Genetic changes in agronomic and phenologic traits of Iranian wheat cultivars grown in different environmental conditions

Mehdi Joudi · Ali Ahmadi · Valiollah Mohammadi · Alireza Abbasi · Hamid Mohammadi

Abstract Information on genetic gains in different traits of wheat is important in breeding cultivars with improved grain yield. Changes in agronomic and phenologic traits resulting from breeding in Iranian wheat cultivars were studied. Eighty one wheat cultivars released from 1930 to 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 in the Moghan region during 2010–2011. Improvements in grain yield were 31 and 20 kg ha^{-1} y^{-1} in Karaj (under WW and DS conditions) and at Moghan, respectively. In response to DS, grain yield loss was less in modern than in old wheat cultivars, suggesting that, in line with grain yield improvement, breeding has increased the resistance of wheat to terminal DS. Significant genetic changes over time were found for HI, grain number per square meter and spike dry weight at anthesis in all conditions tested. No changes were observed for above–ground dry matter and 1,000 grain weight. Dates of booting and anthesis decreased significantly from old to modern cultivars, and the amount of decrease was more evident at Karaj. Karaj experiments showed that length of the grain filling period, the anthesis—maturity phase, was increased significantly by breeding. However, this trend was not found in the Moghan experiment. These findings indicate that there was an interaction between genetic gains in different traits and environmental conditions in which the genetic gains were studied.

Keywords Genetic gain · Grain yield · Harvest index · Phenological events · *Triticum aestivum*

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Introduction

Wheat is the most important source of carbohydrates in a majority of countries. It provides more nourishment for people than any other food source. Grain yield of wheat has increased noticeably during recent decades. Increases in wheat grain yield over time can

be attributed to the adoption of both better crop management practices (such as sowing time, fertilizer application, and disease control) and cultivars with higher yield potential (Sener et al. 2009).

Genetic gains in wheat yield have been associated with changes in different plant characteristics (Feil 1992; De Vita et al. 2007). The changes in plant characteristics are not, however, consistent and vary with environment. For example, many researchers reported that increased grain yield in modern wheat cultivars was associated with the presence of dwarfing genes and decreased plant height (Royo et al. 2007). However, Sener et al. (2009) studied 16 bread wheat cultivars in the Mediterranean region of Turkey and found that there were no significant differences in plant height between old and new cultivars.

From the point of view of biomass production, there are reports showing that this character has not been modified significantly by breeding (Royo et al. 2007; Calderini et al. 1995) suggesting that selection for grain yield did not lead to cultivars with greater total biomass. These results are not in agreement with Shearman et al. (2005) who stated that a linear increase in grain yield with year of release was due to a counteracting curvilinear increase in above-ground dry matter (AGDM).

The timing of phenological events represents one of the most important factors for adaptation and yield in a given environment (Motzo and Giunta 2007). As agronomic traits, information about genetic gains associated with phenologic events does not show consistent change during the past decades. Peltonen-Sainio and Peltonen (1994) evaluated 10 Finnish spring wheat cultivars and showed that wheat breeders had shortened the length of the grain filling period (GFP) (period from anthesis to physiological maturity) by 2–3 days in the last 50 years. In contrast, Isidro et al. (2011) worked on 24 durum cultivars (12 Italian and 12 Spanish grown throughout the 20th century in Italy and Spain) and reported that there was no significant difference in the anthesis—maturity phase between old and new cultivars. The period of release significantly influenced the duration of other growth phases in their study. Interestingly, increased GFP in modern durums wheat was reported by De Vita et al. (2007).

Weather conditions have pronounced effects on genetic gains in yield by wheat crops over time. For example, in regions with stresses not necessarily occurring late in the growing season (e.g. Canada or Argentina) breeding has not changed the time of anthesis, whereas in Mediterranean regions (e.g. Western Australia or Spain) the time to anthesis tends to reduce systematically as new cultivars have been released (Slafer et al. 2005, and references therein). Thus breeding effects measured on a specific trait in one agro-ecological situation are not necessarily similar in other situations.

There is no report, to our knowledge, of breeding effects on large numbers of wheat cultivars released during different periods, when they are cultivated simultaneously under irrigated and drought stress conditions. Also, little is known about genetic gains in wheat grown in semi-arid conditions such as in Iran where grain development takes place under high temperature and high radiation conditions. Therefore, changes in some agronomic traits and phenological events in Iranian wheat cultivars released from 1930 to 2006 were studied in two latitudes of Iran representing contrasting environmental conditions.

Materials and methods

Cultivars

Seventy five Iranian bread wheat, two foreign bread wheat, and four durum cultivars released from 1930 to 2006 were considered in the current work (Table 1). They were commonly grown in Iran during this period and covered up to 90 % of the total area of cultivation.

Sites of experiments

Experiments were performed at Karaj and Parsabad-Moghan, representing contrasting environmental conditions. Karaj is situated in the north-central part of Iran (35°49′N, 51°0′E and 1,312 m asl) 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 north-west Iran (39°36′N, 47°57′E and 45 m asl) has a warm Mediterranean climate, with cold winters, humid spring and summers with average annual precipitation of 271 mm.

Monthly metrological data for the duration of the experiments are presented in Table 6.

Table 1 Wheat cultivars used in the Karaj and Parsabad-Moghan experiments

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

[a] According to plant height in the Karaj experiment and under well-watered conditions, plant heights were classified in three groups: <80 cm = dwarf; 80–100 cm = semi-dwarf; >100 cm = tall

Agronomic trials

Karaj experiments

Trials were conducted over crop seasons 2007–2008 and 2008–2009. In each season, two experiments were conducted simultaneously under well-watered (WW) and terminal drought stress (DS) conditions at the agriculture research farm of Tehran University. The 81 cultivars were sown on Nov 1–3, 2007 and on Nov 10–11, 2008. Seeding rates was adjusted by cultivar according to 1,000 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 4 m long with 0.2 m spacing.

Fertilizer applied was 200 kg ha^{-1} of diammonium phosphate ($(NH_4)_2HPO_4$) and 100 kg ha^{-1} of urea ($CO (NH_2)_2$) 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 2007–2008 and 2008–2009 seasons, WW and DS plants were irrigated five times from sowing to heading (when 50 % of the plots had reached heading (Zadoks GS 55)). From this point, DS plants were no longer irrigated whereas WW plots were irrigated a further three times in 2007–2008 and four times in 2008–2009 until maturity (Zadoks GS 94). Approximately, 55 mm of irrigation water was applied each time.

Parsabad-Moghan experiment

This field experiment was carried out under WW conditions at the agriculture research farm of Moghan College of Agriculture and Natural Resources, University of Mohaghegh Ardabili, during the 2010–2011 season. The 81 cultivars were sown (300 seeds m^{-2}) on Nov 17–19, 2010. The experimental design, plot direction, row number and spacing, and fertilizer applications were as described above. The rows were 2 m long. Recommended practices were used for control of weeds and fungal diseases. The plants were irrigated five times from sowing to maturity. Approximately, 55 mm of water were applied at each irrigation. High relative humidity and low total evaporation during the growing season (Table 6) could explain why water input for the WW plants at Parsabad-Moghan were less than that of WW experiments at Karaj.

Phenological events

The dates of booting, heading, anthesis, and physiological maturity were recorded. To achieve this, the plots were monitored every 2 days. Booting date was recorded when about half of the main shoots showed emerged awns 1 cm beyond the flag leaf sheath (GS 45). Heading date was recorded when about half of the main shoots showed emerged spikes (GS 55), and anthesis was recorded when about half of the main shoot spikes had visible anthers (GS 65). Dates of physiological maturity were recorded when peduncles on about half of the plants in plots were completely yellow. GFP was recorded as the period from anthesis to physiological maturity. As temperatures varied between years, and with the objective of including temperature effects on the lengths of growth phases (Isidro et al. 2011), all developmental stages were expressed in the form of thermal time (TT), calculated as $\sum [(T_{max} + T_{min}/2) - T_b]$, in which T_{max} and T_{min} are site daily maximum and minimum temperatures, and T_b is the base temperature (5 °Cd).

Agronomic traits

At maturity, 1 m^2 per plot sections were cut at ground level and weighed (AGDM). Spike dry weight was determined on 3 randomly selected spikes and the average obtained. Grain yield per m^{-2} was obtained after threshing. Harvest index (HI) was calculated by dividing grain yield m^{-2} by AGDM m^{-2} × 100. Thousand grain weight was determined for each plot. The number of grains m^{-2} was calculated by dividing grain yield by 1,000 grain weight (Aggarwal et al. 1990).

Statistics

For individual experiments, analyses of variance (ANOVA) were carried out using SAS statistical software (SAS Institute 1994). In the Karaj experiments, data from WW and DS conditions were analyzed separately in each growing season 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) and their means were used. Data from the Moghan experiment were analyzed according to a lattice design and adjusted means were considered.

Measured parameters were regressed against year of cultivar release to obtain genetic gain and to study changes in different plant characteristic over time using linear equations that were fitted to the data. Among tested cultivars, the years of release for 11 cultivars were unknown; they were not, therefore, considered in regression analysis. Relationships between traits were studied by correlation analysis. Regression and correlation analyses were performed using SPSS statistical software Version 17.0 (SPSS Inc. 1998).

Results

Karaj experiment

Large variations were found among cultivars for grain yield under WW conditions; grain yields ranged from 2,720 to 10,320 kg ha^{-1} (Table 2). Overall, new wheat cultivars produced more grain yield than old ones. Linear regression analysis of grain yield against year of release indicated that annual gains in grain yield were 31 kg ha^{-1} y^{-1} (Fig. 1a).

Grain yields differed significantly under DS conditions (Table 2). In most cases, the most productive cultivars were modern and intermediate cultivars. Old cultivars were lower yielding. There was a linear increase in grain yield with breeding of 31 kg ha^{-1} y^{-1} (Fig. 1a).

DS decreased the grain yields of tested cultivars (Table 2). Averaged among cultivars, grain yields decreased from 7,510 under WW to 3,720 kg ha^{-1} under DS. Depending on cultivars, the amount of grain yield loss ranged from 8 to 78 % (data not shown), showing different responses of wheat cultivars to imposed terminal drought. When the grain yield reductions were compared between modern and old

cultivars, it was found that performance and/or tolerance of the modern cultivars had been improved by breeding under stress conditions (Fig. 2).

AGDM ranged from 11,220 to 25,570 kg ha^{-1} under WW conditions. There was no significant association between AGDM and year of cultivar release (Fig. 1b). Under WW conditions, AGDM was positively correlated with grain yield (Table 3).

Imposed terminal drought stress decreased the AGDM of wheat plants. On average, AGDM decreased from 20,170 under WW to 15,760 kg ha^{-1} under DS. Under terminal drought conditions, there were no significant differences in AGDM between old and new cultivars and no association was observed with year of release (Fig. 1b).

HI ranged from 23 to 49 % under WW conditions; it increased at a rate of 0.17 % per year from 1930 (Fig. 1c). In response to DS, HI decreased across all plant materials. Under terminal drought, this trait increased at a rate of 0.20 % per year from older to modern cultivars (Fig. 1c).

Numbers of grains per square meter increased linearly with year of release in both WW and DS conditions (Fig. 1d). The same trend was observed for spike dry weight at maturity (Fig. 1e).

Average 1.000 grain weights were 47.2 and 35.1 g under WW and DS conditions, respectively. There was no significant difference in 1,000 grain weight between older and new cultivars (Fig. 1f).

Cultivars differed markedly in booting date; thermal time varied from 1,111 to 1,439 °Cd (Table 4). When duration of sowing–booting was related to the year of release, thermal time decreased by 1.3 °Cd y^{-1} (Fig. 3a). Cycle length from sowing to anthesis showed similar trends, being longer in older cultivars (Fig. 3b).

Table 2 Basic statistics [minimum and maximum value, mean, standard deviation (SD) and coefficient of variance (CV)] for agronomic traits of 81 wheat cultivars grown under well watered (WW) and drought stress (DS) conditions at Karaj station during the 2007–2008 and 2008–2009 growing seasons

|	Grain yield (kg ha^{-1})		Above-ground dry matter (kg ha^{-1})		Harvest index (%)		Grain number per square meter		Spike dry weight (g)		1000–grain weight (g)	
	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS
Minimum	2,720	1,120	11,220	11,040	23	8	7,074	3,993	1.67	1.41	36.5	19.5
Maximum	10,320	6,560	25,570	19,940	49	37	25,674	18,399	4.55	3.91	60.1	48.8
Mean	7,510	3,720	20,170	15,760	38	24	16,055	10,722	2.70	2.01	47.2	35.1
SD	1,390	1,060	2,800	1,420	5.3	6.4	3,352	3,065	0.48	0.40	5.4	6.4
CV	19	28	14	9	14	27	21	29	18	20	11	18
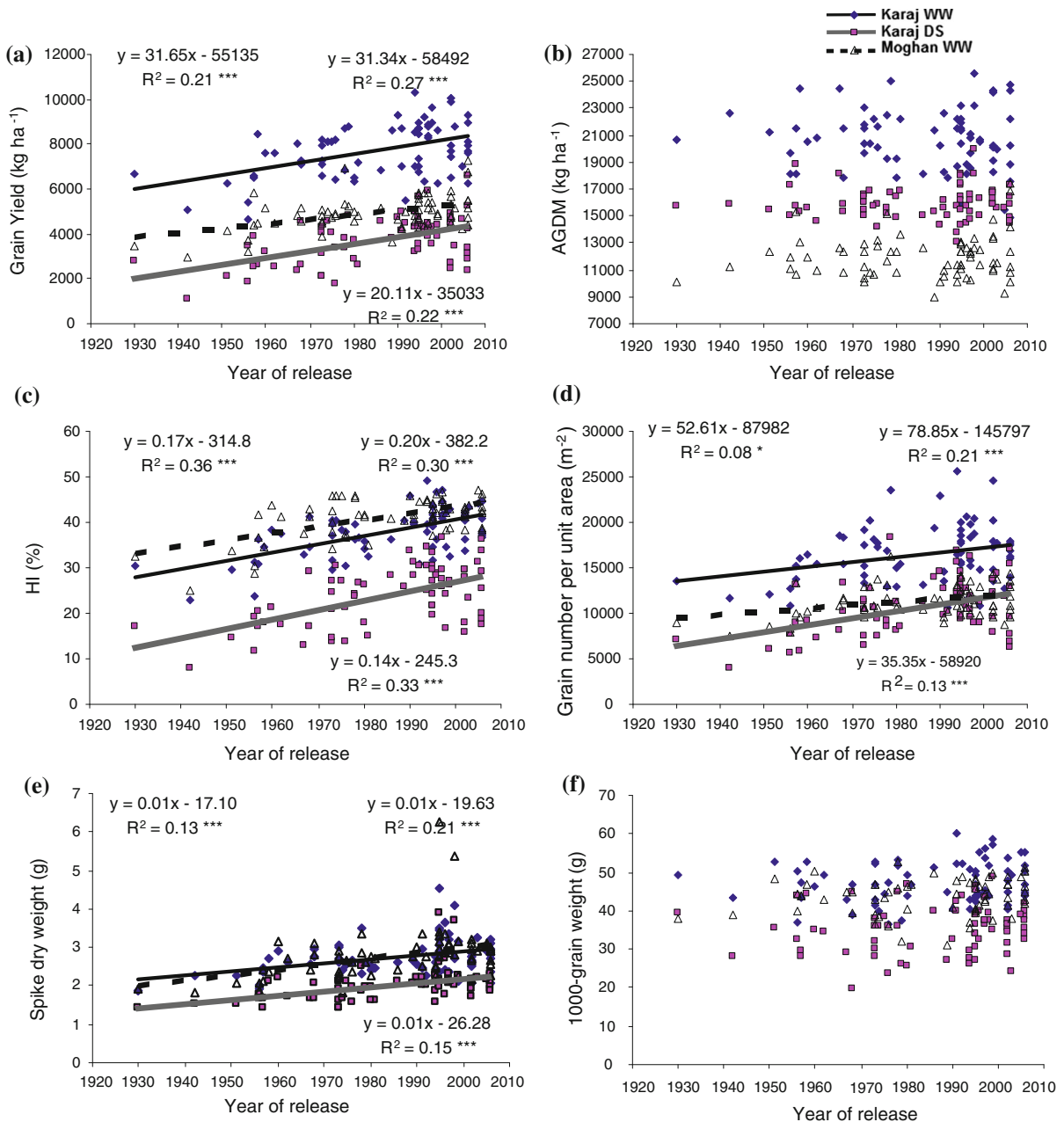
Fig. 1 Relationships between year of cultivar release and **a** grain yield, **b** AGDM, **c** HI, **d** grain number per unit area, **e** spike dry weight, and **f** 1,000 grain weight in Iranian wheat cultivars released from 1930 to 2006. Each lozenge (Karaj–WW) and square (Karaj–DS) point represents 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

The earliest and the latest cultivars accumulated 2,222 and 2,397 °Cd from sowing until maturity, respectively. Drought stress imposed at anthesis caused earlier maturity (Table 4). Averaged among

cultivars, thermal time from sowing to maturity was decreased from 2,285 °Cd in WW to 2,105 °Cd in DS conditions. Under WW conditions, the duration of the sowing—maturity phase was shortened significantly
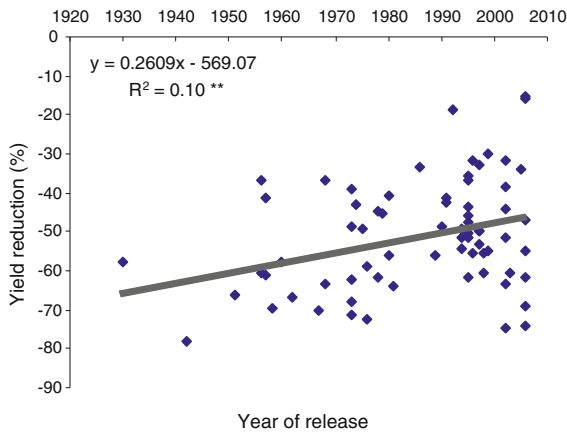
Fig. 2 Relationship between year of cultivar release and grain yield reduction in Iranian wheat cultivars released from 1930 to 2006 and cultivated in the Karaj experiment under well watered (WW) and drought stress (DS) conditions. Grain yield reduction was calculated as [(WW grain yield–DS grain yield/WW grain yield)] × 100. Each point represents the mean value of one cultivar across 2007–2008 and 2008–2009

in modern compared to old cultivars. However, this trend was not observed under DS conditions (Fig. 3d).

The GFP, the anthesis—maturity phase, on average accounted for 39 and 34 % of the duration from sowing to maturity under WW and DS conditions, respectively (Table 4). GFP ranged from 744 to 997 °Cd in WW conditions and from 616 to 872 °Cd under DS. Under both regimes, there were significant differences between old and modern cultivars in GFP phase which was longer in the modern than old cultivars (Fig. 3e).

Moghan experiment

Grain yield ranged from 2,930 to 7,460 kg ha^{-1} (Table 5). Linear regression analysis showed that the annual gain in grain yield was 20 kg ha^{-1} y^{-1} (Fig. 1a).

The lowest and the highest values of AGDM were 8,560 and 17,360 kg ha^{-1}, respectively (Table 5). There was no significant association between AGDM and year of cultivar release (Fig. 1b). HI varied from 25 to 47 % and was higher in modern and intermediate cultivars compared to old cultivars. HI improvement was 0.14 % per year (Fig. 1c).

Grain number per square meter and spike dry weight were affected by breeding, as they increased at a rate of 35 grains m^{-2} y^{-1} and 0.01 g spike dry weight y^{-1}, respectively (Fig. 1d, e). As for the Karaj experiments, no significant differences in 1,000 grain weight were detected between old and modern cultivars (Fig. 1f).

Large variations were found among tested cultivars with respect to thermal time from sowing to booting. The difference between the highest and the lowest GDD was 199 °Cd, 39 % less than that observed at Karaj under WW conditions (Tables 4, 5). The length of the sowing—anthesis period ranged from 1,287 to 1,584 °Cd. Mean anthesis TT was 1392 °Cd (Table 5). Thermal time from sowing to anthesis decreased from old to modern cultivars (Fig. 3b). The earliest and the latest cultivars accumulated 2,076 and 2,265 °Cd from sowing to maturity, respectively. Overall, wheat plants tested at Moghan completed their life cycles earlier than those tested at Karaj under WW conditions (Fig. 3d). The length of GFP in the Moghan experiment was 16 % less than at Karaj under WW conditions (Tables 4, 5). Unlike Karaj under WW and DS conditions, no significant differences in duration of GFP between old and modern cultivars were found at Moghan (Fig. 3e).

Discussion

Progress in wheat grain yield was achieved by breeding. Genetic improvement can be obtained in a

Table 3 Correlation coefficients among grain yield, AGDM and harvest index (HI) of 81 wheat cultivars grown at Karaj during 2007–2008 and 2008–2009 under WW and DS conditions, and at Parsabad-Moghan station during 2010–2011 under WW conditions

ns Non significant

** Significant at $P = 0.01$

			Grain yield	AGDM	HI
Karaj experiments	WW	Grain yield	1		
		AGDM	0.66**	1	
		HI	0.61**	−0.14^{ns}	1
	DS	Grain yield	1		
		AGDM	0.31**	1	
		HI	0.91**	−0.06^{ns}	1
Parsabad-Moghan Experiment	WW	Grain yield	1		
		AGDM	0.79**	1	
		HI	0.46**	−0.15^{ns}	1

Table 4 Basic statistics [minimum and maximum value, mean, standard deviation (SD) and coefficient of variation (CV)] for phenologic traits of 81 wheat cultivars grown under well watered (WW) and drought stress (DS) conditions at Karaj station during 2007–2008 and 2008–2009 growing seasons. Phenologic traits were measured based on thermal time (°Cd)

	Booting	Anthesis	Booting–anthesis	Physiologic maturity		Grain filling period	
	WW	WW	WW	WW	DS	WW	DS
Minimum	1,111	1,254	109	2,222	1,967	744	616
Maximum	1,439	1,631	243	2,397	2,269	997	872
Mean	1,214	1,392	178	2,285	2,105	893	718
SD	56	67	25	32	53	50	48
CV	5	5	14	1	3	6	7

target environment either directly by selection for a primary trait (such as grain yield) or indirectly by selection of a secondary trait that is putatively related to higher yield potential (Araus et al. 2008). Researchers suggest that complementation of the first method with the second may be required to further improve grain yield (Araus et al. 2008). The traits that are important in grain yield can be assessed in different ways. One approach involves retrospective studies, comparing genotypes released in different eras as a result of previous breeding programs (Araus et al. 2002). Comparisons of cultivars bred in different periods can throw light on evolutionary trends in different characteristics of wheat grown in a given region, and provide the most direct estimate of breeding progress (De Vita et al. 2007).

The Karaj experiments showed that the average genetic gain in grain yield was 31 kg ha^{-1} y^{-1} both in WW and DS conditions. In a study in which 16 bread wheat cultivars were examined in the Mediterranean region of Turkey, Sener et al. (2009) reported that national bread wheat yields increased by an average of 20.8 kg ha^{-1} y^{-1} from 1925 to 2006. Much higher rates of yield increase due to genetic improvement were reported in the UK (Shearman et al. 2005). Lower yield improvement in Mediterranean regions was attributed to a low ability to improve yields through either genetic or management improvement, and different approaches such as source and sink manipulation may be necessary for the further improvement in wheat yields (Sener et al. 2009, and references therein).

Iranian wheat cultivars grown in the Moghan experiment showed an improvement of 20 kg ha^{-1} y^{-1} in grain yield, 11 kg less than that observed in Karaj experiments. These results are comparable to the results of Sanchez-Garcia et al. (2013) who worked on a set of 28 Spanish bread wheat genotypes at four sites with different climatic conditions, and reported that genetic gains in yield ranged from 7.7 to 66.5 kg ha^{-1} y^{-1} depending on the conditions under which the cultivars were tested. It suggests a very high dependence of the estimated genetic gains on environmental conditions.

Wheat cultivars responded differently to the imposed DS under Karaj conditions. Overall, modern cultivars produced more grain yield than old cultivars under DS conditions. Moreover, the yield reduction in modern cultivars was less than old cultivars (Fig. 2). These results suggest that in line with yield improvement, breeding has increased resistance of Iranian wheat cultivars to terminal drought stress. However, it should be noted that these findings do not imply that modern Iranian wheat cultivars show superiority in any given drought treatment, because the frequency, timing, duration and severity of drought stress are variable. In this respect, Ceccarelli et al. (1998) stated that the carryover effect of high yield potential takes place only up to a given level of stress and disappears under severe stress.

Changes in grain yield may be interpreted at one level as due to changes in biomass or to changes in partition of dry matter between straw and grain (Perry and D'Antuono 1989). Our experiments showed that there was no significant correlation between AGDM and year of release. These results are consistent with other studies on bread wheat (Calderini et al. 1995) and durum (De Vita et al. 2007). They are not, however, consistent with the results of Miri (2009) who worked on 15 Iranian bread wheat cultivars in Arsanjan, Fars Province, in southern Iran (29°55′N, 53°19′E, 1,810 m asl) where the winters are cold and summers are hot and dry. He reported an improvement of AGDM with year of cultivar release. A lack of consistent increases in AGDM through breeding does not imply that this character is not related to past yield
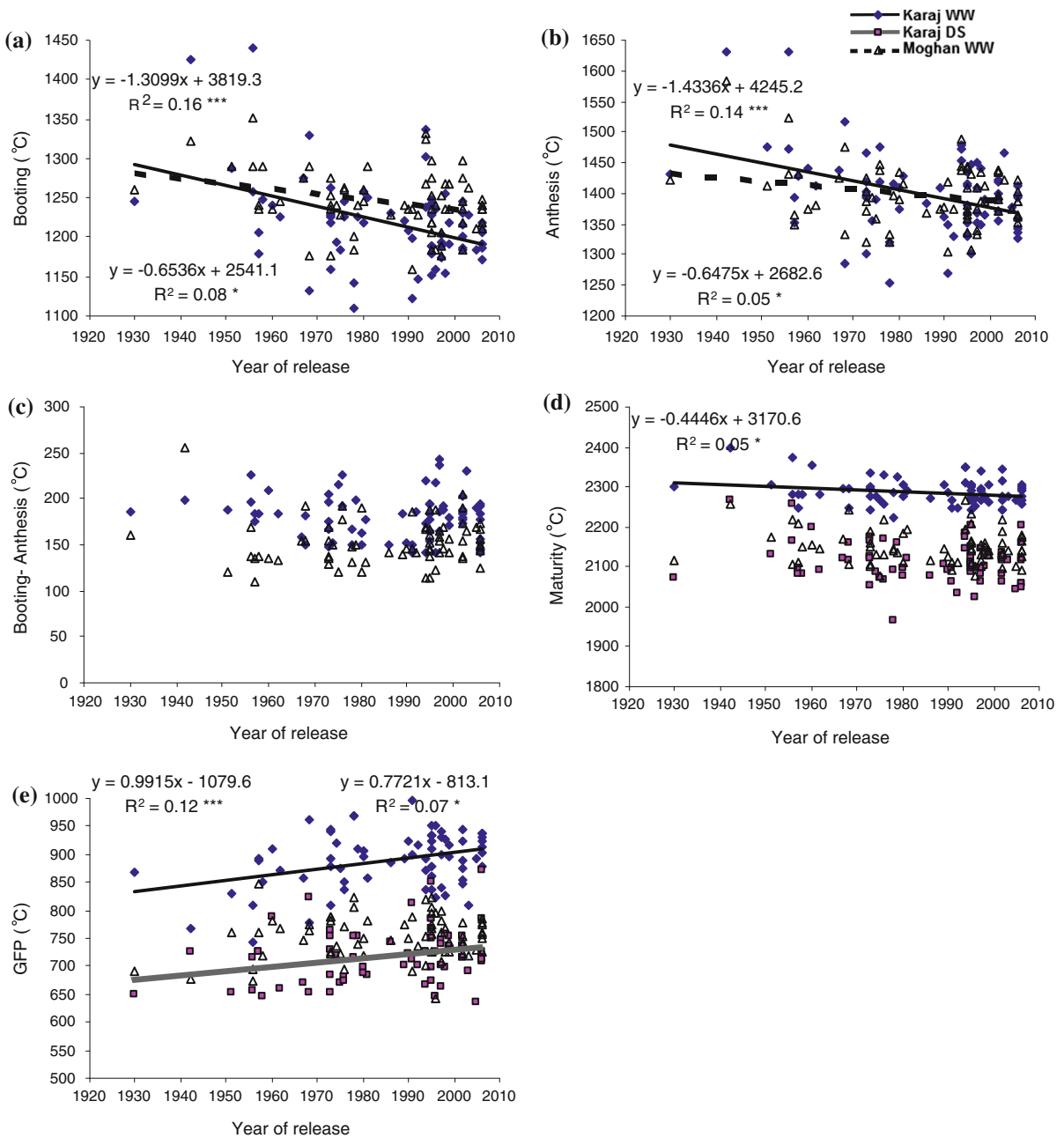
Fig. 3 Relationships between year of cultivar release and thermal time (°C) from sowing to **a** booting, **b** anthesis, **c** booting—anthesis, **d** physiological maturity, **e** grain filling period (GFP) in Iranian wheat cultivars released from 1930 to 2006. Each lozenge (Karaj–WW) and square (Karaj–DS) point represents the mean value of one cultivar across 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 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

increases, because there is a positive and significant correlation between AGDM and grain yield in all conditions tested (Table 3). It was reported that modern wheat cultivars show higher radiation use efficiency

(RUE) after anthesis than their predecessors because of increased demand for a larger sink in modern cultivars (Araus et al. 2008). Improved RUE indicates increases in photosynthetic tissues per unit leaf area and, therefore,

Table 5 Basic statistics [minimum and maximum value, mean, standard deviation (SD) and coefficient of variation (CV)] for measured agronomic traits and phenological events of 81 wheat cultivars grown under well watered condition at Parsabad-Moghan station during 2010–2011 growing season. Phenological events were measured based on thermal time (°Cd)

	Grain Yield (kg ha⁻¹)	Above-ground dry matter (kg ha⁻¹)	Harvest index (%)	Grain number per square meter	Spike dry weight (g)	1000-grain weight (g)	Booting	Anthesis	Booting–anthesis	Physiological maturity	Grain filling period
Minimum	2,930	8,560	25	7,575	1.57	31.1	1,152	1287	109	2,076	643
Maximum	7,460	17,360	47	16,596	6.25	52.9	1,351	1584	257	2,265	849
Mean	2,145	11,860	41	11,289	2.72	43.6	1,240	1392	153	2,145	752
SD	810	1,670	4	1,762	0.65	4.6	41	50	24	42	40
CV	17	14	10	16	24	11	3	4	16	2	5

increased AGDM. While maintaining its level during the entire life cycle, increased AGDM after anthesis in the modern wheat group could meet increased grain demand directly (via current production) or indirectly (via remobilization of stored carbohydrates) (Joudi et al. 2012).

A steady increase in HI occurred during progression from old to modern cultivars. Progress in HI was most apparent in the Karaj experiments (Fig. 1c). The highest amount of HI observed in new wheat cultivars (Fig. 1c) suggest that HI could be improved further in Iranian wheat cultivars, if an upper limit of 62 % for HI is accepted (cited in Shearman et al. 2005).

In many cases yield variation and yield progress is associated with changes in grain number (Fischer 2011). The results of our experiments showed that the number of grains per square meter increased linearly from old to modern cultivars (Fig. 1d). Similar results were reported by others (Royo et al. 2007). Shearman et al. (2005) reported that genetic gains in number of grains per square meter were associated with changes over time in both number of spikes per square meter and number of grains per spike. Fischer (2011) stated that there is a close link between grain number and dry weight accumulation in spikes (g m⁻²) at flowering. Abbate et al. (1995) claimed that grain number (m²) was more closely related to spike nitrogen content (g m⁻²) than to spike dry weight (g m⁻²). Regardless of the reasons for increased grain number per square meter, improvement in this character during past decades suggests that the total amount of available assimilates was sufficient to support the development of higher numbers of grains per m⁻² in modern cultivars (De Vita et al. 2007).

Overall, spike dry weight at maturity was higher in modern wheat cultivars. The improvement of spike dry weight was attributed to increased spike size as well as higher grain number per spike. Araus et al. (2008) reported that reduced plant height in modern wheat cultivars enhanced partitioning towards the growing spikes, which in turn results in an increased spike dry matter associated with more grains per unit land area.

Our studies showed that 1,000 grain weight remained unchanged during the past decades and that the rise in grain yield was not due to increased 1,000 grain weight. These findings are in line with the results of other researchers (Sadras 2007; Sanchez-Garcia et al. 2013). Lack of significant changes in 1,000 grain weight in modern wheat cultivars along with increased grain number per square meter (see above) suggests that grain yields of the cultivars used under the

conditions imposed are controlled more by sink than by source strength (Ahmadi et al. 2009).

Phenologic traits are of critical importance as they may not only confer adaptability to particular environments but also influence yield improvement through increasing yield potential (Borras et al. 2009). Iranian wheat cultivars are grown under conditions in which moisture and temperature are most often favorable for vegetative growth during autumn and early spring. However, grain filling often occurs when temperatures are increasing and moisture supply is decreasing. The common end–results of these stresses are grain shriveling, reduced test weight and loss in yield (Blum 1998). Early flowering in Mediterranean regions could be an important trait to escape water stress and thus to improve water use efficiency (Slafer et al. 2005). The Karaj experiments showed that the time of booting and anthesis had decreased significantly in modern wheat cultivars (Fig. 3a, b). This was paralleled by a significant rise in the grain filling period since the total lengths of life cycles were only marginally reduced (Fig. 3d, e). De Vita et al. (2007) worked on durum wheat cultivars with similar results to those of our Karaj experiments. The trends in phenologic events observed at Karaj were not evident at Moghan. Sener et al. (2009) worked on bread wheat cultivars in Mediterranean regions and reported that there were no significant differences between modern and old genotypes in respect to the period from the heading to physiologic maturity. All of these results suggest that there are interactions between environments and phenological events in the wheat plants. Therefore, in countries with high environmental variation experimental research needs to be carried out over multiple environments in order to have a better understanding of genetic changes in phenologic traits of plants caused by breeding during past decades.

The duration of booting—anthesis was not affected by year of cultivar release under the conditions tested (Fig. 3c). These findings are not consistent with the results of Isidro et al. (2011) who stated that the duration of the booting to anthesis period in Spanish and Italian durum wheat cultivars would increase with breeding. These results suggest that different strategies were used by breeders to achieve higher grain yields in wheat.

Conclusions

Improved knowledge about the causes of increased grain yield in plants can be used to predict strategies for further progress. Comparisons of old and modern wheat cultivars increase information on evolutionary trends in morphologic, phenologic, physiologic, and agronomic characteristics of wheat grown in a given region.

Our studies in two regions of Iran clearly showed that genetic gains in different traits varied with environment. For example, improvements in grain yield in modern cultivars were estimated at 31 and 20 kg ha^{-1} y^{-1} in Karaj and Moghan, respectively. While a significant increase in GFP was observed in the Karaj experiments, this trend was not found in the Moghan experiment. These findings indicate that there are interactions between genetic gains in different traits and the environment in which trait improvements are studied. Therefore, when similar experiments are performed by researchers, special attention should be paid to the environmental conditions. This interaction might explain in part why the changes in plant characteristics are not consistent and vary with environment (see Introduction).

The current work showed that the amount of yield loss in modern wheat varieties cultivated under conditions of terminal drought stress was less than in old cultivars, indicating that in line with grain yield, breeding has increased resistance to terminal drought stress in Iranian wheat cultivars. Most wheat cultivation areas across Iran are arid or semiarid, and are subject to drought and heat stresses during grain filling, resulting in severe grain yield reductions. Future climate scenarios predict further reductions in winter rainfall and an increase in temperature and atmospheric CO_2 (Ludwig and Asseng 2010). As for the impact of climate changes on water resources in Iran, it has been predicted that, in general, current wet regions of the country will receive more rainfall while dry regions will receive less (Abbaspour et al. 2009). Therefore, a shortage of water will be the most important yield-limiting factor for Iranian farmers, suggesting that breeding for drought adaptation mechanisms needs to increase in order to address future environmental change.

Appendix

See Table 6.

Table 6 Climatic data for the wheat growing seasons 2007–2008 and 2008–2009 at Karaj and for 2010–2011 at the Parsabad-Moghan research station

	Maximum air temperature (°C)			Minimum air temperature (°C)			Maximum relative humidity (%)			Minimum relative humidity (%)		
	Karaj 2007–2008	Karaj 2008–2009	Moghan 2010–2011	Karaj 2007–2008	Karaj 2008–2009	Moghan 2010–2011	Karaj 2007–2008	Karaj 2008–2009	Moghan 2010–2011	Karaj 2007–2008	Karaj 2008–2009	Moghan 2010–2011
November	17.5	13.6	17.4	5.7	4.2	7.2	68	87	93	27	16	61
December	8.1	9.2	16.2	−0.8	−1.0	5.4	84	81	92	44	44	59
January	−1.5	7	9.6	−10	−1.6	0.4	92	82	90	61	44	58
February	6	11.6	9.6	−3.1	2.5	0.1	84	81	88	49	43	51
March	21.7	17.5	9.6	7.7	5.2	1.8	56	64	94	19	39	60
April	24.3	17.7	17.8	11	5.9	6.2	59	79	92	18	23	50
May	27.8	26.7	22.1	13.1	13.3	12	60	68	95	18	34	65
June	33.7	31.9	29.6	15.5	16	18	66	66	93	17	24	54
July	36.2	36.7	34.1	19.4	19.9	20.9	61	58	86	27	18	41

	Rainfall (mm)			Snow (cm)			Total evaporation (mm)		
	Karaj 2007–2008	Karaj 2008–2009	Moghan 2010–2011	Karaj 2007–2008	Karaj 2008–2009	Moghan 2010–2011	Karaj 2007–2008	Karaj 2008–2009	Moghan 2010–2011
November	33.2	42.4	8.6	–	–	–	117.8	58.7	33.8
December	69.8	12.7	2.1	–	–	–	–	–	–
January	60.2	18.1	22.8	415	11.0	–	–	–	–
February	16	43.0	20.5	79	0.0	–	–	–	–
March	3.2	20.5	32.8	–	–	–	–	–	–
April	4.1	58.7	11.8	–	–	–	168.5	97.8	95.6
May	5.2	18.4	32.5	–	–	–	217	206.0	111.2
June	0.2	5.3	64.3	–	–	–	302	288.1	177.9
July	0.1	0.0	0.2	–	–	–	351	391.3	261.3

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