

Soil moisture deficit drives assimilate remobilization and grain yield variability in bread wheat genotypes

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Abstract

Soil moisture deficit and drought, exacerbated by climate change, frequently affect crop yields. This study aimed to evaluate the physiological and agronomic responses of bread wheat (*Triticum aestivum* L.) genotypes under soil moisture deficit conditions. Field experiments were conducted using a randomized complete block design during the 2015–2016 growing season at the Agricultural and Natural Resources Research Station in southwestern West Azerbaijan Province, Iran. The study treatments were full irrigation and irrigation cutoff at the flowering stage with seven bread wheat genotypes and the Orum, Zare, Zarin, and Mihan cultivars. The bread wheat grain yield and its components, and some physiological traits like the contribution of photosynthesis, assimilate remobilization, and harvest index (HI) were determined in this study. A significant reduction was observed in yield components (spikelets/spike, grains/spike, grain weight/spike, and spike weight) under drought stress. The Mihan cultivar exhibited the highest spikelets/spike (15), grains/spike (38), grain weight/spike (1.62 g), and spike weight (2.17 g). The intensification of drought stress increased the contribution of remobilization of stored assimilates by 25%. The Mihan cultivar had the highest remobilization rate at 52%, while line C-91-7 and line C-91-5 had the lowest at 27 %. The HI decreased by 20% under soil water deficient stress. The Mihan cultivar, with a HI of 50%, and C-91-8, with 41%, had the highest and lowest HI, respectively. The mean comparison of the contribution of the current photosynthesis trait to wheat grain yield from full irrigation to severe water shortage dropped to 41.2%. Under full irrigation and irrigation cutoff conditions, line C-91-4 had the highest grain yield, with 8747 kg/ha and 5039 kg/ha, respectively. Furthermore, the highest grain yield under full irrigation and irrigation cutoff treatment was related to the Mihan cultivar, with 7569 kg/ha and 4856 kg/ha. Based on these findings, the Mihan cultivar and C-91-4 line are recommended for cultivation in semi-arid regions facing water limitations. Understanding physiological traits and yield components is critical for selecting drought-tolerant wheat varieties in the context of climate change.

Keywords: Soil water deficit, Bread wheat, Assimilate remobilization, Photosynthesis, Yield components

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INTRODUCTION

Soil moisture deficit and drought stress are among the most critical and widespread environmental factors negatively impacting agricultural production worldwide (Rahdari & Hoseini, 2012). Wheat, one of the major cereal crops, is cultivated globally and serves as a staple food for approximately one-third of the world's population (Rahman et al., 2008; Abdelsalam et al., 2019). Among the various abiotic stresses, water deficit is particularly detrimental, adversely affecting chlorophyll content, qualitative traits, and the individual components of wheat grain yield, ultimately leading to substantial yield losses (Raza et al., 2012; Tesfaye et al., 2013; Raza et al., 2014;

Wasaya et al., 2021; Ahmad et al., 2022). Drought stress severely impacts photosynthesis, leading to stomatal closure and reduced CO₂ supply, making it a highly sensitive process (Li et al., 2021; Naseer et al., 2022).

The selection of drought-tolerant genotypes can reduce damage to crops, and testing these genotypes can lead to the development of new cultivars and potential genetic improvement (Zafar-ul-Hye et al., 2007; Chowdhury et al., 2021). Wheat genotypes and varieties impact genetic engineering success, and genotype screening aids in selecting parents and breeding processes by assessing transformation, regeneration, tissue culture, and callus induction efficiency (Vendruscolo et al., 2008; Abid et al., 2014). Various indices have been proposed for selecting genotypes based on grain yield. Among these, a higher harvest index (HI) under drought stress conditions is one of the important criteria for selecting genotypes (Giunta et al., 1995; Rezadoost & Roshdi, 2006; Sanjarei Pirvatlou & Yazdansepa, 2009). The increase in grain yield potential of new wheat varieties has primarily been achieved by enhancing the harvest index (Araus et al., 2002). Remobilizing photosynthetic materials can be different under soil moisture scarcity between wheat genotypes (Meng et al., 2017). Consistent with this, Elyassi et al. (2010) reported that the Shahryar wheat cultivar had the highest remobilization of photosynthetic materials (80 g/m²) among other studied varieties under pre-anthesis drought stress. They also reported that the maximum remobilization efficiency under pre-anthesis stress treatment belonged to the Shahriar cultivar (53%), while the highest efficiency under post-anthesis stress was observed in the tall Toos cultivar (34%). Aligned with this, Gent (1994), over a three-year experiment, concluded that the carbohydrates stored in the wheat stem are important for grain filling but stated that the amount of current carbohydrates for grain filling is limited under drought stress conditions.

Additionally, wheat genotypes can exhibit different ranges of yield components including spike weight, number of spikelets per spike (spikelets/spike), grain weight/spike, number of grains per spike (grains/spike), and 1000-grain weight under drought stress (Ahmad et al., 2022; Javed et al., 2022). Furthermore, Subhani and Chowdhry (2000), by correlation and causation analysis of bread wheat under drought and irrigation conditions, also found that grain yield had a direct positive correlation with the traits of flag leaf area, plant height, spike length, grains/spike, 1000-grain weight, plant biomass, and HI under drought stress, but negative correlation with the trait of days to spike emergence. Emam et al. (2007) reported that the reduction in the grains/spike and the 1000-grain weight were the main causes of decreased grain yield under drought stress conditions under post-anthesis, while drought stress had no significant effect on the spikelets/spike and spikes/m².

Therefore, selecting genotypes with high tolerance to limited soil moisture according to yield components and physiological traits (Mutanda et al., 2024) is significant in gaining higher grain yield, especially in arid ecosystems. This research investigates the impact of soil water deficit stress on photosynthesis and remobilization in wheat genotypes and the relationship between yield and yield components under drought conditions. In the context of these facts, this study screened wheat genotypes in semi-arid regions of Northwest Iran (West Azerbaijan Province) for moisture deficit resistance. We hypothesized that changes in physiological traits and yield components under soil water deficiency, which affect the grain yield of different wheat genotypes, can help us introduce a wheat genotype or cultivar with a higher yield than other studied genotypes for cultivation in these cold and arid regions.

MATERIALS AND METHODS

Study area

Field research was conducted during 2015-2016 at the Agricultural and Natural Resources Research Station in the southeastern part of West Azerbaijan Province, Iran (46°05' E longitude and 36°00' N latitude). The elevation of the study area was 1142 m above sea level. The meteorological data for the experimental site during the 2015–2016 growing season are presented in Table 1. Long-term meteorological data showed the area's mean annual rainfall was 280 mm. The area's minimum and maximum mean temperatures were about -5.7°C and 26.2 °C, respectively.

The soil at the experimental site is a silty loam. Composite soils were collected from a depth of 0-30 cm, processed and analyzed for particle size analysis, pH, calcium carbonate (CaCO₃) concentration, and electrical conductivity (ECe) using the standard methodologies (Bauyoucos, 1954; McLean, 1965; Allison & Moodie, 1965; and Black et al. 1983). The modified Walkley-Black method was used to determine soil organic carbon (SOC) content (Jackson, 1958). The Kjeldahl digestion and distillation method was used for measuring total nitrogen (Bremner, 1982), while Olsen (1954), the ammonium acetate method (Carson, 1980), and DTPA extraction (Lindsay & Norvell, 1978) were used to determine available phosphorus (P), potassium (K), and micronutrients (iron and zinc). The soil had an ECe of 0.81 dS/m and a pH of 8 (Table 2).

Experiment design

The experiment followed a randomized complete block design with three replicated plots of 4.8 m² for each treatment. Treatments were full irrigation and irrigation cutoff at the flowering stage with seven bread wheat genotypes and the Urum, Zare, Zarin, and Mihan cultivars, with the cultivar as the control. According to the soil analysis results, 73.6 kg N ha⁻¹ was applied in the form of 160 kg/ha urea fertilizer (46% nitrogen) in three stages: 20 kg/ha during soil preparation (before planting), 70 kg/ha at the tillering stage, and 70 kg/ha at the stem elongation stage of wheat. Additionally, 38.25 kg K/ha was applied as 85 kg/ha potassium sulfate (45% potassium),

and 23 kg P /ha was applied as 100 kg/ha diammonium phosphate (23% phosphorus) concurrently with planting. Zinc was applied at a rate of 3.38 kg Zn/ha in the form of 15 kg/ha zinc sulfate, applied in a band at a depth of 3–4 cm beneath the plants.

Table 1. Meteorological Data of the Experimental Site in the 2015–2016 Growing Season

Months	Temperature (°C)			Relative humidity (%)			Total Evaporation (mm)	Total Precipitation (mm)
	Average	Min	Max	Average	Min	Max		
October	16	7.1	25	53	28	77	145.1	0.8
November	11	2.9	19	55	31	79	61.4	5.6
December	3.7	-1.8	9.1	64	41	87	0	17.8
January	-5.7	-11.4	-1.0	65	43	88	0	1.3
February	-2.6	-7.1	2	72	54	90	0	42.3
March	6.2	0.1	12.5	61	36	86	0	38.2
April	8	-4	20	57	30	84	72.9	37.6
May	15.8	1.6	31.2	50	2	77	182.2	36.1
June	19.4	6.4	32.4	46	21	71	225.7	9.6
July	25.1	11.4	38.8	47	26	69	290	8.8
August	26.2	12	40.4	45	24	66	308	0
September	23.5	9.4	37.6	53	28	78	207	23.3

Table 2. Selected soil physical and chemical properties

Soil properties	Unit	Values
Electrical conductivity (ECe)	(dS/m)	0.81
pH		8
Saturation moisture	(%)	33
Calcium Carbonate	(%)	11.4
Sand	(%)	16
Silt	(%)	58
Clay	(%)	26
Soil organic carbon	(%)	0.83
Total nitrogen	(%)	0.12
Exchangeable potassium	(mg/kg)	250
Available phosphorus	(mg/kg)	11.2
Available iron	(mg/kg)	6.24
Available zinc	(mg/kg)	0.74

Wheat planting was performed in October with clean, disinfected seeds, with a planting density of 450 seeds/m². Following planting, one irrigation in the fall was applied to facilitate the germination and establishment of the seedlings. Weed management was executed utilizing the pesticide 2,4-D (2,4-Dichlorophenoxyacetic acid).

To assess dry matter remobilization to the grains at two growth stages—pollen shedding and physiological maturity—20 randomly selected plants from each experimental plot were harvested at ground level and oven-dried at 72°C for 48 hours. Upon crop maturation, the total plant weight, spike weight, grain weight/spike, and number of grains per spike (grains/spike) were measured from the harvested samples. The amount, efficiency, and ultimately the contribution of the remobilization of dry matter from vegetative tissues to the grain were calculated using the methods of Cox et al. (1986) and Papakosta and Gagianas (1991) as follows:

Assimilate Remobilization contribution (%) = (Transferred dry matter / Grain yield) × 100

Assimilate Remobilization contribution - 100 = Current photosynthesis contribution

The grain yield was harvested by removing 50 cm from the beginning and end of each plot using a Wintersteiger cereal combine and then converted to kg/ha.

Statistical analyses

Statistical analyses and graph plotting were performed using SPSS and Excel software. To identify significant variations, analysis of variance and the mean data comparison were performed using Duncan's multiple range test at a $p \leq 0.05$ unless otherwise mentioned.

RESULTS AND DISCUSSION

Grain yield components

The effects of soil moisture deficit (drought stress) and genotypes on the wheat yield components were significant. The highest values of wheat yield components were observed in the full irrigation treatment (Table 3). In contrast, one of the effects of water deficit stress in the early growth stages of wheat stem elongation and spike formation is the reduction in the number of spikelets per spike. Kilic and Yağbasanlar (2010) indicated that the spikelets/spike were positively correlated with wheat yield under soil moisture deficit. The spikelets/spike exhibited a 14.3% reduction under soil moisture deficit compared to full irrigation conditions. The difference between the highest and lowest spikelets/spike among the wheat genotypes was 30.7% (Table 3).

The highest number of spikelets per spike (15) was observed in Mihan, Zare, and C-91-9, while the lowest (11) was recorded in C-91-5. Water scarcity stress led to the formation of fewer grains in the spike, such that the highest grains/spike was determined in full irrigation with 29 grains, and the lowest was in the water scarcity stress treatment with 25 grains/spike (Table 3). Our results correlated with the results of Praba et al. (2009), who reported that water stress significantly reduces plant height, grains/spike, spike weight, and grain weight/spike. Likewise, Başer et al. (2024) reported a significant reduction in the grains/spike under limited soil moisture conditions.

Wheat genotypes showed significant differences in grains/spike (53.3%). The Mahin variety had the highest grains/spike (38), while C-91-5 had the lowest (22) grains/spike. Water stress in all genotypes caused a reduction (21.7%) of grain weight/spike. Pour-Aboughadareh et al. (2020) reported a significant reduction in the grains/spike of the wheat genotypes under drought stress compared to the control. Similarly, Akbari Mogaddam et al. (2002) stated that water stress during the spike emergence stage reduces grain yield, with the most significant impact on grain weight among the yield components. The highest (1.62 g) and lowest (0.98 g) grain weight/spike were observed in genotypes Mihan and C-91-8, respectively. Furthermore, under soil water deficit, spike weight exhibited a 23.4 % reduction compared to full irrigation. Denčić et al. (2000) concluded that kernel weight/spike positively impacted wheat grain yield under drought stress.

The Mihan cultivar had the highest spike weight (2.17 g), while line number 5 (C-91-5) had the lowest (1.32 g). The grain yield exhibited significantly different values under irrigation treatments. Under soil water deficit stress, the grain yield was reduced by 41.7% (Table 3). Considering that increasing soil water deficiency led to a reduction in grain yield components such as spikelets/spike, grains /spike, and grain weight/spike, the decrease in grain yield with increasing water stress was not unexpected. Javed et al. (2022) found a positive correlation between wheat grain yield and yield components under soil water deficit. Shahryari and Mollasadeghi (2011) reported that water stress decreased grain yield and its components across all studied genotypes.

Several studies (Siddique et al., 2000; Guttieri et al., 2001) have reported reductions in wheat grain yield under water deficit stress. According to Sanjari and Shiri (2000), this reduction is primarily associated with a decrease in grains per spike and the number of spikes per unit area. Among the cultivars studied, the highest grain yield (6894 kg/ha) was recorded for Mihan, while the lowest (5025 kg/ha) was observed in Line C-91-5 (Table 3). Tahmasebi Sarvestani et al. (2001) found that the Sabalan variety had the highest average yield (2214 kg/ha) under different irrigation treatments, whereas the Sardari variety had the lowest (1502 kg/ha). They noted that applying a single irrigation at the milk stage in Sabalan led to a 54% increase in grain yield compared to the control.

Table 3. Irrigation and genotype effects on yield components of wheat.

Treatments	Spikelets /spike	Grains /spike	Grain weight /spike (g)	Spike weight (g)	Harvest index (HI)	Grain yield (kg/ha)
Irrigation						
Full irrigation	14x [♂]	29x	1.29x	1.75x	50x	7410x
Irrigation cutoff	12y	25y	1.01y	1.34y	40y	4317y
Genotypes						
Orum	13bc [‡]	26cde	1.16bc	1.59bc	46bc	5951bc
Zare	15a	25cde	1.05bcd	1.38ef	46bc	5465bc
Mihan	15a	38a	1.62a	2.17a	50a	6213ab
Zarrin	14ab	26cde	1.09bcd	1.41cdef	45bcd	5951abc
C-91-4	14ab	30b	1.20b	1.58bcd	43cd	6894a
C-91-5	11d	22e	1.02cd	1.32f	43cd	5025c
C-91-6	12c	24de	1.12bcd	1.49cdef	44cd	5475bc
C-91-7	13bc	27bcd	1.15bc	1.54bcde	44cd	5724bc
C-91-8	13bc	23e	0.98d	1.46cdef	41d	5893bc
C-91-9	15bc	24de	1.05bcd	1.40def	44cd	5642bc
C-91-10	13bc	28bc	1.20b	1.68b	48ab	6265ab

In each column, the means that have the same lower-case letter (x vs. y[♂]) or (a, b, c, d, e, f[‡]) are not significantly different between irrigation treatments or wheat genotypes, based on DMRT at the 5% probability level

The HI was determined at 50% and 40% in the full irrigation and irrigation cutoff treatments, respectively. The difference between the two irrigation treatment levels in HI was 20% in this study. Previous studies (Bayoumi et al., 2008; Khakwani et al., 2012) reported that wheat genotypes' physiological and agronomic traits and HI significantly decreased under drought conditions. Ahmadi et al. (2006) observed a significant interaction between drought stress and the timing of nitrogen fertilizer application on grain yield and related physiological traits in wheat. They highlighted that the soil moisture regime notably influences grain yield and HI. These traits significantly decreased under drought-stress conditions. Likewise, Tavakoli (2003) concluded that supplementary irrigation of rainfed wheat fields directly and positively increased the HI and grain yield. Sharifi and Rahmanian (2001) also reported that applying soil moisture stress in wheat fields reduces the ripening period, the HI, and the grain yield. The average of the HI of the studied genotypes in the experiment varied, with a difference of 18% between the lowest and highest harvest indexes among the genotypes. The Mihan cultivar, with a harvest index of 50%, and line C-91-8, with 41%, had the highest and lowest HI, respectively (Table 3).

Both irrigation wheat genotypes significantly affected wheat grain yield (Figure 1). Among genotypes, Line C-91-4, with 8747 kg/ha under full irrigation treatment, had the highest grain yield, while C-91-5, with 6066 kg/ha under soil water stress treatment, had the lowest grain yield. Considering that line C-91-4 had a higher grains/spike and grain weight under full irrigation treatment, the high grain yield of this genotype was predictable. With increased irrigation intervals and intensified water stress in all genotypes, grain yield was decreased. In cultivars such as Zarin and Urum, the reduction in grain yield under drought conditions compared to full irrigation was more than 50%, whereas in the Mihan cultivar, this difference was about 33% (Figure 1). The highest grain yield in the irrigation cutoff treatment was related to the Mihan cultivar, with 4856 kg/ha. Although the Zarin and Urum cultivars had the highest grain yield under full irrigation conditions, their grain yield significantly decreased under water stress conditions. One of the main reasons for the severe reduction in their grain yield was the wrinkling of the grains and a reduction (40%) in grain weight. In contrast, the Mihan cultivar showed a 22% reduction in grain weight under water stress conditions.

Considering that the trend of changes in the traits of the spikelets/spike and the grains/spike of the genotypes at different irrigation levels was almost the same, and water stress uniformly reduced these traits in all genotypes, the high grain weight (or thousand-grain weight) should be considered as one of the most important components of grain yield under water stress conditions as a criterion for selecting drought-tolerant genotypes (Akbari Mogaddam et al., 2002; Rezadoust & Roshdi, 2006; Sanjari Pireivatlou & Yazdansepas, 2008). Under drought stress conditions, the genotype C-91-4 and Mihan cultivar, probably due to higher grain weight, produced high grain yields of 5039 and 4856 kg/ha, respectively (Figure 1)

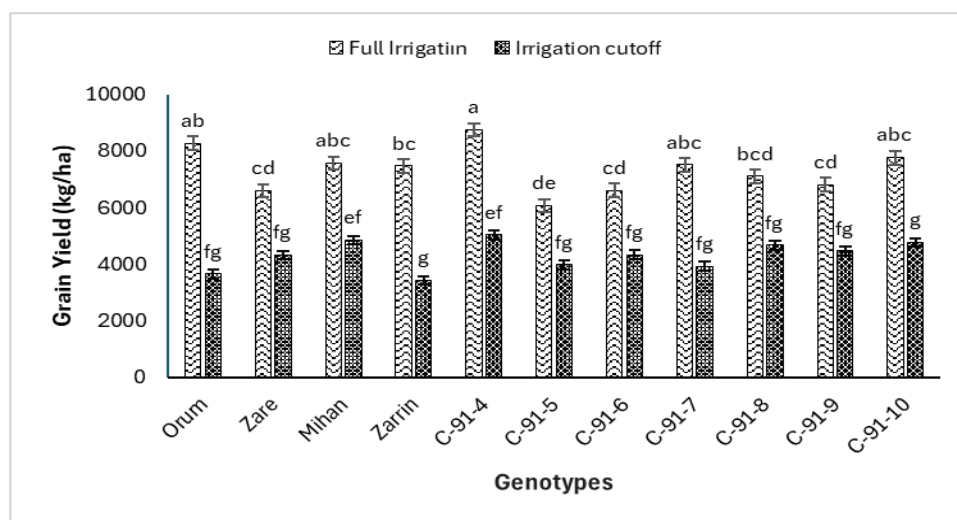


Figure 1. The mean of grain yield of wheat genotypes under different levels of full irrigation and irrigation cutoff (water stress) treatments (Different letters indicate significant differences at the 5% and 1% probability level)

Photosynthesis and assimilate remobilization

Results indicated that varying irrigation levels significantly influenced the contribution of remobilized photosynthetic materials (assimilate remobilization) to grain yield. Under non-stress conditions, remobilized assimilates were determined to be 32%, which increased to 40% as drought stress intensified (Figure 2). Soil water stress significantly enhanced stem reserve mobilization, ranging from 16% to 68%, compared to non-stress conditions (Gurumurthy et al., 2023).

Gent (1994), in a three-year study, concluded that carbohydrates stored in wheat stems are crucial for grain filling, particularly under drought conditions where current photosynthesis is limited. Similarly, Tiryakioğlu (2024) reported that, under water-limited regimes, wheat dry matter remobilization was primarily derived from pre-anthesis reserves, especially under irrigation until anthesis and until physiological maturity.

Vosoghi Rad et al. (2022) found that the peduncle internode significantly affected stem height across all durum wheat genotypes, with lower internodes showing the highest levels of dry matter remobilization under both drought and normal conditions. In the present study, significant genotypic differences in assimilate remobilization were observed, with rates ranging up to 63.3%. The Mihan cultivar showed the highest remobilization rate (52%), while lines C-91-7 and C-91-5 exhibited the lowest (27%) (Table 4).

Plaut et al. (2004) also reported considerable variation in dry matter remobilization from vegetative organs to grains among wheat cultivars under drought conditions, with the Sonka variety outperforming the Batavia variety in this regard. These findings align with Ehdaie et al. (2006), who, in evaluating 11 wheat genotypes, observed significant genetic diversity in remobilization capacity. The remobilized dry matter stored in the peduncle, lower internode, and lower stem nodes ranged from 43 to 171 mg, 81 to 272 mg, and 198 to 474 mg, respectively, under water deficit conditions.

Both irrigation regime and genotype significantly influenced the contribution of current photosynthesis to grain yield (Figure 2 and Table 4). On average, current photosynthesis was determined to be 68% under non-stress conditions, but this dropped to 40% under severe water stress (Figure 2). This underscores the critical role of current photosynthesis as a selective mechanism in grain filling. Since remobilization processes—both in accumulation and transfer—require energy, their activity diminishes when current photosynthetic assimilates are sufficient for grain development (Naderi et al., 2000).

The studied genotypes also differed significantly in their reliance on current photosynthesis, with a 34% variation. Lines C-91-5 and C-91-7 showed the highest contributions from current photosynthesis (73%), while the Mihan cultivar had the lowest (48%) (Table 4). However, despite their higher current photosynthesis rates, C-91-5 and C-91-7 exhibited reduced grain yields due to lower yield component performance. In contrast, the Urum variety, with a high current photosynthesis rate (67%) and favorable yield components, achieved the highest grain yield (8274 kg/ha) under full irrigation (Figure 1). This highlighted the importance of current photosynthesis for grain filling under optimal conditions.

Therefore, maintaining an active and healthy green leaf area is essential to sustain photosynthetic capacity, particularly under non-stress environments. In plant communities, solar energy capture through photosynthesis is fundamental. Research in crop physiology has consistently shown that the final yield of agricultural crops depends largely on both the size and efficiency of their photosynthetic systems.

Table 4. Irrigation and Genotypes effects on Assimilate remobilization contribution and Current photosynthesis contribution

Treatments	Assimilate remobilization contribution (%)	Current photosynthesis contribution (%)
Irrigation		
Full irrigation	32y [♂]	68x
Irrigation cutoff	40x	40y
Genotypes		
Orum	33cd [‡]	67b
Zare	39bc	61cd
Mihan	52a	57d
Zarrin	34cd	66b
C-91-4	41b	59cd
C-91-5	27d	73a
C-91-6	28d	72a
C-91-7	27d	73a
C-91-8	32cd	68b
C-91-9	38bc	62c
C-91-10	43b	48e

In each column, the means that have the same lower-case letter (x vs. y[♂]) or (a, b, c, d, e, f[‡]) are not significantly different between irrigation treatments or wheat genotypes, based on DMRT at the 5% probability level

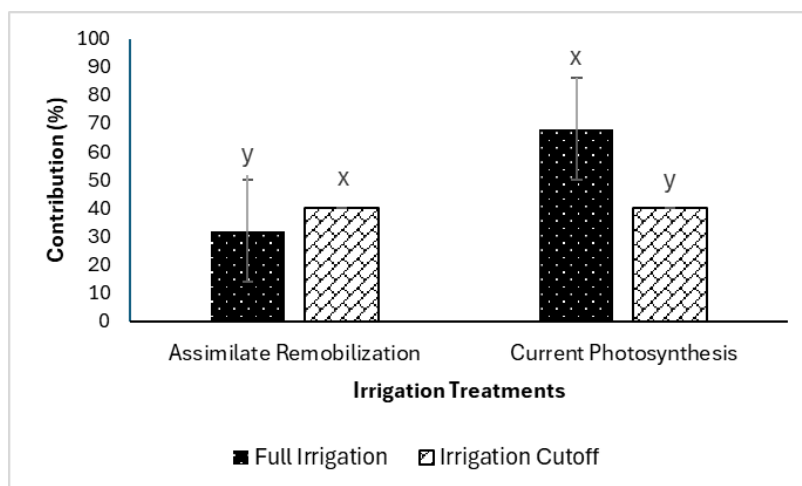


Figure 2. The mean comparison of assimilate remobilization and current photosynthesis contributions under full irrigation and irrigation cutoff (drought stress) treatments

CONCLUSION

This study highlights the significant impact of soil moisture deficit on wheat grain yield and its key components. Drought stress notably reduced spikelets/spike, grain weight/spike, spike weight, and grains/spike, especially during critical growth stages such as spike development and grain filling. Physiological responses, including a reduced harvest index and diminished contribution from current photosynthesis, further contributed to yield losses, shifting reliance toward assimilate remobilization for grain filling.

Among the genotypes tested, drought-tolerant lines like Mihran and C-91-4 maintained comparatively higher yields under stress conditions, underscoring the importance of selecting and breeding for traits associated with stress resilience. The Mihran cultivar, with a high harvest index (50%), remobilization rate (52%), and moderate current photosynthesis contribution (57%), demonstrated strong adaptability and yield stability in semi-arid environments.

The findings underscore the necessity of incorporating traits such as enhanced assimilate remobilization, sustained photosynthetic activity, and optimized grain weight into breeding programs. Developing wheat varieties with these adaptive traits will be crucial for maintaining productivity under increasing water constraints. This research offers valuable insights for wheat breeders and agronomists working to improve drought resilience and ensure food security in water-limited regions.

Compliance with Ethical Standards

Peer-review

Externally peer-reviewed.

Declaration of Interests

The authors have no conflict of interest to declare.

Author contribution

The author confirms sole responsibility for the study's conception, design, analysis, interpretation, and manuscript preparation

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