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Determination of physiological traits related to terminal drought and heat stress tolerance in spring wheat genotypes

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ABSTRACT: Terminal drought and heat stress are two most important environmental factors affecting wheat in south-west of Iran.To determine physiological traits related to both terminal drought and heat stress tolerance, this research was conducted in three separate experiments with 15 spring wheat genotypes in two cropping seasons (2010-11 and 2011-12), under warm and semi-arid climate field conditions in south west of Iran. In control (irrigated) and drought-stressed experiments, genotypes were sown at optimum planting date, while for heat-stressed experiment planting date was delayed. In drought stress experiment irrigations were done until flowering stage. All experiments were conducted in randomized complete block design with three replications. Flag leaf area (FLA), days to flowering (DTF), biomass at flowering stage (BMF), leaf relative water content (RWC), flag leaf chlorophyll content (Chlo), canopy temperature (CT), stomatal conductance of flag leaf (SC), light extinction coefficient (k), grain filling period (GFP), grain filling rate (GFR), thousand grain weight (TGW), grain yield, and stress susceptibility index (SSI) were measured and recorded. Results of correlation and principal component analysis showed that Chlo, GFR and TGW were associated with both terminal drought and heat stress tolerance. It can be concluded that under both terminal drought and heat stress conditions, these traits could be more focused in wheat breeding programs. Furthermore, results of slicing of genotype× environmental conditions interaction showed grain yield reduction of durum cultivars were not significant under terminal drought stress as compared to bread wheat genotypes (6.1% and 28.6%, respectively). All wheat genotypes showed significant grain yield reduction under terminal heat stress condition, except for cv. Dena. High yielding genotypes under non-stressed condition showed significant grain yield reduction, when subjected to a stressed condition (36.2% and 45.8% under terminal drought and heat stress conditions, respectively); consequently based on SSI these genotypes were not classified into tolerant group (1.45 and 1.48 under terminal drought and heat stress conditions, respectively).

Key words: wheat physiology; grain yield; stress susceptibility index.

INTRODUCTION

Declining water resources and global climate change associated with global warming are two global environmental issues. Both factors are anticipated to increase the intensity of drought and heat stress experienced by crops (Reynolds et al., 2007).Drought and heat stress are two most important environmental factors affecting crop growth, development, and yield.Understanding of the effect of drought and heat stress will be critical in evaluating the impact of climate change on crop production. Both drought and heat stress affect physiological, growth, development, yield, and quality of crops. Short- and long-term stresses can significantly influence growth and yield processes, particularlywhen stresses occur at sensitive stages (Prasad et al., 2008).

Physiological traits are ideal selection criteria for drought adaptation. Recently,these traits have acquired increasing importance in wheat breeding programs, because of a greater understanding of their relative contribution to grain yield (Araus et al., 2002; Reynolds et al., 2005; Olivares-Villegas et al., 2007) Understanding of physiological traits that determine wheat grain yield in different conditions may be useful for assisting future wheat breeding. Genotypes with physiological traits conferring higher grain yield potential usually perform better under stress conditions. Breeders also need to release cultivars which are adapted to different conditions, so identifying physiological traits that may confer simultaneously high grain yield potential and tolerance to stresses would be essential. These traits must allow the plants to capture more resources or to use them more efficiently (Slafer and Araus, 2007).

In recent years genetic gains in yield potential have been far lower than what is expected. Slafer and Araus (2007) believed that further improvements need the integration of new tools and strategies to complement traditional breeding approaches. Two issues that might contribute to complementing traditional breeding are molecular biology and crop physiology.A number of physiological traits have been reported to be associated with grain yield under both heat- and drought-stressed conditions. These traits include remobilization of stem carbohydrates (Blum, 1998; Asseng and van Herwaarden, 2003), canopy temperature (Blum et al., 1989; Reynolds et al., 1998), ground cover (Rawson, 1986; Richards et al., 2002), and chlorophyll protection or stay-green (van Herwaarden et al., 1998; Reynolds et al., 2000).

Reynolds et al. (2007) reported that under drought condition, the best expression of canopy temperature and carbon isotope discrimination suggested potential yield gains of approximately 10 and 9% above the best yielding cultivars, respectively; while under heat stress condition, canopy temperature and remobilization of stem carbohydrates suggested potential yield gains of approximately 7 and 9% respectively. They also pointed-out that under drought, canopy temperature associated with water uptake, and carbon isotope discrimination associated with transpiration efficiency andunder heat stress, stomatal conductance, leaf chlorophyll content, and canopy temperature were associated with radiation use efficiency. Negative strong correlation between water use and canopy temperature at grain filling stage indicated association between water extraction from soil and canopy cooling at this stage.

Olivares-Villegas et al. (2007) showed that canopy temperature measured under irrigated and reduced irrigated conditions was not strongly associated with yield, but under drought condition it had significant negative correlation with yield. They noted that genotypes with cooler canopy outperformed in stress condition, but not only this trait caused higher photosynthetic activity in tolerant group, they also had greater flag leaf chlorophyll content. Moreover,they found a negative significant correlation between canopy temperature and flag leaf chlorophyll content.

The relative yield performance of genotypes in stress and favorable environment seems to be a common starting point in identifying the desirable genotypes for stress condition (Mohammadi et al., 2010). A number of methods have been proposed to consider yield stability of genotypes in a wide range of environmental conditions, the main objective of those were comparing the performance in the inverse conditions and selecting genotypes adapted to both conditions (Ehdaie et al., 1988; Falconer, 1990; Fernandez, 1992). Selection under favorable, stressed, and simultaneously in both conditions were three main strategies, suggested to select tolerant genotypes (Calhoum et al., 1994). Several indices have been proposed to describe the behavior of a given genotype under stress and non-stress conditions (Mohammadi et al., 2010).An index to determine stress tolerance is stress susceptibility index (SSI) (Fisher and Maurer, 1978). It was based on realized reduction of yield under stressed condition. This index can be used to identify genotypes with yield stability under stressed conditions, and as an indicator index to differentiate between tolerant and sensitive genotypes (Bahar and Yildirim, 2010).

Under warm and semi-arid climate conditions in south-west of Iran, introducing tolerant wheat genotypes has specific importance to stabilizing wheat production. Understanding relationship between grain yield and physiological traits related to abiotic stress tolerance can be used as efficient tools in breeding programs and identifying ideotypes of the crop for the target environments. On the other hand determination of physiological traits contributing to different abiotic stress tolerance mechanisms is a shortcut to select genotypesfor stressed conditions, and then releasing them for the target environments. The objective of this research was to study the relationship between some physiological and phenological traits, grain yield and stress tolerance in spring wheat genotypes under both terminal drought and heat stresses, as well as to determinethecommon traits related to tolerance to both stresses.

MATERIALS AND METHODS

This research was conducted in three separate experiments with 15 spring wheat genotypes (table 1) in two cropping seasons (2010-11 and 2011-12), under warm and semi-arid climate conditions innorth of Khouzestan province in south west of Iran (32° 22' N, 48° 07' E). In control (irrigated) and drought-stressed experiments, genotypes were sown at optimum planting date (mid-December), while for heat-stressed experiment planting date was delayed (late January). In control and heat-stressed experiments irrigations were applied, without any limitations. In droughtstress experiment irrigations were applied until flowering stage. All experiments were conducted in a randomized complete block design with three replications. Fertilizers and weed control were applied based on research recommendation for the region. Plants were sown in plots 5 m long and 1.2 m wide consisting of eight rows with 15 cm rowspacing.

Physiological and Phenotypic Measurements

Flag leaf area (FLA): To measure FLA,areas of 5 young-fully expanded flag leaves from five randomly selected plants per plot were measured andthe average was recorded.

Days to flowering and biomass at this stage (DTF and BMF)

Days to flowering were recorded from thedate of emergence to the date when 50% of the spikes werefully emerged in each plot. Biomass measured immediately after flowering consisted of all aboveground tissue from 1 m^2 in each plot.Fresh biomass was oven-dried at 70°C for 48 h for dry weight measurement.

Leaf relative water content (RWC)

To measure RWC at flowering and grain filling stages (RWCF and RWCGF), three fresh flag leaves were detached from each plot and weighed immediately to record fresh weight. Fresh leaves were floated in distilled water for 24 h. Excess water of leaves were wipedoff and weighed to record saturated weight, and then oven-dried at 70°C for 48 h for dried weight measurement. The RWC was computed using the following equation:

RWC= (FW-DW)/ (SW-DW) ×100

Where FW, DW, SW were fresh weight, dry weight, and saturate weight, respectively.

Flag leaf chlorophyll content (Chlo)

Chlorophyll content was assessed on flag leaves at the flowering stage (ChloF) and during grain filling (ChloGF) with a self-calibrating chlorophyll meter (Model SPAD 502). An average chlorophyll content of five randomly selected flag leaves per plot was recorded.

Canopy temperature (CT)

Canopy temperature was measured with an infrared thermometer two times at the flowering stage (CTF) and during grain filling (CTGF), as described byReynolds et al. (1998) and Olivares-Villegas et al. (2007). Five measurements per plot were taken.

Stomatal conductance of flag leaf (SC)

Stomatal conductance was measured two times at the flowering stage (SCF) and during grain filling (SCGF) using a portable porometer at 11:00-14:00 hrs on three flag leaves per plot, and the average recorded.

Light-related traits

Photosynthetic Active Radiationat the above and ground level of the canopy was measured using a ceptometer (Decagon AccuPAR LP-80) at the flowering stage at 11:00-14:00 hrs. Light extinction coefficient (k) was computed using the following equation:

$$K = \left[\frac{-ln\left(\frac{PAR_t}{PAR_i}\right)}{LAI} \right]$$

Where PAR_i andPAR_t,were PAR at above the canopy and at the ground level, respectively and LAI was leaf area index.

Traits related to grain growth

To assess grain filling period (GFP) and grain filling rate (GFR), days from anthesis to physiological maturity wererecorded as GFP and grain filling rate (GFR) was calculated by dividing final grain weight toGFP. 1000 grains were separated and then their weight was measured as TGW.

Grain yield

Grain yield was measured by hand-harvesting a bordered area of 1.4 m^2. To estimate harvest index a random subsample of 100 spike-bearing culms was removed from each plot, dried, weighed, and threshed, and HI wasestimated by the ratio of the grain weight to biomass of the subsample (Reynolds et al., 2007).

Stress susceptibility index (SSI)

SSI was calculated by the following equation (Fisher and Maurer, 1978):

$$SSI = \frac{1-\left(Y_s/Y_P\right)}{1-\left(\bar{Y}_s/\bar{Y}_P\right)}$$

Where Y_s and Y_p, were grain yield in stressed, non-stressed conditions and $\bar{Y}_s$ and $\bar{Y}_p$ were mean grain yield in stressed and non-stressed conditions, respectively.

STATISTICAL METHODS

Data was analyzed using SPSS18.0 for correlation analysis between traits, MINITAB14 for PCA analysis, and SAS 9 for combined analysis of variance.

RESULTS AND DISCUSSION

Genotypes were classifiedinto three groups (table 2), based on least significant difference of grain yield in comparison with cv. Chamran as the checkin non-stressedexperiment, including:

Genotypes with higher grain yield than the check (group A, mean grain yield was 734.1 g.m^{-2})
Genotypes without significant difference with the check (group B, mean grain yield was558.7 g.m^{-2})
Genotypes with lower grain yield than the check (group C, mean grain yield was 489.7 g.m^{-2})

Results of the combined ANOVA (not shown) showed genetic variation for grain yield among the spring wheat genotypes under different conditions. Results of slicing analysis of genotype×environmental condition interaction in combined analysis of variance indicated that compared to the bread wheat genotypes, grain yield reduction of durum cultivarswas not significant under terminal drought stress (28.6% and 6.1%, respectively). Among bread wheat genotypes, grain yield reduction of S-80-18 and S-83-3 lines was not significant under terminal drought stress.All wheat genotypes except for cv. Dena (13% grain yield reduction) showed a significant grain yield reductionunder terminal heat stress condition. These finding indicated that some of the genotypes which were studied in this research had tolerance mechanisms to terminal stress condition.

Regarding to the results of the slicing analysis, stress susceptibility index (SSI), which is based on realize grain yield decrease in stressed conditions, was used to classify tolerant and sensitive genotypes under stressed conditions (table 2).The results indicated that high yielding genotypes under non-stressed condition (line No. 514 and cv. Star) showed a significant grain yield reduction, when subjected to a stressed condition (the mean grain yield reductions of them were 36.2% and 45.8% under terminal drought and heat stress conditions, respectively); consequently based on SSI were not classified into tolerant group (the mean SSI of them were 1.45 and 1.48 under terminal drought and heat stress conditions, respectively).So breeding for higher performance in a desirable condition could not often cause to high performance in stressed conditions and stress tolerance.

Olivares-Villegas et al. (2007) reported that high yielding genotypes in a favorite condition werenot in outperforming genotypes under stressed environment. However, selection for high performance is necessary in order to yield production in desirable conditions (Turner and Begg, 1981; Rajaram, 1995; Slafer et al., 1996) and in conditions where environmental stress isnot permanent limiting factor; but there is some evidence justified that, when environmental stress is a permanent constraint,selection for specific traits related to stress tolerance would increase yield significantly (Richards, 1996; Quarrie et al., 1999; van Ginkel et al., 1998; Araus et al., 2002).

To determine traits related to stress tolerance,genotypes were divided into tolerant and sensitive groupsbased on SSI under both terminal drought and heat stress conditions (table2). Results showed that durum wheat genotypes were more tolerant than bread wheat genotypes under terminal drought stress condition (mean SSI of durum and bread wheat genotypes were 0.24 and 1.12, respectively). This finding was in agreement with results of Shrif Alhosainy (1998) and Saleem (2003),who reported that under terminal drought stress, durum wheat genotypes showed lower yield reduction than bread wheat genotypes.

The results of correlation analysis between SSI and physiological traits in tolerant genotypes under both terminal drought and heat stress showed a negative significant correlation between SSI and flag leaf chlorophyll content at the flowering stage (-0.79* and -.0.84** under terminal drought and heat stress conditions, respectively).

Kandic et al. (2009) noted that leaf senescence had negative significant effect on yield, and accelerated leaf chlorosis occurred under drought stress caused yield reduction. They also pointed out under both drought and heat stressed condition, delayed leaf chlorosis was suggested as a useful trait for small grain crops breeding. Furthermore, Reynolds and Trethowan (2007) indicated leaf chlorophyll content or stay green was associated with transpiration efficiency, which causes to the improvement of WUE under drought condition. Richards et al. (2001) reported leaf stay green probably was an indicator of soil water status and deeper root systems; furthermore it means presence of higher photosynthetic apparatus for more assimilation and water soil extraction. Leaf senescence or stay green was used as selection criteria for sorghum breeding in USA and

Australia (Reynolds and Tuberosa, 2008). Saeedpour (2012) reported that drought stress caused leaf senescence by accelerated loss of chlorophyll and soluble proteins. He also pointed out that leaf senescence occurred earlier in sensitive genotype than in tolerant one.

Association between SSI and flag leaf chlorophyll contentunder heat stress condition corresponded with other researchers'findings (Reynolds et al., 2007; Reynolds and Trethowan, 2007; Kandic et al., 2009). According to theconceptual model suggested by Reynolds and Trethowan (2007), leaf chlorophyll content or stay green involved in heat tolerance metabolism, which associated with transpiration efficiency; so this contributed to the improvement of WUE and RUE under drought and heat stress, respectively. Reynolds et al. (1994) also reported that stay green was used widely for heat tolerance breeding. They indicated photosynthesis rate and leaf chlorophyll content measured during grain filling were associated with yield. Fanizza et al (1991) used chlorophyll meter to screen germplasm for heat tolerance.

Table 1. spring wheat genotypes and their origin

Genotype	Type	Origin
Zagros	Bread wheat	CIMMYT
Kouhdasht	Bread wheat	CIMMYT
Pishtaz	Bread wheat	Iran
Chenab	Bread wheat	Pakistan
Star	Bread wheat	CIMMYT
S-78-11	Bread wheat	Iran
Chamran	Bread wheat	CIMMYT
Vee/Nac	Bread wheat	CIMMYT
S-80-18 (HD160/5/Tob/ Cno / 23854 /3/ Nai60// Tit/ Son64 /4/ LR/ Son64)	Bread wheat	CIMMYT
S-83-3 (Atilla50//Attila/Bacanora)	Bread wheat	Iran
BAZ (WAXWING/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ)	Bread wheat	CIMMYT
2ndEBWYT-514 (Oasis/SKauz//4*Bcn/3/2*Pastor)	Bread wheat	CIMMYT
Behrang	Durum wheat	CIMMYT
Dena	Durum wheat	CIMMYT
Karkheh	Durum wheat	ICARDA

Table 2. Grouping of spring wheat genotypes based on grain yield in non-stressed condition and SSI under both terminal stressed conditions

genotypes		Grain yield (g/m^2)			SSI_D	SSI_H
		control	drought	heat		
Group A	2ndEBWYT-514	734.6	530.3	362.4	1.11	1.63
	Star	733.5	406.9	433.2	1.78	1.32
	Chamran	595.5	394.1	402.5	1.35	1.05
	S-78-11	582.6	415.2	430.2	1.15	0.84
	BAZ	549.7	288.2	426.7	1.9	0.72
Group B	S-80-18	549.2	470.9	420.4	0.57	0.76
	Chenab	546.9	391.9	401.7	1.13	0.86
	Pishtaz	545.7	398.2	406.1	1.08	0.83
	Vee/Nac	541.4	454.6	422.4	0.63	0.71
	Zagros	518.5	368.1	402.8	1.16	0.72
Group C	S-83-3	507.0	427.0	322.3	0.63	1.18
	Behrang	500.6	469.1	286.8	0.25	1.38
	Kouhdasht	485.2	372.4	329.5	0.93	1.03
	Karkheh	480.4	434.8	264.3	0.38	1.45
	Dena	446.3	436.3	388.3	0.09	0.42
	Mean	554.5	417.2	380.0	0.94	0.99
		63.67	112.54	66.11		

SSI_D: Drought Susceptibility Index, SSI_H: Heat susceptibility Index, Tolerant genotypes under drought and heat stress has SSI≤1.

There was a negative significant correlation between SSI and grain filling rate (GFR) under heat stress (-0.74*) and a positive correlation between flag leaf chlorophyll content and GFR and between GFR and TGW under both stressed conditions (tables 4 and 5). These results indicated that flag leaf chlorophyll content and thereby green leaf duration, contributed to longer maintenance of current photosynthesis to grains. On the other hand genotypes with longer stay green capacity, utilized available resources efficiently and had higher photosynthetic efficiency under stressed condition, consequently current photosynthesis had a greater effect on grain filling. Reynolds et al. (2001) noted that photo-assimilation was the most important limiting factor in heat stress condition, especially when stress intensified during grain filling due to increased demand of assimilates in this period. Ehdaie and Waines (1996) also reported current photosynthesis especially from flag leaf was the most important source of carbohydrate storage for wheat kernels. Amount and rate of translocation of storage material and assimilates from current photosynthesis of plants depend on speed of plants reaction and reception of environmental cues, enzyme, hormonal and vascular systems efficiency; especially under stressed environment. Interaction function of these factors is expressed by grain filling rate and duration and had key roles in the stability of yield (Naderi et al., 2000).

Correlation between SSI and light extinction coefficient (k) was negatively significant under heat stress (-0.82*). It is indicated that genotypes with more light extinction ability, utilized light efficiently compare to other genotypes. Based on the result of this study higher light extinction coefficient might be a useful mechanism to avoid photo-inhibition and tolerance of increased temperature under heat stress. According to conceptual model of Reynolds and Trethowan (2007), improved RUE contributed to higher yield and tolerance under heat stress condition.

In this research, we observed that some tolerant genotypes had specific morphological traits. Among genotypes which were studied in this research, cv. Dena was the most tolerant genotype (SSI was 0.09 and 0.42 under drought and heat stress conditions, respectively). It had pubescence spike, which may had a role in its tolerance under both stressed conditions. Also in this research Vee/Nac genotype was one of the most tolerant genotypes under both drought and heat stress conditions (SSI was 0.63 and 0.71 under drought and heat stress conditions, respectively), which showed the most visible leaf rolling, that probably contributed to both heat and drought stress tolerance. Also, both of the mentioned genotypes were among the early maturity genotypes in this research (table 3). Modhej et al. (2010) reported higher leaf rolling and earliness in Vee/Nac, previously. According to the conceptual model of Reynolds and Trethowan (2007) leaf pubescence and rolling contributed to photo-protection and may associated with WUE and RUE under drought and heat stressed condition, respectively. Morphological traits such as leaf wax and rolling may reduce incoming radiation and contribute to photo-protection (Richards et al., 2002). Leaf rolling may be an indicator of plant water status and consequently deeper root system. Also, it may be an adaptive feature to avoid leaf senescence and maintain leaf area (Richards et al., 2001). Other researchers reported early maturity genotypes were suitable to the tolerance of stress. Because they had faster developmental phases and were exposed to stress lesser, especially terminal stresses; as they complemented their growth cycle before the occurrence of terminal stresses and hence damage of stresses on them was lesser (Blum, 1993; van Ginkel et al., 1998).

Results of the principal component analysis (PCA) under terminal drought and heat stress showed that SSI was in the opposite direction of flag leaf chlorophyll content, grain filling rate and thousand grain weight. These findings confirmed the results of correlation analysis, which indicated that chlorophyll content, GFR and TGW contributed to the maintenance of the current photosynthesis and hence stress tolerance. Naderi et al. (2000) pointed out that under favorite conditions, higher GFR and GFP may have more desirable outcome, but according to the goals of breeding strategies in arid and semi-arid environments, higher GFR may be more useful than GFP in these sites. PCA results showed a strong correlation between yield and harvest index (HI) under drought stress, which corresponded with the finding of Reynolds et al. (2007). They reported HI consisted of soluble carbohydrates in stem and biomass at anthesis stage, which partitioned to developing grains. Reynolds and Trethowan (2007) suggested that HI was one of the most important drivers of yield under both drought and heat stress conditions.

The results of PCA showed a negative association between SSI and light extinction coefficient (k) under heat stress, which is similar to the results of correlation analysis as described earlier. Also, PCA showed a strong association between yield and biomass shortly after flowering stage under heat stress, which probably due to expend of storage assimilates in vegetative period for grain filling under stressed condition. Since under stressed environment, current photosynthesis declines and remobilization of storage assimilates can perform as a compensation mechanism. These finding were in agreement with the results described elsewhere (Blum, 1998; Asseng and van Herwaarden, 2003; Reynolds et al., 2007).

CONCLUSION

Our results showed that some physiological and morphological traits could contribute to both drought and heat stress tolerance of wheat genotypes. Reynolds and Trethowan (2007) believed that some useful traits under drought stress may be useful under heat stress. Our results showed that flag leaf chlorophyll content, grain filling rate and thousand grain weights were associated with stress tolerance under both conditions. So it can be concluded that under both terminal drought and heat stress conditions, breeders can have special attention on these traits and focus on them in breeding programs. Furthermore, the results showed that some morphological traits such as pubescence spike and leaf rolling could have an effect on higher stress tolerance under both conditions.

Our findings indicated that under terminal drought stress, durum wheat genotypes did not show a significant grain yield reduction compared to bread wheat genotypes, which indicated that these genotypes had mechanisms, which confer them terminal drought tolerance. According to the results of this research, higher chlorophyll content, GFR and TGW of durum wheat genotypes might contribute to their terminal drought tolerance (mean ChloF, ChloGF, GFR and TGW of durum genotypes were 54.4, 55.2, 1.55 and 36.7, respectively). Higher GFR of durum wheat genotypes than bread wheat genotypes was reported previously by Modhej et al. (2011).

Table 3. traits measured under different conditions

Genotype	CTF (°C)			CTGF (°C)			RWCF (%)			RWCGF (%)			SCF (mmolm^{-2}s^{-1})			SCGF (mmolm^{-2}s^{-1})			ChloF			ChloGF		
	C	D	H	C	D	H	C	D	H	C	D	H	C	D	H	C	D	H	C	D	H	C	D	H
2ndEBWYT-514	17.1	17.7	24.2	25.3	27	32.5	75	75	75	65	65	92	105.8	101.5	141.6	69.8	76.5	121.9	51.2	50.5	51.2	50.9	50.1	49
BAZ	16.4	17.1	24.1	26.4	27.2	32.7	86	81	64	65	65	87	104.8	127.4	117.3	106.6	49	115	46.9	46.8	49	47.3	45.9	47.7
S-80-18	15.8	16.5	24.2	24.6	26.1	32.6	87	84	72	52	61	81	92.6	111.9	142.1	74.1	35.1	54	46.5	45.6	49.2	48.6	49	49
Chamran	17	17.5	23.9	24.8	26.5	32.5	78	81	68	58	60	84	104	103.1	116	93.2	29.4	89	48.6	48.8	50.6	52.1	50.1	50
Zagros	15.6	16	24.3	24.3	26.4	32.2	85	85	69	57	58	78	93.4	103.4	135	133.4	64.2	72	49	47.2	49	49.9	49.9	48.9
Behrang	16	16.8	24.1	25	26.8	31.6	79	82	65	59	55	82	86.2	91.5	139	84.2	38.6	87	54.9	53.6	56.8	57.8	56.2	58.5
Kouhdasht	15.8	16.7	24.3	25.6	26.3	32	79	72	68	59	59	82	115.2	97.9	128.9	130.1	51.4	61	47.5	47.5	49.2	46.8	50.3	50.5
Karkheh	16.1	17.5	22.8	24.8	26.9	31.2	83	75	73	62	60	82	94.5	93.5	150.4	119.1	66.4	103.1	53.7	54.5	54.1	53.6	52.1	53.8
S-83-3	15.8	16.6	23.6	25.1	27.3	32.5	84	79	77	62	67	85	124.2	105.2	135.4	60.1	55.9	84	50.1	50.1	50.1	51.3	50	50.3
S-78-11	16.1	17.4	23.5	24.4	26.9	32.4	79	65	70	60	59	82	117	91	103.8	76.2	44.4	77	49.7	49.7	49.2	51.5	55.4	51.7
Dena	16.8	17.8	24.3	24.9	26.8	32.1	75	63	67	59	61	80	93.4	85.2	136.4	94.1	33.4	106.4	55.2	55.2	54.7	54.1	53.7	55.9
Vee/Nac	16	16.8	23.5	24.4	27.2	32.3	87	74	66	57	58	78	108.9	96.3	201.6	122	76.1	86	50.8	50.8	51.4	51.4	49.1	50
Star	17.2	17.4	22.5	23.4	25.3	28.6	85	83	85	69	69	87	149.8	98.3	164	133.4	44.7	131.4	55.2	55.2	55.4	54.9	55.2	54.8
Chenab	17.2	17.5	23.8	25.5	24.4	32.7	85	83	76	51	54	81	120.4	115.9	141.1	106.2	56.5	97.5	50.7	50.7	49.7	49.7	51.3	50.7
Pishtaz	16.7	17.3	24.2	24.2	26.3	31.3	76	73	71	62	66	85	127.1	110.5	112.8	122.2	47.2	90	50.4	50.4	50.2	49.2	49.3	47.4
Mean	16.4	17.1	23.8	24.8	26.5	31.9	82	77	71	60	61	83	109.2	102.2	137.7	101.6	51.3	91.7	50.7	50.4	51.3	51.3	51.2	51.2
$LSD_{5\%}$	.85	.92	1.13	.88	1.15	2.54	4.94	6.54	3.8	3.53	5.53	5.37	15.37	23.32	27.99	31.74	14.9	28.82	1.44	.98	1.29	1.98	1.55	1.4

Genotype	FLA (cm^2)			BM (g/m^2)			DTF (day)			HI (%)			k			GFP (day)			GFR (mg/day)			TGW(g)		
	C	D	H	C	D	H	C	D	H	C	D	H	C	D	H	C	D	H	C	D	H	C	D	H
2ndEBWYT-514	31	29.2	23.3	1326.56	1326.56	801.76	88	88	64	40	35	37	.55	.55	.43	29	27	23	1.35	1.12	1.31	34.3	32.4	29.7
BAZ	26.1	22.8	18.6	1084	1084	937.28	82	82	59	34	25	41	.34	.34	.53	30	25	27	1.45	1.16	1.11	38.7	31.1	28.4
S-80-18	24	23.8	23.4	1112.8	1112.8	738.4	85	86	63	34	39	37	.4	.4	.53	32	28	25	1.12	1.09	1.09	33.6	28.5	25.6
Chamran	22.1	21.9	19.1	957.28	957.28	1011.36	87	88	64	35	32	42	.43	.43	.4	29	24	22	1.19	1.16	1.28	34.3	30.8	28.3
Zagros	28.9	26.9	24.6	942.4	942.4	830.08	86	86	61	37	28	40	.58	.58	.44	28	26	26	1.42	1.23	1.25	36.5	31.9	29.1
Behrang	31.5	30.3	28.4	1102.56	1102.56	782.4	83	84	66	40	39	40	.32	.32	.44	30	27	25	1.69	1.52	1.38	44.6	37.7	32.5
Kouhdasht	32	31.1	25.5	1110.4	1110.4	985.92	85	85	63	38	31	42	.44	.44	.33	32	29	26	1.23	1.26	1.2	35.6	34.9	28
Karkheh	34.5	32.2	32.7	1145.12	1145.12	1012.32	87	86	67	40	36	39	.52	.52	.39	29	25	22	1.88	1.62	1.8	47.2	39	34.4
S-83-3	30.2	28.3	19.4	1180.8	1180.8	794.08	90	90	68	44	36	39	.54	.54	.43	29	26	24	1.23	1.24	1.12	33	30.5	25.3
S-78-11	30.8	26.5	26.2	1180.16	1180.16	1013.6	91	91	66	41	41	39	.56	.56	.35	26	23	21	1.39	1.38	1.21	34.6	29.1	25
Dena	27.5	21.5	22.9	1104.64	1104.64	856.16	86	86	61	41	36	39	.52	.52	.6	31	24	26	1.45	1.51	1.36	40.1	33.4	31.9
Vee/Nac	25	21	17.8	1033.92	1033.92	757.12	85	85	61	36	38	46	.37	.37	.44	32	24	25	1.19	1.34	1.07	33.5	31.1	24.9
Star	31.8	29.2	23.9	1399.84	1399.84	1182.08	95	94	71	39	31	35	.44	.44	.42	30	26	21	1.22	.99	1.3	34.3	26.1	26.4
Chenab	34.4	33.4	27.9	1317.6	1317.6	845.92	87	87	63	43	36	34	.43	.43	.37	29	24	25	1.27	1.21	1.06	33.9	28.2	26.9
Pishtaz	26.2	27.1	19.7	1116.16	1116.16	1226.88	90	91	64	37	40	38	.63	.63	.32	30	27	27	1.28	1.25	1.01	36.6	33.9	25.7
Mean	29.1	27	23.6	1140.96	1140.96	918.4	87	87	64	39	35	39	.47	.47	.43	30	26	24	1.36	1.27	1.24	36.7	31.9	28.1
$LSD_{5\%}$	3.47	4.2	1.12	382.01	382.01	164.68	1	1	2	8	4	3	.21	.21	.13	3	3	3	.17	.21	.16	2.4	2.3	1.4

C: control, D: drought, H: heat, CTF and CTGF: canopy temperature at flowering and grain filling stages, RWCF and RWCGF: relative water content at flowering and grain filling stages, SCF and SCGF: stomatal conductance at flowering and grain filling stages, ChloF and ChloGF: chlorophyll content at flowering and grain filling stages, FLA: flag leaf area, BM: biomass shortly after flowering, DTF: days to flowering, HI: harvest index, k: light extinction coefficient, GFP and GFR: grain filling period and rate, TGW: thousand grain weight.

Table 4. correlation between traits of tolerant genotypes under terminal drought stress

Traits	CT-F	CT-GF	RWC-F	RWC-GF	SC-F	SC-GF	Chlo-F	Chlo-GF	FLA	BM	DTF	HI	k	GFP	GFR	TGW	SSI
CT-GF	.20^{ns}																
RWC-F	.76*	-.17^{ns}															
RWC-GF	-.07^{ns}	.26^{ns}	-.04^{ns}														
SC-F	-.80*	-.32^{ns}	.71^{ns}	.45^{ns}													
SC-GF	-.06^{ns}	.58^{ns}	-.04^{ns}	.03^{ns}	.01^{ns}												
Chlo-F	.82*	.56^{ns}	-.48^{ns}	-.21^{ns}	-.87*	.06^{ns}											
Chlo-GF	.48^{ns}	.10^{ns}	-.14^{ns}	-.48^{ns}	-.72^{ns}	-.44^{ns}	.74^{ns}										
FLA	-.10^{ns}	-.08^{ns}	.30^{ns}	-.08^{ns}	-.00^{ns}	.10^{ns}	.07^{ns}	.29^{ns}									
BM	.01^{ns}	.06^{ns}	.20^{ns}	.69^{ns}	.27^{ns}	-.20^{ns}	.02^{ns}	.06^{ns}	.58^{ns}								
DTF	-.12^{ns}	.42^{ns}	.07^{ns}	.97**	.48^{ns}	.10^{ns}	-.12^{ns}	-.38^{ns}	.01^{ns}	.73^{ns}							
HI	-.11^{ns}	.18^{ns}	.51^{ns}	-.19^{ns}	.15^{ns}	-.14^{ns}	.14^{ns}	.18^{ns}	-.41^{ns}	-.24^{ns}	-.10^{ns}						
k	.48^{ns}	.26^{ns}	-.47^{ns}	.79*	-.07^{ns}	.08^{ns}	.24^{ns}	-.16^{ns}	.11^{ns}	.68^{ns}	.73^{ns}	-.45^{ns}					
GFP	-.65^{ns}	-.73^{ns}	.50^{ns}	-.10^{ns}	.53^{ns}	-.38^{ns}	-.71^{ns}	-.13^{ns}	.49^{ns}	.24^{ns}	-.13^{ns}	-.32^{ns}	-.31^{ns}				
GFR	.79*	.40^{ns}	-.42^{ns}	-.39^{ns}	-.87*	.14^{ns}	.95**	.75^{ns}	.28^{ns}	-.02^{ns}	-.31^{ns}	.03^{ns}	.14^{ns}	-.55^{ns}			
TGW	.49^{ns}	.09^{ns}	-.18^{ns}	-.52^{ns}	-.67^{ns}	.10^{ns}	.65^{ns}	.71^{ns}	.69^{ns}	.11^{ns}	-.44^{ns}	-.23^{ns}	-.00^{ns}	-.05^{ns}	.85*		
SSI	-.70^{ns}	-.21^{ns}	.24^{ns}	.18^{ns}	.61^{ns}	.42^{ns}	-.79*	-.75^{ns}	.20^{ns}	-.02^{ns}	.14^{ns}	-.52^{ns}	-.08^{ns}	.56^{ns}	-.67^{ns}	-.33^{ns}	
Yield	-.05^{ns}	.12^{ns}	.47^{ns}	-.23^{ns}	.11^{ns}	-.18^{ns}	.17^{ns}	.21^{ns}	-.41^{ns}	-.26^{ns}	-.15^{ns}	.99**	-.45^{ns}	-.32^{ns}	.07^{ns}	-.19^{ns}	-.56^{ns}

Table 5. correlation between traits of tolerant genotypes under terminal heat stress

Traits	CT-F	CT-GF	RWC-F	RWC-GF	SC-F	SC-GF	Chlo-F	Chlo-GF	FLA	BM	DTF	HI	k	GFP	GFR	TGW	SSI
CT-GF	-.30^{ns}																
RWC-F	-.05^{ns}	.02^{ns}															
RWC-GF	.17^{ns}	-.09^{ns}	-.14^{ns}														
SC-F	-.33^{ns}	.17^{ns}	-.16^{ns}	-.65^{ns}													
SC-GF	.03^{ns}	-.01^{ns}	-.40^{ns}	.46^{ns}	-.11^{ns}												
Chlo-F	.15^{ns}	-.30^{ns}	-.28^{ns}	-.30^{ns}	.31^{ns}	.40^{ns}											
Chlo-GF	-.07^{ns}	.09^{ns}	-.03^{ns}	-.43^{ns}	.09^{ns}	.22^{ns}	.79*										
FLA	-.07^{ns}	.32^{ns}	.74*	-.30^{ns}	-.34^{ns}	-.30^{ns}	-.19^{ns}	.36^{ns}									
BM	.07^{ns}	-.70^{ns}	.06^{ns}	.66^{ns}	-.67^{ns}	.27^{ns}	-.12^{ns}	-.26^{ns}	-.14^{ns}								
DTF	-.38^{ns}	-.25^{ns}	.64^{ns}	.00^{ns}	-.38^{ns}	-.48^{ns}	-.22^{ns}	.07^{ns}	.53^{ns}	.43^{ns}							
HI	-.31^{ns}	-.08^{ns}	-.819*	-.22^{ns}	.56^{ns}	.09^{ns}	.19^{ns}	-.08^{ns}	-.74**	-.19^{ns}	-.44^{ns}						
k	.47^{ns}	.36^{ns}	-.51^{ns}	-.10^{ns}	.20^{ns}	.18^{ns}	.47^{ns}	.39^{ns}	-.24^{ns}	-.58^{ns}	-.68^{ns}	.19^{ns}					
GFP	.71*	-.31^{ns}	-.25^{ns}	.26^{ns}	.11^{ns}	.40^{ns}	.18^{ns}	-.33^{ns}	-.53^{ns}	.08^{ns}	-.70^{ns}	.05^{ns}	.34^{ns}				
GFR	.27^{ns}	.06^{ns}	-.32^{ns}	-.38^{ns}	-.16^{ns}	.10^{ns}	.51^{ns}	.75*	.30^{ns}	-.23^{ns}	-.16^{ns}	.06^{ns}	.52^{ns}	-.18^{ns}			
TGW	.65^{ns}	.00^{ns}	-.32^{ns}	-.08^{ns}	-.15^{ns}	.49^{ns}	.56^{ns}	.52^{ns}	.07^{ns}	-.16^{ns}	-.57^{ns}	-.09^{ns}	.66^{ns}	.45^{ns}	.75*		
SSI	-.43^{ns}	.07^{ns}	.55^{ns}	.27^{ns}	-.21^{ns}	-.34^{ns}	-.84**	-.68^{ns}	.24^{ns}	.32^{ns}	.55^{ns}	-.29^{ns}	-.82*	-.31^{ns}	-.74*	-.80*	
Yield	-.57^{ns}	.38^{ns}	-.26^{ns}	.31^{ns}	-.02^{ns}	-.25^{ns}	-.61^{ns}	-.47^{ns}	-.26^{ns}	.01^{ns}	.16^{ns}	.37^{ns}	-.19^{ns}	-.45^{ns}	-.41^{ns}	-.69	.52^{ns}

CTF and CTGF: canopy temperature at flowering and grain filling stages, RWCF and RWCGF: relative water content at flowering and grain filling stages, SCF and SCGF: stomatal conductance at flowering and grain filling stages, ChloF and ChloGF: chlorophyll content at flowering and grain filling stages, FLA: flag leaf area, BM: biomass shortly after flowering, DTF: days to flowering, HI: harvest index, k: light extinction coefficient, GFP and GFR: grain filling period and rate, TGW: thousand grain weight.

*, **, and ns were significant at 5% and 1% probability levels and non-significant, respectively.

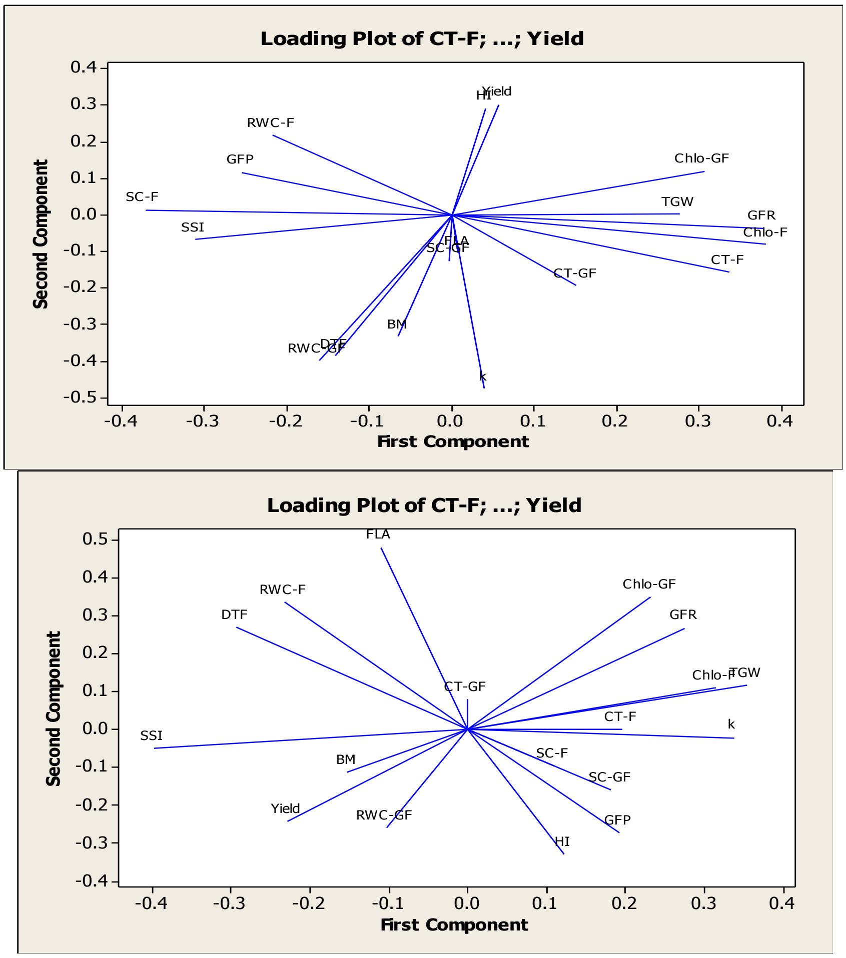

Figure 1. CTF and CTGF: canopy temperature at flowering and grain filling stages, RWCF and RWCGF: relative water content at flowering and grain filling stages, SCF and SCGF: stomatal conductance at flowering and grain filling stages, ChloF and ChloGF: chlorophyll content at flowering and grain filling stages, FLA: flag leaf area, BM: biomass shortly after flowering, DTF: days to flowering, HI: harvest index, k: light extinction coefficient, GFP and GFR: grain filling period and rate, TGW: thousand grain weight.

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