

Differential Floral Developmental Patterns in Some Recently Released Iranian Bread Wheat Cultivars

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ABSTRACT

Wheat floret primordia develop in a rather narrow window of time, mostly coinciding with stem elongation. That is why the stem elongation phase is considered a critical period for grain number and yield determination. Under controlled conditions, floral primordia development of 10 mostly adopted bread wheat cultivars including Bayat, Azadi, Falat, Navid, Chamran, Marvdasht, Pishtaz, Shiraz, Sirvan, and Baharan, which were released during the last five decades, was studied in detail at Shiraz University, Shiraz, Iran. Floral primordia monitoring showed that visible floral degradation among wheat cultivars occurred at several floral developmental stages from green anther (GA) to anthesis (AN). Floral degradation period started from yellow anther stage and was longer in cultivars with lower grain number per spike (Bayat, Navid, Shiraz and Azadi cultivars). Also, cultivars that started stem elongation earlier, such as Sirvan, Baharan, Chamran, and Falat, had extended period for stem elongation and produced higher grain number per spike. Overall, it appeared that under short growing seasons of semi-arid regions, in which delay in flowering usually results in more floral mortality during GA to AN, cultivars with earlier stem elongation could be more efficient in production of grains.

Keywords: Floral degradation, Floret primordia number, Floral score, *Triticum aestivum* L.

INTRODUCTION

Improvement in wheat (*Triticum aestivum* L.) yield is essential to ensure food security in the future (Reynolds *et al.*, 2009). However, it appears that further increases in wheat yield potential, particularly in semi-arid regions with late season water stress, might simply not be possible (González *et al.*, 2011b). For better understanding of the yield-limiting factors, a survey of the physiological changes associated with genetic gains is essential (Aisawi *et al.*, 2015). When analyzing physiological determinants of cereal productivity, yield is commonly divided into its two major components: the number of grains set per m², and the average weight of these grains. It has been reported that the capacity of the canopy to provide assimilates to fill the

grains does not appear to limit grain growth in a wide range of growing conditions and genotypes (Borrás *et al.*, 2004; Gonzalez-Navarro *et al.*, 2016; Serrago *et al.*, 2013), even under Mediterranean conditions (Acreche and Slafer, 2006; Cartelle *et al.*, 2006). Thus, to achieve relevant genetic gains in yield potential, further improvement in sink-strength is essential; which means that identification of traits affecting the grain number is necessary (Acreche and Slafer, 2006; Cartelle *et al.*, 2006; Fischer, 2011; Haghshenas *et al.*, 2013; Pedro *et al.*, 2012; Pirasteh Anosheh *et al.*, 2016; Reynolds *et al.*, 2009; Sadras and Slafer, 2012; Shekoofa and Emam, 2010; Slafer *et al.*, 2014).

It is known that there is genetic variation within well-adapted modern wheat cultivars in grain number due to differences in spike growth during pre-anthesis period, i.e. between terminal spikelet and anthesis

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(Pedro *et al.*, 2011). Grain number in wheat is determined over the time that the juvenile spike is growing rapidly, during the stem elongation phase (Fischer, 1985; Slafer and Rawson, 1994). During the floret developmental processes, many (6-12) floret primordia are generated and then a rather large proportion of those degenerate, such that not more than usually five to six fertile florets can be found at anthesis (Kirby, 1974). At anthesis, the ovaries of these florets fertilize and then, immediately after anthesis, a proportion of these fertilized ovaries abort during the lag phase, and the rest set grains and finally determine the grain yield at maturity (Guo *et al.*, 2016). Thus, in any spikelet there is a period of generation of potential floret primordia, followed by a plateau of variable duration and, then, a period of floret death (González *et al.*, 2011a). Fischer (2011) summarized that spike and stem compete for assimilates during stem elongation period and extending this period could be a way to increase the fertile floret number. Better adaptation of spike growth to environmental conditions can improve floret fertility as well as grain yield. Since in Mediterranean region, with short growing seasons, drought and high temperature stresses at post flowering stage limit yield formation, delays in flowering usually result in yield reductions. On the other hand, early flowering could improve pollination and thus increase grain set and finally grain yield (Haghshenas *et al.*, 2013; Motzo and Giunta, 2007).

The development of each floret primordium within a spikelet can be studied using the scale developed by Waddington *et al.* (1983). This scale identifies different stages of a floret primordium, from W3 (glume primordium present) to W10 (styles curved outwards with stigmatic branches spread wide and pollen grains present on stigmatic hairs) (Figure 1). It has been reported that differences in the number of grains per m² in cereals could be due to both environmental effects and genotypic differences (Slafer *et al.*, 2006). However, evidence for whether these differences

among genotypes and responses to the environment are related to the processes of generation or degeneration of floret primordia, is rather scarce. One possible reason for this is that analysis of the fate of floret primordia is difficult and time-consuming. Therefore, more work is needed to enrich our knowledge of how floral development and abortion processes will determine final grain number and grain yield in each widely grown modern cultivar.

The objective of the present study was to examine how the pattern of floret development during pre-anthesis period could affect grain number and yield of recently released bread wheat cultivars.

MATERIALS AND METHODS

Plant Material

This study was carried out at the greenhouse of School of Agriculture, Shiraz University, using 10 wheat cultivars (Bayat, Azadi, Falat, Navid, Chamran, Marvdasht, Pishtaz, Shiraz, Sirvan, and Baharan), which were released during the last five decades. These cultivars were carefully chosen to be well-adapted to Shiraz weather conditions (Table 1).

Growth Conditions

The experimental design was CRD (Completely Randomized Design) with six replications. In 4th January, 2021, ten seeds of each wheat cultivar were hand sown at depth of 2.5 cm in 5 kg pots filled with the field soil. The soil had a loamy-silty-clay texture, with clay, silt, and sand contents of 39, 46, and 15%, respectively, and the pH of the soil extract was 7.7. Nitrogen fertilizer was applied at the rate of 150 kg ha⁻¹ (as urea) in three equal splits i.e. at planting, mid tillering, and anthesis. The pots were watered when necessary to avoid water stress. The greenhouse temperature was

Table 1. Characteristics of cultivars used in the study.

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

25°C (± 5), with 60% (± 5) humidity and light intensity varied in the range of 600-1,000 $\mu\text{mol m}^{-2} \text{s}$.

Measurements

There were six pots for each cultivar, and each pot was considered as a replicate. Three pots were sampled to monitor floret development and the remaining (three for each cultivar) were kept intact to determine the final number of grains per spike at maturity. Destructive sampling was performed once or twice a week to follow apical development. In this way, for each cultivar, one sample was taken from each pot. In each sampling, the main shoots were dissected under a binocular microscope (LEITZ WETZLAR, GERMANY) to determine the timing of double ridges as well as terminal spikelet initiation (Kirby and Appleyard, 1987). Also, from terminal spikelet to flowering, each 2 or 3 days, one plant per experimental unit was sampled, and the main shoot was dissected to count the total number of floret primordia under a binocular microscope (Gonzalez-Navarro *et al.*, 2016). Floret primordia number at seven floral developmental stages were recorded: Terminal Spikelet (TS) (completion of spikelet initiation); White Anther (WA) (lemmas of floret 1 and floret 2 completely enclosed stamens and other structures);

Green Anther (GA) (glumes cover all but the tips of florets); Yellow Anther (YA) (glumes were fully formed and the lemmas of the first three florets were visible) (Kirby and Appleyard, 1987); Tipping (TP) (ZG49, first awns visible); Heading (HD) (ZG55, 50% of spikes visible); and Anthesis (AN) (ZG65, 50% of spikes with anthers) (Zadoks *et al.*, 1974).

In addition, at each sampling, the floral score of each floret within a particular spikelet was determined following the scale of Waddington *et al.* (1983), mostly based on pistil development from stage W3.5 to W10 (see Figure 1). Floret primordia were considered fertile when they were at W10 (styles curved and stigmatic branches spread wide, pollen grains on well-developed stigmatic hairs) or immediately before that stage (when the stigmatic branches were curved with green anthers) (Guo and Schnurbusch, 2015) (see Figure 1). In contrast with fertile florets, aborted florets were dry and transparent. The analyzed spikelets were in the basal (fourth spikelet from the base of the spike), central (middle spikelet position of the spike), and apical (fourth spikelet from the top of the spike) positions of the spike (Ferrante *et al.*, 2010). At Physiological Maturity (PM), spikes of main shoot in three replicates were used to determine final grain number per spikelet. In each of these spikes, each spikelet was separated and the grains filled normally

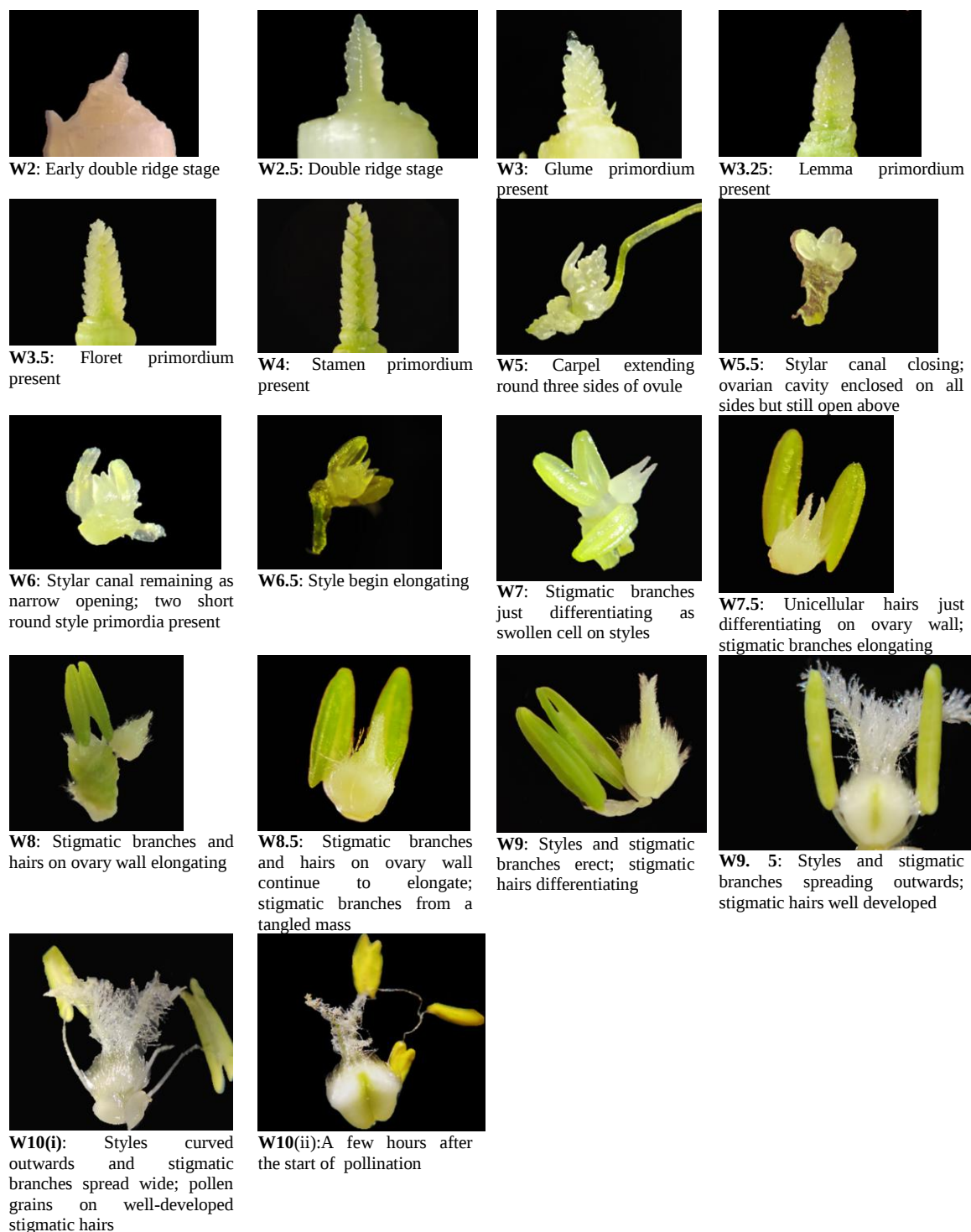


Figure 1. Wheat floral developmental stages from early spikelet primordia differentiation through terminal spikelet to anthesis, with details of selected floret developmental stages (Waddington *et al.*, 1983). The pictures are not to scale; as a reference, the length of apex in W2.5= 1 mm, W3.5= 2.2 mm, and the ovary dimensions in W10= 3.5 mm length and 1.60 mm width.

were determined. ‘Normal grains’ were those which were completely developed, not shriveled, and had a size that was not particularly reduced (Guo *et al.*, 2016). Grain set (%) was calculated as the ratio of final grain number (at maturity) to fertile florets (at anthesis), expressed as a percentage (Ferrante *et al.*, 2013), and was calculated separately for each position (apical, central, and basal).

Thermal Time (TT) was used to identify the duration of each stage and was calculated as the summation of daily average temperature, with a base temperature of 0°C (McMaster and Wilhelm, 1997).

The collected data were subjected to analysis of variance (ANOVA) using statistical program SAS 9.1 and the means were compared by Duncan’s multiple-range test ($P \leq 0.01$).

RESULTS AND DISCUSSION

Fate of Floret Primordia

Cultivars had significantly different fertile florets per spikelet at basal, central, and apical spikelet positions (Tables 2, 3 and 4). The maximum floret primordia number per spikelet was consistently found at the GA stage. Higher fertile florets per spikelet were found in Baharan, Sirvan, Chamran, and Falat cultivars at central (10.02, 9.87, 9.50 and 9.39, respectively), apical (9.67, 9.53, 9.15 and 9.04, respectively) and basal (9.81, 9.66, 9.32 and 9.19, respectively) spikelets. Shiraz, Bayat and Navid cultivars produced the lowest fertile florets per spikelet in the apical, central, and basal spikelets. Indeed, maximum fertile florets across spikelet positions and genotypes ranged between 7.59 to 10.02 (Tables 2, 3, and 4). Guo and Schnurbusch (2015) also

Table 2. Living florets (primordia) number per spikelet in apical spikelets at seven floral developmental stages and grain number per spikelet at Physiological Maturity (PM) in ten wheat cultivars.^a

Cultivars	TS	WA	GA	YA	TP	HD	AN	PM
Sirvan	2.70 ± 0.36 ^{ab}	5.53 ± 0.25 ^a	9.53 ± 0.02^b	9.52 ± 0.02 ^b	9.48 ± 0.02 ^a	4.53 ± 0.35 ^{cd}	4.25 ± 0.05 ^d	3.42 ± 0.02 ^b
Baharan	3.03 ± 0.35 ^a	5.30 ± 0.26 ^{ab}	9.67 ± 0.06^a	9.64 ± 0.05 ^a	9.63 ± 0.04 ^a	5.70 ± 0.3 ^{ab}	4.75 ± 0.02 ^a	3.59 ± 0.02 ^a
Chamran	2.73 ± 0.25 ^{ab}	5.16 ± 0.15 ^{ab}	9.15 ± 0.02^c	9.13 ± 0.03 ^c	9.26 ± 0.56 ^a	5.80 ± 0.2 ^a	4.40 ± 0.02 ^c	3.11 ± 0.01 ^c
Falat	2.33 ± 0.28 ^{abc}	5.40 ± 0.36 ^a	9.04 ± 0.03^d	9.02 ± 0.02 ^d	8.61 ± 0.03 ^b	5.46 ± 0.3 ^{ab}	4.33 ± 0.05 ^{cd}	2.91 ± 0.03 ^d
Pishtaz	1.93 ± 0.4 ^{bc}	5.23 ± 0.25 ^{ab}	8.64 ± 0.04^e	8.61 ± 0.03 ^e	5.93 ± 0.1 ^c	5.31 ± 0.03 ^b	4.82 ± 0.03 ^a	2.74 ± 0.01 ^e
Marvdasht	2.63 ± 0.4 ^{ab}	4.60 ± 0.36 ^b	8.57 ± 0.04^e	8.41 ± 0.01 ^f	4.93 ± 0.1 ^d	4.76 ± 0.05 ^c	4.58 ± 0.02 ^b	2.83 ± 0.03 ^{de}
Azadi	2.16 ± 0.47 ^{bc}	3.56 ± 0.4 ^c	8.21 ± 0.08^f	4.86 ± 0.02 ^g	4.84 ± 0.04 ^d	4.83 ± 0.04 ^c	4.81 ± 0.06 ^a	2.85 ± 0.06 ^d
Navid	1.13 ± 0.11 ^d	2.80 ± 0.26 ^d	7.80 ± 0.02^h	4.22 ± 0.04 ⁱ	4.18 ± 0.02 ^e	4.10 ± 0.01 ^{de}	3.99 ± 0.01 ^e	2.10 ± 0.02 ^f
Shiraz	2.16 ± 0.15 ^{bc}	3.86 ± 0.15 ^c	7.92 ± 0.02^g	4.51 ± 0.01 ^h	4.23 ± 0.02 ^e	3.88 ± 0.02 ^e	3.90 ± 0.01 ^f	2.02 ± 0.01 ^{fg}
Bayat	1.66 ± 0.15 ^{cd}	2.26 ± 0.25 ^d	7.87 ± 0.02^{gh}	3.59 ± 0.04 ^j	3.92 ± 0.02 ^e	3.90 ± 0 ^e	3.90 ± 0.01 ^f	1.94 ± 0.09 ^g

^a Data are presented as the mean±SD (Standard Deviation), n= 3. The bold text suggests that maximum floret primordia number occurred during GA stage, while grey boxes indicate the time windows when visible floral degradation occurred. Means followed by the same letter in each column are not significantly different, Duncan’s test ($P \leq 0.01$).

**Table 3.** Living florets (primordia) number per spikelet in central spikelets at seven floral developmental stages and grain number per spikelet at Physiological Maturity (PM) in ten wheat cultivars.^a

Cultivars	TS	WA	GA	YA	TP	HD	AN	PM
Sirvan	4.70 ± 0.98 ^{ab}	6.23 ± 0.30 ^b	9.87 ± 0.03^b	9.88 ± 0.04 ^a	9.84 ± 0.03 ^a	6.03 ± 0.15 ^c	4.85 ± 0.04 ^b	4.12 ± 0.02 ^b
Baharan	5 ± 0.2 ^a	7.26 ± 0.25 ^a	10.02 ± 0.06^a	9.87 ± 0.03 ^a	9.86 ± 0.02 ^a	7.53 ± 0.25 ^a	5.13 ± 0.03 ^a	4.20 ± 0.04 ^a
Chamran	4 ± 0.1 ^b	6.10 ± 0.17 ^b	9.50 ± 0.02^c	9.48 ± 0.03 ^b	9.44 ± 0.03 ^{ab}	6.60 ± 0.1 ^b	4.48 ± 0.03 ^d	3.48 ± 0.03 ^c
Falat	3.83 ± 0.15 ^b	5.93 ± 0.11 ^b	9.39 ± 0.03^c	9.35 ± 0.03 ^c	8.93 ± 0.04 ^b	6.26 ± 0.55 ^{bc}	4.48 ± 0.01 ^d	3.41 ± 0.02 ^d
Pishtaz	4.13 ± 0.15 ^{ab}	5.73 ± 0.25 ^b	9.02 ± 0.08^d	8.93 ± 0.04 ^d	7.60 ± 0.17 ^c	6.28 ± 0.03 ^{bc}	4.89 ± 0.02 ^b	3.16 ± 0.01 ^f
Marvdasht	3.96 ± 0.05 ^b	5.76 ± 0.40 ^b	8.92 ± 0.04^d	8.81 ± 0.03 ^e	6.73 ± 0.64 ^d	5.79 ± 0.23 ^c	4.65 ± 0.05 ^c	3.27 ± 0.01 ^e
Azadi	3.93 ± 0.11 ^b	5.06 ± 0.11 ^c	8.58 ± 0.11^e	5.32 ± 0.01 ^f	5.24 ± 0.05 ^e	5.03 ± 0.13 ^d	4.93 ± 0.05 ^b	3.23 ± 0.05 ^{ef}
Navid	2.26 ± 0.25 ^c	4.26 ± 0.30 ^d	8.16 ± 0.04^f	4.33 ± 0.01 ⁱ	4.21 ± 0.01 ^f	4.18 ± 0.01 ^e	4.12 ± 0.03 ^f	2.52 ± 0.02 ^h
Shiraz	3.76 ± 0.25 ^b	5.03 ± 0.15 ^c	8.27 ± 0.02^f	4.64 ± 0.03 ^g	4.45 ± 0.02 ^f	4.35 ± 0.03 ^e	4.23 ± 0.10 ^e	2.62 ± 0.02 ^g
Bayat	2.90 ± 0.36 ^c	3.20 ± 0.26 ^e	8.22 ± 0.02^f	4.43 ± 0.01 ^h	4.05 ± 0.55 ^f	4.06 ± 0.19 ^e	3.93 ± 0.06 ^g	2.37 ± 0.01 ⁱ

^a Data are presented as the mean±SD (Standard Deviation), n= 3. The bold text suggests that maximum floret primordia number stage occurred during GA stage, while grey boxes indicate the time windows when visible floral degradation occurred. Means followed by the same letter in each column are not significantly different, Duncan's test (P≤ 0.01).

Table 4. Living floret (primordia) number per spikelet in basal spikelets at seven floral developmental stages and grain number per spikelet at Physiological Maturity (PM) in ten wheat cultivars.^a

Cultivars	TS	WA	GA	YA	TP	HD	AN	PM
Sirvan	2.90 ± 0.36 ^{ab}	5.20 ± 0.2 ^b	9.66 ± 0.02^b	9.64 ± 0.02 ^a	9.61 ± 0.01 ^a	4.76 ± 0.51 ^d	4.39 ± 0.04 ^c	3.65 ± 0.04 ^b
Baharan	3.46 ± 0.55 ^a	6 ± 0.2 ^a	9.81 ± 0.06^a	9.6 ± 0.03 ^a	9.63 ± 0.02 ^a	5.56 ± 0.28 ^{bc}	4.81 ± 0.03 ^a	3.81 ± 0.01 ^a
Chamran	2.96 ± 0.05 ^{ab}	5.06 ± 0.11 ^b	9.32 ± 0.05^c	9.30 ± 0.05 ^b	9.26 ± 0.05 ^{ab}	5.86 ± 0.32 ^{ab}	4.44 ± 0.03 ^c	3.29 ± 0.02 ^c
Falat	2.73 ± 0.25 ^{abc}	5.23 ± 0.25 ^b	9.19 ± 0.3^c	9.12 ± 0.07 ^c	8.75 ± 0.04 ^b	4.66 ± 0.15 ^{de}	4.41 ± 0.03 ^c	3.26 ± 0.02 ^c
Pishtaz	2.50 ± 0.5 ^{bc}	4.76 ± 0.25 ^b	8.81 ± 0.08^d	8.75 ± 0.04 ^d	6.16 ± 1.04 ^c	6.15 ± 0.02 ^a	4.85 ± 0.05 ^a	2.98 ± 0.03 ^e
Marvdasht	2.80 ± 0.26 ^{ab}	4.16 ± 0.37 ^c	8.71 ± 0.04^d	8.47 ± 0.06 ^e	5.29 ± 0.36 ^d	5.19 ± 0.01 ^{cd}	4.60 ± 0.04 ^b	3.04 ± 0.03 ^e
Azadi	2.46 ± 0.45 ^{bc}	3.20 ± 0.2 ^d	8.37 ± 0.11^e	4.96 ± 0.10 ^f	4.94 ± 0.10 ^{de}	4.91 ± 0.11 ^d	4.89 ± 0.11 ^a	3.13 ± 0.04 ^d
Navid	1.40 ± 0.1 ^d	3.03 ± 0.20 ^d	7.59 ± 0.04^f	4.24 ± 0.03 ^h	4.19 ± 0.01 ^{ef}	4.13 ± 0.02 ^{ef}	4 ± 0.04 ^d	2.30 ± 0.01 ^f
Shiraz	2.43 ± 0.20 ^{bc}	3.30 ± 0.26 ^d	8.09 ± 0.03^f	4.57 ± 0.03 ^g	4.25 ± 0.02 ^{ef}	4.14 ± 0.03 ^{ef}	3.92 ± 0.05 ^d	2.22 ± 0.03 ^g
Bayat	1.90 ± 0.17 ^{cd}	1.93 ± 0.20 ^e	8.01 ± 0.03^f	4.02 ± 0.01 ⁱ	3.97 ± 0.02 ^f	3.94 ± 0.03 ^f	3.92 ± 0.03 ^d	2.23 ± 0.02 ^g

^a Data are presented as the mean±SD (Standard Deviation), n= 3. The bold text suggests that maximum floret primordia number occurred during GA stage, while grey boxes indicate the time windows when visible floral degradation occurred. Means followed by the same letter in each column are not significantly different, Duncan's test (P≤ 0.01).

reported that the maximum floret primordia number per spikelet occurred at GA stage.

Regardless of wheat cultivars, the final grain number per spikelet at apical spikelet positions was fewer than basal and central spikelets. Grain set percent (final grain number at PM to fertile florets at AN) in apical spikelets was 62.64% (Figure 2), while grain set percentage for basal and central spikelets were 67.32% (Figure 3) and 70.36% (Figure 4), respectively. It appeared that the apical spikelets failed to set grains owing to the competition among spikelets in different positions. This speculation fits not only with the pattern described here, but also with the study of Ferrante *et al.* (2013) who observed that floret 3 did not reach the stage of fertile florets in the apical spikelet positions. They observed that the number of fertile florets at anthesis was increased by ~30% in response to N fertilization. This effect was evident on floret developmental rates from the third floret primordium onwards. Therefore, it appears that the large variation of final grain number and reduced spikelet fertility in apical spikelets might be due to preferential resource allocation to the mid-bottom part of the spike as also being argued by Guo and Schnurbusch (2015). It might be concluded that there are still large

opportunities for improving fertile florets number in apical spikelets. This observation needs to be confirmed by further studies.

Final grain number per spikelet at PM was different among cultivars. Generally, Baharan, Sirvan, and Chamran cultivars had 4.20, 4.12 and 3.48 grains per spikelet, respectively which was significantly higher than other cultivars (Table 3) at central spikelets. It has been argued that increasing the grain number per spikelet, increases the grain yield (Mohamed and Marshall, 1979). Generally, Baharan, Sirvan and Chamran cultivars had produced more grains at apical (3.59, 3.42 and 3.11 grains) (Table 2), central (4.20, 4.12 and 3.48 grains) (Table 3) and basal (3.81, 3.65 and 3.29 grains) (Table 4) spikelet positions, respectively. Navid and Bayat cultivars produced lowest grains at apical, central, and basal spikelets (Tables 2, 3 and 4). The highest grain set percentage was observed in Sirvan (80.50, 84.89 and 83.01) and Baharan (75.59, 81.82 and 79.10) cultivars at apical, central, and basal positions, respectively (Figures 2, 3 and 4). Indeed, pre-anthesis stem dry mass accumulation plays an important role in floral development and grain filling (Bidinger *et al.*, 1977). Therefore, floret primordia may benefit from an increase in different structural parts of the main shoot

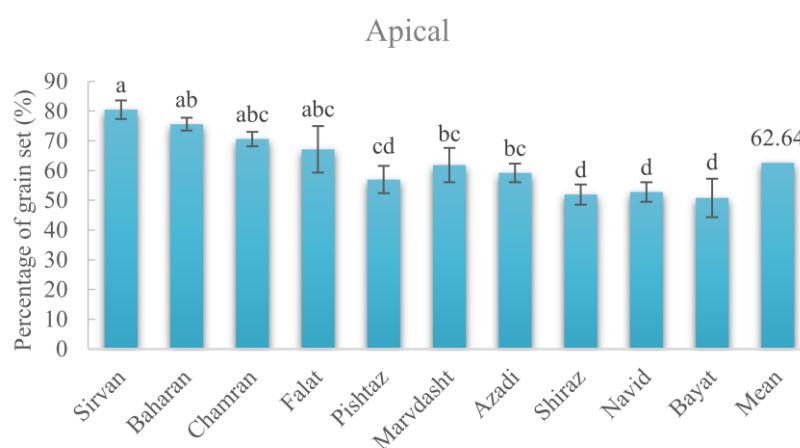


Figure 2. Grain set percentage for apical spikelets in wheat cultivars. Bars represent mean $\pm$ SD (Standard Deviation), $n = 3$. Different letters indicate that differences between cultivars were significant at $P < 0.01$ (Duncan's test).

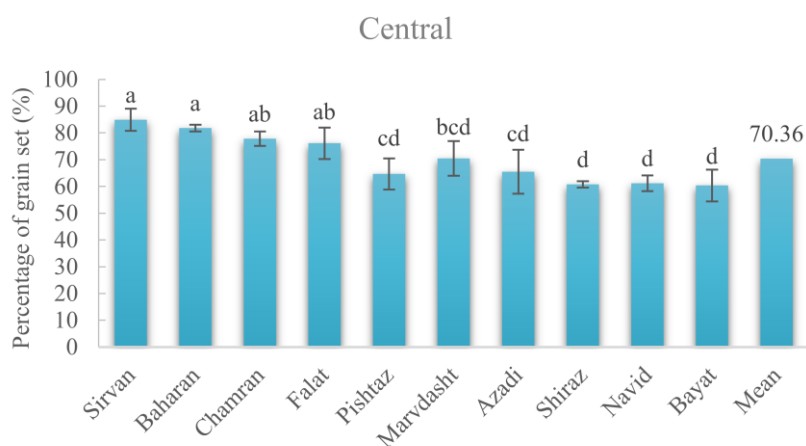


Figure 3. Grain set percentage for apical spikelets in wheat cultivars. Bars represent mean $\pm$ SD (standard deviation), n= 3. Different letters indicate significant differences between cultivars $P < 0.01$ (Duncan's test).

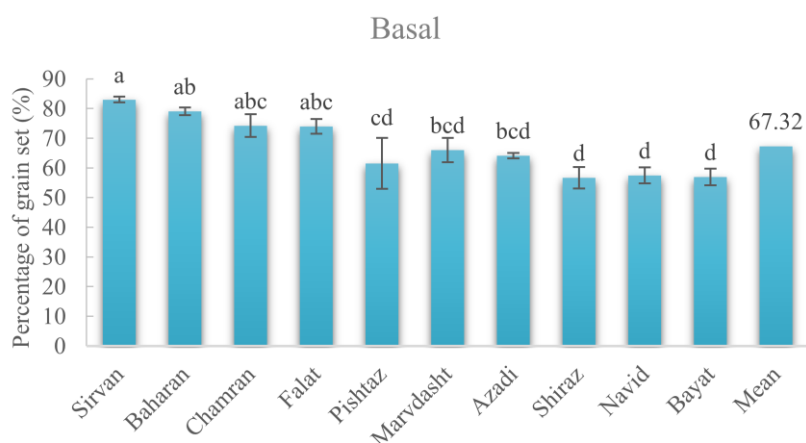


Figure 4. Grain set percentage for basal spikelets in wheat cultivars. Bars represent mean $\pm$ SD (standard deviation), n= 3. Different letters indicate significant differences between cultivars $P < 0.01$ (Duncan's test).

(i.e. more biological yield) and, so, final grain number could increase. Undoubtedly, in the future, the goal of many wheat breeding programs would be to increase the relationship between potential yield capacity and biomass production (Aisawi *et al.*, 2015; Emam *et al.*, 2007; Fischer, 2007; Pedro *et al.*, 2012). In other words, the major part of increasing the potential production capacity of different wheat cultivars will depend on increasing biomass production (Emam and Seghatoleslami, 2005; Dastfal *et al.*, 2011; Pirasteh Anosheh *et al.*, 2016, Shekoofa and Emam, 2010).

It has already been reported that floret abortion occurs when the juvenile spikes grow fast (stem elongation phase) (Fischer

and Stockman, 1980; Kirby, 1974). Indeed, during the stem elongation phase, stem competes with the spike for assimilates, and this competition determines the final number of grains (González *et al.*, 2011b; Pirasteh Anosheh *et al.*, 2016). Therefore, if more assimilates are allocated to spikes, the spike fertility would be improved and, finally, grain yield will increase (Fischer, 2011; Foulkes *et al.*, 2011).

As shown in Tables 2, 3, and 4, visible floral degradation (grey boxes in tables) in exemplified cultivars occurred at several floral developmental stages from GA to AN. Generally, visible floral degradation in apical and basal spikelet positions occurred simultaneously with central spikelet

positions. Floral degradation in Bayat, Navid, Shiraz and Azadi cultivars started from YA stage, so, these cultivars had longer floral degradation period than others. This longer period resulted to lower final grain number in these cultivars. Meanwhile, visible floral degradation was very short in Sirvan, Baharan, Chamran, and Falat cultivars (occurred at HD stage) and this led to more grain number (Tables 2, 3, and 4).

The spike has the potential for a large number of floret primordia. Since the metabolic cost required to initiate floret primordia is markedly lower than that required to survive them, firstly, plants initiate more primordia, however, only a relatively small fraction of those can reach the stage of fertile floret at AN, depending on the spike growth rate (Fischer, 2007; Kirby and Appleyard, 1987; Pirasteh Anosheh *et al.*, 2016). Nevertheless, in determination of final fertile florets, the survival of the florets is much more vital than the floret initiation *per se*. Ferrante *et al.* (2013) concluded that “since the plasticity of a given component could be expected to be inversely related to the cost/benefit associated with that component, therefore, the crop would accommodate environmental variation by preferential production of components, which involve low cost or net fitness benefits”. Probably, the determining factor here is the demand for assimilates, because this amount during the first stage (initiation of florets) is much less than that for the next stages, i.e. survival of florets. In summary, it appears that it is an evolutionary strategy, in which a large number of floret primordia should be initiated, however, not more than usually five to six fertile florets can be found at anthesis. Then, those that could be safely filled survive and produce grains (Ferrante *et al.*, 2010).

Floret Development

Floret development differed among cultivars (Figure 5). Shiraz, Bayat, and

Navid cultivars were late flowering and required 865.29, 850.66 and 1113.52 TT from sowing to anthesis. In contrast, Sirvan, Baharan, Chamran, and Falat cultivars entered W10 earlier than other cultivars (Figure 5 and Supplementary).

It has been argued that the higher respiration rate due to higher air temperature in late flowering cultivars can reduce the grain number, and hence the grain yield (Fisher, 2011). Adaptation of crop to environmental conditions can coincide the transition from vegetative to reproductive phase with favorable conditions. In temperate regions with long growing seasons, late flowering cultivars might be of interest, because they can store more assimilates during the vegetative phase, which can be used later in the season (Cockram *et al.*, 2007; Pirasteh Anosheh *et al.*, 2016). However, in the Mediterranean region, short growing seasons, drought, and high temperature stresses at post flowering stages limit yield formation, so, early flowering could ensure a better pollination (Motzo and Giunta, 2007). Haghshenas *et al.*, (2013) also observed that the early ripening cultivar was superior to middle-ripening cultivar and avoided post-anthesis moisture stress. They concluded that shorter growing period, was associated with lower post-anthesis stresses and hence higher grain yield.

The majority of previous studies worldwide showed that, since the ability of the canopy to provide assimilates to fill the grains is not limited as such, the mean grain weight was almost constant, however, the difference in grain number mainly contributes in the yield differences (Dastfal *et al.*, 2011; Emam and Borjian, 2000; Gonzalez-Navarro *et al.*, 2016; Pedro *et al.*, 2011; Shekoofa and Emam, 2010; Waddington *et al.*, 1986). Therefore, it appeared that further attempt for better understanding of the factors that play a role in determining the number of grains is of prime importance for yield improvement in bread wheat (Borrás *et al.*, 2004; Slafer *et al.*, 2014; Pirasteh Anosheh *et al.*, 2016).

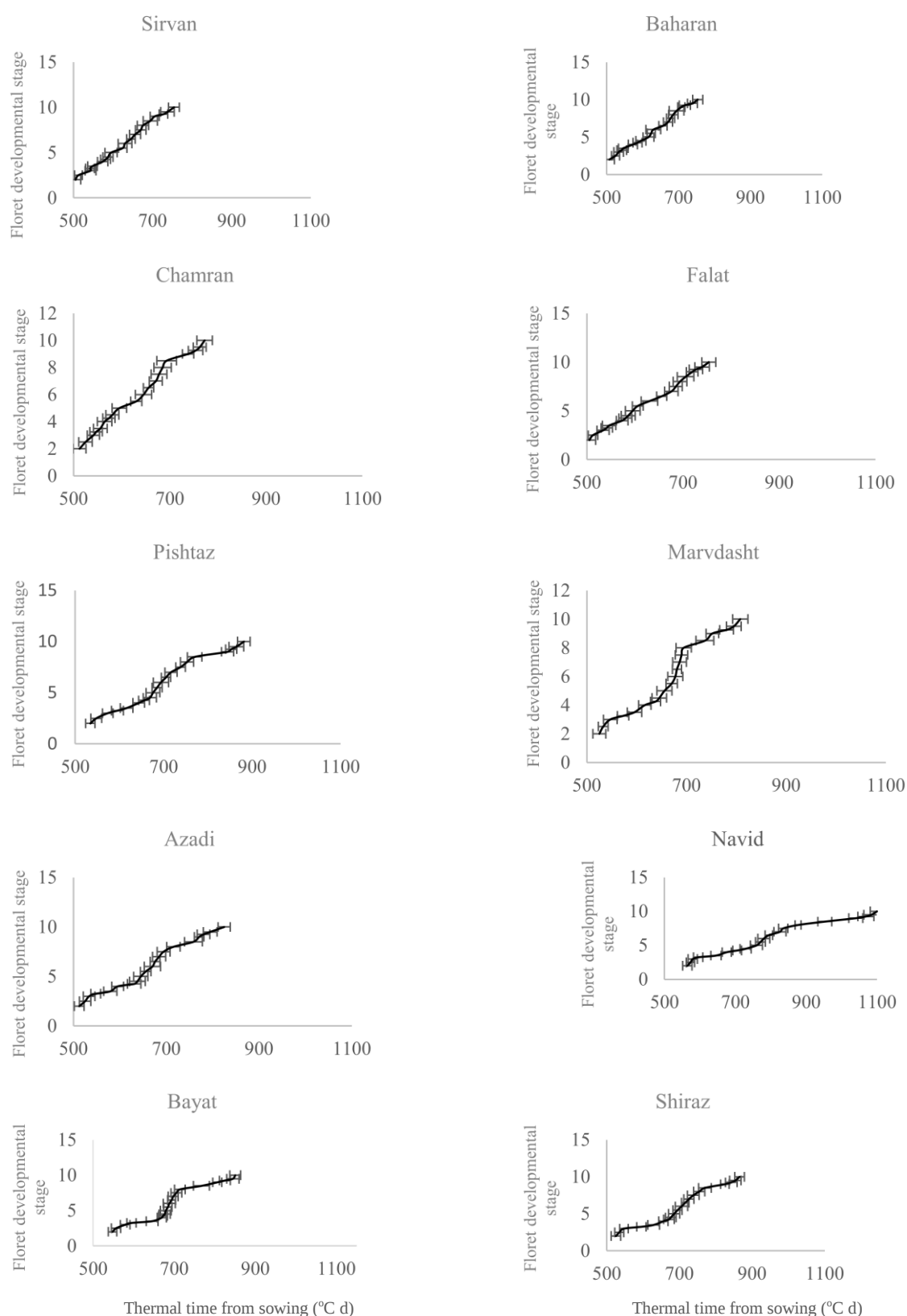


Figure 5. Floret development stage in wheat cultivars: during the stem elongation phase for florets 2 proximal with respect to the rachis in central spikelet positions. Floret development was assessed through frequent determination of floret stages following the scores of the scale of Waddington *et al.* (1983). Scores lower than W3.5 correspond to spike rather than floret development.

Table S1. Thermal time required for floret development in ten wheat cultivars. Floret development was assessed through frequent determination of floral stages following the scores of the scale presented by Waddington et al., (1983) (see Fig. 1).

	W 2	W 2.5	W 3	W 3.25	W 3.5	W 4	W 4.25	W 4.5	W 5	W 5.5
Bayat	548.03 ± 2.6 ^b	556.46 ± 4.08 ^b	579.05 ± 3.62 ^a	594.71 ± 4.18 ^a	645.39 ± 5.04 ^a	669.19 ± 3.69 ^a	672.33 ± 2.51 ^b	676.62 ± 4.14 ^b	679.33 ± 3.05 ^b	684.45 ± 4.07 ^b
Azadi	512.6 ± 2.50 ^d	525.1 ± 5 ^c	533.73 ± 4.02 ^c	548.03 ± 2.66 ^c	579.71 ± 4.51 ^c	595.38 ± 5.04 ^d	631.22 ± 6.51 ^d	637.89 ± 7.53 ^c	645.39 ± 5.04 ^c	655.79 ± 5.18 ^d
Falat	505.35 ± 5.03 ^d	512.6 ± 2.50 ^d	533.73 ± 4.02 ^c	541.45 ± 3.50 ^c	546.36 ± 5.53 ^f	573.55 ± 4.07 ^e	580.38 ± 5.50 ^{ef}	585.8 ± 5.22 ^{de}	595.38 ± 5.04 ^e	605.87 ± 5.22 ^f
Navid	564.63 ± 5.04 ^a	573.55 ± 4.07 ^a	580.05 ± 5 ^a	595.38 ± 5.04 ^a	645.39 ± 5.04 ^a	675.95 ± 5.26 ^a	705.45 ± 5.06 ^a	729.09 ± 5.54 ^a	759.92 ± 6.28 ^a	771.39 ± 7.07 ^a
Chamran	512.6 ± 5.10 ^d	525.1 ± 7.10 ^c	541.45 ± 4 ^{bc}	547.03 ± 5.04 ^c	555.8 ± 5.50 ^f	564.63 ± 7.79 ^e	573.55 ± 5.18 ^f	580.71 ± 4.26 ^e	595.38 ± 5.26 ^e	630.22 ± 5 ^e
Marvdasht	525.1 ± 5 ^c	532.73 ± 2.53 ^c	547.03 ± 6.26 ^b	572.88 ± 3 ^b	595.38 ± 5.04 ^d	616.32 ± 5.50 ^e	637.89 ± 2.59 ^d	645.39 ± 5.04 ^e	655.79 ± 5.18 ^e	670.19 ± 5.01 ^e
Pishiaz	534.4 ± 2.50 ^c	547.7 ± 5 ^b	573.55 ± 3.50 ^a	595.38 ± 6.26 ^a	616.32 ± 5.18 ^c	643.72 ± 5.04 ^b	655.79 ± 4.07 ^c	668.85 ± 5.02 ^b	675.95 ± 5.04 ^b	685.12 ± 5.01 ^b
Shiraz	525.1 ± 5 ^c	534.4 ± 5.10 ^c	547.03 ± 4.38 ^b	595.38 ± 5.04 ^a	628.89 ± 7.16 ^b	655.79 ± 5.18 ^b	671.19 ± 6.52 ^b	675.95 ± 5.26 ^b	685.12 ± 5 ^b	694.7 ± 5.66 ^b
Sirvan	505.35 ± 5.03 ^d	512.6 ± 2.50 ^d	543.4 ± 5.10 ^c	542.11 ± 2.58 ^c	548.03 ± 2.66 ^f	574.21 ± 5.18 ^e	581.38 ± 4.14 ^{ef}	587.53 ± 2.2 ^{de}	595.38 ± 5.04 ^e	624.64 ± 4.50 ^e
Baharan	507.35 ± 6.10 ^d	524.43 ± 4.06 ^c	533.06 ± 5 ^c	541.78 ± 5.01 ^c	546.03 ± 5.22 ^c	572.88 ± 5 ^e	585.86 ± 5.22 ^e	595.05 ± 4.59 ^d	616.32 ± 5.50 ^d	623.64 ± 5.12 ^e

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

	W 6	W 6.5	W 7	W 7.5	W 8	W 8.5	W 9	W 9.25	W 9.5	W 10
Bayat	688 ± 2.64 ^{cd}	693.7 ± 4.03 ^c	697.66 ± 2.51 ^c	705.45 ± 5.06 ^c	714 ± 3.60 ^c	767.39 ± 8.35 ^b	806.14 ± 5.37 ^d	824.97 ± 5 ^c	844.65 ± 5.03 ^c	850.66 ± 5.03 ^c
Azadi	670.19 ± 5.0 ^e	675.95 ± 5.26 ^d	684.79 ± 4.52 ^d	694.37 ± 5.11 ^{cd}	715.87 ± 5.22 ^e	758.84 ± 7.85 ^b	771.05 ± 3.58 ^e	780.39 ± 5.50 ^d	794.97 ± 5 ^d	824.97 ± 5 ^d
Falat	630.22 ± 5.0 ^g	655.79 ± 5.18 ^e	675.95 ± 5.26 ^{de}	685.12 ± 5 ^{de}	693.7 ± 4.03 ^d	705.45 ± 5.06 ^d	719.2 ± 5.18 ^g	726.75 ± 6.14 ^f	739.67 ± 5.03 ^f	753.59 ± 6.04 ^g
Navid	780.72 ± 4.0 ^a	794.97 ± 5 ^a	826.3 ± 7.10 ^a	835.45 ± 5.06 ^a	777.29 ± 2.51 ^a	953.04 ± 7.55 ^a	1040.37 ± 13.8 ^a	1068.6 ± 16.2 ^a	1084.6 ± 13.0 ^a	1113.52 ± 12.0 ^a
Chamran	645.39 ± 4.0 ^f	655.79 ± 5.06 ^e	671.19 ± 4.10 ^e	677.62 ± 8.02 ^{ef}	685.12 ± 8 ^{de}	770.05 ± 8 ^d	738 ± 5.03 ^f	753.59 ± 7 ^c	762.17 ± 4.14 ^e	881.57 ± 8.03 ^f
Marvdasht	677.62 ± 2.5 ^{de}	680.66 ± 3.05 ^d	686.12 ± 3.55 ^d	690 ± 3.60 ^{de}	694.37 ± 5.11 ^d	737 ± 6.24 ^c	751.92 ± 6.54 ^f	780.39 ± 5.50 ^d	794.97 ± 5 ^d	807.8 ± 7.51 ^e
Pishiaz	693.7 ± 5.04 ^c	705.45 ± 5.18 ^b	716.54 ± 3.54 ^b	738.34 ± 2.50 ^b	752.92 ± 5 ^b	693.37 ± 3.50 ^b	844.65 ± 7.55 ^b	852.94 ± 4.06 ^b	864.62 ± 6.52 ^b	772.39 ± 5.82 ^b
Shiraz	705.45 ± 5.0 ^b	715.87 ± 5.22 ^b	726.09 ± 5.34 ^b	738 ± 7.55 ^b	754.25 ± 5.16 ^b	770 ± 5 ^b	824.97 ± 5 ^c	842.65 ± 8.08 ^{bc}	853.94 ± 5.58 ^{bc}	865.29 ± 5.02 ^c
Sirvan	630.22 ± 5.0 ^g	645.39 ± 5.04 ^e	655.79 ± 5.18 ^f	670.19 ± 5.01 ^f	675.95 ± 5.26 ^e	694.37 ± 5.11 ^d	705.45 ± 5.06 ^g	727.75 ± 2.53 ^f	738 ± 7.55 ^f	754.25 ± 5.16 ^g
Baharan	629.89 ± 8.5 ^g	656.45 ± 6.05 ^e	670.52 ± 2.50 ^{ef}	677.62 ± 2.50 ^{ef}	685.12 ± 3 ^{de}	694.37 ± 8.07 ^d	707.45 ± 3.14 ^g	717.54 ± 7.50 ^f	738.67 ± 3.51 ^f	753.25 ± 5.51 ^g

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



Since the potential number of grains in wheat is determined during spike growth phase, which coincided with the stem elongation stage, it appeared that earlier start of stem elongation in some studied cultivars (Sirvan, Baharan, Chamran, and Falat with 548.03, 546, 555.8 and 546.36 TT from sowing to W3.5, respectively (Figure 5). In contrast, Navid and Bayat cultivars needed 645 TT from sowing to W3.5 (Figure 5). It has already been reported that floret abortion occurs when the juvenile spikes grow fast (stem elongation phase) (Fischer and Stockman, 1980; Kirby, 1974). Indeed, during the stem elongation phase, stem competes with the spike for assimilates, and this competition determines the final number of grains (González *et al.*, 2011b; Pirasteh Anosheh *et al.*, 2016). Therefore, if more assimilates could be allocated to spikes, the spike fertility would be improved, and finally the grain yield will increase (Fischer, 2011; Foulkes *et al.*, 2011). It could be concluded that when the reproductive phase is longer, this can contribute to higher assimilate acquisition by the spikes, and higher proportion of floret primordia that are competent at anthesis. In the present study, it was found that Navid, Bayat, and Shiraz cultivars with 191.31, 110.97 and 100 TT from W8 to W9 had longer floret abortion periods, respectively (Figure 5). However, Baharan, Falat, and Sirvan cultivars with 41.42, 43.05 and 51.8 TT from W8 to W9, respectively, had shorter floret abortion periods (Figure 5). Other studies also focused on the important role of floret abortion period in determining the number of grains (Kirby, 1974; González *et al.*, 2011b). Recently Guo and Schnurbusch (2015) also demonstrated that delaying visible floral degradation in wheat was associated with increased fertile floret number at anthesis.

In conclusion, based on the results of this study, we found a strong fluctuation in maximum fertile floret number across genotypes and spikelet positions. Regardless of wheat cultivar, the final grain number per spikelet at apical spikelet positions was

fewer than at basal and central spikelets. Such positional effects suggest a good opportunity for improving fertile floret number, in particular for apical spikelets, since basal and central spikelets generally had higher fertile florets per spikelet. Further support is provided by such agronomic practices as appropriate N fertilization.

Floral primordia monitoring showed that GA stage was associated with the maximum floret primordia number per spikelet. Visible floral degradation in exemplified cultivars occurred at several floral developmental stages from GA to AN, which was longer in cultivars with lower fertile florets per spike. Understanding the dynamics of floret initiation and survival may be instrumental in achieving a more comprehensive perception of wheat grain yield determination.

In summary, grain number in wheat is largely determined during the stem elongation phase. Extending this growth period could provide the opportunity for improvement of the fertile florets. Since in the Mediterranean region short growing seasons, drought, and high temperature stresses at post flowering stages limit yield formation, cultivars with earlier stem elongation could produce more grains per spike, and higher grain yield.

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الگوهای نمودی متفاوت گلچه‌های گندم در برخی ارقام گندم نان ایرانی که به تازگی عرضه شده اند

م. جهانی دوقزلو، و.ی. امام

چکیده

نمو گلچه‌ها در بازه‌ی زمانی کوتاهی مصادف با مرحله ساقه رفتن انجام می‌شود. این موضوع دلیل اهمیت این مرحله را به عنوان یک دوره مهم در تعیین تعداد دانه و در نتیجه عملکرد دانه نشان می‌دهد. بنابراین پژوهشی با هدف مقایسه‌ی الگوهای نمودی گلچه‌های ده رقم گندم شامل بیات، آزادی، فلات، نوید، چمران، مرودشت، پیشناز، شیراز، سیروان و بهاران در گلخانه تحقیقاتی دانشگاه شیراز اجرا شد. پایش نمود گلچه‌ها نشان داد که زمان شروع سقط گلچه‌ها در ارقام مختلف، متفاوت بود. به نحوی که در ارقامی که تعداد نهایی دانه در آنها کمتر بود (بیات، نوید، شیراز و آزادی) از مرحله‌ی بساک زرد شروع شد و طول مرحله‌ی سقط گلچه در آنها طولانی‌تر بود. از طرفی ارقام سیروان، بهاران، چمران و فلات با ورود زودتر به مرحله ساقه رفتن، طول این مرحله نمودی را گسترش دادند که در نهایت موجب تولید تعداد بیشتری دانه در سنبله شد. به طور کلی، به نظر می‌رسد در مناطق نیمه خشک با فصل رشد کوتاه و تنش‌های خشکی و گرمای انتهای فصل، تاخیر در گلدهی موجب افزایش سقط گلچه‌ها شده و بنابراین ارقامی که زودتر به ساقه‌روی وارد شوند می‌توانند با افزایش بازه‌ی زمانی تولید دانه، دانه‌ی بیشتری تولید می‌کنند.