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GRAPHICAL DIALLEL ANALYSIS FOR QUANTITATIVE TRAITS IN DURUM WHEAT

Rangel DRAGOV[1], Krasimira TANEVA[1], Boryana HADZHIIVANOVA[1], Maria VIDEVA[1], Boyana TODOROVA[1], Rositsa CHOLAKOVA[2]

[1]Agricultural Academy, Field Crops Institute - Chirpan, Georgi Dimitrov Blvd, 6200,
Chirpan, Bulgaria
[2]Agricultural Academy, Maritsa Vegetable Crops Research Institute,
32 Brezovsko shosse Street, 4000, Plovdiv, Bulgaria

Corresponding author email: rositsa.cho@abv.bg

Abstract

The aim of the study is to determine the genetic system controlling traits related to productivity in durum wheat and to identify the parents and their correct usage for achieving optimal results. A diallel cross without reciprocals was conducted with five modern durum wheat varieties at the Field Crops Institute - Chirpan. The inheritance of traits involves incomplete, complete and overdominance. Productivity tillering, spikelets number per spike and grain weight per spike are controlled by a simply additive-dominant genetic system with epistasis from complementary type. For the traits: plant height, spike length, and thousand kernel weight, the inheritance control is accomplished by a simply additive-dominant genetic system. All traits increased by accumulation of dominant genes, except productivity tillering. Complexly breeding valuable genotype with more dominant gene simultaneously several traits are the variety Progress. It can be successfully used to improve the traits related to productivity in durum wheat breeding programs.

***Key words**: additive-dominance model, epistasis, traits rise, durum wheat.*

INTRODUCTION

Durum wheat (*Triticum durum* Desf.) is an important agricultural crop, widely cultivated for pasta production and other high-protein, gluten-rich food products. It is a raw material mainly used for human consumption. Over the past decades, the increasing global population has necessitated a significant rise in crop yields. Breeding programs for durum wheat predominantly rely on hybridization to generate genetic diversity, which is crucial for effective breeding and the creation of new genotypes. The selection of parents used for crossing is a fundamental step in achieving high breeding efficiency. The acquisition and assessment of these genotypes assist in creating new ones adapted to changing climatic conditions. Establishing the genetic control systems governing inheritance is fundamental for achieving optimal breeding outcomes. In the context of durum wheat, graphical diallel analysis is an underutilized approach that provides valuable insights. This method allows breeders to efficiently utilize parental lines as donors and optimize their breeding potential. The genetic system controlling productivity-related traits exhibits various inheritance patterns. In most cases, an additive-dominant genetic system governs these traits, although some are also influenced by non-allelic interactions (epistasis). One of the key advantages of graphical diallel analysis is its ability to account for epistatic gene interactions. Epistasis can either enhance or reduce the degree of dominance (Hayman, 1957). In quantitative genetics, two primary types of epistasis are recognized: complementary (recessive gene) and duplicate (dominant gene) (Mather, 1967). Both types of epistasis play significant roles in the inheritance of quantitative traits in durum wheat. Hayman (1954a), Jinks (1955; 1956), and Whitehouse et al. (1958) demonstrated that the simplest way to extract information from diallel crosses is through the graphical representation of the covariance (Wr) of each row against its variance (Vr). Graphical diallel analysis provides valuable information regarding the genetic nature of the studied quantitative traits, as well as the nature of recessive and dominant genes in the parents.

Furthermore, it offers insight into which types of genes contribute to increased or decreased trait values.

Several researchers have conducted diallel analyses of productivity-related traits. However, studies focusing on durum wheat remain relatively scarce, and different genetic systems governing the traits have been observed depending on the parental lines used. Kashif et al. (2003) reported the predominant role of complete dominance in the inheritance of spike length and epistasis, which complicates selection efficiency. For thousand kernel weight, they reported incomplete dominance and a lack of epistasis. Ivanovska et al. (2003) investigated plant height in F_1 and F_2 generations of a seven-parent durum wheat diallel cross. They found that overdominance played a general role in inheritance in F_1, while incomplete dominance was reported in F_2. Ismail et al. (2003) reported incomplete dominance in F_1 and F_2, with dominant genes predominant in the parents for plant height and spike length, while overdominance was observed for thousand kernel weight. Aydogan & Yagdi (2004) concluded that overdominance was the principal inheritance pattern for all examined traits in their study. Inamullah et al. (2006) suggested that the accumulation of recessive genes was responsible for achieving higher results for productivity tillering and spike length, while dominant genes led to increased thousand kernel weight. They reported that incomplete dominance was the primary inheritance pattern for thousand kernel weight, while overdominance was predominant for the other traits. Gami et al. (2010) proposed that plant height and spike length were enhanced by the accumulation of recessive genes. Nazeer et al. (2011) observed overdominance for spike length and grain weight per spike, whereas incomplete dominance played a primary role in the inheritance of all other traits. Zaazaa et al. (2012) and Ijaz & Kashif (2013) conducted diallel analyses on grain weight per spike and highlighted its direct correlation with yield levels. They reported that this trait was controlled by an additive-dominant genetic system with epistatic interactions, emphasizing the importance of epistasis in trait expression. Adel & Ali (2013) performed graphical diallel analysis and concluded that incomplete dominance played a crucial role in the inheritance of productivity tillering, whereas overdominance was observed for plant height. Fellahi et al. (2015) investigated productivity tillering and found that it was controlled by a simple additive-dominant genetic system. Kultu & Olgun (2015) confirmed that spike length and grain weight per spike were controlled by an additive-dominant genetic system with non-allelic interactions. Sadeghzadeh-Ahari et al. (2015) noted that the examined traits increased as a result of the accumulation of either dominant or recessive genes. Shehzad et al. (2015) reported that most of the studied traits exhibited overdominance in their inheritance. All these studies identified genotypes carrying dominant or recessive genes that are suitable for improving specific traits. Some of these genotypes are globally recognized varieties. These varieties can be effectively utilized to enhance individual traits in breeding programs, ultimately improving durum wheat productivity. This approach accelerates the breeding process and facilitates the achievement of desirable outcomes for plant breeders.

The aim of this study is to determine the genetic system controlling productivity-related traits in durum wheat. Specifically, it seeks to identify the types of genes responsible for enhancing yield-related traits and, most importantly, to determine which parental lines carry these genes.

MATERIALS AND METHODS

Five modern durum wheat varieties were included as parents in a diallel cross scheme. The Victoria variety was developed at the Field Crops Institute (FCI) Chirpan and was certified by the Patent Office in 2008. It is a medium-stemmed variety with good lodging resistance and high tillering capacity. Its vegetative period is similar to that of the Predel variety - it heads simultaneously and matures 1-2 days later. It has a more erect flag leaf. The spike is medium in length, dense, white, and pointed in profile, belonging to var. *Valenciae*. Awns are distributed along the entire spike length and are longer relative to the spike. The variety is characterized by yellow, semi-elongated grains, with a thousand kernel weight ranging from 44 to 46 g and vitreousness of 85-95%. The test weight is 79-80 kg/hl. It exhibits good rust resistance and moderate resistance to powdery mildew. The variety has a high yield potential exceeding 8500 kg/ha, good winter hardiness, and phenotypic stability across different years. The Deni variety was developed at Field Crops Institute - Chirpan using the pedigree selection method and was certified by the Patent Office in 2012. It has a high yield potential and belongs to the group of medium-early varieties. The stem reaches a height of 90-95 cm. It has a white, pubescent spike (var. *Valenciae*) with long, white, uniformly pointed awns. The grains are medium-sized, with a thousand kernel weight of 48-50 g. The test weight is high, ranging from 80 to 82 kg/hl. Based on biochemical and technological parameters, the variety is considered a high-quality accession. It has a high vitreousness, reaching up to 87% in certain years. It possesses good resistance to powdery mildew and moderate resistance to rusts. The variety exhibits high tillering capacity and good winter hardiness. It is suitable for producing high-quality pasta products and pearled durum wheat. The Superdur variety was developed in Austria by the breeding company *ProbsdorferSaatzucht* and was listed in the European variety catalog in 2000. It is a winter-type variety with high cold tolerance. It belongs to *var. Leucomelan (ALEF) KOERN.* According to the varietal description, the spike is white with dark awns, elongated, dense, and flat. The variety is medium-stemmed with good lodging resistance. It is characterized by amber-yellow grains with very high virtuousness, exceeding 86%. The grains are large, with a thousand kernel weight of 48–54 g, and a test weight of 78–80 kg/hl. The variety demonstrates high resistance to rusts and moderate resistance to powdery mildew. Its technological properties are superior, with grain protein content reaching up to 15% and wet gluten content exceeding 32%. The Progress variety was recognized as an original variety in 1990. It belongs to var. *Leucurum Al.*, characterized by white to pale-yellow, non-pubescent spikes and awns. The spike is cylindrical, slightly tapered at the top, and approximately 8.5 cm in length. The grains are very large, with a thousand kernel weight of 55-60 g and a test weight of 80-82 kg/hl. The variety exhibits good drought and winter hardiness. It shows moderate resistance to brown and black rust as well as powdery mildew. It has favorable values for protein content and wet gluten in the grain. It is classified as a medium-early variety in terms of the vegetative period. The productivity potential exceeds 7500 kg/ha. Due to its large and well-nourished grains, it is highly suitable for producing pearled durum wheat and other pasta products. The Predel variety was recognized in 2010 and is currently the national yield standard in Bulgaria. It is characterized by high and stable yields across different years, with a productivity potential exceeding 8500 kg/ha. The variety is medium-stemmed (85-95 cm) with very good lodging resistance. It belongs to the medium-early group. The spike is white, slightly pubescent, with white awns (var. *Valenciae*). It is of medium length and has a moderate spikelets density. The variety demonstrates good resistance to rusts and powdery mildew and exhibits enhanced drought tolerance. The grains are yellow, medium-sized (thousand kernel weight 44-47 g), and slightly elongated. The test weight reaches up to 82.4 kg/hl. Vitreousness varies across years, consistently exceeding 85%. Predel has a high carotenoid content, which ensures a stable color in pasta products. It carries a genetic marker for high gluten quality – gamma gliadin 45 allowing for high and stable pasta quality over the years. In terms of technological and biochemical properties, it matches or surpasses the standard variety in quality. The combination of high yield and excellent pasta-making qualities makes it one of the most valuable durum wheat varieties in Bulgaria.

The diallel crosses among the five varieties were performed without reciprocal crosses. Hand-pollination was conducted at the beginning of heading under field conditions, using 30 spikes per cross. A total of ten crosses were performed. The genotypes were arranged in a randomized block design with three replications in the breeding garden of Field Crops Institute - Chirpan. The parents and F_1 hybrids were sown in two rows, while F_2 hybrids were sown in five rows handmade in beds. The bed length was two meters, with an inter-row spacing of twenty cm and an intra-row spacing of five cm. A total of 20 plants were selected per parent, F_1 crosses and F_2 crosses at full maturity. The experiment was conducted in the breeding trial field of Field Crops Institute - Chirpan over three consecutive years (2014-2016). The recommended technology for durum wheat cultivation was applied. The preceding crop was field pea harvested for green fodder. Nitrogen fertilization was applied once in spring as a top-dressing at a rate of 100 kg active nitrogen substance per hectare. Weed control was performed with a single treatment using a combination of two herbicides. No fungicides were applied for disease and pest control. The three study years were characterized by higher temperatures compared to the long-term period. The first and second years had normal precipitation during the vegetative period, whereas the third year had 20% less rainfall than the long-term average. Six quantitative traits were analyzed: plant height, productivity tillering, spikelets number per spike, spike length, grains weight per spike and thousand kernel weight.

The graphical diallel analysis was conducted following the methods of Hayman (1954a; 1954b; 1957; 1958; 1960), Jinks (1954), Mather (1967), and Mather & Jinks (1971). The diallel analysis program by Aksel& Johnson (1962) was used. The diallel graphs were presented without eliminating parents that cause non-allelic interactions to obtain adequate genetic information. The genetic inheritance systems of quantitative traits were determined using a graphical regression analysis following Hayman (1954a) and Jinks (1954). The interpretation was based on the following assumptions: homozygous parents, diploid segregation, no difference in reciprocal crosses, independent action of non-allelic genes and independent gene distribution among parents. Homozygosis of the parents was ensured as durum wheat is a self-pollinating crop. Diploid segregation was assumed based on typical disomic inheritance in durum wheat. According to Hayman (1954), measuring the average degree of dominance on the graph confirms the absence of multiple allelism and the independent gene distribution among parents. The graphical representation and interpretation were performed using the Vr/Wr coordinate system and the regression line $Wr = a \pm bVr$. In the absence of inter-locus interactions, variety points on the diagram should fall within a limiting parabola calculated as $Wr^2 = Vr.Vp$ and be distributed along the regression line (b = 1). If the regression coefficient (b) significantly differs from unity, the presence of non-allelic interactions (epistasis) is assumed. A coefficient significantly lower than unity indicates complementary epistasis by recessive gene, while a coefficient greater than unity indicates duplicate epistasis by dominant gene. The degree of dominance is certin by the crossing of regression line with the Wr ordinate. When cross above the origin it indicates incomplete dominance. When cross around the origin it indicates complete dominance. If regression line cross below the origin it indicates overdominance. The location of genotypes along the regression line indicates which genes, recessive or dominant genes are more in parents of diallel cross. Points located close to the origin indicate parents with more dominant genes, while points located closer to the intersection of the regression line with the limiting parabola indicate parents with more recessive genes. The correlation coefficient $r_{Yr(Wr+Vr)}$ shows whether dominant or recessive factors control trait expression. A positive r indicates that higher trait values are associated with recessive genes, while a negative value suggests that dominant genes contribute to higher trait values. Variation in quantitative traits contains variation due to genetic causes, which is inherited, and variation due to environmental conditions, which is not inherited.

RESULTS AND DISCUSSIONS

A major contribution to the development of a successful breeding program for durum wheat is the proper utilization of genetic diversity. Identifying high-potential parents and crossing them is essential for the recombination of genes in newly created genotypes. The evaluation of the breeding value of parents as starting material for improving specific traits particularly productivity is crucial for achieving the ultimate goal. Graphical analysis provides a comprehensive explanation of the behavior of dominant and recessive genes in the parents and indicates the contribution of individual parents to inheritance. This helps in selecting parents as donors for improving newly developed genotypes. This study found significant differences between genotypes (analysis of variance not shown), and based on this, the following results have been presented:

Plant height

Figure 1 shows the graphical analysis for two generations: F_1 and F_2. The regression line for both generations crosses above zero, indicating that inheritance is governed by incomplete dominance. Incomplete dominance is thus the underlying genetic basis of this trait. In both graphs (Figure 1), the regression line shows a decline that significantly differs from zero but not significantly from unity.

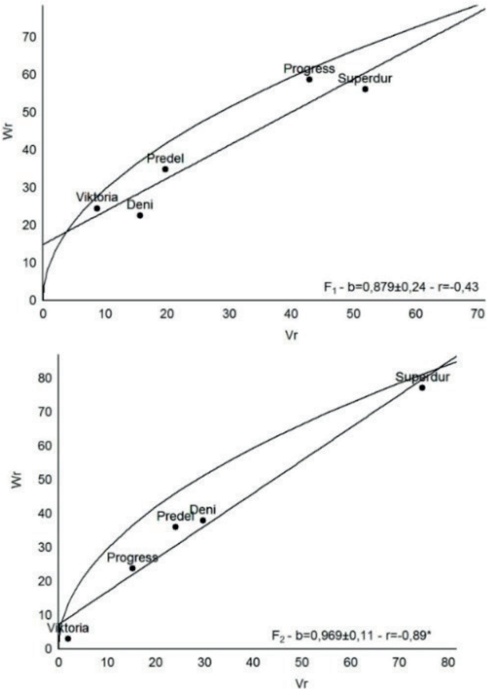

Figure 1. Graphical diallel analys for Plant height in F_1 and F_2; b – regression coefficient; $r_{Yr(Wr+Vr)}$- correlation coefficient; * - $p \leq 0.05$

Therefore, we can infer that plant height is controlled by a simple additive-dominant genetic system. Similar results have been reported by other researchers (Gami et al., 2010; Yao et al., 2011; Kutlu & Olgun, 2015; Shehzad et al., 2015). It is interesting to examine the relationship between the trait values in parents and their sum. The correlation coefficients (r) are negative in both generations, and in F_2, the correlation is statistically significant. This suggests that dominant genes are associated with increased plant height in durum wheat. In Figure 1, the configuration of the graphs in both generations shows that the Victoria variety is located near to the origin of the coordinate system. This indicates that Victoria likely contains more dominant genes. Conversely, the Superdur variety appears to possess the highest number of recessive genes, as shown consistently in both generations. Thus, we can assume that its short-stemmed nature is determined by the action of recessive genetic factors. It is worth highlighting the high breeding value of the Superdur variety. When used as a parent, dwarf plants appear as early as the F_2 generation and are likely to remain stable in subsequent segregating generations.

In the two generations, the other three varieties occupy an intermediate position and exhibit greater variation in the coordinate system across generations. This suggests that they contain an equal proportion of dominant and recessive genes.

Productivity tillering

The graphs for this trait are presented in Figure 2. In the figure, the regression line crosses below the starting point in F_1, indicating overdominance. In the F_2 generation, the regression line crosses the ordinate near the starting point, suggesting complete dominance. Overdominance in the expression of this trait was also reported by Shehzad et al. (2015). It is evident that the trait in durum wheat is determined by a genetic system involving complementary epistasis in both generations. This is demonstrated by the regression coefficient "b", which is significantly less than one, causing the regression line to bend downward to a circumstantial angle.

The correlation coefficient (r) is positive but not statistically significant. Therefore, the accumulation of recessive genes increases the values of the trait. This is consistent with the findings of Inamullah et al. (2006).

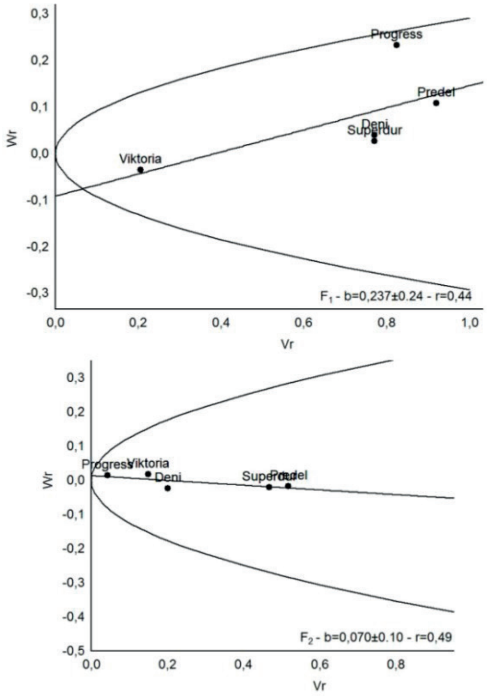

Figure 2. Graphical diallel analys for productivity tillering in F_1 and F_2; b – regression coefficient; $r_{Yr(Wr+Vr)}$- correlation coefficient

The parental points are significantly spaced apart and lie between the regression line and the parabola. This is attributed to the genotype-environment interaction in the expression of the trait. The positions of the parent points change across generations, which is explained by genotype - environment interaction. Based on the location of the parental points at the beginning and end of the crossing between the regression line and the parabola, it can be concluded which varieties have more dominant genes and which have more recessive genes. It is noteworthy that in both generations, the varieties are located near the origin of the coordinate system, indicating they have more dominant genes.

Spike length

The graphs for this trait are presented in Figure 3. In both generations (F_1 and F_2), the regression line intersects the origin of the coordinate system (Vr/Wr) above zero, indicating that incomplete dominance controls the inheritance of the trait. The regression lines in both generations suggest that inheritance is governed by a simple additive-dominant genetic system. This is consistent with the results obtained by other authors (Nazeer et al., 2011; Shehzad et al., 2015). The correlation coefficients (r) obtained for the F_1 generation (Figure 3) indicate that the increase in trait values is due to the accumulation of dominant genes. This correlation is significant in the F_1 generation and should be taken into consideration. However, in the second generation, the correlation coefficient is not significant and is negative. Therefore, the values of the trait increase with the accumulation of dominant genes. In the first generation, the Victoria variety contains more recessive genes, while Progress and Superdur varieties are located near the origin, indicating they have more dominant genes.

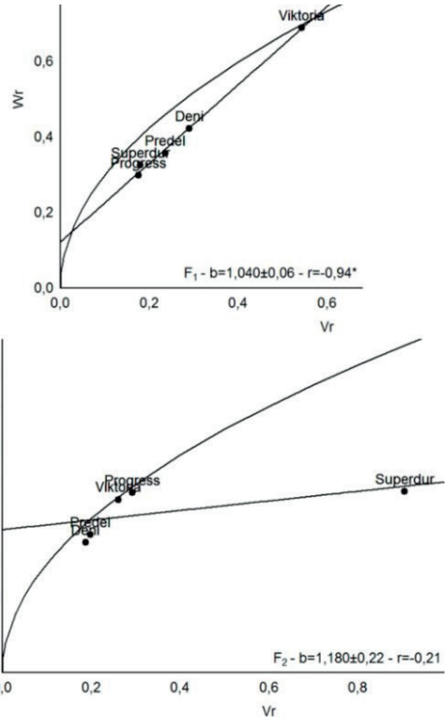

Figure 3. Graphical diallel analys for Spike length in F_1 and F_2; b – regression coefficient; $r_{Yr(Wr+Vr)}$- correlation coefficient; * - $p \leq 0.05$

The rest of the varieties are located in the middle, which indicates they are with equal dominant and recessive genes.

In the second generation, all varieties are located near to the beginning and have low values of (Wr + Vr), since the parabola remains open on the chart at the end. Therefore they have more dominant genes.

Spikelets number per spike

Graphical diallel analysis is presented in Figure 4. In generation F_1, the regression line intersects the coordinate system below the starting point, which means that overdominance is of essential importance. In the second generation, complete dominance have major role. The results are also in sync with other authors (Nazeer et al., 2011; Fellahi et al., 2015; Shehzad et al., 2015). The slope of the regression line indicates that in inheritance of this trait presence complementary epistasis.

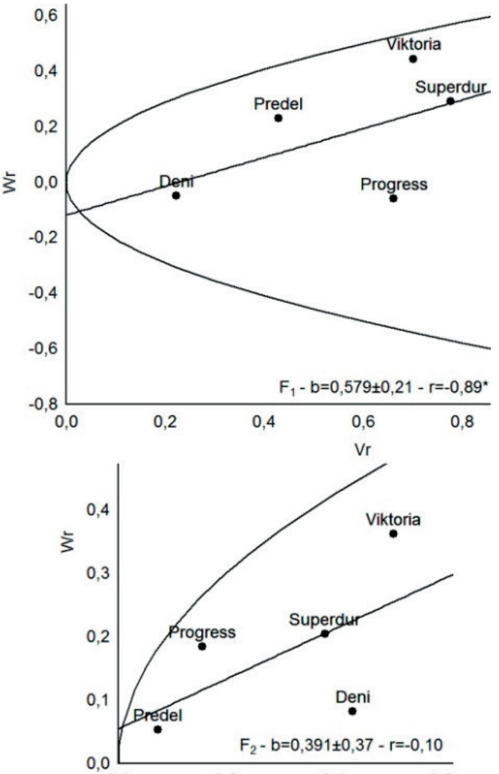

Figure 4. Graphical diallel analys for Spikelets number per spike in F_1 and F_2; b – regression coefficient; $r_{Yr(Wr+Vr)}$- correlation coefficient; * - $p \leq 0.05$

The correlation coefficient r shows dominant genes increasing values of the trait (Figure 4). In the first generation correlation coefficient is significant. Gami et al. (2010) reported the same statement for this trait and cunclude dominance genes are important for this trait. In second generation correlation coefficient is again negative and unproven. From the graphs for the F_1 generation, Deny variety have more dominant genes. In second generation with the most dominant genes is Predel variety. The dispersion (distance) of the points from the regression line is also impressive, which shows the great influence of the environment on the expression of the trait.

Grains weight per Spike

The graphs of graphical analysis of both generations is presented in Figure 5. The regression line intersects Wr below and show overdominance. Other authors also report that overdominance is involved in the inheritance of the trait (Vanda & Houshmand, 2011; Nazeer et al., 2011; Shehzad et al., 2015). In Figure 5, the regression coefficients b in both generations does not differ from zero and differs from unity indicates the participation epistasis of complementary type. Epistasis for this trait was reported before from other authors (Zaazaa et al., 2012; Ijaz & Kashif, 2013; Kutlu & Olgun, 2015). Dominant genes are responsible for increasing the trait. Correlation coefficients are significant and this statement remains valid. In the first generation, all varieties are near to the Wr and they have more dominant genes. The most dominant genes have varieties Victoria and Progress. In second generation in Predel and Progress dominant genes prevails when in Superdur prevails recessive genes. The Victoria and Deni varieties are with equal dominant and recessive genes. Progress variety have more dominant genes and that makes it extremely important.

Thousand kernel weight

The regression line intersects the ordinate of the coordinate system above the starting point in both generations, indicating that incomplete dominance plays a important role in the inheritance of the trait (Figure 6). Incomplete dominance in the inheritance of the trait have also been reported by other authors (Inamullah et al., 2006; Fellahi et al., 2015).

The values of the regression coefficients in both generations differed significantly from zero and did not differ significantly from unity (Figure 6).

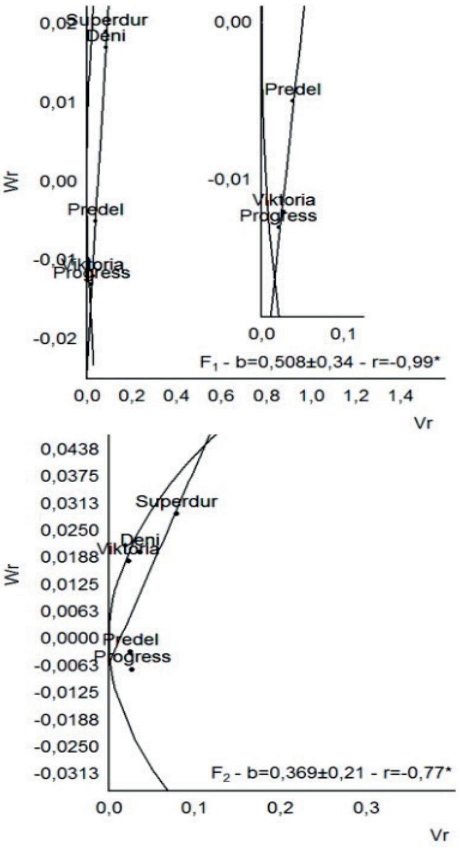

Figure 5. Graphical diallel analys for grains weight per spike in F_1 and F_2; b – regression coefficient; $r_{Yr(Wr+Vr)}$ - correlation coefficient; * - $p \leq 0.05$

Therefore, in both generations F_1 and F_2 in our set of parental varieties, control in inheritance of the trait has a simple additive-dominant genetic system. Shehzad et al. (2015) reported the same statement like in our case. The correlation coefficient r in the both generation is negative and the trait are increase with accumulation of dominant genes. In the case of our study, the correlation coefficients are significant and it can be relied on that this trait is increased by the dominant genes. In generation F_1, the Victoria and Progess varieties has greatest number of dominant genes. Other varieties are with equal dominant and recessive genes. In the F_2 generation with the most dominant genes is the Progress variety.

In generations F_1 and $F_2$the traits plant height, spike length and thousand kernel weight are under control of additive-dominant genetic system.

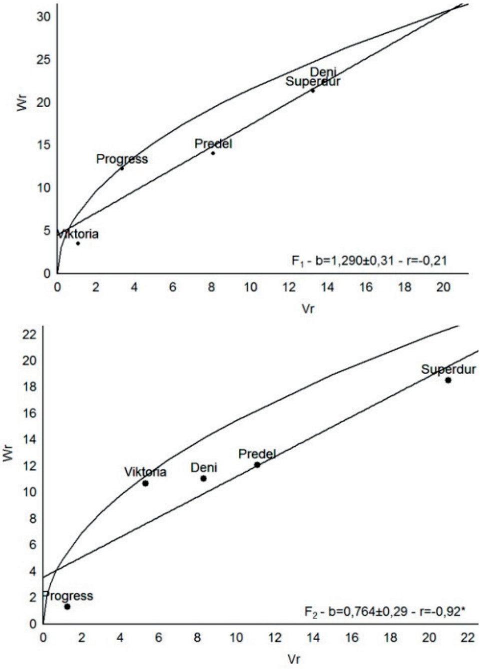

Figure 6. Graphical diallel analys for thousand kernel weight in F_1 and F_2; b – regression coefficient; $r_{Yr(Wr+Vr)}$ - correlation coefficient; * - $p \leq 0.05$

When this genetic system participates in inheritance, individual selection is very effective and improvement of traits can be expected. For other traits in both generations is observed epistatic interactions of genes from complementary type. Manifestations of complementary epistasis affect disintegration, and selection can continue into later segregating generations. It is possible to select different valuable forms in different years in the same cross. The results obtained indicate that the most suitable for individual selection using classical methods are the traits like plant height, spike length and thousand kernel weight. It should be noted that the main structural element of the yield - thousand kernel weight - has no manifestations of epistasis. For a significant increase of the traits, it is of great importance which genes accumulate. The correlation coefficients in some cases are significant and this information is essential. Despite the unproven values for correlation coefficient the traits related to the productivityin most cases are increase with dominant genes. In most cases these are the varieties Progress and Victoria. The Progress variety is extremely valuable in terms of breeding, as there are more dominant genes for the traits like grains weight per spike and thousand kernel weight. For productivity tillering which recessive genes are important for increasing the values of the trait, may have better results in the later segregating generations, which allows for a longer selection.

CONCLUSIONS

The trait plant height in durum wheat is controlled by a simple additive-dominant genetic system. Dwarf plants can be obtained with accumulation of recessive genes. Incomplete dominance plays an important role in the expression of this trait. The trait productivity tillering is controlled by complementary epistasis and recessive genes increase the values of this trait. Both complete dominance and overdominance are involved in its expression. The trait spike length is controlled by a simple additive-dominant genetic system. Dominant genes are responsible for its increase, and incomplete dominance plays a major role in its expression. The trait spikelets number per spike is controlled by complementary epistasis. The accumulation of dominant genes increases this trait. Both incomplete dominance and overdominance are essential for its expression. The inheritance of the trait grain weight per spike is governed by complementary epistasis. Trait values increase with the accumulation of dominant genes, and overdominance plays a major role. The trait thousand kernel weight in durum wheat is controlled by a simple additive-dominant genetic system. Dominant genes are associated with increased trait values, and incomplete dominance plays an essential role in its inheritance. The Progress variety is extremely valuable in breeding due to its higher proportion of dominant genes for both grain weight per spike and thousand kernel weight. Since dominant genes are responsible for increasing two of the main elements of productivity, this variety is of significant importance.

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