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Grain Filling Rate and Duration in Bread Wheat Under Irrigated and Drought Stressed Conditions

AG Sanjari Pireivatlou[1*], RT Aliyev[2] and B Sorkhi Lalehloo[3]

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[1]Agricultural and Natural Resources Research Station of Ardabil, Ardabil, Iran
[2]Azerbaijan National Academy of Science, Genetic Resources Institute, Baku, Republic of Azerbaijan
[3]Seed and Plant Improvement Institute (SPII), Karaj, Iran
*Corresponding author Email: a.sangarip@yahoo.com

Abstract
Eleven wheat cultivars were evaluated at 10-day intervals, beginning from anthesis, under irrigated and drought stress conditions during 2006-2007. The effects of irrigation, genotype and date of harvest were significant for most of the studied characters. Water deficit decreased pre-and post-anthesis assimilation rate, grain weight per spike, grain number per spike and 1000 grain weight about 5.7, 24.5, 21.2, 15.7 and 6.4 %, respectively. Mobilization, mobilization efficiency and contribution of pre-anthesis assimilates to kernels were considerably increased under drought stress condition. Grain weight, grain growth rate and contribution of current assimilates to grain filling decreased under drought stress about 7.18, 22.1 and 29.6 %, respectively. However, the effective grain filling period was considerably increased in the stressed plants. Grain filling rate was correlated with the accumulation of dry matter at maturity, grain weight per spike and grain number per spike in the irrigated and drought stressed environments (r=0.87** and 0.53, r=0.87** and r=0.62*, r=0.75* and r=0.63*, respectively). A negative correlation was found between effective grain filling period and grain yield/spike under irrigation (r =-0.65*) and drought stress (r =-0.76**) conditions. Furthermore, positive correlations between grain filling rate and grain yield were obtained in the irrigated and drought stressed environments (r = 0.87** and r = 0.62*, respectively). It seems that accumulation of pre-anthesis assimilates (mainly under drought stress), short effective grain filling period and high grain filling rate are major factors for producing higher grain yield in wheat under both irrigated and drought stress conditions.

Keywords: Drought stress, Effective grain filling period, Grain filling rate, Wheat

Introduction
Genetic variability exists among winter cereal genotypes in response to environmental factors such as drought stress condition, and thus, selection of genotypes for each production area is feasible (Gooding *et al*. 2003). Based on Santiveri *et al*. (2002), grain dry weight at maturity was determined by the rate of dry

weight accumulation and the length of dry weight accumulation period. The assimilate supply problem may be compounded by further reductions in photosynthesis due to water stress and suggests that the reduction in grain number caused by stress at this critical period is proportional to the reduction in leaf-area development and hence, in available assimilate during about 25 days before anthesis (Fischer 1980). Grain growth and development in wheat depend on C from three sources: current assimilates produced by photosynthesis in leaves and stems, mobilization of the stored carbohydrates and N containing compounds within these organs and their subsequent transport to the spike and growing kernels, and assimilates produced by the spike (Bradford and Hasio 1982, Sanjari Pireivatlou and Yazdasepas 2009). Van Herwaarden *et al*. (1998) showed that under dry conditions, the apparent contribution of stored assimilates could be 75-100% of grain yield, compared with 37-39% under rainfall conditions. In fact, a high correlation was found between the use of non-structural carbohydrates stored in stems and grain yield under drought conditions (Gavuzz *et al.* 1997). Wheat crops grown in dry land areas may depend more on the stem reserves for grain filling than crops grown under well-watered conditions (Ehdaie *et al.* 2006). There are two components involved in the extent of contribution of stored reserves to grain yield in wheat; the first is the ability to store assimilates in the stem and the second is the efficiency of the crop to mobilize and translocate the reserved materials to the grains. The second component is a function of sink strength in a genotype, which depends on the number of grains per spike and mean grain weight (Ehdaie and Waines 1996). Stored reserves and their contribution to grain can be estimated by measuring post-anthesis changes in the internode dry matter (Hunt1997, Cruz-Aguado *et al*. 2000), changes in internode water soluble carbohydrate content during grain-filling period (Blum *et al*. 1994), or by difference between shoot dry weight at anthesis and at maturity excluding the grains (Flood *et al*. 1995). Grain filling duration seems to be more affected by environmental factors than grain filling rate (Wiegand and Cuellar 1981, Royo *et al*. 2000).

Genetic variation for the duration of grain filling has been reported for wheat (Bruckner and Frohberg 1987). However, final grain weight has also been suggested to be proportional to grain filling rate (Wiegand and Cuellar 1981), because grain filling duration is largely influenced by temperature under terminal stress conditions. Therefore, selection of genotypes with high grain filling rates appears to be a successful strategy for increasing grain yield (Van Sanford 1985, Bruckner and Frohberg 1987, Knott and Gebeyehou 1987), especially for regions where grain filling duration is restricted by high temperatures (Wiegand and Cuellar 1981, Bruckner and Frohberg 1987). Lack of relationship between grain yield and grain filling duration has been reported for wheat (Nass and Reisser 1975, Van Sanford 1985, Bruckner and Frohberg 1987). Grain growth of field crops is initially slow, enters a linear phase where the growth rate is fast and then slows down toward maturity (Yoshida 1981). Cho *et al.* (1988) divided rice grain filling duration into three phases: lag phase of five days from heading, linear increasing phase of 5–20 days after heading and late grain filling period thereafter. However, grain filling patterns frequently demonstrate genotypic variations in many cereal crops. Yoshida (1981) suggested that effective grain filling duration, where grain growth is linear, is more important than the duration of ripening from the date of heading to the time when maximum grain weight is attained (Yashida 1981). The rate of dry matter accumulation by kernels was considerably decreased by water deficit in wheat cultivars (Plaut *et al*. 2004). Przulj and Momellovie (2003) reported that in the years with favorable growing conditions during vegetative growth, the main portion of dry matter was stored before anthesis, while in the years with unfavorable conditions during the same period significant amounts of dry matter were accumulated during grain filling as well. The more adapted cultivars continued the accumulation of dry matter and nitrogen during the grain filling period, while in the less adapted ones the main portion accumulated before anthesis (Przulj and Momellovie 2003). Austin *et al.* (1977) reported that a major quantity of pre-anthesis dry matter was used for sinks other than kernel and found that only 73 % of the losses of vegetative weight were used for kernel growth. Respiratory (Rawson and Evans 1971) and dead leaf losses (Bidenger *et al*. 1977) can account for the rest of losses. Modern cultivars seem to be relatively less sink-limited during post-anthesis than their predecessors (Shearman *et al*. 2005), as the semi dwarf wheat seems less sink-limited than the traditional tall wheat.

The major purposes of this study were to understand the accumulation rates of dry matter during pre-anthesis and the effects of grain filling rate and grain filling duration on grain yield in bread wheat genotypes under irrigated and drought stressed conditions.

Material and Methods

Eleven diverse wheat cultivars (Table 1) were evaluated under two water treatments (well watered and drought stress) in 2006-2007. Each experiment was laid out in a randomized complete block design with three replications. Seeds were planted on 15th October 2006, in a clay loam soil at Agricultural and Natural Resources Research Station of Ardabil (38^{o} 15´ N, 48^{o} 20´ E, with an elevation about 1350 m above sea level), Iran. Plants in the normal condition were irrigated five times from planting until they reached physiological maturity (i.e. at planting, tillering, booting, anthesis and milk stages). In the normal condition, plants received 672.4 mm of water (406 mm irrigation + 266.4 mm rain year-1) and those in drought stress condition received only 266.4 mm seasonal rainfall during the 2006-2007 growing year. However, 78.7% of this rainfall was received before booting stage, 19.6 % between booting and heading stage (4.0-4.9 sub-stage of Zadoks), and 1.7% fell between heading and early grain filling period (6.0 to 7.0 sub-stage of Zadoks). Based on the climatic data of Ardabil region, a period of drought was occurred during grain filling stage of wheat in June and July. The absolute maximum and mean temperatures in the grain filling period were 30˚C and 8.0˚C, respectively. Average temperatures were optimum during grain filling period (data not shown).

Each plot consisted of two rows, 2 m in length. Inter-row spacing was 30 cm and kg

Table 1. The pedigree, origin and growth habit of wheat cultivars under study

No	Pedigree	Origin	Growth habit
1	Siosson/M-73-4/3/Bez-2B/Cgn/Veratza	Iran	Spring and semi dwarf
2	MV17	Hungary	Winter and semi dwarf
3	Kal/Bb//Cj"s"/3/Hork"s"/4/Mv17/5/Gascogne/3/P101/Anza//1-66-49	Iran	Winter and semi dwarf
4	Gaspard/6/Bow"s"/Crow"s"/5/Omid/4/Hys//Drc*2/7c/3/2*Rsh	Iran	Winter and semi dwarf
5	Mv-92-2854//Rsh*2/10120	Iran	Winter and semi dwarf
6	ID800994w/Vee//F900K/3/Pony/Opata	9^{th} EYT^{+}	Winter and semi dwarf
7	Es14//Sitta//Agri/Nac	9^{th} EYT^{+}	Spring and semi dwarf
8	Sardari (landrace)	Iran	Facultative and tall
9	Agri/Nac//Atilla	Iran	Facultative and semi dwarf
10	Siossons	France	Winter and semi dwarf
11	Landrace	Azerbaijan	Spring and tall

+International Elite Yield Trial, CIMMYT

interplant spacing was 3 to 5 cm. The land was fallowed in the previous year and 100 kg ha^{-1} urea was utilized at the tillering stage. All cultural practices (i.e., hoeing, weeding, fertilization, etc.) were practiced uniformly, except for irrigation which was based on the respective treatments. Data for grain growth rate (GGR), effective grain filling period (EGFP), mobilization of reserves (MDM), mobilization efficiency (ME), contribution of pre-anthesis assimilates (CPAA) and contribution of current assimilates (CCA) *viz*., plant height, plant weigh, grain weight per spike, grain number per spike, *etc*. were collected by harvesting five spikes from main stems and primary tillers (Gooding *et al.* 2003) at 10-day intervals (five times) from anthesis to physiological maturity.

The following parameters related to dry matter mobilization were estimated in this research:

1. Pre-anthesis and post-anthesis dry matter accumulation (mg per plant).
2. Mobilization of dry matter (mg per plant) = dry matter at anthesis – dry matter (leaf + culm + chaff) at maturity.
3. Mobilization efficiency (%) = Mobilization of dry matter /dry matter at anthesis ×100.
4. Contribution of assimilates to grain (%) = Mobilization of dry matter /grain weight ×100 (Papakosa and Gagianas 1991).

Effective grain filling period= grain dry weight at maturity/ linear grain growth rate (Santiveri *et al*. 2002).

Analysis of variance (ANOVA) was performed for each character in each experiment. The combined ANOVA was also performed for irrigation experiments. Associations between characters were examined by calculating correlation coefficients. Means were compared using the LSD test (Steel *et al*. 1997).

Results and Discussion

The combined ANOVA showed significant effect of irrigation, date of harvest, genotype and genotype × irrigation interaction on most of the studied characters (data are not shown).

Heading time of wheat cultivars was reduced under drought stress condition as compared with the irrigated condition (161.5 and 159.8 days, respectively). Sardary, a tall landrace, had the earliest heading time, whereas a tall landrace from Azerbaijan republic, had the latest heading time under both well watered and drought stress conditions.

Drought, on the average, reduced the aboveground dry matter by 5.7 and 24.5% at anthesis and maturity, respectively. Furthermore, significant differences were found between genotypes in terms of this character at anthesis under drought stress condition. The landrace from Azerbaijan Republic had the highest aboveground dry matter (3170 mg) and the genotype No. 6 had the lowest amount (1555 mg) under this condition (Table 2). Thereby contribution of pre-anthesis assimilates to grain under drought stress condition was higher in the landrace of Azerbaijan Republic (88.5%) than the genotype No. 6 (59.3%) (Table 2). It seems that the landrace from Azerbaijan reserved high amount of non-structural assimilates in the pre-anthesis growth stage and mobilized them into grains under drought stress condition. Ehdaie and Waines (1996) also reported the same results for Iranian landraces.

There were no significant differences among genotypes for dry matter at maturity and grain weight per spike under drought stress condition. Genotypic variation for this trait was considerably decreased at maturity under drought stress condition (Table 2). Although the genotypic differences were not significant at this condition, however, the highest and lowest aboveground dry matter reduction belonged to genotypes No. 9 and landrace of Azerbaijan Republic (50.2% and 19.1%, respectively). It is assumed that this reduction from anthesis to maturity was due to the utilization of assimilates for kernel development. The average contribution of pre-anthesis dry matter to kernel weight was 30.7% and 55.9% in the irrigated and drought stress conditions, respectively (Table 2). Some genotypes, such as No. 9 and No. 8, lost much more dry matter from anthesis to maturity in the irrigated condition (38.7 and 34.6 %, respectively). Thus, a major quantity of pre-anthesis dry matter was used for sinks other than kernels. Austin *et al*. (1977) found that only 73 % of the loss of vegetative weight were attributed to kernel growth. Respiration (Rawson and Evans 1971) and dead leaves (Bidenger *et al*. 1977) could be responsible for the rest of the loss. The highest reduction of grain weight per spike (48.9%) under drought stress condition was also found in the genotype No. 6. However, grain weight per spike was increased (5.1%) in the genotype No. 3 under drought stress condition.

Drought reduced grain number per spike by 15.7%. Fisher (1980) also reported the reduction in grain number per spike under water stress environment. However, the amount of reduction varied for different genotypes. The highest reduction (46.1%) was found in the genotype No. 6 in contrast with the genotype No. 3, in which grain number per spike was increased under drought stress condition (9.7%). On the other hand, grain number per spike in irrigated and drought stress conditions were similar in relation to the landrace of Azerbaijan Republic.

Mobilization of dry matter and mobilization efficiency were increased under drought stress condition by 60.1% and 74.9%, respectively. However, genotypes responded differently to drought for the amount of pre-anthesis dry matter translocation and translocation efficiency.

Contribution of pre-anthesis dry matter to kernels was increased under drought stress by 82.1%. Mobilization of pre-anthesis assimilates, mobilization efficiency and contribution of pre-anthesis assimilates to kernels under drought stress condition, were higher in the drought tolerant variety of Sardary, Agri/Nac/Atilla and the landrace of Azerbaijan as compared with other varieties. These genotypes had dry matter mobilization of 1115, 1105, 1591 mg, mobilization efficiency of 54.4, 50.2, 50.2% and pre-anthesis assimilate contribution of 86.8, 94.8, 88.5%, respectively (Table 2). Van Herwaarden *et al*. (1998) reported that under dry conditions in the field, the apparent contribution of stored assimilates could be 75-100% of the grain yield as compared with 37-39% under high rainfall conditions. According to the results obtained, genotype No. 9, with 94.8 % of dry matter contribution to grain, produced 1165 mg grain per spike, whereas genotype No. 1, with 23.5 % of assimilate contribution to grain, produced 2220 mg grain per spike (Table 2). This shows that genotypes with larger amount of assimilate contribution to grain tended to have lower grain yields. The coefficient of `determination (R^2) between mobilization of pre-anthesis assimilates and grain yield was only 0.07, which means that the mobilization of dry matter was not useful for high grain yield production. The relationship between the contribution of pre-anthesis assimilates to grain yield and drought tolerance is not well understand, as also reported by Przulj and Momcilovic (2003). Drought, on the average, decreased dry matter accumulation in kernels by 6.4%, however, reduction varied in different genotypes. Genotype No. 2, showed highest reduction (19.1 %) but, in Sardary, Agri/Nac/Atilla and Siosson the rate of dry matter accumulation by kernels increased under drought stress condition (Table 1), as also reported by Plaute *et al*. (2004).

Drought stress decreased grain weight at maturity by 7.18 %. However, the reduction varied in different wheat genotypes. The highest reduction was occurred in genotype No. 2, by 19.1%, whereas in genotypes No. 8, 9 and 10 the grain weight at maturity increased by 0.48, 8.2 and 9.7 %, respectively. Grain growth rate and contribution of current assimilates to developing grains were also decreased under drought stress condition by 22.1 and 29.6%, respectively. The highest reduction was observed in genotype No. 2 (44.9%) and the rate of grain growth in genotype No. 5 was substantially increased (32.3%) under drought stress condition. The mean values observed for effective grain filling period and grain filling rate suggest that there was compensation between both traits especially in genotypes No. 1 and No. 5 under drought stress condition and No. 1 and No. 11 under irrigated condition, where the highest rate but the shorter duration were found (Table 3). In fact, a negative phenotypic correlations (r =-0.73** and r =-0.84** under irrigated and drought stress conditions, respectively) were observed between these two traits across the genotypes. The grain filling rate in genotypes No, 1, 2, 4, 6, 8, 9 and 11 decreased, whereas the effective grain filling period increased under drought stress condition in contrast with the irrigated condition. The amount of grain filling under drought stress condition in genotypes No. 3, 5 and 10 were increased, whereas the duration

of grain filling was decreased as compared with the irrigated condition. In conclusion, the higher rates were accompanied by the shorter duration across the genotypes studied, as also reported by Gooding *et al*. (2003).

Data about grain growth was well described by the logistic model proposed by Darroch and Baker (1990), because the coefficients of determination obtained were higher than 98% in most cases (Figures 1 to 14). Grain filling duration depended strongly on the environment, which accounted for 22.1% of the total variation. Probably genotypic variations were partially responsible for the observed differences in the grain filling duration. A reduction of 46.7% in grain filling duration was observed in the latest flowering genotype (No. 11) as compared with the earliest genotype, No. 8 (Table 3).

Differences between genotypes for grain filling duration were significant (Table 3). There was no evidence that grain filling in primary tillers suffered more from the stress than in main stem. For example coefficient of determinations between grain weight and grain number were 0.71 and 0.66 under irrigated and drought stress conditions, respectively (Figures 1 and 2). Under irrigated condition, the grain weight of the winter genotypes was 39.8 mg, whereas in the spring genotypes this ranged between 44.4 mg for the genotype No. 7 (Es14//Sitta//Agri/Nac), and 46.6 mg for the genotype No. 11 (Landrace of Azerbaijan Republic) (Table 3) whereas, on the average, the same grain weight was found in the winter and spring genotypes, as reported by Santiveri *et al*. (2002).

The timing and duration of the stresses coincided broadly with the different phases of grain development. The period from day 1 to 10 appeared to cover a lag phase, associated with cell division, and the start of the linear phase of grain growth. The period from day 11 to 40 broadly corresponded to the linear phase of grain growth in the irrigated plants (Figure 2). When stress was applied during this period (Figure 2), day 40 occurred after the end of the linear phase of grain filling. The period from day 41 to 50 occurred after maximum dry matter content was attained and therefore, coincided with the maturation period. All stresses imposed before the end of linear phase of grain growth reduced final mean grain weight (Table 3, Figure 2). This reduction was most marked when drought stress occurred between days 40 and 50 after anthesis (Figure 2). On the average, the effect of drought stress between days 11 and 40 was approximately additive (Figure 2), as reported earlier (Gooding *et al*. 2003). Drought stress also reduced grain number per spike (Table 3).

The period of lag phase was from day 1 to 20 and from day 20 to 40 and broadly corresponded to the linear phase of grain growth, when stress was imposed during this period (Figure 3), and day 40 occurred after the end of the linear phase of grain filling. The period from day 41 to 50 occurred after maximum dry matter content was attained and therefore, coincided with the maturation period in the genotype No. 1. All stresses imposed before the end of the linear phase of grain growth, reduced final mean grain weight by

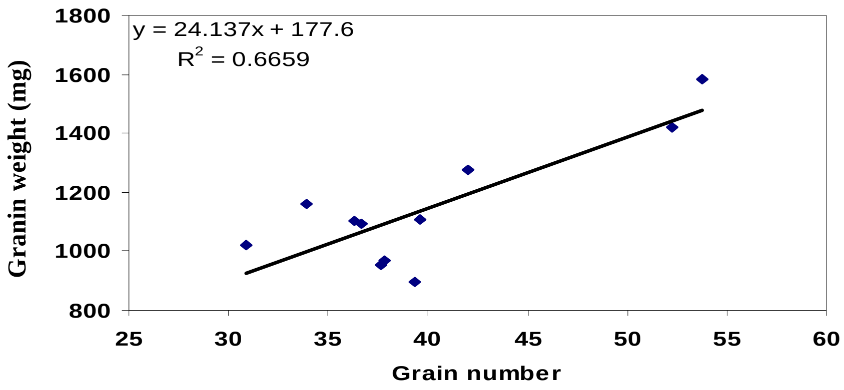

Figure 1. Relationship between grain weight and grain number on wheat genotypes under irrigated condition

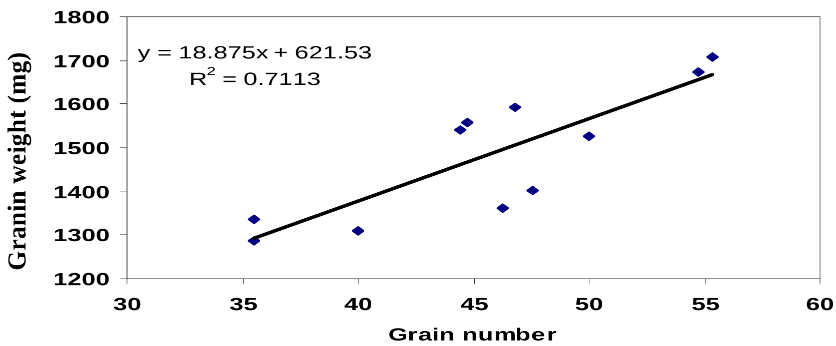

Figure 2. Relationship between grain weight and grain number on wheat genotypes under rainfed condition

12.4% (Table 3, Figure 3). This reduction was mostly marked when drought stress occurred between days 40 and 50 after anthesis (Figure 3). The effect of drought stress between days 20 and 40 has been reported to be additive (Gooding *et al*. 2003) as it was in our experiment (Figure 3).

All stresses applied before the end of the linear phase of grain growth reduced final grain weight (Table 3, Figures 4 to 12). This reduction was considerable when drought stress occurred between days 1 and 20 after anthesis (Figures 4 to 12). Effect of drought stress between days 21 and 40 was approximately additive upon exposure to the stress condition (Figures 4 to 12). Reductions in the final grain weight were mostly attributable to an earlier end to the grain filling when stress was applied and day 40 occurred after the end of the linear phase of grain filling. All stresses imposed before the end of the linear phase of grain growth reduced final grain weight by 12.4, 19.1%, 4.3%, 16.7%, 2.6%, 6.6%, 11.7% and 16.1% for the genotypes No. 1, 2, 3, 4, 5, 6, 7 and 11, respectively (Table 3, Figures 4, 5, 6, 7, 8, 9, 10 and 14). This reduction was most marked when drought stress occurred between days 40 and 50 after anthesis. On the average, the effect of drought stress between days 11 and 40 was additive across genotypes.

In the genotypes No. 8 and 10, the period of lag and linear grain growth were from day 1 to 20 and from day 21 to 40, respectively. The linear grain growth in the genotypes No. 8 and 10 were more additive under drought stress than irrigated condition so that grain filling continued until the end of physiological maturity and no reduction was observed in grain weight. In the genotype No. 9, the period from days 1-10 was lag period under both irrigated and drought condition. The linear grain growth was more additive under drought stress than irrigated conditions (Figure 11).

Grain filling rate was negatively and significantly correlated (r= -0.68) with the contribution of assimilates to developing kernels in the irrigated condition. Under irrigated and drought stress conditions, phenotypic correlations of grain filling rate with grain weight per spike (*r*= 0.87, *r*= 0.62) and grain number per spike (*r*= 0.71, *r*= 0.63) were significant. Furthermore, a significant positive correlation coefficient between grain filling rate and accumulation of dry matter at maturity (*r*=0.87) was observed in the irrigated environment. The observed values for effective grain filling period and grain filling rate suggested the compensation between these traits in both drought stress and irrigated plants. In fact, a significant negative phenotypic correlation was observed between these traits under irrigated and drought stress conditions (*r* =−0.73, r=-0.84, respectively). The same result was also reported by Goodong *et al.* (2003).

Mobilization of dry matter from vegetative organs to developing kernels was significantly correlated with accumulation of post-anthesis assimilate (r= -0.72), grain weight per spike (r= -0.74), grain number per spike (r= -0.73) and contribution of pre-anthesis assimilate to kernels (r= 0.95) in the irrigated environment. However, this character was only significantly correlated

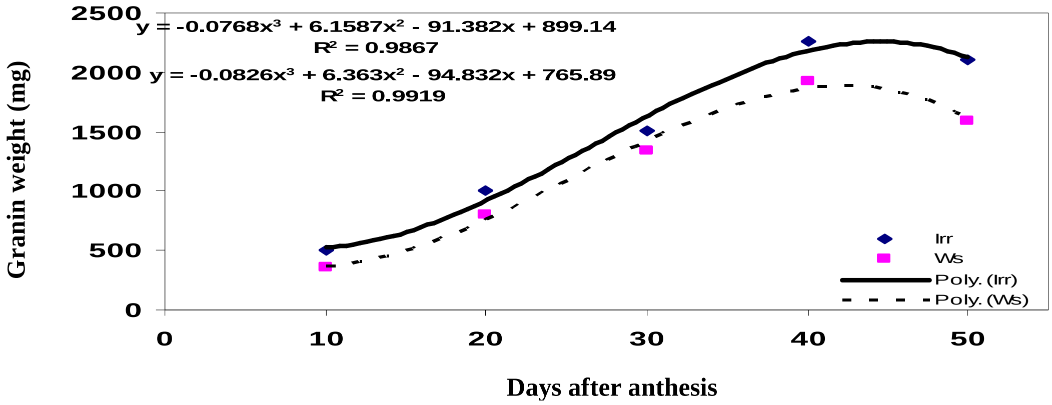

Figure 3. Changes in grain weight of wheat genotypes under irrigated and drought stress conditions

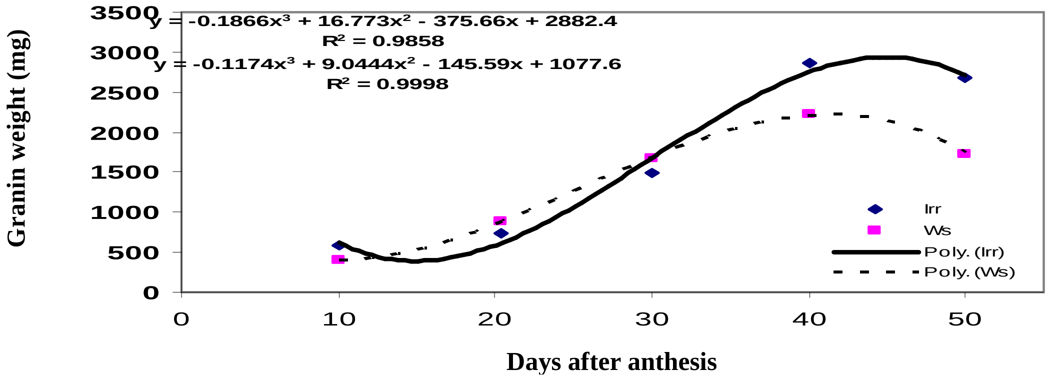

Figure 4. Effective grain filling in the wheat genotype No. 1 under irrigated and drought stress conditions

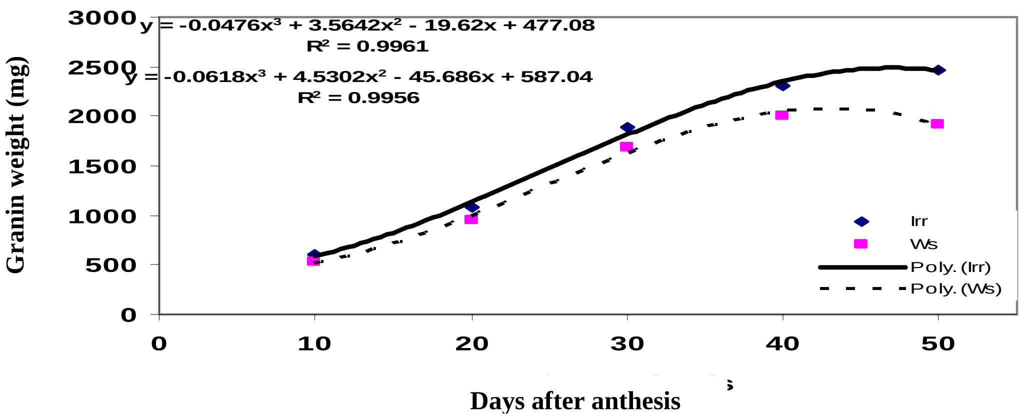

Figure 5. Effective grain filling in the wheat genotype No. 2, under irrigated and drought stress conditions

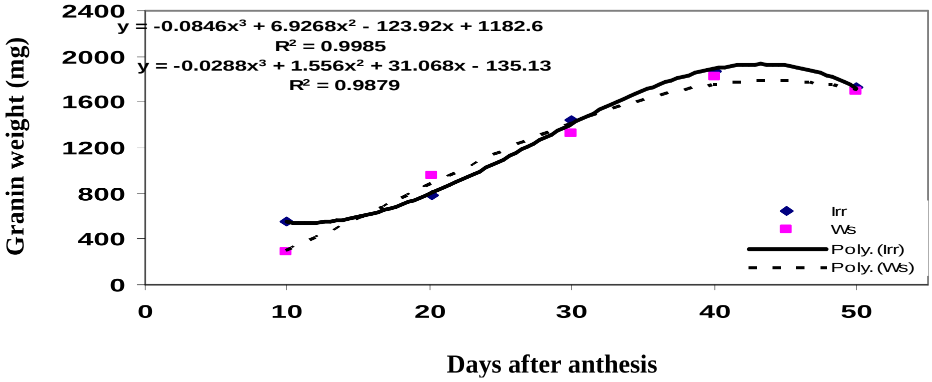

Figure 6. Effective grain filling in the wheat genotype No. 3, under irrigated and drought stress conditions

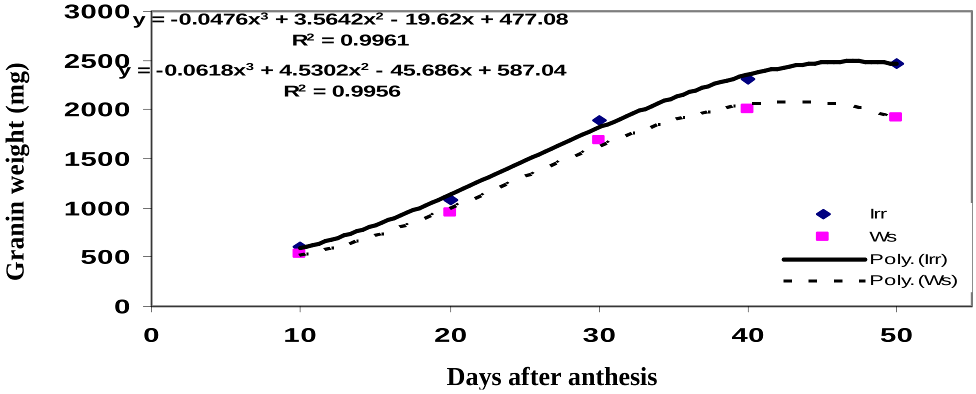

Figure 7. Effective grain filling in the wheat genotype No. 4, under irrigated and drought stress conditions

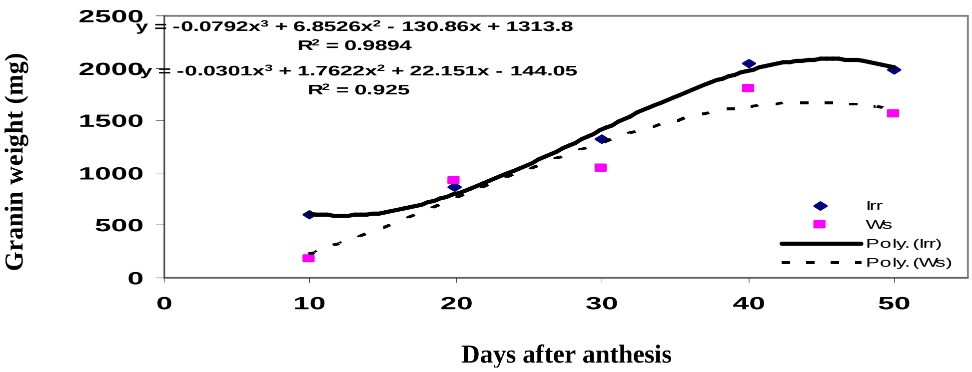

Figure 8. Effective grain filling in the wheat genotype No. 5, under irrigated and drought stress conditions

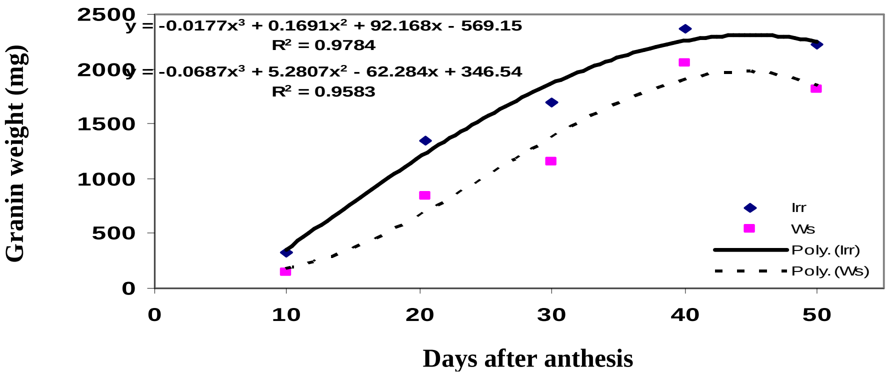

Figure 9. Effective grain filling in the wheat genotype No. 6 under irrigated and drought stress conditions

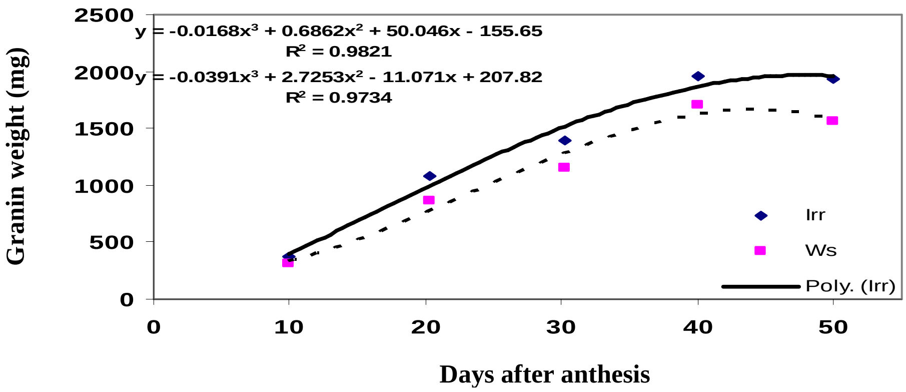

Figure 10. Effective grain filling in the wheat genotype No. 7 under irrigated and drought stress conditions

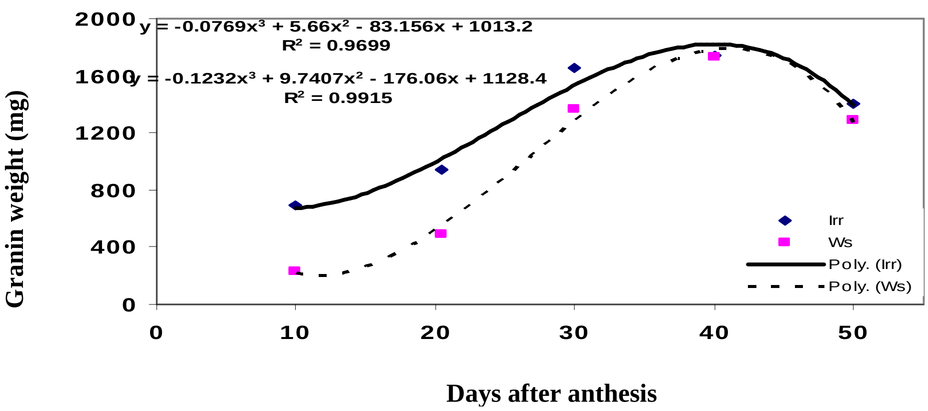

Figure 11. Effective grain filling in the wheat genotype No. 8 under irrigated and drought stress conditions

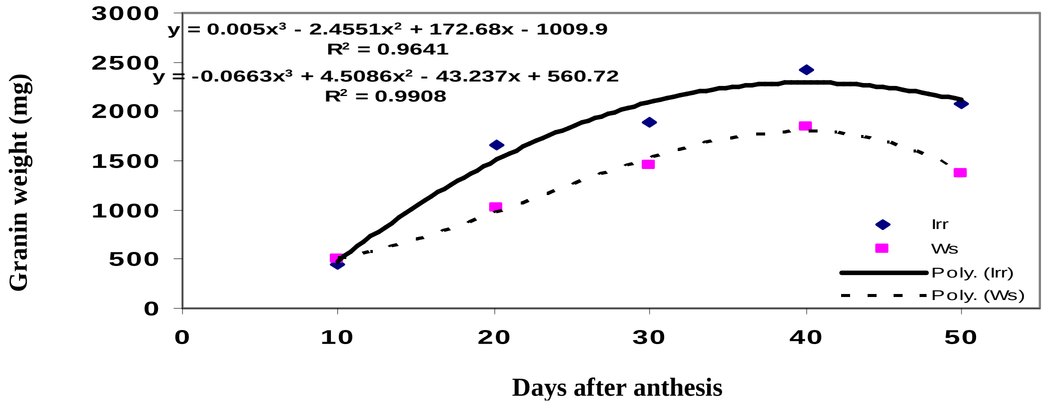

Figure 12. Effective grain filling in the wheat genotype No. 9 under irrigated and drought stress conditions

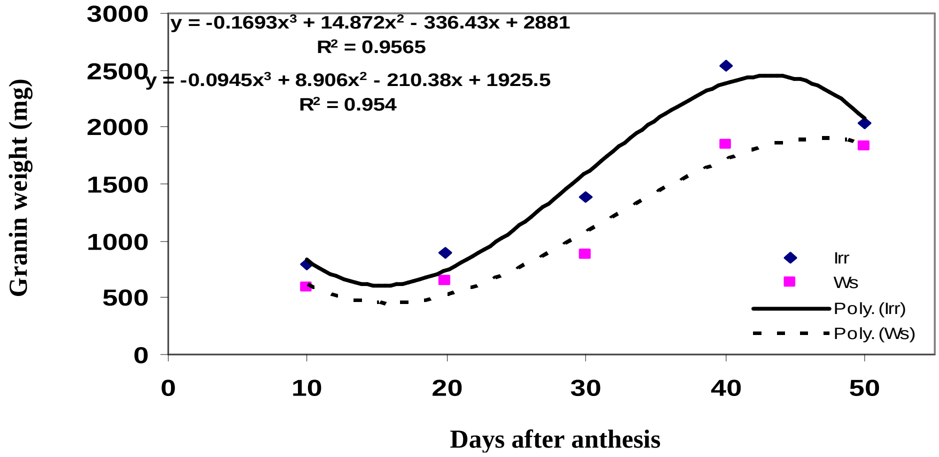

Figure 13. Effective grain filling in the wheat genotype No. 10 under irrigated and drought stress conditions

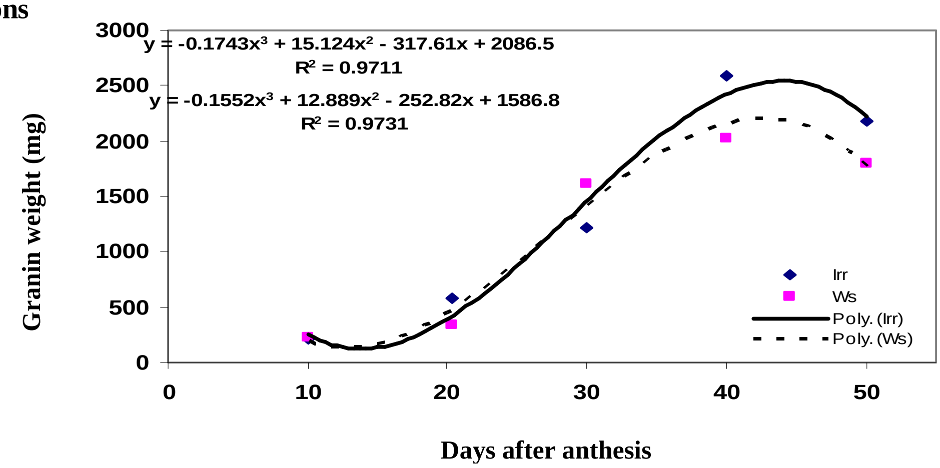

Figure 14. Effective grain filling in the wheat genotype No. 11 under irrigated and drought stress conditions

with the contribution of pre-anthesis assimilate to kernels (r=0.87) and grain weight (r= 0.61) under drought stress condition. Gavuzzi *et al*. (1997) reported high correlation of grain yield

with the storage of non-structural carbohydrates in the drought condition.

Significant phenotypic correlation coefficients of effective grain filling period with grain weight (r= -0.70, r= -0.67), accumulation of pre-anthesis assimilates (r= -0.6, r= -0.76) and grain filling rate (r= -0.73, r= -0.84) were observed under irrigated and drought stress conditions, respectively. Effective grain filling period was also significantly correlated with accumulation of post-anthesis assimilates (r= -0.79) and grain number per spike (r= 0.68) in in the drought stressed plants. In addition, a phenotypic correlation coefficient of 0.56 was found between grain number per spike and accumulation of pre- anthesis assimilates under drought stress condition. According to Fischer (1980), who reported the same results, the assimilate supply problem may be compounded by further reductions in photosynthesis due to water stress, so it was suggested that the reduction in seed number caused by stress at this critical period is proportional to the reduction in leaf area development and hence, in available assimilates during approximately 25 days before anthesis.

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Table 2. Translocation of dry matter (TDM), contribution of pre-anthesis assimilates to grain (CPA) and translocation efficiency (TE) of the stem internodes in bread wheat genotypes under well watered and drought stress conditions during 2006-2007.

	Irrigated condition								Drought stress condition							
	Vegetative organs (above grand dry matter) (mg)		Yield (mg/ plant)	Grain/ spike	1000 grain weight (g)	TDM (mg)	TE (%)	CPA (%)	Vegetative organs (above grand dry matter) (mg)		Yield/ spike (mg)	Grain/ spike	1000 grain weight (g)	TDM (mg)	TE (%)	CPA (%)
No.	Anthesis	Maturity							Anthesis	Maturity						
1	2990	5440	2677	69.0	38.7	227	7.6	8.5	2725	4424	2220	65.5	33.9	521	19.1	23.5
2	2800	5734	2672	63.0	42.3	-262	0.0	0.0	2400	3395	1612	47.0	34.2	617	25.7	38.3
3	3050	4004	1730	41.0	41.7	776	25.4	44.8	2750	3600	1818	45.0	39.9	968	35.2	53.2
4	2305	4972	2213	55.0	40.8	-454	0.0	0.0	2549	3534	1762	45.5	37.0	577	22.6	32.7
5	3000	4202	1988	53.0	38.1	786	26.2	39.5	2555	3275	1562	43.5	37.1	841	32.9	53.8
6	2630	4290	2370	58.5	41.1	710	27.0	30.0	1555	2047	1210	31.5	38.4	718	46.2	59.3
7	2743	4022	1940	43.0	44.4	661	24.1	34.1	2975	3903	1712	43.5	39.2	784	26.3	45.8
8	2710	3182	1408	33.0	41.7	936	34.5	66.5	2455	2625	1285	31.0	41.9	1115	54.4	86.8
9	2285	2977	1580	46.0	34.3	888	38.5	56.2	2200	2260	1165	30.5	36.7	1105	50.2	94.8
10	2235	3844	2037	57.5	35.0	428	19.1	21.0	2565	3688	1825	47.0	38.4	702	27.4	38.5
11	3855	5217	2185	47.0	46.6	823	21.3	37.7	3170	3377	1798	47.0	39.1	1591	50.2	88.5
Mean	2691.2	4353.1	2072.7	51.5	40.4	501.7	20.3	30.7	2536.3	3284.4	1633.5	43.4	37.8	803.4	35.5	55.9
LSD 5%	996.9	2156	925.1	22.3	11.29	-	-	-	903.2	2411	1160	24.7	14.25	-	-	-
Changes under drought stress relative to irrigated condition									-5.7	-24.5	-21.2	-15.7	-6.4	60.1	74.9	82.1

Table 3. Grain weight (GW) at maturity, linear grain growth rate (LGGR), effective grain filling period (EFGP), contribution of pre-anthesis assimilates (CPAA) and contribution of current assimilates (CCA) in wheat genotypes under irrigated and drought stress conditions

Genotype	Irrigated condition					Drought stress condition				
	GW (mg)	LGGR (mg/grain /day)	EGFP	CPAA (%)	CCA (%)	GW (mg)	LGGR (mg/grain /day)	EGFP	CPAA (%)	CCA (%)
1	38.7	60.2	0.64	8.5	91.5	33.9	41.1	0.85	23.5	67.5
2	42.3	48.8	1.16	0.0	100.0	34.2	26.9	1.27	38.3	67.3
3	41.7	33.0	1.35	44.8	55.2	39.9	38.0	1.18	53.2	46.8
4	40.8	43.9	0.96	0.0	100.0	34.0	33.4	1.31	32.7	67.3
5	38.1	34.1	1.11	39.5	60.5	37.1	45.1	1.07	53.8	46.2
6	41.1	49.6	0.82	30.0	70.0	38.4	30.0	1.29	59.3	40.7
7	44.4	33.5	1.45	34.1	65.9	39.2	28.5	1.38	45.8	54.2
8	41.7	27.6	1.52	66.5	33.5	41.9	24.6	1.94	86.8	13.2
9	33.9	23.8	1.47	56.2	43.8	36.7	20.1	2.15	94.8	5.2
10	35.0	41.2	1.88	21.0	79.0	38.4	28.6	1.36	38.5	61.5
11	46.6	57.6	0.81	37.7	62.3	39.1	36.6	1.15	88.5	11.5
LSD 5%	11.30	30.45	0.82	30.7	-	14.25	28.1	1.03	55.9	-
Mean	40.4	41.2	1.20	30.75	62.2	37.5	32.1	1.36	55.9	43.8
Changes under drought stress relative to irrigated conditions						-7.18	-22.1	13.3	81.8	-29.6