectively, as compared to parental segregations. Number of kernels/spikelet, 1000-kernel weight and number of fertile spikes/plant scored low percentages of transgression i.e. 36.30, 18.52 and 42.96, respectively, as compared to parental segregants.

The considerable relative values of both genotypic and phenotypic coefficients of variation may be attributed to the creation of new variation in the hybrid population under study (WM10 x Gemmeiza 9), which can play a significant role in increasing the efficiency of wheat

improvement via selection. The success of wheat breeding programs depends on the selection of superior breeding lines which ultimately depends on the variability knowledge of wheat germplasm. It is important to note that all traits in the present study exhibited transgressive segregations in F_3 generation, indicating that both parents harbored positive alleles.

The polygenic segregation patterns in F_3 generation refers to the heterozygosity of the traits of selected transgressive segregation from F_2 generation. The occurrence of exceptional transgressive segregation for number of spikelets/spike and related traits in F_2 population and in the subsequent F_3 generation suggests the presence of complementary QTL alleles in the two parents of the hybrid population under study. Moreover, the novel transgressed alleles in this population should be used as a new useful variation. This is of great importance especially in self-pollinated crops like wheat, where the germplasm base for wheat breeding is narrow as illustrated by de Vicente and Tanksley (1993). Therefore, this hybrid population has great potential for generating novel recombinations of wheat varieties with exceptional characteristics for improving grain yield and yield-related traits.

Number of kernels per spike is one of the main components of wheat (Sreenivasulu and Schnurbusch, 2012 and Guo *et al.*, 2018). Grain yield in wheat is more closely associated with the number of kernels than the kernel weight (Fisher

2008, 2011 and González-Navarro *et al.*, 2015). The number of kernels per spike is determined by the number of spikelets per spike and the number of kernels per spikelet. The results of the present study showed that final transgressed kernel number per spike was increased in F_3 generation. This increase in transgressed number of kernels per spike is due to the increase in transgressed number of spikelets per spike rather than the increase in number of kernels per spikelet. The final increase in grain yield per plant is the result of the increase in transgressed number of kernels per spike rather than the increase in kernel weight. Therefore, it seems likely that further increase in grain yield in this investigation is due to the improvement of grain number. These results consistent with previous work in wheat (Reynolds *et al.* 2001, 2005; González *et al.*, 2014 and Guo *et al.*, 2018).

Previous studies have demonstrated that the evidence of creation of transgressive segregations in hybrid populations of wheat (Yadav *et al.*, 1998; Yadav *et al.*, 1992; Lee and Shaner, 1985; Smith, 1966 and Nilsson-Ehle, 1911). Mujeeb-Kazi and Villareal, (2002) demonstrated that Nilsson-Ehle, a cereal breeder in Sweden, made the first wheat crosses in the early years of the twentieth century and used the pedigree system to handle breeding materials. They also stated that, Nilsson-Ehle, (1911) demonstrated the existence of polymorphic factors, and he thus gave a scientific basis to transgressive segregation.

Several genetic hypotheses have been proposed to explain the appearance of transgressive phenotypes in segregating hybrid populations (Grant, 1975; Riesberg *et al.*, 1999; Riesberg *et al.*, 2003 and Shivaprasad *et al.*, 2012). Among the proposed hypotheses, the best supported genetic mechanisms causing transgressive segregation are complementary action of genes and the nonadditivity of allelic effects between loci or epistasis (Riesberg *et al.*, 1999; Riesberg *et al.*, 2003 and Ditrlich-Reed and Fitzpatrick, 2013). According to the complementary action of genes, hybrid individuals that combine "plus" alleles from both parents or "minus" alleles from both parents are likely to have extreme phenotypes. Grant, (1975) called this an oppositional multiple gene system. The epistasis hypothesis predicts that non-additivity of allelic effects or interactions between gene loci from different parents can cause extreme phenotypes in hybrid populations (Riesberg *et al.*, 1999 and Goulet *et al.*, 2017). Several QTLs studies of transgressive segregating traits support complementary action of genes, epistasis, or both (de Vicente and Tanksley, 1993; Hagiwara *et al.*, 2006 and Mao *et al.*, 2011). Increased mutation rate, the exposure of recessive alleles in segregating hybrid populations, and overdominance are other hypotheses that have been proposed for explanation of transgressive segregation phenomenon (Riesberg *et al.*, 1999). Genomic analyses have suggested

a role for small interfering RNAs as additional mechanisms underlying transgressive segregation (Shivaprasad *et al.*, 2012).

Correlation coefficients between studied traits in F₃ population

Simple correlation coefficients between all possible pairs of studied traits in F₃ population are presented in Table (6). Positive and significant correlation coefficients between grain yield/plant and number of fertile spikes/plant, 1000-kernel weight, number of kernels/spike, number of spikelets/spike and number of kernels/spikelet were estimated. Number of fertile spikes/plant had the highest positive and highly significant correlation coefficient with grain yield/plant (0.79**). High positive and significant correlation coefficients occurred between number of kernels/spike and number of spikelets/spike (0.40**) and between number of kernels/spike and number of kernels/spikelet (0.80**).

The positive correlation coefficients between grain yield/plant and number of fertile spikes/plant, number of spikelets/spike and number of kernels/spike indicate that indirect selection for these traits would be accompanied by high yield and will be effective for the improvement of grain yield in this transgressive hybrid population. Hsu and Walton, (1970), Sidwell *et al.*, (1976) and Al-Bakry *et al.*, (2017) found that grain yield was

positively correlated with number of fertile spikes/plant, number of kernels/spike, number of spikelets/spike and number of kernels/spike. The high positive and significant correlation coefficients occurred between number of kernels/spike and number of spikelets/spike and between number of kernels/spike and number of kernels/spikelet indicate that number of kernels/spikelet and number of spikelets/spike are important in this transgressive hybrid population in the determination of number of kernels/spike. Therefore, selecting for an increase in the number of spikelets/spike or the number of kernels/spikelet or both will increase the number of kernels/spike. The high positive and significant correlation coefficients occurred between number of kernels/spike and number of spikelets/spike and between number of kernels/spike and number of kernels/spikelet obtained in this study are in agreement with the results reported by Sidwell *et al.*, (1976).

Number of fertile spikes/plant had negative correlation coefficients with 1000-kernel weight, number of kernels/spike, and number of kernels/spikelet. Number of spikelets/spike had the highest negative correlation coefficient with 1000-kernel weight (-0.41^{**}). Negative correlation coefficient between 1000-kernel weight and number of kernels/spike was estimated. Negative and significant

correlation coefficient between number of spikelets/spike and number of kernels/spikelet was also observed.

The negative correlation coefficients of 1000-kernel weight with number of spikelets/spike, number of kernels/spike and number of fertile spikes/plant indicates that the simultaneous improvement of kernel weight and these traits may be difficult. Sidwell *et al.*, (1976), Al-Bakry, (2010) and Al-Bakry, (2017) found that kernel weight was negatively correlated with number of spikelets/spike and number of kernels/spike. Hsu and Walton, (1970) also found that kernel weight was strongly negatively correlated with tiller number.

Recently, De los Reyes, (2019) and Pabuayon *et al.*, (2020) referred to the role of transgressive segregants as an outstanding source for adaptive traits of different biotic and abiotic stresses and for yield related traits. They also mentioned that transgressive segregants have not been fully exploited up till now to reach for novel improved genotypes in the 21st century. Accordingly, the promising transgressive segregants selected in this investigation that have recombinations of desirable transgressed traits must be utilized in wheat breeding program for maximizing yield potential. Finally, further studies on the identification of quantitative trait loci (QTLs) controlling the transgressed number of spikelets per spike, number of ker-

nels per spike and grain yield are necessary for more understanding the genetics of these important traits.

SUMMARY

The present study was conducted to create new genetic variation in the hybrid population WM10 × Gemmeiza9 of bread wheat, phenotypic evaluation of F₂ and F₃ segregated populations for number of spikelets/spike, number of kernels/spike, number of kernels/spikelet, number of fertile spikes per plant, 1000-kernel weight and grain yield per plant and to estimate interrelationships between all possible pairs of studied traits. An exceptional transgressive segregation exceeded its parental phenotypic values in positive direction for number of spikelets/spike, number of kernels per spike and grain yield per plant was selected from F₂ generation. In F₃ generation, considerable high estimates of genotypic and phenotypic coefficients of variation for grain yield/plant, number of kernels/spike, number of fertile spikes/plant, 1000-kernel weight and number of spikelets/spike were observed. Positive and significant correlation coefficients between grain yield/plant and number of spikelets/spike, number of kernels/spike, number of kernels/spikelet, number of fertile spikes/plant, and 1000-kernel weight were estimated, indicating that indirect selection for these traits would be accompanied by high grain yield in this transgressed hybrid population.

High positive and significant correlation coefficients occurred between number of kernels/spike and number of spikelets/spike and between number of kernels/spike and number of kernels/spikelet. These results indicated that number of spikelets/spike and number of kernels/spikelet are important in this transgressive hybrid population in the determination of number of kernels/spike.

REFERENCES

- Al-Bakry M. R. I., (2004). Improvement of wheat for drought tolerance by using some biotechnological and nuclear techniques. Ph. D. Thesis, Fac. Agric., Cairo Univ., Egypt.
- Al-Bakry M. R. I., (2010). Inheritance of induced glaucousness, grain yield, and yield-related traits in bread wheat (*Triticum aestivum* L.). Egypt. J. Genet. Cytol. 39: 15-27.
- Al-Bakry M. R. I., Al-Naggar A. M. M., Ghareeb Zeinab E. and Mohamed Samia G. A., (2017). Gene effects and interrelationships of spike traits in bread wheat. Egyptian J. of Plant Breeding, 21 (1): 85-98.
- Broers L. H. M. and Jacobs T., (1989). The inheritance of host plant effect on latency period of wheat rust in spring wheat. II. Number of segregating factors and evidence for transgressive segregation in F₃ and F₄ generations. Euphytica, 44: 207-217.

- Burton G. W., (1952). Quantitative inheritance in grasses. In: Proceedings of the 6th International Grassland Congress. pp: 277-283.
- De los Reyes B. G., (2019). Genomic and epigenomic bases of transgressive segregation - New breeding paradigm for plant phenotypes. *Plant Science*, 288 (2019) 110213.
- de Vicente M. C. and Tanksley S. D., (1993). QTL analysis of transgressive segregation in an interspecific tomato cross. *Genetics*, 134: 585-596.
- Dittrich-Reed D. R. and Fitzpatrick B. M., (2013). Transgressive hybrids as hopeful monsters. *Evol. Biol.*, 40: 310-315.
- FAO., (2009). How to feed the World in 2050. FAO, Rome.
- FAO., (2016). <http://www.fao.org/world-foodsituation/csdb/en/>.
- Fischer R. A., (2008). The importance of grain or kernel number in wheat: a reply to Sinclair and Jamieson. *Field Crops Res.*, 105: 15-21.
- Fischer R. A., (2011). Wheat physiology: a review of recent developments. *Crop Pasture Sci.*, 62: 95-114.
- González F. G., Aldabe M. L., Terrile I. I. and Rondanini D. P., (2014). Grain weight response to different postflowering source:sink ratios in modern high-yielding Argentinean wheats differing in spike fruiting efficiency. *Crop Sci.*, 54: 297.
- González-Navarro E. O., Griffiths S., Molero G., Reynolds P. M. and Slafer A. G., (2015). Dynamics of floret development determining differences in spike fertility in an elite population of wheat. *Field Crops Res.*, 172: 21-31.
- Goulet B. E., Roda F. and Hopkins R., (2017). Hybridization in Plants: Old Ideas, New Techniques. *Plant Physiology*, Vol. 173: 65-78.
- Grant V., (1975). *Genetics of Flowering Plants*. Columbia University Press, New York.
- Grant V., (1981). *Plant Speciation*. Columbia University Press, New York.
- Guindon M. F., Martin E., Cravero V. and Cointry E., (2018). Transgressive segregation, heterosis and heritability for yield-related traits in a segregating population of *Pisum sativum* L. *Expl Agric.*, 1-11. Cambridge University Press. Doi: 10.1017/S0014479718000224
- Guo Z., Zhao Y., Röder M. S., Reif J. C., Ganai M. W., Chen D. and Schnurnusch T., (2018). Manipulation and prediction of spike morphology traits for the improvement of grain yield in wheat. *Scientific*

- Reports, 8: 14435.
- Hagiwara W. E., Onishi K., Takamura I. and Sano Y., (2006). Transgressive segregation due to linked QTLs for grain characteristics of rice. *Euphytica* 150: 27-35.
- Hsu P. and Walton P. D., (1970). The inheritance of morphological and agronomic characters in spring wheat. *Euphytica* 19: 54-60.
- Kim S. K., Kim J. and Jang W., (2017). Past, Present and Future Molecular Approches to Improve Yield in Wheat. In: Ruth Wanyera editor. *Wheat Improvement, Management and Utilization*. DOI: 10.5772/63694.pp. 17-37.
- Koseoglu K., Adak A., Sari D., Sari H., Oncu F. Ceylan and Toker C., (2017). Transgressive segregations for yield criteria in reciprocal interspecific crosses between *Cicer arietinum* L. and *C. reticulatum* Ladiz. *Euphytica*, 213: 116.
- Lee T. S. and Shaner G., (1985). Transgressive segregation of length of latent period in crosses between slow leaf-rusting wheat (*Triticum aestivum*) cultivars. *Phytopathology*, 75: 643-647.
- Mackay I. J., Cockram J., Howell P. and Powell W., (2020). Understanding the classics: the unifying concepts of transgressive segregation, inbreeding depression and heterosis and their central relevance for crop breeding. *Plant Biotechnology Journal*, pp. 1-9.
- Mao D., Liu T., Xu C., Li X. and Xing Y., (2011). Epistasis and complementary gene action adequately account for the genetic bases of transgressive segregation of kilograin weight in rice. *Euphytica*, 180: 261-271.
- Mujeeb-Kazi A. and R. Villareal L., (2002). Wheat. In: Evolution and adaptation of cereal crops. Chopra V. L. and Prakash S. (Eds.). Science Publishers, Inc., Enfield, NH, USA.
- Nilsson-Ehle H., (1911). Kreuzungsuntersuchungen an hafer und weizen. *Lunds Univ. Areskript*, 7: 1-84.
- Pabuayon I. C. M., Kitazumi A., Cushman K. R., Singh R. K., Gregorio G. B., Dhatt B., Zabet Moghaddam M., Walia H. and Reyes B. G. De los, (2020). Transgressive segregation for salt tolerance in rice due to physiological coupling and uncoupling and genetic network rewiring. *bioRxiv preprint* doi: <https://doi.org/10.1101/2020.06.25.171603>
- Raval L., Pithia M. S., Mehta D. R., Mungra K. S. and Shah Siddhi, (2018). Spectrum of variation and transgressive segregation in F₂ generation of desi chickpea. *Electronic Journal of Plant Breeding*, 9 (1):

- 18-24.
- Reynolds M., Pellegrineschi A. and Skovmand B., (2005). Sink-limitation to yield and biomass: a summary of some investigations in spring wheat. *Ann. Appl. Biol.*, 146: 39-49.
- Reynolds M. P., Calderini D. F., Condon A. G. and Rajaram S., (2001). Physiological basis of yield grains in wheat associated with the LR 19 translocation from *Agropyron elongatum*. *Euphytica*, 119: 137-141.
- Rieseberg L. H., Archer M. A. and Wayne R. K., (1999). Transgressive segregation, adaptation and speciation. *Heredity*, 83: 363-372.
- Rieseberg L. H., Widmer A., Arntz A. M., and Burke J. M., (2003). The genetic architecture necessary for transgressive segregation is common in both natural and domesticated populations. *Philos Trans R Soc Lond B Biol. Sci.*, 358: 1141-1147.
- Semenov M. A. and Stratonovitch P., (2013). Designing high-yielding wheat ideotypes for changing climate. *Food and Energy Security.*, 2(3): 185-196. Doi: 10. 1002/fes3.34.
- Shivaprasad P. V., Dunn R. M., Santos B. A., Bassett A. and Baulcombe D. C., (2012). Extraordinary transgressive phenotypes of hybrid tomato are influenced by epigenetics and small silencing RNAs. *EMBO J.*, 31: 257-266.
- Shreya S., Ainmisha S. and Vashanti R. P., (2017). Transgressive segregation study in F₃ population of four groundnut crosses. *International Journal of Current Microbiology and Applied Sciences*, 6: 2054-2059.
- Sidwell R. J., Smith E. L. and McNew R. W., (1976). Inheritance and interrelationships of grain yield and selected yield-related traits in a hard red winter wheat cross. *Crop Sci.*, 16: 650-654.
- Singh P. and Narayanan S. S., (2000). *Biometrical Techniques in Plant Breeding*. Kalyani Publishers, New Delhi, India.
- Smith G. S., (1966). Transgressive segregation in spring wheat. *Crop Sci.*, 6: 310-317.
- Snedecor G. W. and Cochran W. G., (1967). *Statistical Methods*. Sixth edition, Iowa State University Press, Ames, Iowa.
- Sreenivasulu N. and Schnurbusch T., (2012). A genetic playground for enhancing grain number in cereals. *Trends Plant Sci.*, 17: 91-101.
- Tilman D., Balzer C., Hill J. and Befort B. L., (2011). Global food demand

- and the sustainable intensification of agriculture. Proc. Natl. Acad. Sci. USA., 108 (50): 20260-20264. DOI: 10.1073/pnas.1116437108
- Vega U. and Frey K. J., (1980). Transgressive segregation in inter- and intraspecific crosses of barley. Euphytica, 29: 585-594.
- Yadav B., Tyagi C. S. and Singh D., (1998). Genetics of transgressive segregation for yield and yield components in wheat. Ann. Appl. Biol., 133: 227-235.
- Yadav B., Ram B., Sethi S. K. and Luthra O. P., (1992). Genetics of field resistance and transgressive segregation leaf rust of wheat (*Triticum aestivum* L. em. Thell.). Cereal Research Communication, 20: 41-48.
- Zhou Y., Conway B., Miller D., Marshall D., Cooper A., Murphy P., Chao S., Brown-Guedira G. and Costa J., (2017). Quantitative trait loci mapping for spike characteristics in hexaploid wheat. Plant Genome, 10 (2).
<https://doi.org/10.3835/plantgenome2016.10.0101>

Table (1): Parental and F₁ means (\pm S.E.), heterobeltiosis and inbreeding depression estimates for spikelets per spike and related traits.

Trait	Parents		F ₁ mean \pm S.E.	Heterobeltiosis	Inbreeding depression
	WM10 \pm S.E.	Gemmeiza9 \pm S.E.			
No. of spikelets /spike	22.0 \pm 0.06	24.96 \pm 0.15	23.47 \pm 0.18	- 5.97	1.49
No. of kernels /spike	87.0 \pm 0.97	80.22 \pm 0.44	87.05 \pm 0.83	0.06	0.01
No. of kernels /spikelet	3.95 \pm 0.05	3.21 \pm 0.02	3.71 \pm 0.04	-6.07	- 1.62
Grain yield/plant (g)	19.11 \pm 0.58	28.01 \pm 0.79	51.19 \pm 1.34	82.76	37.43
1000-grain weight (g)	54.91 \pm 1.09	42.58 \pm 0.31	57.00 \pm 0.65	3.81	7.40
No. of spikes /plant	4.00 \pm 0.13	8.20 \pm 0.27	10.40 \pm 0.34	26.83	30.19

Table (2): Parental, F₂ population means (\pm S.E.) and ranges for spikelets per spike and related traits grown during 2018/2019 season.

Trait	Parents		F ₂ population		
	WM10 \pm S.E.	Gemmeiza9 \pm S.E.	Range		Mean \pm S.E.
			Min.	Max.	
No. of spikelets /spike	21.90 \pm 0.08	23.90 \pm 0.12	18	38	23.12 \pm 0.13
No. of kernels /spike	84.0 \pm 1.17	77.35 \pm 0.42	55.0	142.5	87.04 \pm 0.97
No. of kernels /spikelet	3.83 \pm 0.04	3.24 \pm 0.02	2.12	5.68	3.77 \pm 0.06
No. of spikes /plant	3.76 \pm 0.14	7.80 \pm 0.25	2	17	7.26 \pm 0.20
1000-grain weight (g)	50.78 \pm 1.14	45.84 \pm 0.40	33.43	74.27	52.78 \pm 0.49
Grain yield /plant (g)	16.28 \pm 0.61	27.41 \pm 0.86	10.10	85.15	32.03 \pm 0.88

Table (3): Parental, F₃ population means (\pm S.E.), and ranges for spikelets per spike and related traits grown during 2019/2020 season.

Trait	Parents		F ₃ population		
	WM10 \pm S.E.	Gemmeiza9 \pm S.E.	Range		Mean \pm S.E.
			Min.	Max.	
No. of spikelets/spike	22.3 \pm 0.06	24.26 \pm 0.16	22.00	38.00	30.13 \pm 0.31
No. of kernels/spike	87.0 \pm 1.22	82.12 \pm 0.36	60.42	194.50	114.93 \pm 1.94
No. of kernels/spikelet	3.90 \pm 0.07	3.38 \pm 0.06	2.39	6.10	3.83 \pm 0.06
No. of spike /plant	4.20 \pm 0.11	7.89 \pm 0.24	4.00	19.00	10.49 \pm 0.29
1000-grain weight (g)	50.25 \pm 0.94	46.01 \pm 0.56	34.15	64.72	50.35 \pm 0.50
Grain yield/plant (g)	18.36 \pm 0.84	29.81 \pm 0.89	19.70	115.11	59.80 \pm 1.82

Table (4): Variability parameters in F₃ generation for spikelets per spike and related traits grown during 2019/2020 seasons.

Trait	PCV(%)	GCV(%)	ECV (%)
No. of spikelets/spike	42.78	41.82	0.96
No. of Kernels/spike	444.87	432.99	11.88
No. of Kernels/spikelet	13.31	12.79	0.52
No. of spikes/plant	111.34	106.76	4.58
1000-kernel weight (g)	68.32	46.20	22.12
Grain yield /plant (g)	747.12	720.30	26.82

Table (5): Number and percentage of parental and transgressive segregants for number of spikelets/spike and related traits in F₃ hybrid population of the cross WM 10 × Gemmeiza 9.

Trait	Parental segregants		Transgressive segregants	
	No.	%	No.	%
No. of spikelets/spike	28	20.74	107	79.26
No. of kernels/spike	31	22.96	104	77.04
No. of kernels/spikelet	86	63.70	49	36.30
No. of spikes/plant	77	57.04	58	42.96
1000-grain weight (g)	110	81.48	25	18.52
Grain yield/plant (g)	26	19.26	109	80.74

Table (6): Correlation coefficients between studied traits of the F₃ transgressive segregation population.

Trait	No. of kernels/spike	No. of kernels/spikelet	1000-kernel weight	No. of spikes/plant	Grain yield/plant
No. of spikelets/spike	0.40**	- 0.21*	- 0.41**	0.01	0.21*
No. of kernels/spike		0.80**	- 0.14*	- 0.16*	0.36**
No. of kernels/spikelet			0.13	- 0.25**	0.27**
1000-kernel weight				- 0.08	0.21*
No. of spikes/plant					0.79**

Simple correlation coefficient with $n-2 = 133$ df, must exceed 0.16 and 0.21 to be significant at the 0.05 (*) and 0.01 (**) probability levels, respectively, (Snedecor and Cochran 1967).

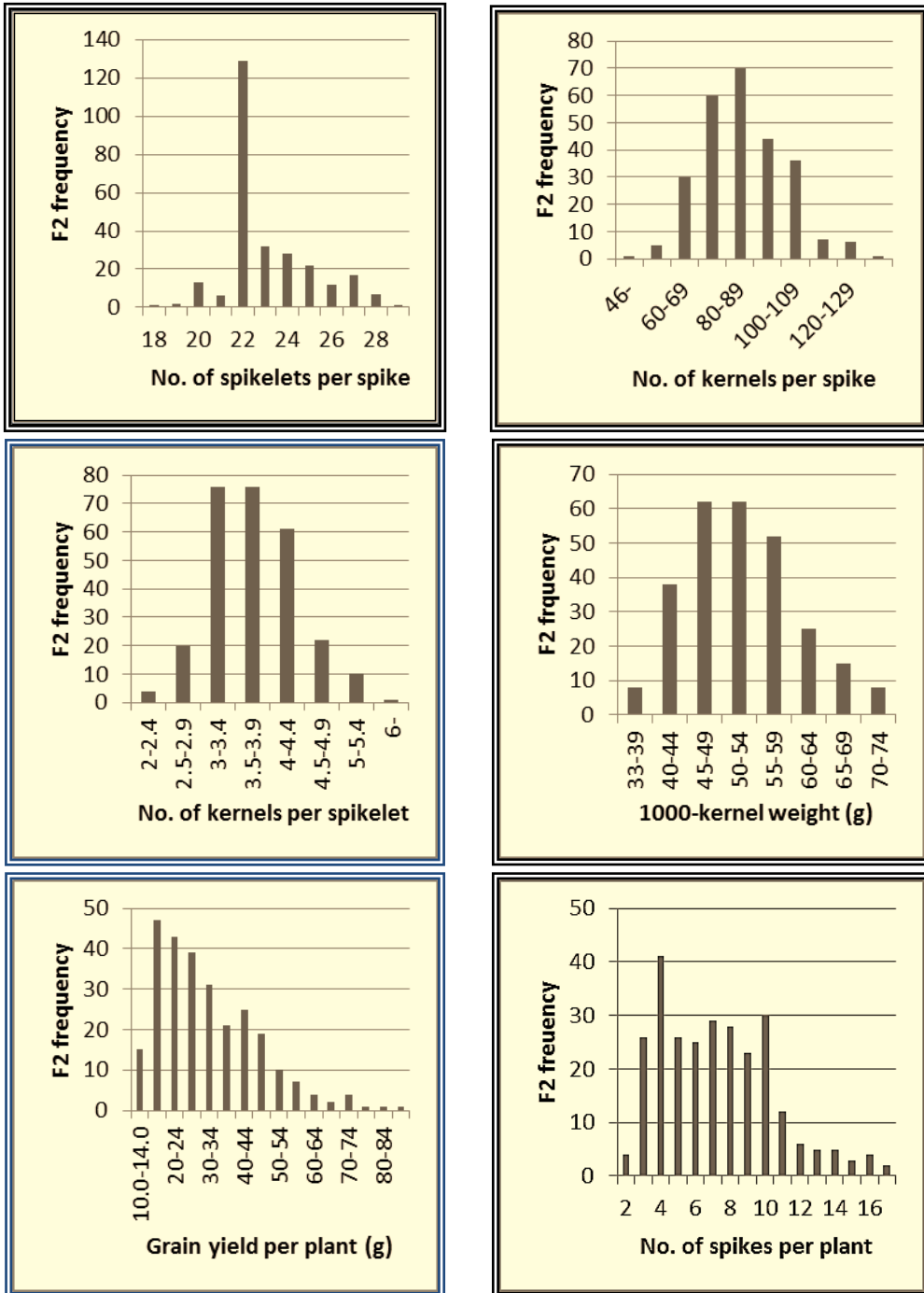


Fig. (1): Frequency distribution of number of spikelets/spike, number of kernels/spike, number of kernels/spikelet, 1000-kernel weight, grain yield/plant and number of spikes per plant in F₂ generation of the hybrid population WM10 × Gemmeiza 9.



Fig. (2). Spike of the novel transgressive segregant of bread wheat containing 38 spikelets/spike.

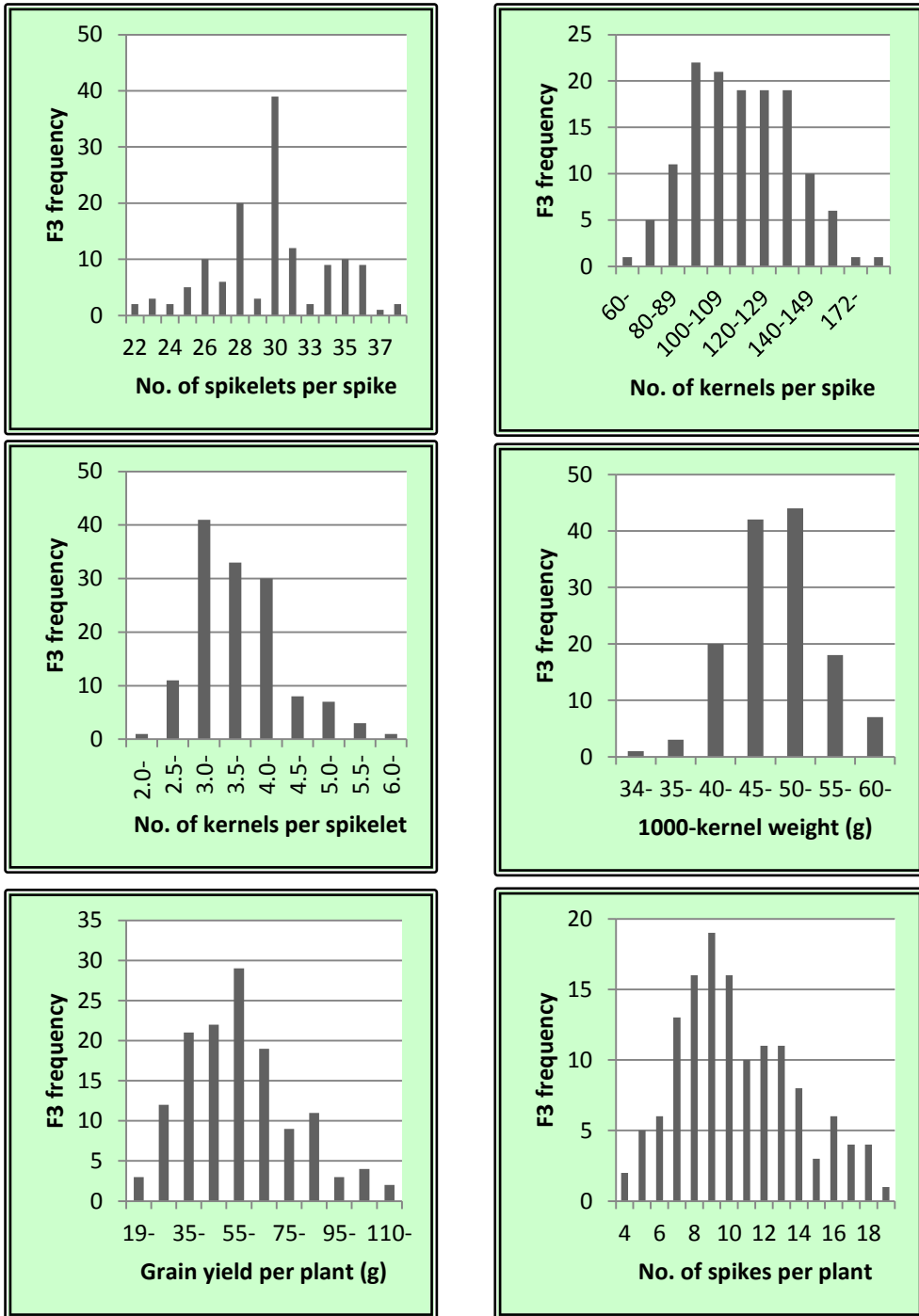


Fig. (3): Frequency distribution of number of spikelets/spike, number of kernels/spike, number of kernels/spikelet, 1000-kernel weight, grain yield/plant and number of spikes per plant in F₃ generation of the hybrid population WM10 × Gemmeiza 9.