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Genotype by tillage interaction and performance progress for bread and durum wheat genotypes on irrigated raised beds

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A B S T R A C T

Agronomic systems based on zero tillage and residue retention are becoming more important due to their potential for climate change adaptation through the reduction of soil erosion and improved water availability. Denser soil surface conditions and large amounts of crop residues, however, may be a constraint for early plant establishment, especially in irrigated production areas with high yield potential. Genotype by tillage interactions for yield are not well understood and it is unknown whether tillage should be an evaluation factor in breeding programs.

Twenty-six CIMMYT bread (*Triticum aestivum*) and durum (*Triticum turgidum*) wheat genotypes, created between 1964 and 2009, were tested for yield and agronomic performance at CIMMYT's experimental station near Ciudad Obregon, Mexico, over six years. Treatments included conventional and permanent raised beds with full and reduced irrigation. The objectives were to study breeding progress in distinct agronomic systems and to elucidate the importance of tillage and genotype by tillage interaction for yield and agronomic traits.

Breeding progress was achieved irrespective of agronomic treatment. Tillage influenced plant growth and number of grains per m^2 in both wheat types. In bread wheat, genotype by tillage interaction was significant for yield, test weight, and growth parameters. However, no cross-over effects were detected and rank changes were small. In durum wheat, genotype by tillage interaction was only significant for plant growth. The results do not indicate the need for separate breeding programs. However, the question of a need for selection under zero tillage to increase breeding progress is yet to be answered.

1. Introduction

Intensive tillage is an important component of conventional crop production systems. Physical disturbance loosens and aerates the upper soil layer creating optimal germination conditions for crops. However, intensive tillage, especially in combination with removal of crop residues, can lead to soil degradation and erosion (Montgomery, 2007).

Conservation agriculture (CA) is based on minimum soil movement, residue retention, and crop diversification. Conservation agriculture has the potential to improve soil resilience and increase sustainability of crop production (Hobbs et al., 2008). Zero tillage (ZT) is the most extreme form of minimum soil movement. When combined with crop residue retention, it improves top soil structure which in turn impacts soil flora and fauna and subsequently disease pressure (Verhulst et al., 2010). The retention of crop residue also influences the growing environment. Residue cover of the soil has positive effects on water infiltration by slowing down rain drops and preventing aggregate breakup and crust formation (Le Bissonnais, 1996). Crop residue also improves water infiltration rates by improved soil structure (Singh et al., 2016) and reducing runoff (Zhang et al., 2007). Residue cover can also lead to better soil temperature regulation. Moreover, CA can reduce production costs by reducing labor and fuel inputs necessary for conventional tillage operations. Erenstein and Laxmi (2008) summarized eleven studies from the Indo-Gangetic Plains (IGP) and found that ZT reduced tractor time and fuel use on average by 81%. Reduction of fuel input in turn leads to reduction of greenhouse gas emissions. An important advantage of ZT is the possibility of timelier sowing, since no prior tillage is needed. This reduces turnaround time significantly and is important in systems where more than one crop is grown per year. In regions with late season heat, like the IGP, timely sowing is of high importance as it allows the crop to escape extreme stress at the end of the growing cycle and can lead to higher yields (Erenstein and Laxmi,

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2008).

Despite the many benefits of CA, different production conditions may result in challenges for crop production. Crop residues can be a constraint for crop growth as they may increase incidence of soil borne disease that survive on stubble and are carried over to the next crop (Chan et al., 1989). Large amounts of crop residues can be a physical constraint during seedling establishment (Wuest et al., 2000) Zero tillage can also increase soil surface bulk density, making it more difficult for seedlings to establish roots (Chan et al., 1989).

The differences between CA and conventional crop production systems can be expected to influence crop performance and yield. For example, Verhulst et al. (2011a) observed slower initial growth of wheat on permanent beds (PB) in the central Mexican highlands. This observation confirms earlier studies. Riley (1998) reported slower initial growth in spring barley and wheat and Vyn et al. (1991) reported slower growth of winter wheat under reduced tillage treatments. Many studies have compared yield under ZT and conventional tillage. Verhulst et al. (2011a) and Vyn et al. (1991) reported that delayed early growth under ZT was compensated for later in the season, resulting in no yield differences with conventional till (CT). In conditions with high residue loads, Rebetzke et al. (2005) observed improved emergence and biomass production of wheat genotypes with long coleoptiles than genotypes with regular length coleoptiles. Rebetzke et al. (2017) compared low and high vigor genotypes and found significantly higher yields associated with high vigor genotypes.

Herrera et al. (2013) summarized results from 14 studies on bread wheat and observed mixed results. In four studies there was no yield difference between ZT and CT, in six studies yield was higher under CT and in four higher under ZT. Pittelkow et al. (2015) conducted an extensive meta-analysis on crop yields in ZT and CT. Their analysis included 678 studies, representing 50 crops and 63 countries. Across all crops and environments, yields were reduced in ZT by 5.1%. However, results varied widely between crop species and agro-ecological environments. For example ZT reduced yield of root crops on average by 21.4%. In contrast, oilseed, cotton, and legume crops in ZT did not have lower yield. In wheat, yield reduction was relatively low at 2.6%. Zero tillage systems across all tested crops performed best under rainfed conditions in dry environments, where yields matched or exceeded those under CT for all crop categories. Under these conditions wheat yields were increased on average by about 2% relative to CT. These observations indicate an influence of genetic and morphological characteristics as well as environment and management factors on crop performance in ZT. It is clear that the question of ZT effects on yield does not have a simple answer. Tillage interacts with other management and environmental factors, and genotypes add their effects as well. Whether crops should be bred to adapt to the cropping system, or conservation agriculture, needs to be determined.

Herrera et al. (2013) pointed out that although area under CA is increasing, these conditions are not represented in the selection conditions of most breeding programs. However, if targeted breeding programs were to be developed for different tillage practices, it would need to be assured that relevant genotype by tillage interaction (G × T) exists, especially for grain yield performance.

Genotype by tillage interactions have been studied by various researchers (e.g.: Ciha 1982; Hall and Cholick 1989; Cox 1991; Cox and Shelton 1992; Hwu and Allan 1992). Trethowan et al. (2012) studied a diverse set of bread wheat cultivars and found highly significant G × T for grain yield and quality parameters. Moreover, they developed a mapping population and were able to map quantitative trait loci associated with variation for yield in ZT. In the review by Herrera et al. (2013), G × T effects on yield were significant in eight cases and in six they were not. One important concern mentioned by the authors was that almost all genotypes were selected under CT. Therefore, it is possible that adaptation to ZT and G × T is limited.

In our study, CIMMYT durum wheat (*Triticum turgidum*) and bread (common) wheat (*Triticum aestivum*) genotypes, developed between 1964 and 2009, were grown over six consecutive years in four agronomic environments, including conventionally tilled (CB) and permanent raised beds (PB), each with full (FI) and reduced irrigation (RI). The objectives were (1) to study breeding progress in CIMMYT-derived wheat genotypes in four distinct agronomic treatments and (2) to shed further light on the importance of tillage and G × T interaction for yield and agronomic traits.

2. Materials and methods

2.1. Plant material

The bread and durum wheat genotypes used were developed by CIMMYT breeding programs. Thirteen durum wheat genotypes created between 1970 and 2009 and thirteen bread wheat genotypes developed between 1964 and 2006 were screened for growth and agronomic traits. The wheat materials included a basic set of historically important CIMMYT varieties and the best materials that were available from the CIMMYT breeding programs when the study initiated. All genotypes were selected under CT conditions. In earlier years flat planting was used, while bed systems were established in the early 1990's. A full list of genotypes is provided in Table S1.

2.2. Experimental set-up

The experiments were conducted during the winter growing seasons (November to May) 2009/10 to 2014/15 at CIMMYT's experimental station near Ciudad Obregon, Sonora, in northwestern Mexico (lat. 27.33 N, long. 109.09 W, 38 masl). The station is characterized by an arid climate with highly variable rainfall. Mean annual precipitation is 308 mm (1993–2015). During the growing seasons used in the study, average rainfall was 55 mm with large differences between years, ranging from 5 to 122 mm. Annual reference evaporation is approximately 1800–2000 mm (Verhulst et al., 2011a,b,c,d). Long-term mean annual temperature is 23.5° C (1993–2015) with monthly mean temperatures ranging from 16° C in January to 31° C in July/August. According to the World Reference Base the soil is classified as a Hyposodic Vertisol (Calcaric, Chromic) (Verhulst et al., 2009).

Agronomic performance of bread and durum wheat genotypes was determined in four distinct agronomic systems, each corresponding to a different environment and all involved sowing on raised beds: 1) conventionally tilled beds with full irrigation (CB-FI), 2) conventionally tilled beds with reduced irrigation (CB-RI), 3) permanent beds with full irrigation (PB-FI), and 4) permanent beds with reduced irrigation (PB-RI). Permanent beds and conventionally tilled treatments were located in adjacent blocks. Permanent beds were reshaped when necessary, but the top of the beds were not tilled. Prior to experiment initiation, the PB area had been under ZT for three years. In autumn 2005 the entire experimental area was tilled (one pass with a chisel plough to 50 cm and a moldboard plough to 40 cm and two passes with a disc plough to 20 cm). In subsequent years beds were reshaped without tillage prior to planting in PB environments. In CB environments soil was tilled after harvest and before sowing with a disk plough to 20 cm. New beds were formed before planting. The trial was irrigated during the summer fallow period to germinate weeds and volunteers. These were controlled with glyphosate under PB and tillage under CB (Verhulst et al., 2011a).

Bread and durum wheat genotypes were tested with three replicates together in the same randomized complete block design. Each plot was 8 m^2, consisting of two 80 cm wide and 5 m long beds sown with two rows of wheat with 26 cm distance between rows and at a sowing density of 250 seeds m^{-2}. In all agronomic systems a seeding irrigation was applied. Full irrigation treatments received three or four additional irrigations (approximately 520 mm water per season), to avoid moisture stress; RI treatments received one additional irrigation at around heading (approximately 240 mm per season). Irrigation was

Table 1
Abbreviation and definition of 14 investigated traits.

Abbreviation	Trait definition
DaGr	Days from flowering to maturity
FLO	Days to flowering, measured in days after emergence
GPR	Grain production rate from flowering to maturity [kg ha^{-1} day^{-1}]
Grm2	Number of grains per m^2
GrSp	Number of grains per spike
HEI	Plant height [cm]
HI	Harvest index, calculated from 50 stems
MAT	Days to maturity, measured in days after emergence
NDVI1	NDVI, early vegetative growth
NDVI2	NDVI, maximum growth (highest recorded NDVI value)
Spm2	Spikes per m^2
TGW	Thousand grain weight [g]
TWT	Test weight [kg hL^{-1}]
YLD	Grain yield at 12% moisture [kg ha^{-1}]

applied as furrow irrigation. At the start of the season, 103 kg N ha^{-1} and 23 kg P ha^{-1} was applied as a band application in the center of the beds. At first node, the RI treatment received an additional 100 kg N ha^{-1} and the FI treatment received 175 kg N ha^{-1} banded in the furrow. Weeds, pests, and diseases were controlled chemically. Fungicides for rusts (*Puccinia* sp.) were applied preventively. The trial was sown between end of November and beginning of December. With the exception of season 2010/11, where seeding irrigation was applied three days after sowing, all other sowing received pre-sowing irrigation approximately 21 days prior to sowing. In 2011/12 due to an atypical rainfall event, the experiment was sown into residual moisture. Harvest took place between end of April and beginning of May.

2.3. Data collection

Weather data were obtained from a weather station approximately 2 km from the experimental site.

During the six growing seasons, 14 growth and agronomic traits were measured for all wheat genotypes (Table 1). During the growing period days from emergence to flowering (FLO), plant height (HEI), and days to maturity (MAT) were recorded. Plant growth was approximated by the normalized difference vegetative index (NDVI) using a GreenSeeker™ Handheld Optical Sensor Unit (NTech Industries, Inc., USA). Throughout the experiment, NDVI readings were recorded at regular intervals and growth curves were created based on the obtained data. For analysis, two values were selected; one measurement during early (vegetative) growth (NDVI1), around four weeks after planting, and the maximum NDVI value (NDVI2). After maturity, 50 stems were cut and their total weight and grain weight determined to calculate harvest index (HI) (Pask et al., 2012). Plots were combine harvested and grain weight and moisture content determined to calculate yield at 12% moisture content (YLD). After harvest, thousand grain weight (TGW), and test weight (TWT) were measured. Grain filling was determined as days from flowering to maturity (DaGr), grain production rate as yield divided by the days from flowering to maturity (GPR) expressed in kg ha^{-1} day^{-1}. The number of spikes per m^2 (Spm2), number of grains per m^2 (Grm2), number of grains per spike (GrSp) were also calculated.

2.4. Statistical analysis

Statistical analysis was completed using SAS 9.4 (SAS Institute, 2013). Pearson's correlation coefficients were calculated using PROC CORR. Correlation analyses were conducted separately for bread and durum wheat, across agronomic systems and separately for agronomic systems. Across years trait means for each genotype were also calculated.

A linear mixed model was conducted using PROC MIXED by wheat type and in a second analysis by wheat type and irrigation regime. Agronomic system, genotype, agronomic system*genotype, and block nested in agronomic system were treated as fixed effects. Year, agronomic system*year, genotype*year, and agronomic system*genotype*year were considered random effects. Variables were considered statistically significant if $P < 0.05$. Means and standard errors for traits were calculated with PROC MIXED. Multiple pairwise means separation tests were conducted using the Tukey Honestly Significant Difference method (Kramer, 1957, 1956; Tukey, 1953) at 95% confidence level using the%PDMIX800 macro within SAS 9.4 (Saxton, 1998).

Regression analysis was completed using a standard linear model. Genotype means, calculated for each agronomic system, were used to calculate rates of change for all traits with year of creation:

$$y_i = a + bx_i + u$$

where y_i is the trait mean of i^{th} genotype, x_i is the creation year of the ith genotype, a is the intercept, b is the slope and u is the residual error.

3. Results

3.1. Experimental conditions

Fig. 1 shows monthly evapotranspiration, precipitation, minimum, maximum, and average temperatures from 2009 to 2015. Average annual temperature and total precipitation during the six experimental years were similar to the long term average. The average temperature for the six years was 23.7 °C (range 22.7–24.7 °C), compared to the long term average of 23.5 °C. In early February 2011 frost occurred during three consecutive days, which was approximately 60 days after sowing and may have affected flower development. Precipitation varied widely between years, which is common in the region. The lowest rainfall (161 mm) was recorded in 2011 and the highest in 2010 (545 mm). The average rainfall over six years was 344 mm, 36 mm more than the long term average of 308 mm. During the study period, around 15% of precipitation occurred during the growing seasons (November to May), with a range of 3% to 27%.

3.2. Correlations

3.2.1. Bread wheat

Early plant growth (NDVI1) showed high correlations with NDVI2 ($r = 0.79$) and HEI ($r = 0.91$). Early plant growth was moderately correlated with GPR and yield with $r = 0.62$. Correlation between NDVI1 and TGW was $r = 0.79$, similar to the correlation between TGW and YLD with $r = 0.73$ (Table 2). In all agronomic systems YLD had the highest correlation to GPR ($r = 0.85$ to $r = 0.96$) because GPR is a calculated derivative of YLD. TGW also significantly correlated to YLD in all four agronomic systems ($r = 0.69$ to $r = 0.75$) (Table 3). Early vegetative growth moderately correlated to YLD under PB-RI. In the other three systems correlation was low ($r = 0.52$ to 0.59; CB-FI n.s.). Maximum growth showed statistically significant correlations to YLD under RI but not under FI (Table 3).

3.2.2. Durum wheat

In durum wheat the highest correlation was detected between YLD and GPR ($r = 0.93$) as observed for bread wheat. Very high correlations were also observed between TGW and HI ($r = 0.90$) and between Grm2 and FLO time ($r = 0.89$). Yield also correlated well with FLO ($r = 0.78$), Grm2 ($r = 0.68$), and GrSp ($r = 0.66$) (Table 4). The number of grains per spike was significantly correlated with YLD in all four agronomic systems ($r = 0.57$ to $r = 0.66$) (Table 5). In contrast to bread wheat, TGW did not correlate with YLD in durum wheat. Correlation between NDVI1 and YLD was not significant but showed a negative trend in FI. In RI significant correlations between NDVI2 and

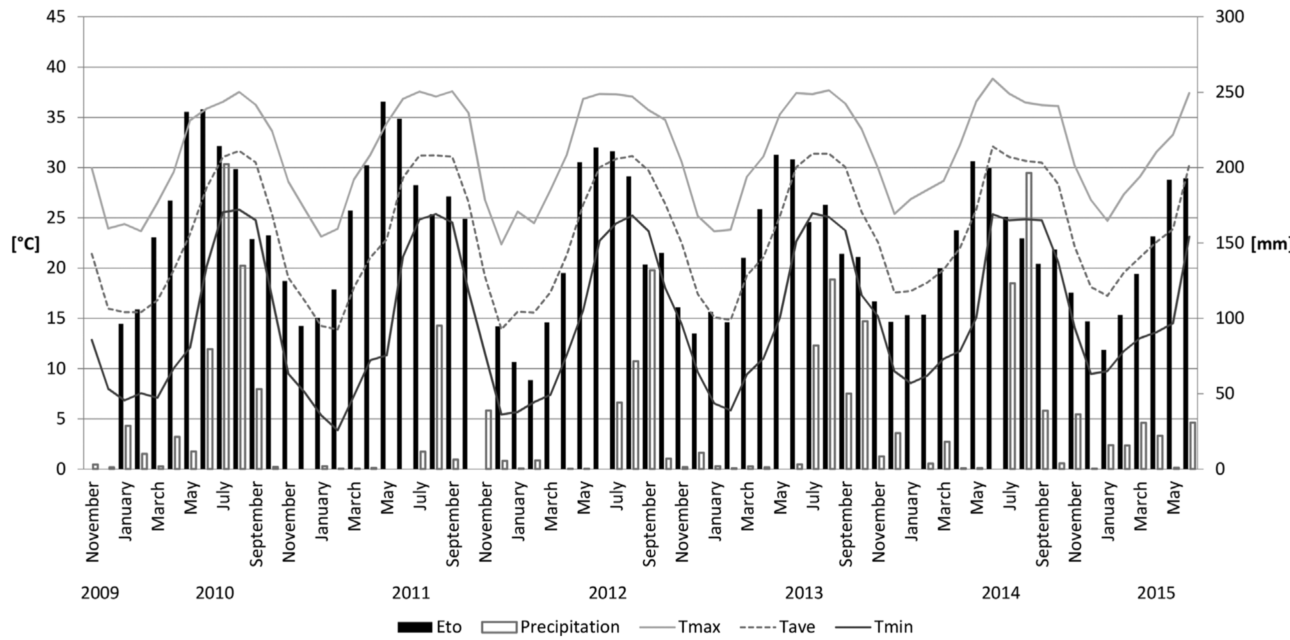

Fig. 1. Monthly climate conditions for the growing season November 2009 to May 2015 at the experiment station near Ciudad Obregon. Minimum and maximum temperatures are monthly average temperatures.

YLD were observed on CB (r = 0.76) and PB (r = 0.63) (Table 5).

3.3. Breeding progress and trait performance

3.3.1. Bread wheat

3.3.1.1. Crop growth. Early vegetative growth differed more between the two tillage systems CB and PB than between FI and RI. On CB under FI NDVI1 genotype means ranged between 0.47 and 0.61, and were similar to the RI means (0.45–0.62). On PB NDVI1 was lower than on CB, with PB-FI genotype means of 0.37–0.48 and PB-RI values of 0.39–0.52. There were differences in early plant vigor with a trend towards increase early vigor from older genotypes to more recent ones. Lowest NDVI1 was recorded for a genotype created in 1985 and highest for a genotype created in 2000. The regression of NDVI1 on year of creation was positive in all four agronomic systems and the effect was significant for PB-FI, PB-RI, and CB-FI, whereas the effect was marginally significant for CB-RI (P = 0.06; Tables S6 and S7).

Maximum NDVI ranged between 0.7 and 0.87 and, thus, had a smaller range than NDVI1. Maximum NDVI of the oldest genotypes was generally very similar to the newest ones, but with the smallest value for NDVI2 observed in a genotype from 1979. Differences between the agronomic systems were small, but CB-FI consistently performed best

Table 3
Bread wheat; Correlations of yield with 13 traits separately for each agronomic system.

	CB-FI	CB-RI	PB-FI	PB-RI
NDVI1	0.52	**0.59**	**0.57**	**0.72**
NDVI2	0.31	**0.63**	0.48	**0.59**
HEI	0.37	**0.68**	0.47	**0.73**
FLO	0.16	−0.39	−0.25	**−0.68**
MAT	−0.18	−0.26	−0.35	−0.53
Spm2	−0.36	−0.08	−0.12	0.08
DaGr	−0.36	0.38	−0.02	0.55
GPR	**0.92**	**0.85**	**0.95**	**0.96**
Grm2	0.11	−0.23	−0.02	0.24
GrSp	0.46	−0.06	0.10	0.02
HI	0.37	0.13	0.46	0.23
TGW	**0.70**	**0.75**	**0.69**	**0.73**
TWT	0.40	0.26	0.47	0.45

Bold numbers indicate statistically significant (P < 0.05) correlations; trait abbreviations: see Table 1.

Table 2
Pearson correlation coefficients between traits across agronomic systems for bread wheat (N = 13).

	NDVI2	HEI	FLO	MAT	Spm2	DaGr	GPR	Grm2	GrSp	HI	TGW	TWT	YLD
NDVI1	**0.79**	**0.91**	0.05	0.01	−0.27	−0.08	**0.62**	−0.51	−0.02	−0.36	**0.79**	−0.19	**0.62**
NDVI2		**0.70**	0.08	0.03	0.10	−0.10	**0.58**	−0.04	−0.18	−0.54	0.44	0.04	**0.55**
HEI			−0.08	−0.19	−0.35	−0.08	**0.57**	−0.52	0.06	−0.42	**0.75**	−0.05	**0.55**
FLO				**0.83**	−0.22	**−0.76**	0.02	−0.13	0.16	−0.43	−0.16	**−0.69**	−0.27
MAT					0.02	−0.27	−0.19	−0.10	−0.09	−0.43	−0.20	**−0.72**	−0.29
Spm2						0.40	−0.36	**0.60**	**−0.84**	−0.16	−0.54	0.27	−0.22
DaGr							−0.26	0.11	−0.38	0.24	0.04	0.34	0.13
GPR								−0.05	0.35	0.15	**0.67**	0.16	**0.92**
Grm2									−0.07	0.10	**−0.71**	0.41	−0.04
GrSp										0.26	0.17	−0.10	0.20
HI											0.12	0.27	0.26
TGW												−0.04	**0.73**
TWT													0.29

Bold numbers indicate statistically significant (P < 0.05) correlations; trait abbreviations: see Table 1.

Table 4
Pearson correlation coefficients between traits across agronomic systems for durum wheat (N = 13).

	NDVI2	HEI	FLO	MAT	Spm2	DaGr	GPR	Grm2	GrSp	HI	TGW	TWT	YLD
NDVI1	0.34	−0.32	−0.32	**−0.57**	−0.48	−0.23	−0.24	**−0.63**	−0.38	0.34	**0.59**	−0.05	−0.30
NDVI2		0.31	**0.73**	0.21	0.25	**−0.72**	**0.64**	0.40	0.39	−0.34	−0.25	0.50	0.55
HEI			0.48	0.17	0.51	−0.44	0.35	**0.63**	0.43	**−0.72**	**−0.76**	0.34	0.14
FLO				**0.68**	**0.71**	**−0.56**	**0.81**	**0.89**	0.52	**−0.64**	**−0.70**	0.43	**0.78**
MAT					0.52	0.23	0.28	**0.67**	0.34	−0.51	**−0.60**	0.11	0.46
Spm2						−0.34	0.43	**0.80**	−0.04	**−0.81**	**−0.84**	−0.13	0.34
DaGr							**−0.75**	−0.42	−0.30	0.27	0.24	−0.47	−0.52
GPR								**0.72**	**0.66**	−0.25	−0.38	**0.69**	**0.93**
Grm2									0.55	**−0.74**	**−0.89**	0.34	**0.68**
GrSp										−0.13	−0.32	**0.79**	**0.66**
HI											**0.90**	0.04	−0.13
TGW												−0.07	−0.27
TWT													**0.66**

Bold numbers indicate statistically significant ($P < 0.05$) correlations; trait abbreviations: see Table 1.

Table 5
Durum wheat; Correlations of yield with 13 traits separately for each agronomic system.

	CB-FI	CB-RI	PB-FI	PB-RI
NDVI1	−0.43	0.04	−0.50	0.07
NDVI2	0.40	**0.76**	0.31	**0.63**
HEI	0.30	0.13	0.19	−0.07
FLO	**0.77**	0.54	**0.74**	**0.62**
MAT	**0.65**	0.01	**0.59**	0.03
Spm2	0.28	0.15	0.38	0.12
DaGr	−0.28	−0.49	−0.37	**−0.75**
GPR	**0.91**	**0.87**	**0.92**	**0.94**
Grm2	**0.77**	0.48	**0.73**	0.53
GrSp	**0.66**	**0.57**	**0.63**	**0.61**
HI	0.19	−0.02	−0.05	0.02
TGW	−0.17	−0.15	−0.20	−0.13
TWT	**0.75**	0.54	**0.75**	**0.57**

Bold numbers indicate statistically significant ($P < 0.05$) correlations; trait abbreviations: see Table 1.

and PB-RI the worst. Regression of trait performance on year of creation was only significant for PB-RI.

3.3.1.2. Physiological and agronomic traits. Plant height ranged between 74 and 107 cm (Table S2), but tillage type did not have significant impact on differences in trait performance (Table S4). Irrigation regime, however, influenced HEI significantly (Table S5), with FI plants growing taller (84–107 cm) than RI plants (74–91 cm). There was no trend in height associated with year of genotype creation.

Flowering time varied widely between genotypes. As for HEI, tillage system did not have a significant influence on FLO, but irrigation did. Under FI, plants flowered between 80 and 87 days after emergence, whereas RI plants flowered earlier; between 75 and 81 days after emergence. The regression of FLO on year of creation was not significant. Earliest and latest flowering was observed in genotypes from the 1980's.

For MAT and DaGr the results were similar to FLO. Trait performance was significantly influenced by irrigation regime, but not tillage. Moreover, there was no breeding trend over years, but values fluctuated. Maturity ranged between 127 and 132 days after emergence under FI and between 117 and 122 days under RI. Days from flowering to MAT ranged from 44 to 50 days with FI and from 39 to 43 under RI.

3.3.1.3. Yield and yield related traits. Grain production rate breeding progress was detected at statistically significant levels in CB-FI, PB-FI, and PB-RI. For CB-RI the regression of GPR on year of creation was not statistically significant ($P = 0.09$) but the trend was the same as observed in the other three agronomic systems (Tables S6 & S7). Grain production rate ranged from 131 to 181 kg ha^{-1} day^{-1} for FI and from 95 to 124 kg ha^{-1} day^{-1} for RI conditions.

For TGW significant breeding progress was observed in all four agronomic systems (Fig. 2). Under FI TGW ranged between 32 and 45 g. The mixed model analysis identified a significant difference between PB and CB under RI conditions, with TGW between 29 and 39 g for CB-RI and 27–37 g for PB-RI.

Breeding progress for YLD was statistically significant in all four investigated environments (Fig. 2 and Table S6). The highest coefficient of determination was $R^2 = 0.69$ for PB-FI. For CB-FI the R^2 was 0.59. Under RI, R^2 was smaller (CB-RI = 0.35, PB-RI = 0.36). Yield of the 13 investigated genotypes ranged between 6.2 and 8.0 t ha^{-1} under FI and between 3.8 and 5.1 t ha^{-1} under RI conditions. The average annual yield increase was 36.8 kg ha^{-1} for PB-FI, 35.9 kg ha^{-1} for CB-FI, 22.3 kg ha^{-1} for PB-RI, and 12.6 kg ha^{-1} for CB-RI.

The five yield related traits GrSp, Grm2, HI, Spm2, and TWT did not show significant regression of trait performance on year of creation with the adjusted R^2 ranging between −0.09 and 0.12. The number of grains per spike ranged between 37 and 52 under FI and between 28 and 42 under RI. For Grm2 the oldest and newest genotypes had a similar performance, and under FI between approximately 14,000 and 19,000 grains per m^2 were produced. Harvest index ranged from 42 to 50% and there were no statistically significant differences between tillage or irrigation regimes. For Spm2 no effect of irrigation was detected in CB. For CB and PB-FI, Spm2 was between 302 and 476, but in PB-RI the average numbers were lower; 278–398 spikes per m^2. Test weight under FI conditions ranged between 79 and 82 kg hL^{-1}. Under RI there were differences between CB and PB. Under CB-RI, TWT was between 77 and 81 kg hL^{-1} and under PB-RI test weight was lower, ranging from 75 to 79 kg hL^{-1}.

3.3.2. Durum wheat

3.3.2.1. Crop growth. Early vegetative crop growth decreased with year of creation. This trend was visible and significant in all four agronomic systems. NDVI1 values ranged from 0.31 to 0.43 in CB, from 0.25 to 0.31 in PB-FI, and from 0.26 to 0.34 in PB-RI. For NDVI2 no breeding progress was observed. Under FI NDVI2 values ranged between 0.8 and 0.86 and under RI between 0.73 and 0.83. Differences between tillage types were not significant, but plants on CB performed slightly better (Tables S6 and S8).

3.3.2.2. Physiological and agronomic traits. Plant height was between 86 and 98 cm for FI and ranged from 71 to 85 cm for RI. The regression of HEI on year of creation was not statistically significant. Breeding progress was observed for FLO in all four agronomic systems. The newer genotypes flowered between three and four days later than the oldest genotype. R^2 for FLO on year of creation ranged between 0.39 and 0.53; highest values were observed under PB conditions. Days to flowering ranged from 75 to 83 days after emergence under FI and from

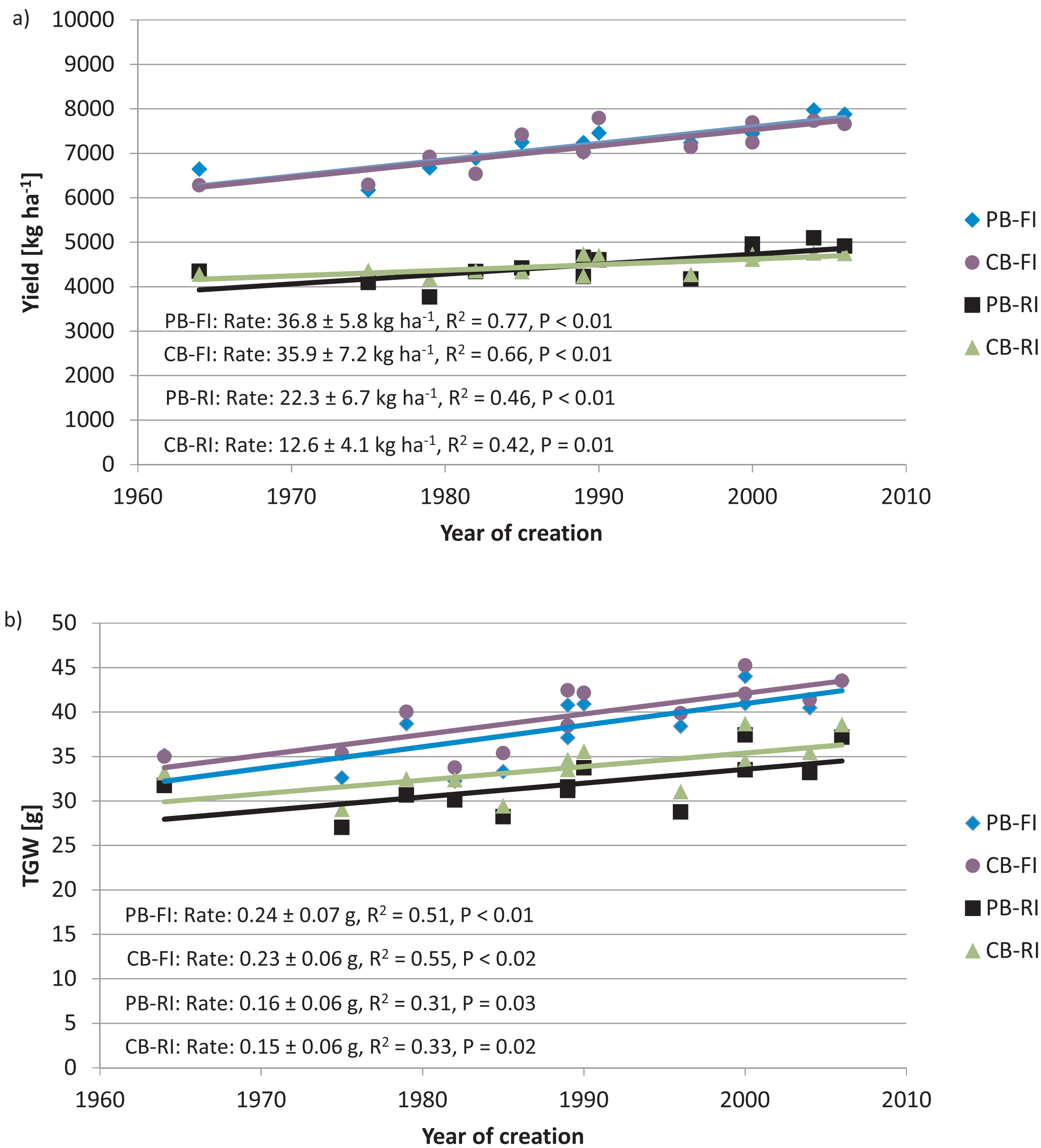

Fig. 2. Breeding progress for bread wheat yield (a) and TGW (b) from 1964 to 2006. Regression lines indicate statistical significance ($P < 0.05$).

72 to 77 days under RI.

Days to maturity ranged from 124 to 129 with FI and 114–119 in RI. The regression of MAT on year of creation was statistically significant for PB-FI ($R^2 = 0.27$). However, the oldest genotype matured around the same time as the newer genotypes. No breeding progress was observed for DaGr, which ranged from 44 to 51 under FI and 39–44 days under RI.

3.3.2.3. Yield and yield related traits. For six of the seven traits, significant regression of trait performance on year of creation was recorded for at least one agronomic system (Tables S6 and S8). Harvest index was the only trait where no significant effect was observed, but ranged from 46 to 53% under FI and 37–49% under RI.

Yield and number of grains per m^2 improved over time under all tested conditions. Grain production rate significantly improved in all systems except CB-RI. R^2 for the three traits was between 0.3 and 0.67, with highest values for plants grown under FI. Yield was between 3.8 and 5.1 t ha^{-1} under RI and between 6.5 and 8.7 t ha^{-1} under FI (Fig. 3). Average annual yield increase was 30.1 kg ha^{-1} for PB-FI, 28.1 kg ha^{-1} for CB-FI, 11.8 kg ha^{-1} for PB-RI, and 9.5 kg ha^{-1} for CB-RI. Grains per m^2 ranged from 6721 to 11,741 under RI and from 11,401 to 17,716 under FI. Grain production rate was between 135 and 189 kg ha^{-1} day^{-1} under FI and between 94 and 134 kg ha^{-1} day^{-1} under RI conditions.

Grains per spike and TWT had a significant regression of trait performance on year of creation under FI. Adjusted R^2 for GrSp was 0.44 for CB-FI and 0.3 for PB-FI. However, under PB-RI a trend towards higher GrSp was visible, although the trend was not statistically significant ($P = 0.064$). The number of grains per spike was between 39 and 54 under FI and 26 and 38 under RI. For TWT the adjusted R^2 was 0.33 in CB-FI and 0.26 in PB-FI. Test weight ranged between 81 and 84 kg hL^{-1} under FI and CB-RI and was slightly lower (80–83 kg hL^{-1}) under PB-RI.

Thousand grain weight ranged from 34 to 52 g with no effect of agronomic system observed. Under RI, TGW decreased from oldest to newest genotypes (adjusted R^2 was 0.28 under CB-RI and 0.37 under PB-RI).

The number of spikes per m^2 was not influenced by agronomic system and ranged between 245 and 409. A positive trend of breeding progress towards more spikes per m^2 was observed in all four systems

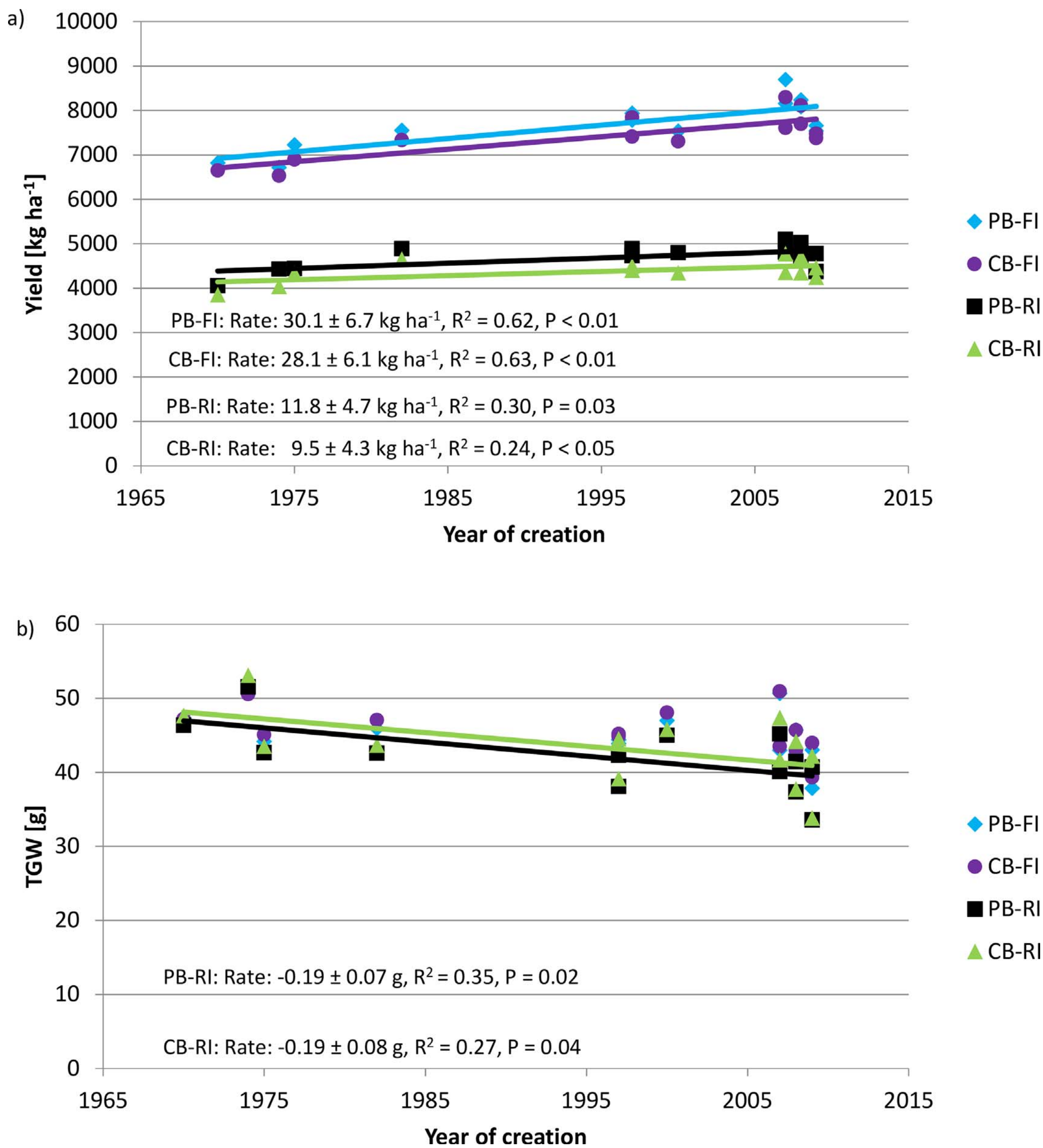

Fig. 3. Breeding progress for durum wheat yield (a) and TGW (b) from 1970 to 2009. Regression lines indicate statistical significance ($P < 0.05$).

but was only significant under PB-RI ($R^2 = 0.29$).

3.4. Genotype, system, and genotype × system effects

3.4.1. Bread wheat

For bread wheat the genotype had a significant effect on all investigated traits (Tables S3–S5). Tillage system influenced Grm2 and NDVI1 under FI. Grains per m^2 were increased under PB to 16,632 compared to 15,939 grains per m^2 in CB. Early vegetative growth was higher with CB with an average NDVI of 0.53 compared to 0.42 on PB. Under RI the tillage effect was significant for NDVI1, NDVI2, TGW, and TWT. On average, better trait performance (higher value) was achieved under CT (Table S2). The average value of NDVI1 was 0.55 on CB compared to 0.45 on PB. Maximum NDVI was 0.82 on CB and 0.77 on PB. Thousand kernel weight was slightly higher on CB as well; 33.7 g compared to 31.9 g on PB. Test weight was also slightly increased with CB. The average TWT with CB was 78.9 kg hL^{-1} compared to 77.5 kg hL^{-1} under PB conditions.

Under FI, G × T was observed for GPR, HEI, TGW, and YLD. Under RI treatment G × T was observed for GPR, Grm2, NDVI2, and YLD.

3.4.2. Durum wheat

In durum wheat, genotype had a significant influence on performance of all investigated traits (Tables S3–S5). The tillage system had less influence compared to bread wheat. Under FI, NDVI1 was reduced under PB conditions (0.28) compared to CB (0.38) and also under RI conditions; PB (0.31) compared to CB (0.39). The number of grains per m^2 was higher in PB (10,159) than CB (9199). The G × T effect was only significant for NDVI2 under RI.

4. Discussion

4.1. Breeding progress

In comparison to many previous studies on yield progress, wheat genotypes from the early 20th century were not included in this study. The oldest bread wheat genotype was from 1964 and the oldest durum wheat genotype from 1970. These genotypes were developed after the introduction of the two semi dwarfing genes *Rht-B1b* (*Rht1*) and *Rht-D1b* (*Rht2*) (Peng et al., 1999) to the CIMMYT breeding programs. Therefore, all genotypes considered are semi-dwarf. For this reason no major breeding progress on plant height and harvest index was observed. These two factors, which were largely responsible for early yield increases in the 20th century (Austin et al., 1980), were not of importance for yield improvement of the investigated genotypes.

4.1.1. Bread wheat

In bread wheat, statistically significant breeding progress was observed for five traits. For NDVI2, progress was only observed in PB-RI. For NDVI1 and GPR, breeding progress was observed in three environments (not in CB-RI), and for yield and TGW in all four. Even when breeding progress was not statistically significant for all four agronomic treatments, a tendency toward breeding progress was apparent. In all cases, adjusted R^2 was higher under FI conditions than under RI and, thus, most statistically significant effects were detected under FI. Only two effects were observed with CB-RI, while with PB-RI there were five effects. Although heritability was high for most traits, in general it was lower under reduced irrigation conditions, with lowest values under CB-RI, and this may explain why fewer effects were detected for this condition. For grain production rate, a broad-sense heritability (H^2) of 56% for CB-RI was considerably lower than for the three remaining agronomic systems, where H^2 for this trait was about 90% (for details on heritability values, see Table S9). It has been observed in many studies that experiments under stress conditions (e.g. reduced irrigation) are difficult to reproduce, since it is difficult to repeat the exact stress situation (Poorter et al., 2012). Under reduced irrigation, soil water content tended to be slightly higher for PB than CB between planting and heading stage, when the first auxiliary irrigation was given (data not shown). During this phase, the stress can be expected to be slightly higher with CB and this may be the reason why the least effects were detected under CB-RI conditions. It also shows that it is more difficult to achieve improvements under stress conditions and that crops need to have a broad adaptation to succeed under varying stress conditions. Another important reason could be that a majority of the genotypes included in the study were released for FI conditions, as this is the main production system in southern Sonora. Despite this, yield improvements in all tested systems show that adaptation to a range of production systems is present in CIMMYT germplasm.

The strongest yield progress was observed under FI, which was expected due to the release of most of the genotypes specifically for these conditions. This is reflected in the high heritabilities of 95% and 93% for PB and CB, respectively. Between 1964 and 2006 yield was increased by 0.60% (35.9 kg ha^{-1}) and 0.62% (36.8 kg ha^{-1}) per year under CB-FI and PB-FI, respectively. Yield increase under FI was similar for both tillage systems, which is an observation also made by Kitonyo et al. (2017). They tested 14 Australian wheat varieties released between 1958 and 2011 under conventional tillage and no-till and observed a yield increase of 21 kg ha^{-1} yr^{-1}, irrespective of tillage system.

Under CB-RI a yield progress of only 0.31% per year was lower than under FI. In contrast, breeding progress under PB-RI was 0.56%, which was almost as high as under FI. Again, this is reflected in differences in heritability between the two tillage systems. Under PB-RI, heritability was as high as under FI conditions, whereas under CB-RI it was only 74%. While under RI older genotypes had poorer performance on PB than CB, yield progress was stronger on PB, and genotypes released after 1995 performed better under PB-RI than CB-RI. It is possible that better water availability on PB, especially early in the season during floret formation, led to higher yield progress under RI conditions.

The observation of higher yield progress in more favorable environments (better water availability, in this case) is in accordance with De Vita et al. (2007), who conducted yield progress experiments with durum wheat under different nitrogen fertilization levels. They found that genetic gains in grain yield, kernels m^{-2}, and protein yield were greatest under the best nitrogen availability. This highlights the importance of good agronomic practices to take advantage of breeding progress.

Bread wheat yield was highly correlated to GPR and TGW. Grain production rate is calculated as grain production from flowering to maturity in kg ha^{-1} day^{-1}. Thus, it is a derivative of yield, which explains its high correlation. In opposition to early modern varieties, yield increase in the investigated set could not be explained by increased HI. Instead, the increase of TGW over time and the strong correlation (r = 0.73) with YLD indicate that an increase of kernel weight was an important factor for yield improvement between 1964 and 2006. Qin et al. (2015) tested more than 1850 Chinese wheat varieties released between 1920 and 2014. They found that the yield of varieties released between 1980 and 2014 had positive correlations with TGW and kernel number per spike, and that breeding progress had been achieved for these three traits. Sanchez-Garcia et al. (2015) studied dry matter accumulation and partitioning in Spanish bread wheat varieties released during the 20th century. They described that in varieties released after 1972, HI did not change considerably. They observed higher spike weight and argued that enhanced photosynthesis in the last phase of plant development contributed to increased grain filling in modern varieties.

4.1.2. Durum wheat

In contrast to bread wheat, breeding progress was observed for almost all traits (ten out of fourteen) in durum wheat in at least one agronomic system.

Days to flowering increased from 1970 to 2009 by about three to four days, depending on agronomic system. Later flowering can be an advantageous trait in regions where frost during flowering is a risk. This is the case in the Yaqui valley, where this experiment was conducted. De Vita et al. (2007) observed a decrease in heading time from 1900 to 1970 by about 13 days, subsequently, until 1990 when heading date slightly increased again. Days to maturity increased slightly in the CIMMYT material, however, the effect was only statistically significant under PB-FI. Waddington et al. (1987) found that CIMMYT varieties released in the early 1970's matured slightly earlier than varieties released later and until 1985. This trend was not observed in Italian durum material released between 1900 and 1990. The overall trend described by De Vita et al. (2007) was a decline in days to maturity. However, the data for varieties released between 1970 and 1990 appeared more as a cluster and did not present a clear negative trend.

Earlier flowering is a desired trait to prolong grain filling. In regions with late season drought, early flowering ideally is combined with earlier maturity to escape drought during grain filling. In contrast to earlier studies (De Vita et al., 2007; Waddington et al., 1987) we did not observe changes in grain filling period due to simultaneous increase in both FLO and MAT.

Durum wheat yield increases over time of creation was observed in all four agronomic environments. The relative increase over 39 years was higher in FI than in RI environments, where gains for CB-FI was about 0.45% and 0.47% in PB-FI, while under RI the annual increase was lower, 0.27% in CB-RI and 0.31% in PB-RI. Higher yield increases under FI was reflected in a very high heritability of around 95% (Table S9) compared to lower values of 76.7% for PB-RI and 63.4% for CB-RI. Yield increase was higher on PB under both FI and RI, a trend common to both bread wheat and durum wheat. Improved water availability in PB (Verhulst et al., 2010) possibly enabled wheat plants to realize a greater part of their yield potential.

Yield increases for durum wheat have been described in several studies. De Vita et al. (2007) studied breeding progress in Italian durum cultivars released between 1900 and 1990 and found an average annual increase of 19.9 kg ha^{-1}. A similar annual increase was observed by Pecetti and Annicchiarico (1998). They tested Italian durum landraces and genotypes developed until the 1970's in moderately favorable environments in Syria and found an average annual yield increase of 17 kg ha^{-1}. McCaig and Clarke (1995) also report an average annual yield increase of 17 kg ha^{-1} due to breeding progress in their analysis of Canadian durum wheat varieties.

Significant correlations were detected between YLD and GrSp in all agronomic environments. The importance of GrSp for YLD in durum wheat was also described by García Del Moral et al. (2003). Correlation between YLD and Grm2 also played a role, but was only significant under FI. Breeding progress for Grm2 was significant in all environments, while GrSp was only improved under FI. Isidro et al. (2011) reported that the number of fertile florets per spikelet and per spike did not change over time. However, they observed a decrease of floret abortion by 24% in modern (released in or after 1988) varieties than those released prior to 1946. They discuss favorable conditions for floret development, like extended period from booting to anthesis and improved carbon partitioning to the spikes. In our trial breeding, progress for Grm2 was not significant under RI, especially on CB, where drought stress tends to be more pronounced than in PB. The explanation may be in the observation made by Isidro et al. (2011), that under water deficit the favorable longer time for floret development cannot be used effectively.

Correlation between Grm2 and GrSp had a positive trend but was only statistically significant under CB-RI. Correlations between Grm2 and Spm2 were moderate to strong and statistically significant in all agronomic systems. For Grm2, Spm2 appears to be more important than GrSp. In terms of breeding progress GrSp was more important under FI and Spm2 under RI. Royo et al. (2007) reported breeding progress for number of spikes per plant, number of grains per spike, and number of grains per m^2. Although the material they tested had a much higher range in terms of release date than our material, they did not observe significant changes in TGW over time. However, they did find a slight decrease in TGW over time. This corresponds to the effect we detected in our experiments, where a decrease in TGW was significant under RI and a similar trend was also visible under FI. De Vita et al. (2007) found a positive TGW trend from 1900 to 2000. However, seed weights varied widely and grain weights did not continuously rise.

4.2. Tillage and genotype × tillage interaction effects

Overall tillage effects were few. More effects were observed under RI than under FI, in accordance with the observation that greatest differences between tillage systems are found under water-limited conditions. Reduced tillage, especially with crop residue retention, is known to improve water holding capacity and reduce evaporation and, thus, improve water availability to plants (Verhulst et al., 2011c). Under water-limited conditions, like the RI regime in our experiment, differences between CB and PB beds might be greater than when water is sufficiently available. The tillage effect, in this case, would therefore be an effect of water availability. Yield progress and average yield (not statistically significant) were higher under PB for both irrigation regimes and wheat types.

Even though a trend of higher yield on PB was apparent, the mixed model revealed only a small number of significant tillage effects. Number of grains per m^2 tended towards higher values on PB than on CB. The effect was significant for bread wheat under FI and durum wheat under RI. Early plant growth of bread and durum wheat on CB outperformed plants on PB, irrespective of irrigation regime. This supports the findings of Verhulst et al. (2011a), who reported that early plant growth was slower in PB, due to physical and biological constrains (Watt et al., 2005). Thousand grain weight, NDVI2, and TWT also showed a slight trend towards higher values under CB. However, the effect was only significant for bread wheat under RI.

Few G × T interactions were observed. For durum wheat no interaction was observed under FI and only one under RI. Maximum NDVI showed an interaction with tillage system. However, no crossover effects were detected. Two out of 13 genotypes performed equally well under PB and CB. The other genotypes showed lower performance but with varying relative performance compared to CB, leading to several rank changes. While it was expected to see higher NDVI values under PB with reduced irrigation than on CB, as an approximation for biomass production, we observed the opposite effect. It is possible that the imposed drought stress was not severe enough to express the water conserving effect of PB and, thus, growth impeding factors of zero tillage and crop residues were observed. The method of applying stress may also have played a role. Under rainfed conditions, CA allows better infiltration in the case of heavy rainfalls, resulting in more water availability compared to conventional systems. In the irrigated experiments, the soil profile under both tillage treatments became saturated equally after each irrigation.

CIMMYT material is known to be adapted to a wide range of environments. This might also be a reason why genotype performance was stable across agronomic environments in our experiment and few G × T interactions were found. Not many studies on G × T interaction in durum wheat have been published. Thompson and Hoag (1987) studied durum wheat under ZT. They found no differences in yield and test weight between CT and ZT.

In bread wheat, a G × T interaction was observed for YLD and GPR in FI and RI with cross over effects as well as rank changes within the tested genotypes. One reason why more G × T were found in bread wheat than durum wheat may be that the genotypes used in this study were derived from targeted breeding programs for irrigated and rainfed conditions and therefore comprised higher variation than the durum genotypes. Under FI, G × T effects were also observed for HEI and TWT, whereas under RI Grm2 and NDVI2 showed G × T effects. Crossover effects were more pronounced under FI and rank changes were observed for all traits.

Although some interaction effects were found, the importance of these might be small. In almost all cases there was no significant difference between CB and PB. In a more detailed analysis we compared CB and PB separately for each genotype. No differences in performance of individual genotypes were detected for key traits like GPR and YLD.

Similar to our study, Hall and Cholick (1989) and Cox (1991) investigated wheat varieties under CT and ZT treatments. Both studies found G × T interaction, but tillage main effect was not statistically significant. Herrera et al. (2013) reviewed G × T effects in wheat and maize. Five out of twelve studies on spring and winter wheat did not find G × T effects. Out of the seven that did find effects, some failed to identify tillage main effects, leaving in doubt the importance of the interaction.

The need to develop breeding programs including ZT is being discussed, however, a definitive answer has not yet been found. Carena et al. (2009) reviewed studies on G × T in maize. In their selection of studies only a few reported G × T interaction. Moreover, in cases where G × T was described, there were other treatment factors (e.g. N treatment, short time under ZT) that likely influenced the results. The authors also pointed out that where G × T was detected, the best performing varieties performed best under all treatments. Thus, Carena et al. (2009) concluded that different breeding programs for different tillage systems were not necessary for maize from the current state of knowledge.

Herrera et al. (2013) showed mixed results in terms of G × T for wheat. However, the percentage of studies that find G × T is higher than in maize and, thus, there might be more need for targeted improvement. On the other hand, these mixed results can be interpreted as tillage itself does not cause the greatest effect, but instead alters other parameters depending on environmental conditions. Tillage would rather have an indirect effect and this could explain why tillage main effects as well as G × T are not always apparent. Almost all genotypes have been developed under CT and it is unclear if crop yield under ZT would benefit more from selection under ZT conditions. To answer this question and to see whether specific adaptive traits become visible under ZT selection, parallel selection experiments under both conditions could be conducted. While it is still uncertain if selection for ZT is beneficial, varietal performance testing for release conducted under ZT could be beneficial if they are to be grown under ZT.

Farmers that are adopting CA for the benefits like improved soil quality, improved yields in water limited conditions, cost savings and reduction of greenhouse gas emissions from fuel use, can expect the same benefits from improved varieties as farmers continuing to use conventional systems. Farmers in regions with two crops per year and late season heat stress, like the Indo-Gangetic Plains, can benefit from timelier planting of the wheat crop after rice under CA. Heat escape due to timely planting can increase yields (Erenstein and Laxmi, 2008). Though planting date was not part of this study, CIMMYT's wheat breeding program is developing wheat varieties adapted to early planting conditions.

Additionally, this study was done with bed planting. In many areas of the world, farmers continue to plant on the flat, including in irrigated conditions. Early released materials used in this study were bred using these flat planting conditions. While our study did not include treatments planted on the flat, these conditions are included in yield potential trials for all CIMMYT varieties before they are released. This is to ensure that released genotypes perform well under different agronomic conditions.

5. Conclusion

For the tested materials, it can be concluded that breeding progress was achieved in all agronomic systems, even though selection was done under conventional tillage. Moreover, genotypes performed similarly on conventionally tilled beds and permanent beds. For bread wheat, G × T was more frequent than for durum wheat, however, overall G × T was of little importance. The results do not indicate the need for separate breeding programs for zero and conventional tillage. However, the question of whether selection under conservation agriculture or zero tillage conditions could result in better progress under conservation agriculture, and possibly as well under conventional conditions, is yet to be answered.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2017.11.011.

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