The Physiological Basis of the Genetic Progress in Yield Potential of CIMMYT Spring Wheat Cultivars from 1966 to 2009

K. A. B. Aisawi, M. P. Reynolds, R. P. Singh, and M. J. Foulkes*

ABSTRACT

Our objective was to investigate the physiological basis of genetic progress in grain yield in CIMMYT spring wheat (*Triticum aestivum* L.) cultivars developed from 1966 to 2009 in irrigated, high-potential conditions. Field experiments were conducted during three growing seasons in northwest Mexico (2008–2009, 2009–2010, and 2010–2011) examining 12 historic CIMMYT semidwarf spring wheat cultivars released from 1966 to 2009. The linear rate of genetic gain in grain yield was 30 kg ha^{-1} yr^{-1} (0.59% yr^{-1}; $R^2 = 0.58$, $P = 0.01$). Grain yield progress was associated with increased aboveground dry matter (AGDM) at harvest ($R^2 = 0.80$, $P < 0.001$) and heavier grain weight ($R^2 = 0.46$, $P < 0.05$). There was a positive linear association between AGDM and plant height ($R^2 = 0.43$, $P < 0.05$) and between grain weight and the date of complete canopy senescence (CCS) among the 12 cultivars ($R^2 = 0.36$, $P < 0.05$). There was no change in grains per square meter or harvest index (HI) with year of release (YoR). Grain weight was positively associated with potential grain weight (PGW), and PGW, in turn, was positively associated with rachis length per spikelet among the cultivars. Overall spike dry matter (DM) per square meter at anthesis (GS61) +7 d did not change with YoR. There was a trend for a linear increase in AGDM of fertile shoots (expressed as g m^{-2}) at GS61 +7 d with YoR, but this was counteracted by spike partitioning decreasing overall during the 43-yr period from 0.25 to 0.23. There was a linear increase in preanthesis flag-leaf stomatal conductance with YoR ($P < 0.05$). There was no change in grain growth response to a degraining treatment imposed at GS61 +14 d (mean grain weight response +5.5%) indicating that the degree of source limitation to grain growth appeared to be small and unchanged in the older and modern cultivars. Generally, these results indicated that the rate of genetic progress in CIMMYT spring wheat has slowed but has not plateaued in recent decades, while genetic gains were associated with increase in both potential and final grain weight.

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Abbreviations: AGDM, aboveground dry matter; CCS, complete canopy senescence; CGR, crop growth rate; CTD, canopy temperature depression; DM, dry matter; FE, fruiting efficiency; GN, grain number per square meter; GPS, grains per spike; GS, growth stage; HI, harvest index; PGW, potential grain weight; RUE, radiation-use efficiency; SPI, spike-partitioning index; TGW, 1000-grain weight; WSC, water-soluble carbohydrate; YoR, year of release.

Several studies have examined grain yield progress in sets of historic CIMMYT spring wheat cultivars and advanced lines. Waddington et al. (1986) observed genetic progress for 17 cultivars of 59 kg ha^{-1} yr^{-1} (1.1% yr^{-1}) from 1950 to 1982 in northwest Mexico. Sayre et al. (1997) reported progress of grain yield in northwest Mexico for eight CIMMYT cultivars from 1962 to 1988 of 67 kg ha^{-1} yr^{-1} (0.88% yr^{-1}). Manes et al. (2012) examined genetic progress globally in the CIMMYT semiarid wheat yield trials over a 17-yr period (1994 to 2010) and found grain yield as a percentage of the check cultivar Dharwar Dry increased at a rate of 31 kg ha^{-1} yr^{-1} (~1% yr^{-1}). The genetic grain yield progress of 26 spring wheat advanced lines released by CIMMYT from 1977 to 2008 was evaluated by Lopes et al. (2012); grain yield progress was linear and ~35 kg ha^{-1} yr^{-1} (0.7% yr^{-1}). Generally, these

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investigations indicated that the rate of genetic progress in CIMMYT spring wheat has slowed but has not plateaued in recent decades. There are also several other studies worldwide that do show recent genetic gains for wheat yield potential, for example, Zhou et al. (2007), Zheng et al. (2011) and Xiao et al. (2012) in China; Peltonen-Sainio et al. (2009) in Finland; Shearman et al. (2005), Mackay et al. (2011), and Clarke et al. (2012) in the United Kingdom; Sanchez-Garcia et al. (2013) in Spain; and Sadras and Lawson (2011) in Australia. However, there are also some cases in which the genetic progress appears to be showing a plateau, for example, winter wheat in the great plains of North America between 1984 and 2008 (Graybosch and Peterson, 2010) and spring wheat in Chile between 1990 and 2000 (Matus et al., 2012) and in Brazil between 1999 and 2009 (Beche et al., 2014). In addition, Brisson et al. (2010) found genetic progress in yield potential in France had been counteracted from 1990 onward by climate change (particularly by heat stress).

Knowledge of the changes in physiological traits associated with genetic gains in yield potential is essential to improve understanding of yield-limiting factors and to inform future breeding strategies. Studies of the physiological basis of genetic gains in grain yield in sets of historic wheat cultivars worldwide have generally shown number of grains per square meter (usually because of number of grains per spike) and HI to be positively associated with grain yield progress (e.g., Waddington et al., 1986; Sayre et al., 1997; Austin et al., 1989; Slafer et al., 1990; Brancourt-Hulmel et al., 2003). Fischer et al. (1998) reported higher stomatal conductance preanthesis for spring wheats released from 1962 to 1988 in northwest Mexico under fully irrigated conditions and found a positive association between grain yield and grains per square meter and, in one year out of the three, a positive association between crop growth rate (CGR) and radiation-use efficiency (RUE) in the 3-wk period before flowering. Greater light-saturated photosynthetic rate was found in the more recent cultivars. Shearman et al. (2005) found genetic progress in grain yield of UK winter wheat from 1972 to 1995 was from about 1980 onward based mainly on improvement in harvest biomass associated with a higher RUE in the stem-elongation period, driving increases in grains per square meter and stem soluble carbohydrate reserves. Changes in the flag leaf with breeding progress at CIMMYT (e.g., smaller, more erect flag leaves, higher N per unit area) (Fischer et al., 1998) were similar to those reported for winter wheat progress in the United Kingdom (e.g., smaller, more erect flag leaves, higher DM per unit area) (Shearman et al., 2005). Xiao et al. (2012) reported genetic gain in grain yield of winter wheat released from 1962 to 2006 in Shandong Province, China, was 62 kg ha^{-1} yr^{-1}, largely associated with increased grains per square meter and biomass together with increased HI and reduced plant height. Significant genetic changes were also observed for leaf area index (total leaf area per ground area), flag-leaf chlorophyll content, and stem water-soluble carbohydrate (WSC) content at anthesis and flag-leaf photosynthesis rate during grain filling. Similar to the findings of Shearman et al. (2005), increases in grains per square meter and biomass were apparently achieved through improving crop photosynthesis at and after heading, and increased stem WSC in stems at anthesis. Beche et al. (2014) reported genetic gains in grain yield of 29.9 kg ha^{-1} yr^{-1} in spring wheat in Brazil from 1940 to 2009 were associated with gains in HI, biomass, and grains per square meter; and that pre- and postanthesis stomatal conductance and leaf photosynthesis rate and postanthesis leaf chlorophyll content were positively associated with grain yield. In addition, grain-yield progress of CIMMYT advanced lines released from 1977 to 2008 was associated with fewer days to heading, cooler canopy temperature at grain filling, increased stay green, and higher grain weight (Lopes et al., 2012).

Grain yield under optimal conditions appears to be mainly limited by grain number per square meter. In the studies cited above, grain weight was almost always reported not to increase with YoR. A physiological model for analyzing grain number per square meter (GN) was proposed by Fischer (1983):

$$\mathrm{SDW_a} = D_\mathrm{s} \times \mathrm{CGR} \times F_\mathrm{s} \qquad [1]$$

where SDW$_a$ is the dry weight of spikes at anthesis (per unit area basis), D_s is the duration of spike growth, and CGR and F_s are, respectively, the rate of aboveground dry accumulation and the fraction of this DM growth partitioned to the spike averaged over the spike-growth period.

In the model of Fischer (1983) also:

$$\mathrm{GN} = \mathrm{SDW_a} \times \mathrm{FE} \qquad [2]$$

where FE is the fruiting efficiency, defined as the number of grains per unit spike DW at anthesis.

This model will be referred to in the present analysis of the physiological basis of GN among a set of historic CIMMYT semidwarf cultivars introduced from 1966 to 2009. Moreover, the importance of increasing the total grain sink size, not only by increasing grains per square meter but also the PGW, will be considered. In this respect, a degraining treatment (removal of 50% of the spikelets) was imposed at 14 d postanthesis (GS61) to study source–sink relationships in the 12 cultivars. Lopes et al. (2012) reported grain yield progress of CIMMYT advanced lines from 1977 to 2008 was associated with increased grain weight as mentioned above.

The present paper aims to (i) quantify changes in GN, grain weight, HI, and harvest AGDM associated with grain yield progress for a set of 12 representative CIMMYT spring wheat cultivars developed between 1966 and 2009 in the irrigated, high-potential environment of northwest Mexico and (ii) identify the physiological basis of these changes by examining phenology, DM production and partitioning, CGR, flag-leaf traits, and source–sink balance and PGW according to a degraining treatment imposed at GS61 +14 d.

MATERIALS AND METHODS

Experimental Site and Design

Experiments were conducted at the CIMMYT Norman E. Borlaug Experimental Station near Ciudad Obregon, northwest Mexico (20°27′ N, 54°109′ W; 38 m asl) in three seasons (2008–2009, 2009–2010, and 2010–2011; hereafter, referred to as the years 2009, 2010, and 2011, respectively). The site is in an intertropical region and the experiments were performed in high-potential conditions under optimum irrigation (Reynolds et al., 2007). The soil type is coarse sandy clay, mixed montmorillonitic typic calciorthid, low in organic matter (<1%) and slightly alkaline (pH 7.7) (Limon-Ortega et al., 2002). In each of the experiments, 12 cultivars released from 1966 to 2009 were examined (Table 1). The cultivars were selected because they were the most widely grown CIMMYT releases during the 43-yr period from 1966 to 2009. A randomized complete block design was implemented with four replications. Each plot consisted of two beds, each of which was 4-m long and 0.8-m wide with two rows 30 cm apart per bed (and two rows 50 cm apart between beds).

At growth stage (GS) 61 (onset of anthesis) +14 d (Tottman, 1987), 15 randomly selected fertile (those with a spike) shoots per plot were tagged and all the spikelets were removed from one side of the spike to determine the effect of degraining on grain weight at harvest in three replicates. Fifteen randomly selected control shoots were also tagged at this stage in the same three replicates.

Plot Management

The sowing dates were 18 Nov. 2008, 3 Dec. 2009, and 3 Dec. 2010. In each experiment, plots were irrigated using a gravity-based system with flood irrigations four to six times during the crop cycle at 3- to 4-wk intervals to supply adequate moisture to avoid water stress during the growing season. After sowing, four applications of irrigation were made in each of 2009 and 2010 and six applications in 2011. The fertilizer application regime was the same in all seasons. The first application of N (50 kg ha^{-1}) was applied as urea during land preparation followed by 40 kg ha^{-1} of P as triple-super P at sowing. The second application of N (50 kg ha^{-1}) as urea was added at the time of first irrigation. Herbicides were applied in each season during early tillering in December as Buctril (1300 mL ha^{-1}; Bayer Crop Science) for broad-leaf weeds and Axial (500 mL ha^{-1}; Syngenta) for narrow-leaf weeds. In each season, a fungicide application as Folicur (500 mL ha^{-1}; Bayer Crop Science) was applied four times from approximately onset of stem extension to early grain filling during January to March. Insecticides as Aflix (1 L ha^{-1}; Sandoz) and Lorsban (1400 mL ha^{-1}; Dow AgroSciences) were applied in each season at around early- to mid stem extension during January to February.

Table 1. Year of release, the presence of *Rht-B1b* and *Rht-D1b* semidwarfing genes, and the *1BL/1RS* translocation for 12 CIMMYT spring wheat cultivars released from 1966 to 2009.

Genotype	Year of release	*Rht* semidwarfing genes	Presence of *1BL/1RS* translocation
Siete Cerros	1966	*Rht-B1b*	No
Pavon	1976	*Rht-D1b*	No
Seri	1982	*Rht-B1b*	Yes
Bacanora	1988	*Rht-B1b*	Yes
Attila (PBW 343)	1990	*Rht-B1b*	Yes
Baviacora	1992	*Rht-B1b*	Mixed
Tarachi	2000	*Rht-B1b*	No
Tacupeto	2001	*Rht-B1b*	No
Roelfs	2007	*Rht-B1b*	No
Navojoa	2007	*Rht-B1b*	No
Becard	2009	*Rht-B1b*	No
Line 1[†]	2009	N/A[‡]	N/A

[†] Pedigree: Croc_1/Ae Squarrosa (205)//Borl95/3/Prl/Sara/Tsi/Vee$^{\#}$5/4/Fret2.

[‡] N/A, data not available.

Crop Measurements

Crop Growth Analysis

Dates of onset of stem extension (GS31; growth stage 31), flag-leaf emergence (GS39), anthesis (GS61) (Tottman, 1987), and CCS (when 50% of the shoots had no flag leaf or spike green area and less than 10% of the stem remained green) were recorded in each plot of three replicates in all years. In 2009 and 2010, growth of the aboveground plant material was analyzed at GS31 (in each plot of two replicates in 2009 and of three replicates in 2010) and at GS61 +7 d (in each plot of three replicates in 2009 and 2010). In each case, plant material was sampled in two 50-cm-length rows of the bed (0.4 m^2), situated at least 50 cm from the end of the plot. Genotypes were sampled on the actual calendar dates that they reached the specific stage, that is, genotypes were sampled on different dates. At GS31, plants were counted in the 0.5 × 0.8 m quadrat area before sampling.

At GS31 and GS61 +7 d, plants were cut off at ground level and the number of fertile and infertile shoots was counted. At GS31, infertile shoots were classified as those that either had no green area or for which the newest fully expanded leaf was completely senesced; the remaining shoots were classified as fertile. At GS61 +7 d, fertile shoots were classified as those with a spike; the remaining shoots were classified as infertile. The weight of the infertile shoots was recorded after drying for 48 h at 75°C. A subsample of 15 fertile shoots was taken by fresh weight and separated into (i) spikes, (ii) flag-leaf lamina, (iii) remaining lamina, and (iv) stem with attached leaf sheath, depending on the developmental stage. Dry matter of crop components (leaf lamina, stem and leaf sheath, etc.) was obtained by weighing components of the 15-shoot subsample after drying for 48 h at 75°C.

In 2009 and 2010, rachis length and spikelet number per spike were recorded on 12 randomly selected spikes per plot at GS61 +7 d in three replicates. Percentage WSC concentration in stems and attached leaf sheaths was estimated at GS61 +7 d and at maturity in 10 randomly selected fertile shoots per plot in three replicates, using the anthrone method of Yemm and Willis (1954) as described by Gay et al. (1998). In relation to the grain number model of Fischer (1983), the spike-growth period was presently estimated as onset of stem extension (GS31, Tottman, 1987) to anthesis (GS61) +7 d. The CGR was calculated as the accumulated AGDM from GS31 to GS61 +7 d divided by the number of calendar days for this period. The spike-partitioning index (SPI) was calculated as the ratio of the spike DM to the fertile-shoot DM at GS61 +7 d. The FE was calculated as the number of grains per unit spike dry weight at GS61 +7 d.

At harvest, the 15 tagged degrained shoots (i.e., 50% spikelets removed) and 15 tagged control shoots were sampled in each plot. The spikes were then threshed and their grains counted and weighed after drying for 48 h at 75°C. The dry weight of the stem and the attached leaf sheaths was also weighed after drying for 48 h at 75°C.

In each experiment, after maturity was reached, grain yield was measured by machine harvesting a plot area of 4.8 m^2 in each plot in four replicates and values adjusted to 0% moisture content. Before machine harvesting, 100 spike-bearing shoots were removed from each plot and the plant material was dried for 48 h at 75°C and weighed, and the spikes were then threshed. Dry weight of grains from 100 spikes was recorded. From this lot, 200 grains were randomly counted and weighed to determine the 1000-grain weight (TGW). The grains per spike (GPS) was calculated by dividing the grain weight per shoot (g) by the TGW(g)/1000. The spikes per square meter was then calculated by dividing the machine-harvested grain yield (g m^{-2}) (from 4.8 m^2 area) by the product of GPS and TGW(g)/1000. Finally, aboveground biomass was calculated by dividing the machine-harvested grain yield (from 4.8 m^2 area) by the HI (from the 100-shoot sample).

Stomatal Conductance and Canopy Temperature Depression

In 2010, stomatal conductance was measured using the Decagon SC-1 Leaf Porometer (Decagon Devices, Inc.) approximately weekly from flag-leaf emergence (GS39) until mid-to-late grain filling in each plot of three replicates; there were two measurements preanthesis and five measurements in the 30 d postanthesis. Measurements were taken on the middle of the adaxial surface of the flag leaf, which was fully exposed to the sunlight for four leaves per plot from 11:00 to 15:00 on clear, sunny days. In 2009 and 2010, canopy temperature was determined by using a hand-held (Sixth Sense LT300) infrared thermometer (Total Temperature Instrumentation, Inc.) in each plot of three replicates. Readings were taken at an angle of approximately 30° to the horizontal approximately 0.5 m above the canopy. Two readings per plot were made around midday during cloudless periods. In the preanthesis period, there were two measurements from GS39 to GS61 in each year, and in the postanthesis period, there were two measurements in 2009 (approximately 20 and 30 d post-GS61), and one measurement in 2010 (approximately 20 d post-GS61). Air temperature was measured at the same time as the canopy temperature and canopy temperature depression (CTD) was calculated as follows:

$$\mathrm{CTD} = T_{\mathrm{a}} - T_{\mathrm{c}} \qquad [3]$$

where T_a is the air temperature and T_c is the canopy temperature.

Statistical Analysis

Standard analysis of variance (ANOVA) procedures were used to calculate treatment means, standard errors, and significant differences between treatments using the GenStat program (VSN International, 2010). The significance of the treatment effects was determined by ANOVA including year as random and cultivar as fixed main effect, and their interactions. Treatment means were compared using the LSD of the means of Fisher, calculated from standard errors of the difference of the means using appropriate degrees of freedom, when the ANOVA indicated significant differences. For ANOVAs across years, Bartlett's test ($P = 0.05$) was used to test for the homogeneity of variances, and years were regarded as random effects. The mean square for the year effect was tested against an error *A* mean square representing the variation between blocks. The mean square of the cultivar and year effects was tested against an error *B* mean square representing residual variation. Treatment means were compared using the LSD.

Where the effect of cultivar was statistically significant, associations between traits and between traits and grain yield among cultivars were examined through correlation, regression (linear and nonlinear), and multivariate biplot analysis procedures based on the cultivar mean values across years using the GenStat program.

RESULTS

Development, Plant Height, and Plant Establishment

Cultivar ranges averaging over years for dates of onset of stem extension (GS31), anthesis (GS61), and CCS were 8, 10, and 7 d, respectively (Table 2). The year × cultivar interaction was not statistically significant for any of the growth stages (data not shown) (Table 2). There was no change in date of GS31 with YoR. There was a nonlinear change in date of GS61 with YoR; days from sowing to GS61 increased up to approximately 1980 and then decreased (quadratic $R^2 = 0.73$, $P < 0.03$; Table 2). There was a linear change in date of CCS with YoR, with days from sowing to CCS overall increasing by 5 d over the 43-yr period ($R^2 = 0.37$, $P < 0.05$). The duration of GS61 to CCS initially decreased to approximately 1980 and then increased with an overall increase of 4 d across the 43-yr period (quadratic $R^2 = 0.67$, $P = 0.07$). There was no systematic change in the duration from sowing to GS31 or for the stem-elongation phase (GS31–GS61) with plant breeding. Averaging over years, plant height ranged from 89.4 to 109.6 cm among the cultivars ($P < 0.001$; Table 2) and increased linearly by 0.25 cm yr^{-1} with YoR ($R^2 = 0.37$, $P < 0.05$).

Table 2. Number of days after sowing to growth stages (GS) 31 and 61 and complete canopy senescence (CCS), days for phenophases, and plant height and plants per m^2 for 12 CIMMYT spring wheat cultivars. Values for dates of growth stages and phenophase durations represent means in 2009 and 2010. Values for plant height and plants per m^2 represent means in 2009, 2010, and 2011.

Cultivar (year of release)	GS31	GS61	Days from GS31 to GS61	CCS	Days from GS61 to CCS	Plant height	Plants per m^2
	d					cm	
Siete Cerros (1966)	46.0	84.5	38.5	135.0	50.5	93.8	172.8
Pavon (1976)	48.0	90.5	42.5	139.5	49.0	101.0	185.5
Seri (1982)	48.0	91.5	43.5	137.5	46.0	90.8	176.7
Bacanora (1988)	53.5	91.5	38.0	136.0	44.5	89.4	139.2
Attila (1990)	47.0	94.0	47.0	137.0	43.0	99.3	183.0
Baviacora (1992)	48.5	91.5	43.0	142.0	50.5	103.8	202.3
Tarachi (2000)	49.5	90.5	41.0	138.5	48.0	99.1	182.5
Tacupeto (2001)	47.5	91.5	44.0	140.0	48.5	99.5	196.4
Roelfs (2007)	46.0	87.5	41.5	138.0	50.5	109.6	174.7
Navojoa (2007)	46.5	92.5	46.0	142.0	49.5	103.8	199.4
Becard (2009)	51.0	86.5	35.5	140.5	54.0	101.2	179.4
Line 1 (2009)	45.0	85.5	40.5	140.5	55.0	101.4	181.4
SED[†] (cultivar)	1.32	0.83	1.52	0.38	0.88	1.16	12.84
df	44	44	44	44	44	66	66

[†] SED, standard error of the differences.

Table 3. Grain yield, harvest aboveground dry matter (AGDM), harvest index, spikes per m^2, grains per spike, grains per m^2, and grain weight for 12 CIMMYT spring wheat cultivars released from 1966 and 2009. Values represent means in 2009, 2010, and 2011

Cultivar (year of release)	Combine grain yield	Harvest AGDM	Harvest index	Spikes per m^2	Grains per spike	Grains per m^2	Grain weight
	g m^{-2}						mg
Siete Cerros (1966)	589.8	1391.1	0.424	347.2	50.3	17,455	34.1
Pavon (1976)	588.4	1430.8	0.412	405.7	42.3	16,576	35.3
Seri (1982)	601.7	1282.4	0.468	294.7	50.1	14,617	40.8
Bacanora (1988)	695.6	1508.4	0.461	391.1	50.9	19,803	35.3
Attila (1990)	687.0	1559.0	0.440	403.5	39.6	15,853	43.0
Baviacora (1992)	722.1	1607.3	0.448	327.0	49.9	15,956	44.8
Tarachi (2000)	637.6	1451.8	0.439	356.1	44.1	15,552	40.9
Tacupeto (2001)	653.6	1541.1	0.423	383.1	42.1	16,051	40.7
Roelfs (2007)	673.0	1583.9	0.424	324.9	46.7	15,087	44.6
Navojoa (2007)	724.1	1680.8	0.431	401.5	42.7	17,088	42.4
Becard (2009)	742.1	1620.2	0.457	375.2	44.3	16,531	44.9
Line 1 (2009)	731.6	1690.9	0.433	437.5	39.7	16,934	43.0
Mean	670.5	1529.0	0.439	370.6	45.2	16,459	40.8
SED[†] cultivar (df 99)	12.69	40.27	0.0076	11.02	1.292	349.4	0.584
Correlation with yr of release	0.76**	0.77**	0.06	0.26	−0.47	−0.17	0.78**
Correlation with grain yield	–	0.89***	0.30	0.36	−0.26	0.23	0.68*

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

[†] SED, standard error of the differences.

Averaging over years, plants per square meter ranged from 139 to 202 ($P < 0.05$; Table 2). Among 11 of the 12 cultivars, there were no significant differences in the range 177 to 202 plants m^{-2}. Bacanora at 139 plants m^{-2} had fewer plants per square meter than several other cultivars. There was no significant association between plants per square meter and either spikes per square meter at harvest ($R^2 = 0.04$) or grain yield ($R^2 = 0.02$) within the 12 cultivars (Table 3).

Grain Yield and Yield Components

Grain yield ranged from 588 to 742 g m^{-2} among cultivars ($P < 0.001$; Table 3; Fig. 1), and the year × cultivar interaction was not statistically significant (data not shown). There was a linear genetic gain in grain yield of 0.030 t ha^{-1} yr^{-1} (0.59% yr^{-1}, relative to grain yield in 1966; $R^2 = 0.58$, $P < 0.001$; Table 4; Fig. 1). Overall, grains per square meter ranged from 14,607 to 19,803 ($P < 0.001$)

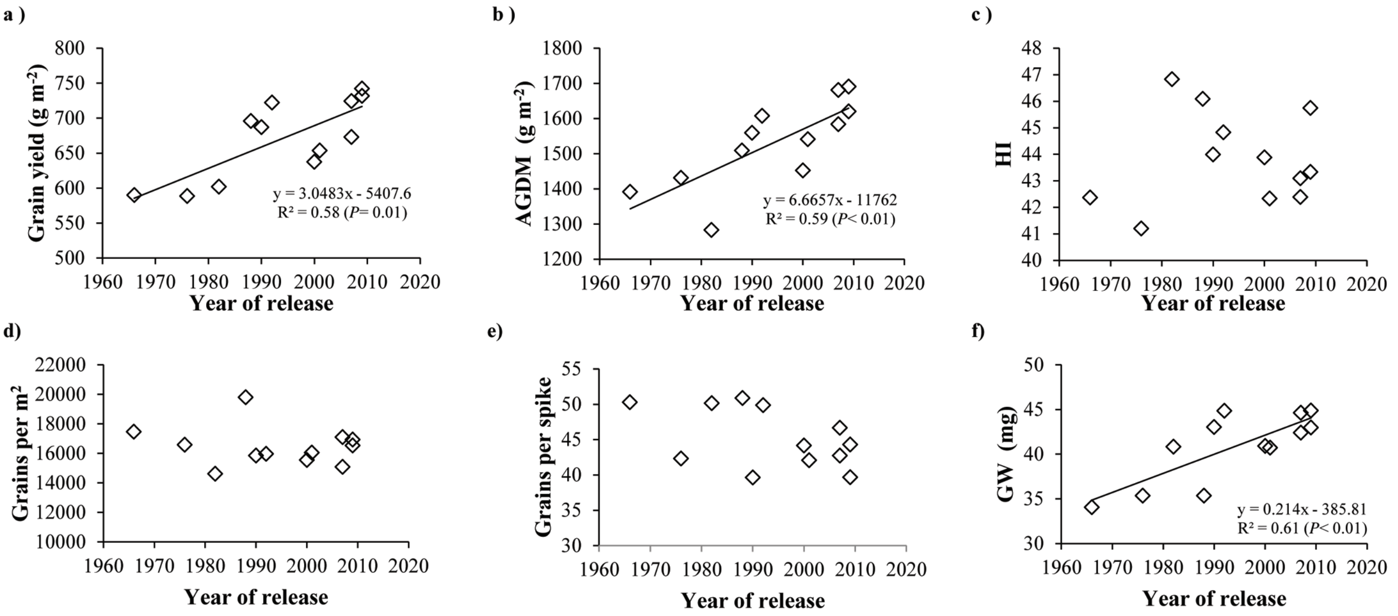

Figure 1. Regression of year of release on (a) grain yield (0% moisture content), (b) aboveground dry matter (AGDM) at harvest, (c) harvest index (HI, %), (d) grains per m^2, (e) grains per spike, and (f) grain weight (GW, 0% moisture content) for 12 CIMMYT spring wheat cultivars released from 1966 to 2009. Values represent mean of 2009, 2010, and 2011.

Table 4. Fitted parameter estimates for linear changes in crop traits with year of release for 12 CIMMYT spring wheat cultivars released from 1966 and 2009. Linear function ($y = a + bx$) was fitted to 3-yr cultivar means (2009, 2010, and 2011).

	Parameter estimates ($y = a + bx$)	
Trait	y (as in 1966)	$b \pm$ SE
Yield and yield components		
Combine grain yield, g m^{-2}	589.8	3.048 ± 0.813**
Grains per m^2	17,455.1	–15.7 ± 29.6ns‡
Spikes per m^2	347.2	0.755 ± 0.899ns
Grains per spike	50.3	–0.1412 ± 0.0830ns
Grain weight, mg	34.1	0.2140 ± 0.0545**
AGDM and HI†		
AGDM harvest, g m^{-2}	1391.1	6.67 ± 1.75**
HI, %	42.4	0.0086 ± 0.0388ns
Plant height, cm	93.8	0.243 ± 0.102*
df		10

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† AGDM, aboveground dry matter; HI, harvest index.

‡ ns, not significant.

among cultivars, but there was no association with YoR. Similarly spikes per square meter and grains per spike ranged from 295 to 437 m^{-2} ($P < 0.001$) and 39.6 to 50.1 ($P < 0.001$), respectively, among cultivars, but there were no associations with YoR (Table 3 and Table 4). Grain weight ranged from 34.1 to 44.9 mg among cultivars and was linearly positively associated with YoR ($R^2 = 0.61$, $P < 0.01$; Table 3; Fig. 1). Averaging over years, there was a positive linear association between grain yield and grain weight among cultivars ($R^2 = 0.46$, $P < 0.05$), whereas there was no significant association between grain yield and grains per square meter.

Overall, AGDM ranged from 1282 to 1691 g m^{-2} among the cultivars ($P < 0.001$; Table 3) and increased linearly with YoR over the 43-yr period by 6.67 g m^{-2} yr^{-1} ($R^2 = 0.59$, $P < 0.01$; Table 3, 4; Fig. 2); the year × cultivar interaction was not statistically significant (data not shown). Grain yield ($R^2 = 0.80$, $P < 0.001$) and plant height ($R^2 = 0.48$, $P < 0.05$) were each positively linearly associated with AGDM. Overall HI ranged among the cultivars from 0.41 to 0.47 and a nonlinear (quadratic) relationship was found between grain yield and HI over the 43-yr period ($P < 0.001$; Table 3; Fig. 1, 2). Grain yield increased with HI up to values of ~0.45 and then decreased slightly at higher values of HI. There was a trend for a negative linear association among the genotypes between plant height and HI ($R^2 = 0.27$; $P = 0.08$).

Dry Matter Production and Partitioning at Anthesis and Crop Growth Rate

Averaging across 2009 and 2010, there was a weak trend for a linear increase in AGDM at GS61 +7 d with YoR ($R^2 = 0.23$, $P = 0.11$; Table 5). There was a positive linear association between plant height and AGDM at GS61 +7 d ($R^2 = 0.34$, $P < 0.05$). Nonlinear changes in DM partitioning indices with YoR were observed. Spike partitioning index increased from 1966 up to approximately 1980 and then decreased to 2009 (quadratic; $R^2 = 0.48$; $P = 0.085$); there was a small decrease in SPI from 0.25 to 0.23 over the 43-yr period (Table 5). There was a negative linear association between plant height and SPI ($R^2 = 0.42$; $P < 0.05$). Stem-and-leaf-sheath partitioning index increased mainly

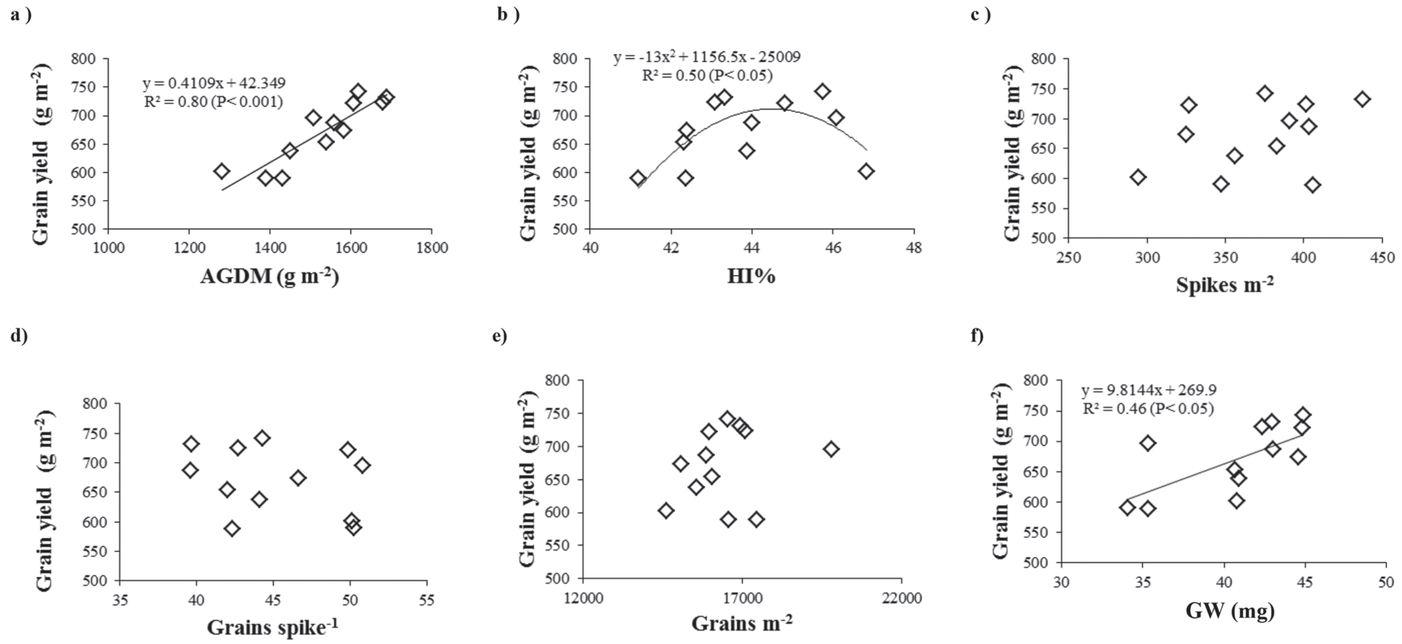

Figure 2. Regression of grain yield (0% moisture content) on (a) aboveground dry matter (AGDM) at harvest , (b) harvest index (HI, %), (c) spikes per m^2, (d) grains per spike, (e) grains per m^2, and (f) grain weight (GW) for 12 CIMMYT spring wheat cultivars released from 1966 to 2009. Values represent mean of 2009, 2010, and 2011.

Table 5. Fertile and infertile shoots dry matter (DM), spike DM, spike-partitioning index, fruiting efficiency, stem-and-leaf-sheath DM, stem-and-leaf-sheath partitioning index, lamina DM, and lamina partitioning index at GS61 +7 d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009. Values represent means in 2009 and 2010.

Cultivar (year of release)	Fertile shoots DM	Infertile shoots DM	Spike DM	Spike partitioning index‡	Fruiting efficiency	Stem DM	Stem partitioning index	Lamina DM	Lamina partitioning index
	———— g m^{-2} ————				grains g^{-1}	g m^{-2}		g m^{-2}	
Siete Cerros (1966)	757.3	33.9	188.7	0.249	100.6	404.6	0.534	164.0	0.217
Pavon (1976)	980.5	37.8	262.8	0.269	70.0	510.2	0.521	207.5	0.210
Seri (1982)	831.0	29.9	232.3	0.282	67.3	432.6	0.520	166.2	0.198
Bacanora (1988)	863.2	36.3	231.1	0.268	92.1	462.9	0.536	169.2	0.196
Attila (1990)	891.5	27.0	234.6	0.262	72.7	495.1	0.556	161.9	0.182
Baviacora (1992)	823.2	32.9	201.0	0.244	85.6	449.1	0.546	173.1	0.210
Tarachi (2000)	814.9	30.1	217.3	0.268	77.1	445.3	0.546	152.3	0.186
Tacupeto (2001)	939.4	31.6	267.5	0.284	66.1	492.8	0.524	179.1	0.191
Roelfs (2007)	1001.8	36.8	213.7	0.214	77.1	571.8	0.571	216.3	0.215
Navojoa (2007)	1000.7	29.8	256.2	0.256	71.0	566.1	0.566	178.3	0.178
Becard (2009)	967.4	46.6	229.9	0.239	79.3	547.9	0.564	189.6	0.197
Line 1 (2009)	834.9	25.8	195.0	0.233	93.0	467.8	0.560	172.1	0.207
Mean	892.1	33.2	227.5	0.256	79.3	487.2	0.545	177.4	0.199
SED† cultivar (df 44)	48.68***	7.39ns§	14.58***	0.0087***	5.62***	28.28***	0.0106***	12.86 ***	0.0072***
Correlation (yr of release)	0.48	0.01	0.09	−0.41	−0.22	0.64*	0.72**	0.20	−0.37
Correlation (grain yield)	0.29	0.10	−0.12	−0.50¶	0.14	0.48	0.74**	0.07	−0.25

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† SED, standard error of the differences.

‡ Partitioning indices for spike, stem, and lamina calculated as a proportion of the fertile shoots DM.

§ ns, not significant.

¶ Significant at the 0.10 probability level.

Table 6. Crop growth rate (CGR) from GS31 to GS61 +7 d and stem-and-leaf-sheath water soluble carbohydrate (WSC) DM at GS61 +7 d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009. Values represent means in 2009 and 2010.

Cultivar (year of release)	CGR GS31 to GS61 +7 d	Stem WSC GS61 +7 d
	g m^{-2} d^{-1}	g m^{-2}
Siete Cerros (1966)	17.0	53.1
Pavon (1976)	20.2	72.1
Seri (1982)	16.6	95.6
Bacanora (1988)	21.0	96.8
Attila (1990)	16.1	114.0
Baviacora (1992)	16.6	69.2
Tarachi (2000)	16.4	96.9
Tacupeto (2001)	18.1	96.5
Roelfs (2007)	20.4	70.7
Navojoa (2007)	18.9	106.8
Becard (2009)	24.4	67.0
Line 1 (2009)	17.1	52.6
Mean	19.7	82.6
SED† cultivar (df)	1.29*** (33)	9.76*** (44)
Correlation (yr of release)	0.30	0.10
Correlation (grain yield)	0.33	0.01

*** Significant at the 0.001 probability level.

† SED, standard error of the differences.

after approximately 1980 with an overall increase from 0.53 to 0.56 over the 43-yr period (quadratic $R^2 = 0.60$, $P < 0.01$) and was positively linearly associated with plant height among the cultivars ($R^2 = 0.43$, $P < 0.05$). There was no change in leaf lamina partitioning index with YoR. The overall effect of the changes in AGDM and DM partitioning was that spike DM at GS61 +7 d differed among cultivars in the range 188.7 to 267.5 g m^{-2} ($P < 0.001$); there was no change in spike DM per square meter at GS61 +7 d with YoR. Grains per square meter was not associated with spike DM per square meter among the 12 cultivars but showed a positive linear association with the FE ($R^2 = 0.34$; $P < 0.05$), which ranged among the cultivars from 66.1 to 100.6 grains g^{-1} ($P < 0.001$; Table 5). However, there was no change in the FE with YoR.

Averaging over 2009 and 2010, CGR during the stem-extension phase differed among cultivars in the range 16.6 to 24.4 g m^{-2} d^{-1} ($P < 0.01$; Table 6). Aboveground DM accumulated during stem extension was not associated with the number of days from GS31 to GS61 +7 d but was positively linearly associated with the CGR from GS31 to GS61 +7 d ($R^2 = 0.53$, $P < 0.05$). Crop growth rate during stem extension also showed a positive linear association with AGDM at GS61 +7 d among the cultivars ($R^2 = 0.53$; $P < 0.05$).

There was a nonlinear change in stem WSC at GS61 +7 d per square meter with YoR with the amount of stem WSC increasing from 1966 to approximately 1990 and then decreasing to 2009 (quadratic, $R^2 = 0.46$, $P = 0.06$; Table 6); overall stem WSC per square meter changed little over the 43-yr period. A similar quadratic regression between the amount stem WSC remobilized to the grain (difference between stem WSC at GS61 +7 d and maturity) and YoR was observed (data not shown; mean 65.9 g m^{-2}; genetic range 30.4–83.7 g m^{-2}). Differences in the amount of stem WSC at GS61 +7 d among cultivars were associated with stem WSC% at GS61 +7 d ($R^2 = 0.69$; $P < 0.01$; data not shown; mean 17.1%; genetic range 11.2–23.0%) and not stem DM per unit area (g m^{-2}) ($R^2 = 0.11$; $P = 0.30$) (Table 5).

Leaf and Canopy Traits

In 2010, preanthesis stomatal conductance differed among cultivars in the range 162 to 294 mmol m^{-2} s^{-1} ($P < 0.001$). There was a strong trend for preanthesis stomatal conductance to increase linearly with YoR among the cultivars ($R^2 = 0.32$; $P = 0.06$) and a positive linear association between preanthesis stomatal conductance and grain yield ($R^2 = 0.48$; $P < 0.05$). No associations were found between postanthesis stomatal conductance and either YoR or grain yield. Averaging over 2009 and 2010, CTD during the postanthesis period increased linearly with YoR among cultivars ($R^2 = 0.33$, $P = 0.05$) and there was a positive linear association among the cultivars with grain yield ($R^2 = 0.66$, $P < 0.001$, Fig. 3) and grain weight ($R^2 = 0.27$, $P = 0.08$). Associations between preanthesis CTD and YoR and grain yield, however, were not statistically significant. The duration of canopy senescence from GS61 to CCS increased by 4 d over the 43-yr period; there was a nonlinear change in senescence duration with YoR (quadratic $R^2 = 0.64$, $P < 0.05$), with senescence duration increasing from approximately 1980. Overall, grain yield and grain weight were not associated with senescence duration among the 12 cultivars; although, among the 10 cultivars released since 1982, there was a trend for a positive linear association between each of grain yield ($R^2 = 0.32$, $P = 0.08$) and grain weight ($R^2 = 0.36$, $P = 0.06$) and senescence duration.

Spike Traits

Averaging across 2009 and 2010, rachis length ranged among cultivars from 10.8 to 13.9 cm ($P < 0.001$) but was not associated with YoR (Fig. 4). Fertile spikelets per spike ranged from 16.8 to 21.9 ($P < 0.001$) and initially increased with breeding but then decreased from approximately 1990 (Fig. 4b) (quadratic $R^2 = 0.58$; $P < 0.05$). Rachis length was not associated with either fertile spikelets per spike or grain yield among cultivars. However, there was a trend for rachis length per fertile spikelet to increase linearly with YoR ($R^2 = 0.27$; $P = 0.08$) (Fig. 4b), and this trait was positively linearly associated with grain weight among cultivars ($R^2 = 0.46$; $P < 0.05$) (Fig. 4c).

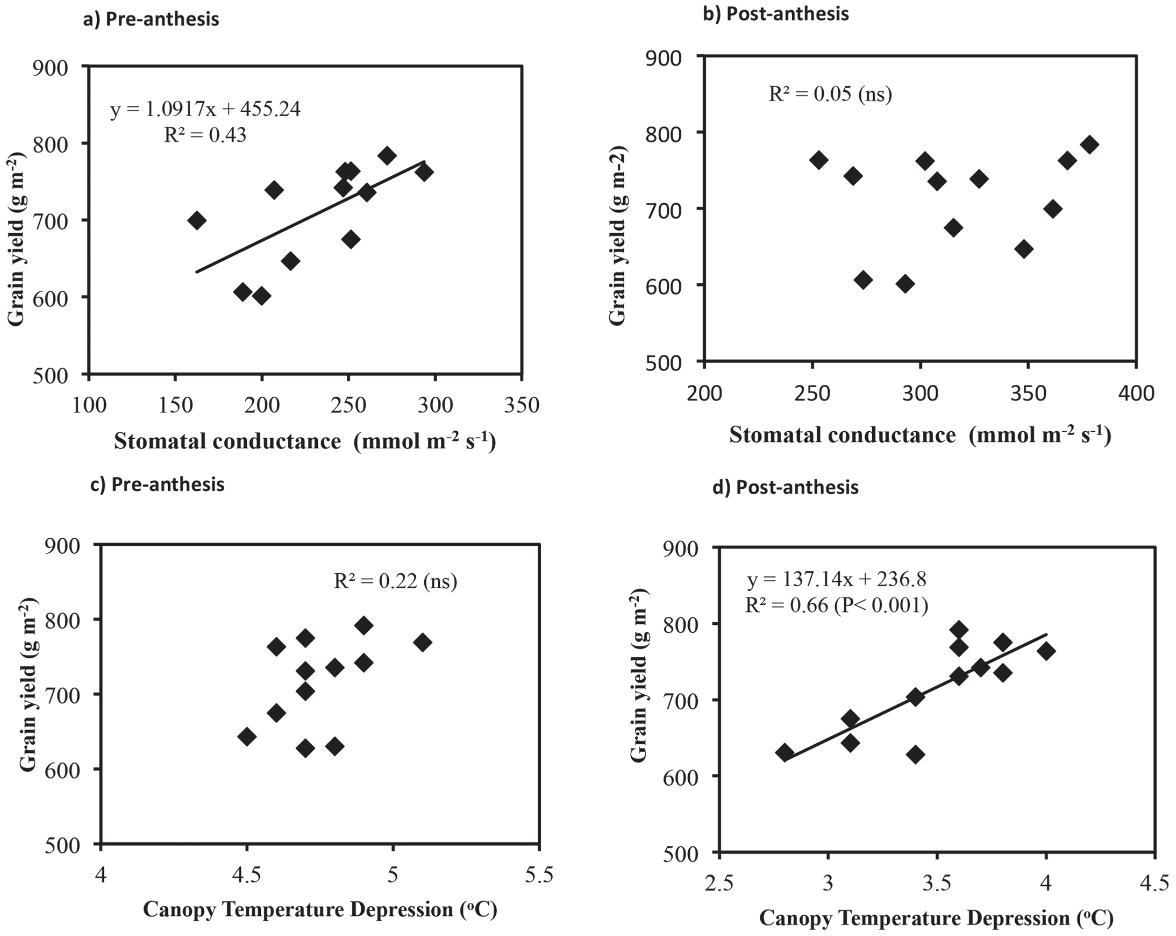

Figure 3. Linear regression of (a) grain yield on preanthesis flag-leaf stomatal conductance, (b) grain yield on postanthesis flag-leaf stomatal conductance, (c) grain yield on preanthesis canopy temperature depression, and (d) grain yield on postanthesis canopy temperature depression for 12 CIMMYT spring wheat cultivars released from 1988 to 2009. Values for (a) and (b) are for 2010. Values for (c) and (d) represent the means of 2009 and 2010.

Responses to Degraining

To assess whether grain growth among the cultivars was limited by grain source or grain sink size, a degraining treatment was performed at GS61 +14 d. Grain growth responses to degraining of approximately 0 to 10% are indicative of sink limitation of grain growth, whereas those of approximately 10 to 20% are indicative of colimitation of grain growth by sink during the earlier phase of grain fill and source during the latter phase of grain fill (Acreche and Slafer, 2009). It was hypothesized that the extent of sink limitation of grain growth may have decreased with plant breeding, with genetic gains in postanthesis source not matching those in sink. Averaging across cultivars, degraining increased grain weight from 42.7 (control treatment) to 45.0 mg (degraining treatment) (5.5%; $P < 0.001$; Table 7). Only weakly significant differences were found among cultivars in the percentage increase in grain weight in response to degraining in the range 0.5 to 13.2% ($P = 0.097$; Table 7), and the interaction between degraining treatment and cultivar was only weakly significant ($P = 0.087$). There was no association among genotypes between the percentage increase in grain weight with degraining and YoR. Stem-and-leaf-sheath weight per shoot was increased from 1.64 g in the control to 1.79 g in the degraining treatment (9.6%; $P < 0.001$), and there was a trend for the percentage increase to differ among cultivars in the range 2.2 to 21.0% ($P = 0.07$). The association between the percentage increase in stem-and-leaf-sheath weight per shoot with degraining and YoR was not significant.

Trait Correlations

A biplot showing associations between grain yield, yield components, and physiological traits is shown in Fig. 5. The biplot confirms the strong positive correlations between each of aboveground biomass, grain weight, plant height, and grain yield among the 12 cultivars. The positive correlation between FE and grains per square meter and between each of preanthesis stomatal conductance and postanthesis CTD and grain yield were also confirmed. Spike partitioning index was negatively correlated with grain yield and plant height. The positive association between rachis length per spikelet and grain weight was also confirmed.

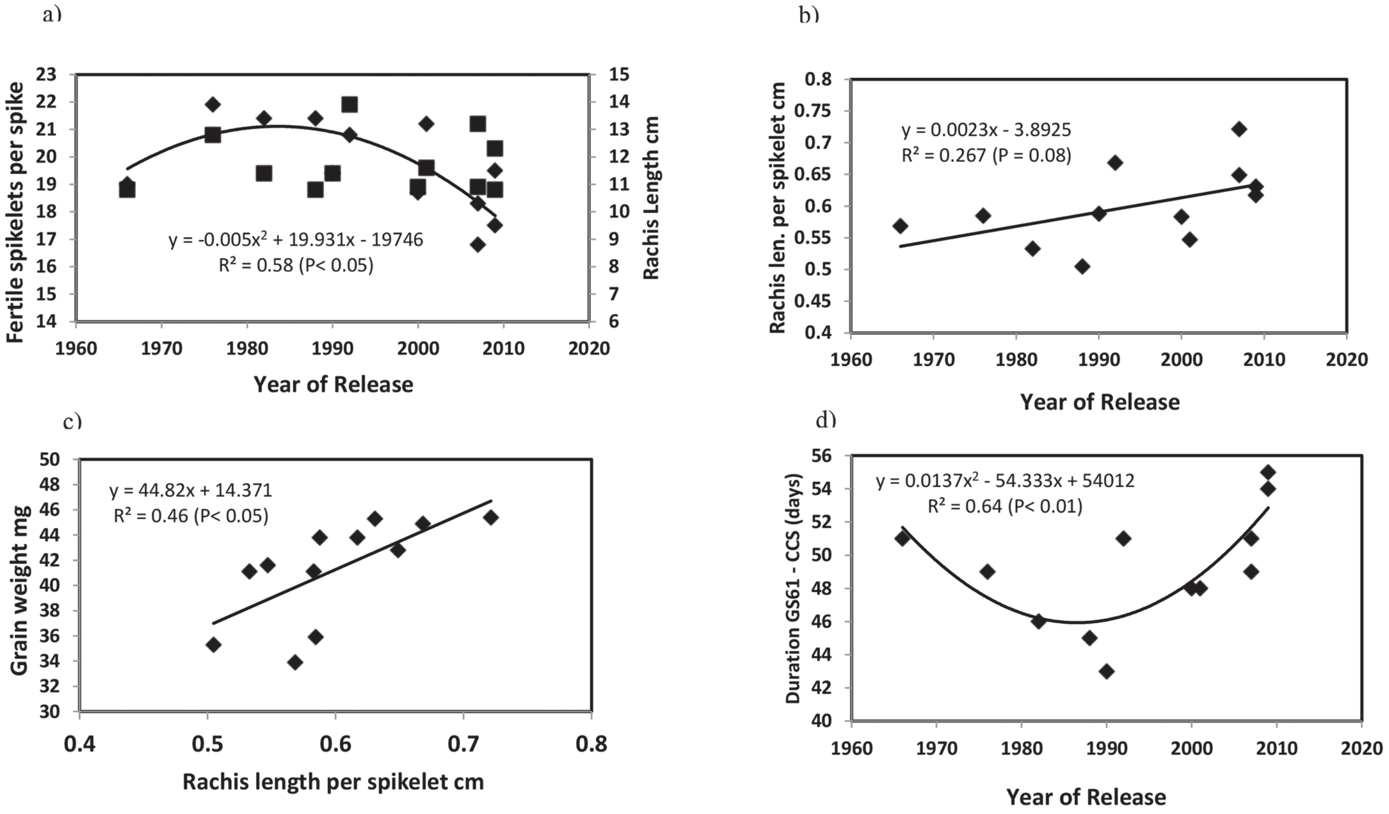

Figure 4. Regression of (a) fertile spikelets per spike (diamonds) and rachis length (squares) on year of release, (b) rachis length per spikelet on year of release, (c) grain weight on rachis length per spikelet, and (d) duration from anthesis (GS61) to complete canopy senescence (CCS) on year of release for 12 CIMMYT spring wheat cultivars. Values represent the mean of 2009 and 2010.

DISCUSSION

First we will discuss the physiological basis of the genetic gains in grain yield and associated changes in physiological traits with plant breeding in the CIMMYT spring wheat cultivars, including changes in resource capture and assimilate allocation in the pre- and postanthesis periods. Then, we will discuss the implications for future wheat breeding.

Genetic Progress in Grain Yield and Yield Components

Grain yield potential increased linearly in spring wheat cultivars released in CIMMYT from 1966 to 2009 by 30 kg ha^{-1} yr^{-1} (0.59% yr^{-1}). Previous studies at the same site on sets of historic spring wheat cultivars showed slightly higher rates of genetic gain of 50 kg ha^{-1} yr^{-1} from 1950 to 1982 (Waddington et al., 1986) and 57 kg ha^{-1} yr^{-1} from 1962 to 1988 (Sayre et al., 1997) (expressing grain yield at 0% moisture content equivalent to the present study). Present results indicated that the rate of genetic progress in CIMMYT spring wheat has slowed but has not plateaued in recent decades. Present results are therefore in agreement with extensive international yield trials that show continued genetic progress in CIMMYT spring wheat in recent decades (Manes et al., 2012; Lopes et al., 2012; Sharma et al., 2012).

In the present study, there was no association between genetic progress in grain yield and grains per square meter. Genetic grain yield progress from 1966 to 2009 was therefore associated with grain weight. The majority of previous studies worldwide showed that grain yield progress in wheat was mainly associated with grains per square meter (e.g., Perry and D'Antuono, 1989; Waddington et al., 1986; Sayre et al., 1997; Abbate et al., 1998; Shearman et al., 2005) rather than individual grain weight. Lopes et al. (2012), however, recently also found grain yield progress of CIMMYT advanced lines from 1977 to 2008 was associated with increased grain weight and not grains per square meter.

The reduction in plant height with the CIMMYT semidwarf cultivars introduced during the 1960s improved grains per square meter by favoring spike partitioning during the preanthesis phase (Fischer and Stockman, 1986). In the study of Waddington et al. (1986) there were two tall varieties and 15 semidwarfs released from 1950 to 1982. In our study, all the cultivars studied were semidwarf genotypes released between 1966 and 2009. This may partly explain why increases in grains per square meter and HI with plant breeding were observed in the study of Waddington et al. (1986) but not in our study. Most previous studies on wheat did not show genetic progress in grain weight (e.g., Perry and D'Antuono, 1989; Sayre et al., 1997;

Table 7. Effect of degraining treatment at GS61 +14 d on stem and leaf sheath dry matter (Stem DM) per fertile shoot and individual grain weight of 12 CIMMYT spring wheat cultivars released from 1966 to 2009. Values represent means in 2009 and 2010.

Cultivar (year of release)	Stem DM			Grain weight		
	Control	Degrained	% increase	Control	Degrained	% increase
	g shoot^{-1}			mg		
Siete Cerros (1966)	1.62	1.82	12.5	36.0	36.2	0.5
Pavon (1976)	1.60	1.72	7.4	38.0	39.7	4.2
Seri (1982)	1.58	1.74	10.8	40.6	44.0	8.3
Bacanora (1988)	1.34	1.47	8.7	37.5	39.6	5.8
Attila (1990)	1.40	1.69	20.1	44.6	47.2	5.8
Baviacora (1992)	2.08	2.24	7.6	45.1	51.0	13.2
Tarachi (2000)	1.62	1.66	2.2	44.4	45.4	2.1
Tacupeto (2001)	1.58	1.67	5.2	42.9	44.6	3.8
Roelfs (2007)	2.06	2.27	10.3	47.9	49.3	3.0
Navojoa (2007)	1.55	1.66	7.4	45.6	46.7	2.4
Becard (2009)	1.55	1.79	15.5	45.4	48.6	7.1
Line 1 (2009)	1.70	1.82	7.3	44.1	48.2	9.3
Mean	1.64	1.79	9.6	42.7	45.0	5.5
SED[†] cultivar (df = 44)	0.085***	0.073***	4.65[‡]	1.44***	0.75***	3.78[‡]
Correlation (yr of release)	0.21	0.16	–0.18	0.85**	0.78**	0.16
Correlation (grain yield per shoot)	0.82**	0.73**	n/a[§]	0.42	0.50[†]	n/a

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

[†] SED, standard error of the differences.

[‡] Significant at the 0.10 probability level.

[§] n/a, not applicable.

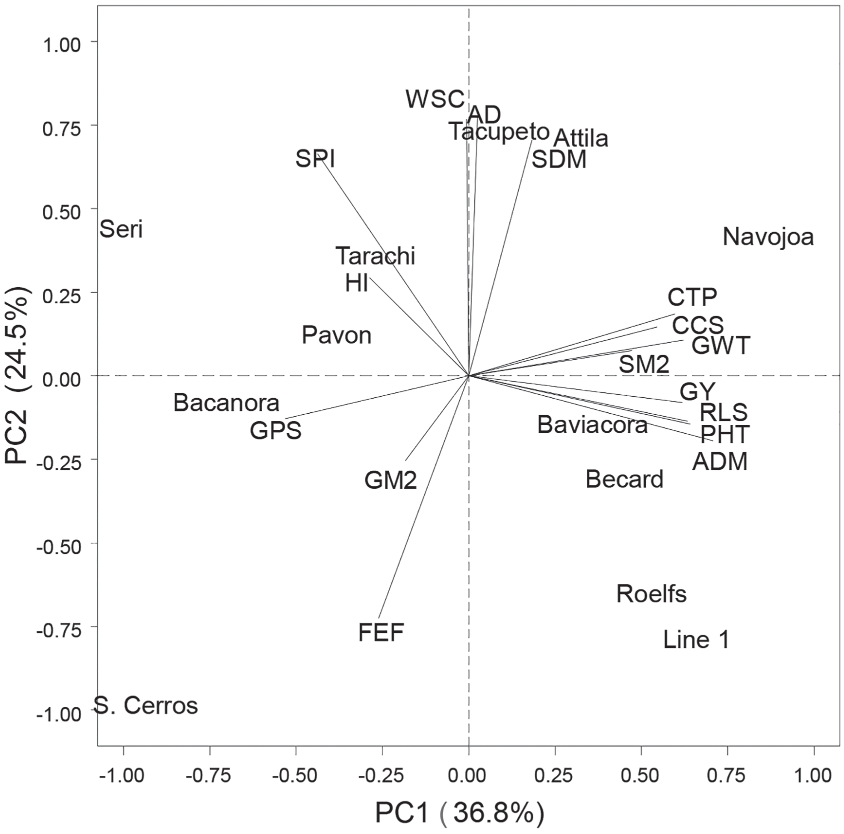

Figure 5. Biplot of grain yield, yield components, and physiological traits for 12 CIMMYT spring wheat cultivars. Values represent the mean of 2009 and 2010. AGDM, aboveground dry matter; CTPOST, canopy temperature depression postanthesis; FE, fruiting efficiency; FSP, fertile spikelets per spike; GM2, grains per m^2; GPS, grains per spike; GSPRE, stomatal conductance preanthesis; GWT, grain weight; GY, grain yield; HI, harvest index; PHT, plant height; RCL, rachis length; SDMA, spike dry matter at GS61 +7 d; SM2, spikes per m^2; SPI, spike-partitioning index; SRL, rachis length per spikelet; WSC, stem-and-leaf-sheath water-soluble carbohydrate at GS61 +7 d.

Brancourt-Hulmel et al., 2003; Shearman et al., 2005; Brisson et al., 2010; Acreche et al., 2008). With the introduction of the semidwarf cultivars, there was a tendency for grain weight to decrease associated with more grains in distal positions in spikelets with lower PGW (Waddington et al., 1986). Nevertheless, a few recent studies have indicated that grain weight has contributed to yield progress (Cox et al., 1988; Morgounov et al., 2010; Tian et al., 2011; Zheng et al., 2011; Lopes et al., 2012). Our results indicated that PGW has likely increased and contributed to the genetic gains in final grain weight, since grain weight in the degrained spikes increased linearly with YoR. Where source per grain is effectively increased by 100% in the degrained spikes, the final grain dry weight is an indicator of PGW. Our results showed no change with plant breeding in either rachis length or fertile spikelets per spike and no correlation between these two traits among genotypes, but indicated rachis length per spikelet increased with YoR and was linearly positively associated with grain weight. It is possible that an increase in rachis length per spikelet favored larger PGW through either increasing spike photosynthesis per grain during the critical phase before (Calderini et al., 1999a; Ugarte et al., 2007) or after (Calderini et al., 1999b) anthesis for determination of PGW or alleviating mechanical constraints to the volume of the floret cavities within the spike. The increase in grain weight in the CIMMYT spring wheats over the 43-yr period may have been partly associated with direct selection for larger grains associated with increased seedling vigor.

Present results indicated the duration from GS61 to CCS increased from approximately 1980. Overall, postanthesis senescence duration was not associated with grain yield or grain weight among the 12 cultivars, but among the 10 cultivars released since 1982 there was a trend for a positive linear association between CCS and each of grain yield ($R^2 = 0.28$, $P = 0.07$) and grain weight ($R^2 = 0.36$, $P < 0.05$). These results are consistent with a previous study, which attributed recent genetic increases in grain yield in CIMMYT spring wheats partly to postheading stay-green traits (Lopes et al., 2012). Further work is justified to test whether the genetic gains in grain yield associated with extended senescence duration were related to a delayed onset or a slower rate of canopy senescence.

Genetic Progress in Physiological Components of Grain Yield

Results showed that plant height has increased linearly with plant breeding. This increase was positively associated with aboveground biomass, which appeared to explain most of the genetic progress in grain yield. The increase in harvest biomass was mostly explained by increased postanthesis AGDM accumulated from GS61 +7 d to harvest, which was linearly associated with harvest biomass among cultivars ($R^2 = 0.55$, $P < 0.05$); whereas, preanthesis biomass accumulated from sowing to GS61 +7 d was not associated with harvest biomass ($R^2 = 0.18$, $P = 0.18$) among the cultivars. These results support the idea that improving harvest biomass through selecting for taller cultivars among semidwarf genotypes has been a target in recent breeding strategies at CIMMYT. It is possible the raised-bed planting system used in the experiments, and which is used in the CIMMYT bread wheat yield potential selection breeding trials at Ciudad Obregon, may have favored the selection of taller lines, with taller lines being better adapted to capture radiation in the 50-cm gap between beds within a plot during vegetative growth before canopy closure. For example, Fischer et al. (2005), in the same site in northwest Mexico, reported the response of range of bread wheat cultivars to raised-bed plots compared with flat plots under full irrigation during the period 1988 to 2005. Results suggested that the main consideration determining the responses to raised-bed planting system was the ability of the cultivar to capture the solar radiation falling in the gap between the beds in the critical preanthesis period therefore favoring taller, later, and less-erect genotypes. This may partly explain the positive association between plant height and AGDM in the present experiments observed for AGDM at both GS61 +7 d ($R^2 = 0.33$, $P = 0.05$) and harvest ($R^2 = 0.43$, $P < 0.05$) among the 12 genotypes. Present results showed no genetic gain in CGR during the stem-elongation phase but a linear genetic gain in preanthesis stomatal conductance ($R^2 = 0.32$, $P = 0.06$) and a positive correlation between preanthesis stomatal conductance and grain yield ($R^2 = 0.43$, $P < 0.05$). Fischer et al. (1998) reported similar effects for CGR and preanthesis stomatal conductance from 1962 to 1988 in CIMMYT spring wheat releases. The trend for aboveground DM at GS61 +7 d to increase with YoR in our study is consistent with the increase in stomatal conductance preanthesis. However, the increased AGDM at GS61 +7 d did not lead to more grains per square meter, mainly because SPI decreased over the 43-yr period from 0.25 to 0.23; spike DM per square meter at GS61 +7 d did not change with YoR. Therefore, it is possible the correlation between preanthesis stomatal conductance and grain yield was a spurious correlation with both traits increasing with YoR but not directly mechanistically linked.

Turning to consider changes in resource-capture traits during the postanthesis period, our results showed genetic progress in grain weight in northwest Mexico has not been associated with changes in stem WSC accumulation or stem WSC remobilization. Consequently, grain weight increases were apparently associated with increases in current photosynthesis postanthesis. This is consistent with a linear increase in postanthesis CTD with YoR, indicative of an increase in canopy photosynthesis during grain filling and a positive linear association between postanthesis CTD and grain yield ($R^2 = 0.66$, $P < 0.001$) and grain weight ($R^2 = 0.27$, $P = 0.08$). In the 1 yr in which stomatal conductance was measured (2010), there was a positive linear relationship between postanthesis CTD and postanthesis stomatal conductance as expected ($R^2 = 0.46$, $P < 0.05$), although postanthesis stomatal conductance itself was not associated with grain yield. Several previous studies also showed phenotypic correlations between CTD and genetic grains in grain yield among CIMMYT wheat releases (e.g., Fischer et al., 1998 and Lopes et al., 2012). Overall the contribution of stem WSC to grain yield in the current study (calculated as stem WSC remobilization as a proportion of grain yield) was relatively low, varying among cultivars in the range 0.05 to 0.13 compared with some other field investigations, for example, 0.21 reported by Borrell et al. (1989) for spring wheat in field experiments in Australia and a range of 0.23 to 0.39 reported by Foulkes et al. (2002) for six winter wheat cultivars in experiments in the United Kingdom under irrigated conditions. Shearman et al. (2005) found a range of stem WSC of 244 to 391 g m^{-2} measured shortly after anthesis for eight winter wheat cultivars introduced from 1972 to 1995 in the United Kingdom and a positive correlation with grain yield (R^2 0.51, $P < 0.05$). Present results could indicate that under the high-radiation environment in northwest Mexico, stem WSC is likely to be a less important yield determinant than in lower-radiation environments, for example, the United Kingdom. The trend for differences in grain weight responses to degraining among cultivars ($P = 0.087$) suggested differences in source–sink balance among the cultivars. Results indicated that most cultivars in this historic set were generally sink limited rather than source limited or colimited by source and sink. Several previous studies concluded grain growth of wheat was mainly sink limited under optimal conditions (Borras et al., 2004; Snyder et al., 1993; Miralles and Slafer, 1995; Slafer and Savin, 1994; Cartelle et al., 2006). However, Acreche and Slafer (2009) reported that for wheat genotypes released from 1940 to 2005 in Spain, grain weight was unchanged by removing the upper half of the spike in the old cultivars but increased in the newest cultivars. They suggested the modern cultivars exhibited a colimitation of grain growth by source and sink. Fischer and HilleRis Lambers (1978) also reported in responses to a treatment that reduced grains per spike by about 80%, old tall bread wheats showed low source limitation (final grain weight response <10%), whereas most modern semidwarf cultivars showed responses up to 50%) and higher grain yields. It is possible that some of the cultivars in the present study also exhibited colimitation of grain growth by source and sink, that is, those with grain weight response to degraining >10%. Nevertheless, our results did not indicate any systematic change in the extent of sink limitation with plant breeding since the proportional grain weight response to degraining did not change with YoR.

Implications for Future Wheat Breeding

Since the introduction of semidwarfing genes into spring wheat germplasm at CIMMYT, our results indicated the present strategy to increase yield in irrigated, high-potential environments has increased harvest biomass production while maintaining HI. The increase in biomass appears to have contributed to increases in grain yield through heavier grains rather than more grains per square meter. Therefore, relevant future investigations may include the mechanistic basis of genetic gains in PGW involving the regulation of biochemical and structural properties of the ovary and pericarp cell walls before and after anthesis (Foulkes et al., 2011). The basis of the positive relationship between rachis length per spikelet and PGW we detected should also be further investigated, that is, whether this an allometric relationship with larger spikelets relating to larger PGW or whether there are also effects of enhanced spike photosynthesis per spikelet or removal of physical restrictions to grain development with increased size of glumes, paleas, and lemmas. Our results suggested that recent gains in biomass since approximately 1985 were associated with a tendency for a decrease in HI from ~0.47 to 0.43, in turn, associated with increased plant height. The plant height of the most recently introduced CIMMYT spring wheat was ~100 cm, which is significantly higher than the optimum range of plant height of 70 to 90 cm reported for modern wheat cultivars in many environments worldwide grown on flat planting systems, for example, in China (Zhou et al., 2007; Zheng et al., 2011), the United Kingdom (Clarke et al., 2012), Spain (Sanchez-Garcia et al., 2013), and Australia (Sadras et al., 2012). There may be limited scope to exploit plant height further for enhancing aboveground biomass, as further plant height increases would likely have implications for decreased lodging resistance (Berry et al., 2007). Therefore, for future gains in yield potential of CIMMYT spring wheats it will be important to identify strategies for increasing grain sink while maintaining plant height (Foulkes et al., 2011; Reynolds et al., 2012). It can be speculated that increasing plant height may have also been an advantageous trait for biomass production with regard to the raised-bed planting system in the present experiment, with taller lines being better adapted to capture radiation in the 50-cm gap between beds within a plot during vegetative growth before canopy closure and also during the critical period determining grain number from booting to anthesis (Fischer et al., 2005). There was positive linear relationship between plant height and AGDM at GS31 among the 12 cultivars ($R^2 = 0.50$, $P < 0.01$; data not shown).

Our results indicated that, theoretically, a grain yield of 15.30 t ha^{-1} could be achieved under irrigated conditions in northwest Mexico by combining the maximum values of fertile-shoot AGDM at GS61 +7 d (1271 g m^{-2}), SPI (0.284), FE (83.1 grains g^{-1}), and PGW (51.0 mg) expressed among the 12 cultivars. Future progress will require an improved understanding of any trade-offs between these traits. Present results indicated a linear negative relationship between grains per square meter and grain weight ($R^2 = 0.31$, $P = 0.06$). Although the association between SPI and FE was not significant among the 12 cultivars, there was a linear negative relationship between SPI and FE among the eight cultivars released since 1990 ($R^2 = 0.73$, $P < 0.01$). A negative relationship between grains per square meter and grain weight has been frequently observed among wheat genotypes (Foulkes et al., 2011) and a negative relationship between SPI and FE in wheat has also previously been reported in some studies (e.g., Gaju et al., 2009; González et al., 2011; Lázaro and Abbate, 2012). With regard to the trade-off between grains per square meter and grain weight, it is encouraging that results on a Bacanora (high grain per square meter) × Weebil (high grain weight) spring wheat double-haploid cross in Chile showed it is possible to combine high grain number and grain weight in double-haploid lines with yield gains of 17 and 27% in two seasons compared to the highest yielding parent Weebil, and there was no evidence for a strong source limitation of grain growth during grain filling (Bustos et al., 2013). The physiological basis of the trade-off between SPI and FE is still unclear. One possible avenue to minimize the trade-off may be improvement of vascular connections within the rachilla, since floret fertility of more distal florets still may be limited by resistance according to the vascular connections within the rachilla (Bancal and Soltani, 2002). Future work to enhance wheat yields should also seek to enhance stay-green, for example, by maximizing canopy N accumulation and slowing post-anthesis N remobilization (Derkx et al., 2012; Gaju et al., 2011, 2014). In addition, the root system of modern wheat may not be large enough at depth to take up sufficient water and nutrients to support future gains in biomass, so breeders should also consider strategies for deeper root distribution in future breeding programs alongside strategies to raise aboveground biomass (Reynolds et al., 2007; Lynch, 2007). The present results also confirm the scope for the application of canopy temperature and stomatal conductance as selection criteria for wheat yield potential in irrigated, high-potential environments (Fischer et al., 1998; Reynolds et al., 2007).

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