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Research Article

The impacts of earlier flowering on grain yield of winter wheat cultivars under semi-arid conditions

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ABSTRACT- The timing of wheat anthesis, often coinciding with late-season drought stress, can significantly reduce grain number and yield. Field and greenhouse experiments conducted at Shiraz University, Shiraz, Iran, during the 2019–2021 growing seasons investigated how early flowering may mitigate yield reduction. The study aimed to assess the impact of phenological timing on yield components and overall yield performance. Ten widely adopted cultivars, introduced over the past five decades, were used. The high-yielding cultivars (Baharan, Sirvan, and Chamran) exhibited significantly more grains per spike and a greater biological yield. This increased phytomass production was accompanied by a higher harvest index. Stem elongation began earlier in the superior cultivars, while cultivars with extended flowering periods (Navid, Bayat, and Shiraz) had the lowest grain yield. Floret development monitoring revealed that floret degradation occurred earlier and lasted longer in low-yielding cultivars, beginning from the yellow anther stage. In contrast, high-yielding cultivars experienced a shorter floret abortion period, from heading to anthesis. In semi-arid regions, early flowering and reduced floret abortion periods may enhance grain yield. Unlocking the full potential of superior cultivars requires a deeper understanding of the genetic mechanisms driving early flowering in these varieties.

INTRODUCTION

Bread wheat (*Triticum aestivum*) is a major source of carbohydrates, protein, and essential nutrients for billions of people, particularly in regions such as Asia, Europe, and North Africa. Increasing its production is crucial for global food security (Sierra-Gonzalez et al., 2021). To identify yield-limiting factors effectively, understanding the physiological changes associated with genetic advancements is essential (Aisawi et al., 2015; Beche et al., 2014). Extensive research has consistently shown that wheat yield increases over the past century are linked to the steady genetic gains in harvest index (HI) across diverse growing environments. These yield gains are primarily driven by improvements in spikelet grain number and spikes per plant density, highlighting the importance of these factors in bread wheat yield enhancement (Calderini et al., 2001; Slafer et al., 2023). Previous studies have demonstrated that wheat plants can supply sufficient assimilates for grain filling, even under post-flowering stress conditions.

Therefore, increasing sink capacity, particularly the grain number (GN), appears to be a crucial strategy for enhancing wheat yield potential (Gonzalez-Navarro et al., 2016; Slafer et al., 2014, 2022). While wheat growth before terminal spikelet initiation does not appear to directly affect the ultimate GN, the growth pattern from terminal spikelet onwards plays a significant role in grain establishment. Research indicates that during stem elongation (STE), competition for photosynthates arises between the developing stem and the juvenile spike (PirastehAnosheh et al., 2016; Slafer et al., 2022). Based on this understanding, we hypothesize that extending the duration of the STE phase (i.e., spike growth phase) could provide more assimilates for the rapidly growing spike, potentially enhancing floret survival, increasing the GN, and improving yield performance (Gonzalez-Navarro et al., 2016; Jahani Doghozlou & Emam, 2022; Slafer et al., 2023). Alterations in wheat phenology, specifically the timing of growth and reproductive phases, can significantly influence yield potential (Motzo & Giunta, 2007). The GN in wheat is a polygenic trait influenced by multiple factors, from the terminal spikelet phase through to shortly after the onset of anthesis (AN), including tiller loss, floret primordia development and degeneration, and the rate of aborted grains (Slafer et al., 2023).

During STE, up to twelve floret primordia are initiated, but a significant proportion undergo degeneration, with typically five to six florets being fertilized at AN. Following fertilization, some developing ovaries abort, while the remaining ones mature into grains (Kirby, 1974). Recent studies have shown that improved spike fertility is more strongly associated with the survival of initiated florets than with

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the initiation of additional florets (Ferrante et al., 2020; Jahani Doghozlou & Emam, 2022; Ochagavía et al., 2021; Vahamidis et al., 2019). Given the variation in developmental stage duration, particularly the duration of rapid spike growth prior to flowering, across wheat cultivars, these differences may help explain the variation in the GN per spike observed across cultivars (Fischer, 1985). Despite the significance of floret primordia development and degeneration, detailed studies on these processes are limited due to their time-consuming and labor-intensive nature. In this study, we employed the Waddington scale (W#) to monitor floret primordium development, encompassing stages W3 to W10 (Fig. 1) (Waddington et al., 1983).

In Mediterranean climates, the timing of wheat AN, which often coincides with late-season heat and/or drought stress, can significantly reduce GN and yield (Acreche & Slafer, 2009). Modern wheat cultivars have been reported to exhibit a continual trend towards earlier AN dates (Jahani Doghozlou & Emam, 2022; Motzo & Giunta, 2007). These cultivars have been bred to optimize AN timing, thereby enhancing their adaptability to prevailing environmental conditions (Ochagavía et al., 2021). However, further exploration is needed to fully understand the potential benefits of early flowering in wheat. Additionally, examining the physiological changes associated with the transition from older to modern cultivars provides a valuable framework for understanding the mechanisms underlying grain yield (GY) improvement (Alonso et al., 2018; Pedro et al., 2012). This study investigates the relationship between phenological stage duration and GY in ten wheat cultivars introduced over the past fifty years under semi-arid conditions. The primary objective is to assess the impact of phenological timing on yield components and overall GY. Following the observation of phenological variations among cultivars in the field experiment, a detailed phenological monitoring study was conducted.

MATERIALS AND METHODS

Experimental setup and location

Two experiments were conducted during the 2019–2020 and 2020–2021 growing seasons at Shiraz University, Iran. Experiment I (2019–2020) was carried out in the research field of the School of Agriculture (29°50′N, 52°46′E; elevation 1810 m above sea level), characterized by a Mediterranean precipitation pattern with a long-term average annual temperature of 13.4 °C and annual precipitation of 386 mm (Haghshenas et al., 2021). This field experiment evaluated yield, yield components, and phenological development in ten widely cultivated wheat cultivars (Bayat, Azadi, Falat, Navid, Chamran, Marvdasht, Pishtaz, Shiraz, Sirvan, and Baharan), each introduced in the region over the past fifty years. Experiment II (2020–2021) was conducted in a controlled greenhouse environment at Shiraz University to enable detailed phenological monitoring. Floral development of individual florets within juvenile spikes was assessed using the Waddington scale (Waddington et al., 1983) and the Kirby and Appleyard scoring system (Kirby & Appleyard, 1984). The soil used in both experiments had a loamy-silty-clay texture, consisting of 39% clay, 46% silt, and 15% sand. The soil extract showed a pH of 7.7, indicating neutral to slightly alkaline conditions, and contained 0.36% organic carbon within the 0–30 cm depth.

Experimental design

In Experiment I (Field experiment), the field experiment was arranged as a randomized complete block design (RCBD) with three replications. Each plot measured 1.6 × 2.5 m^2 and consisted of eight rows spaced 20 cm apart. Seeds of the ten wheat cultivars were hand-sown at a density of 250 plants m^{-2} on November 20, 2021, within the region's standard sowing window. Irrigation was applied at ten-day intervals using a drip tape system, following local agronomic practices. Based on soil analysis, nitrogen was supplied at a rate of 150 kg ha^{-1} in the form of urea, divided into three equal applications: before sowing, at mid-tillering, and at AN. No pesticides were applied, and weeds were managed manually through hand weeding.

In Experiment II, the greenhouse study followed a completely randomized design (CRD) with six replications. Three replications were designated for monitoring apical development, while the remaining three were left intact to assess the final GN per spikelet at maturity. Sowing was carried out on January 4^{th}. Uniform seeds of the ten wheat cultivars were hand-sown in 5 kg pots filled with field-collected soil. As in the field experiment, each pot received 150 kg ha^{-1} of nitrogen (as urea) applied in three equal portions: before sowing, at mid-tillering, and at AN, based on the results of soil analysis (Table 1). During the experiment, temperatures ranged from 13-34 °C, and relative humidity was maintained between 55-60%.

Measurements

Phenological stages—including STE (ZG30), booting (BO, ZG40), AN (ZG60), and physiological maturity (PM, defined as the point when 50% of the plants in each plot reached the respective stage)—were recorded based on the Zadoks growth scale (Zadoks et al., 1974). Growing degree days (GDD) for each phenological stage were calculated by summing the daily mean temperatures exceeding a base temperature of 0 °C, with the accumulated thermal time (TT) expressed in degree-days (McMaster & Wilhelm, 1997). At harvest, plants from a 1 m^2 area in the center of each plot were collected for yield analysis. The GN per spike was determined by counting grains from 10 randomly selected main stem spikes. After a 48-hour drying period at 72 °C, the spikes were threshed, and the dry weight of 500 grains per plot was measured to estimate the thousand-grain weight (TGW). Biological yield (BY, total aboveground dry matter), HI, and GY were recorded for each plot. Additional agronomic characteristics of the cultivars are presented in Table 2.

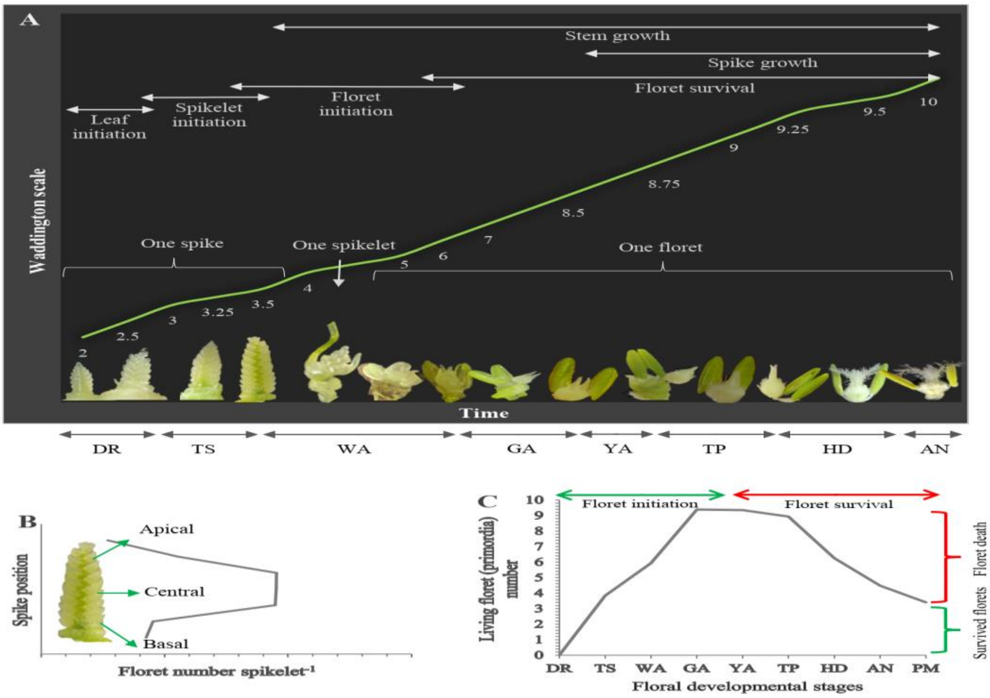

Fig. 1. (A) Graphical time course of key wheat floral developmental stages from early spikelet primordia differentiation (W2; double ridges) to anthesis (W10), based on "Waddington scale" (Waddington et al., 1983). Also, the corresponding floral developmental stages proposed by Kirby and Appleyard (Kirby & Appleyard, 1984) based on the frequent sampling result in this experiment are demonstrated; Double ridges (DR), terminal spikelet (TS), white anther (WA), green anther (GA), yellow anther (YA), tipping (TP), Heading (HD), anthesis (AN), and physiological maturity (PM). The pictures are not to the scale; as a reference, the length of apex in W2.5 = 1mm, W3.5 = 2.2 mm, and the ovary dimensions in W10 = 3.5 mm length and 1.60 mm width. (B) Illustrating the mapping of florets in different spikelets of the spike positions. (C) The dynamics of living floret primordia; floret generation, maximum number of florets at green anther stage followed by floret degeneration.

Experiment II: For a detailed assessment of wheat cultivar phenology, frequent sampling was conducted once or twice per week. At each sampling point, a median plant from each cultivar was excised at the soil surface, and apical development was examined under a binocular microscope. The initiation timing of double ridges and terminal spikelets was recorded. From the terminal spikelet stage until AN, samples were collected two to three times weekly. The main spike of each plant was carefully dissected under magnification to determine the total number of initiated floret primordia, following the method of Gonzalez-Navarro et al. (2016), at three specific spikelet positions: basal (fourth from the base), central (middle of the spike), and apical (fourth from the top), as described by Ferrante et al. (2010) (Fig. 1C). Floret primordia counts were performed at seven key floral developmental stages described by Kirby and Appleyard (1987), including the terminal spikelet stage (when spikelet initiation was complete), the white anther stage (when the lemmas of florets one and two fully enclosed all internal structures), the green anther stage (when glumes covered all but the tips of the florets), and the yellow anther stage (when the lemmas and glumes of the first three florets became visible). These were followed by the tipping stage (ZG49, when awns first appeared), the heading stage (ZG55, when 50% of spikes were visible), and finally the AN stage (ZG65, when 50% of spikes had extruded anthers) (Jahani Doghozlou & Emam, 2022; Fig. 1). Floral development of individual florets within each spikelet was also recorded using the Waddington scale (Waddington et al., 1983), and TT (expressed in °C days) was calculated for each developmental stage using a base temperature of 0 °C (McMaster & Wilhelm, 1997). Florets that reached stage W10 (AN) or just prior to it were classified as fertile, while those that appeared dry and transparent were considered aborted (Guo et al., 2015). At PM, in the remaining three replicates, fully developed and non-shriveled grains were counted at each spikelet position (basal, central, and apical) on the main shoot spike, using the same spatial scheme applied during floret primordia recording. Grain set percentage for each position was then calculated by dividing the final GN by the maximum number of the fertile florets, following the method described by Ferrante et al. (2013).

Data analyses

Data analysis was performed using analysis of variance (ANOVA) with SAS 9.1 software. Means comparison were executed through Duncan's multiple range test at a significance level of $P \leq 0.01$.

RESULTS

Wheat cultivars grain yield comparison

ANOVA revealed significant differences in GY among the wheat cultivars ($P \leq 0.01$) (Table 3). Sirvan and Baharan cultivars, producing 5307.3 and 5365.0 kg grain ha^{-1}, respectively, were the highest-yielding cultivars. Baharan, Sirvan, and Chamran cultivars exhibited higher grains per spike, averaging 45.3, 45.0, and 44.0 grains per spike, respectively (Table 4). In contrast, Shiraz, Azadi, Bayat, and Navid cultivars had lower GY, with values of 3326.7, 3142.0, 2932.7, and 2733.6 kg ha^{-1}, respectively. These cultivars also had the lowest grains per spike, averaging 38.3, 39.3, 34.7 and 31.7 grains per spike, respectively (Table 4).

In this study, TGW did not exhibit significant variation among cultivars and had no significant effect on wheat GY (Table 4), however, significant differences in BY were observed among the cultivars ($P \leq 0.01$). The higher-yielding cultivars (Baharan, Sirvan, and Chamran) produced the highest BY, with values of 11330, 11241.3, and 10896.7 kg ha^{-1}, respectively. Conversely, Azadi, Shiraz, Navid, and Bayat cultivars, which exhibited lower GY, also had lower BY, with values of 8765.3, 8343.3, 7541.0, and 7488.3 kg ha^{-1}, respectively (Table 4). (Slafer et al., 2014). HI also differed significantly among cultivars ($P \leq 0.01$). The high yielding cultivars (Baharan, Sirvan, and Chamran) had higher harvest indices (45.3%, 45%, and 43.3%, respectively; Table 4).

Duration of phenological phases

Phenological phases were found to be significantly different among cultivars (Table 5). The superior cultivars were early flowering, in such a way that Sirvan, Baharan, and Chamran cultivars with 1285, 1283, and 1323 °Cd TT in the field experiment (Fig. 2) and 754, 753, and 772 °Cd TT in the greenhouse (Fig. 3; Supplementary Table S1) were earlier flowering cultivars. However, Navid, Bayat, Shiraz, and Azadi cultivars with 1515.0, 1462.0, 1436.0, and 1385.0 °Cd TT, respectively, in the field (Fig. 2) and 1113.0, 850.0, 865.0, and 881.0 °Cd TT in the greenhouse experiment (Fig. 3; Supplementary Table S2) reached AN later than other cultivars. Baharan, Sirvan, Falat, and Chamran cultivars, which required 1934.0, 1980.0, 2032.0, and 2035.0 °Cd TT from sowing to PM respectively, completed their life cycle earlier than others, so that they can be categorized as the earliest ripening ones (Fig. 2). In contrast, the Navid, Shiraz, and Azadi cultivars, which were lower-yielding (Table 4), needed 2346.0, 2314.0, and 2246.0 °Cd TT, respectively, from sowing to ripening, and were the latest ripening cultivars (Fig. 2).

In our study, the wheat cultivars Sirvan, Baharan, Falat, and Chamran exhibited an earlier onset of STE, with TT values from sowing to STE of 845.0, 855.0, 884.0, and 864.0 °Cd, respectively, under field conditions (Fig. 2). These same cultivars showed comparable TT values from sowing to W3.5—corresponding to the onset of STE according to the Waddington scale—in the greenhouse experiment, with accumulated TT of 548.0, 546.0, 555.0, and 546.0 °Cd, respectively (Fig. 3; Supplementary Table S2). Notably, these early-developing cultivars also demonstrated improved GY performance (Table 4). Conversely, cultivars such as Navid, Bayat, Shiraz, and Azadi, which recorded the lowest GY (Table 4), were characterized by a delayed entry into the STE phase, requiring greater thermal accumulation. In the field experiment, these cultivars reached STE after accumulating 1022.0, 1002.0, 996.0, and 949.0 °Cd, respectively (Fig. 2), while in the greenhouse, corresponding TT values to reach STE were 645.0, 645.0, 628.0, and 616.0 °Cd (Fig. 3; Supplementary Table S1). Further analysis in the field experiment revealed that Navid, Bayat, and Shiraz cultivars exhibited extended durations of the floret abortion phase—defined as the period between BO and AN —with TT values of 363.0, 339.0, and 298.0 °Cd, respectively (Fig. 4). In contrast, the superior-yielding Baharan and Sirvan cultivars showed significantly shorter durations of this phase, requiring only 202.0 and 208.0 °Cd, respectively. A more detailed evaluation of floret development stages indicated that Navid, Bayat, Azadi, and Shiraz experienced prolonged floret abortion periods during the W8 to W9 stages, accumulating 263.0, 92.0, 91.0, and 70.0 °Cd, respectively. On the other hand, Baharan and Sirvan exhibited more rapid progression through these stages, with lower TT requirements from W8 to W9, indicating shorter floret abortion periods (Fig. 3; Supplementary Table S2).

Spike fertility pattern

The results of this experiment showed that wheat cultivars produced significantly different fertile floret numbers at the basal, central, and apical spikelet positions across seven floral developmental stages ($P \leq 0.01$). Across all cultivars and spikelet positions, maximum floret primordia spikelet^{-1} was also observed at the green anther stage (Fig. 5; Supplementary Table S4, Table S5, and Table S6). At the green anther stage, Baharan, Sirvan, and Chamran cultivars exhibited maximum floret primordia numbers per spikelet of 9.8, 9.7, and 9.3, respectively, at the basal position (Fig. 5; Supplementary Table S5). For the central position, these cultivars had maximum counts of 10.0, 9.9, and 9.5, respectively (Fig. 5; Supplementary Table S4). Finally, at the apical position, the maximum counts were 9.7, 9.5, and 9.1, respectively (Fig. 5; Supplementary Table S3). At the green anther stage, Shiraz, Bayat, and Navid cultivars exhibited the lowest fertile floret counts per spikelet at the apical, central, and basal positions, respectively (Fig. 5; Supplementary Table S4, Table S5, and Table S6) (Prieto et al., 2018).

In the present study, the onset of visible floral degradation varied among wheat cultivars, occurring at different floral developmental stages ranging from the green anther to AN. Interestingly, the pattern of degradation was consistent across apical, central, and basal spikelets. Bayat, Navid, Shiraz, and Azadi cultivars exhibited a prolonged visible floral degradation period, commencing at the yellow anther stage. Thus, Bayat, Shiraz, and Navid cultivars exhibited the lowest final GN, with 1.9, 2.0, and 2.1 grains at the apical position (Fig. 5; Supplementary Table S3), 2.4, 2.6, and 2.5 grains at the central position (Fig. 5; Supplementary Table S4), and 2.2, 2.2, and 2.3 grains at the basal position (Fig. 5; Supplementary Table S5), respectively. Visible floral degradation in Sirvan, Baharan, Chamran, and Falat cultivars commenced at the heading stage across apical, central, and basal spikelets (Fig. 5; Supplementary Table S4, Table S5, and Table S6).

At PM, Baharan, Sirvan, and Chamran cultivars exhibited the highest final GN, with 3.6, 3.4, and 3.1 grains at the apical position (Fig. 5; Supplementary Table S3), 4.2, 4.1, and 3.5 grains at the central position (Fig. 5; Supplementary Table S4), and 3.8, 3.6, and 3.3 grains at the basal position (Fig. 5; Supplementary Table S5), respectively.

Significant variation in mean grain formation percentage was recorded among cultivars. Sirvan (80.5, 84.9, and 83.0) and Baharan (75.6, 81.8, and 79.1) cultivars exhibited the highest mean grain set percentages at the apical, central, and basal positions, respectively (Table 6). While Bayat, Shiraz, and Navid cultivars GS were 50.8%, 52%, and 52.8% in apical, 60.4%, 60.8%, and 61.2% in central and 57%, 56.7%, and 57.5% in basal (Table 6) spikelet positions. Across all wheat cultivars, the mean number of living florets (primordia) at the apical spikelet position consistently remained lower than at the central and basal positions throughout floral development from the TS to PM (Fig. 5; Supplementary Table S4, Table S5, and Table S6). Furthermore, the mean grain set percentage was highest in central spikelets (70.3%), followed by basal (67.3%) and apical (62.6%) spikelets (Table 6).

DISCUSSION

According to the results the wheat cultivars with higher GY, had also higher GN per spike. This suggested that GN, rather than grain weight, was the primary determinant of wheat GY (Martín M Acreche et al., 2008; Borrás et al., 2004; Sadras, 2021; Slafer et al., 2014, 2022). Serrago et al. (2023) also, by comparing two- and six-rowed barley types, reported that increases in the GY were primarily driven by an increased GN per spike, with minimal variation in grain weight or spike density.

In this study it was demonstrated that wheat cultivars with higher GY had also higher phytomass production. It has been indicated that increased biomass accumulation throughout the pre-AN period can contribute to higher GY (PirastehAnosheh et al., 2016). The CIMMYT wheat breeding program has demonstrated a consistent increase in GY, averaging 0.6% per year from 1966 to 2009, with a positive correlation between GY and biomass production (Aisawi et al., 2015). This suggests that future breeding programs should prioritize improving the relationship between potential GY and BY (Firoozabadi et al., 2023; Pedro et al., 2012). However, it is important to note that achieving higher GY requires not only increased biomass production but also a corresponding increase in HI.

Indeed, a higher HI indicates that more dry matter from vegetative stem tissues is allocated to the above-ground sink organs (Martín M Acreche et al., 2008; Mondal et al., 2020). While the highest HI observed in this study (45%) was lower than the theoretical maximum proposed by Austin et al. (1980). It suggests that breeding programs have yet to fully optimize this trait (Aisawi et al., 2015). This raises the question of whether the theoretical maximum (62%) is truly achievable under Mediterranean conditions (Slafer et al., 2023).

Crop adaptation to the growing environment is crucial for optimum yield, enabling the synchronization of phenological phases with favorable conditions. Grain set, a highly plastic process, is particularly sensitive to AN timing (Pessarakli, 2021; Reynolds et al., 2001; Tétard-Jones & Leifert, 2011). Therefore, when breeders introduce a new cultivar for a region, the AN time is of prime importance, and when this trait is optimized, then other traits could be improved (Slafer et al., 2023).

The schematic representation of the importance of AN time is illustrated in Fig. 4. It shows why adjusting the AN time is vital in influencing the adaptation of a crop in a given environment. Indeed, AN earlier or later than the optimal range will cause the crop to face excessive cold or heat temperatures. Generally, in temperate regions with an extended growing season, prolonging the vegetative growth period enables plants to accumulate more assimilates, which can then be remobilized at a later stage (Cockram et al., 2007). However, in Mediterranean regions characterized by terminal heat and drought stresses (Fig. 4), late-flowering cultivars were susceptible to damage from these unfavorable conditions (Haghshenas et al., 2021). Conversely, early-flowering cultivars experienced normal pollination (Jahani Doghozlou & Emam, 2022; Motzo & Giunta, 2007). As summarized by Fischer (2011), under conditions of late flowering stresses, increased respiration can occur due to the crop's exposure to high temperatures, which ultimately reduces yield.

The time and duration of different phenological phases, especially AN time, could be considered as a reliable basis for breeding programs to introduce new cultivars which are optimized for crop phenology. Due to the terminal stresses in semi-arid areas, similar to the present study, cultivars which can cope better with these stresses, appear to be more suitable. One of the proposed solutions to address this issue is the concept of "drought escape", where the crop adjusts its phenology in a way that the flowering and grain filling stages do not coincide with the late-season stresses. This allows the plant to escape, either partially or entirely, from the terminal stress conditions (Pessarakli, 2021; Reynolds et al., 2001; Slafer et al., 2023). Exposure to post-flowering stresses causes a reduction in GY due to the failure in normal grain set (Haghshenas et al., 2021) or incomplete grain filling (Zamani et al., 2024). However, it should be noted that selection of early flowering/maturing cultivars, as a strategy for escaping terminal stresses, should be taken cautiously. As shown in Fig. 4, in early flowering conditions, there is a possibility that the sensitive pollination stage is associated with frost risk and late flowering of wheat could involve a greater risk of terminal drought or heat stress.

Table 1. Physical and chemical properties of the soil at 0–30 cm depth

Soil Texture	Organic matter (%)	pH	Electrical conductivity ($dS.m^{-1}$)	Nitrogen (%)	Potassium ($mg.kg^{-1}$)	Phosphorus ($mg.kg^{-1}$)
Loam-Silty	0.4	7.8	0.5	0.1	450.0	17.0

Table 2. Characteristics of cultivars used in this experiment

Wheat cultivars	Release year	Growth period	Climate	Origin
Bayat	1976	Middle-ripening	Temperate	Native
Azadi	1979	Middle-ripening	Temperate	Native
Navid	1990	Middle-ripening	Cold	Turkey - Oregon (United States)
Falat	1991	Early-ripening	Tropical and subtropical	Mexico (CIMMYT)
Chamran	1997	Early-ripening	Tropical and subtropical	Mexico (CIMMYT)
Marvdasht	1999	Middle-ripening	Temperate	Native
Pishtaz	2002	Relatively early-ripening	Temperate	Native
Shiraz	2002	Middle-ripening	Temperate	Native
Sirvan	2011	Early-ripening	Temperate with drought stress at the end of the season	Mexico (CIMMYT)
Baharan	2014	Early-ripening	Temperate with drought stress at the end of the season	Mexico (CIMMYT)

Table 3. Analysis of variance (ANOVA) for grain yield (GY), biological yield (BY), harvest index (HI), number of grain (GN) per spike, and thousand grain weight (TGW)

SOV	df	GY	BY	HI	GN	TGW
Block	2	68824.0^{**}	5260.0^{ns}	4.8^{*}	12.9^{ns}	5.5^{ns}
Cultivar	9	2087794.0^{**}	5072626.0^{**}	59.9^{**}	1.5^{**}	27.4^{**}
Error	18	8034.3	30873.0	1.1	4.4	3.3
CV (%)		9.7	7.8	4.0	5.2	4.7

*, **, and ns: Significant at 0.05, 0.01, and not significant, according to Duncan's multiple range test ($P \leq 0.01$).

Table 4. Mean comparison of grain yield (GY), biological yield (BY), harvest index (HI), number of grain (GN) per spike, and thousand grain weight (TGW) of ten wheat cultivars in field experiment

Wheat cultivar	GY (kg ha^{-1})	BY (kg ha^{-1})	HI (%)	GN spike^{-1}	TGW (g)
Bayat	$2932.7^{e} \pm 125.1$	$7488.3^{g} \pm 438.1$	$39.2^{de} \pm 1.2$	$34.7^{de} \pm 2.5$	$39.2^{a} \pm 1.7$
Azadi	$3142.0^{de} \pm 139.0$	$8765.3^{e} \pm 362.2$	$37.7^{def} \pm 1.6$	$39.3^{bc} \pm 2.1$	$33.4^{c} \pm 2.0$
Navid	$2733.6^{e} \pm 249.0$	$7541.0^{g} \pm 334.2$	$36.2^{f} \pm 2.2$	$31.7^{e} \pm 2.1$	$38.9^{ab} \pm 2.2$
Falat	$4569.0^{bc} \pm 189.9$	$10428.3^{c} \pm 161.8$	$43.8^{bc} \pm 1.2$	$43.3^{ab} \pm 2.5$	$37.3^{ab} \pm 0.8$
Chamran	$4977.7^{ab} \pm 260.9$	$10896.7^{b} \pm 192.7$	$45.7^{ab} \pm 0.1$	$44.0^{ab} \pm 2.0$	$39.9^{a} \pm 1.9$
Marvdasht	$3404.3^{d} \pm 247.5$	$9243.3^{d} \pm 335.0$	$36.8^{ef} \pm 1.3$	$39.7^{bc} \pm 2.1$	$35.6^{bc} \pm 2.3$
Pishtaz	$4456.3^{c} \pm 232.8$	$10397.7^{c} \pm 338.9$	$42.8^{c} \pm 0.9$	$41.7^{abc} \pm 1.5$	$39.6^{a} \pm 0.6$
Shiraz	$3326.7^{d} \pm 183.6$	$8343.3^{f} \pm 400.8$	$39.9^{d} \pm 0.3$	$38.3^{cd} \pm 2.5$	$40.1^{a} \pm 1.8$
Sirvan	$5307.3^{a} \pm 161.4$	$11241.3^{a} \pm 208.9$	$47.2^{a} \pm 0.6$	$45.0^{a} \pm 2.0$	$41.1^{a} \pm 0.8$
Baharan	$5365.0^{a} \pm 240.5$	$11330.0^{a} \pm 338.3$	$47.3^{a} \pm 0.8$	$45.3^{a} \pm 2.6$	$41^{a} \pm 0.9$

Data are presented as the mean ± SD (standard deviation); $n = 3$. Means followed by the same letter in each column are not significantly different, according to Duncan's multiple range test ($P \leq 0.01$).

Table 5. Analysis of variance (ANOVA) for thermal time (growing degree days; GDD) in ten wheat cultivars for sowing (S), stem elongation (STE), booting (BO), anthesis (AN), and physiological maturity (PM) phases

SOV	df	S-STE	STE-BO	BO-AN	AN-PM
Block	2	39.4^{ns}	128.6^{ns}	60.6^{ns}	1193.9*
Cultivar	9	12195.1**	6096.9**	8723.5**	17411.3**
Error	18	220.1	354.6	80.8	279.0
CV (%)		1.6	10.0	3.4	2.2

*, **, and ns: Significant at 0.05, 0.01, and not significant, according to Duncan's multiple range test ($P \leq 0.01$).

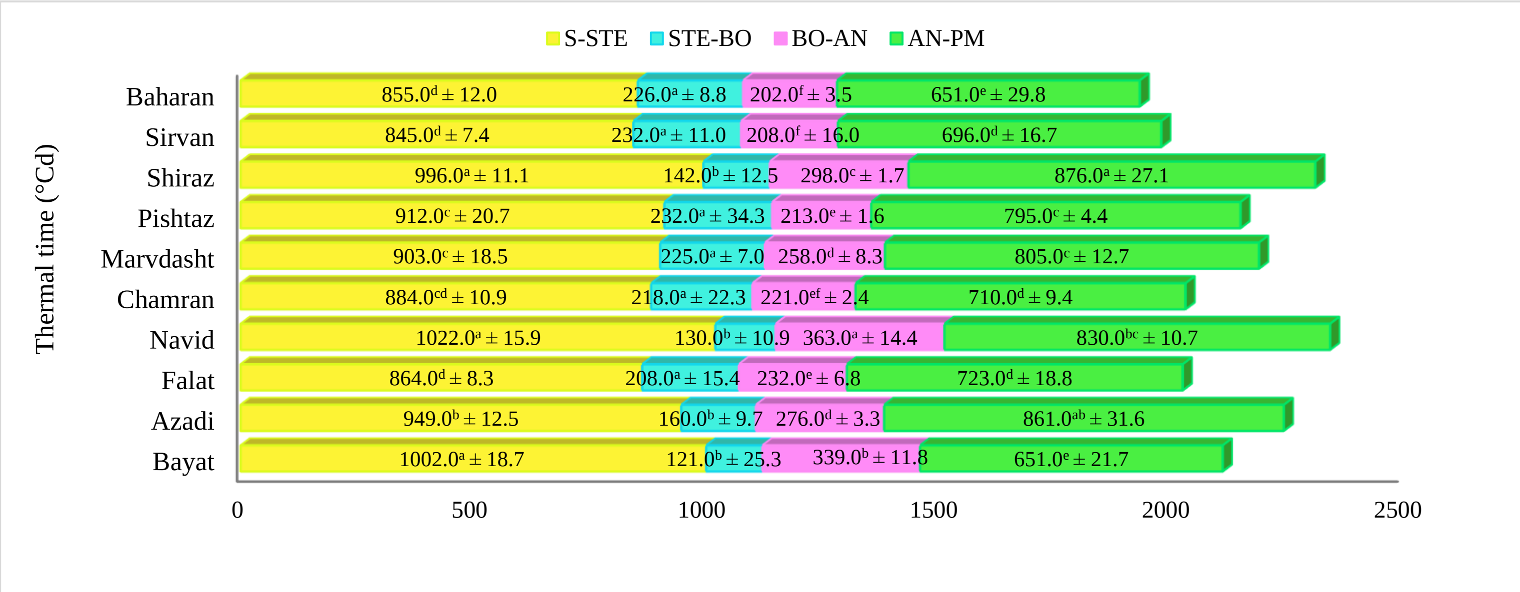

Fig. 2. Thermal time (growing degree days; GDD) of ten wheat cultivars from sowing to maturity in semi-arid conditions; Sowing (S), stem elongation (STE), booting (BO), anthesis (AN), and physiological maturity (PM). Data were presented as the mean ± SD (standard deviation); $n = 3$. In each color means followed by the same letter are not significantly different among cultivars ($P \leq 0.01$).

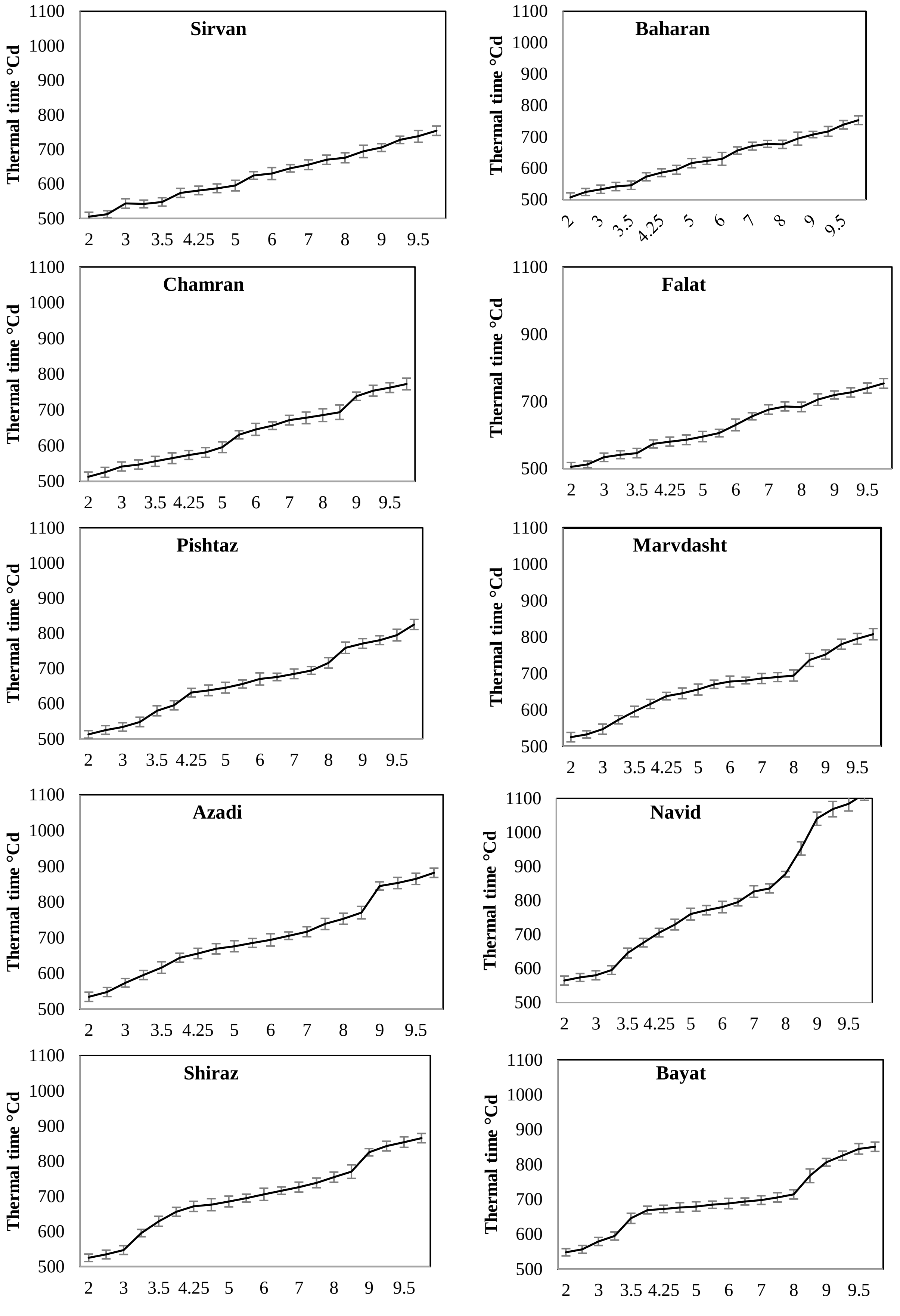

Fig. 3. Floral development of ten wheat cultivars based on Waddington scale through frequent sampling during the stem elongation (STE) phase for florets 2 in central spikelet positions. Scores lower than W3.5 correspond to the spike rather than floret development. Bars represent mean ± SD (standard deviation); *n* = 3.

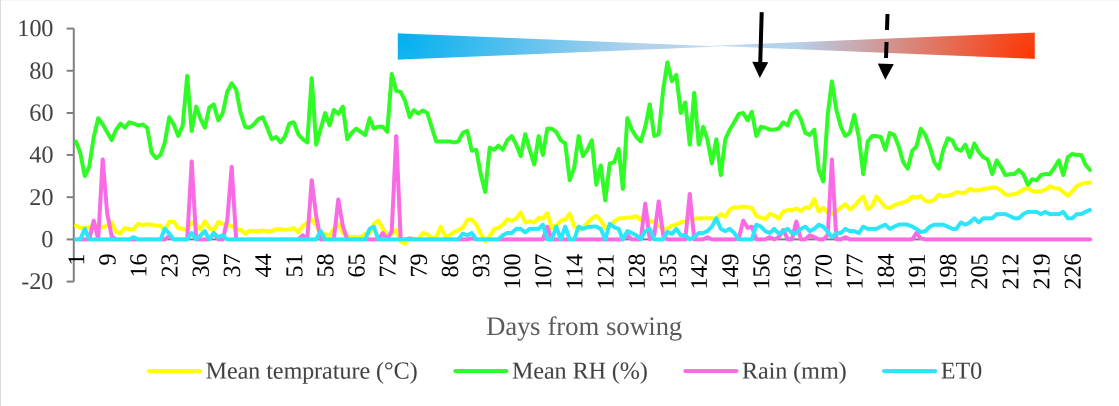

Fig. 4. The meteorological data of the 2019-2020 growing season (field experiment); Relative humidity (RH), evapotranspiration (ET0). The solid and dashed black arrows show the flowering time of the earliest and latest flowering cultivars (i.e., Sirvan and Navid cultivars), respectively.

While GN in wheat is influenced by developmental stages from sowing to shortly after AN, its potential is primarily determined during the STE stage, which occurs a few weeks prior to AN (Ferrante et al., 2020; Fischer, 2007). It has been hypothesized that extending the duration of STE, which coincides with the spike growth phase, would provide increased assimilate for the rapidly developing spike, leading to improved floret survival and, consequently, higher GN and yield (Gonzalez-Navarro et al., 2016; Miralles et al., 2000). In this period, stem and spike compete for assimilates and the number of florets that succeed in this competition determines the final GN and wheat yield (González et al., 2011; PirastehAnosheh et al., 2016). Therefore, enhancing the supply of photosynthetic products for the spike and its florets could enhance spike fertility and GY (Fischer, 2011; Foulkes et al., 2011; Murchie et al., 2023). A longer STE phase allows the wheat plant to accumulate more dry matter (Roychowdhury et al., 2023), potentially increasing the availability of assimilates for the spike and its florets. This could lead to a higher proportion of florets reaching the fertile stage.

Four primary strategies have been proposed to increase GN in wheat (Philipp et al., 2018; Tilley et al., 2019; Xie et al., 2016):

(i) Minimizing competition from non-productive organs, such as sterile tillers; (ii) Enhancing spikelet density per spike; (iii) Prolonging the spike growth stage; (iv) Mitigating floret degeneration by ensuring adequate carbon, water, and nutrient supply. The period of floret abortion, which commences at BO and extends to AN, overlaps with STE, a phase characterized by rapid growth of both the stem and the developing spike (Kirby, 1974; Slafer et al., 2021)

The significance of the floret abortion period and its influence on final GN has been noted by other researchers as well (Ferrante et al., 2020; Gonzalez-Navarro et al., 2016). Indeed, a delay in floret abortion, characterized by a shorter BO to AN period, has been associated with an increased number of fertile florets at AN and ultimately, a higher final GN (Guo et al., 2015). While Ochagavía et al. (2021) observed minimal variation in AN time among wheat cultivars, they found significant differences in the duration of individual phenological phases. Furthermore, they concluded that variations in fertile florets at AN were more strongly associated with the florets' ability to survive than the floret degeneration period. This finding aligns with extensive prior research on environmental impacts on spike growth before AN (Ferrante et al., 2013; González et al., 2003, 2005). During the period from the onset of STE to BO, floret development exhibits minimal responsiveness to spike growth. Furthermore, environmental factors appear to have a negligible impact on the initiation of floret primordia during this phase. Consequently, wheat genotypes exhibit minimal variation in the maximum number of viable floret primordia (Ochagavía et al., 2021). However, the period from BO to AN, known as the floret abortion period, appears to be highly sensitive for floret development and spike growth. During this phase, the floret degeneration process significantly influences the performance of different wheat genotypes (Slafer et al., 2023).

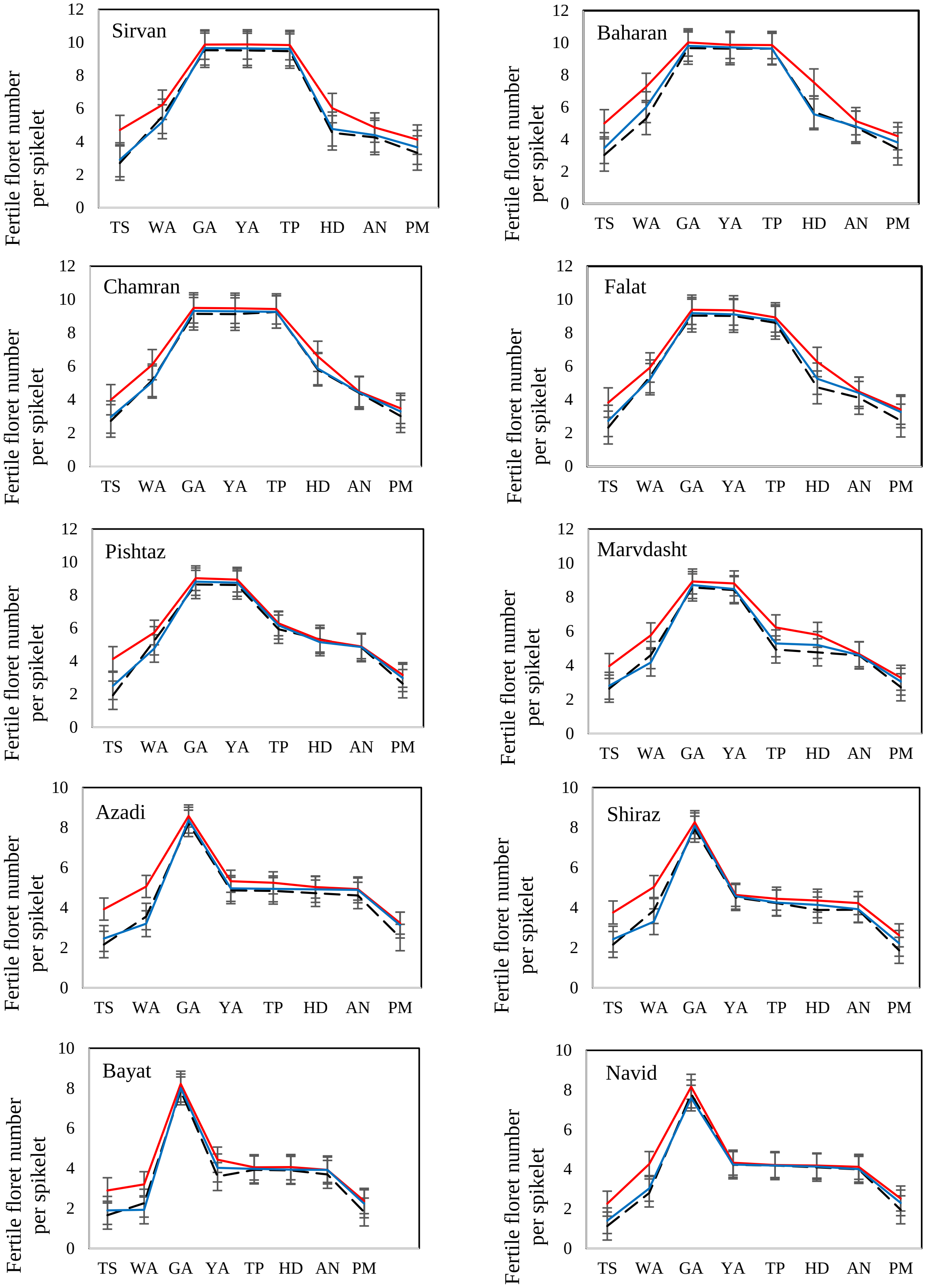

Fig. 5. Living florets per spikelet in apical (– – –), centr(——) , and basal (——) spikelets at seven floral developmental stages; Terminal spikelet (TS), white anther (WA), green anther (GA), yellow anther (YA), tipping (TP), heading (HD), and anthesis (AN) in ten wheat cultivars, according to Duncan’s multiple range test ($P \leq 0.01$).

Table 6. Percentage of grain set in wheat cultivars for the greenhouse experiment

Wheat cultivar	Grain set (%)		
	Apical	Central	Basal
Sirvan	80.5[a]	84.9[a]	83.0[a]
Baharan	75.6[ab]	81.8[a]	79.1[ab]
Chamran	70.6[abc]	77.8[ab]	74.2[abc]
Falat	67.1[abc]	76.1[ab]	74.0[abc]
Pishtaz	57.0[cd]	64.7[cd]	61.4[cd]
Marvdasht	61.9[bc]	70.5[bcd]	66.0[bcd]
Azadi	59.2[bc]	65.5[cd]	64.1[bcd]
Shiraz	52.0[cd]	60.8[d]	56.7[d]
Navid	52.8[d]	61.2[d]	57.5[d]
Bayat	50.8[d]	60.4[d]	57.0[d]
Mean	62.6	70.4	67.3

Means followed by the same letter in each column are not significantly different, according to Duncan's multiple range test ($P \leq 0.01$).

The maximum floret primordia number per spikelet, a key indicator of wheat yield potential, which was observed at the green anther stage is in line with the findings of Gou and Schnurbusch (2015). Previous studies have also further highlighted the importance of maximum floret primordia number, fertile floret number, and final GN or grain set percentage as key factors contributing to cultivar differences in the floral generation and degeneration process (Ferrante et al., 2020; Jahani Doghozlou & Emam, 2022; Serrago et al., 2008; Vahamidis et al., 2019). Following the attainment of peak floret primordia number at the green anther (GA) stage, the floral degradation process commences, leading to the determination of fertile floret number at AN. Subsequently, during the lag phase between AN and the watery ripe period, a portion of these pollinated florets undergo abortion (Fig. 1C). Therefore, investigating the dynamic interplay between floret generation and degeneration processes can provide valuable insights into the underlying mechanisms driving GY variation among cultivars.

It has been hypothesized that throughout the evolutionary history of wild grass progenitors, a considerable number of floret primordia developed irrespective of environmental conditions. Subsequently, a significant proportion of these florets were aborted, with only five to six reaching the fertile stage at AN, contingent upon the availability of resources (González et al., 2011). This process underscores the critical importance of viable floret primordia survival in enhancing spike fertility, rather than simply floret initiation itself (Guo & Schnurbusch, 2015). The demand for assimilates during the floret initiation phase (ascending portion of the curve in Fig. 1C) was lower than during the floret survival phase (descending portion of the curve in Fig. 1C). This suggests that the plant prioritizes survival by producing a large number of relatively inexpensive primordia during a period of low assimilate demand. Subsequently, only those primordia capable of normal development survive and contribute to grain set. Fertility of florets per spikelet has been recognized as a strong predictor of GN per spike, a key determinant of final GY (Vahamidis et al., 2019). Furthermore, more BY, especially in the pre-AN period, can be a good supplier for floret nutritional needs, so that the floret primordia development could benefit from such an increase in dry matter accumulation and, finally, more increased BY, particularly during the pre-AN period, can provide a greater supply of nutrients to support floret development. This enhanced nutrient availability can promote floret primordia development, ultimately leading to the increased GN and yield. Indeed, our field experiment, revealed that cultivars with higher BY, produced more grains per spike and the low-yield cultivars had fewer grains per spike and lower GY (Table 4).

Mean grain set percentage was found to be highest in central spikelets followed by basal and apical spikelets. This suggests that apical spikelets may be less competitive for resources compared to central and basal spikelets. Backhaus et al. (2023) observed that competition among spikelets at apical, central, and basal positions can result in complete grain abortion in apical spikelets of certain wheat cultivars. This phenomenon is likely attributed to preferential assimilate allocation towards the mid-bottom portion of the spike, leading to reduced spike fertility and ultimately, grain abortion in apical spikelets. Furthermore, it has been reported that lower GN in apical spikelets compared to central and basal spikelets, are often due to the failure of floret 3 to reach fertility. This suggests that enhancing the fertility of floret 3 in apical spikelets could potentially increase GY. This has recently been shown that primordia development in labile florets (florets 3 and 4) in contemporary cultivars could be fast and these florets could complete their development normally and reach the fertility stage, while labile florets development in traditional cultivars has been shown to have a rather delayed onset of development and do not have enough time to complete their development and set the grains (Ferrante et al., 2020).

The availability of assimilates to distal florets appears to be a critical factor in controlling both floret retention and grain formation. Further research is warranted to elucidate the mechanisms by which assimilate distribution influences grain set in wheat cultivars.

CONCLUSION

High-yielding wheat cultivars exhibited a higher GN per spike, with no detectable trend in TGW. These superior cultivars also demonstrated a greater BY. Significant variation in phenological phases was observed among cultivars. Late-flowering cultivars exhibited the lowest GY. Conversely, early-flowering cultivars demonstrated a phenological adaptation that allowed them to avoid late-season stresses such as heat and drought during flowering and grain filling. The findings of this study support the hypothesis that extending the duration of STE enhances assimilate availability for the rapidly developing spike, promoting floret survival and ultimately increasing GN and yield.

The peak floret primordia spikelet^{-1} was achieved at the green anther stage, while variation was found among cultivars for the onset of visible floral degradation, occurring at different floral developmental stages from green anther to AN. The visible floret abortion period was longer in the low-yielding cultivars and started from the yellow anther stage. Across all wheat cultivars, the mean grain set percentage was the highest at central spikelets, followed by basal spikelets, while apical spikelets exhibited the lowest percentage. This pattern suggests that prioritized assimilate allocation towards the mid-basal spike regions may contribute to reduced fertility in apical spikelets. A thorough understanding of floret generation and degeneration dynamics is crucial for gaining a comprehensive understanding of wheat GY formation.

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CRediT AUTHORSHIP CONTRIBUTION STATEMENT

Conceptualization: Maryam Jahani Doghozlou and Yahya Emam; Methodology: Maryam Jahani Doghozlou and Yahya Emam; Software: Maryam Jahani Doghozlou and Yahya Emam; Validation: Maryam Jahani Doghozlou, Yahya Emam, and Afshin Zamani; Formal analysis: Maryam Jahani Doghozlou; Investigation: Maryam Jahani Doghozlou, Yahya Emam, and Afshin Zamani; Data curation: Maryam Jahani Doghozlou and Yahya Emam; Writing—original draft preparation: Maryam Jahani Doghozlou; Writing—review and editing: Maryam Jahani Doghozlou, Yahya Emam, and Afshin Zamani; Visualization: Maryam Jahani Doghozlou, Yahya Emam, and Afshin Zamani; Supervision: Yahya Emam; Project administration: Yahya Emam; Funding acquisition: Yahya Emam.

DECLARATION OF COMPETING INTEREST

The authors declare no conflicts of interest.

ETHICAL STATEMENT

This study was performed in line with the principles of the Declaration of Helsinki. Approval was granted by the Ethics Committee of Shiraz University.

DATA AVAILABILITY

The authors confirm that the datasets analyzed during the current study are available from the corresponding author on request.

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