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Changes in Stem and Spike Related Traits Resulting from Breeding in Iranian Wheat Cultivars: Associations with Grain Yield

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Abstract

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This study investigated changes in stem and spike characteristics resulting from breeding in Iranian wheat cultivars, and their relationship with grain yield. Eighty-one wheat cultivars released between 1930 and 2006 were examined under well-watered (WW) and terminal drought stress (DS) conditions at Karaj during 2007–2008 and 2008–2009 and under WW conditions at Parsabad in the Moghan region during 2010–2011. Genetic improvement over time in specific stem weight (SSW) along with significant positive correlations between this trait and grain yield were observed at Karaj under DS conditions and at Parsabad, suggesting that SSW could be used as an indirect selection criterion for yield in these environments. Time-dependent changes in spike dry weight showed that the accumulation of photoassimilates in the spike from anthesis to 16 days after anthesis (16 DAA) was not changed by breeding. However, during the 16 DAA – maturity phase, modern cultivars had more photoassimilates allocated to the spike than the old ones. This suggests that the sink is more limited during early grain growth than during the end of grain filling.

Keywords: partitioned photoassimilates; sink limitation; stem specific weight; *Triticum aestivum*; *Triticum durum*

Wheat (*Triticum* spp.) is an important cereal crop and serves as a staple food in many countries. This crop is grown on 220 million ha throughout the world producing approximately 729 million t of grain. In Iran, the area under wheat cultivation in 2014 was 7.3 million ha with the production of 10.6 million t (FAO 2014).

Although the grain yield of wheat has increased noticeably during recent decades, challenges to wheat production are still considerable (Reynolds *et al.* 2007). Understanding agronomical and physiological traits associated with grain yield is important for plant breeders who develop cultivars with improved yield and for performing more basic research at a physiological and molecular level.

Leaf tissue is the main photosynthetic organ of plants. However, non-leaf organs such as stem, spike bracts and awns also have photosynthetic capability (Zhang *et al.* 2011). At the later grain filling stage, leaves turn senescent, limiting the contribution of current assimilates to the grain. Therefore, a substantial amount of the carbohydrates used during late grain filling in wheat must come from stem reserves (Ehdaie *et al.* 2006) and spike photosynthesis (Tambussi *et al.* 2005).

Stem length and weight are two characteristics of wheat which have long been considered by scientists. Past genetic gains in wheat plants have been widely associated with increased harvest index and grain per m^2 and decreasing stem length (Royo *et al.* 2007).

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Most likely, selection for decreased plant height has led to decreased stem weight. Alvaro *et al.* (2008) worked on 12 Italian and 12 Spanish durum cultivars released at different periods and reported that main stem (stem + sheaths) weight and area were higher in old than in modern cultivars. Specific weight of stem (stem weight/stem length) is another trait which can be considered in wheat breeding programs. Unlike stem length and weight, information about stem specific weight, its relationship with grain yield as well as its change during past breeding programs are incomplete and need further study.

Partitioning post-anthesis photoassimilates to the spike has an important role in grain yield formation. The capability by which the wheat spike captures post-anthesis photosynthesis can be considered as an indication of sink strength (Fischer 2011). This parameter can be measured as a difference in spike weight at different phases of spike development (see below). It is not clear how breeding activity has changed this trait. If its change is consistent with grain yield enhancement, it can be used as a promising trait in wheat breeding programs.

The present study was undertaken in order to study the relationships of stem and spike characteristics with grain yield in Iranian wheat cultivars released from 1930 to 2006 and cultivated at two latitudes of Iran representing contrasting environmental conditions.

MATERIAL AND METHODS

Seventy-five Iranian bread wheat (*T. aestivum* L.) cultivars, two foreign bread wheat (Kauz and Montana), and four durum (*T. durum* Desf.) cultivars (Yavarus, Simine, Shovamald, and Stark) released from 1930 to 2006 were considered in the present work (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 Karaj and Parsabad, representing contrasting environmental conditions. Karaj is situated in the north-central part of Iran (35°49'N, 51°0'E and 1312 m a.s.l.) and has an arid Mediterranean climate, with cold winters, temperate spring and dry summers, with average annual precipitation of 243 mm. Parsabad, located in the Moghan region in northwestern Iran (39°36'N, 47°57'E and 45 m a.s.l.) has a warm Mediterranean climate, with cold winters, humid spring and summers with average annual precipitation of 271 mm (Figure 1).

At Karaj, trials were conducted over crop seasons 2007–2008 and 2008–2009. In each season, experiments were conducted simultaneously under well-watered (WW) and terminal drought stress (DS) conditions at the Agriculture Research Farm of Tehran University. At Parsabad, a field experiment was carried out under WW conditions at the Agriculture Research Farm of the Moghan College of Agriculture and Natural Resources, University of Mohaghegh Ardabili, in the 2010–2011 growing season. The 81 cultivars were sown (300 seeds/m^2) on Nov 1–3, 2007 and on Nov 10–11, 2008 at Karaj and on Nov 17–19, 2010 at Parsabad station. The details of the experiments have been presented elsewhere (Joudi *et al.* 2014).

In each plot, three main stems (including the spike) from the two middle rows were harvested randomly at anthesis, 16 days after anthesis (16 DAA), and physiological maturity. They were immediately dried in a forced-air dryer at 70°C for 48 h to minimize respiration and weight loss. The length and weight of stem (excluding leaf sheaths) were recorded. Stem specific weight (SSW) was calculated as the ratio of its weight (mg) to its length (cm). Spike weight was also recorded at each sampling time. Therefore, since there was no further significant increase in chaff weight (i.e., rachis and glumes without grain) after anthesis (Ehdaie *et al.* 2008), the magnitude of partitioned photoassimilates to the spike (grain) during anthesis – 16 DAA (MPP A – 16 DAA) was estimated as the difference in spike dry weight at 16 DAA and at anthesis. Also, the magnitude of partitioned photoassimilates to the spike during 16 DAA – physiological maturity (MPP 16 DAA – M) was estimated as the difference in spike dry weight at physiological maturity and at 16 DAA (Joudi 2016). At maturity, 1 m^2 per plot sections was cut at the ground level and grain yield was obtained after threshing.

Figure 1. Map of Iran and geographical position of the experimental sites

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Table 1. Wheat cultivars used in the Karaj and Parsabad-Moghan experiments (among the tested cultivars, the years of release for 11 cultivars were unknown; they were not, therefore, considered in regression analysis)

Cultivar name	Origin	Year of release in Iran	Cultivar name	Origin	Year of release in Iran
Arta	Iran	2006	Gholestan	CIMMYT	1986
Akbari	Iran	2006	Sabalan	Iran	1981
Bam	Iran	2006	Bistun	Iran	1980
Daria	CIMMYT	2006	Kaveh	Mexico	1980
Sepahan	Iran	2006	Azadi	Iran	1979
Sistan	ICARDA	2006	Alborz	CIMMYT	1978
Moghan 3	Iran	2006	Naz	CIMMYT	1978
Stark	CIMMYT	2005	Baiat	Iran	1976
Shovamald	CIMMYT	2003	Karaj 3	Iran	1976
Pishtaz	Iran	2002	Chenab	Pakistan	1975
Dez	CIMMYT	2002	Moghan 2	CIMMYT	1974
Shahriar	Iran	2002	Arvand	Iran	1973
Shiraz	Iran	2002	Khazar 1	Mexico	1973
Crossed Falat Hamun	Iran	2002	Karaj 1	Iran	1973
Hamun	Iran	2002	Karaj 2	Iran	1973
Azar2	Iran	1999	Moghan 1	Mexico	1973
Marvdasht	Iran	1999	Inia	CIMMYT	1968
Spring BC Roshan	Iran	1998	Navid	Iran	1968
Winter BC Roshan	Iran	1998	Shahi	Iran	1967
Chamran	CIMMYT	1997	Adl	Iran	1962
Simine	Iran	1997	Khalij	Iran	1960
Shirodi	CIMMYT	1997	Roshan	Iran	1958
Kavir	Iran	1997	Sorkhtokhm	Iran	1957
Yavarus	CIMMYT	1996	Shole	Iraq	1957
Zakros	ICARDA	1996	Azar 1	Iran	1956
Atrak	CIMMYT	1995	Omid	Iran	1956
Estar	CIMMYT	1995	Tabasi	Iran	1951
Alvand	Iran	1995	Shahpasand	Iran	1942
Alamut	Iran	1995	Sardari	Iran	1930
Darab 2	CIMMYT	1995	Bulani	Iran	–
Zarrin	–	1995	Somaye 3	China	–
Mahdavi	Iran	1995	Frontana	Brazil	–
Niknazhad	ICARDA	1995	Fongh	China	–
Soissons	France	1994	Crossed Alborz	Iran	–
Gascogne	France	1994	Crossed Shahi	Iran	–
Gaspard	France	1994	Verinak	CIMMYT	–
Rasul	CIMMYT	1992	DN-11	CIMMYT	–
Marun	Iran	1991	WS-82-9	–	–
Hirmand	Iran	1991	Kauz	–	–
Falat	CIMMYT	1990	Montana	–	–
Ghods	Iran	1989			

Recorded data were analysed separately for each type of conditions according to a lattice design and adjusted means were considered (Joudi *et al.* 2014). Measured parameters were regressed against the year of cultivar release to obtain genetic gain and to study changes in different plant characteristics over time using linear equations that were fitted to the data. Among the tested cultivars, the years of

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release for 11 cultivars were unknown; they were not, therefore, considered in regression analysis. The Pearson correlation coefficient was calculated to study the relationships between grain yield and measured traits. Student's *t*-test was used to test the significance of the correlation coefficient. Regression and correlation analysis were performed using SPSS statistical software Version 17.0 (SPSS 1998).

RESULTS

Karaj experiments. At anthesis, stem weight ranged from 851 to 1550 mg under WW conditions (Table 2). There was no significant association between stem weight and year of release (Figure 2a). Cultivars differed markedly in SSW which varied from 11 to 19.5 mg/cm (Table 2). SSW was significantly higher in modern cultivars, compared to the old ones (Figure 2c).

Averaged among WW cultivars, stem weight increased from 1198 mg at anthesis to 1390 mg at 16 DAA (Table 2). Under these conditions, stem weight was significantly lower in modern cultivars in comparison with the old ones (Figure 2b). Stem weight decreased in response to terminal drought stress. Under DS conditions, there was no significant association between stem weight and year of release (Figure 2b). Under WW conditions, mean SSW was 17 mg/cm, 13% more than SSW at anthesis. This trait had been improved by breeding. The same trend was observed for SSW under DS conditions (Figure 2d).

The magnitude of partitioned photoassimilates to the spike during anthesis – 16 DAA ranged from 0.44 to 1.42 g and from 0.45 to 1.16 g under WW and DS conditions, respectively (Table 2). No significant association was found between this trait and year of release (Figure 2e). The spike of tested cultivars accumulated photoassimilates differently from 16 DAA to maturity. This parameter increased significantly in modern cultivars under both water regimes (Figure 2f).

Under WW and DS conditions, large variations in grain yield were found among cultivars (Table 2). Overall, new wheat cultivars produced higher grain yield than the old ones (Figure 2g).

Parsabad-Moghan experiment. At anthesis, stem weight ranged from 553 to 1553 mg (Table 2). This trait was not associated with the year of release (Figure 2a). A large variation in SSW was found at anthesis, which ranged from 8.9 to 20.2 mg/cm (Table 2). Like in Karaj experiments, SSW was higher in modern cultivars than in the old ones (Figure 2c).

Table 2. Basic statistics for stem weight (mg) and stem specific weight (SSW, mg/cm) measured at anthesis and 16 days after anthesis (16 DAA), magnitude of partitioned photoassimilates to the spike during anthesis – 16 days after anthesis (MPP A – 16 DAA, g) and during 16 days after anthesis – maturity (MPP 16 DAA–M, g), grain yield (kg/ha) in 81 wheat cultivars grown at Karaj during 2007–2008 and 2008–2009 under well-watered (WW) and drought stress (DS) conditions, and at Parsabad station during 2010–2011 under WW conditions

	Anthesis				16 days after anthesis														
	Karaj		Parsabad		Karaj				Parsabad		Karaj				Parsabad		Karaj		Parsabad
	stem weight	SSW	stem weight	SSW	stem weight		SSW		stem weight	SSW	MPP A – 16 DAA		MPP 16 DAA – M		MPP A – 16 DAA	MPP 16 DAA – M	grain yield		
	WW	WW	WW	WW	WW	DS	WW	DS	WW	WW	WW	DS	WW	DS	WW	WW	WW	DS	WW
Minimum	851	11	553	8.9	1038	763	12.9	9.8	1083	13.6	0.44	0.45	0.23	0.07	0.47	0.06	2710	1120	2930
Maximum	1550	19.5	1553	20.2	1851	1732	22.2	21.3	2138	24.6	1.42	1.16	1.92	1.07	2.21	1.25	10320	6560	7460
Mean	1198	15	972	14	1390	1192	17	15	1604	19	0.79	0.71	1.20	0.56	1.38	0.66	7510	3720	4900
SD	132	1.87	172	2.23	172	183	1.87	2.07	253	2.74	0.16	0.13	0.33	0.23	0.39	0.21	1390	1060	810
CV	11	12	18	16	12	15	11	14	16	14	20	18	27	41	28	32	19	28	17

SD – standard deviation; CV – coefficient of variation

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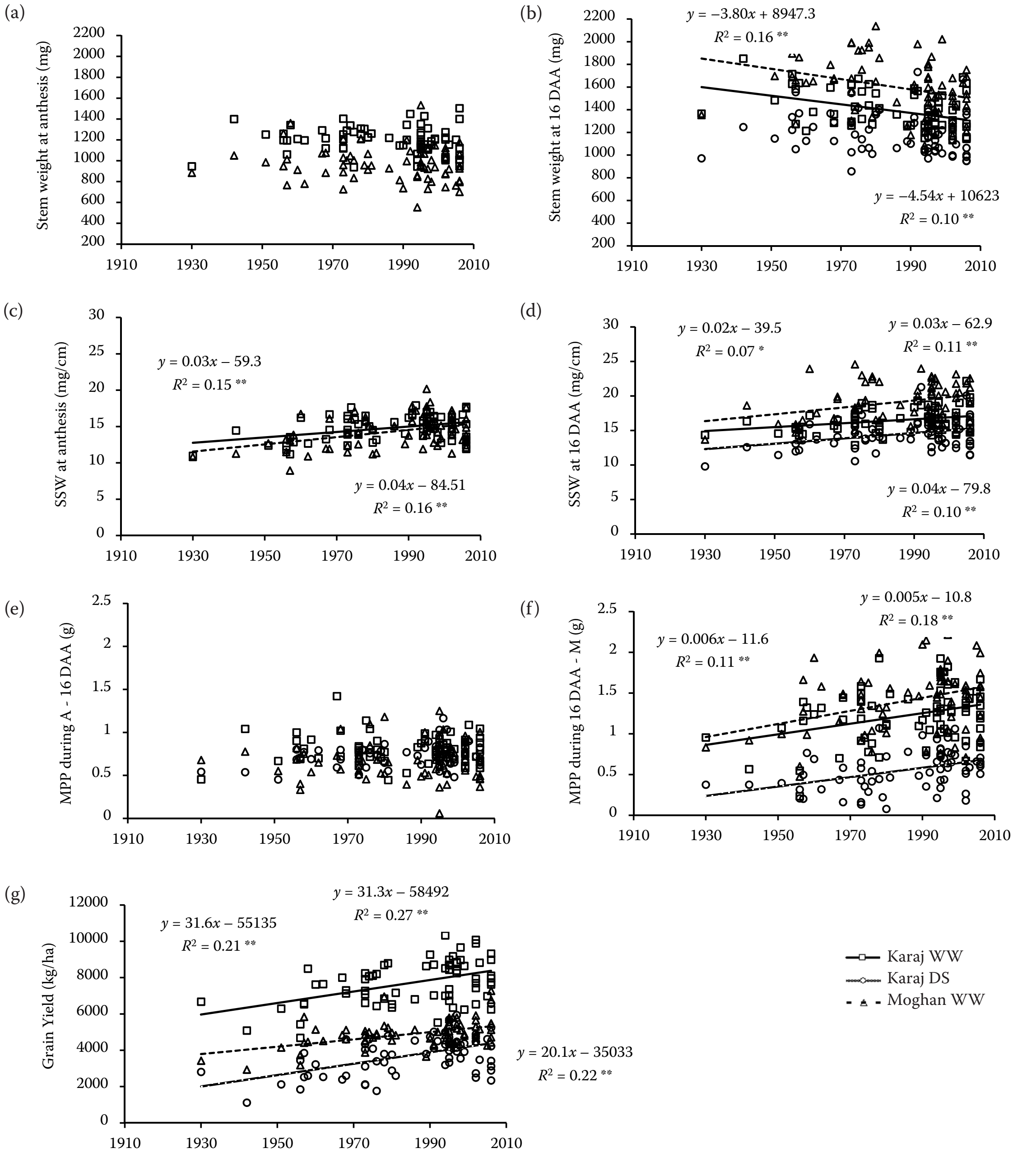

Figure 2. Relationships between year of cultivar release and (a) stem weight at anthesis, (b) stem weight at 16 DAA, (c) stem specific weight (SSW) at anthesis, (d) SSW at 16 DAA, (e) magnitude of partitioned photoassimilates to the spike during anthesis – 16 days after anthesis (MPP A–16 DAA) and (f) during 16 days after anthesis – maturity (MPP 16 DAA – M), and (g) grain yield in Iranian wheat cultivars released from 1930 to 2006

Each square (Karaj – WW) and circle (Karaj – DS) point represents the mean value of one cultivar across 2 years (2007–2008 and 2008–2009) and each triangle (Moghan – WW) represents the mean value of one cultivar during 2010–2011; only significant linear regressions were plotted; regression equations for the Karaj and Moghan experiments are presented in the upper (Karaj – WW is on the left side; Karaj – DS is on the right side) and lower parts of the figures, respectively

Stem weight and SSW were higher at 16 DAA compared to anthesis (Table 2). Stem weight was lower in modern than in old cultivars. A reverse trend was observed for SSW (Figure 2b, d).

As for the Karaj experiment, there was no difference between old and modern cultivars regarding the capacity to accumulate photoassimilates in spike during the phase anthesis – 16 DAA. During the

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phase 16 DAA – maturity, spikes of modern cultivars accumulated more photoassimilates compared to the old ones (Figure 2e, f).

Wheat cultivars differed markedly in grain yield which ranged from 2930 to 7460 kg/ha. Grain yield was positively associated with the year of release (Figure 2g).

DISCUSSION

Optimizing grain yield of wheat is the main issue for breeders worldwide. Understanding relationships between morphological and physiological traits and grain yield across different environmental conditions could help plant breeders to develop wheat cultivars with improved and stable grain yield.

At anthesis, no significant difference in stem weight was detected between old and modern cultivars. Except in Karaj and under DS conditions, however, stem weight was lower in modern than in old cultivars at 16 DAA (Figure 2a, b). Conversely, Alvaro *et al.* (2008) found that stem weight was higher in old than in modern cultivars. In most cases, no significant correlations were found between grain yield and stem weight (Table 3), suggesting a complex relationship between stem weight and grain yield in wheat.

A significant increase in stem specific weight occurred over years of release (Figure 2c, d). To our knowledge, this is the first report on an increase of SSW with breeding. This type of change in SSW along with significant positive correlations between SSW and grain yield that were found at Karaj under DS conditions and at Parsabad (Table 3) suggest that SSW could be considered as a promising trait in wheat programs.

It is now accepted that the wheat stem makes a major contribution to the final grain yield. Carbohydrate accumulation and then their remobilization from the stem are important sources of photoassimilates for grain filling (Ehdaie *et al.* 2006). Potential stem storage as a sink is determined by stem length and SSW (Blum 1998). The Rht_1 and Rht_2 dwarfing genes of wheat were found to reduce reserve storage by 35% and 39%, respectively, and reduce stem length by 21% (Blum 1998). As the total amount of stem contributions to grain yield was the same in the taller and shorter cultivars (Joudi unpublished), the decrease in carbohydrate accumulation and remobilization imposed by length reduction is expected to be compensated by higher SSW in the shorter cultivars. Joudi *et al.* (2012) reported that both carbohydrate amounts and remobilization efficiency per unit stem length were higher in modern cultivars, as compared to the old ones. Therefore, the reduction of stem length (data not shown) and an increase of SSW in modern cultivars suggest that plant breeders should pay more attention to SSW than to stem weight or length.

There was no significant difference between old and modern cultivars with respect to spike dry weight increase from anthesis to 16 days afterwards. Nonetheless, modern wheat cultivars allocated more photoassimilates to their spike from 16 DAA to maturity in all conditions tested (Figure 2e, f). Interestingly, partitioning of photoassimilates from 16 DAA to maturity showed a positive correlation with grain yield (Table 3). From anthesis to 16 DAA, grain

Table 3. Pearson correlation coefficients between grain yield (g/m^2) and stem weight (mg) and stem specific weight (SSW, mg/cm) measured at anthesis and 16 days after anthesis (16 DAA), magnitude of partitioned photoassimilates to the spike during anthesis – 16 days after anthesis (MPP A–16 DAA, g) and during 16 days after anthesis – maturity (MPP 16 DAA–M) in 81 wheat cultivars grown at Karaj during 2007–2008 and 2008–2009 under well-watered (WW) and drought stress (DS) conditions, and at Parsabad station during 2010–2011 under WW conditions

		Grain yield
Karaj WW	Stem weight at anthesis	– 0.13^{ns}
	Stem weight at 16 DAA	– 0.26*
	SSW at anthesis	0.12^{ns}
	SSW at 16 DAA	0.09^{ns}
	MPP A–16 DAA	0.18^{ns}
	MPP 16 DAA–M	0.47**
Karaj DS	Stem weight at anthesis	0.003^{ns}
	Stem weight at 16 DAA	0.005^{ns}
	SSW at anthesis	0.45**
	SSW at 16 DAA	0.43**
	MPP A–16 DAA	0.21^{ns}
	MPP 16 DAA–M	0.32**
Parsabad WW	Stem weight at anthesis	0.05^{ns}
	Stem weight at 16 DAA	– 0.08^{ns}
	SSW at anthesis	0.26*
	SSW at 16 DAA	0.14^{ns}
	MPP A–16 DAA	0.10^{ns}
	MPP 16 DAA–M	0.30**

^{ns}not significant; *, **significant according to Student's *t*-test at the P = 0.05 and 0.01 level, respectively

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size is set in the spike. Later on, formed grains take photoassimilates actively until physiological maturity (Saini & Westgate 2000). Several studies have reported an excess of photoassimilates in wheat and suggested the control of grain yield by sink rather than source strength (Borras *et al.* 2004 and references therein). Considering that spike dry weight during the phase anthesis – 16 DAA has not been changed significantly by breeding during the past decades, we propose here that most probably, the sink limitation in wheat is imposed more during the anthesis – 16 DAA phase than during 16 DAA – maturity. Therefore, plant breeders dealing with sink limitation should pay more attention to the early grain growth than the late one.

CONCLUSIONS

It can be concluded that relationships between agro-morphological traits and grain yield are not consistent and vary with environment. Among stem related traits, stem specific weight increased linearly with the year of release, and showed significant positive correlations with grain yield at Karaj under DS conditions and at Parsabad, suggesting that this trait could be used as an indirect selection criterion for yield in these environments. Based on time-dependent changes that were observed for spike dry weight, it was proposed that the sink limitation in wheat is imposed more during anthesis – 16 DAA than during 16 DAA – maturity. These traits might represent valuable indirect selection criteria to be incorporated into breeding programs dealing with wheat grain yield enhancement.

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