International Journal of Agriculture, Environment and Food Sciences

e-ISSN: 2618-5946 https://dergipark.org.tr/jaefs

DOI: https://doi.org/10.31015/2025.2.27 Int. J. Agric. Environ. Food Sci. 2025; 9 (2): 539-550

Bread wheat responses to post-generative drought and heat stress: physiological, yield and quality implications

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Article History
Received: April 6, 2025
Accepted: May 24, 2025
Published Online: June 25, 2025

Article Info
Type: Research Article
Subject: Cereals and Legumes

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Available at
https://dergipark.org.tr/jaefs/issue/91914/1670880

Abstract

Post-generative drought and heat stress significantly impact wheat physiology, yield, and grain quality. This study investigated the effects of four different soil moisture levels (100%, 75%, 50%, and 25% of (WHC) water holding capacity) combined with heat stress (≥30ºC) conditions on four bread wheat cultivars from stem elongation to harvest in semi-controlled green house conditions. This study examined the physiological responses of the plants as assessed by flag leaf area, SPAD chlorophyll measurements and changes in dry matter, from anthesis to harvest. Yield formation parameters, including the number of grains per ear and ear yield, were analyzed alongside grain quality traits such as crude protein, fiber, starch content, and flour color parameters (L*, a*, b*). Additionally, total phenolic content and antioxidant activity were evaluated to determine the impact of water stress on wheat's bioactive compounds.The results revealed that severe water deficit (50% and 25% WHC) led to a significant decline in flag leaf area, SPAD chlorophyll values and dry matter accumulation in anthesis and post anthesis stages, and also grain yield. The cultivars responded to increasing water stress conditions as accelerated senescence as a results of a decrease in chlorophyll and biomass production values. However, water deficiency (50 and 25% WHC) influenced quality traits differently, with causing increases in protein content, total phenolic content and antioxidant activity. It is clear that increasing temperature and drought conditions will cause wheat yield reductions supported by physiological responses. The findings provide significant insights into wheat yield and quality response under water-limited conditions, simulating spring rainfall deficiency and increasing temperatures in post-generative growth stages.

Keywords: *Triticum aestivum* L., Drought, Phenology, SPAD, Yield, Quality, Antioxidant

Cite this article as: Yigit, A. (2025). Bread wheat responses to post-generative drought and heat stress: physiological, yield and quality implications. International Journal of Agriculture, Environment and Food Sciences, 9 (2): 539-550. https://doi.org/10.31015/2025.2.27

INTRODUCTION

Wheat is grown in many regions of the world because of its adaptability to different environments. It has long been a staple food, providing daily starch and energy. It is also one of the most important cereals in terms of health and nutrition, as it contains phytochemicals, vitamins and minerals that contribute to good health (Shewry and Hey, 2015). However, this plant will face significant challenges in production levels, which is of critical importance with regard to daily nutrition and health, and is expected to occur due to climate change, particularly in Mediterranean climate regions (Tita et al., 2025). Climate change poses significant challenges to global food security and cereal crop production by altering food availability and utilization. Increasing climate variability (increasing variability in temperature and precipitation) influences crop development and yield potential, with the extent of these effects dependent on phenological responses (a shift in timing of the most sensitive phases: anthesis etc.) to extreme weather conditions (Bracho-Mujica et al., 2024). Wheat researchers are closely monitoring these changes to mitigate potential risks that are projected and may occur in the future.

In Mediterranean climates, the distribution of rainfall is as critical as the total seasonal precipitation for wheat yield formation. It has been estimated that a 1% change in mean temperature during April and May results in a 1.4% decrease in wheat production in major wheat-growing regions, including Central Anatolia, the Mediterranean region, Southeast Anatolia, West Marmara and West Black Sea of Türkiye (Demirhan and Bayraktar, 2025). Spring rainfall, in particular, exerts a pivotal role in determining yield outcomes due to its alignment with key phenological stages such as heading, flowering, and grain filling in addition to winter water budget (Passioura, 2007). It has been demonstrated that spring rainfall can serve as a buffer against terminal drought, a common constraint in Mediterranean regions where precipitation sharply declines from late spring onward. In instances where spring rainfall is inadequate, wheat crops are usually faced to residual soil moisture during the most important crucial phenological stages (Flohr et al., 2020). It has been determined that this situation has a significant impact on the effects of heat stress, particularly during the processes of anthesis and early grain filling. At these times, elevated temperatures within the canopy can have a deleterious effect on pollen viability and the subsequent reduction in grain set (Farooq et al., 2011).

Anthesis time is known to be the most important phenological developmental period in cereals, which determines the number of grains (results of sterility/fertility of spikelets) per ear and thus the yield. During this period, plants are highly sensitive to the most important abiotic (temperature and water scarcity) and biotic (insect and disease agents) stress factors. The timing and shifting in these crucial phenological stages (anthesis and post-anthesis) cause to face to stress conditions (drought and heat: >32-36°C) that result with greatly reduced grain formation and development of wheat plants resulting high yield variability. Heat stress conditions cause anther sterility by affecting pollen cell and microspore and high temperature of above 30ºC during anthesis may result with complete sterility depending on wheat genotypes (Akter and Rafiqul Islam, 2017). During the wheat growing season, 1°C increase in the average temperature value causes a decrease in wheat yield by approximately 5-8%. (Mirosavljević et al., 2024; Craufurd and Wheeler, 2009). In addition ear initiation and expansion may be affected by drought at stem elongation stage resulting as reducing plant biomass and the number of grains per ear which is limiting the higher yield potential (Pantha et al., 2024).

SPAD readings have been shown to have the potential to improve yield and quality prediction and allow for further evaluations to what extent is this relationship affected by the environment. SPAD values are also used in breeding programs for screening and selection of drought tolerant wheat cultivars. Additionally assessment of photosynthetic pigments is an important indicator of senescence related to yield and its components (Barutçular et al., 2016). It was posited that SPAD measurements represent a significant approach in the prediction of grain yield, and that generative period measurements are more efficacious than vegetative period measurements for this purpose (Monostori et al., 2016). In general, SPAD chlorophyll measurements provide essential information about the tolerance mechanism of genotypes under drought conditions. The stay-green trait in wheat is characterized by the prolonged greenness of flag leaf (after anthesis) during grain filling periods supporting dry matter accumulation by sustaining photosynthetic activity in plant's organs even under combined stress conditions (Sultana et al., 2021).

In overall, spring drought and heat stress significantly not only influence yield and its formation but also the chemical composition of wheat grains, particularly affecting protein and is quality. It has been demonstrated that the total protein content and gluten content increase by 65% and 32%, respectively, when subjected to combined heat and drought stress in comparison with control conditions (Lama et al., 2023). In addition, wheat flour color is an important in bakery products for appearance. Heat and drought stress can lead to decrease in brightness color spectrum (L*) of flour which means to appear darker. It is also plausible to observe redness (a*) and yellowness (b*) which are related to protein and pigment concentrations change in grain under combined stress conditions.

In contrast, whole wheat grain is distinguished by its significant contributions to health. It is notable for its high content of phenolic compounds and vitamins, which underscore its importance in daily nutrition and its role in promoting overall health and well-being. These health contributing compounds are mainly located in the outer layers of grain such as aleurone, testa and pericarp (Martini et al., 2015). It is evident that stress conditions result in alterations to the morphological and chemical structures of grains. Consequently, there can be considerable changes in the amount of these chemicals.

As a result, the aim of this study is to simulate the drought and heat stresses that occur in the most important important generative periods related to grain structure and yield formation of wheat to examine the changes in physiological, yield and important quality characteristics of the plant. In general terms, the objective of this study mentioned as follows;

a. To reveal the changes in flag leaf SPAD chlorophyll value and dry matter accumulation under stress conditions during the generative period,

b. To determine the level of change of important quality traits under stress conditions,

c. To examine the change in grain structure at the color level and to examine the response of the antioxidant activity and phenolic contents of the grain under stress conditions,

d. To examine the senescence of the wheat cultivars examined under limited irrigation conditions and high temperature conditions.

MATERIALS AND METHODS

Experimental design and conditions

The experiment was conducted and designed to create two distinct stress-inducing environments in semi-controlled greenhouse conditions to located at Aydın Adnan Menderes University, Faculty of Agriculture in Aydın. The commonly grown 4 bread wheat cultivars adapted to in Aegean parts of Türkiye used as plant material named Ceyhan 99, Efe, Masaccio and Osmaniyem. Experimental soil was collected from the field area at 0-30 cm depth before sowing the seeds and then analyzed for physico-chemical properties and water holding capacity (%). The experimental soil characteristics are loamy sand with slightly alkaline pH level (8.3). The organic content of the soil is low (1.6 %) while phosphorus (10.7 ppm), potassium (305 ppm), calcium and magnesium were high level in the pot experimental soil. All the materials were sown to 25 cm diameter pots according to split plot design with three replications (5 plants/pot) in 2022. In all trials, N fertilization was applied to plants at the pre-sowing, tillering and stem elongation stages at rates of 0.39, 1.15 and 0.825 kg/ha, respectively.

To adjust and simulate the environmental constraints with minimized water supply 4 irrigation levels of 25 % ($IR_{25\%}$), 50 % ($IR_{50\%}$), 75 % ($IR_{75\%}$) of the maximum water holding capacity (WHC; $IR_{100\%}$) were set in the pots by using gravimetric calculation method. For this purpose, WHC 100% was calculated as;

[WHC 100%: (Weight saturated soil-Weight dry soil)/Weight dry soil)*100] by assessing the soil moisture level by using calibrated cylinders (100 cm^3) of the fully saturated water (3 h in water for saturation and the draining of 2 h) and of the dry soil (24 h, 105ºC). The simulation of post-generative drought conditions was conducted through the application of daily irrigation to pots from the stem elongation stage (BBCH 31) to harvest of the plants. In order to induce conditions of drought and heat stress, the internal temperature of the greenhouse was hourly recorded during the generative development periods (Figure 1). During the course of the experiment in generative growth stages, which spanned 45 days, the maximum temperature recorded within the greenhouse was higher than upper limit (≥ 30º C) on 35 days. This resulted in heat stress during all of the observed generative growth periods.

Evaluated parameters and measurement details

For this study, the extended BBCH-scale for cereals were used to describe the all phenological stages of wheat plants (Meier, 2018). Agronomic, physiological, quality and antioxidant properties such as number of grains per ear (GN), ear yield (g: EY), flag leaf area (cm^2, $LeafA_{FLAG}$), SPAD chlorophyll change observations in anthesis and post-anthesis stages: SPAD measurement in anthesis ($SPAD_{ANT}$: BBCH 65), SPAD measurement in medium milk stage ($SPAD_{MILK}$: BBCH 75), SPAD measurement in soft dough stage ($SPAD_{DOU}$: BBCH 85), total biomass dry matter calculations in anthesis and post-anthesis stages: total biomass dry matter (%) in anthesis (DM_{ANT}: BBCH 65), total biomass dry matter (%) in medium milk stage (DM_{MILK}: BBCH 75), total biomass dry matter (%) in soft dough stage (DM_{DOU}: BBCH 85), grain protein, starch, fiber ratios (%), total phenolic content (µg GAE/g), total antioxidant activity (% DPPH radical scavenging) and grain color (brightness: L*, redness: a* and yellowness: b*) were investigated.

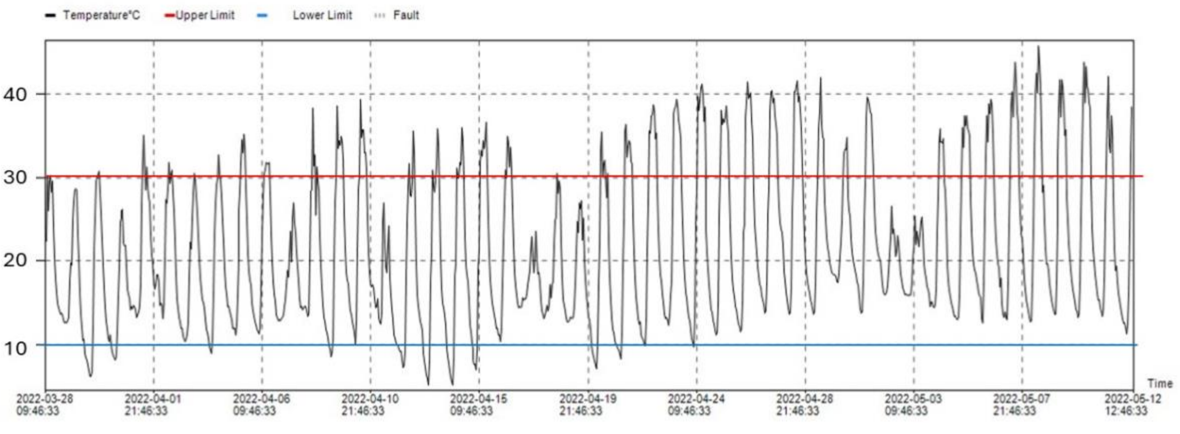

Figure 1. Daily hourly recorded temperature data during generative growth periods (Elitech Data logger; upper limit: ≥30ºC)

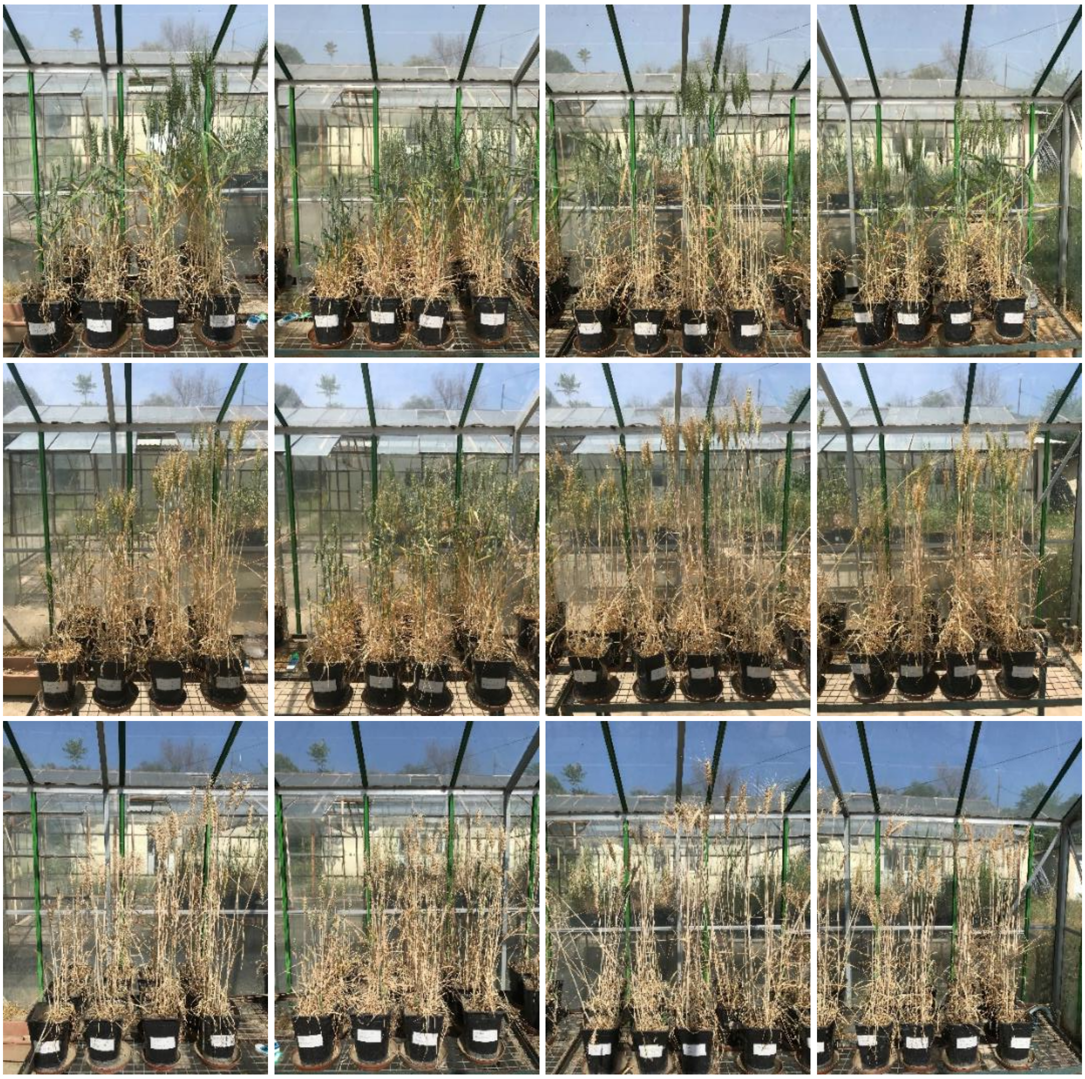

Figure 2. Images of senescence of wheat plants affected by combined stress conditions in grain filling periods (a: BBCH 75: Medium milk stage, b: BBCH 85: Soft dough stage, c: BBCH 99: Harvest; the order of the irrigation regimes from the left to the right is $IR_{25\%}$, $IR_{50\%}$, $IR_{75\%}$ and $IR_{100\%}$ and for cultivars: Ceyhan 99, Masaccio, Efe and Osmaniyem)

With the combination of heat and water stress conditions Soil Plant Analysis Development flag leaf (SPAD) chlorophyll content was measured to observe the senescence of plants during generative growth stages mentioned above. The chlorophyll measurements were conducted by using chlorophyll meter (SPAD-502, Konica Minolta, Japan). The flag leaf area measurement was performed by using LICOR (Lincoln, NE, USA) LI-3000C portable leaf area meter when flag leaf of plants fully visible (BBCH 47). Subsequent to the SPAD measurements, dry matter content measurements (24 h, 105ºC) were made by sampling randomly selected wheat plants above ground biomass (Figure 2.). After harvest the seeds were milled to whole wheat flour (0.8 mm) for quality and antioxidant analysis stored at +4ºC. The Near Infrared Reflected Spectroscopy (NIRS) method was used to analyze crude protein, starch and fiber content of wheat flour using Bruker MPA TM (Bruker, Ettlingen, Germany). The spectral grain color analysis of wheat flour was measured by using HunterLab Color Flex device (Reston, Virginia, USA). To determine total phenolic content and antioxidant activity of wheat flour acidic methanol solution (HCL/methanol/water, 1:80:10 v/v) was used and mixed with 1 g ground whole wheat flour under nitrogen gas for 1 h, then centrifuged (5000 rpm, 20 min.) then transferred to tubes and stored at +4ºC until phenol and antioxidant analysis. Folin-Ciocalteu method was used to determine total phenolic content described by Kaluza et al. (1980) and Ragaee et al. (2006) by using gallic acid as standard. For the total antioxidant activity of wheat samples, the 2,2-diphenyl-1-picrylhydrazyl (DPPH) free radical scavenging method was used. In the last, the absorbance measurements of total phenolic content (725 nm) and antioxidant activity (517 nm) extracts were determined by Thermo Scientific spectrophotometer (Beta et al., 2005; Ma et al., 2014).

The data was subjected to analysis of variance for each parameter and all data were analyzed by using ANOVA and LSD test ($p \leq 0.05$) techniques in the "agricolae" package in R Studio v4 (de Mendiburu, 2019) statistical analysis software.

RESULTS AND DISCUSSION

ANOVA results for all parameters

According to ANOVA statistical analysis results, significant interaction ($p \leq 0.01$ and 0.05) was identified between variety and irrigation interaction (IrrixCul), with notable changes observed in anthesis and post-anthesis dry matter composition and chlorophyll concentration (SPAD), quality, and antioxidant properties except for flag leaf area and protein ratio of bread wheat varieties under varying water stress conditions. Irrigation in different WHC values in post-generative periods of wheat caused statistically significant differences ($p \leq 0.01$) in all evaluated parameters (except grain yellowness color; b*). At the same time, the cultivar factor also had a significant effect ($p \leq 0.01$ and 0.05) on all the characteristics that were analyzed (Table 1 and Table 2).

Table 1. Analysis of variance on irrigation regimes and cultivars for agronomic and physiological characteristics

		Mean squares								
Source	Df	G_N	E_Y	$LeafA_{FLAG}$	$SPAD_{ANT}$	DM_{ANT}	$SPAD_{MILK}$	DM_{MILK}	$SPAD_{DOU}$	DM_{DOU}
IR	3	695.2**	0.93**	487.6**	200.7**	119.6**	1098.0**	764.2**	1236.6**	143.8**
Cul	3	144.0**	0.37**	217.4**	404.7**	11.9ns	905.9**	719.7**	626.7**	1058.8**
IRxCul	9	21.2**	0.05**	20.3ns	63.7**	26.9*	151.8**	238.6**	74.4**	221.3**
Error	24	2.42	0.01	14.4	0.64	9.77	3.20	17.1	7.5	15.5

IR: Irrigation regimes; Cul: Cultivar; G_N: Number of grains per ear; E_Y: Ear Yield (g); $LeafA_{FLAG}$: Flag leaf area (cm^2); $SPAD_{ANT}$: SPAD chlorophyll value in anthesis stage (BBCH 65); DM_{ANT}: Total biomass dry matter (%) in anthesis stage; $SPAD_{MILK}$: SPAD chlorophyll value in medium milk stage (BBCH 75); DM_{ANT}: Total biomass dry matter (%) in medium milk stage; $SPAD_{DOU}$: SPAD chlorophyll value in soft dough stage (BBCH 85); DM_{ANT}: Total biomass dry matter (%) in soft dough stage.

Table 2. Analysis of variance on irrigation regimes and cultivars for quality and antioxidant characteristics

		Mean squares							
Source	Df	Protein	Starch	Fiber	L*	a*	b*	Phe	Aac
IR	3	47.5**	19.7**	2.65**	5.73**	0.22**	0.28ns	4055.2**	2.56**
Cul	3	6.46*	106.0**	3.79**	3.23**	0.71**	5.11**	8907.3**	6.37**
IRxCul	9	3.78ns	21.9**	0.55**	2.81**	0.29**	0.36*	4590.3**	9.19**
Error	30	1.73	1.35	0.02	0.34	0.03	0.13	43.9	0.31

Protein: Crude Protein Ratio (%); Starch: Crude starch ratio (%); Phe: Total phenolic content (µg GAE/g); Aac: Total antioxidant activity (DPPH %)

The results of ear yield formation, SPAD chlorophyll content and dry matter

The impact of heat stress, both in the pre- and post-anthesis phases, on grain number and yield traits in wheat has proven to be a subject of significant interest. The previous study demonstrates that pre-anthesis heat stress exerts a more pronounced negative effect on grain number resulted with grain abortion, while post-anthesis heat stress primarily reduces grain weight, ultimately lowering total yield (Kim et al., 2024).

From the onset of the generative development period, substantial losses occurred in yield and flag leaf area traits under varying levels of water and heat stress conditions applied to bread wheat varieties adapted to the region due to the escalation in combined stress. A subsequent analysis of the G_N revealed a broad distribution ranging from 7.16 to 31.8 across varying water holding capacity levels. A particularly notable finding was that under conditions of water stress ($IR_{25\%}$ and $IR_{50\%}$), the number of grains decreased significantly, with the highest values being attained at the $IR_{100\%}$ (26.8) doses and $IR_{75\%}$ (22.1). However, it is noteworthy that the Masaccio cultivar exhibited lower values in the majority of water treatments in comparison to other cultivars (Table 3).

The analysis of water stress conditions in terms of single ear yield revealed that the Efe cultivar exhibited superior performance in both limited irrigation and full irrigation scenarios, surpassing the other cultivars. Notably, at an irrigation level of 50% ($IR_{50\%}$), which is considered a restricted moisture condition, Efe exhibited a notably higher ear yield of 1.09 g. In contrast, a substantial decline in E_Y was observed in all varieties under limited irrigation ($IR_{25\%}$). Notably, the Ceyhan-99, Efe and Osmaniyem varieties exhibited the highest yield values at full water holding capacity ($IR_{100\%}$). At the level of all water treatments and cultivars, Ceyhan-99 reached the highest yield value of 1.110 g at the $IR_{100\%}$ dose, and Efe reached the highest yield value of 1.113 g at the $IR_{75\%}$ dose (Table 3.). It is hypothesized that the lower values of Masaccio in the G_N and E_Y compared to the other cultivars may be due to the cultivar's comparatively later and slower development. It is notable that this variety exhibits a notably high yield potential (approx. 9-10 t/ha) within the region, provided that sufficient soil moisture (with supplemental irrigation in ear formation) is available during the extended generative period.

Table 3. Number of grains per ear (G_N), ear yield (E_Y, g/ear) and flag leaf area ($LeafA_{FLAG}$, cm^2) results under combined stress conditions during post generative periods of bread wheat cultivars

		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
G_N	$IR_{25\%}$	9.61 hi	9.99 h	7.16 i	8.81 hi	8.89
	$IR_{50\%}$	18.8 e	22.6 d	15.3 fg	17.3 ef	18.5
	$IR_{75\%}$	22.8 cd	26.0 b	14.1 g	25.5 bc	22.1
	$IR_{100\%}$	31.8 a	28.0 b	19.3 e	28.1 b	26.8
	Mean C.	20.7	21.6	14.0	19.9	
Lsd IR: 1.94; Lsd C: 1.31; Lsd IR*Cul: 2.74						
		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
E_Y (g)	$IR_{25\%}$	0.243 i	0.416 ghi	0.246 i	0.373 hi	0.320
	$IR_{50\%}$	0.783 cde	1.093 ab	0.463 fgh	0.586 efg	0.731
	$IR_{75\%}$	0.830 cd	1.113 a	0.553 fgh	0.893 bc	0.847
	$IR_{100\%}$	1.110 a	1.033 ab	0.663 def	1.036 ab	0.960
	Mean C.	0.741	0.914	0.481	0.722	
Lsd IR: 0.07; Lsd C: 0.11; Lsd IR*Cul: 0.20						
		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
$LeafA_{FLAG}$ (cm^2)	$IR_{25\%}$	10.5	9.37	8.17	13.5	10.3 C
	$IR_{50\%}$	15.4	14.1	7.42	18.6	13.9 C
	$IR_{75\%}$	24.5	20.8	13.3	20.3	19.7 B
	$IR_{100\%}$	26.8	28.1	15.0	29.2	24.8 A
	Mean C.	19.3 A	18.1 A	11.0 B	20.4 A	

Lsd IR: 3.61; Lsd C: 3.24

Pre-anthesis drought stress has been shown to reduce leaf area and chlorophyll content, leading to reduced photosynthetic capacity and potential yield loss. Post-anthesis drought stress also affects chlorophyll content. Ahmadi-Lajihani and Emam (2016) suggests that higher chlorophyll content under water deficit conditions is associated with increased photosynthetic rates. Maintaining stay-green duration of flag leaf with greater leaf area during grain filling contributes to improved yield under drought stress.

It was determined that the flag leaf area of wheat plants decreased significantly depending on the limited soil moisture and high temperature conditions initiated during the stem elongation (BBCH 31) to harvest period and heat stress. A marked decline in $LeafA_{FLAG}$ was observed in response to declining soil moisture levels, particularly in cases where a linear decrease occurred, commencing from the point of full water-holding capacity ($IR_{100\%}$) and progressing towards conditions of limited irrigation conditions ($IR_{50\%}$ and $IR_{25\%}$). As given in Table 3, the Masaccio cultivar had the smallest $LeafA_{FLAG}$ in addition to other yield parameters ($p\leq0.01$).

The analysis of flag leaf SPAD chlorophyll values and dry matter changes was conducted during the anthesis and post-anthesis phenological growth periods. This analysis was undertaken to determine the senescence levels of plants and to observe dry matter accumulation in wheat plants under conditions of limited soil moisture and high temperature stress (Figure 3). It is noteworthy that, Ceyhan-99 cultivar has attained the highest SPAD values with the least chlorophyll change in all development periods under the condition of $IR_{75\%}$. In addition, studies have shown that drought-tolerant wheat varieties maintain higher leaf chlorophyll content under drought conditions than sensitive genotypes. This trait is positively correlated with higher yield under stress (Ghaffar et al. 2023).

In addition to the variation in SPAD chlorophyll, when the changes in dry matter accumulation during these developmental periods was analyzed, the cultivar Efe, which has the highest ear yield E_Y, g), caused the highest dry matter accumulation during the grain filling periods (DM_{MILK} and DM_{DOU}) and reflected the assimilates it stored positively as yield, even under water and heat stress. Furthermore, both the Ceylan-99 and Efe cultivars demonstrated the capacity to maintain their yield values, exhibiting reduced senescence and enhanced assimilate accumulation under conditions of combined stress. In general, the level of greenness of the flag leaves of the cultivars decreased significantly under restricted irrigation conditions, and they had the lowest value at $IR_{25\%}$ under water stress conditions, especially at dough maturity. At the end of this growth period, Efe exhibited the highest accumulation of dry matter at the highest water holding capacity ($IR_{100\%}$) under water and heat stress, while the Ceyhan-99 with its high level of almost ≈80% dry matter accumulation at $IR_{50\%}$ under restricted irrigation conditions, achieved significant results under both stress conditions (Figure 3.).

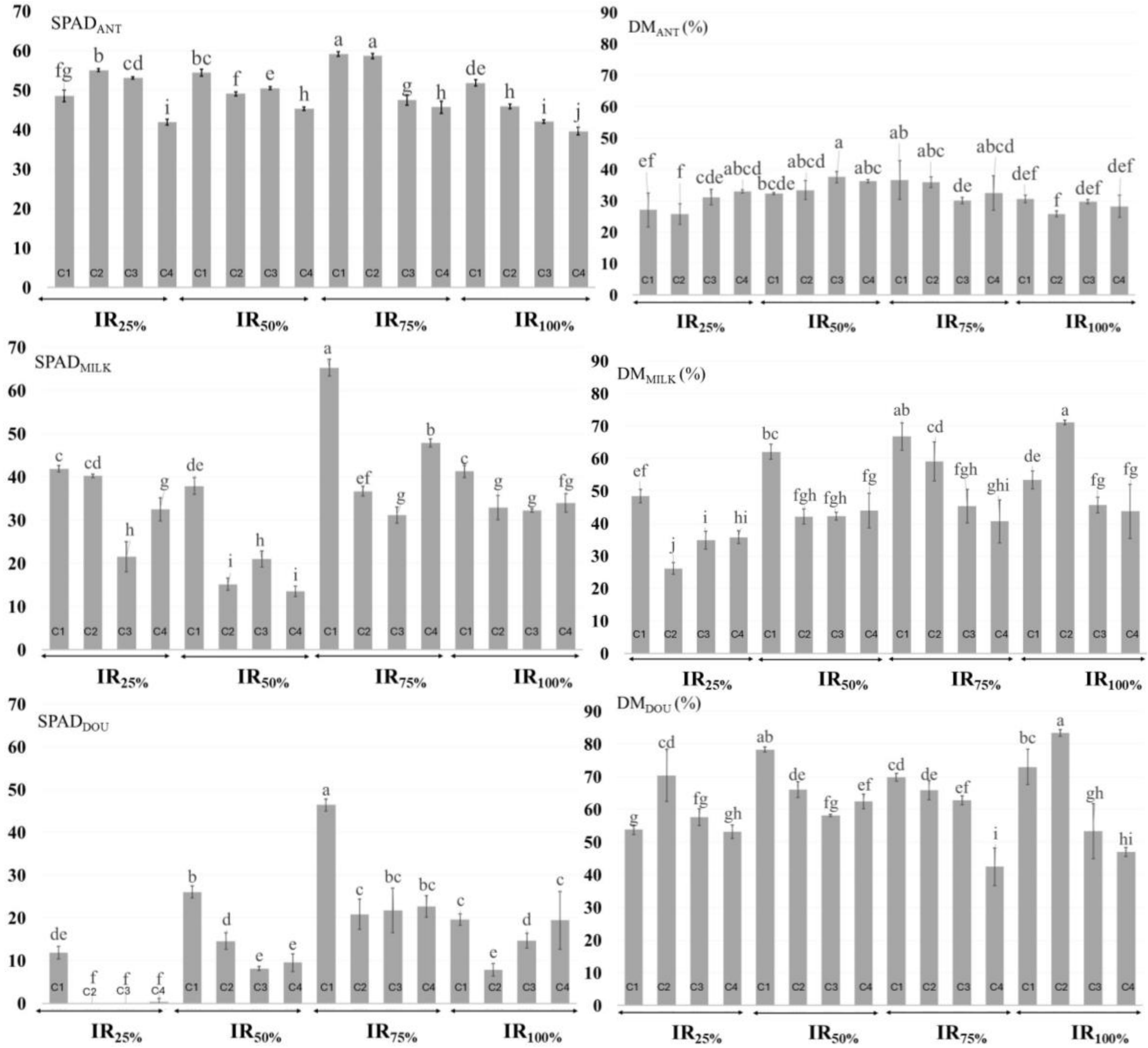

Figure 3. Flag leaf SPAD chlorophyll and dry matter content change in anthesis and post-anthesis growth periods in water and heat stress conditions (C1: Ceyhan 99, C2: Efe, C3: Masaccio, C4: Osmaniyem)

As was evidenced in previous studies, drought conditions have been demonstrated to result in a considerable decline in both chlorophyll concentration and total biomass in wheat. A study involving 40 local wheat cultivars found that drought stress led to notable decreases in shoot and root fresh and dry biomass, plant height, flag leaf area, and total chlorophyll content (SPAD). Specifically, the reduction in total chlorophyll content under drought stress was found to be 35% (Ghaffar et al. 2023).

It is imperative to maintaining the soil moisture within the (optimal range of) 75% to 100% of soil water holding capacity to ensure optimal yield in wheat during these critical developmental phases, which frequently align with the spring season. It is widely acknowledged that a decline in spring precipitation, consequent to climate change, has the potential to engender substantial reductions in yield components during these developmental phases (grain-filling) of plant growth (Nazim Ud Dowla et al., 2018).

The results of grain quality and flour color characteristics

In the context of combined stress conditions, Ceyhan 99 exhibited a notable increase in yield, chlorophyll and dry matter accumulation, while Efe demonstrated a marked enhancement in protein and fiber ratios. While the protein ratio in grain increased significantly (16.2 and 17.3%) under limited water conditions, the protein ratio decreased (14.6 and 12.7%) under sufficient moisture conditions. The protein content of wheat increased by approximately 36% under the highest restricted irrigation dose (IR$_{25\%}$). Post-anthesis heat and drought stress have been demonstrated to significantly influence the protein content and composition of wheat grains. A number of studies have reported an increase in total protein content under such stress conditions. For instance, Fernie et al. (2022) reviewed that exposure to temperatures exceeding 30°C led to a 0.78% to 0.82% increase in grain protein content for every unit increase in heat degree days above this threshold. A similar outcome was reported by another study, which found that a 2-day heat treatment at 38°C, applied 20 days after flowering, resulted in a 5.0% and 2.7% increase in total protein content for two different wheat cultivars, compared to control conditions. Moreover, a combination of heat and drought stress has been documented to enhance total protein content by 65% and gluten content by 32% in comparison with control conditions (Lama et al., 2023). As a result, these stressors demonstrated significant positive influence on grain protein value, particularly affecting dough properties and end-use quality.

Table 4. Grain quality characteristics results under combined stress conditions during post generative periods of bread wheat cultivars

		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
Protein (%)	$IR_{25\%}$	17.0	16.2	16.9	19.1	17.3 A
	$IR_{50\%}$	18.5	15.4	16.2	14.5	16.2 A
	$IR_{75\%}$	15.6	14.3	14.7	13.8	14.6 B
	$IR_{100\%}$	14.0	12.8	12.5	11.6	12.7 C
	Mean C.	16.2 A	14.7 B	15.1 B	14.7 B	
Lsd IR: 1.22; Lsd C: 1.12						
		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
Starch (%)	$IR_{25\%}$	58.8 de	56.9 ef	59.5 cd	67.1 a	60.6
	$IR_{50\%}$	55.4 f	59.5 cd	60.1 cd	64.9 b	60.0
	$IR_{75\%}$	56.4 f	65.1 b	65.0 b	64.0 b	62.6
	$IR_{100\%}$	59.8 cd	64.4 b	61.2 c	63.5 b	62.2
	Mean C.	57.6	61.5	61.5	64.9	
Lsd IR: 1.11; Lsd C: 0.99; Lsd IR*Cul: 1.94						
		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
Fiber (%)	$IR_{25\%}$	3.38 de	4.56 a	3.77 c	2.61 g	3.58
	$IR_{50\%}$	3.79 c	3.43 d	3.34 de	2.51 gh	3.26
	$IR_{75\%}$	4.15 b	3.73 c	3.09 f	2.27 hi	3.31
	$IR_{100\%}$	3.14 ef	2.34 hi	2.36 h	2.11 i	2.48
	Mean C.	3.61	3.51	3.14	2.37	

Lsd IR: 0.19; Lsd C: 0.11; Lsd IR*Cul: 0.24

In general, the starch ratio values decreased in limited irrigation dose, while the Osmaniyem variety reached the highest value with 67.1% in $IR_{25\%}$ dose. It is notable that the starch ratio (55.4-67.1%), which constitutes a significant proportion of the grain, exhibits a decline under stress conditions. The Ceyhan 99 variety demonstrated notable performance in terms of yield and protein ratio, while exhibiting low starch ratio values under both limited and full irrigation conditions. Conversely, the Osmaniyem variety exhibited a contrasting response, exhibiting the lowest fiber ratio values under all water doses. The highest fiber ratio values were obtained at the highest restricted water level. Under conditions of water and temperature stress, an increase in protein and fiber ratio values was observed at 25% of soil water holding capacity level (Table 4).

Pre- and post-anthesis drought and heat stress have been demonstrated to exert a significant influence on the color attributes of wheat grains, the L* (brightness), a* (redness), and b* (yellowness) values. It can be mentioned that water and heat stress during the grain-filling period constitute significant abiotic factors that are capable of constraining both grain yield and quality in wheat. While the study primarily focuses on yield and protein content, it implies that water scarcity and heat stress can also affect grain quality parameters, which may include color attributes (Mahdavi et al. 2022). Heat stress during grain development has been reported to affect grain appearance, including color attributes. Specifically, heat stress can lead to changes in grain brightness (L*), redness (a*), and yellowness (b*), although the extent of these changes depends on the timing and severity of the stress, as well as the genotype (Hafeez et al. 2023).

An examination of the results pertaining to the L* of flour color revealed that the maximum value was attained at $IR_{50\%}$ under conditions of limited irrigation. Conversely, as the moisture content increased, the brightness value diminished. While Ceyhan-99 exhibited the lowest value on a cultivar basis, divergent results were obtained, particularly regarding interactions. In the case of limited irrigation ($IR_{50\%}$), the brightness rate increased for the Ceyhan-99, Efe and Osmaniyem cultivars, while Masaccio reached the highest values under full water conditions ($IR_{100\%}$) and restricted irrigation conditions ($IR_{25\%}$), although no clear result was obtained. It is hypothesized that there will not be sufficient level of assimilate accumulation in the grain filling stage under limited irrigation conditions and starch ratio will be less as an important factor in the increase of L* value. While this hypothesis is supported by the findings of low starch and L* ratios in Ceyhan99 under $IR_{25\%}$ conditions, the overall outcomes of the water-variety interaction are complex (Table 5).

Table 5. Bread wheat grain color (Brightness: L*, redness: a*, and yellowness: b*) results under combined stress conditions during post generative periods of bread wheat cultivars

		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
L* Brightness	$IR_{25\%}$	80.3 f	83.8 a-d	83.8 abc	81.6 f	82.4
	$IR_{50\%}$	83.8 abc	84.5 a	83.6 a-d	84.0 ab	84.0
	$IR_{75\%}$	83.4 bcd	82.3 ef	82.9 cde	83.3 bcd	83.0
	$IR_{100\%}$	82.8 de	83.6 a-d	84.4 a	83.2 b-e	83.5
	Mean C.	82.6	83.6	83.7	83.0	
Lsd IR: 0.629; Lsd C: 0.484; Lsd IR*Cul: 0.978						
		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
a* Redness	$IR_{25\%}$	2.14 b-e	1.71 fg	2.09 cde	1.98 def	1.98
	$IR_{50\%}$	2.41 b	1.86 efg	1.95 def	2.19 bcd	2.10
	$IR_{75\%}$	2.32 bc	2.36 bc	1.70 fg	1.69 fg	2.02
	$IR_{100\%}$	2.92 a	1.60 g	2.34 bc	2.30 bc	2.29
	Mean C.	2.45	1.88	2.02	2.04	
Lsd IR: 0.197; Lsd C: 0.145 Lsd IR*Cul: 1.94						
		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
b* Yellowness	$IR_{25\%}$	10.5 def	11.2 ab	10.2 def	10.4 def	10.6
	$IR_{50\%}$	11.5 a	11.3 ab	9.64 g	10.5 cde	10.7
	$IR_{75\%}$	11.4 a	11.7 a	9.92 fg	10.4 def	10.9
	$IR_{100\%}$	11.7 a	11.1 abc	10.1 efg	10.8 bcd	10.9
	Mean C.	11.3	11.3	9.99	10.5	

Lsd IR: 0.19; Lsd C: 0.288; Lsd IR*Cul: 0.608

With regard to the redness (a*) value, the Ceyhan-99 variety was distinguished by its redder flour colour in comparison to the other varieties under all water conditions. The interaction between the Irri*Cul factor was not clearly determined by obtaining high/low values at full and limited irrigation doses. With regard to yellowness (b*), Ceyhan-99 exhibited elevated values in all water conditions except $IR_{25\%}$. The grain b* color value of the Ceyhan-99 was found to decrease significantly under limited water conditions. Furthermore, a comparison of Ceyhan-99 and Efe cultivars revealed that they exhibited higher values in all water conditions when compared to other cultivars. It is particularly noteworthy that the Ceyhan-99 and Efe varieties exhibited higher values in yellowness, a trait that is a significant criterion for quality (Table 5.). Although direct studies on these parameters under such stress conditions are limited, more targeted studies are required on these parameters. In summary, while direct measurements of L*, a*, and b* values under post-anthesis drought and heat stress are scarce, existing research suggests that such stress conditions can alter grain color. These changes are likely due to disruptions in pigment biosynthesis and deposition, as well as accelerated grain maturation.

The results of grain antioxidant activity and phenolic content

The total phenolic content and antioxidant activity of wheat grain, which is of significance to human health and is the most consumed daily food, demonstrated significant variation among the cultivars at differing water levels. Notably, the total phenol content and antioxidant activity exhibited their lowest values (2652 µg GAE/g, 31.6%) at full irrigation doses. Post-anthesis drought and heat stress have been demonstrated to significantly influence the accumulation of phenolic acids and antioxidant properties in wheat grains. A study examining six durum wheat cultivars under varying growth conditions found that ferulic acid was the predominant phenolic acid, ranging from 390.1 to 785.6 µg/g dry matter across all cultivars and conditions. It is of particular interest that severe drought conditions resulted in an increase in ferulic acid and total phenolic acids. Conversely, heat stress primarily enhanced the accumulation of minor individual phenolic acids rather than total phenolic acids (Laddomada et al., 2021). Osmaniyem exhibited the highest total phenol content (3431 µg GAE/g at $IR_{25\%}$ and 3381 µg GAE/g at $IR_{50\%}$) at limited irrigation doses, while the Ceyhan-99 exhibited the lowest content (2127 µg GAE/g at $IR_{100\%}$ full water holding capacity). With regard to antioxidant activity, the lowest value (31.6%) was observed at full water holding capacity. Furthermore, the Masaccio variety exhibited the highest antioxidant activity value at $IR_{50\%}$ under limited soil moisture conditions, while the Ceyhan 99 variety demonstrated the lowest antioxidant activity value (28.7%) at $IR_{100\%}$ (Table 6).

Table 6. Total phenolic acid content given in gallic acid equivalent (µg/g) and DDPH radical scavenging activity (total antioxidant: % inhibition) results under combined stress conditions during post generative periods of bread wheat cultivars

		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
Total Phenolic (µg GAE/g)	$IR_{25\%}$	2959 d	2863 d	2859 d	3431 a	3028
	$IR_{50\%}$	2173 fg	2874 d	2519 e	3381 ab	2737
	$IR_{75\%}$	2573 e	3251 c	2866 d	3239 c	2982
	$IR_{100\%}$	2127 g	2939 d	3291 bc	2250 f	2652
	Mean C.	2458	2982	2884	3075	
Lsd IR: 69.8; Lsd C: 55.0; Lsd IR*Cul: 110.5						
		Ceyhan-99	Efe	Masaccio	Osmaniyem	Mean IR.
Total Aac (DPPH %)	$IR_{25\%}$	33.2 bcd	32.2 ef	32.9 cde	32.6 def	32.7
	$IR_{50\%}$	31.1 gh	33.6 bc	34.6 a	30.0 i	32.3
	$IR_{75\%}$	32.9 cde	33.9 ab	32.1 ef	30.6 hi	32.4
	$IR_{100\%}$	28.7 j	31.7 fg	32.0 ef	34.0 ab	31.6
	Mean C.	31.5	32.9	32.9	31.8	
Lsd IR: 0.49; Lsd C: 0.48; Lsd IR*Cul: 0.93						

CONCLUSION

The drought that has occurred in recent years has had a detrimental effect on both winter and summer crops due to the spring and summer drought conditions in the Aegean region of Türkiye. This research focuses on the critical developmental stages of wheat, where climate factors notably impact yields, end-use quality and also health benefits. The evaluation of the obtained results indicated that the water and heat stress conditions applied from the stem elongation period onwards exerted a significantly negative impact on yield formation in the ear, flag leaf area, flag leaf SPAD chlorophyll change and biomass dry matter formation. However, it was determined that cultivars with optimal yield levels were more prominent than those with very high yield potential in the region, in terms of both yields, SPAD and dry matter accumulation. This finding suggests that these cultivars possess a higher tolerance for increasing stress conditions, exhibiting a lesser effect on yield characteristics and plant senescence levels. Consequently, it can be concluded that these cultivars, which also stand out in terms of some quality characteristics, can better tolerate adverse climate conditions. For instance, drought and heat stress have been demonstrated to have a detrimental effect on flag leaf chlorophyll content and dry matter accumulation in bread wheat (*Triticum aestivum* L.). However, the extent to which these effects manifest varies between genotypes, thereby suggesting that breeding programs with a focus on stress tolerance could mitigate these adverse effects.

In general terms, it has been found that the flag leaf senescence level in wheat increases and the yield potential decreases significantly under combined stress (drought and heat) levels. However, some quality, phenol and antioxidant activity characteristics have changed positively. The findings of this study, conducted under controlled conditions, indicate that the yield potential of wheat plants is significantly diminished under conditions of generative period stress. It is further understood that adverse conditions will occur in the production amount due to the effect of climate change. It is therefore concluded that conducting further studies under field conditions is of great importance in order to provide clearer information.

Compliance with Ethical Standards

Peer-review

Externally peer-reviewed.

Declaration of Interests

There are not any conflict of interest.

Author contribution

A.Y; experiment conceptualization, methodology, data processing, investigation, writing and editing.

Acknowledgments

A.Y is greateful to Prof. Dr. Ömer Erincik and Assist. Prof. Dr. Sevdiye Yorgancı (Aydın Adnan Menderes University, Faculty of Agriculture, Department of Plant Protection) for the experimental facility support (greenhouse). A.Y also sincerely thanks to Dr. Nermin Yaraşır and M.Sc. Melike Demirel Şimsek for their valuable help and assistance with green house experiment observations.

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