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RELATIONSHIP BETWEEN GRAIN YIELD AND YIELD COMPONENTS OF THE ETHIOPIAN DURUM WHEAT GENOTYPES AT VARIOUS GROWTH STAGES

[RELACIÓN ENTRE LA PRODUCCIÓN DE GRANO Y SUS COMPONENTES EN GENOTIPOS DE TRIGO DURUM DE ETIOPIA A VARIOS ESTADÍOS DE CRECIMIENTOS]

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SUMMARY

Water availability is the main constraint limiting durum wheat production in many parts of the world. Knowledge of the phenotypic and genotypic relationship between grain yield and its various components is an important step in developing selection criteria under water stress environment. To assess the usefulness of some of the agronomic traits as indicators of grain yield, eighteen durum wheat genotypes were evaluated under water stress treatments induced at three growth stage together with a well-watered control in plastic pots during 2006/07 growing season. The water stress treatments used were continuous stress from tillering to physiological maturity (M1), stress from anthesis to physiological maturity (M2) and stress from grain-filling stage to physiological maturity (M3). The water levels were maintained in the range of 35-50% field capacity in the stress treatments while above 75% in the control treatment. Harvest index and grain-filling rate were positively associated with grain yield under all water regimes while number of kernels per spike and aboveground biomass yield were correlated with grain yield under water stress conditions only. Path analysis revealed that grain-filling rate and grain-filling period had high positive direct effect on grain yield under continuous stress from tillering to crop maturity and well-watered conditions. Aboveground biomass and harvest index had positive direct effect on grain yield under stress treatment from flowering through crop maturity. Similarly, grain filling rate and harvest index had positive direct effect on yield while biomass yield and kernel number per spike had high indirect positive effect on grain yield through grain filling rate and harvest index under water stress from grain filling to crop maturity. Therefore, selection for higher grain filling rate and longer grain filling period under optimal moisture supply to severe stress environment whereas higher biomass yield, harvest index and kernels per spike are expected to improve the yield of durum wheat under moderate water stressed environments.

Key words: durum wheat; water stress; grain-filling rate.

RESUMEN

La disponibilidad de agua es una de las limitantes para la producción de trigo durum en muchas partes del mundo. El conocimiento de la relación entre aspectos fenotípicos y genotípicos de la producción y sus componentes es un paso importante para desarrollar criterios de selección en ambientes con estrés hídrico. Con el objetivo de conocer la utilidad de algunas variables agronómicas como indicadores del rendimiento de grano se evaluó 18 genotipos bajo condiciones de estrés hídrico inducido en tres etapas de crecimiento manteniendo un control positivo irrigado durante las estaciones de cultivo 2006/07. Los tratamientos de estrés hídrico fueron de la siembra a la madurez fisiológica (M1), de la floración a la madurez fisiológica (M2) y del llenado del grano a la madurez fisiológica (M3). .Los niveles de agua se mantuvieron en el rango de 35 a 50% de la capacidad de campo para los tratamientos de estrés hídrico y arriba del 75% para el control. El índice de cosecha y llenado de grano estuvo positivamente asociado con el rendimiento de grano en todos los tratamientos y el número de granos por espiga y la biomasa aérea estuvieron asociados con el rendimiento del grano en tratamientos con estrés hídrico. La tasa de llenado de grano y el período de llenado tuvieron un efecto positivo directo en el rendimiento en condiciones de estrés continuo de la siembra a la madurez, así como en condiciones de riego suficiente (control). La biomasa aérea y el índice de cosecha tuvieron un efecto positivo directo en el rendimiento en condiciones de estrés de la floración a la madurez. De manera similar, la tasa de llenado y el índice de cosecha tuvieron un efecto positivo directo en rendimiento, mientras que la biomasa y el número de granos por espiga tuvieron un efecto positivo indirecto en el rendimiento de grano en condiciones de estrés del llenado de grano a la madurez. Por lo tanto, la selección para mayor tasa de llenado de grano, períodos de llenado de grano más largos en condiciones de aporte óptimo de humedad a estrés severo en contraste con mayor biomasa, índice de cosecha y número de granos por espiga son los indicares para un mayor rendimiento del trigo durum en condiciones de estrés hídrico moderado.

Palabras clave: trigo durum; estrés hídrico; tasa de llenado de grano.

INTRODUCTION

Both bread wheat (*Triticum aestivum* L.) and durum wheat ***(****Triticum turgidum* L. *durum****)*** are widely cultivated in Ethiopia. The total area for both crops is about 1.685 million hectares with a corresponding production of 3.08 million tons annually (CSA, 2010). Durum wheat is an indigenous crop with a wide genetic diversity in the country (Hailu et al, 1991). It occupies 40% of the total wheat area and the country is one of the largest producers of durum wheat in sub-Saharan Africa (Efrem et al. 2000). However, the bulk of durum wheat is produced under rainfed condition, often in places where rainfall is infrequent in distribution and scarce during the grain-filling period. The random variations of rainfall from year to year and across locations in Ethiopia usually affect crop yield (Simane et al., 1993, Deselegn et al., 2001). Selection of wheat genotypes with better adaptation to water stress increases the productivity of rainfed wheat (Rajaram, 2001). Selection for yield under drought stress conditions is, however, complicated by low heritability and large genotype-environment interaction (van Oosterom et al, 1993). This interaction can occur as a consequence of differential responses by genotypes to yearly variation in quantity of rainfall or its distribution (van Ginkel et al., 1998) and thus, it limits the breeding efficiency (Ceccarelli et al., 2000). The efficiency of a breeding program, therefore, can be increased by selection for traits associated with performance under stress, which are less prone to show significant genotype x environment interaction (Gonzalez et al., 2007). Phenological and agronomic characteristics are generally attractive to breeders because they are easy and cheap to measure.

In environmental conditions that are characterized by exposing plant growth to drought developing increasingly during the late reproductive and grain-filling phases, the natural outcome of breeding for adaptation has been the selection for earliness (Loss et al., 1994). The duration of grain filling and the growth cycle also contribute greatly to wheat yield under these conditions (Simane et al., 1993, Gracia del Moral et al., 2003). Increase in crop biomass contributes to the improvement of cereal yield under water stress conditions. At grain filling stage, a proportion of this biomass is available to the grain development (Shakhatreh et al., 2001). It is also desirable that this proportion is high to obtain better yields and a higher harvest index (Siddique et al., 1989). Harvest index also depends on the availability of water during grain filling and the partitioning of carbohydrates that stored before anthesis (Richards et al., 2002).

For improvement in yield, study of yield contributing components in respect of their genetic mechanism is very important. Information regarding genotypic and phenotypic correlations between quantitatively inherited plant characters and their direct and indirect effects on grain yield as a result of varietal response proved to be a useful tool for increasing the yield per unit area through selection (Khan et al., 2010). However, there is little information that shows the relationship between grain yield and its various components of the Ethiopian durum wheat genotypes under different water stress conditions. This experiment was, therefore, conducted to determine the direct and indirect relationship between yield and different traits of durum wheat genotypes that have different origin under different water supply conditions.

MATERIALS AND METHODS

Plating materials and design

The study was conducted in a lathhouse at Sinana Agricultural Research Center (SARC) during the 2006/07 main season. It is located at 7° 7’N latitude, 40° 10’ E longitude and 2400 m.a.s.l altitude in Bale Zone of Oromia Region, Ethiopia. Eighteen durum wheat (*Triticum turgidum L. durum*) genotypes consisting landraces [B5-5B, S-17B, and WA-13], commercial cultivars [Asassa, Bekelcha, Boohai, Egersa, Foka, Gerardo, Ilani, Kilinto, Obsa, Oda, Quamy, Tob-66 and Yeror] and advanced lines from the breeding program [CDSS93Y107 and CD94523] were used for this study. Plants were grown in 21 cm diameter and 18 cm length plastic pots filled with a textural class of clay (49.7% clay, 27.3% silt and 23% sand). Each pot was filled with 4 kg uniformly air-dried soil (17.1% moisture). The field capacity and permanent wilting point of the soil were 47.8% and 11.5%, respectively. Pots were arranged in Randomized Complete Block Design (RCBD) in factorial combination of the eighteen genotypes and four water regimes with three replications. A total of 216 pots, 12 pots were assigned to each genotype. 2g N and 2 g P_2O_5 fertilizers were applied to each pot during planting and additional 0.5 g N was applied at the first tillering. Planting was done on August 10, 2006. Eight seeds were sown per pot and the seedlings were thinned to four at two leaf growth stages. Five hundred ml of water was added to each pot every other day for a period of a month until the plants reach four leaf growth stages.

Water Stress Treatment

Following the Zadock's scale (Zadoks et al., 1974), plants were subjected to water stress at different growth stages: stress continuously from tillering to physiological maturity (M1), stress from anthesis to physiological maturity (M2), and stress from grain-filling stage to physiological maturity (M3) and well-watered control (C) treatments. The water levels were maintained in the range of 35-50% field capacity in the stress treatments while above 75% in the control treatment. These water stress conditions are designed to simulate the environments that experience very low water supply after crop establishment in different parts of the country. During the stress period, plants were left without water for 12 days by withholding irrigation until early morning wilting is observed. Then pots were weighted and irrigated until the weight of every pot became equal to the weight of the predetermined water level. The amount of water depleted from pots was obtained by weighing pots every two to three days, and the loss in weight was restored by watering pots with the amount of water equal to the loss in weight.

Data Collection and Analysis

Data were collected for mature plant height (cm), days to heading (DH) (when spike completely emerged from the flag leaf ligule) and days to physiological maturity (DM) (when the entire plant turns to yellow). The length of vegetative period (VP) was calculated as days from sowing to anthesis (growth stage 65 according to Zadoks *et al*. (1974). Duration of grain filling period (GFP) was considered to be the days from anthesis to physiological maturity (growth stage 91). Grain-filling rate (GFR) was determined as the ratio of final dry grain yield (mg/plant) to the duration of grain-filling period. Data were also collected for number of kernels per spike, 100 kernel weight, spike length, air-dried aboveground biomass and grain yield per plant. Harvest index was determined as the proportion of grain yield to the overall aboveground biomass per plant.

Linear correlation and stepwise regression analyses were conducted to determine the association between grain yield and yield components and their relative contribution in predicting the grain yield of durum wheat genotypes under different water regimes, respectively. Path coefficient analysis was also performed to partition the correlation coefficient into direct and indirect effects of component character on grain yield as described by Dewey and Lu (1959). Sets of simultaneous equations were used to calculate the direct and indirect effects of traits based on the crop ontogeny for the following characters using a method described by Gracia del Moral et al (2003) :
(1) duration of vegetative period (VP),
(2) duration of grain filling period (GFP),
(3) biomass yield (BY),
(4) harvest index (HI),
(5) number of kernel per spike (KS),
(6) kernel weight (KW) ,
(7) grain-filling rate (GFR) and
(8) grain yield (GY).

$r_{58}= P_{58} + r_{57}P_{78} + r_{56}P_{68}$
$r_{78}= r_{57}P_{58} + P_{78} + r_{76}P_{68}$
$r_{68}= r_{56}P_{58} +r_{76}P_{78} +P_{68}$

$r_{56}=P_{56} + r_{52}P_{26} + r_{57}P_{76}$
$r_{26}=r_{52}P_{56} + P_{26} + r_{27}P_{76}$
$r_{76}= r_{57}P_{56} +r_{27}P_{26} +P_{76}$

$r_{17}=P_{17} +r_{15}P_{57} +r_{12}P_{27}$
$r_{57}=r_{15}P_{17} +P_{57} + r_{52}P_{27}$
$r_{27}=r_{13}P_{17} + r_{52}P_{57} + P_{27}$

$r_{12}= P_{12} + r_{15}P_{52}$
$r_{52}= r_{15}P_{12} + P_{52}$

In equation:
$r_{12}= P_{12} + r_{15}P_{52},$
$P_{12} =$ direct effect of character 1 on 2 (path coefficient)
$r_{15}P_{52}$ = indirect effect of character 1 on 2 via 5. Similar definitions apply to other equations. The causal system assumed was based on the ontogeny of the cereal plant, and it is shown in Figure 1.

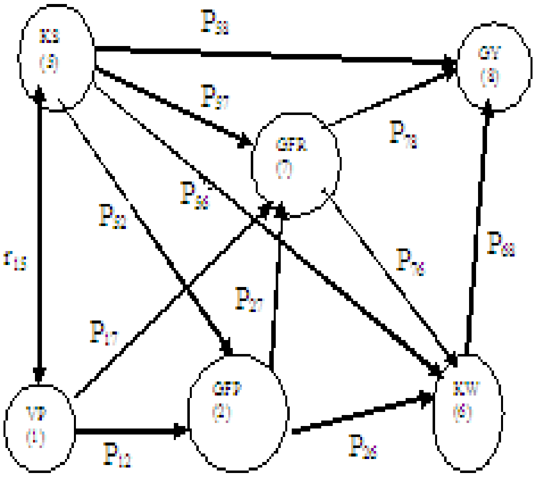

Figure 1. Path coefficient diagrams showing the relationships among duration of vegetative period (VP), duration of grain-filing period (GFP), numbers of kernels per spike (KS), hundred kernel weight (KW), grain-filling rate (GFR) and grain yield (GY). The single headed arrow indicates path coefficients and the double-headed arrow indicates simple correlation coefficient.

RESULTS AND DISCUSSION

Correlation studies

The Pearson correlation coefficients between grain yield and the major yield components under different water stress treatments are shown in Table 1. Although the correlation coefficients were non-significant, days to heading, days to maturity and vegetative period were negatively correlated with grain yield under all water treatments. The negative association between grain yield and days to heading and maturity indicates the importance of earliness under water deficit condition (Gonzalez et al., 2007, Solomon et al., 2003a). Slafer et al. (2005) stated that selection for earliness has two important consequences on the physiology of cereal yields: first, it increases the likelihood to escape drought, and second, it improves the partitioning of the total water used by the crop actually absorbed and transpired after anthesis.

Grain yield showed a positive significant correlation with plant height under water stress from tillering to crop maturity, which suggests that under this condition the yield depends on the achievement of better vegetative development and larger stem reserve mobilization (Khan et al., 2010). However, the correlations were negative and non significant under late stress and well-watered conditions because of the fact that stress were induced when plant approached to its maximum growth. Spike length showed positive but non-significant correlation with grain yield across all water regimes. Number of kernel per spike and aboveground biomass were positively significantly correlated with grain yield under all water stress treatments while harvest index and grain-filling rate were positively associated with grain yield under all the water regimes (Table 2). Several authors also reported the positive correlations between grain yield and spike length (Villegas et al., 2007), grain yield and kernel weight (Simane et al., 1993; Leilah et al., 2005) and number of kernels per spike and grain yield (Simane et al., 1993; Gracia del Moral et al., 2003; Slafer et al., 2005). Such positive relationship between number of kernels and grain yield seems to be derived from the fact that grain yield in wheat is frequently sink limited (Slafer et al., 2005), and for this reason, the number of kernels per spike has been reported as a promising trait in increasing wheat grain yield, especially under drought conditions (Simane, et al., 1993; Dencic et al., 2000; Slafer et al., 2005).

Positive and significant associations were noted between aboveground biomass and grain yield and between harvest index and grain yield per plant under all water stress treatments. This result agrees with the previous findings of several researchers (Simane et al., 1993; Elias, 2003; Solomon et al., 2003b; Misra et al., 2006). The significant correlation between grain yield and biomass is expected under water deficit conditions because assimilates are available to the grain development through dry matter re-allocation (Shakhatreh, et al., 2001).

Grain yield under continuous stress from tillering to crop maturity (M1) was not strongly correlated with the grain yield in the M2 ($r = 0.37$), M3 ($r = 0.09$) and C ($r = 0.12$) treatments. On the other hand, a positive and significant relationship ($r = 0.69$; $p < 0.01$) was noticed between the grain yield of mild-stressed (M3) with that of the grain yield of the control treatment. The lack of correlation between the grain yield under continuous stress from tillering up to crop maturity with that of the grain yield recorded under late-season stress and well-watered treatments indicated that specific adaptation strategy is employed by studied genotypes. This result suggested that different breeding strategy will be followed for durum wheat improvement under severe water stress, mild- stressed and non-stressed environmental conditions. Ceccarelli *et al.* (1987) and Ceccarelli and Grando (1991) indicated that progress in yield and adaptation in drought-affected environments can be achieved only by selecting genotypes under prevailing conditions in the target environments. On the other hand, a positive and significant relationship noticed between the grain yield of late-stress treatments with that of the grain yield of the control treatment indicates the possibility of selecting superior genotypes under favorable condition that could give relatively high yield under terminal stressed environments. This supports the ideas of van Ginkel *et al*. (1998)], Araus *et al*. (2002) and Richards (2000) and that selection for yield under near optimum condition would be acceptable method for selecting crops grown under mild-moisture stress conditions.

Path coefficient and stepwise regression

The phenotypic correlation coefficients and the relative contribution (partial and cumulative R2) of selected yield components in predicting the yield of durum wheat genotypes under different water stress treatments are given in Tables 2, 3, 4 and 5. Results of path analysis at phenotypic level in the M1 treatment showed that grain-filling rate (0.818) and grain-filling period (0.227) had high positive direct effects on grain yield per plant (Table 2). The highest positive indirect effect on grain yield was observed from number of kernels per spike via grain-filling rate (0.701) followed by kernel weight and biomass via grain-filling rate. Similarly, the genotypic path indicated that grain-filling rate followed by grain-filling period had maximum positive direct effect on grain yield (Table 2). Kernel number per spike, biomass yield and harvest index had maximum positive indirect effect on grain yield via grain-filling rate. This result shows that selection of genotypes with high grain-filling rate and relatively longer grain-filling period would increase grain yield in durum wheat under limited water supply condition from tillering to crop maturity. Grain filling period is an important trait in wheat that ultimately affects the overall grain yield by increasing seed weight and used as selection criteria in wheat breeding program (Masood et al., 2005). However, in terminal water-stressed environment, it would be better to select for high grain-filling rate rather than longer grain-filling period since the latter is more subjected to the influence of environmental conditions such as high temperature that could prematurely stop grain growth and accelerate physiological maturity (Gonzalez et al., 2007).

Maximum positive phenotypic direct effect on grain yield was exerted by aboveground biomass (0.438) followed by harvest index (0.371) in the M2 treatment (Table 3). However, grain filling rate and kernel number per spike exerted the maximum positive indirect effect on grain yield per plant via biomass yield and HI. Genotypic path also indicated that biomass yield followed by harvest index and grain-filling rate had maximum positive direct effect on grain yield per plant. Maximum positive indirect effects were also exerted by grain-filling rate and number of kernel per spike via biomass and harvest index (Table 3). These traits are also showed positive relationship with grain yield and thus direct selection for higher biomass and harvest index would be helpful to increase yield under water stress that started from flowering periods. Reynolds *et al*. (2007) have also established the importance of total biomass for the yield increase in wheat especially under drought stress conditions. A higher biomass production under drought stress conditions, particularly during grain filling period, would have an advantage because the translocation of assimilates from the vegetative parts of a plant to seeds contribute significantly to yield (Royo et al., 2000).

Table 1. Pearson correlation coefficients of grain yield with different pheno-agronomic characters of durum wheat genotypes grown under water stress induced at three growth stages and well-watered condition.

Characters	**M1^a**	**M2**	**M3**	**C**
Days to heading (DH)	-0.359	-0.399	-0.209	-0.252
Days to maturity (DM)	-0.402	-0.316	-0.054	-0.083
Vegetative growth period (VP)	-0.446	-0.348	-0.224	-0.153
Plant height (PH)	0.362*	-0.218	-0.252	-0.430
Spike length (SL)	0.021	0.406	0.010	0.178
No of spikelet per spike (SPS)	0.162	0.093	-0.121	-0.284
No. of kernels per spike (KS)	0.896**	0.510*	0.560**	0.180
No. of kernels per spikelet (KPSK)	0.603**	0.419	0.502**	0.526*
Hundred kernel weight (KW)	0.756**	0.034	0.097	0.243
Harvest index (HI)	0.578**	0.789**	0.717**	0.770***
Total aboveground biomass(BY)	0.787***	0.800**	0.817***	0.452
Grain filling period (GFP)	0.296	0.210	0.101	0.216
Grain filling rate (GFR)	0.964***	0.922***	0.948***	0.851**

*, ** and *** significant at $P < 0.05$, 0.01 and 0.001, respectively.

Table 2. Phenotypic and genotypic path coefficient showing direct and indirect effect of seven characters on grain yield of durum wheat genotypes grown under water deficit treatment induced from tillering to crop maturity (M1).

Trait	Direct effect	Indirect effect via							Total indirect effect	Total effect
		VP^b	GFP	BY	HI	KS	KW	GFR		
					Phenotypic path					
VP	0.015		-0.175	-0.043	0.002	-0.029	-0.011	-0.205	-0.461	-0.446
GFP	0.227	-0.011		0.028	0.002	0.015	0.008	0.027	0.069	0.296
BY	0.073	-0.009	0.086		-0.001	0.043	0.013	0.582	0.714	0.787
HI	0.042	0.001	0.014	-0.001		0.029	0.007	0.486	0.536	0.578
KS	0.060	-0.007	0.058	0.052	0.020		0.012	0.701	0.836	0.896
KW	0.019	-0.008	0.094	0.048	0.015	0.037		0.551	0.737	0.756
GFR	0.818	-0.004	0.008	0.052	0.025	0.052	0.013		0.146	0.964
					Genotypic path					
VP	0.016		-0.160	-0.052	0.000	-0.025	-0.014	-0.217	-0.468	-0.452
GFP	0.207	-0.013		0.032	0.004	0.013	0.011	0.060	0.107	0.314
BY	0.086	-0.010	0.078		0.002	0.041	0.016	0.603	0.730	0.816
HI	0.043	0.000	0.018	0.005		0.026	0.009	0.510	0.568	0.611
KS	0.054	-0.008	0.051	0.065	0.021		0.014	0.698	0.841	0.895
KW	0.024	-0.010	0.094	0.057	0.016	0.033		0.528	0.718	0.742
GFR	0.805	-0.004	0.015	0.064	0.027	0.047	0.016		0.165	0.970

Phenotypic residual effect = 0.0018 and genotypic residual effect =0.0006, ^{b}VP = Vegetative period, GFP = Grain-filling period, BY = Aboveground biomass yield, HI Harvest index, KS = Number of kernels per spike, KW = Hundred kernel weight and GFR = Grain filing rate

Table 3. Phenotypic and genotypic path coefficients showing direct and indirect effect of six characters on grain yield of durum wheat genotypes grown under water stress treatment induced from anthesis to crop maturity (M2)

Trait	Direct effect	Indirect effect via						Total indirect effect	Total effect
		VP	GFP	BY	HI	KS	GFR		
					Phenotypic path				
VP	0.051		-0.090	-0.185	-0.066	-0.052	-0.006	-0.399	-0.348
GFP	0.110	-0.041		0.120	0.040	0.037	-0.056	0.100	0.210
BY	0.438	-0.021	0.030		0.098	0.033	0.222	0.362	0.800
HI	0.371	-0.009	0.012	0.116		0.021	0.278	0.418	0.789
KS	0.066	-0.039	0.061	0.216	0.120		0.086	0.444	0.510
GFR	0.346	-0.001	-0.018	0.281	0.298	0.016		0.576	0.922
					Genotypic path				
VP	0.056		-0.068	-0.196	-0.070	-0.049	-0.004	-0.443	-0.387
GFP	0.085	-0.045		0.126	0.043	0.035	-0.043	0.076	0.161
BY	0.473	-0.023	0.023		0.108	0.031	0.170	-0.141	0.332
HI	0.440	-0.009	0.008	0.116		0.020	0.212	-0.084	0.356
KS	0.064	-0.043	0.047	0.229	0.139		0.066	0.417	0.481
GFR	0.269	-0.001	-0.014	0.300	0.348	0.016		0.381	0.650

Phenotypic residual = 0.0004 and genotypic residual = 0.0058 ^{b} Symbols are the same as shown in Table 3

Grain-filling rate followed by biomass yield and grain-filling period exerted the highest positive direct effect on grain yield per plant in the M3 treatment (Table 4). While the highest positive indirect effect was exerted on grain yield by aboveground biomass and harvest index via grain-filling rate (0.513).

Kernel number per spike also exerted high indirect effect on grain yield through grain filling rate (0.311) and HI (0.136). The highest genotypic direct effect on grain yield was observed from grain-filling rate followed by biomass and harvest index. Grain-filling rate and number of kernel per spike had relatively higher genotypic indirect effect on grain yield via harvest index as compared to the rest of the traits considered (Table 4).

Similarly, grain filling rate (0.672) and grain filling period (0.346) had maximum positive phenotypic direct effect on grain yield of wheat under well-watered condition (Table 5). HI followed by aboveground biomass also exerted maximum positive indirect effects on grain yield through grain-filling rate. On the other hand, genotypic path indicated that harvest index followed by grain-filling rate, biomass and grain filling period had the maximum direct effect on grain yield (Table 5). As the direct effect as well as the correlation is positive, therefore, direct selection for higher grain filling rate, higher harvest index, biomass yield and longer grain filling period is recommended for obtaining higher yield under moderate water supply environments. The total biomass production and the proportion of the biomass allocated to the grains (HI) determine the final grain yield in wheat (Royo et al., 2000). The grain weight is also determined by the rate at which the grain accumulates the dry matter and the duration over which it occurs (Villegas et al., 2005).

Phenotypic residual= 0.0040 and genotypic residual= 0.0013[b] Symbols are the same as shown in Table 3

Stepwise regression analysis revealed that 99.2% of the total grain yield variation was explained by grain-filling rate (92.2%) and grain-filling period (7%) under continuous water stress from tillering to crop maturity (Table 6). As shown from the same table, grain-filling rate together with grain filling period explained more than 95% of the grain yield variation of the tested genotypes across water regimes. This shows that these two traits are the major yield determining parameters of durum wheat across different water supply environments, and can be used as suitable selection criteria for improving the grain yield of durum wheat in different water supply environments. The contribution of grain-filling period to the total grain yield variation increased relatively as the moisture availability increased. Therefore, selection of genotypes with longer grain-filling duration would increase grain yield under mild-water stressed conditions. The positive effect of long grain-filling period on grain yield has been previously reported (Simane et al., 1993; Royo et al., 2001; Villegas et al., 2005). Longer grain-filling period allows high accumulation of assimilates into the grain, which results in heavier kernels and higher yields. Nevertheless, longer grain-filling period should increase grain yield, provided that the later stages of grain filling do not occur under terminal drought stress (Gebeyehu et al., 1982).

Table 4. Phenotypic and genotypic path coefficients showing direct and indirect effect of six characters on grain yield of durum wheat genotypes grown under water stress treatment induced from grain filling stage to crop maturity (M3)

Trait	Direct effect	Indirect effect via						Total indirect effect	Total effect
		VP	GFP	BY	HI	KS	GFR		
				Phenotypic path					
VP	-0.022		-0.139	-0.059	-0.018	0.013	0.001	-0.202	-0.224
GFP	0.200	0.015		0.053	-0.007	-0.010	-0.150	-0.099	0.101
BY	0.218	0.006	0.049		0.038	-0.007	0.513	0.599	0.817
HI	0.187	0.002	-0.007	0.044		-0.020	0.512	0.530	0.717
KS	-0.027	0.010	0.073	0.057	0.136		0.311	0.587	0.560
GFR	0.711	0.000	-0.042	0.157	0.134	-0.012		0.237	0.948
				Genotypic path					
VP	-0.038		-0.119	-0.079	-0.023	0.021	0.006	-0.156	-0.194
GFP	0.172	0.026		0.069	-0.008	-0.017	-0.137	-0.265	-0.093
BY	0.280	0.011	0.042		0.049	-0.012	0.450	0.249	0.529
HI	0.247	0.004	-0.006	0.056		-0.033	0.448	0.218	0.465
KS	-0.044	0.019	0.066	0.075	0.186		0.278	0.649	0.605
GFR	0.624	0.000	-0.038	0.202	0.177	-0.019		-0.302	0.322

Phenotypic residual = 0.0027 and genotypic residual= 0.0020 [b] Symbols are the same as shown in Table 3

Table 5. Phenotypic and genotypic path coefficients showing direct and indirect effect of six characters on grain yield of durum wheat genotypes grown under well-watered condition (C)

Trait	Direct effect	Indirect effect via						Total indirect effect	Total effect
		VP	GFP	BY	HI	KS	GFR		
Phenotypic path									
VP	-0.023		-0.275	0.008	-0.048	-0.004	0.189	-0.130	-0.153
GFP	0.346	0.018		-0.023	0.087	0.004	-0.216	-0.130	0.216
BY	0.242	-0.001	-0.033		-0.064	-0.001	0.309	0.210	0.452
HI	0.307	0.004	0.099	-0.050		0.002	0.408	0.463	0.770
KS	0.008	0.012	0.152	-0.041	0.083		-0.034	0.172	0.180
GFR	0.672	-0.007	-0.111	0.111	0.186	0.000		0.179	0.851
Genotypic path									
VP	-0.020		-0.196	0.010	-0.074	-0.009	0.134	-0.115	-0.135
GFP	0.245	0.016		-0.036	0.139	0.008	-0.152	-0.286	-0.041
BY	0.365	-0.001	-0.024		-0.102	-0.003	0.219	-0.275	0.090
HI	0.482	0.003	0.071	-0.078		0.005	0.287	-0.197	0.285
KS	0.019	0.010	0.104	-0.064	0.128		-0.025	0.124	0.143
GFR	0.473	-0.006	-0.079	0.170	0.292	-0.001		-0.091	0.382

Table 6. Stepwise regression showing the relative contribution (partial and model R^2) in predicting grain yield per plant of durum wheat genotypes grown under water stress induced at three growth stages.

Character included	Partial R^2	Model R^2	SE of estimate	Probability
M1[a]				
Grain-filling rate (GFR)	0.922	0.920	0.070	$p < 0.001$
Grain-filling period (GFP)	0.070	0.990	0.023	$p < 0.001$
Kernel ash content (m_aG_a)	0.001	0.991	0.022	$P < 0.01$
Final Equation	Grain yield (g plant^{-1}) = -0.730 + 0.046 GFR +0.016GFP			
M2				
Grain-filling rate (GFR)	0.877	0.874	0.156	$p < 0.05$
Grain-filling period (GFP)	0.113	0.990	0.049	$p < 0.01$
Hundred kernel weight	0.002	0.992	0.046	$P < 0.001$
Final equation	Grain yield (g plant^{-1}) = -1.648 + 0.044 GFR +0.038GFP			
M3				
Grain-filling rate (GFR)	0.843	0.838	0.274	$p < 0.01$
Grain-filling period (GFP)	0.106	0.949	0.159	$p < 0.01$
Biomass yield	0.005	0.987	0.121	$P < 0.01$
Final equation	Grain yield (g plant^{-1})=-2.283+ 0.046GFR + 0.051GFP			
C				
Grain-filling rate (GFR)	0.858	0.855	0.207	$p < 0.01$
Grain-filling period (GFP)	0.136	0.985	0.074	$p < 0.01$
Hundred kernel weight	0.001	0.990	0.060	$P <0.01$
Final equation	Grain yield (g plant^{-1})= - 2.39+ 0.047GFR+ 0.045GFP			
Across all moisture regimes				
Grain-filling rate (GFR)	0.929	0.929	0.232	$p < 0.01$
Grain-filling period (GFP)	0.059	0.988	0.097	$p < 0.01$
Water use efficiency (WUE_g)	0.001	0.989	0.093	$P < 0.01$
Final equation	Grain yield (g plant^{-1})= -1.904 + 0.047GFR+ 0.041GFP			

CONCLUSION

Durum wheat yield under continuous water stress from tillering through crop maturity and well-watered conditions appears to be determined by grain-filling rate and grain-filling period while biomass yield, harvest index and grain-filling rate seems to be the most important factors in determining grain yield under late-water stress conditions. Therefore, selection for high grain filling rate and longer grain filling period under optimal moisture supply to severe water stress environments and higher biomass yield, harvest index and large kernels per spike are expected to improve the yield of durum wheat under moderate water stress environments. These traits, thus, can be used as indirect selection criteria for higher grain yield of durum wheat under different water supply environments.

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