

Research Article

GENETIC ANALYSES FOR SOME CHARACTERISTICS IN DURUM WHEAT (*Triticum durum* Desf.)Yalçın COŞKUN*¹İrfan ÖZBERK¹Ayşe COŞKUN²

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ABSTRACT

This study aimed to assess and use of some genetics factors such as additive, dominance and non allelic interactions affecting generation means and variances for some quantitative characteristics of basic generations [P₁, P₂, F₁ (2 family), F₂ (4 family), B₁ (4 family) and B₂ (4 family)] derived from the cross between Ozberk and Firat-93 cultivars of *Triticum durum*. Except canopy temperature and SDS sedimentation value, simple additive dominance model (m, [d], [h]) was not found to be adequate to describe generation means indicating the presence of non allelic interactions. Parameters for means of generations obtained from biometrical equations were found to be overlapping partially those of computer software (MEAN FIT). H (dominance) and E (environmental) variations turned out to be significant frequency. Variance components obtained from biometrical equations and computer software (VAR FIT) overlapped. Utilizing from variance components of best fit, h²_n for number of grain spike⁻¹ was only estimated as 18.26 %. The h²_b values were found to be less than 50 % for both estimation methods (formulas and computer software). It was concluded that the similarity of parents for the characteristics under study, limited number of sampling, the presence of micro environmental variations resulted in absence of genuine genetic variations or the presence of some undetected genetic parameters depending on inadequacy of basic generations. Taking into account the presence of epistasis nearly for all characteristics, delay selection is recommended.

Key Words: Wheat, basic generations, heritability, components of means and variances

MAKARNALIK BUĞDAYDA (*Triticum durum* Desf.) BAZI KARAKTERLERDE GENETİK ANALİZLER

ÖZET

Bu araştırmada Özberk ve Firat-93 makarnalık buğdayların melezlenmesinden elde edilen temel generasyonlar [P₁, P₂, F₁ (2 aile), F₂ (4 aile), B₁ (4 aile) ve B₂ (4 aile)] yardımıyla bazı agronomik karakterlerdeki genetik varyasyon ve kalıtım araştırılarak elde edilen bilgilerin ıslah programında kullanılması amaçlanmıştır. Kanopi sıcaklığı ve SDS sedimantasyon değeri dışında anılan tüm karakterler için F₁ ana ve babaya ait değerler dışında yer almıştır. Bu da dominans etkilerin varlığını göstermektedir. Jenerasyon ortalamaları üzerindeki genetik etkiler biyometrik eşitlikler ve bilgisayar programı yardımıyla araştırılmış ve tane verimi ile SDS sedimantasyon dışındaki tüm karakterler için basit eklemeli dominans model (m, d, h) yeterli bulunmamış, iki genli interaksiyon modelleri bu etkileri ifade etmede daha yeterli bulunmuştur. Ölçülen tüm karakterlerde anaya ve cinsiyete bağlı etkiler tespit edilmemiştir. Formüller yardımıyla bulunan ortalama öğeleri ile en iyi uyumlu modelin ortalama öğeleri kısmen uyuşmuştur. Ele alınan karakterlerdeki genetik varyasyon bilgisayar programı ve biyometrik eşitlikler yardımıyla hesaplanmıştır. Genellikle H ve E'den oluşan dominans ve çevresel varyans tespit edilmiştir. Formüller yardımıyla yapılan hesaplamalarda bulunan D ve H genellikle bilgisayar programı bulgularıyla örtüşmektedir. Eşitlikler yardımıyla bulunan geniş anlamda kalıtım derecesi (h²_b) değerleri % 50'nin altında gerçekleşmiş ve bazı karakter için dar anlamda kalıtım derecesi (h²_n) değerleri tahmin edilememiştir. En iyi uyumlu modele ait varyans parametreleri kullanılarak yapılan tespitlerde başakta tane sayısı (h²_n=% 18.26) dışında h²_n değeri tahmin edilememiştir. Sonuç olarak anaç çeşitlerin anılan karakterler bakımından birbirlerine yakın olmaları, örnekleme sayılarının bazı karakterler için yetersiz olması, mikro çevresel varyasyonlar ve temel jenerasyonlar modelindeki bazı yetersizlikler anılan karakterler için genetik varyasyon ve kalıtım derecelerinin saptanmasını güçleştirmiştir. Ancak anılan karakterler için allelik olmayan interaksiyonların varlığı dikkate alınarak seleksiyonun geciktirilmesi önerilebilir.

Anahtar Kelimeler: Buğday, temel generasyonlar, kalıtım derecesi, varyans öğeleri

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INTRODUCTION

The wheat production of Turkey in 2006 was 16.5 million tons. Southeast Anatolia Region meets 10% of wheat production of Turkey with 1.6 million tons. The durum wheat production of Turkey in 2006 was 3.5 million tons. Southeast Anatolia Region meets 38% of durum wheat production of Turkey with 1.33 tons (Anonymous, 2009a).

High grain yield and grain protein content with suitable milling and cooking quality are basic criteria of selection in wheat breeding (Cho et al., 2001). Plant height, spike length, spikelets numbers per spike, grain numbers per spike, thousand kernel weights are some other criteria for selection in wheat breeding (Chowdhry et al., 1992; Lariak et al., 1995). Ketata et al. (1976) showed that narrow sense heritability estimations ranged from moderate to high degrees for plant height and grain weights and this was found to be relatively low for grain yield. Ozberk and Kirtok (2003) reported that narrow sense heritability estimates were high for spike length and thousand kernel weights and low for plant height due to the same genetics background of parents. Novoselovic et al. (2004) reported that narrow sense heritability estimations were 54-81 % for plant height, 9-76 % for number of spikes per plant, 11-99.8 % for number of grain per spike and 23-73 % for grain weights per spike and 49.7-72 % grain yield per plant. In another study, Yagdi et al. (2007) reported quite low broad sense heritability estimations for spike length (35.48 %), plant height (9.07 %), number of grain per spike (2.97 %), grain weights per spike (3.0 %), grain yield (5.61 %) and SDS sedimentation value (13.89 %) in durum wheat. Non-additive gene effects have an important role in genetic control of spike length (Sharma et al., 2003). Additive gene effects also have an important role in genetic control of number of grain per spike (Sharma and Sain, 2003). Bilgin et al. (2009) reported that estimation of broad sense heritability for grain yield was 33 % in durum wheat. There is highly positive correlation between grain protein content and cooking quality in durum wheat (Autran and Galterio, 1989; Dexter and Matsuo, 1980). Grain protein content is affected by environment and also negatively correlated with grain yield in wheat (Cox et al., 1985). The most important criteria for selection in durum wheat are grain protein content, gluten strength, pigment quantity and oxidative enzyme activities. Proteins of LMW-2 glutenin at Glu-B3 loci and γ -45 gliadin at Glu-B1 loci are most important proteins for gluten strength and high cooking quality (Yildirim et al., 2008). Yildirim et al. (2008) reported that durum wheat cultivar Firat-93 contains the proteins of LMW-2 glutenin in Glu-B3 loci and γ -45 gliadin in Glu-B1 loci. Santra et al. (2005) indicated that dominance effect was significant for low β -carotene content of wheat and the broad sense heritability was estimated as 67-93 %. Clarke et al. (2006) revealed that

heritability of yellow pigment in durum wheat was polygenic and the broad sense heritability of pigment concentration was high (88-95 %) for multi-years and multi-locations testing, but it was low (34 %) for single year or single location. Yalvac et al. (1999) showed that SDS sedimentation values in durum wheat were between 13.8 ml and 24.5 ml. in central Anatolia. Yagdi and Sozen (2009) reported that estimations of narrow sense heritability values were 0.72% for SDS sedimentation and 30.43% for spike length in durum wheat. Some researchers (Santra et al., 2005; Clarke et al., 2006; Reimer et al., 2008; Patil et al., 2008; Patil et al., 2009; Singh et al., 2009) reported that grain color in durum wheat was controlled by two or more genes.

In biometrical genetics, the effects of genes are not identified individually. Overall genetical phenomena are described through additive action, dominance, non-allelic interactions, linkage and so on. This approach makes possible to investigate various segregating and non segregating generations that are related to each other by descent with a view to arriving at a comprehensive picture of the genetics architecture of the material (Özberk, 1992).

This study aimed to assess genetic variability and inheritance of some important agronomical characteristics through basic generations derived from newly released (Özberk) and widely grown (Firat-93) durum wheat varieties.

MATERIALS and METHODS

Basic generations (P₁, P₂, F₁, F₂, BC₁ and BC₂) were derived from the crosses between Özberk and Firat-93. Field trials were carried out employing randomized complete block design with three replications in 2007-2008 cropping seasons in the experimental cold frame of Harran University. Plot size was 1 m x 2 rows (0.4 m²) with a 30 cm row space. Five plants for canopy temperature 10 plants for other characteristics under study were sampled in each plot. Whole plot sample was taken into account for grain color, SDS sedimentation and grain yield plot⁻¹. A base fertilization of 6 kg da⁻¹ pure nitrogen and 6 kg da⁻¹ pure phosphorus was applied at sowing applying 20.20.0 chemical fertilizer. In late joining and early shooting stage in spring, 6 kg da⁻¹ pure nitrogen was applied as Ammonium Nitrate (33%) Material was irrigated twice in dough stage. But the amount of irrigation water was not measured. Chemical control for broad and narrow leaf weeds was practiced in the experiment.

Experimental field was typically red, clayed structure, calcareous and low organic matter content (Dinc, 1988).

In the study number of days to heading, canopy temperature, plant height, grain number spike⁻¹

¹, grain weight spike⁻¹, grain yield plot⁻¹, Sodium Dodecyl Sulfate (SDS) sedimentation (by Anonymous, 1983) and grain color (cracked grain b value by Anonymous, 2001) were scored.

Statistical genetic methods

Early generations, like P₁, P₂, F₁, F₂, BC₁ and BC₂ derived from a cross between two pure breeding varieties allow an extensive array of biometrical procedures to be applied and thus provide a great deal of information about genetic control (Özberk, 1992). An analysis of variance was performed on the various generations to detect the presence or absence of genetic and environmental variations by JMP 5 0 1 statistical software program (Anonymous, 2002). The scaling test of Mather (1949) with $A=2\bar{B}_1 - \bar{F}_1 - \bar{P}_1$, $B=2\bar{B}_2 - \bar{F}_1 - \bar{P}_2$, $C=4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$ were performed to detect the presence of non-allelic interactions on generation means. A joint scaling test attributed to Cavalli (1952) as well as Mather and Jinks (1971) were also conducted to test adequacy of 3 parameters (m, d, h) model. Generation means for each character were further investigated by the method of Mather and Jinks (1982) to fit a 6-parameter model (m, d, h, I, j, l) through computer software of Meanfit (Anonymous, 1991). Bartlett's test was performed to test for presence of micro environmental interactions. Presence of micro environmental interactions was detected through Bartlett's test. In model fitting by weighted least squares of Hayman (1960) was employed and statistically significant second degree statistics were estimated through the computer program Varfit (Anonymous, 1991). The heritability estimates were calculated as described below;

h^2_n : $\frac{1}{2}D/VF_2$ (Warner, 1952).

h^2_b : $(\frac{1}{2}D + \frac{1}{4}H)/VF_2$ (Warner, 1952).

h^2_n : $\frac{1}{2}D/(\frac{1}{2}D + \frac{1}{4}H + E)$ (Mather and Jinks, 1982).

h^2_b : $(\frac{1}{2}D + \frac{1}{4}H)/(\frac{1}{2}D + \frac{1}{4}H + E)$ (Mather and Jinks, 1982).

h^2_n : narrow sense heritability

h^2_b : broad sense heritability

D: additive component of variation

H: dominance component of variation

E: Environmental component of variation

VF₂: Within family variance of F₂ generation

Results for means of generation means, variances components and heritability degrees obtained from biometrical equations and computer software program were summarized by Table 1.

Number of days to heading:

Taking into account the Figure 1; dominance with positive direction for 'numbers of days to heading' are seen by mean of F₁ families which are higher than those of parents. Transgressive segregations were present in F₂ or Back Cross (BC) families which have higher values than those of both parents.

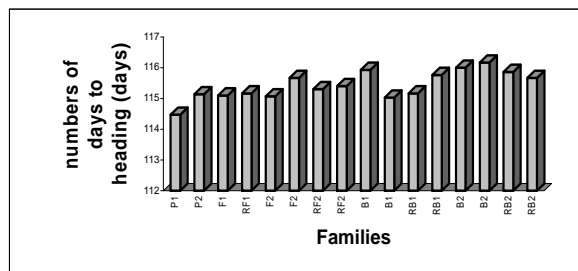


Figure 1. Numbers of days to heading of families (days)

It was found through the variance analyses that there were not statistically significant differences between families for all generations except B₁.

Maternal effect and sex linkage were not present for number of days to heading. Complete dominance for late maturity was observed. It was estimated that genes of early maturing ability accumulated in one of the parents.

Estimation of components of mean by 'meanfit' software showed that there were some non significant parameters in the perfect fit model. But the best fit model was adequate with parameters m, [d], [h], [i] and [l]. It means that the number of days to heading is controlled by more of one gene pair. Similar results were found by other researchers (Johnson et al., 1966; Amaya et al., 1972; Sun et al., 1972).

Estimation of components of variance by 'Varfit' software showed that best fit model was adequate with F and E, parameters D and H were not significant statistically. Similar results were found by other researchers (Johnson et al., 1966; Amaya et al., 1972; Sun et al., 1972).

RESULTS and DISCUSSION

Amount of average total rainfalls in March and April in 2008 were lower than average of last 35 years and also average temperatures of same period were higher than average of last 35 years (Anonymous, 2009b).

Dominance ratio, narrow sense heritability (h^2_n) and broad sense heritability (h^2_b) for number of days to heading were not estimated by methods employed under study due to absence of D and H.

Canopy temperature:

Looking at the Figure 2; dominance effect with negative direction for canopy temperature can be seen by means of F_1 families which are lower than those of parents. Transgressive segregations were present in F_2 and in Back Cross (BC) families have higher or lower values than both parents.

It was found by variance analyses that there were not statistically significant differences between families for all generations except B_1 and B_2 generations.

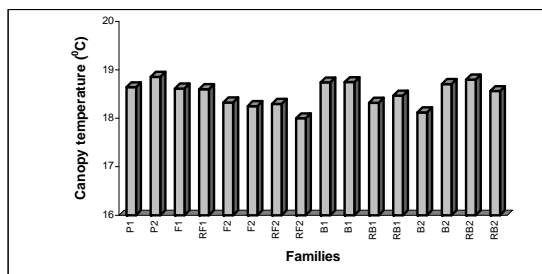


Figure 2. Canopy temperature of families (°C)

Maternal effect and sex linkage were not present for canopy temperature but an over dominance effect for low canopy temperature was present. It was also revealed that the genes for low canopy temperature accumulated in one of parents.

Estimations of components of mean by 'meanfit' software showed that there were some non significant parameters in the perfect fit model. But the best fit model was adequate with parameters m , $[h]$ and $[i]$. It means that the number of days to heading is controlled by more of one pair of genes. In this model, $[d]$, $[j]$ and $[l]$ were not significant statistically. It was concluded that dominance and additive x additive effects are important for inheritance of canopy temperature.

Estimation of the variance components by 'varfit' software indicated that best fit model was adequate describing variance components with only the parameter E. In this model, parameters D, H and F were not significant statistically. Generations with low canopy temperature resulted in relatively high grain yield. Similar results were found by Reynolds et al. (1998) and Ayeneh et al. (2002). It was concluded that only environmental variance had significant effect on canopy temperature or the basic generations are not adequate to detect the existing variation.

Referring Mather and Jinks (1982) method, h^2_n and h^2_b for canopy temperature were found to be equal (44.98%). Narrow heritability (h^2_n) was estimated as 71.34% referring Warner (1952). It was

concluded that selection for this character may be practiced in early generations.

Plant height:

Dominance effect with positive direction for plant height is shown by Figure 3. The means of F_1 families are higher than those of parents. Transgressive segregations are present for this characteristic (the means of some F_2 and Back Cross (BC) families have higher values than both parents). Variance analyses indicated that there were not statistically significant differences between families for all generations except P_1 and P_2 generations. Maternal effect and sex linkage were not present for plant height but over dominance for tall plant height was present. It was also estimated that genes of tall plant height accumulated in one of parents. Estimations of components of means by 'meanfit' software showed that perfect fit model didn't describe the components of means significantly but the best fit model was adequate with parameters m , $[h]$, $[j]$ and $[l]$. In this model parameters $[d]$ and $[i]$ were not significant statistically. It means that the number of days to heading is controlled by more than one pair of genes. Similar results were found by other researchers (Johnson et al., 1966; Amaya et al., 1972; Sun et al., 1972; Bhatiya et al., 1987; Collaku and Harrison, 2005).

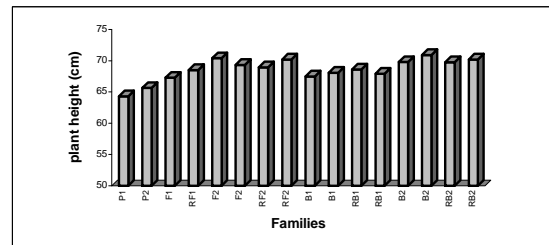


Figure 3. Plant height of families (cm)

Variance components were estimated through 'varfit' and this indicated that the best fit model with significant H, F and E parameter described all genetic variation in this characteristic. D was not significant statistically. Similar results in wheat were found by other researchers (Johnson et al., 1966; Amaya et al., 1972; Sun et al., 1972; Bhatiya et al., 1987; Collaku and Harrison, 2005). It was concluded that there was no genuine genetic variation for this characteristic between parents. Narrow heritability (h^2_n) for plant height were not estimated but h^2_b was estimated as 57.97% by biometrical equations and 40.65% employing the parameter found through 'varfit'.

Number of grain spike⁻¹:

Figure 4 shows the presence of dominance effect with positive direction for number of grains per spike. The means of F_1 families are higher than those of parents. Transgressive segregations were present, means of some F_2 and Back Cross (BC) families were higher than those of both parents.

variance analyses indicated that there were not statistically differences between families for all generations except F₁ generation.

Maternal effect and sex linkage were not present for number of grain spike⁻¹ but over dominance for this characteristic was present. Similar result was reported by Dağüstü (2008). It was also found that genes of high number of grain spike⁻¹ accumulated in one of the parents.

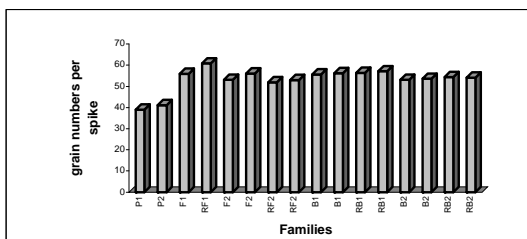


Figure 4. Grain numbers per spike of families

Estimations of components of mean by meanfit showed that due to the presence of some non significant parameters, the perfect fit model was not fit to describe the generation means adequately. But the best fit model was adequate with parameters m, [h], [j] and [l]. In this model, [d] and [i] were not significant statistically. It means that number of days to heading is controlled by more than one pair of genes. Similar results were found by Bhatiya et al., (1987); Sharma and Sain, (2004); Collaku and Harrison, (2005). Estimation of components of variance by varfit showed that best fit model was adequate with D and E for this characteristic. H and F were not significant statistically. It was concluded that this characteristic is only affected by additive and environmental variation. Similar results were obtained by other researchers (Bhatiya et al., 1987; Collaku and Harrison, 2005; Yagdi et al., 2007).

Narrow heritability (h^2_n) and broad heritability (h^2_b) for number of grain spike⁻¹ were equal and estimated as 42.25 % by equations, and 18.26 % by the parameters obtained from computer software. Narrow heritability (h^2_n) was estimated as 77.06 % by Warner (1952) method. Similar results were found by other researchers (Novoselovic et al., 2004; Ali et al., 2008).

Grain weights spike⁻¹:

According to figure 5; dominance effect with positive direction for grain weights per spike is present, the means F₁ families are higher than those of parents. Transgressive segregations are also present and the means of some F₂ or Back Cross (BC) families are higher than those of both parents.

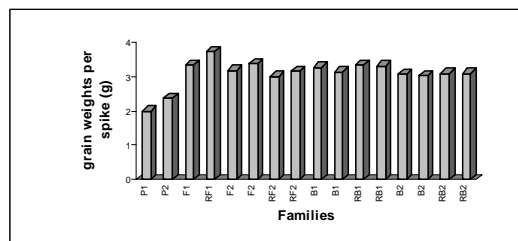


Figure 5. Grain weights per spike of families (g)

It was found by variance analyses that there were not statistically significant differences between families for all generations except F₁ generation.

Maternal effect and sex linkage were not present for grain weights spike⁻¹ but over dominance for high grain weights spike⁻¹ was present. It was also estimated that genes of high grain weights spike⁻¹ accumulated in one of the parents.

Estimation of components of mean by meanfit showed that perfect fit model was not found to be fit with some non significant parameters but the best fit model was adequate with parameters m, [d], [h], [j] and [l] in this model, [i] was not significant statistically. It means number of days to heading is controlled by more than one pair genes. Similar results were found by other researchers (Johnson et al., 1966; Bhatiya et al., 1987; Collaku and Harrison, 2005; Yagdi et al, 2007).

Estimations of components of variance by varfit indicated that the best fit model was adequate with parameter H and E. In this model; D and F were not significant statistically. Similar results were found by other researchers (Johnson et al., 1966; Bhatiya et al., 1987; Collaku and Harrison, 2005; Yagdi et al, 2007).

h^2_n for grain weights spike⁻¹ was not estimated but h^2_b were estimated as 50.26 % by equations and 36.35 % by using the parameters obtained from varfit.

Grain yield plot⁻¹:

According to Figure 6; dominance with positive direction for grain yield per plot is present for this characteristic. The means of F₁ families are higher than those of parents. Transgressive segregations are also present The means of some F₂ or Back Cross (BC) families are higher than those of both parents.

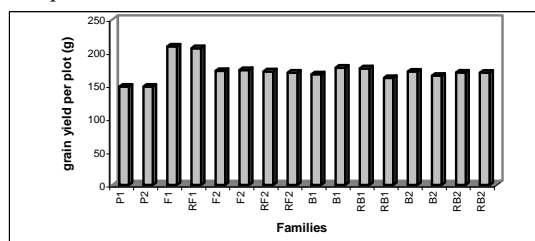


Figure 6. Grain yield per plot of families (g)

It was found by variance analyses that there were not statistically differences between families for all generations.

Maternal effect and sex linkage were not present for grain yield plot⁻¹ but over dominance for high grain yield plot⁻¹ was present. It was also estimated that genes of high grain yield plot⁻¹ accumulated in one of the parents.

Estimations of components of means by computer program revealed that the perfect fit model was not fit but the best fit model was adequate with parameters m and [h]. In this model [d], [i], [j] and [l], were not significant statistically. Similar results were found by other researchers (Johnson et al., 1966; Bhatiya et al., 1987; Collaku and Harrison, 2005).

Estimations of components of variance by varfit showed that the best fit model was adequate with parameters F and E, in this model; D and H were not significant statistically. It was concluded that differences of grain yield plot⁻¹ was mainly controlled by environmental variance (E) and additive x dominance interaction (F). Similar results were found by other researchers (Amaya et al., 1972; Sun et al., 1972).

h^2_n and h^2_b for grain yield plot⁻¹ could not be estimated by both equations and computer software.

SDS sedimentation value

A dominance effect with negative direction for SDS sedimentation is shown by Figure 7. The means of F₁ families are lower than those of parents. Transgressive segregations also present The means of some F₂ and Back Cross (BC) families are higher or lower values than those of both parents.

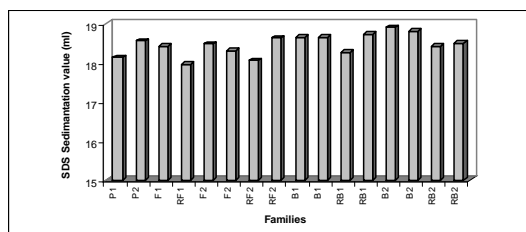


Figure 7. SDS sedimentation values of families (ml)

It was found by variance analyses that there were not statistically differences between families for all generations.

Maternal effect, sex linkage and heterosis were not present for SDS sedimentation. It was also estimated that genes for SDS sedimentation were normally distributed in both parents.

Estimations of components of means by meanfit indicated that the perfect fit model was not fit but the best fit model was adequate with parameter m, in this model [d], [h], [j], [l] and [i] were not

significant statistically. Simple additive-dominance model described generation means adequately.

Estimation of components of variance by computer program showed that the best fit model was adequate with parameter E, in this model, parameters D, H and F were not significant statistically. It was concluded that SDS sedimentation was controlled by only environmental variance. Similar results were found by Yagdi and Sozen (2009).

h^2_n for SDS sedimentation value was not estimated but h^2_b were estimated as 40.77 % by biometrical equations used in the study.

Grain color (cracked grain b value):

According to Figure 8; A dominance effect toward negative direction is present for cracked grain b value. The means of F₁ families are lower than those of parents. Transgressive segregations are also present. The means of some of F₂ or Back Cross (BC) families are lower values than those of both parents.

It was found by variance analyses that there were not statistically differences between families for all generations.

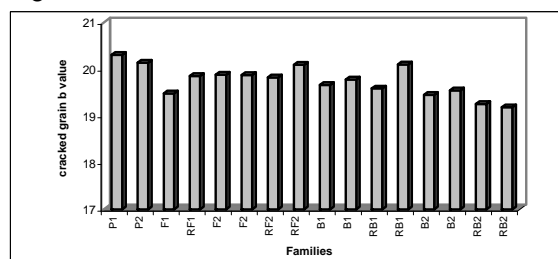


Figure 8. Cracked grain b values of families

Maternal effect and sex linkage were not present but over dominance for lower b value was present. It was also estimated that genes for b value gathered in one of the parents.

Estimations of components of means by meanfit revealed that the perfect fit model was not fit but the best fit model was adequate with parameters m, [h], [j], [l] and [i] in this model. It means number of days to heading is controlled by more than one pair of genes. Parameter [d] was not significant statistically. It was indicated absence of genuine genetic variation between parents. It was concluded that grain color in durum wheat was controlled by two or more genes. Similar results were reported by other researchers (Merrit, 1988; Santra et al., 2005; Clarke et al., 2006; Reimer te al., 2008; Patil et al., 2008; Patil et al., 2009; Singh et al., 2009).

Estimations of components of variance by varfit indicated that the best fit model was adequate with parameter E, in this model; D, H and F were not significant statistically. It was concluded that grain color was controlled by only environmental variance.

h^2_n for grain color was not estimated but h^2_b were estimated as 40.17 % by biometrical equations used in the study.

Due to the similarities of both parents for the characters under study, genuine genetics variation couldn't be detected. Further more, limited sampling size, the presence of micro environmental variations and the some weakness of basic generations model might be resulted in the presence of some genetic variation undetected. The presences of non allelic interactions for many characteristics recommend us to refer delay selection.

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Table 1. Parameters for means of generations, variance components and heritability degrees obtained from formulas and computer software program.

Events	Number of days to heading	Canopy temperature	Plant height	Number of grain spike ⁻¹	Grain weights spike ⁻¹	Grain yield plot ⁻¹	SDS sedimentation value	Grain color (cracked grain b value)
d by formulas	0.33	0.105	0.67	1.1	0.19	0.075	0.206	-0.0830
h by formulas	0.33	-0.135	2.92	18.35	1.37	40.83	-0.153	-0.5543
D by formulas	-	0.2253	-	73.72	-	-	-	-
H by formulas	-	-	42.75	-	0.61	-	1.384	0.2232
h ² n by formulas referring Mather and Jinks (1982)	-	44.98 %	-	42.25 %	-	-	-	-
h ² b by formulas referring Mather and Jinks (1982)	-	44.98 %	57.97 %	42.25 %	50.26 %	-	40.77 %	40.17 %
h ² n by formulas referring Warner (1952)	-	71.34 %	-	77.06 %	-	-	-	-
Mean components from best fit model	m, d, h, i, l	m, h, i	m, h, j, l	m, h, i, l	m, d, h, j, l	m, h	m	m, h, i, j, l
Variance components from best fit model	F, E	E	H, F, E	D, E	H, E	F, E	E	E
h ² n by variance components from best fit model	-	-	-	18.26 %	-	-	-	-
h ² b by variance components from best fit model	-	-	40.65 %	18.26 %	36.35 %	-	-	-

m: effect of mean, d: additive effect, h: dominance effect, i: additive x additive effect, j: dominance x dominance effect, l: additive x dominance effect
D: additive variance, H: dominance variance, F: interactions of additive x dominance variance, E: environmental variance