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Trade-offs between grain number, grain weight and fruiting efficiency of different bread wheat genotypes in response to anthesis drought stress

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Abstract: Cereal crops in Morocco are mainly cultivated under rainfed conditions of dryland regions. Under these conditions, they are mostly exposed to drought stress that affects different yield components. We studied the effect of anthesis drought stress on the relationships among the components of grain number (GN), thousand grains weight (TGW), fruiting efficiency (FE) and yield. And we examined fruiting efficiency (FE= grains set per g of spike dry weight at anthesis) as promising trait for further increasing yield without compromising yield components. Greenhouse experiments were conducted on 2019/2020, 2020/2021 and 2021/2022 cropping seasons. Two contrasting water regimes, irrigated and stressed treatments at anthesis growth stage were assessed. Results showed that anthesis drought stress affects negatively all components studied. Substantial decrease of 10%, 16%, 9% and 34% were recorded for GN, TGW, FE, and yield, respectively, under water stress compared to irrigated treatments. Two genotypes, namely 15/42 and Achtar, were found to be the most adapted to both stressed and irrigated conditions. Under stressed conditions yield becomes less correlated with GN (r = 0.36) and FE (r = 0.37) and more correlated with TGW (r = 0.56*). GN becomes less correlated with FE (r = 0.02) and TGW (r = -0.14). While, FE becomes more correlated with TGW (r = 0.73*). To the extent of this study, FE was found as promising selection criterion under stress conditions without compromising TGW component.

Keywords: wheat; water stress; anthesis; fruiting efficiency; grain number; thousand grain weight.
Abbreviations: GN_Grain number; TGW_thousand grains weight; FE_fruiting efficiency; ns_no-significant; p_P_{value}; r, coefficient of correlation.

Introduction

Water is the main factor limiting crop production of arid and semi-arid regions. The amount of rain and its distribution, affect the crop growth and productivity (Alqudah et al., 2011; Khakwani et al., 2012). Previews studies reported several effects of anthesis drought stress on metabolic, morpho-physiologic, and agronomic traits of wheat (Qaseem et al., 2019; Fan et al., 2022; Ru et al., 2022). However, the amount of these effects varied with genotypes and across environments (Elía et al., 2016; Ferrante et al., 2017; Terrile et al., 2017; Pretini et al., 2020).
Concerning agronomic traits; number of grains per unit area and average grain weight are the main components of yield. The grains number is determined during flowering time (Alqudah et al., 2011; Liu et al., 2015). It recognizes a decrease under water stress due to pollen abortion in the young microscope stage of pollen development, and spikelets and florets abortion in the floral development stage (Ji et al., 2010; Mahrookashani et al., 2017; Slafer et al., 2023). Other causes of grain loss may be related to reduced spike dry weight at anthesis (SDWa) (Terrile et al., 2017; Rivera-Amado et al., 2019; Pretini et al., 2021), or reduced duration of the late reproductive phase (Gonzalez-Navarro et al., 2016). Similarly, grain size started its construction just before anthesis which make it vulnerable to anthesis drought stress and to the lack of sufficient assimilate to fill the grain during grain filling growth stage (Ji et al., 2010; Weldearegay et al., 2012). However, longer phase from terminal spikelet to anthesis, results in later grain filling conditions and consequently smaller grains (Gonzalez-Navarro et al., 2016).
One of the alternatives for further increasing yield is increasing fruiting efficiency (grains set per unit of spike dry weight at anthesis). Increasing FE may be achieved by an accelerated rate of floret development, an enhanced partitioning of spike assimilates, a long stem elongation duration, or by reducing the abortion of grains (Gonzalez-Navarro et al., 2016; Terrile et al., 2017; Slafer et al., 2023). The fruiting efficiency has been used recently in breeding program as a promising trait to enhance grain number and therefore grain yield of wheat crop (Ferrante et al., 2015;

Table 1. Year of release and the pedigree of the genotypes studied.

Genotypes	Year of release	Pedigree
15/42	2020	BT1735/ACHTAR//HUBARA-8
44/10/17	-	MINO
132-88	-	UP2338*2/KKTS*2//YANAC
132-93	-	BAJ #1/KISKADEE #1
Achtar	1988	HORK/YMH//KAL/BB
Amal	1993	Bow's'/Buc's'

Table 2. Means of treatments, mean squares and significance of ANOVA.

	GN/S	TGW (g)	FE (grains.g_{spike}^{-1})	Yield (g/pot)
Mean irrigated treatments	25.14 ±0.83	29.19 ±0.88	35.22 ±1.53	9.42 ±0.34
Mean stressed treatments	22.59 ±0.90	24.40 ±1.35	31.91 ±1.35	6.26 ±0.36
Source of variation (mean square $^{ns, *, **, ***}$)				
Water regime (WR)	176.46^{**}	619.44^{**}	296.08^{ns}	269.611^{***}
Genotype (G)	121.44^{***}	65.42^{ns}	184.82^{ns}	3.885^{ns}
Year (Y)	4734.07^{***}	1353.48^{***}	3400.35^{***}	129.961^{***}
WR x G	12.64^{ns}	35.84^{ns}	29.82^{ns}	2.438^{ns}
WR x Y	84.79^{*}	390.31^{**}	1052.22^{***}	34.336^{**}
G x Y	78.33^{**}	72.141^{ns}	140.36^{ns}	7.978^{ns}
WR x G x Y	18.76^{ns}	9.32^{ns}	82.36^{ns}	4.356^{ns}

± standard error. ns: no-significant; *: significant at p<0.05; **: highly significant at p<0.01; ***: very highly significant at p<0.001.

Joudi et al., 2016; Gerard et al., 2019; Curin et al., 2021; Pretini et al., 2021). The eco-physiological model defined above encompasses the grain number as the result of the spike dry weight and fruiting efficiency at anthesis (Pretini et al., 2021). However, the trade-off recorded between FE and grain weight may limit its usefulness (Gonzalez-Navarro et al., 2016; Terrile et al., 2017; Slafer et al., 2023). In response to that, the objectives of this study were to identify the best-performant genotypes among six bread wheat genotypes exposed to anthesis drought stress, to underly the resulting relationship among yield, grain number, grain weight and fruiting efficiency, and to discuss the resulting trade-offs between these traits.

Results

Effect of anthesis drought stress on grain number, grain weight, fruiting efficiency and yield

Analysis of variance revealed significant difference (p<0.05) between water regimes (WR) for GN/S, TGW and yield. Average decrease of 10%, 16%, 9%, 34% were observed for GN, TGW, FE and yield, respectively, under water stress compared to control treatment (Table 2). Highly significant difference (p<0.001) between genotypes was recorded for NG/S. In fact, all genotypes recorded substantial decrease due to water stress in GN/S, TGW, FE and yield. However, 15/42 and Achtar genotypes recorded small amount of decrease between water regimes for GN/S and FE components. Amal variety recorded the same value of TGW (25 g) under both water regimes. And the three genotypes, Amal, Achtar and 15/42 recorded small amount of decrease in yield between both water regimes (Fig. 1).

The range of variation in GN/S among genotypes oscillated between 20 and 29 grains under irrigated regimes (9 grains of difference), while this range lowered to 6 grains of difference when it is exposed to stress (Fig. 1a). Likewise, TGW showed a range of 9 g of difference between genotypes (from 26 to 35 g) when it was irrigated, while this range was lowered to 3 g when it was exposed to water stress (Fig. 1b). Similarly, FE ranged between 28 and 41 (13 grains/$g._{spike}$ of difference) when it was irrigated, while this range was lowered to 7 grains/$g._{spike}$ (from 29 to 36) when it was subjected to water stress (Fig. 1c). Finally, grain yield recorded a range from 9 to 11 g/pot when it was irrigated, while it ranges around 6 g/pot when it was stressed (Fig. 1d).

Genotypes ranking under stressed and irrigated environments

The results of the centered scatter plot revealed that the six genotypes studied varied noticeably in reaction to stressed or irrigated environment for each trait. 15/42 and Achtar genotypes showed the best performance under stressed environments for grain number component (GN/S) (Fig. 2a). For thousand-grain weight (TGW), all genotypes except 132-93 performed better in stressed environment (Fig. 2b). Whereas, for the fruiting efficiency trait (FE), 132-93, 15/42, and Achtar genotypes showed the best performance under stressed conditions (Fig. 2c). Finally, for grain yield, 15/42, Amal, and Achtar genotypes performed better in stressed environment (Fig. 2d).

Trade-offs: grain number, grain weight, fruiting efficiency and yield

As shown in Table 3, Grain number (GN) recorded significant and positive correlation with FE (r = 0.48*) under irrigated conditions. This trend was changed under stressed conditions by reducing the positive correlation to r = 0.02. On the other side, significant negative correlation between GN and TGW (r = - 0.66*) was recorded under irrigated conditions. While under stressed conditions, this negative correlation becomes much lower (r = - 0.14). Additionally, FE recorded a negative correlation with TGW (r = - 0.11) under irrigated conditions. This trend was changed under stressed conditions by favoriting the positive correlation between FE and TGW (r = 0.73*). Finally, yield recorded significant (<0.001) and positive correlation with GN (r = 0.76*) and FE (r = 0.61*), and significant and negative correlation with TGW (r = - 0.50*) under irrigated conditions. While under stressed conditions it records less positive correlation with

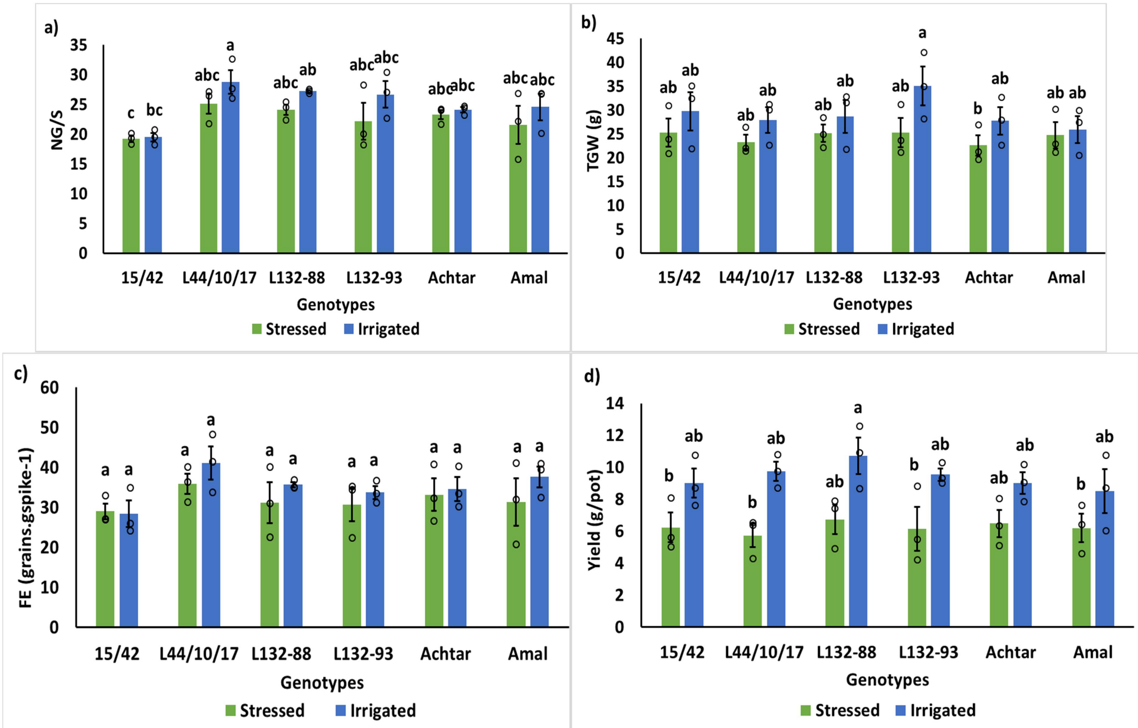

Fig 1. Means of genotypes under stressed and irrigated treatments for a) grain number per spike (GN/S); b) thousand-grain weight (TGW); c) fruiting efficiency (FE); and d) yield. Different small letters indicate significant difference according to Tukey's test.

Table 3. Pearson's correlation coefficients of different traits under irrigated (above) and stressed (below) conditions

Correlations		Irrigated			
	-	NG/S	TGW	FE	Yield
Stressed	NG/S	-	-0.66*	0.48*	0.76*
	TGW	-0.14	-	-0.11	-0.50*
	FE	0.02	0.73*	-	0.61*
	Yield	0.36	0.56*	0.37	-

*: significant correlation at p<0.05.

GN (r = 0.36) and FE (r = 0.37) and high positive correlation with TGW (r = 0.56*).

Discussion

The present study assessed the effect of water stress at anthesis growth stage on grain number per spike (GN/S), thousand grain weight (TGW), fruiting efficiency (FE) and yield traits. The resulting trade-offs between these traits were discussed.

Water stress applied at anthesis, acts as an indirect method of thinning the grains, it caused substantial decrease in GN/S (10%), TGW (16%), FE (9%) and yield (34%) (Table 2). Reduced grain number under water stress was estimated between 20 to 60% (Jatoi et al., 2011; Mahrookashani et al., 2017; Qaseem et al., 2019). This decrease was related to ovarian abortion or pollen sterility (Alqudah et al., 2011; Mahrookashani et al., 2017). In our study the tolerant varieties in this component, were 15/42 and Achtar genotypes, they maintained a lower decrease and they are those adapted to stressed environments (Figs. 1a and 2a). Likewise, anthesis water stress caused a decrease in TGW. The estimated decrease ranges between 10% and 30% (Jatoi et al., 2011; Mahrookashani et al., 2017). Amal variety was less affected by this stress and was the most adapted to stressed environments for this component (Figs. 1b and 2b).

In fact, anthesis drought stress in some cases may led to less reduction in TGW, which could be due to less formed grain numbers which conduct to heavier grains (Weldearegay et al., 2012). Similarly, FE recorded substantial decrease under water stress. 15/42 and Achtar genotypes maintained less reduction and are well positioned on the stressed environment (Figs. 1c and 2c). The FE is the final result of floret development rate and the proportion of kernel formed per fertile floret per unit of spike dry weight (Slafer et al., 2015; Elía et al., 2016; Garcia et al., 2019). In fact, higher persistence of floret primordia, and/or a reduced level of grain abortion characterize the efficient genotypes (Slafer et al., 2015; Elía et al., 2016; Garcia et al., 2019). Also, Amal, Achtar and 15/42 genotypes recorded the lowest decrease in grain yield, which reflect their ability to resist water stress (Fig. 1d). This result is in line with the centered environment biplot result, which ranked these three genotypes as the best performant genotypes to stressed environment (Fig. 2d). The recorded decrease in grain yield under anthesis drought stress was previously reported by several studies on the wheat crop (Khakwani et al., 2012; Weldearegay et al., 2012). And it was estimated at 40 to 50% of grain yield loss (Mahrookashani et al., 2017; Qaseem et al., 2019).

The strong positive correlation between GN and FE (r = 0.48*) under irrigated conditions, indicates a great

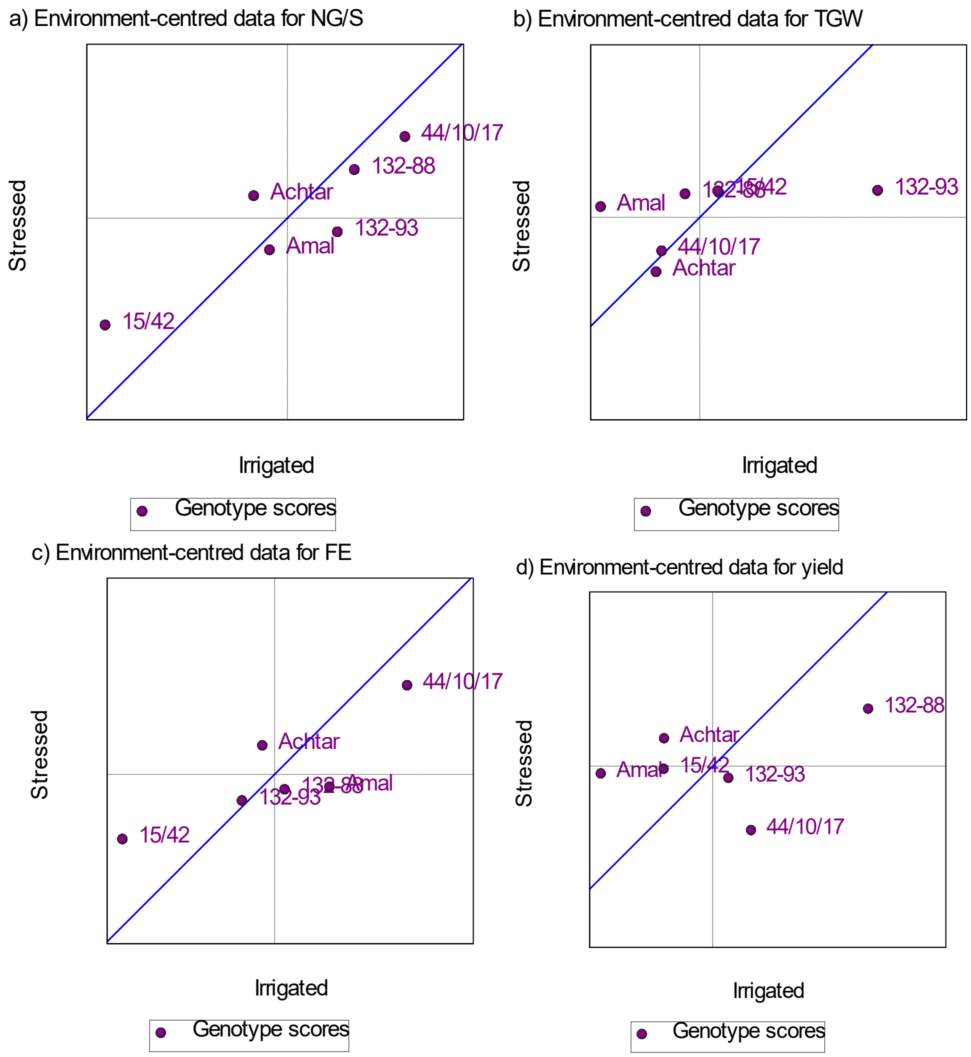

Fig 2. Genotypes ranking according to their performance in irrigated or stressed environment for a) grain number per spike (GN/S), b) thousand-grain weight (TGW), c) fruiting efficiency (FE), and d) yield.

contribution of GN to FE (Table 3). In fact, the positive relationship between FE and GN in normal conditions makes FE as a promising trait for further increasing GN (Rivera-Amado et al., 2019; Zhang et al., 2019; Pretini et al., 2021; Sierra-Gonzalez et al., 2021). However, this relationship was reduced (r = 0.02) by water stress (Table 3), which reduces the potential contribution of GN to FE. While, the strong negative correlation between GN and TGW (r = -0.66*) under optimal conditions reflects the great trade-off between these two components (Table 3). In fact, the normal trend of the relationship between GN and TGW is negative (Gonzalez-Navarro et al., 2016; Terrile et al., 2017; Sierra-Gonzalez et al., 2021). Because of germplasm that can maintain high GN is not able to maintain high TGW (Ji et al., 2010). Under stressed conditions, this negative correlation becomes much lower (r = -0.14) (Table 3), indicating that at this stress level, TGW was not limited by the sink capacity but by the compensation effect between GN and TGW. Similarly, FE recorded a negative correlation with TGW (r = -0.11) under optimal conditions, which indicate the great trade-off between FE and TGW (Table 3). Thus, genotypes with high fruiting efficiency will have smaller fertile florets or smaller grains (García et al., 2014; Ferrante et al., 2015; Slafer et al., 2015; Gonzalez-Navarro et al., 2016; Rivera-Amado et al., 2019). This trend was changed under stressed conditions by favoring the positive correlation between FE and TGW (r = 0.73*) (Table 3).

The positive correlation between GN and FE and the recorded trade-offs between TGW and GN and between TGW and FE under optimal conditions (Table 3), reflect that any increase in GN and subsequently in FE could be at the expense of TGW. In fact, the negative correlation between TGW and FE components could be caused by different processes; the most reported one is that the increase in FE would increase the proportion of grains of smaller potential size, which represents the grains from the distal position, without necessarily reducing the potential size of grains already existing under low FE situations (Ferrante et al., 2015; Terrile et al., 2017; Garcia et al., 2019). And this negative correlation was explained by the reduced demand of individual florets to develop normally, the final size of the fertile floret will be smaller by increasing FE (the same amount of resources to satisfy normal growth, by smaller florets) (Slafer et al., 2015). Consequently, the negative correlation between TGW and FE would not present any trade-off with TGW (Ferrante et al., 2012; González et al.,

2014; Terrile et al., 2017; Garcia et al., 2019; Gerard et al., 2019).
The positive correlations between yield and GN (r = 0.76*) and FE (r = 0.61*) indicate the important contributions of these traits to yield. Analyzing all sources of variation, genotypic or environmental, yield was found to be closely correlated to grain number (Ferrant et al., 2012; Elía et al., 2016). And several studies suggest FE as a secondary or physiological trait for yield improvement (Pretini et al., 2021). Overall, the extent of the relationship between yield and GN and FE components decreased with water stress (GN: r = 0.36, FE: r = 0.37), and the recorded trade-off between yield and TGW (r = -0.50*) becomes lower under stress conditions (r = 0.56).

Materials and methods

Site description

A greenhouse experiment was carried out at National Institute of Agricultural Research, Settat - Morocco (N: 33.167 and W: 7.4). During three cropping seasons: 2018/2019, 2019/2020 and 2021/2022. The soil used is a vertisol with a clay texture, an alkaline pH (8.2), and a medium organic matter (2.7%).

Crop managements and treatments

Six genotypes (15/42, 44/10/17, 132/88, and 132/93, Achtar and Amal) were tested for their ability to tolerate anthesis water stress. Table 1 gives the characteristics of the genotypes studied. Sowing was carried out on the 20^{th}, 24^{th} and 16^{th} December of the three cropping seasons consecutively, 2018/2019, 2019/2020 and 2021/2022. A pot of 10-liter containing 1/3 compost and 2/3 soil was used. Sufficient nutrients were applied. Weed, disease and insect were controlled. The treatments consisted of the control with sufficient irrigation twice a week from sowing to the end of grain filling, and stressed treatment consisted of restricting irrigation at anthesis for 15 days (from the beginning of anthesis to the beginning of grain filling). The experimental design was a split-plot with three replications.

Plant measurements

Five plants were harvested after the period of water stress to measure the spike dry matter at anthesis. And a sample of 15 plants was taken at harvest to measure the grain number per spike (GN/S), thousand grain weight (TGW), fruiting efficiency (FE: grains set per g of spike dry weight at anthesis) and yield in each treatment.

Statistical analysis

Analysis of variance (ANOVA) was used to extract the effect of genotype, water regime and their interaction. Mean comparison test of Tukey was used to classify the treatments. Genotype ranking using a centered scatter plot was recorded by GGE-biplot. A pearson's correlation analysis was recorded. All statistical analyses were performed using GenStat software, 15^{th} edition (VSN International, Hermel Hempstead, UK, 2011).

Conclusion

Anthesis drought stress reduced all components studied. However, the persistence of genotypes was evaluated by their ability to maintain a low reduction under water stress in comparison to irrigated treatment. Two genotypes, namely 15/42 and Achtar, were found to be the most adapted to both stressed and irrigated conditions. The high correlation between GN and FE under irrigated conditions makes FE as promising trait to take in consideration in breeding program. However, its importance is reduced under stress conditions. While, the recorded trade-off between FE and TGW under irrigated conditions decreased under stressed conditions, the origin of that indicate that increasing FE could be achieved without compromising TGW. To the extent of this study, further investigation of the physiological process of florets development and grain filling is needed.

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Conflict of Interest

The authors declare no conflict of interest.

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