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GENOTYPIC VARIATIONS FOR PHOTOASSIMILATES PARTITIONING TO THE GRAINS DURING EARLY DEVELOPMENT OF ENDOSPERM IN WHEAT: ASSOCIATION WITH GRAIN WEIGHT

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There is little information on genotype variations for photoassimilates partitioning to the grains during early development of endosperm in wheat. Eighty–one wheat cultivars were examined in the Moghan region of Iran during 2010–2011 and 2013–2014 growing seasons. The amount and rate of photoassimilates partitioning to the grains were measured in the tested cultivars during anthesis–16 days after anthesis (DAA) and 16 DAA–maturity phases using time dependent changes in spike dry weight. There were substantial genetic variations in the amount and rate of partitioned photoassimilates to the grains during anthesis–16 DAA and 16 DAA–maturity phases. Part of these variations could be attributed to cultivars differences in anthesis time, spike dry weight at anthesis, and grain number per spike. Taking them into accounts, there were some cultivars but they differed in partitioned photoassimilates toward grains during anthesis–16 DAA and 16 DAA–maturity phases, further supporting the idea that breeding for photoassimilates partitioning during these phases was a possibility. The results yielded for 2013–2014 showed that there is close association between photoassimilates partitioning to the grain during anthesis–16 DAA and individual grain weight. The results suggest that in case wheat breeders could improve photoassimilates partitioning to the grains during anthesis–16 DAA, it would result in increased grain size and weight in the wheat.

Key words: grain growth stages, grain weight, photoassimilates partitioning, wheat

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INTRODUCTION

Wheat is grown on 220 million hectares throughout the world producing approximately 729 million tons of grain. In Iran, the area under wheat cultivation during 2014 was 7.3 million hectares with a production of 10.6 million tons (FAO, 2014).

Grain yield of wheat has increased noticeably since the beginning of the twentieth century. However, in the last decades, strategies of conventional breeding have been insufficient to keep improvement rate similar to the past, suggesting efficiency losses in breeding programs (GARCÍA *et al*., 2011). Understanding agronomical, phenological, and physiological traits associated with grain yield can help wheat breeders to accelerate genetic improvement in grain yield potential.

Grain yield in wheat have been divided into its components, namely, grain number and grain weight. In many cases, yield variation and yield progress are associated with changes in grain number (FISCHER, 2011), while clear associations have not been reported between grain yield improvement and thousand grain weight (SANCHEZ–GARCIA *et al*., 2013; JOUDI *et al*., 2014). The reasons for such association between grain yield progress and thousand grain weight have not been fully understood and have remained unsolved (FISCHER, 2007).

Most of the researchers have reported that there is an excess of photoassimilates during wheat grain filling period (BORRAS *et al*., 2004; MIRALLES and SLAFER, 2007; AHMADI *et al*., 2009; FOULKES *et al*., 2011), and the frequently reported negative relationship between grain number and average grain weight does not necessarily reflect competition among grains for limited assimilates (FOULKES *et al*., 2011 and references therein). In this respect, GAJU *et al*. (2009) studied two CIMMYT spring lines of large spike phenotype (LSP1 and LSP2) and one check cultivar (Bacanora) in the growth room and irrigated field conditions and reported that higher potential grain weight in LSP1 was achieved without sacrificing grain number per spike dry matter, suggesting that it may be possible to uncouple these two parameters genetically as a route to increasing yield potential.

Final grain weight in wheat is determined as the product of the rate and the duration of grain growth (MORITA *et al*., 2005). There is a strong correlation between the length of the grain filling duration (GFD) and grain dry weight among wheat genotypes (TEWOLDE *et al*., 2006). Another study showed that wheat genotypes with the highest grain dry weights exhibited shorter duration and higher maximum rates of grain filling (AL–KARAKI, 2012). DIAS and LIDON (2009) declared that in durum and bread wheat, grain filling rate (GFR) may be more important than GFD to increase the grain weight (as the GFD is more affected by the environment), particularly for the regions which have a grain filling duration restricted by high temperature.

Grain growth and development of wheat could be divided into three phases (SAINI and WESTGATE, 2000). Phase I is started from anthesis and extended until 15 to 20 days after anthesis (DAA). During this period, the albumin is developed and the cellularization of endosperm is finalized. The total number of cells in the endosperm at the end of cellularization phase is closely associated with final grain weight and has been hypothesized as the main factor controlling the rate of starch accumulation during the linear grain filling phase (BROCKLEHURST, 1977). Phase II is a period during which starch deposition reaches its maximum rate since its accumulation has already started at about 7–14 DAA, depends upon environmental conditions that are predominant during grain development (JENNER *et al*., 1991; HURKMAN *et al*., 2003). Phase III is the last stage of grain development where dry matter accumulation ceases and the grain loses its water content.

Numerous studies have been carried out about the amount and rate of photoassimilates partitioning toward grains in wheat (DEMOTES–MAINARD and JEUFFROY, 2001; EHDAIE *et al*., 2008; DIAS and LIDON, 2009). However, such parameters have been recorded during anthesis–maturity phase and, to my best knowledge, no study has investigated them separately during anthesis–16 DAA and 16 DAA–maturity phases. I hypothesized that there are genetic variations for the amount and rate of photoassimilates partitioning to the grains during anthesis–16 DAA phase. It was also assumed that wheat cultivars with higher values of amount and rate of photoassimilates partitioning during anthesis–16 DAA phase would have increased grain weight at physiological maturity. With those hypotheses, eighty–one wheat cultivars were cultivated during 2010–2011 and 2013–2014 growing seasons in the Moghan region of Iran. The amounts and rate of photoassimilates partitioned to the grains were measured during anthesis–16 DAA and 16 DAA–maturity phases. Possible associations between these traits and individual grain weight were also explored.

MATERIALS AND METHODS

Cultivars and site of experiments

Seventy–five Iranian bread wheat cultivars, two foreign bread wheat (Kauz and Montana), and four durum cultivars (Yavarus, Simine, Shovamald, and Stark) released from 1930 to 2006 were considered in the current study (Table 1). They were commonly grown in Iran during this period and covered up to 90% of the total area of cultivation (JOUDI *et al*., 2014). Experiments were performed at Parsabad–Moghan, located in the north–western of Iran (39º360 N, 47º570 E and 45 m a.s.l.). Parsabad has a warm Mediterranean climate, with cold winters, humid spring and summers with an average annual precipitation of 271mm.

Table 1. Wheat cultivars used in the Parsabad–Moghan experiments during 2010–2011 and 2013–2014 growing seasons.

Cultivars number	Cultivar name	Year of release	Cultivars number	Cultivar name	Year of release
1	Arta	2006	42	Shahi	1967
2	Azadi	1979	43	Shole	1957
3	Azar 1	1956	44	Shovamald	2003
4	Azar2	1999	45	Shahriar	2002
5	Atrak	1995	46	Shirodi	1997
6	Arvand	1973	47	Shiraz	2002
7	Estar	1995	48	Tabasi	1951
8	Akbari	2006	49	Adl	1962
9	Alborz	1978	50	Frontana	–
10	Alvand	1995	51	Falat	1990
12	Omid	1956	53	Ghods	1989
13	Inia	1968	54	Kaveh	1980
14	Spring BC Roshan	1998	55	Gascogne	1994
15	Winter BC Roshan	1998	56	Crossed Alborz	–
16	Bam	2006	57	Crossed Shahi	–

Table 1 continued. Wheat cultivars used in the Parsabad–Moghan experiments during 2010–2011 and 2013–2014 growing seasons.

17	Bulani	–	58	Crossed Falat Hamun	2002
18	Baiat	1976	59	Kavir	1997
19	Bistun	1980	60	Karaj 1	1973
20	Pishtaz	2002	61	Karaj 2	1973
21	Chamran	1997	62	Karaj 3	1976
22	Chanab	1975	63	Gaspard	1994
23	Khazar 1	1973	64	Gholestan	1986
24	Khalij	1960	65	Marun	1991
25	Darab 2	1995	66	Marvdasht	1999
26	Daria	2006	67	Moghan 1	1973
27	Dez	2002	68	Moghan 2	1974
28	Durum Yavarus	1996	69	Moghan 3	2006
29	Rasul	1992	70	Mahdavi	1995
30	Roshan	1958	71	Naz	1978
31	Zakros	1996	72	Navid	1968
32	Zarrin	1995	73	Niknazhad	1995
33	Soisson	1994	74	Hamun	2002
34	Sabalan	1981	75	Hirmand	1991
35	Sepahan	2006	76	Verinak	–
36	Sorkhtokhm	1957	77	DN–11	–
37	Sardari	1930	78	Stark	2005
38	Somaye 3	–	79	WS–82–9	–
39	Siatan	2006	80	Kauz	–
40	Simine	1997	81	Montana	
41	Shahpasand	1942			–

Agronomic trials

Trials were conducted over crop seasons 2010–2011 and 2013–2014 under well–watered conditions at the agriculture research farm of Moghan College of Agriculture and Natural Resources, University of Mohaghegh Ardabili. In the first season, the cultivars were planted on Nov 17–19, 2010, as a recommended date for wheat sowing. In the second season, the wheat cultivars were sown on Dec 11, 2013 as a late sowing date in which plants were exposed to higher temperature during grain filling period. Seeding rates were adjusted by cultivar according to thousand grain weight to achieve a target plant number of 300 m^{-2}. The experimental design was a simple lattice (9×9) with two replications. There were four rows in each plot in a north–south direction; rows were 1m long with 0.2m spacing. Fertilizers applied were diammonium phosphate (200 kg ha^{-1}) and urea (100 kg ha^{-1}) before planting, and 50 kg ha^{-1} of urea top–dressed at jointing (Zadoks GS 31, ZADOKS *et al*., 1974). Herbicides and insecticide were sprayed to prevent or control weeds and insects. In the 2010–2011 and 2013–2014 seasons, plants were irrigated five and four times from sowing to maturity, respectively. Approximately 55 mm of irrigation water was applied each time.

Measured traits

The dates of anthesis and physiological maturity were recorded. To achieve this, the plots were monitored every two days. Anthesis was recorded when half of the main shoot spikes had visible anthers. Dates of physiological maturity were recorded when peduncles on half of the plants in plots turned completely yellow. As temperatures varied between years, and with the objective of including temperature effects on the lengths of growth phases (Isidro *et al.*, 2011), developmental stages were expressed in the form of thermal time (TT), calculated as: $\Sigma [(Tmax+Tmin/2) - Tb]$, where, Tmax and Tmin are site daily maximum and minimum temperatures, and Tb is the base temperature (5°Cd).

In each plot, three main stems from the two middle rows were harvested at random at anthesis, 16 days after anthesis (16 DAA), and at physiological maturity. The main stems were harvested and immediately dried in a forced–air dryer at 70ºC for 48 h to minimize respiration and weight losses. The spikes then were removed from the stems, weighed, and their mean was recorded. Since there is no further significant increase in chaff weight (i. e. rachis and glumes without grain) after anthesis, post anthesis changes in spike dry weight could be used as an indicator of the amount of partitioned photoassimilates to the grains (EHDAIE *et al.*, 2008 and references therein).

The amount of partitioned photoassimilates (APP) to the grains during anthesis–16 DAA and 16 DAA–maturity were calculated as:

The APP during anthesis–16 DAA = spike dry weight at 16 DAA – spike dry weight at anthesis

The APP during 16 DAA–maturity = spike dry weight at maturity – spike dry weight at 16 DAA

Also, the rate of partitioned photoassimilates (RPP) to the grains during anthesis–16 DAA and 16 DAA–maturity were calculated as:

The RPP during anthesis–16 DAA = APP during anthesis–16 DAA / growing degree day (GDD) of anthesis–16 DAA

The RPP during 16 DAA–maturity = APP during 16 DAA–maturity / GDD of 16 DAA–maturity.

In 2013–2014 growing season, individual grain weight was also measured. To achieve this, ten main stems spike were taken at random at maturity and threshed and their average was obtained. Grain number per spike was also recorded. The individual grain weight in the spike was calculated as the ratio of main stem grain yield to grain number per spike.

Statistics

For the traits that were in common between Year 1 (2010–2011 growing season) and Year 2 (2013–2014 growing season), analyses of variance (ANOVA) were performed over two years using SAS statistical software (SAS Institute, 1994). First, data from Year 1 and Year 2 were analyzed separately according to a lattice design. Analyzed data from Years 1 and 2 were considered as replication 1 and 2, respectively. Replications 1 and 2 were then combined based on a randomized complete block design (RCBD) (JOUDI *et al.*, 2014). Relationships between traits (mean of treatments) were studied by correlation analysis which was conducted using SPSS statistical software Version 17.0 (SPSS Inc, 1998).

RESULTS

General

Due to late sowing date, and lower temperature that occurred between December and March during 2013–2014 growing season, establishment of the cultivated plants was delayed until late winter. Hence, thermal times for developmental stages during 2013–2014 were lower than those recorded during 2010–2011 growing season (see below).

Combined ANOVA showed that the main effects for Year were significant for all the traits that were in common between Years 1 and 2 (Table 2). The main effects of cultivar were significant for the most of the measured traits. Cultivar × year interaction was also significant for all of these traits. Significant cultivar × year interaction results from changes in the magnitude of the differences among cultivars in different years or from changes in relative ranking of the cultivars. On the basis of these results, data from Year 1 and 2 are presented separately.

Year 1

Wheat cultivars accumulated, on average, 1392ºC from sowing to anthesis. Thermal time (TT) from sowing to anthesis ranged from 1287 to 1584ºC among examined cultivars (Figure 1a).

At anthesis, mean spike dry weight was 0.58 g. The highest and the lowest spike dry weights at anthesis were 0.31 and 1.20 g, respectively (Figure 1b).

From anthesis to 16 DAA, mean spike dry weight increased significantly to 1.26 g (Figure 1c). Considerable genetic variations were found among cultivars with respect to partitioned photoassimilates to the grains from anthesis to 16 DAA, where it ranged from 0.06 to 1.25 g (Figure 1e). During this phase of grain growth, the higher amounts of photoassimilates partitioning to the grains were generally accompanied with the higher rates of this process and visa versa (Table 3). For example, Alamut, Kaveh, and Karaj 3 showed higher amount and rate of photoassimilates partitioning during anthesis–16 DAA, while Niknazhad, Sorkhtokhm, and Darab 2 exhibited the opposite (Figure 1e and h). There were positive correlations between amount and rate of photoassimilates accumulation in the grain during anthesis–16 DAA and TT from sowing to anthesis (Table 3). The amount and rate of photoassimilates partitioning toward grains during anthesis–16DAA were higher in the late flowering cultivars whereas the apposite trends were observed in the case of early flowering ones (compare Figure 1a, e and h).

At physiological maturity, mean spike dry weight was 2.63 g (Figure 1d). Depending on the cultivars, the amount of partitioned photoassimilates to the grains from 16 DAA to physiological maturity ranged from 0.45 to 2.23 g (Figure 1f). Such considerable variations were also observed in the case of rate of photoassimilates partitioning to the grains during this phase (Figure 1i). The relationships between the amount and rate of accumulated photoassimilates in the grains of tested cultivars during 16 DAA–maturity and TT from sowing to anthesis were significantly negative (Table 3).

Total photoassimilates partitioned to the grains during anthesis– physiological maturity was, on average, 2.05 g (Figure 1g). The proportion of photoassimilates partitioned to the grains during anthesis–16 DAA and 16 DAA–maturity accounted for, on average, 32% and 68% of total photoassimilates accumulated in the grains during grain filling period, respectively.

Table 2. Mean squares for measured traits [growing degree days (GDD) of anthesis and physiologic maturity; spike dry weight (SDW) at anthesis, 16 days after anthesis (16 DAA), and physiologic maturity; amount of partitioned photoassimilates (APP) during anthesis–16 DAA, 16 DAA–maturity, and anthesis–maturity; rate of partitioned photoassimilates (RPP) during anthesis–16 DAA, 16 DAA–maturity, and anthesis–maturity] of 81 wheat cultivars grown in Moghan region of Iran during 2010–2011 and 2013–2014 growing seasons

S. O. V.	d. f.	Mean square										
		GDD of anthesis	GDD of maturity	SDW at anthesis	SDW at 16 DAA	SDW at maturity	APP during anthesis–16 DAA	APP during 16 DAA–maturity	APP during anthesis–maturity	RPP during anthesis–16 DAA	RPP during 16 DAA–maturity	RPP during anthesis–maturity
Replication (Year)	1	19736648**	32408405**	3.070**	27.180**	11.870**	12.080**	3.080**	2.910**	7.560**	1100**	370**
Treatment (Cultivar)	80	2887**	2457**	0.032*	0.154*	0.430**	0.095^{ns}	0.254^{ns}	0.315**	1.350^{ns}	2.930*	1.200**
Error (Year × Cultivar)	80	899**	823**	0.019**	0.104**	0.191**	0.086**	0.215**	0.180**	1.150**	1.850**	0.645**
Averaged Error #	128 ≠	91	258	0.005	0.025	0.067	0.030	0.090	0.070	0.412	0.543	0.206

ns Non significant
* Significant at P = 0.05
** Significant at P = 0.01
# [(Intra Block Error in Year1 + Intra Block Error in Year2)/2]/Number of Replications
≠ (d. f. of Intra Block Error in Year1 + d. f. of Intra Block Error in Year2)

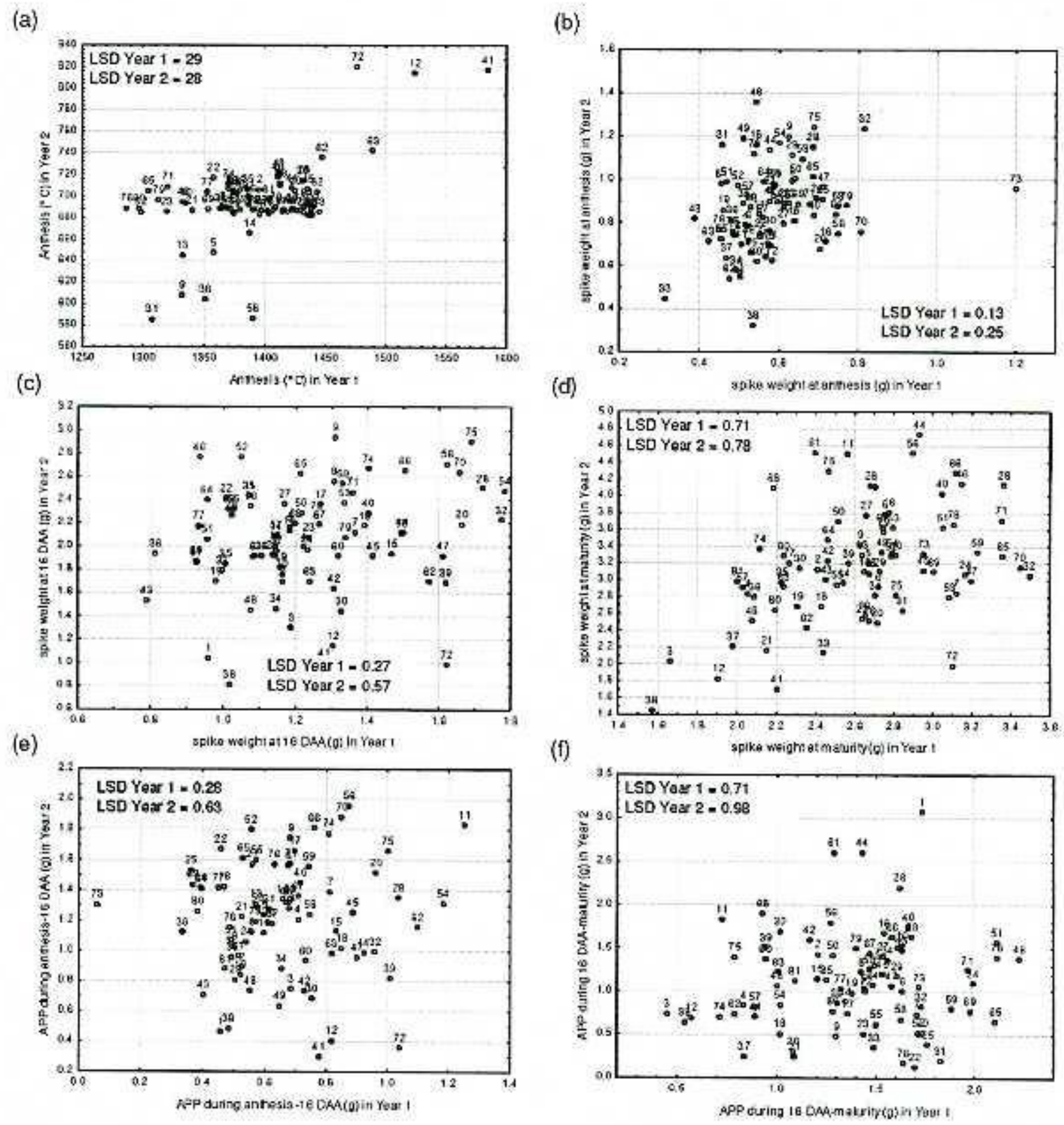

Figure 1. Growing degree days (GDD) for anthesis **(a)**; spike dry weight measured at anthesis **(b)**, 16 days after anthesis (16 DAA) **(c)**, and at physiological maturity **(d)**; amount of partitioned photoassimilates (APP) recorded during anthesis–16 DAA **(e)**, 16 DAA– physiological maturity **(f)**,

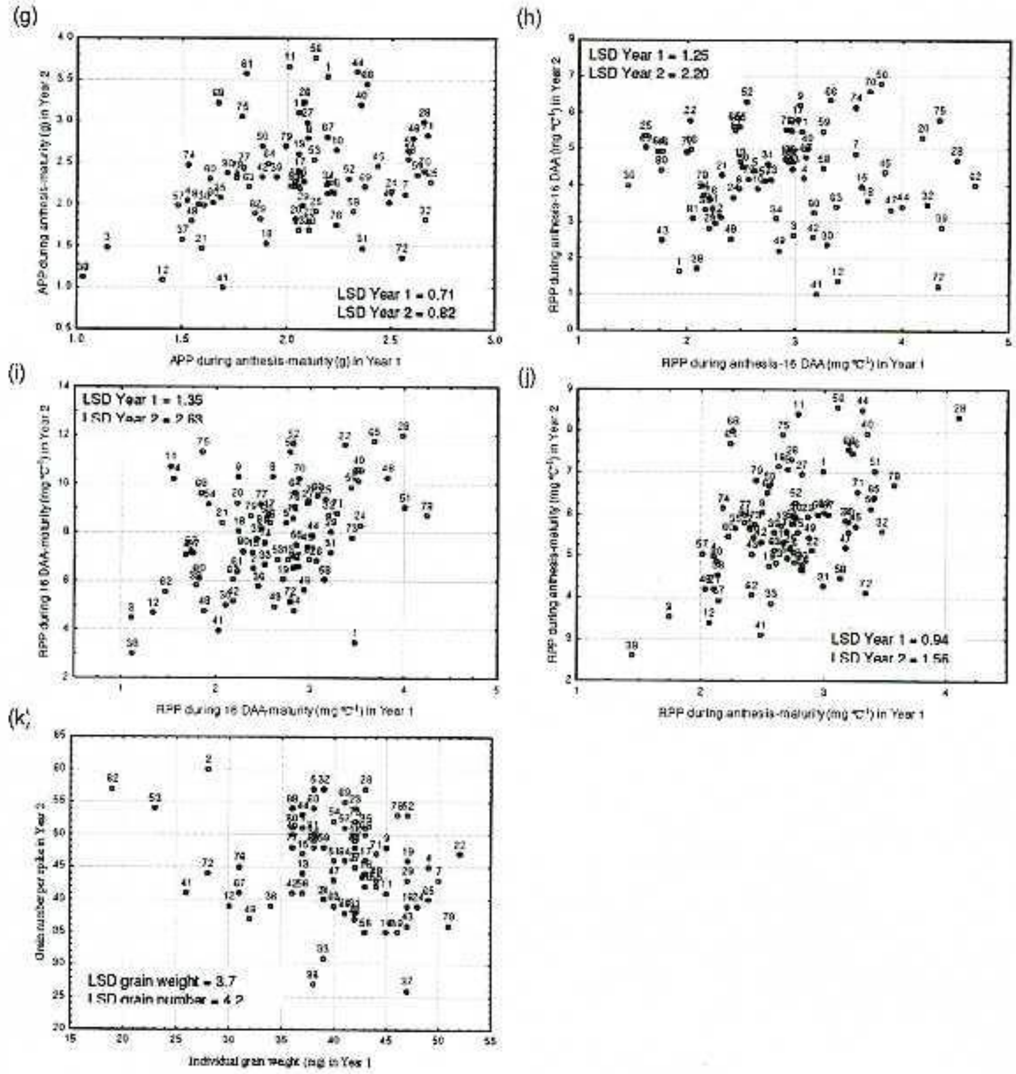

Figure 1 continued. and anthesis– physiological maturity phases (**g**), rate of partitioned photoassimilates (RPP) measured during anthesis–16 DAA **(h)**, 16 DAA–physiological maturity **(i)**, and anthesis–physiological maturity phases **(j)** in 81 wheat cultivars grown at Parsabad–Moghan during 2010–2011 (Year 1) and 2013–2014 (Year 2) growing seasons. Grain number per spike and individual grain weight (k) were measured only during 2013–2014 growing season. Values represent means from three independent main stems. Least significant differences (LSD) values are indicated at 5 % probability level.

Table 3. Correlation coefficients among measured traits in 81 wheat cultivars grown at Parsabad–Moghan during 2010–2011 growing season.

	GDD of anthesis	spike dry weight at anthesis	APP during anthesis–16 DAA	APP during 16 DAA–maturity	APP during anthesis–maturity	RPP during anthesis–16 DAA	RPP during 16 DAA–maturity	RPP during anthesis–maturity
APP during anthesis–16 DAA	0.54 **	– 0.01 ns	1					
APP during 16 DAA–maturity	– 0.50 **	0.23 *	– 0.37 **	1				
APP during anthesis–maturity	– 0.22 *	0.24 *	0.17 ns	0.85 **	1			
RPP during anthesis–16 DAA	0.49 **	– 0.01 ns	0.99 **	– 0.35 **	0.18 ns	1		
RPP during 16 DAA–maturity	– 0.36 **	0.26 *	– 0.30 **	0.95 **	0.84 **	– 0.30 **	1	
RPP during anthesis–maturity	– 0.05 ns	0.26 *	0.28 *	0.75 **	0.95 **	0.28 *	0.82 **	1

ns Non significant
* Significant at 5 % probability level
** Significant at 1 % probability level

Year 2

Cultivars, on average, reached anthesis with 694ºC, 50% less than that observed in year 1. The differences between the highest (818ºC) and the lowest (584ºC) values of anthesis TT was 234ºC (Figure 1a).

The mean spike dry weight at anthesis was 0.86 mg, 48% more than that observed in year 1 (Figure 1b).

During anthesis–16 DAA phase, mean spike dry weight increased significantly to 2.07 g (Figure 1c). Considerable variations were found among cultivars for partitioned photoassimilates to the grains; this parameter varied from 0.30 to 1.96 g (Figure 1e). There was a close relationship between amounts and rates of photoassimilates partitioning to the grains as indicated by correlation analysis (Table 4). Both parameters correlated negatively with TT from sowing to anthesis (Table 4). Partitioning of photoassimilates to the grains during anthesis–16 DAA measured in 2013–2014 did not correlate significantly with those measured during 2010–2011 growing season, which indicates that cultivars ranks for this trait has changed from one year to another (Figure 1e).

Examined wheat cultivars, on average, absorbed 1.11 g photoassimilates to their grains from 16 DAA to maturity. There were significant differences in the grains dry matter accumulation during this phase among wheat cultivars. Such large variations were also found in terms of rate of photoassimilates partitioning to the grains (Fig 1f and i).

Mean total photoassimilates accumulated in the grains during anthesis–maturity was 2.32 g, 11% more than that observed during 2010–2011 growing season (Figure 1g). The proportion of photoassimilates partitioned to the grains during anthesis–16 DAA and 16 DAA–maturity accounted for, on average, 52% and 48% of total photoassimilates accumulated in the grains during grain filling period, respectively.

Individual grain weight, ratio of main stem grain yield to grain number per spike, ranged from 19 to 52 mg (Figure 1 k). Significant differences were also found in terms of grain number per spike, where the highest and the lowest grain number per spike were 26 and 60, respectively

(Figure 1 k). Interestingly, there were significant positive correlations between amount and rate of partitioned photoassimilates to the grains during anthesis–16 DAA and individual grain weight. No significant associations were found between amount and rate of partitioned photoassimilates during 16 DAA–maturity, anthesis–maturity, and individual grain weight (Table 4).

Table 4. Correlation coefficients among measured traits in 81 wheat cultivars grown at Parsabad–Moghan during 2013–2014 growing season.

	GDD of anthesis	spike dry weight at anthesis	APP during anthesis–16 DAA	APP during 16 DAA–maturity	APP during anthesis–maturity	RPP during anthesis–16 DAA	RPP during 16 DAA–maturity	RPP during anthesis–maturity	Grain number per spike	Individual grain weight
APP during anthesis–16 DAA	– 0.36 **	0.17 ns	1						0.13 ns	0.32 **
APP during 16 DAA–maturity	0.11 ns	0.13 ns	– 0.22 *	1					0.17 ns	– 0.06 ns
APP during anthesis–maturity	– 0.12 ns	0.23 *	0.40 **	0.79 **	1				0.24 *	0.14 ns
RPP during anthesis–16 DAA	– 0.38 **	0.17 ns	0.99 **	– 0.23 *	0.40 *	1			0.13 ns	0.32 **
RPP during 16 DAA–maturity	– 0.15 ns	0.14 ns	– 0.19 ns	0.99 **	0.81 **	– 0.20 ns	1		0.29 *	– 0.03 ns
RPP during anthesis–maturity	– 0.08 ns	0.25 *	0.44 **	0.76 **	0.98 **	0.43 **	0.79 **	1	0.33 **	0.17 ns

ns Non significant
* Significant at 5 % probability level
** Significant at 1 % probability level

DISCUSSION

Grain growth and yield of wheat depends upon the assimilate availability (source strength), capacity of the grain to utilize the available substrates (sink strength) and the balance between source–sink strength (AHMADI *et al*., 2009). A large body of evidence demonstrated that sink limits wheat yield more than source strength does (JENNER *et al*., 1991; BORRAS *et al*., 2004; MIRALLES and SLAFER, 2007; FOULKES *et al*., 2011). Therefore, the critical traits to be considered for increasing yield potential must be related to increases in sink size during grain filling, either by increasing the potential size of the grains or by further increasing grain number per square meter (MIRALLES and SLAFER, 2007).

The explanations for non–significant responses of the grain size or weight to the excess of photoassimilates during grain filling have not been fully understood yet (JENNER *et al*., 1991; FISCHER, 2007). In this respect, researchers have reported that some traits show close associations with grain weight. CALDERINI and REYNOLDS (2000), for example, stated that grain weight of wheat was associated with carpel weight at anthesis. FISCHER and HILLERISLAMBERS (1978) working with thirteen wheat cultivars reported that their potential grain weight was associated with spike dry weight at anthesis. The amount of photoassimilates supply during early grain growth has a close association with grain weight as well, actualized by affecting the number of endosperm cell divisions (BROCKLEHURST, 1977) or by effects on potential size of the caryopsis (FISCHER, 2007).

The amount and rate of photoassimilates supply toward grains during anthesis–16 DAA and 16 DAA–maturity phases was studied by measuring spike dry weight changes during 2010–2011 and 2013–2014 growing seasons. Interestingly, cultivated plants during 2013–2014 growing season, characterized by lower accumulated GDD for plant developmental stages, showed priority with respect to measured traits when compared to those grown during 2010–2011 growing season (Figure 1b–j). There is no clear explanation for such results but it is possible that the examined cultivars during 2013–2014 growing season might have produced fewer tillers per main stem. That is to say, these plants partitioned more produced photoassimilates to their main stem's spike and; therefore, they showed superiority in the spike–related traits.

Considerable variations were found for photoassimilates partitioning toward grains during both anthesis–16 DAA and 16 DAA–maturity phases among Iranian wheat cultivars (Figure 1e and f). Part of these variations could be attributed to differences in anthesis time. During 2010–2011 growing season, late flowering cultivars partitioned more photoassimilates during anthesis–16 DAA phase, whereas the opposite trend was observed during 2013–2014 growing season (Table 3 and 4). JOUDI (2016) reported that associations between agronomic and physiological traits and phenological events vary with environment. It was also highlighted that even in a special region there is no simple relationship between these parameters.

Large spike cultivars showed higher amount and rate of photoassimilates partitioning to the grains during anthesis–maturity phase (Table 3 and 4), indicating that spike size should also be taken into account when wheat cultivars are compared with respect to photoassimilates partitioning. It was reported that spike dry weight at anthesis was higher in higher yielding modern wheat cultivars where they showed more grain number per spike and per square meter (ÁLVARO *et al*., 2008; JOUDI *et al*., 2014). This suggests that large spike cultivars have higher potential to capture photoassimilates in comparison with small spike ones.

Grain number per spike could also be considered as a factor influencing photoassimilates partitioning toward grains. Therefore, the number of grain per spike was measured during 2013–2014 growing season and the association between this trait and photoassimilates partitioning toward grains investigated. Generally, wheat cultivars with higher number of grain in their spike showed higher amount and rate of photoassimilates partitioning toward grains during anthesis–maturity phase (Table 4). EHDAEI *et al*. (2008) worked on 11 wheat cultivars grown under irrigated and drought conditions and reported that the linear rate of grain growth was not significantly correlated with grain number per spike or grain weight under both irrigation regimes. However, when linear rate of grain growth was regressed on both numbers of grains per spike and grain weight, the regression was significant under both conditions they were tested.

When differences in anthesis date, spike dry weight at anthesis, and grain number per spike were considered, it was revealed that there were still differences among some cultivars with respect to photoassimilates partitioning toward grains. Flowered at about the same time, Fongh and Niknazhad with the same spike dry weight at anthesis and similar grain number per spike showed noticeable differences in their photoassimilates partitioning to the grain during anthesis–16 DAA and 16 DAA–maturity phases.

It has been reported that the amount of photoassimilates are not sufficient within the growing grain and its endosperm cells. Meanwhile, the concentration of sucrose in the rachis is higher than that observed within the grain, suggesting that there are limitations to the transport of the sucrose into or within the grain (JENNER, 1976). JENNER *et al*. (1991) stated that the simplest postulate explaining the upper limit to sucrose inflow and starch accumulation invokes a transport mechanism with saturable characteristics in the pathway of entry into the endosperm. The exact place of this bottle–neck for sucrose supply into the grain is not clear and it may operate in the stalk of the grain or at the site(s) of unloading and transfers into the endosperm cavity (JENNER *et al*., 1991 and references therein). Therefore, the first possible explanation for the differences in photoassimilates partitioning toward growing grains during anthesis–16 DAA and 16 DAA–physiological maturity, observed among wheat cultivars with the same thermal time of anthesis, spike size at anthesis, and final grain number per spike, could be the differences in the amount of sucrose transport into or within the grain (see also below).

The metabolic activity of the sink organ during its development plays an important role in the rate of photoassimilates accumulation. Biochemical conversion of sucrose to starch is one of the most important components of sink strength and it can be determined by the catalytic activities of one or more of the enzymes involved in this pathway (AHMADI and BAKER, 2001). It was stated that the activity of sucrose synthase, adenosine diphosphorate glucose pyrophosphorylase, starch synthase, and starch branching enzyme are determinant in the process of starch biosynthesis (YANG *et al*., 2004 and references therein). YAN *et al*. (2010) studied four compact– and loose–spike wheat cultivars and reported that superior grains showed a higher starch accumulation rate, endosperm cell number and activity of enzymes including sucrose synthase, uridine diphosphorate glucose pyrophosphorylase, adenosine diphosphorate glucose pyrophosphorylase, soluble starch synthase and granule–bound starch synthase, and subsequently produced higher starch accumulation and grain weight than inferior grains. Thus, the second possible explanation for variations in photoassimilates partitioning during grain filling period, observed among cultivars with the same thermal time of anthesis, spike size at anthesis, and final grain number per spike, could be due to probable variations in catalytic activities of enzymes that are involved in the conversion of sucrose to the starch.

It was hypothesized that higher value of post–anthesis photoassimilates partitioning to the grain during early grain growth would result in higher grain weight at physiological maturity. The results obtained during 2013–2014 growing season revealed a significant positive correlation between photoassimilates partitioning toward grains during anthesis–16 DAA and individual grain weight (Table 4). These results are in line with those of other studies (BROCKLEHURST 1977; YAN *et al*., 2010) which stated that higher amounts of assimilates supply during early grain growth resulted in higher endosperm cells number and increased grain weight at maturity.

CONCLUSION

Our experiments during 2010–2011 and 2013–2014 growing seasons revealed that there are genotypic variations among Iranian wheat cultivars for photoassimilates partitioning toward grains during early development of endosperm (anthesis–16 DAA phase). These variations were partly due to differences in phenological, morphological and agronomical traits. Taking them into account, there were still some cultivars which showed different capacity of photoassimilates partitioning to their grain during anthesis–16 DAA. The possible explanations for such results could be the differences of examined cultivars in sucrose transport into (or within) the grain or their differences in catalytic activities of the enzymes that are involved in the conversion of sucrose to the starch within the grain. However, further investigations are required to get convincing results. Consequently, these observations suggest that breeding for enhanced photoassimilates partitioning towards grain during anthesis–16 DAA could be possible. It should be mentioned that improving photoassimilates partitioning toward grains is a challenging task, as it appears that environmental conditions have pronounced effects on this process (See above). In case such modification could be performed by the wheat breeders, this would result in increased grain size and weight in the wheat plants.

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GENETIČKE VARIJACIJE ZA RASPODELU ASIMILATA U ZRNU TOKOM RANOG RAZVOJA ENDOSPERMA PŠENICE: POVEZANOST SA TEŽINOM ZRNA

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Izvod

Malo je informacija o genetičkim varijacijama u raspodeli fotoasimilata u zrnu tokom ranog razvoja endsperma kod pšenice. Ispitivan je 81 genotip pšenice u reginu Moghan, u Iranu, tokom vegetacionih sezona 2010–2011 i 2013–2014. Količina i brzina raspodele fotoasimilata u zrnu, mereni su tokom cvetanja-16 dana posle cvetanja (DAA) i 16 DAA- u fazi zrelosti, preko promena u suvoj masi klasa. Utvrđene su znatne genetičke varijacije, delom zbog razlika u vremenu cvetanja između kultivara, suvoj masi klasova tokom cvetanja, i broju zrna po klasu. Uzimajući to u obzir neki kultivari su se razlikovali u raspodlei fotoasimilata u zrnu tokom cvetanja-16DAA i 16DAA u fazi zrelosti, podržavajući ideju da oplemenjivanje za raspodelu fotosimilata tokom ovih faza je moguće. Rezultati dobijeni u 2013–2014 pokazali su blisku vezu između raspodele fotasimilata u zrnu tokom cvetanja–16 DAA i pojedinačne težine zrna. Rezultati ukazuju da ukoliko bi oplemenjivači poboljšali raspodelu fotoasimilata u zrnu tokom cvetanja–16 DAA, to bi rezultiralo i u povećanju veličine i težine zrna kod pšenice.

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