Inheritance of Grain Filling Rate and Duration, and Yield Components in Five Durum Wheat Crosses

Mohammad M. Ajlouni[1*] • **Abdul Latief A. Al-Ghzawi**[2] • **Hani Z. Ghosheh**[1*]

[1] Department of Plant Production, Jordan University of Science and Technology, P.O. Box 3030. Irbid, Jordan
[2] Department of Biology and Biotechnology, Faculty of Science, Hashemite University, Jordan

Corresponding author: * majl@just.edu.jo, ghosheh@just.edu.jo

ABSTRACT

To understand the inheritance mechanisms of grain filling rate (GFR), grain filling duration (GFD), yield and yield components, twenty durum wheat landraces were selected from a larger set (~200 accessions) based on their yield and grain filling rate and all reciprocal crosses among them were made by hand emasculation and pollination in the greenhouse. Five crosses which produced adequate amounts of F_1 seeds and their derived F_2s and the parents were used for the purpose of this study. The results showed high heritability, high gain from selection and high coefficient of variation for GFR in two crosses only while GFD showed low values for these parameters in the same crosses. High heritabilities coupled with high gains from selection for yield and yield components indicated that selection for these traits in early generations may be effective. Non additive gene action were found to affect the grain filling duration suggesting that selection in advanced generations may be more appropriate than in early generation. Selection for grain filling rate and number of fertile tillers plant^{-1} can be recommended at early generations for all crosses except crosses 2B × 2A and 4B × 4A. Selection for grain yield might be appropriate in crosses 2B × 2A, 1A × 1B and 4B × 4A in early generation and in advanced generation in the other two crosses. High heritability values for the traits of the cross 2B × 2A, suggested that selection for yield improvement is possible in this cross. The high variability observed in these crosses offers good prospects for its improvement in the future.

_____

INTRODUCTION

Durum wheat (*Triticum turgidum* ssp. *turgidum* conv. *durum* (Desf.) Mac Key) is principally grown under arid and semi-arid areas of the world mainly in the Mediterranean countries (Jaradat 1992; Akar and Ozgen 2007). Its improvement depends on the continuous supply of new germplasm material as donors of genes of agronomic importance. This has been particularly evident in breeding for disease resistance, tolerance to environmental stresses, adaptability, quality characteristics, and higher yield potential (Srivastava *et al.* 1988). The availability of such germplasm depends on the identification of areas of concentration for various traits of agronomic importance, especially within primary and secondary centers of diversity (Bekele 1984). Landraces of durum wheat evolved under arid and semiarid Mediterranean environments, through the long process of domestication, natural and conscious selection, continuous gene flow which led to more adaptive genotypes (Harlan 1975; Jaradat 1992). Therefore, crosses between durum wheat landraces will produce genetic variability which is the basis of selection for further improvement in this crop (Firouzian 2003). Early maturity and higher kernel weight are two important traits for improving wheat production under drought stress environments prevailing in Jordan and many countries in West Asia and North Africa. Final kernel weight is determined by both grain filling rate and grain filling duration (Al-Ghzawi 2007). Grain filling rate is the dry matter accumulation rate for the grain during the linear phase of kernel growth, and is expressed as mg kernel-1 accumulated per growing degree-days-1. Grain filling duration is the duration of photosynthate accumulation and partitioning into grains (Shearman *et al.* 2005) which is considered as an important phase in the life cycle of wheat plants (Reynolds *et al.* 2005). Estimated grain filling duration vary from 17 to 38 days (Gebeyehou *et al.* 1982; Van Sanford 1985). Such differences in the duration are partially explained by differences in prevailing temperatures (Savin and Nicolas 1996; Shearman 2001). Understanding the grain filling processes in durum wheat genotypes may be very helpful in selecting high yielding and drought resistance varieties. In particular, the understanding of the inheritance and the type of gene action for the rate and the duration of grain filling, and final kernel weight would help wheat breeders to increase and stabilize grain yield (Mou and Kronstad 1994). Variable results were reported in the literature with regard to heritability and genetic advance estimates for these traits. For example, heritability estimates of 0.42 for grain filling duration and 0.74 for kernel growth rate were observed in winter wheat crosses (Mou and Kronstad 1994). Furthermore, Deswai *et al.* (1996) reported high heritability and genetic advance values for 1000-grain weight (TGW). Moreover, moderate to high heritability values for TGW were reported by Chowdhry *et al.* (1997) and Mehta *et al.* (1997). Additionally, Saleem *et al.* (2003) found that heritability and genetic advance for TGW ranged from 63-91% and from 8-22%, respectively. High heritability and genetic advance estimates were also observed for grain yield (Saleem *et al.* 2003). But, information is limited regarding the gene action and heritability of grain filling rate and duration in wheat. Rasyad and van Sanford (1992) observed significant additive maternal effects for kernel growth rate. Gene action for kernel weight was predominantly additive in two spring wheat crosses and one winter wheat cross (Mou and Kronstad 1994). Sun *et al.* (1972) found evidence of epistasis, but additive and dominance effects made the major and most consistent contributions to kernel weight in six spring wheat crosses.

Therefore, the present study used a set of durum wheat

_____

landraces differing in grain filling rate to: (a) evaluate the relative importance of grain filling rate and duration in five durum wheat landraces crosses under the semiarid environment (b) determine the mode of inheritance and heritability estimates for the rate and duration of grain filling and other yield components in these crosses.

MATERIALS AND METHODS

Plant material

Twenty durum wheat landraces were selected from a larger set (~200 accessions) based on their yield and grain filling rate as obtained by Al-Ajlouni and Jaradat (1997). A single head from these accessions was selected previously for multiplication to produce pure lines. The selected lines were representing the maximum contrast in terms of grain filling rate. All reciprocal crosses between the twenty landraces lines were made by hand emasculation and pollination in the greenhouse. Five crosses produced adequate amounts of F_1 seeds, and therefore were used to complete this study (**Table 1**). Few F_1 seeds from each cross were planted in pots to produce F_2 seeds. Thirty seeds from the parents, F_1 and F_2 generations of these five crosses were planted in three rows with 30 cm distance between rows and 15 cm within rows. Seeds were planted on January 14 at Maru Agricultural Experiment Station (silty clay soil with pH around 7.9; Al-Karaki 1996) in a randomized complete block design with three replications.

Traits measured

Grain filling rate (mg 100 kernel^{-1} GDD^{-1}: dry matter accumulation rate for the grain during the linear phase of kernel growth and expressed as mg kernel^{-1} accumulated growing degree-days^{-1} using the method reported by Wiegand and Cuellar (1981).
Grain filling duration (day): The duration from anthesis to physiological maturity.
Grain yield per plant (g): weight of the total seeds per plant.
Total seed number per plant: the number of seeds collected from all the fertile spikes per plant.
Main spike seed number: The number of seeds collected from the main spike.
Main spike seed weight: weight of seeds of the main spike.
Number of fertile tillers per plant: number of productive or seed bearing tillers per plant.

Statistical analysis

Data from three replications were pooled to compute means and variances for each population using the MSTAT-C computer software (Michigan State University).
Broad sense heritability (H): Estimated from the total genetic variance, using the variance component technique (Ibrahim *et al.* 1983; Martinez and Foster 1998).
Expected genetic advance (Gs): Estimated for all crosses by the formula GS =K * $\sqrt{VF_2}$ * H. (Allard 1960). Where K * $\sqrt{VF_2}$ the selection differential expression in standard deviation units, K is the truncation selection of the top 10% that has a value of 1.775 as determined from the properties of the normal distribution, and H is broad sense heritability.
Narrow sense heritability (NSH): estimated from the regression of F_2 plants mean with their F_1 parent plant values (Fernandez and Miller 1985; Fehr 1987).
Genetic coefficient of variation (GCV): estimated using Burton (1952) method.

RESULTS AND DISCUSSION

Grain filling rate and duration

Broad and narrow sense heritability estimates for grain filling rate varied from 0.22 to 0.87 and from 0.02 to 0.28, respectively (**Table 2**). Genetic advance from selection for grain filling rate ranged from 0.418 to 2.009 (**Table 3**). Genetic coefficient of variation ranged from 6.017 to 43.89. The crosses 10 B × 10 A and 9 B × 9 A had the highest nar-

Table 1 Grain filling rate and duration, 1000 kernel weight and yield of the parents used for crosses. (Adopted from Al-Ajlouni and Jaradat 1997).

Parent accession number	Grain filling rate (Mg/kernel/GDD)	Yield	1000-kernel weight
High grain filling rate parents			
83089.000 (1A)	0.068	High	68.33
83090.000 (2A)	0.063	High	63.00
83099.000 (4A)	0.058	High	57.76
83087.000 (9A)	0.055	High	55.00
84063.000 (10A)	0.055	High	55.33
Average	0.0598		59.884
Low grain filling rate parents			
84090.000 (1B)	0.027	Low	26.814
9577.000 (2B)	0.029	Low	29.333
84240.000 (4B)	0.034	Low	33.667
84036.000 (9B)	0.038	Low	37.667
84237.000 (10B)	0.038	Low	38.132
Average	0.0332		25.589

row sense heritability and genetic advance values. These results may indicate the presence of an additive gene effects, therefore, the grain filling rate could be improved effectively through selection in early generations in these two crosses. These results are supported by the presence of moderate to high values of genetic coefficient of variation. Even though this study is not design to test the presence of transgressive segregates but the high differences among the parents for this character (0.017 Mg/kernel/GDD) and the above results indicated that we have transgressive segregates in these two crosses and thus, selection might be effective in early generations. These results are in agreement with those obtained Mou and Kronstad (1994) who reported that grain filling rate is influenced mainly by additive gene action. On the other hand, Ehdaie and Waines (1989), and Amin *et al.* (1992) indicated that low values of genetic advance occurred due to dominance and epistasis gene actions.

Broad and narrow sense heritability estimates for grain filling duration ranged from 0.08 to 0.23 and from 0.03 to 0.15, respectively (**Table 2**). Expected genetic advance varied from 0.070 to 1.055. Genetic coefficient of variation ranged from 6.02 to 67.06 (**Table 3**). Low heritability combined with low genetic advances indicates that environmental effect has a large portion of the total phenotypic variation of this trait. Similar low heritability results were obtained by Ehdaie and Waines (1989) and Sharma (1994). The results also indicate that most of the gene action for this trait is non additive, which agreed with the results reported by Mou and Kronstad (1994). Selection for grain filling duration should, therefore, be delayed to later generations.

Yield and yield components

Broad and narrow sense heritability estimates for grain yield plant^{-1} ranged from 0.53 to 0.94 and from 0.01 to 0.75, respectively (**Table 2**). Genetic advance from selection for grain yield plant^{-1} varied from 0.68 to 6.19. Genetic coefficient of variation ranged from 18.02 to 76.09 (**Table 3**). These results agreed with results reported by Amin *et al.* (1992); Ahmed *et al.* (2007). On the other hand, Ehdaie and Waines (1989); Ul Haq and Laila (1991) reported low to moderate values of heritability for grain yield. High heritability combined with high genetic advance in 4B × 4A, 2B × 2A, and 1A × 1B crosses revealed that grain yield was predominantly controlled by additive gene action in these crosses. Therefore, there is a possibility for genetic improvement through direct selection for grain yield, as previously reported by Chowdhry *et al.* (1999) and Ahmed *et al.* (2007). This is also supported by the presence of great differences between parents used in these crosses as indicated by the high values of genetic coefficient of variation for grain yield in these crosses.

Broad and narrow sense heritability estimates for total

Table 2 Broad sense heritability (BSH) and Narrow sense heritability (NSH) for all traits measured for the five crosses.

Cross	10 B X 10 A		9 B X 9 A		4 B X 4 A		2 B X 2 A		1 A X 1 B	
Parameter	BSH	NSH	BSH	NSH	BSH	NSH	BSH	NSH	BSH	NSH
Grain filling rate	0.52	0.19	0.46	0.28	0.31	0.02	0.87	0.05	0.22	0.16
Grain filling duration	0.09	0.04	0.08	0.03	0.23	0.15	0.21	0.14	0.11	0.01
Grain yield per plant	0.53	0.01	0.94	0.01	0.70	0.26	0.93	0.18	0.94	0.75
Total seed number/ plant	0.92	0.14	0.96	0.32	0.93	0.16	0.92	0.79	0.90	0.26
Main spike seed number	0.62	0.10	0.95	0.40	0.95	0.20	0.78	0.26	0.83	0.50
Main spike seed weight	0.78	0.04	0.85	0.21	0.74	0.01	0.91	0.14	0.82	0.79
Number-of fertile tillers/plant	0.55	0.45	0.35	0.16	0.59	0.08	0.54	0.19	0.53	0.20

Table 3 Genetic advance (GS) and Genetic coefficient of variation (GCV%) for all traits of the five crosses.

Cross	10 B X 10 A		9 B X 9 A		4 B X 4 A		2 B X 2 A		1 A X 1 B	
Parameter	GS	GCV	GS	GCV	GS	GCV	GS	GCV	GS	GCV
Grain filling rate	2.009	6.573	1.619	6.017	0.418	37.19	1.331	43.89	0.853	7.418
Grain filling duration	0.089	17.36	0.085	13.73	1.055	7.847	0.753	67.06	0.070	6.02
Grain yield per plant	0.68	18.02	2.33	37.53	1.04	29.10	6.19	76.09	2.33	38.91
Total seed number/ plant	36.73	21.31	45.07	24.28	27.06	19.83	22.56	12.08	30.86	19.2
Main spike seed number	5.31	11.8	10.32	16.23	9.99	18.33	10.35	22.09	10.34	19.18
Main spike seed weight	0.25	17.52	0.31	18.36	0.26	21.53	0.65	27.66	0.39	16.22
Number-of fertile tillers/plant	1.71	26.25	1.14	20.96	1.78	30.15	3.47	45.79	0.6	12.36

seed number plant^{-1} ranged from 0.90 to 0.96 and from 0.14 to 0.79, respectively. Selection for the top 10% among F2-plants provides genetic advances of 22.56 to 45.07, which indicated a minor environmental effect on this trait. Results also indicate that sufficient variation for total seed number plant^{-1} exists in all F2 populations. Heritability and genetic advance were very high for all crosses which indicated the presence of high additive gene effects controlling this trait, and allows for effective selection at early generations. Higher heritability estimates and expected genetic advance were reported for 1000-grain weight and grain yield per plant in wheat crosses were reported by Ehdaie and Waines (1989), Ozkan *et al.* (1997) and Ahmed *et al.* (2007).

Broad and narrow sense heritability estimates for main spike seed number varied from 0.62 to 0.95 and from 0.10 to 0.50, respectively (**Table 2**). Expected genetic advance ranged from 5.31 to 10.35. Genetic coefficient of variation ranged from 11.8 to 22.09 (**Table 3**). High broad and narrow sense heritability combined with high genetic advance in all crosses except for the cross 10B × 10A may indicate that selection could be performed since this trait mainly controls by additive gene action. Same results were obtained by Ehdaie and Waines (1989) and Ozkan *et al.* (1997) who reported that high narrow sense heritability combined with considerable genetic advance in a cross indicate that additive gene effects may control this trait.

Broad and narrow sense heritability estimates for main spike seed weight ranged from 0.74 to 0.91 and from 0.01 to 0.79, respectively (**Table 2**). Expected genetic advance values varied from 0.25 to 0.65 and the genetic coefficient of variation ranged from 16.22 to 27.66 (**Table 3**). The present results indicated that sufficient variation in values for main spike seed weight existed in the five crosses. High heritability and genetic advance estimates for the cross 2B × 2A indicated that effective selection for main spike seed weight is possible in F$_2$ generation of this cross. These results confirm those obtained by Ehdaie and Waines (1989), Amin *et al.* (1992) and Ozkan *et al.* (1997).

Broad and narrow sense heritability estimates for number of fertile tillers per plant ranged from 0.35 to 0.59 and from 0.08 to 0.45, respectively (**Table 2**). Expected genetic advance varied from 0.60 to 3.47. Genetic coefficient of variation ranged from 12.36 to 45.79 (**Table 3**). The cross 2B × 2A showed high values for heritability and had the highest values for genetic advance compared to the rest of the crosses. This could indicate that selection for high tillers number is possible in this cross at early generations. van Sanford and Utomo (1995), found similar results while Chowdhry *et al.* (1999) reported gene action of partial dominance for the number of tillers per plant.

CONCLUDING REMARKS

The crosses in this study represented a wide range of expressions for almost all the traits investigated. High estimates of heritability, gains from selection and genetic coefficient of variation were observed for grain filling rate in two out of the five crosses. With regard to grain filling duration it showed low values for the three genetic parameters in these two crosses. Our results demonstrate the importance of genetic effect, especially the additive gene action in controlling the grain filling rate. But, grain filling duration was found to be highly affected by environmental factors. The high narrow sense heritability values for grain filling rate showed that we can select high yielding genotypes that can perform well under the dryland conditions of the Mediterranean. The presence of high heritability and high gain from selection for the yield and yield components indicated that selection in early generations may be effective and could lead to high improvement in the traits under investigation. The high broad sense heritability values which accompanied by low narrow-sense heritability in some traits indicated the presence of high non additive gene action which suggested that selection in advanced generations may be more appropriate than the early generation selection.

As a result of the above, selection for grain filling rate and number of fertile tillers plants^{-1} for all crosses except crosses 2B × 2A and 4B × 4A can be recommended at early generations. Selection for grain yield might be effecient in crosses 2B × 2A, 1A × 1B and 4B × 4A in early generations and in advanced generations in the other two crosses. The high variability observed in these crosses offers good prospects for durum wheat improvement in the future.

REFERENCES

Ahmed N, Chowdhry MA, Khaliq I, Maekawa M (2007) The inheritance of yield and yield components of five wheat hybrid populations under drought conditions. *Indonesian Journal of Agricultural Science* **8 (2)**, 53-59

Akar T, Ozgen M (2007) Genetic diversity in Turkish durum wheat landraces. In: Buck HT, Nisi JE, Salomón N (Eds) *Wheat Production in Stressed Environments*, Springer, Berlin, Germany, pp 753-760

Al-Ajlouni MM, Jaradat AA (1997) Diversity in durum wheat landraces collected from Jordan I. Quantitative traits. *Cereal Research communication* **25 (2)**, 169-175

Al-Ghzawi ALA (2007) The physiological processes determining grain yield potential in winter wheat. PhD thesis, University of Nottingham, UK, 164 pp

Al-Karaki GN (1996) Effect of phosphorus, *Rhizobium* and *Sitona* weevil control on seed growth, nodulation and yield of lentil under Mediterranean rainfed conditions. *Legume Research* **19 (4)**, 201-210

Allard RW (1960) *Principles of Plant Breeding*, John Wiley and Sons Inc., New York, USA, 490 pp

Amin MR, Barma NCD, Rassaque MA (1992) Variability, heritability, genetic advance and correlation study in some quantitative character in durum wheat. *Rachis News Letter* **11**, 30-32

Bekele E (1984) The biology of cereal landraces 1. Problems of gene conservation, plant-breeding selection schemes and sample size requirement. *Hereditas* **103**, 113-134

Burton GW (1952) Quantitative inheritance in grasses. *Proceedings of the 6th International Grassland Congress*, 1, Pa. State College, August 17–23, National Publishing Company, Washington, D.C., pp 297-283

Chowdhry MA, Iqbal S, Subhani GM, Khaliq I (1997) Heritability of some quantitative characters in bread wheat. *Journal of Animal and Plant Science* **7 (1)**, 27-28

Chowdhry MA, Rasool AI, Khaliq I, Mahmood T, Gilani MM (1999) Genetic of some metric traits in spring wheat under normal and drought environments. *Rachis News Letter* **18**, 34-39

Deswai RK, Grakh SS, Berwal KK (1996) Genetic variability and characters association between grain yield and its components in wheat. *Annals of Biology (Ludhiana)* **12 (2)**, 221-224

Ehdaie E, Waines JG (1989) Genetic variation, heritability and path analysis in Landraces of bread wheat from southwestern Iran. *Euphytica* **41**, 183-190

Fehr WR (1987) *Principles of Cultivar Development* (Vol 1), Macmillan, New York, pp 98-100

Fernandez GCJ, Miller JC (1985) Estimation of heritability by parent-offspring regression. *Theoretical and Applied Genetics* **70 (6)**, 650-654

Firouzian A (2003) Heritability and genetic advance of grain yield and its related traits in wheat. *Pakistan Journal of Biological Sciences* **6 (24)**, 2020-2023

Gebeyehou GD, Knott R, Baker RJ (1982) Relationships among durations of vegetative and grain filling phases, yield components and grain yield in durum wheat cultivars. *Crop Science* **22**, 287-290

Harlan R (1975) Our vanishing genetic resources. *Science* **188**, 618-621

Ibrahim OE, Ohm W, Nyquist WE, Cantrell RP (1983) Inheritance of kernel number per spikelet and its association with plant height in two winter wheat crosses. *Crop Science* **23**, 927-931

Jaradat AA (1992) Breeding potential of durum wheat landraces from Jordan phenotypic diversity. *Hereditas* **116**, 301-304

Martinez JHE, Foster AE (1998) Genetic analysis of heading date and other agronomic characters in barely (*Hordeum vulgare* L.). *Euphytica* **99**, 145-153

Mehta B, Sharma SK, Luthra OP (1997) Genetic architecture of harvest index and yield component characters in wheat. *Annals of Biology (Ludhiana)* **13**, 37-40

Mou B, Kronstad WE (1994) Duration and rate of grain filling in selected winter wheat populations: Inheritance. *Crop Science* **34**, 833-837

Ozkan H, Yagbasanlar T, Gene I (1997) Genetic analysis of yield components, Harvest index and biological yield in bread wheat under Mediterranean climatic conditions. *Rachis* **16**, 49-52

Rasyad A, Van Sanford DA (1992) Genetic and maternal variances and covariance's of kernel growth traits in winter wheat. *Crop Science* **32**, 2239-2243

Reynolds MP, Pellegrineschi A, Skovmand B (2005) Sink-limitation to yield and biomass: a summary of some investigations in spring wheat. *Annals of Applied Biology* **146**, 39-49

Saleem I, Khan AS, Ali Z (2003) Estimating of heritability and genetic advance for grain yield traits in *Triticum aestivum* L. *Journal of Animal and Plant Science* **13**, 52-54

Savin R, Nicolas ME (1996) Effects of short periods of drought and high temperature on grain growth and starch accumulation of two malting barley cultivars. *Australian Journal of Plant Physiology* **23**, 201-210

Sharma RC (1994) Early generation selection for grain filling period in wheat. *Crop Science* **34**, 945-943

Shearman VJ (2001) Changes in the yield-limiting processes associated with the genetic improvement of wheat. PhD thesis, University of Nottingham, UK, pp 148-152

Shearman VJ, Sylvester-Bradly R, Scott RK, Foulkes MJ (2005) Physiological processes associated with recent genetic increases in grain yield in winter wheat in the UK. *Crop Science* **45**, 175-185

Srivastava JP, Damania AB, Pecetti L (1988) Landraces, primitive forms and wild progenitors of macaroni wheat, *Triticum durum*: their use in dryland agriculture. In: Miller ET, Koebner RMD (Eds) *Proceedings of the 7th International Wheat Genetics Symposium*, Cambridge, England, pp 153-158

Sun PLF, Shand HL, Forhberg RA (1972) Inheritance of kernel weight in six-spring wheat crosses. *Crop Science* **12**, 1-5

Ul Haq I, Laila T (1991) Diallel analysis of grain yield and other agronomic traits in durum wheat. *Rachis* **1**, 8-13

van Sanford DA (1985) Variation in kernel growth characters among soft red winter wheats. *Crop Science* **25**, 626-630

van Sanford DA, Utomo H (1995) Inheritance of tillering in a winter wheat population. *Crop Science* **35**, 1566-1569

Wiegand CI, Cuellar JA (1981) Duration of grain filling and kernel weight of wheat as affected by temperature. *Crop Science* **21**, 95-101