



The Effect of Flooding Stress of Varying Durations at Different Growth Stages on Wheat Yield and its Components

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Abstract

This study investigated the effects of flooding stress on bread wheat (*Triticum aestivum* L.) at different growth stages and flooding durations. Two wheat cultivars, flood-tolerant Gönen 98 and susceptible Meta 2002, were subjected to flooding treatments of 10-, 20-, and 30-days during tillering, stem elongation, and heading stages. The research examined various agronomic characteristics, including plant height, number of fertile stems, number of fertile and sterile spikelet, number of grains per unit area, thousand-grain weight, unit area grain yield, biomass and harvest index. Results showed that flooding tolerance varied significantly across growth stages, with stem elongation being particularly susceptible to flooding stress. Short-duration flooding had minimal negative effects and sometimes acted as beneficial irrigation. However, long-duration flooding led to significant reductions in yield components, medium- or long-duration flooding causing up to 74% reduction in some parameters. The study also introduced a Stress Effect Rate (SER) to assess the impact of flooding stress in greater detail. SER values varied depending on flooding duration and growth stage, providing insights into periods of heightened susceptibility to water stress. These findings highlight the importance of considering growth stage-specific flooding tolerance in wheat breeding programs and in developing management strategies for wheat cultivation in flood-prone areas.

Keywords Flooding duration · Growth stages · Stress effect rate · Wheat cultivars

Introduction

Wheat holds a crucial place as a staple food worldwide. It is a vital source of energy, protein, vitamins, and minerals in human nutrition and stands out for its adaptability to diverse climatic conditions. Additionally, it serves as a key raw material for animal feed and various industrial applications (Atchison et al. 2010; Yavas et al. 2012; Tiryakioğlu et al. 2023). Wheat production constitutes an important part of agricultural activities on a global scale and also stands out as a strategic product in world trade (FAO 2025). However, wheat production is increasingly threatened by environmental and economic factors such as global climate change, drought, and dwindling water resources (Bahar and Yildirim 2010; Tiryakioğlu et al. 2024).

Flooding, caused by natural factors like extreme rainfall and snowmelt or human activities such as inadequate infrastructure, results in water exceeding soil absorption capacity and natural drainage paths (Li et al. 2011; Loreti et al. 2016; Beegum et al. 2023). Climate change is exacerbating flood stress, leading to more intense, widespread, and prolonged flooding events (De San Celedonio et al. 2016; Ploschuk et al. 2023; De Castro et al. 2022). In agriculture, flooding directly damages crops by causing root anoxia, which stunts growth and ultimately leads to plant death. This leads to significant yield and economic losses (Abdolshahi et al. 2013; Broughton et al. 2015; Den Besten et al. 2021; Tian et al. 2023). Furthermore, it disrupts soil fertility by leaching essential nutrients, which impairs plant nutrition and ecosystem balance (Broughton et al. 2015; Den Besten et al. 2021).

The tolerance of plants to flooding is determined by various factors. The main factors include are: (i) the sensitivity of the species or cultivar (Manna et al. 2021; Raza et al. 2020; Singh 2023; Ramos Pais 2024), (ii) the developmental stage of the plant at which flooding occurs (Setter and Waters 2003; De San Celedonio et al. 2014; Rivero et

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al. 2022), (iii) the duration of the flooding event (Collaku and Harrison 2002; Malik et al. 2002; Mishra et al. 2023). Unfortunately, the number of studies that address these three factors simultaneously is insufficient. Studies have been conducted by addressing one or two of these factors. Determining wheat yield is a complex process where grain number per unit area is a critical factor, as environmental stressors significantly impact plant productivity by altering seed number and size (González et al. 2005; Rivero et al. 2022). The number of grains per unit area is a function of the number of spikes per unit area and the number of grains per spike (Tiryakioğlu 2024). In wheat, the critical period for yield determination is centered on reproduction, as the flowering season and grain-filling stages are documented as being highly sensitive to abiotic stresses, leading to potential embryos or seed abortion (Rivero et al. 2022; Saharan et al. 2022).

Waterlogging during early growth stages, such as tillering, may allow for physiological adjustments. Consequently, such stress can result in less significant grain yield reductions compared to stress during the highly sensitive reproductive window. In contrast, other studies have shown that early waterlogging can still decrease biomass production during vegetative stages (Malik et al. 2001, 2002; Pang et al. 2004; De San Celedonio et al. 2014; Manna et al. 2021; Rivero et al. 2022). On the other hand, De San Celedonio et al. (2014) reported that waterlogging occurring early in the plant life cycle allows plants to recover from stress through different mechanisms throughout the life cycle once the stress is removed. Robertson et al. (2009) showed that waterlogging in early stages of plant development in wheat delays the tillering period, promoting the emergence of a higher number of tillers and thus delaying the time to flowering. De San Celedonio et al. (2014) reached a similar conclusion, explaining that flowering time is delayed when plants are flooded in the early stages of development. This is likely related to a higher level of tillering, which may compensate for early tillering mortality, resulting in a final spike number per plant equal to or even slightly higher than controls.

There are various studies in the literature on the effect of flooding on different plants. Most of these studies have focused either solely on the stages of development or solely on the duration of exposure. In the present study, trials were conducted using both tolerant and sensitive wheat varieties to evaluate the effects of varying flooding durations at different developmental stages on yield and yield components. Additionally, flooding effects will be analyzed in conjunction with the Stress Effect Rate (SER).

Materials and Methods

Materials

The study was conducted in the research and application area of Hatay Mustafa Kemal University, Faculty of Agriculture, Department of Field Crops (36°19'30"N, 36°11'45"E; 85 m above sea level). Two bread wheat (*Triticum aestivum* L.) cultivars differing in flooding tolerance were used: the flood-tolerant Gönen 98 and the flood-susceptible Meta 2002 (Tiryakioğlu 2015).

Soil Properties

The basic physicochemical properties of the experimental soil were determined prior to the study. The soil was classified as clay-textured (59% clay, 24% silt, 17% sand) with an alkaline pH of 8.18 and low salinity (EC: 0.97 dS m⁻¹). Organic matter (1.33%) and total nitrogen (0.033%) contents were low. Among the available macronutrients, phosphorus was found to be deficient (6.35 ppm), while potassium levels were sufficient (281.3 ppm).

Experimental Design

The experiment was established in containers (86 × 34 × 30 cm) with a total of 72 containers, using a completely randomized design for genotypes (main plot: Gönen 98 and Meta 2002) and growth stages (main factor: tillering, stem elongation, and heading). Flooding duration (0, 10, 20, and 30 days) was arranged as a split-plot factor within genotypes and growth stages, with three replications. The containers were filled with soil taken from the top 30 cm of the field, sieved through a 1 cm mesh. Sowing was done manually in rows to achieve a plant density equivalent to 500 viable seeds m⁻². Before planting, a compound fertilizer (15-15-15) containing nitrogen, phosphorus, and potassium was applied at 13.76 g per container, corresponding to 80 kg ha⁻¹ of pure nutrients. The remaining nitrogen requirement was met during the mid-stem elongation stage (Zadoks Growth Scale, ZGS 33) with ammonium nitrate (26% N), applied at 5.95 g per container, equivalent to 60 kg ha⁻¹ of pure nitrogen.

Irrigation and Flooding Applications

Following sowing, all containers were irrigated uniformly until seedling emergence (10 L per container). After emergence, irrigation continued throughout the growing period by bringing the soil to field capacity. During non-flooding periods (before flooding and after flooding during the recovery phase), irrigation was applied whenever soil moisture

decreased to 20% below field capacity and replenished back to field capacity. Soil moisture content was monitored daily using a digital soil moisture sensor (ProCheck, Decagon Devices Inc.).

Flooding treatments were applied at three growth stages: the beginning of tillering (ZGS 20), stem elongation (ZGS 30), and heading (ZGS 50). The durations included control (0 days), short (10 days), medium (20 days), and long (30 days). Flooding was applied after the soil was fully saturated, creating a minimum water depth of 5 cm above the soil surface. At the end of each flooding period, water was drained through valves located at the bottom of the containers.

Stress Effect Rate (SER)

Plant responses to flooding duration were assessed using the Stress Effect Rate (SER) formula described by Zheng et al. (2023):

$$SER (\%) = \frac{\text{Stress Condition Value} - \text{Control Condition Value}}{\text{Control Condition Value}} \times 100$$

Where, Stress Condition Value=The measured value under stress at day n , Control Condition Value=The corresponding value under non-flooded conditions, SER can take both positive and negative values. A value greater than zero (>0) indicates a beneficial effect of stress, while a value less than zero (<0) indicates a detrimental effect. Results are expressed as percentages.

Statistical Analysis

Data were analyzed using a “completely randomized design for genotypes (A) and periods (B); with flooding duration (C) arranged as a split-plot factor on A and B” through the MSTAT-C software.

Because genotype $\times$ flooding interactions were significant for all traits, the effects of flooding stress were evaluated separately for each genotype. When interactions were significant, general response trends were interpreted

accordingly. The least significant difference (LSD) test was applied for mean comparisons at $p=0.05$. Pearson correlation analysis was performed by using SPSS 27.

The statistical model used in the analysis is presented below:

$$Y_{ijkl} = \mu + A_i + B_j + (AB)_{ij} + \epsilon_{1(ij)k} + C_l + (AC)_{il} + (BC)_{jl} + (ABC)_{ijl} + \epsilon_{2(ijkl)}$$

Where, Y_{ijkl} = Observed response, μ = Overall mean, A_i = Effect of the i th level of factor A, B_j = Effect of the j th level of factor B, $(AB)_{ij}$ = Interaction effect between A and B, $\epsilon_{1(ij)k}$ = Main-plot error, C_l = Effect of the l th level of factor C, $(AC)_{il}$ = Interaction effect between A and C, $(BC)_{jl}$ = Interaction effect between B and C, $(ABC)_{ijl}$ = Three-way interaction effect A $\times$ B $\times$ C, $\epsilon_{2(ijkl)}$ = Sub-plot error.

Results

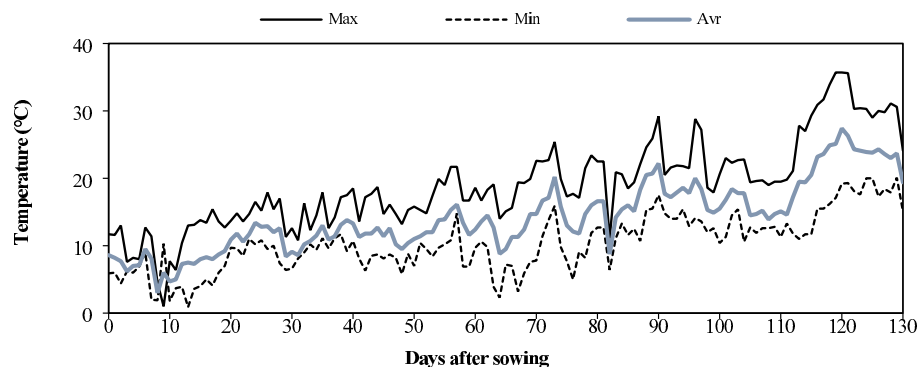
Daily Temperatures and Thermal Period

The changes in daily temperatures in the years studied are given in Fig. 1. Also, the changes in the thermal period from sowing to maturity and from anthesis to maturity can be seen in Fig. 2. It is known that there were suitable growth conditions for wheat production in areas where the average daily temperature is from 10 °C to 25 °C. During the experiment, the lowest monthly average temperature was 3.0 °C and the highest was 26.3 °C. Average temperatures indicated to be suitable for wheat cultivation.

Agronomic Characteristics

The number of fertile stems, the number of fertile spikelets, the number of grains per unit area and thousand-grain weight were affected significantly ($p<0.05$) by genotypes according to the results of ANOVA. However, growth

Fig. 1 Change of the daily maximum, minimum, and average temperature (°C) from sowing to maturity



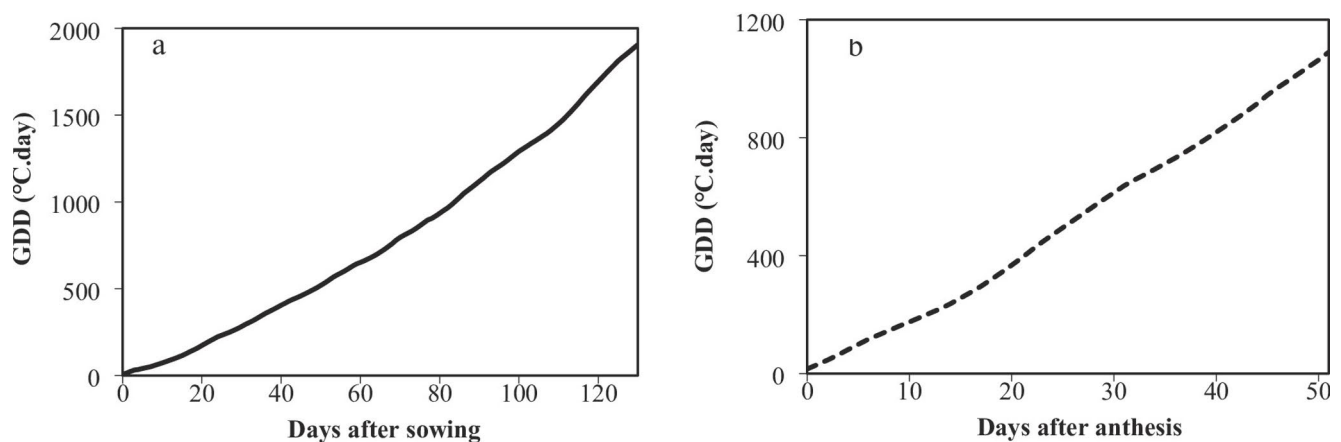


Fig. 2 Change of growing degree days (GDD) from sowing to maturity (a) and from anthesis to maturity (b)

periods and flooding durations affected all parameters significantly (Table 1).

The plant height varied between 51.5 and 61.3 cm according to the mean values for growth stages (Table 2). The highest value was observed in the heading stage, followed by tillering and stem elongation. The plant height was affected more by flooding, especially in the stem elongation stage. For flooding duration, the plant height values ranged from 43.2 cm to 64.3 cm. Short-duration flooding came to the forefront along with the control group with the values of 64.3 cm and 63.3 cm, respectively, while F30 had the minimum value. As expected, the plant height decreased when the plants were exposed to flooding for a long period, like 30 days. According to the genotypes, Meta-2002 was 57.3 cm while Gönen-98 was 56.5 cm.

The number of fertile stems ranged from 427 to 521 for the growth stages, and the maximum value was observed in the tillering stage in contrast to the result of plant height (Table 2). However, similar to the plant height, the number of fertile stems was affected more by flooding, especially in the stem elongation stage. According to the flooding duration, fertile stem number varied between 400 and 627. The highest value was obtained from the control group, followed by short-duration to long-duration, respectively. Therefore, increasing the flooding duration affected the number negatively. Meta-2002 and Gönen-98 had 495 and 465 fertile stems in genotypes.

The number of fertile spikelets was found to be not significant and varied between 13.0 and 13.7 (Table 2). The highest value was observed in the heading stage, followed by tillering and stem elongation. It decreased, especially in the stem elongation stage, exposed to flooding. For the flooding duration, the number of fertile spikelet values ranged from 12.5 to 14.1. Short-duration had the maximum value, while long-duration had the minimum. Similarly to the number of fertile stems, increasing the flooding duration negatively affected the number of fertile spikelets.

Gönen-98 and Meta-2002 had 14.2 and 12.6 fertile spikelet, respectively.

The number of sterile spikelets ranged from 1.76 to 2.36 for the growth stages, and the maximum value was observed in the heading stage, similar to the result for the number of fertile spikelet (Table 2). The stem elongation stage was susceptible to flooding. According to the flooding duration, the number of sterile spikelets varied between 1.82 and 2.25. The highest value was obtained from medium- and short-duration, which were in the same statistical group, followed by the control and long-duration. Meta-2002 and Gönen-98 had the same (2.08) value of sterile spikelet in genotypes.

The number of grains per unit area varied between 9,598 and 11,696 according to the mean values for growth stages (Table 2). The highest value was observed in the tillering stage, followed by heading and stem elongation. As expected, the number of grains per unit area was also affected by flooding, especially in stem elongation, as with sterile and fertile spikelets. For flooding duration, the number of grains per unit area ranged from 8,544 to 14,405. Although control came to the forefront with its highest value, short-duration flooding took to first place among flooding durations. Hence, increasing flood duration dramatically reduced the grain number. According to the genotypes, Meta-2002 was 10,960 while Gönen-98 was 9,904.

Thousand-grain weight ranged from 21.9 g to 29.9 g for the growth stages, and the maximum value was observed in the tillering stage, similar to previous parameters (Table 2). The heading stage was more susceptible to flooding. According to the flooding duration, the thousand-grain weight varied between 16.6 g and 32.4 g. The highest value was obtained from short-duration, followed by the control and medium-duration. Short-duration came to the forefront with its highest value because the short-duration flooding resembled irrigation for the plants. The plants also tolerated the medium-duration flooding. However, the plants exposed to flooding for a long duration almost lost their grain weight

Table 1 The combined ANOVA test and p-value revealed the significant effect of genotypes, periods, and flooding durations for plant height (PH), number of fertile stems (NEA), number of fertile spikelets (NFSp), number of sterile spikelet (NSS), number of grains per unit area (NGA), thousand-grain weight (TGW), unit area grain yield (AGY), biomass (Bio), and harvest index (HI)

Sources		Mean Square									
		SD	PH	NFS	NFSp	NSS	NGA	TGW	AGY	Bio	HI
Genotypes(G)	1	13	ns	16,320	**	50	ns	**	**	ns	ns
Periods(P)	2	590	**	56,398	**	3.19	**	**	**	**	**
G x P	2	53	*	6292	*	3.808	**	**	**	**	**
Error-1	12	18		1532		1.424		1.3	309	7045	12.5
Durations(D)	3	1695	**	352,657	**	7.941	**	**	**	**	**
G x D	3	13	ns	1829	ns	0.377	**	**	**	**	**
P x D	6	387	**	8136	**	3.259	**	**	**	**	**
G x P x D	6	8	ns	8210	**	1.82	**	**	**	**	*
Error-2	36	14		1299		0.647		2.2	454	2249	9.7
CV		6.50		7.51		6.00		6.40	6.66	6.01	9.42

** $p < 0.01$; * $p < 0.05$; ns: non-significant; CV: Coefficient of Variation.

by 50%. Gönen-98 and Meta-2002 had 24.5 g and 26 g thousand-grain weight in genotypes.

The unit area grain yield is one of the indicators that best expresses total yield, especially in trials conducted in containers. It varied between 238 g and 348 g according to the mean values for growth stages (Table 2). The highest value was observed in the tillering stage, followed by stem elongation and heading. As expected, the unit area grain yield was also affected by flooding, especially after the tillering stage, as with the thousand-grain weight. For the flooding duration, the unit area grain yield value ranged from 107 g to 410 g. Besides, increasing flooding, especially long-duration flooding, negatively affected the unit area grain yield and decreased the value by one-third. According to the genotypes, Meta-2002 was 275 g while Gönen-98 was 281 g.

The biomass ranged from 695 to 937 g for the growth stages, and the maximum value was observed in the tillering stage, followed by heading and stem elongation (Table 2). According to the flooding duration, the biomass varied between 454 and 1,050. The highest value was obtained from the short-duration because the short-duration flooding resembled irrigation for the plants. However, being exposed to long-duration flooding decreased the biomass by about 60%. Gönen-98 and Meta-2002 had 799 and 780 biomass in the genotypes.

The harvest index varied between 28.7 and 37 according to the mean values for growth stages (Table 2). The highest value was observed in the tillering stage, followed by stem elongation and heading. As expected, the harvest index was also affected by flooding, especially in the heading stage, as with the thousand-grain weight. For the flooding duration, the harvest index values ranged from 23.2 to 40.5. Control came to the forefront with its highest value, followed by floods of short and medium duration. Besides, increasing flooding negatively affected the harvest index. According to the genotypes, Meta-2002 was 33.2 while Gönen-98 was 32.9.

Correlation

Some components, such as plant height, number of fertile stems, number of fertile spikelets, number of sterile spikelets, number of grains per unit area, thousand-grain weight, biomass, and harvest index, affect the yield in direct or indirect ways. For this reason, it is important to understand the relationship between these yield elements and unit area grain yield (Table 3). The unit area grain yield was highly correlated with biomass ($r=0.92$), number of grains per unit area ($r=0.89$), number of fertile stems ($r=0.85$), and harvest index ($r=0.84$). On the other hand, there were also high correlations between biomass and number of fertile stem ($r=0.87$) and biomass and number of grains per unit area

Table 2 Mean values of different agronomic characters in wheat exposed to flooding stress for various periods at different growth stages, and groups formed according to Lsd test value (Plant height (PH), number of fertile stem (NFS), number of fertile spikelet (NFSp), number of sterile spikelet (NSS), number of grains per unit area (NGA), thousand-grain weight (TGW), unit area grain yield (AGY), biomass (Bio), and harvest index (HI))

Effects	PH	NFS	NFSp	NSS	NGA	TGW	AGY	Bio	HI									
Genotypes																		
Gönen-98	56.5	a	465	b	14.2	a	2.08	a	24.5	a	799	a	32.9	a				
Meta-2002	57.3	a	495	a	12.6	b	2.08	b	26.0	a	275	a	33.2	a				
Growth stages																		
Tillering	57.8	b	521	a	13.5	a	2.12	b	11,696	a	29.9	a	348	a	937	a	37.0	a
Stem elongation	51.5	c	427	c	13.0	a	1.76	c	9598	c	24.1	b	249	b	695	b	33.5	b
Heading	61.3	a	493	b	13.7	a	2.36	a	10,001	b	21.9	c	238	b	737	b	28.7	c
Flooding duration																		
Control	63.3	a	627	a	13.5	b	2.02	b	14,405	a	28.7	b	410	a	1008	b	40.5	a
SD	64.3	a	566	b	14.1	a	2.24	a	12,409	b	32.4	a	391	b	1050	a	37.9	b
MD	56.7	b	400	c	13.4	b	2.25	a	8544	c	23.4	c	204	c	646	c	30.7	c
LD	43.2	c	328	d	12.5	c	1.82	c	6369	d	16.6	d	107	d	454	d	23.2	d
CV	6.50		7.51		6.00		10.50		9.82		6.90		7.66		6.01		9.42	
Lsd _{GS}	2.65		24.62		ns		0.09		392.4		0.62		11.06		52.79		1.95	
Lsd _{FD}	2.50		24.36		0.54		0.15		692.5		0.18		14.4		32.06		2.11	

ns: non-significant; CV: Coefficient of Variation; LSD: Least Significant Difference, SD: Short-duration, MD: Medium-duration, LD: Long-duration of flooding.

($r=0.86$). Consequently, unit area grain yield was mainly correlated with important yield parameters.

Principal Component Analysis (PCA)

The relationships among yield, yield components, genotypes, growth stages, and flooding duration were further explored using PCA. The biplots were generated based on the first two principal components, which explained 73.77% of the total variation (Table 4). PC1 was strongly associated with unit area grain yield (AGY), Bio, number of fertile stems (NFS), number of grains per unit area (NGA), thousand-grain weight (TGW), harvest index (HI), and plant height (PH). PC2 was primarily loaded with the number of fertile spikelets (NFSp) and the number of sterile spikelets (NSS).

Three different biplots were created for the genotype, growth stage, and flooding duration examined in the study. In the generated PCA biplots, it was determined that the AGY, TGW, and HI traits, which were in the same region and had the same direction, were highly correlated with each other. Similarly, the NGA, NFS, and Bio traits, which were in a different region but had the same direction, were also positively correlated with these three traits. The PH trait, located in the same direction, was correlated with these traits as well, although to a lesser extent compared to the others.

In the analysis conducted regarding genotypes (Fig. 3), it was found that the Gönen-98 cultivar was positioned in the positive direction and closer to the other traits; however, it was located in a relatively central position similar to Meta-2002. These results indicate that Gönen-98, which is described as flood-tolerant in the literature, showed a higher correlation with the examined traits compared to the Meta-2002 cultivar, albeit the difference was subtle. However, it is crucial to note that the reported tolerance response of these cultivars (Tiryakioğlu et al. 2015) was specific to the tillering stage. Both the literature and the findings of this study suggest that the flooding response of wheat cultivars can vary significantly depending on the growth stage at which the stress occurs.

The growth stages exposed to flooding were located in different regions (Fig. 4). This situation showed that the periods during which plants were exposed to flooding differed in terms of yield and yield components. The fact that plants exposed to flooding at an early stage (tillering) were in the same region and direction as many of the examined traits indicated that plants could relatively tolerate this stress. The stem elongation stage showed a weak relationship with the NSS, NFSp, and PH traits, which were in a negative direction and a different region. In contrast, these traits were relatively more highly correlated with flooding

Table 3 Correlations and coefficients between unit area grain yield (AGY) and some yield components (Plant height (PH), number of fertile stem (NFS), number of fertile spikelet (NFSp), number of sterile spikelet (NSS), number of grains per unit area (NGA), thousand-grain weight (TGW), biomass (Bio), and harvest index (HI))

NFS	PH	NFS	NFSp	NSS	NGA	TGW	AGY	BIO
	0.74 **							
NFSp	0.48 **	0.30 *						
NSS	0.29 *	0.12 ns	0.01 ns					
NGA	0.60 **	0.81 **	0.41 **	0.06 ns				
TGW	0.46 **	0.62 **	0.16 ns	0.16 ns	0.45 **			
AGY	0.61 **	0.85 **	0.34 **	0.13 ns	0.89 **	0.80 **		
BIO	0.72 **	0.87 **	0.41 **	0.21 ns	0.86 **	0.67 **	0.92 **	
HI	0.35 **	0.60 **	0.12 ns	-0.02 ns	0.66 **	0.83 **	0.84 **	0.59 **

Table 4 Eigenvalues and percentage of variance explained by the principal components from the PCA of agronomic traits under flooding stress

Number	Eigenvalue	Percent (%)	Cum Percent (%)
1	5.435	60.394	60.394
2	1.203	13.372	73.765
3	1.036	11.516	85.281
4	0.579	6.434	91.716
5	0.415	4.617	96.332
6	0.202	2.245	98.577
7	0.113	1.261	99.837
8	0.009	0.106	99.943
9	0.005	0.057	100.000

during the heading stage. This result supports the mean table created from the ANOVA results.

In terms of the duration of flooding exposure (Fig. 5), the analysis showed that plants not exposed to any flooding were more strongly associated with AGY, TGW, and HI. Under short-duration (SD) flooding, plants not only tolerated it but also exhibited a positive relationship, showing a very high correlation especially with traits like NGA, NFS, and Bio, and a low correlation with PH, NSS, and NFSp. As the flooding duration increased (MD and LD), it was observed that the applications were positioned in the opposite direction to yield and yield components in the biplot, and their relationships with these traits gradually weakened. The fact that the medium-duration (MD) flooding application was located relatively close to the center but in the negative region indicated that this application exhibited a variable relationship profile in terms of the examined traits.

Stress Effect Rate

Stress Effect Rate (SER) showed the effect of growth stages and flooding durations on some yield components (Fig. 6). In general, the SER value below zero ($SER < 0$) indicated that both growth stages and flooding durations negatively affected the related parameters. However, a SER value above zero ($SER > 0$) showed that the related parameter is positively affected. In this respect, the control group

was considered as zero, and other values were evaluated accordingly.

The plant height was negatively affected by the flooding, regardless of growth stages. Long-duration flooding significantly reduced plant height, particularly during the early growth stages. However, short-duration flooding in the tillering stage had a neutral effect, while it had positive effects in the stem elongation and heading stages. Besides, plants tolerated the medium- or long-duration flooding in the heading stage more than in the tillering or stem elongation stages.

Medium- or short-duration flooding slightly increased the number of fertile stems in the tillering stage, while long-duration flooding had a negative effect. Plants exposed to medium-duration flooding were negatively affected when the flooding occurred in the stem elongation stage. However, plants tolerated the flooding in the heading stage and even benefited from it.

In contrast to the plant height and the number of fertile stems, the number of fertile spikelets was positively affected by short- and medium-duration flooding in the tillering stage. After this growth stage, however, SER mostly had a negative value for the number of fertile spikelets. It can be concluded that plants were more susceptible after the tillering stage.

The number of sterile spikelet values showed a similar effect in all three growth stages compared to the number of fertile spikelets, and SER had negative values. While relatively fewer losses occurred during short-duration floods, these losses increased nearly three to four times during medium- and long-duration floods. Reduction in the number of sterile spikelets was greater in prolonged floods, especially during the stem elongation stage. Even short-duration flooding caused losses in the number of sterile spikelets regardless of the growth stages.

The number of grains per unit area was also affected by the flooding duration, like the number of sterile spikelets, regardless of the growth stages. Even short-duration flooding during early growth stages caused greater losses, while its effect decreased slightly during later growth stages. In

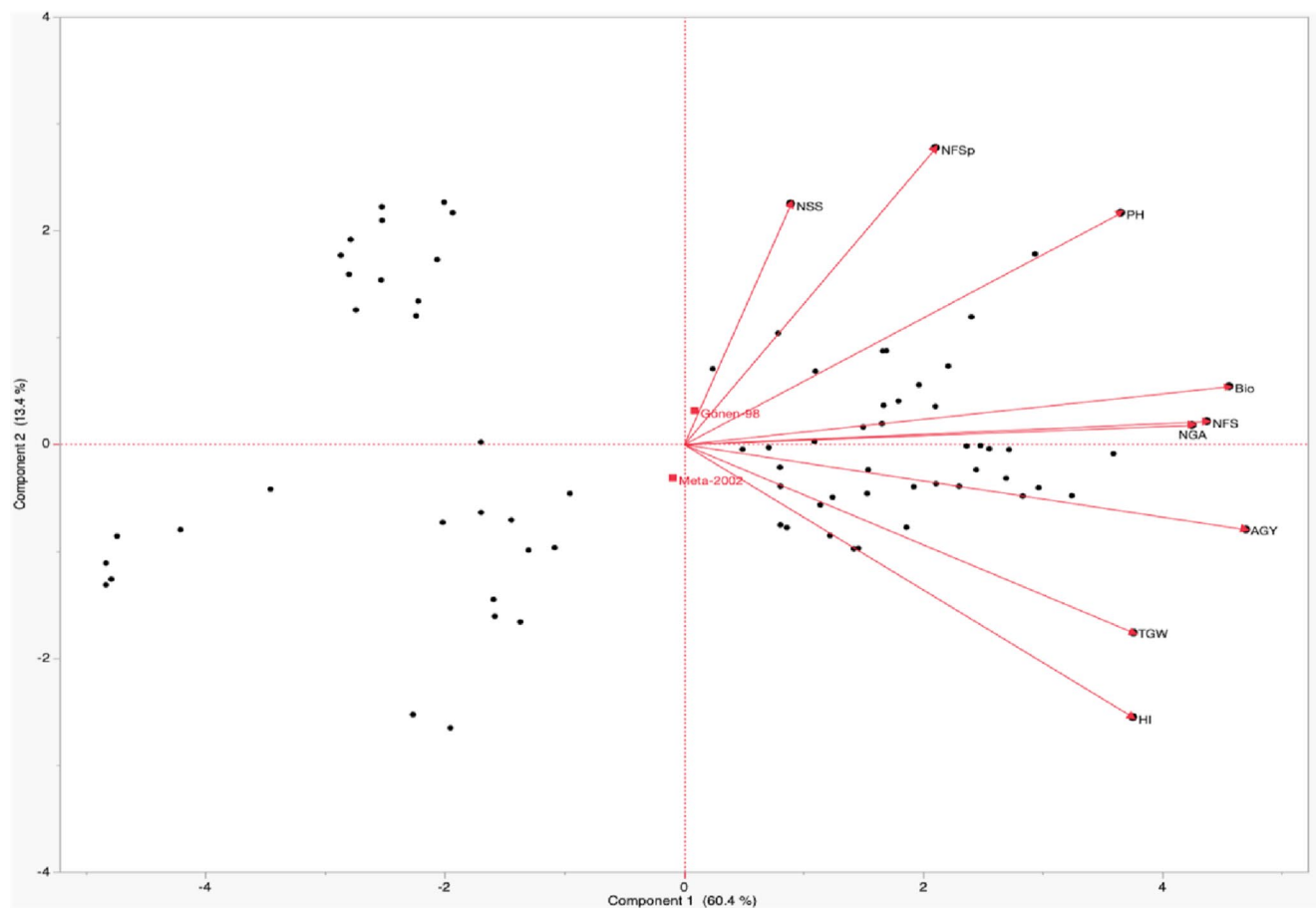


Fig. 3 Principal component analysis (PCA) biplot of agronomic traits under flooding stress, grouped by genotype (Gönen-98 and Meta-2002)

fact, the effect of short-duration flooding during the stem elongation stage was less than that during the tillering stage. It decreased even further during the heading stage. However, the effect of medium- and long-duration flooding was high in almost every growth stage.

Plants tolerated the short-duration flooding in the whole growth period for the thousand-grain weight. In the early growth stage, such as tillering, plants also resisted medium-duration flooding. However, increasing flooding duration caused a loss in thousand-grain weight. This loss was multiplied by the later growth stages. Besides, the plants were susceptible during the heading stage, even exposed to medium-duration flooding.

Unit area grain yield showed a similar effect in the whole growth stages compared to the components, which had positive SERs. While relatively fewer losses occurred during short-duration floods in the tillering stage, these losses increased nearly two to three times during medium- and long-duration floods. The plants resisted short-duration flooding in the stem elongation and heading stages. However, the reduction in the unit area grain yield was greater in

prolonged floods, especially during the stem elongation and heading stages.

BIO, which had a high correlation with AGY, also showed similar results in terms of SER. It showed a slight positive effect against short-duration flooding in all growth stages examined. However, it was significantly affected by medium- and long-duration flooding.

As a final remark, SER may serve as a practical and comparative indicator for future studies aiming to quantify genotype-specific responses across different growth stages and flooding durations.

Discussions

Agronomic Characteristics

Due to global climate change, the frequency and severity of flooding events have been increasing recently (Broughton et al. 2015; Pérez-Jiménez and Pérez-Tornero 2021). Consequently, the exposure of the most widely cultivated crop

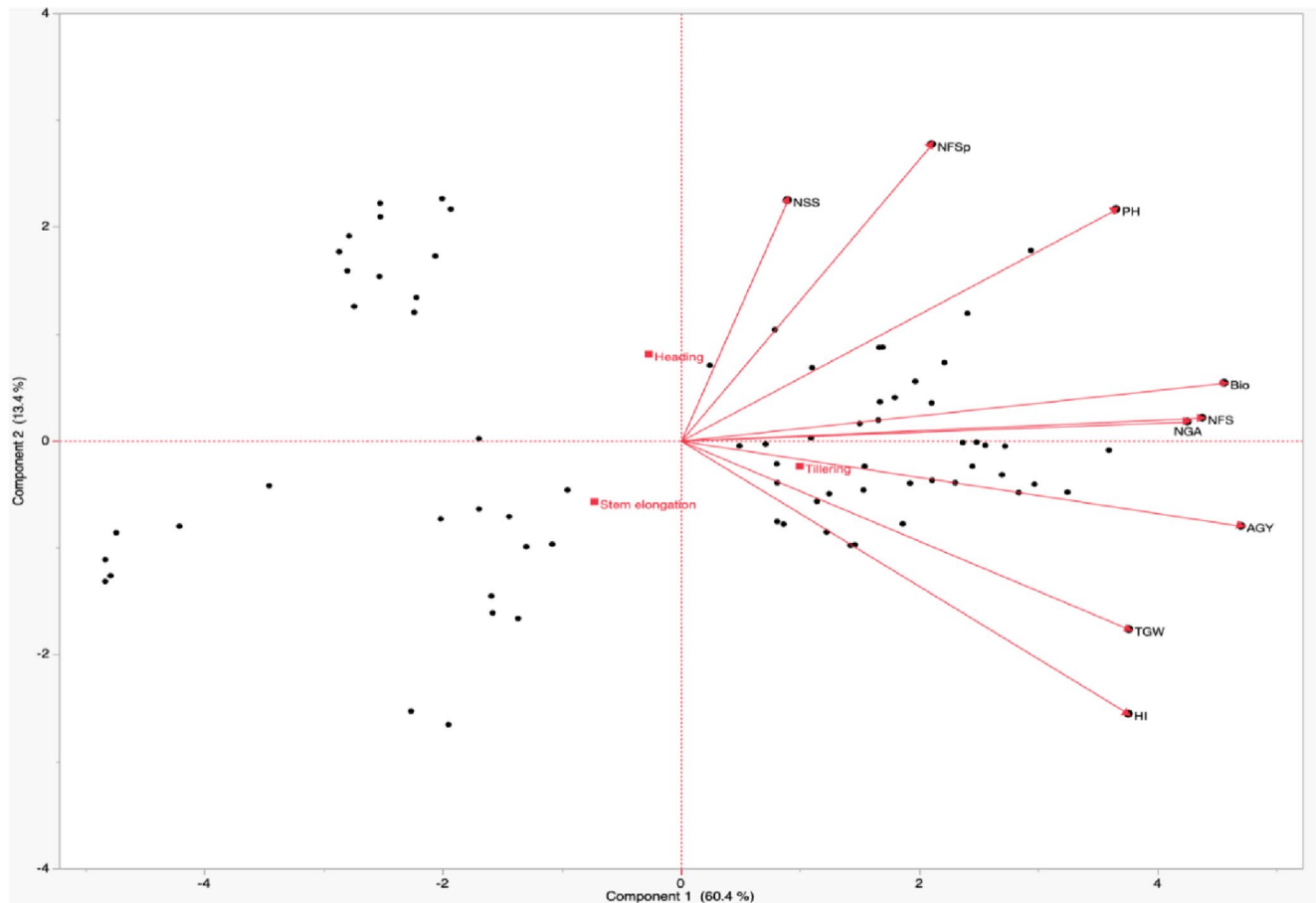


Fig. 4 Principal component analysis (PCA) biplot of agronomic traits under flooding stress, grouped by growth stage (Tillering, Stem Elongation, and Heading)

worldwide, wheat, which has the largest planting area, to this stress is increasing day by day.

The expression of waterlogging stress in wheat plants is influenced by many factors, including the stage of plant development during which it occurs (Bailey-Serres and Voesenek 2008; Magneschi and Perata 2009), how long the effect lasts (Xu et al. 2016), the depth of waterlogging (Garssen et al. 2015), the climate during the stress period (Colmer and Voesenek 2009), soil conditions (Robertson et al. 2009; Pais et al. 2023), topographical factors, even the plant's genetic makeup (Ahsan et al. 2007; Xu et al. 2016), and epigenetic factors. In recent years, the increased frequency and intensity of global climate anomalies have directed researchers toward studies related to this stress. However, most studies (Ploschuk et al. 2023; Wollmer et al. 2018) have examined these factors individually, and there is insufficient literature on the interactions between two or three factors (Nóia Júnior et al. 2023). This study investigated the changes in agricultural traits of wheat at different developmental stages when exposed to waterlogging for short, medium, and long durations, focusing on two

genotypes—one sensitive to stress (Gönen 1998) and one tolerant (Meta 2002) (Tiryakioğlu et al. 2015).

In the present study, although there were differences among genotypic levels in terms of agronomic traits affecting yield such as NFS, NFSp, NGA, and TGW, the Gönen-98 genotype performed well in NGA, and the Meta-2002 genotype performed well in NFS and TGW. Therefore, despite these differences, no significant differences were observed between the two genotypes in terms of AGY values (Table 2). PCA analysis for the genotypes shows that the Gönen-98 variety is positioned closer to and on the positive side of the other examined traits (Fig. 3). In contrast, the Meta-2002 variety is located nearer to the center. The higher correlation of Gönen-98 with the examined traits compared to Meta-2002 supports the idea that this variety is more tolerant to flooding stress. However, the small difference; although it has been previously determined in a study by Tiryakioğlu et al. (2015) that the genotypes respond differently to flooding, this study covers the seedling stage. The current findings indicate that the plant responses to flooding stress are dynamic (Tian et al. 2021) and can vary depending on the growth stages of the plant (Setter and Waters,

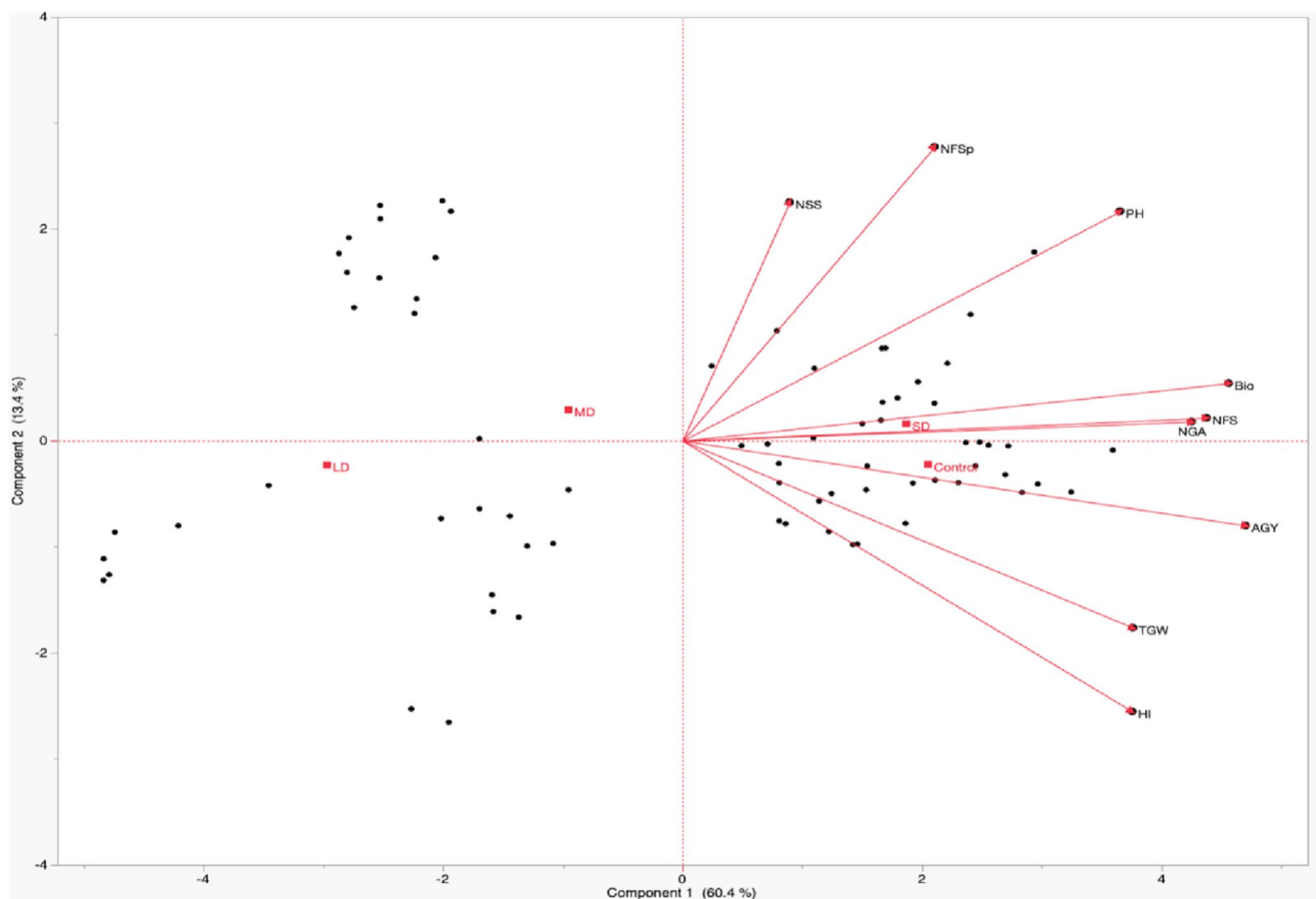


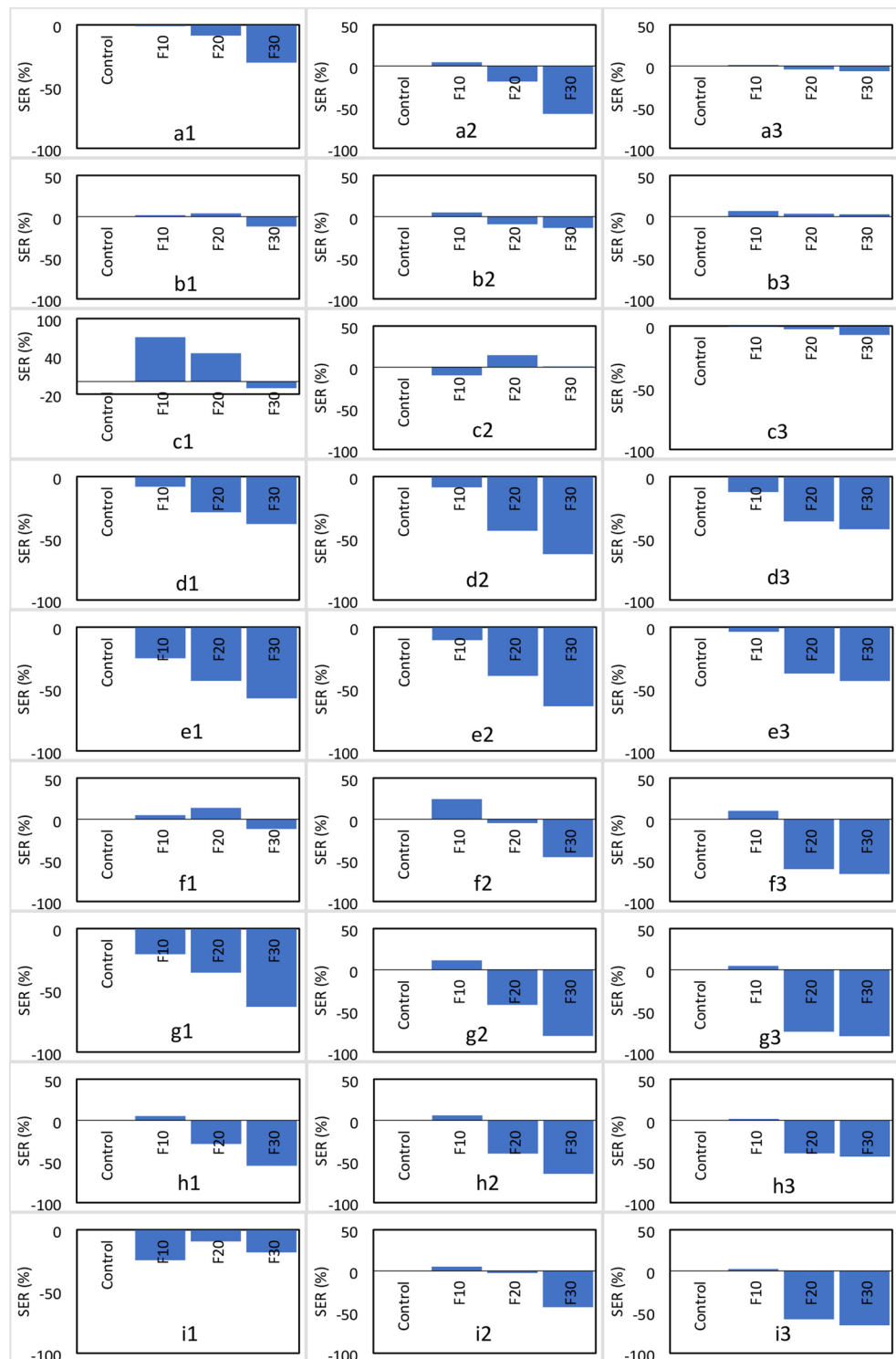
Fig. 5 Principal component analysis (PCA) biplot of agronomic traits, grouped by flooding duration (Control, Short-Duration (SD), Medium-Duration (MD), and Long-Duration (LD))

2003; Tian et al. 2021). Therefore, making a final judgment about the genotype based solely on stage-specific responses is not appropriate. Indeed, Setter and Waters (2003) stated that different tolerance mechanisms exist at the plant and tissue levels in wheat, and thus, genotypic responses can vary according to the plant's developmental stage.

Flood stress varies depending on the plant's growth stages but negatively affects wheat yield and its components (De San Celedonio et al. 2014; Ding et al. 2020; Tian et al. 2021). In our study; it was determined that the most significant negative impact of flooding on grain yield occurs during the heading-grain filling stage, followed by the stem elongation stage (with reductions of 28.45% and 31.61% respectively compared to the jointing stage). However, the difference between these two stages was statistically insignificant. The least affected stage was found to be the jointing stage. The parameters NGA and TGW were decisive in forming this result. It was observed that NGA is determined by NFS. The PCA analysis conducted for different plant growth stages also supports these findings (Fig. 4). Many studies on cereals (Li et al. 2001; Asgari et al. 2012; Liu et al. 2020, 2021; Pais et al. 2023) have shown that the most

sensitive period to flooding is generally the generative stage (especially between stem elongation and flowering). Stress during this period directly affects spike fertility and grain number, leading to the most severe yield losses (Liu et al. 2020, 2021). These findings are quite consistent with our observations. The lower negative impact of flooding during the jointing stage on yield and its components, compared to later developmental stages, is undoubtedly due to the longer recovery period after stress, as well as the fact that the jointing stage involves creating new tillers to replace dead ones (Deng et al. 2009; De San Celedonio et al. 2014; Ding et al., 2020), and the formation of new adventitious roots from damaged root systems (De San Celedonio et al. 2014; De San Celedonio et al. 2017; De Castro et al. 2022). However, such compensatory mechanisms are not present during the stem elongation stage and afterward. De San Celedonio et al. (2014), in their study on wheat and barley, reported that the greatest yield losses occurred when water accumulation was applied from the emergence of the 7th leaf until flowering. Conversely, Wu et al. (2015), in a two-year field study on wheat, found that the highest yield loss due to flooding occurred during the jointing, stem elongation, booting, and

Fig. 6 The effect of stress on some yield components (**a**: plant height, **b**: number of fertile stem, **c**: number of fertile spikelet, **d**: number of sterile spikelet, **e**: number of grains per unit area, **f**: thousand-grain weight, **g**: unit area grain yield, **h**: biomass, **i**: harvest index) in wheat, in which four different periods of flooding [(F0: control, F10: 10 days (short-duration), F20: 20 days (medium-duration), F30: 30 days (long-duration)] were applied in three different development stages (1: tillering, 2: stem elongation, 3: heading) (SER: stress effect rate)



flowering stages when flooding was applied for 35 days, with the most significant impact during the jointing stage. Similarly, a study by Araki et al. (2012) determined that flood tolerance was highest during flowering, followed by the stem elongation stage. The findings of Ren (2016) and Wang (2020) also align with these last two studies. Both

our findings and those of similar studies, as well as studies with different results, demonstrate once again that flood stress is a multifaceted event influenced by many parameters. In conclusion, Tian et al. (2021) conducted a meta-analysis of 2,419 comparisons from 115 studies worldwide to comprehensively evaluate the overall change in grain

yield caused by flooding. Their results indicated that flood stress at different growth stages significantly reduces crop yield, with the most substantial reduction occurring during the reproductive period (41.90%) and vegetative growth stage (34.75%). It was suggested that early-stage flooding might allow plants to recover through various physiological mechanisms. One of these compensatory mechanisms at this stage is the formation of aerenchyma in newly formed adventitious roots (AR). Pan et al. (2021) described AR formation as a typical adaptive change in plant morphology, noting that during prolonged flooding, ARs develop in the internodes of the hypocotyl or at the base of the stem, supporting gas exchange, water, and nutrient absorption. They also indicated that AR formation can partly replace primary roots that die due to hypoxia stress, maintaining metabolic cycles and supporting normal growth and development. In summary, they stated that ARs contain more aerenchyma than primary roots, which enhances both oxygen intake and diffusion capacity.

The negative impact of waterlogging stress on wheat is undoubtedly related not only to the period during which the stress occurs but also to the duration of the stress. However, considering the concept of duration as a direct, quantifiable value like days or hours is not a correct approach. Because, in stress situations where many environmental factors such as waterlogging are effective simultaneously, factors originating from the plant (genotype, developmental stage, etc.) as well as environmental factors like climate conditions, soil structure and composition, topographical features, and even interactions such as genotype-environment interactions all influence the process. For example, in studies conducted under fully controlled conditions where many factors like water culture are managed and an anoxic environment is created in a short time (Barrett-Lenard et al., 1988; Biemelt et al. 1998; Malik et al. 2009), the negative effects of stress on the plant can be immediately observed through parameters such as root responses like water and mineral uptake, stomatal conductance, photosynthesis rate, and transpiration rate. However, under field conditions (Pampana et al. 2016; Ren et al. 2016), these effects may only be observable over a period measured in days or even longer. Therefore, in our study, we chose to express the duration in days based on morphological and physiological changes in the plant, and also to categorize it as ‘short (10 days)’, ‘medium (20 days)’, and ‘long (30 days)’. Because the longer wheat is subjected to waterlogging, the more extensive the damage becomes, and subsequently, the plant’s recovery becomes increasingly difficult. In other words, as the duration of stress increases, the permanence of the damage also increases.

The negative impact of flood stress on all parameters affecting wheat yield shows a very strong linear relationship with duration (Table 3). In our study, it was determined that

both AGY and Bio decreased significantly as the duration of flooding increased. The reduction in AGY was 4.63% after a 10-day (short) flood, 50.24% after a 20-day (medium) flood, and 73.90% after a 30-day (long) flood compared to the control. In Bio, the decreases were 4.17%, 35.92%, and 54.96%, respectively. The PCA analysis results regarding the duration of flood exposure also detailed these findings (Fig. 5). Furthermore, our results are confirmed by other studies (Tian et al. 2019; Zhang et al., 2023). Additionally, according to a meta-analysis conducted by Tian et al. (2021) based on hundreds of studies, it was reported that increasing flood duration leads to reductions in crop yield, with the greatest decreases occurring in field and pot conditions within the range of $15 < D \leq 28$ days (53.19% and 55.96%). In our findings, the increase in Bio value during short-term flooding (10 days) compared to the control is mainly due to the activation of plant compensatory mechanisms during the recovery period following flooding during the tillering stage (data not shown). Indeed, Zhang et al. (2023) stated that early-stage flooding generally results in better recovery because it provides a longer ‘compensation period’ until harvest, and that after stress-induced water withdrawal during the tillering stage, new tillers can form, replacing the dead main stem. Similar findings were reported by De San Celedonio et al. (2014). The absence of this new tiller formation in our results is due to the fact that the formed tillers largely remained sterile in the later stages (data not shown). Since in our study the sowing date was late (January 3), the newly formed tillers during the recovery period after stress could not develop sufficiently to enter the generative phase due to the combined effects of photoperiod and thermoperiod (Masle et al. 1989; Gonzalez et al., 2002) and thus could not attain fertility. In our study, a significant increase of 4.17% in biomass yield was observed compared to the control following short-term flooding (Table 2). This increase is thought to be due to the newly formed tillers during the recovery process after the tillering stage flood. Indeed, Pampana et al. (2016) also reported that short-term flooding could increase wheat yield, but longer durations resulted in significant reductions.

Stress Effect Rate (SER)

A parameter called SER was calculated to assess the impact of flooding stress on wheat in greater detail. The SER values, which varied depending on the duration of flooding (ranging from 10 to 30 days) at different growth stages, helped identify the periods during which wheat plants were more susceptible to water stress. The analyses revealed that SER values were higher at certain growth stages, indicating that yield losses differed based on the timing of stress exposure. These findings highlight the importance of SER

as a criterion in selection studies aimed at developing flood-tolerant wheat genotypes.

Plants face severe stress when their roots are exposed to hypoxia, which causes harmful effects on plants, such as a lack of nutrients, reduction in root growth, and insufficient oxygen (Da-Silva and Do Amarante 2020; Naidoo 2021). They have developed various adaptations that enhance their ability to withstand water stress. If a stress signal is present in the cell, a signaling molecule is activated in response, triggering a quick response in the plant (Da-Silva and Do Amarante 2020; Pérez-Jiménez and Pérez-Tornero 2021).

Decreases in grain yield and biomass deposition are often found in wheat grown under abiotic stresses during the reproductive stage (Li et al. 2013). Plants exposed to flooding in the reproductive stage, such as heading, were more negatively affected than in the vegetative stage (Setter and Waters 2003; De San Celedonio et al. 2014; Ding et al. 2020). In this study, the effect of flooding on grain yield and its components was tested during the growth stages of wheat in which it was exposed to different durations. The SER values for all parameters were generally lower in the tillering stage than in later stages. It was found that the stages from stem elongation to anthesis in wheat were the most sensitive to flooding in terms of yield failures (De San Celedonio et al. 2014). Grain yield has been reported to decrease due to a reduction in tiller number, even when exposed to shorter flooding days (Gupta et al. 2022; Singh et al. 2019). Similar findings also showed that the average grain yield under stress conditions decreased by 26–36% (Golabadi et al. 2006).

In addition to the stages of development during which wheat is exposed to flooding, the duration of exposure is also very important (De San Celedonio et al. 2018). Regardless of the stage of development, serious losses have been observed in plants exposed to long-duration flooding. This situation has resulted in losses of up to 74% in unit area grain yield compared to non-flooding. Our results showed that wheat tolerated the short-duration flooding for some parameters and promoted the yield components compared to medium- or long-duration flooding. However, flooding effects varied across different growth stages, particularly during the vegetative period. Our findings align with those of previous studies, highlighting the sensitivity of wheat to flooding duration and growth stage. The reduced stress effect ratio (SER) values observed during the tillering stage suggest that this period is particularly vulnerable to flooding stress.

Conclusions

The research demonstrated that wheat's tolerance to flooding varies significantly across different growth stages and flooding durations. The stem elongation stage appeared to be particularly susceptible to flooding stress, with notable decreases in agronomic traits, such as plant height, number of fertile stems, and number of fertile and sterile spikelets when flooding occurred during this period. In contrast, flooding during the early growth stages, especially tillering, showed less severe impacts on the plants. Interestingly, grain-related parameters such as number of grains per unit area, thousand-grain weight, and unit area grain yield were most affected by flooding during late growth stages, particularly in the heading stage. This suggests that the timing of flooding is crucial in determining its impact on wheat yield.

The study also revealed that short-duration flooding had minimal negative effects and sometimes even acted as beneficial irrigation, regardless of the growth stage. However, long-duration flooding led to significant reductions in various yield components. These findings highlight the importance of considering growth stage-specific flooding tolerance in wheat breeding programs and in developing management strategies for wheat cultivation in flood-prone areas. Future studies should focus on developing flood-tolerant wheat varieties that can maintain yield stability even when exposed to prolonged flooding, especially during critical growth stages.

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Author contributions MT and AK constructed the hypothesis for the research and planned the methodology. MT supervised the work. MT and AK collected the data. CTA and CBŞ analyzed the data and reviewed the literature. MT, CTA, and CBŞ contributed equally to writing the article.

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Data Availability The data sets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare that they have no conflicts of interest. The original contributions presented in the study are included in the article. Further inquiries can be directed to the corresponding author.

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References

- Abdolshahi R, Safarian A, Nazari M, Pourseyedi S, Mohamadi-Nejad G (2013) Screening drought-tolerant genotypes in bread wheat (*Triticum aestivum* L.) using different multivariate methods. *Arch Agron Soil Sci* 59(5):685–704. <https://doi.org/10.1080/03650340.2012.667080>
- Ahsan N, Lee DG, Lee SH, Kang KY, Bahk JD, Choi MS, Lee IJ, Renaut J, Lee BH (2007) A comparative proteomic analysis of tomato leaves in response to waterlogging stress. *Physiol Plant* 131(4):555–570. <https://doi.org/10.1111/j.1399-3054.2007.00980.x>
- Araki H, Hamada A, Hossain MA, Takahashi T (2012) Waterlogging at jointing and/or after anthesis in wheat induces early leaf senescence and impairs grain filling. *Field Crop Res* 137:27–36. <https://doi.org/10.1016/j.fcr.2012.09.006>
- Asgari H, Cornelis W, Damme P (2012) Wheat (*Triticum aestivum* L.) growth and yield as influenced by flooding and salinity stresses in northern Iran. *Desert* 17:99–104
- Atchison J, Head L, Gates A (2010) Wheat as food, wheat as industrial substance; comparative geographies of transformation and mobility. *Geoforum* 41(2):236–246. <https://doi.org/10.1016/j.geoforum.2009.09.006>
- Bahar B, Yildirim M (2010) Heat and drought resistances criteria in spring bread wheat: Drought resistance parameters. *Sci Res Essays* 5(13):1742–1745
- Bailey-Serres J, Voesenek L (2008) Flooding stress: acclimations and genetic diversity. *Annu Rev Plant Biol* 59:313–339. <https://doi.org/10.1146/annurev.arplant.59032607.092752>
- Barrett-Lennard EG, Leighton PD, Buwalda F, Gibbs J, Armstrong W, Thomson CJ, Greenway H (1988) Effects of growing wheat in hypoxic nutrient solutions and of subsequent transfer to aerated solutions. I. Growth and carbohydrate status of shoots and roots. *Australian J Plant Physiol* 15(4):585–598
- Beegum S, Truong V, Bheemanahalli R, Brand D, Reddy V, Reddy KR (2023) Developing functional relationships between waterlogging and cotton growth and physiology-towards waterlogging modeling. *Front Plant Sci* 14:1174682. <https://doi.org/10.3389/fpls.2023.1174682>
- Biemelt S, Keetman U, Albrecht G (1998) Re-aeration following hypoxia or anoxia leads to activation of the antioxidative defence system in roots of wheat seedlings. *Plant Physiol* 116:651–658
- Broughton S, Zhou G, Teakle NL, Matsuda R, Zhou M, O'Leary RA, Colmer TD, Li C (2015) Waterlogging tolerance is associated with root porosity in barley (*Hordeum vulgare* L.). *Mol Breed* 35(1):27. <https://doi.org/10.1007/s11032-015-0243-3>
- Collaku A, Harrison SA (2002) Losses in wheat due to waterlogging. *Crop Sci* 42(2):444–450. <https://doi.org/10.2135/cropsci2002.4440>
- Colmer TD, Voesenek LACJ (2009) Flooding tolerance: suites of plant traits in variable environments. *Funct. Plant Biol* 36:665–681
- Da-Silva CJ, Do Amarante L (2020) Time-course biochemical analyses of soybean plants during waterlogging and reoxygenation. *Environ Exp Bot* 180:104242. <https://doi.org/10.1016/j.envexpbot.2020.104242>
- De Castro J, Hill RD, Stasolla C, Badea A (2022) Waterlogging stress physiology in barley. *Agronomy* 12(4):780. <https://doi.org/10.3390/agronomy12040780>
- De San Celedonio RP, Abeledo LG, Miralles DJ (2014) Identifying the critical period for waterlogging on yield and its components in wheat and barley. *Plant Soil* 378(1–2):265–277. <https://doi.org/10.1007/s11104-014-2028-6>
- De San Celedonio RP, Abeledo LG, Brihet JM, Miralles DJ (2016) Waterlogging affects leaf and tillering dynamics in wheat and barley. *J Agron Crop Sci* 202(5):409–420. <https://doi.org/10.1111/jac.12151>
- De San Celedonio RP, Abeledo LG, Mantese AI, Miralles DJ (2017) Differential root and shoot biomass recovery in wheat and barley with transient waterlogging during preflowering. *Plant Soil* 417(1):1–18. <https://doi.org/10.1007/S11104-017-3274-1>
- De San Celedonio RP, Abeledo LG, Miralles DJ (2018) Physiological traits associated with reductions in grain number in wheat and barley under waterlogging. *Plant Soil* 429(1–2):469–481. <https://doi.org/10.1007/s11104-018-3708-4>
- Den Besten N, Steele-Dunne S, De Jeu R, Van Der Zaag P (2021) Towards monitoring waterlogging with remote sensing for sustainable irrigated agriculture. *Remote Sens* 13(15):2929. <https://doi.org/10.3390/rs13152929>
- Deng X, Li J, Yang C, Jiang Z, Xiao S, Xhou Z (2009) A preliminary study on PCD aspects and roles of reactive oxygen species during aerenchyma formation in wheat roots under waterlogging. *J Triticeae Crops* 29:832–838
- Ding J, Liang P, Wu P, Zhu M, Li C, Zhu X, Guo W (2020) Identifying the critical stage near anthesis for waterlogging on wheat yield and its components in the Yangtze River Basin, China. *Agronomy* 10(1):130. <https://doi.org/10.3390/agronomy10010130>
- FAO (2025) Food and Agriculture Organization. Accessed 24 July 2025. <https://www.fao.org/faostat/en/#data>
- Garssen AG, Baattrup Pedersen A, Voesenek LACJ, Verhoeven JTA, Soons MB (2015) Riparian plant community responses to increased flooding: a meta-analysis. *Glob Chang Biol* 21:2881–2890. <https://doi.org/10.1111/gcb.12921>
- Golabadi M, Arzani A, Mirmohammadi Maibody SAM (2006) Assessment of drought tolerance in segregating populations in durum wheat. *Afr J Agric Res* 1(5):162–171
- Gonzalez FG, Slafer GA, Miralles DJ (2002) Vernalization and Photoperiod Responses in Wheat Pre-Flowering Reproductive Phases. *Field Crops Res* 74:183–195. [https://doi.org/10.1016/S0378-4290\(01\)00210-6](https://doi.org/10.1016/S0378-4290(01)00210-6)
- González FG, Slafer GA, Miralles DJ (2005) Photoperiod during stem elongation in wheat: is its impact on fertile floret and grain number determination similar to that of radiation? *Funct Plant Biol* 32(3):181–188
- Gupta V, Kumar P, Singh G, Singh C, Sharma A, Tyagi BS, Singh GP (2022) Multi-environment characterization of bread wheat genotypes for waterlogging tolerance. *Genetika* 54(1):161–172. <https://doi.org/10.2298/GENSR2201161G>
- Li J, Dong Q, Yu S (2001) Effect of waterlogging at different growth stages on photosynthesis and yield of different wheat cultivars. *Acta Agron Sin* 27:434–441. <https://doi.org/10.1136/bmj.2.6096.1220>
- Li C, Jiang D, Wollenweber B, Li Y, Dai T, Cao W (2011) Waterlogging pretreatment during vegetative growth improves tolerance to waterlogging after anthesis in wheat. *Plant Sci* 180(5):672–678. <https://doi.org/10.1016/j.plantsci.2011.01.009>
- Li H, Cai J, Jiang D, Liu F, Dai T, Cao W (2013) Carbohydrates accumulation and remobilization in wheat plants as influenced by

- combined waterlogging and shading stress during grain filling. *J Agron Crop Sci* 199(1):38–48. <https://doi.org/10.1111/j.1439-037X.2012.00532.x>
- Liu K, Harrison MT, Ibrahim A, Nuruzzaman Manik SM, Johnson P, Tian X, Meinke H, Zhou M (2020) Genetic factors increasing barley grain yields under soil waterlogging. *Food Energy Secur* 9:e238. <https://doi.org/10.1002/fes3.238>
- Liu K, Harrison M, Archontoulis SV, Huth N, Yang R, Liu DL, Yan H, Meinke H, Huber I, Feng P, Ibrahim A, Zhang Y, Tian X, Zhou M (2021) Climate change shifts forward flowering and reduces crop waterlogging stress. *Environ Res Lett* 16(9). <https://doi.org/10.1088/1748-9326/ac1b5a>
- Loreti E, van Veen H, Perata P (2016) Plant responses to flooding stress. *Curr Opin Plant Biol* 33:64–71
- Magneschi L, Perata P (2009) Rice germination and seedling growth in the absence of oxygen. *Ann Bot* 2181–196. <https://doi.org/10.1093/aob/mcn121Epub> 2008 Jul 25. PMID: 18660495; PMCID: PMC2707302
- Malik AI, Colmer TD, Lambers H, Schortemeyer M (2001) Changes in physiological and morphological traits of roots and shoots of wheat in response to different depths of waterlogging. *Aust J Plant Physiol* 28(11):1121–1131
- Malik AI, Colmer TD, Lambers H, Setter TL, Schortemeyer M (2002) Short-term waterlogging has long-term effects on the growth and physiology of wheat. *New Phytol* 153(2):225–236. <https://doi.org/10.1046/j.0028-646X.2001.00318.x>
- Malik AI, English JP, Colmer TD (2009) Tolerance of *Hordeum marinum* accessions to O₂ deficiency, salinity and these stresses combined. *Ann Botany* 103:237–248
- Manna M, Thakur T, Chirom O, Mandlik R, Deshmukh R, Salvi P (2021) Transcription factors as key molecular target to strengthen the drought stress tolerance in plants. *Physiol Plant* 172(2):847–868
- Masle J, Doussinault G, Sun B (1989) Response of Wheat Genotypes to Temperature and Photoperiod in Natural Conditions. *Crop Sci* 29:712–721. <https://doi.org/10.2135/cropsci1989.0011183X002900030036x>
- Mishra N, Jiang C, Chen L, Paul A, Chatterjee A, Shen G (2023) Achieving abiotic stress tolerance in plants through antioxidative defense mechanisms. *Front Plant Sci* 14:1110622
- Naidoo G (2021) Waterlogging tolerance of the common reeds *Phragmites mauritanus* and *P. australis*. *Afr J Ecol* 59(4):1004–1012. <https://doi.org/10.1111/aje.12884>
- Nóia Júnior RS, Asseng S, Garcia-Vila M, Liu K, Stocca V, dos Santos VM, Weber TKD, Zhao J, Palosuo T, Harrison MT (2023) A call to action for global research on the implications of waterlogging for wheat growth and yield. *Agric Water Manage* 284. <https://doi.org/10.1016/j.agwat.2023.108334>
- Pais IP, Moreira R, Semedo JN, Ramalho JC, Lidon FC, Coutinho J, Maças B, Scotti-Campos P (2023) Wheat Crop under Waterlogging: Potential Soil and Plant Effects. *Plants* 12:149. <https://doi.org/10.3390/plants12010149>
- Pampana S, Masoni A, Arduini I (2016) Grain yield of durum wheat as affected by waterlogging at tillering. *Cereal Res Commun Cereal Res Commun* 44(4):706–716. <https://doi.org/10.1556/0806.44.2016.026>
- Pan J, Sharif R, Xu X, Chen X (2021) Mechanisms of Waterlogging Tolerance in Plants: Research Progress and Prospects. *Front. Plant Sci* 11:627331. <https://doi.org/10.3389/fpls.2020.627331>
- Pang J, Zhou M, Mendham N, Shabala S (2004) Growth and physiological responses of six barley genotypes to waterlogging and subsequent recovery. *Aust J Agric Res* 55(8):895–906. <https://doi.org/10.1071/AR03097>
- Pérez-Jiménez M, Pérez-Tornero O (2021) Short-term waterlogging in citrus rootstocks. *Plants* 10(12):2772. <https://doi.org/10.3390/plants10122772>
- Ploschuk RA, Miralles DJ, Striker GG (2023) Waterlogging tolerance of winter crops: Root mass density and canopy dynamics. *Agron J* 115(5):2506–2520. <https://doi.org/10.1002/agj2.21403>
- Ramos Pais IMP (2024) Exploring bread wheat diversity in waterlogging responses: root system, plant development, ecophysiological traits and yield implications. Doctoral Thesis, NOVA University of Lisbon
- Raza A, Ashraf F, Zou X, Zhang X, Tosif H (2020) Plant adaptation and tolerance to environmental stresses: Mechanisms and perspectives. In M. Hasanuzzaman (Ed.), *Plant ecophysiology and adaptation under climate change: Mechanisms and perspectives I* (pp. 117–145). Springer. https://doi.org/10.1007/978-981-15-2156-0_5
- Ren B, Zhu Y, Zhang J, Dong S, Liu P, Zhao B (2016) Effects of spraying exogenous hormone 6-benzyladenine (6-BA) after waterlogging on grain yield and growth of summer maize. *Field Crop Res* 188:96–104. <https://doi.org/10.1016/j.fcr.2015.10.016>
- Rivero RM, Mittler R, Blumwald E, Zandalinas SI (2022) Developing climate-resilient crops: improving plant tolerance to stress combination. *Plant J* 109(2):373–389
- Robertson D, Zhang H, Palta JA, Colmer T, Turner NC (2009) Waterlogging affects the growth, development of tillers, and yield of wheat through a severe, but transient, N deficiency. *Crop Pasture Sci* 60(6):578–586. <https://doi.org/10.1071/CP08440>
- Saharan BS, Brar B, Duhan JS, Kumar R, Marwaha S, Rajput VD, Minkina T (2022) Molecular and Physiological Mechanisms to Mitigate Abiotic Stress Conditions in Plants. *Life* 12(10):1634
- Setter TL, Waters I (2003) Review of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. *Plant Soil* 253(1):1–34. <https://doi.org/10.1023/A:1024573305997>
- Singh A (2023) Genetic variation in waterlogging tolerance of wheat in sodic soil. *Plant Arch* 23(1):248–252
- Singh S, Singh SP, Pathak AD, Pandey N (2019) Assessment of waterlogging induced physio-biochemical changes in sugarcane varieties and its association with waterlogging tolerance. *J Environ Biol* 40(3):384–392. <https://doi.org/10.22438/jeb/40/3/MRN-898>
- Tian L, Li J, Bi W, Zuo S, Li L, Li W, Sun L (2019) Effects of waterlogging stress at different growth stages on the photosynthetic characteristics and grain yield of spring maize (*Zea mays* L.) under field conditions. *Agric Water Manage* 218:250–258
- Tian LX, Zhang YC, Chen PL, Zhang FF, Li J, Yan F, Dong Y, Feng BL (2021) How Does the Waterlogging Regime Affect Crop Yield? A Global Meta-Analysis. *Front Plant Sci* Feb 19:12:634898. <https://doi.org/10.3389/fpls.2021.634898> PMID: 33679848; PMCID: PMC7933672
- Tian M, Li D, Cisse EHM, Miao L, Zhou J, Yang W, Chen B, Li L, Tian H, Ye B, Yang F (2023) Intra- and interspecific ecophysiological responses to waterlogging stress in two contrasting waterlogging-tolerant arbor species. *Front Plant Sci* 14:1257730. <https://doi.org/10.3389/fpls.2023.1257730>
- Tiryakioğlu M, Akcali CT, Sahin CB, Karanlık S, Ergun N (2023) Genotype by environment interaction and GGE biplot analyses in durum wheat under waterlogging stress. *J Anim Plant Sci* 33(6):1426–1438. <https://doi.org/10.36899/JAPS.2023.6.0681>
- Tiryakioğlu M (2015) The relationship between flag leaf senescence and grain yield of some durum wheat varieties under drought stress during grain filling period. *Tarım Bilim Derg* 21(3):382–393. https://doi.org/10.1501/Tarimbil_0000001341
- Tiryakioğlu M (2024) Dry matter remobilization from different plant parts of six durum wheat genotypes under water-restricted conditions and its compensatory effects on grain yield. *Cereal Res Commun* 52(4):1527–1540
- Tiryakioğlu M, Karanlık S, Arslan M (2015) Response of bread-wheat seedlings to waterlogging stress. *Turkish J Agric Forestry* 39(6):807–816. <https://doi.org/10.3906/tar-1407-124>

- Tiryakioğlu M, Aktaş H, Akçalı CT, Sahin CB (2024) Investigation of yield stability of wheat varieties in different locations by AMMI and GGE-biplot analysis. *J Crop Sci Biotechnol* 27(4):463–473. <https://doi.org/10.1007/s12892-024-00243-6>
- Wang X, Liu D, Wei M, Man J (2020) Spraying 6-BA could alleviate the harmful impacts of waterlogging on dry matter accumulation and grain yield of wheat. *PeerJ* 8:e8193. <https://doi.org/10.7717/peerj.8193>
- Wollmer A-C, Pitann B, Mühling KH (2018) Waterlogging events during stem elongation or flowering affect yield of oilseed rape (*Brassica napus* L.) but not seed quality. *J Agro Crop Sci* 204:165–174. <https://doi.org/10.1111/jac.12244>
- Wu X, Tang Y, Li C, Wu C, Huang G (2015) Chlorophyll Fluorescence and Yield Responses of Winter Wheat to Waterlogging at Different Growth Stages. *Plant Prod Sci* 18(3):284–294. <https://doi.org/10.1626/pps.18.284>
- Xu CM, Chen LP, Wang DY, Chen S, Zhang Xiu-fu, Shi Q-h (2016) Effects of low oxygen stress on the root function and enzyme activities related to nitrogen metabolism in roots of rice seedlings. *Sci Agric Sin* 49(8):1625–1634. <https://doi.org/10.3864/j.issn.0578-1752.2016.08.020>
- Yavas I, Unay A, Aydin M (2012) The waterlogging tolerance of wheat varieties in Western Turkey. *Sci World J* 2012:1–7. <https://doi.org/10.1100/2012/529128>
- Zhang J, Pan B, Shi W, Zhang Y (2023) Monitoring Waterlogging Damage of Winter Wheat Based on HYDRUS-1D and WOFOST Coupled Model and Assimilated Soil Moisture Data of Remote Sensing. *Remote Sens* 15(17):4133. <https://doi.org/10.3390/rs15174133>

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