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Durum wheat selection under zero tillage increases early vigor and is neutral to yield

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ABSTRACT

The combination of zero tillage (ZT) and crop residue retention can substantially improve soil structure and reduce the risk of erosion. Growing conditions for crops are substantially altered in such systems and the question whether specific varieties adapted to ZT conditions need to be developed is not answered. Most published research assessed Genotype by Tillage interactions, which are rarely significant, using genotypes generally developed under CT conditions. CIMMYT's durum wheat breeding program went beyond this approach and performed parallel early generation selection within 16 crosses both in conventional tilled (CT) and ZT soils with the aim of comparing the effect of selection environment (either CT or ZT) on the performance of selected progenies. From 16 initial crosses, 234 lines were selected under CT and 250 under ZT. All 484 lines were subsequently tested for yield and growth traits during three seasons near Ciudad Obregon, Sonora, Mexico in three different testing environments. Those included ZT and CT with full irrigation and CT with reduced irrigation. Early vegetative growth was slightly improved with selection under ZT in all testing environments. Grain yield was highest in ZT testing environment, with a very small average difference in 2013 (0.11 $t\ ha^{-1}$) and larger differences in 2014 (0.65 $t\ ha^{-1}$) and 2015 (0.42 $t\ ha^{-1}$). The differences between selection streams observed for yield were marginal and in most cases not significant.

We conclude that, within the germplasm pool handled in CIMMYT's durum wheat breeding program, selection can be conducted under either tillage conditions without affecting negatively the performance of resulting progenies. The neutrality of selection under ZT in relation to performance of progenies is a likely hypothesis that should be tested in other ZT conditions and germplasm pool combinations.

1. Introduction

Improvement of soil health is an essential part of sustainable intensification of crop production systems (Choudhary et al., 2018). Conservation agriculture (CA), based on minimum tillage, retention of crop residues on the soil surface, and crop diversification, is a key strategy for such intensification. Zero tillage (ZT) in combination with residue retention on the soil surface can substantially improve soil structure. This in turn reduces the risk of soil erosion and improved soil structure leads to better water infiltration, improving system water-use efficiency. Soil cover prevents soil aggregate breakup and crust formation and reduces run-off, thus improving water infiltration further (Verhulst et al., 2010). Evaporation may also be reduced due to soil cover and lead to better water-use efficiency of the system (Cutforth and McConkey, 1997). In surface layers crop residues on top of the soil surface can lead to significantly cooler soil temperatures during warm days, while during the night the insulation effect leads to warmer soils, thus reducing the amplitude between day and night soil temperatures (Oliveira et al., 2001). Conservation agriculture reduces fuel and labor costs, by minimizing tillage operations. Saving time on soil preparation can allow for timelier sowing, often resulting in greater expression of yield potential (Laxmi et al., 2007). The better water infiltration characteristics of soils under CA allow timely machine-sowing after heavy precipitations in environments with wet sowing seasons. This is important in systems where farmers grow more than one crop per year. In regions with late season heat or terminal water stress, timely sowing can help the crop to escape extreme stress at the end of the season and lead to higher yields (Erenstein and Laxmi, 2008).

Conservation agriculture alters the growing conditions for crops. Despite many positive effects of CA, certain constraints arise from ZT and residue cover. During seedling establishment, dense residue cover can be a physical constraint (Wuest et al., 2000). Zero tillage can lead to higher soil surface bulk density, hindering root development of seedlings. Stubble may provide a favorable environment for some pathogens

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to thrive and become problematic for subsequent crops. This imposes higher disease pressures on crops compared to tilled systems (Chan et al., 1989). Residue retention on the soil surface may also temporarily increase N immobilization due to slow decomposition rates (Grahmann et al., 2013).

Early studies of no-till demonstrated reduced early growth in spring wheat (*Triticum aestivum*) in Australia (Cornish and Lymbery, 1987), spring barley and wheat in Norway (Riley, 1998) and winter wheat in Canada (Vyn et al., 1991). The effect was recently confirmed in Mexico by Verhulst et al. (2011a). All four studies report that crops later recovered from the slower initial growth. Yield differences between ZT and CT were compared in a large number of research studies. Pittelkow et al. (2015) conducted a meta-analysis about these differences using 678 studies, representing 50 crops and 63 countries. They found an average yield decrease of 5.1% under ZT. However, when ZT was combined with crop residue retention and crop rotation this effect was reduced. The effect of ZT was also dependent of crop type and climate. In dry rain-fed production systems, ZT systems generally performed best, with higher or equal production compared to tilled systems. The meta-analysis also showed that in cereals, wheat was the least affected by ZT (−2.6%). The results show the need to improve ZT systems in order to close the yield gap between ZT and CT systems, taking into account site and crop specific conditions.

One approach to reduce the negative impact on crops of ZT could involve the development of varieties specifically bred for outstanding performance under ZT and CA based production systems. However, this can only be justified if significant interaction between genotypes and tillage (G × T) exist, including relevant changes in genotype ranking (Carena et al., 2009). Herrera et al. (2013) reviewed G × T effects in wheat. Out of twelve studies, seven found some G × T interactions. However, tilling as main effect was not always significant, hence the importance of the interaction remains unclear. Honsdorf et al. (2018) tested the performance of 26 CIMMYT durum (*Triticum turgidum*) and bread (common) wheat (*Triticum aestivum*) varieties under ZT and CT conditions. In the widely adapted CIMMYT durum wheat germplasm, no G × T effects were detected for yield. In bread wheat, G × T was significant for yield, but no crossover effects were observed and rank changes were small. While many studies show that no relevant G × T exists, it could be argued that, since most breeding programs operate under conventional tillage systems, specific adaptation to zero-till environments was never really “bred into” the crops, in particular in the CIMMYT germplasm. Furthermore, it is not clear how selection under ZT might influence breeding outcome and how selected progenies would perform in either ZT and CT environments. As different tillage practices influence crop performance and development they may affect the breeder’s ability to visually select the best individuals from a given population, thereby affecting the effectiveness of selection (Carena et al., 2009). Few studies have been carried out that compared the outcome of selection streams implemented under ZT and CT.

Maich and Di Rienzo (2014) could not detect any breeding progress when bread wheat lines selected under CT were evaluated under ZT. Hwu and Allan (1992) conducted natural selection experiments in bread wheat. During five seasons, they developed two subpopulations by growing the same origin material under tilled and non-tilled conditions. Subsequently, the authors evaluated the two subpopulations under the same conditions. They found that populations developed on tilled soil performed equally well under both conditions. The subpopulation developed under ZT however, performed better under ZT than CT conditions.

The aim of the present study was to compare the effect of selection under either the conventional tillage system or conservation agriculture on the performance of selected progenies subsequently tested under different relevant growing conditions in CIMMYT’s durum breeding program. Ultimately, our specific objectives were (1) to determine whether selection under ZT resulted in an enhanced performance of progenies under ZT, (2) to assess any positive or negative effect of selection under ZT on the breeding effectiveness (ability to obtain superior lines) for yield and agronomically important traits such as earliness and plant height.

2. Material and methods

2.1. Plant material

Sixteen F_2 generation populations were generated through crosses that are representative of the combinations made every year by CIMMYT’s durum program to address its global breeding objectives. Of these, six were obtained from simple crosses (A x B), 7 from top-crosses ([A x B] x C) and 3 from double crosses ([A x B] x [C x D]). Seed from each of these F_2 populations were divided in two batches to start two parallel selection streams, one under ZT conditions (SELZT) and the other under CT conditions (SELCT). The ZT selection plots had been under conservation agriculture, with no till and direct seeding for more than 5 years, no residue removal and within year rotation with either maize or sorghum as summer crops. The CT selection environment consisted in plots that were fully tilled with complete residue removal. Selection within the segregating populations from the F_2 to the F_5 generations was carried out identically for both streams, selecting at each step single plants with the most attractive phenotypes (disease resistant, early types, short stature and outstanding grain fill). This was done following the “shuttle breeding” scheme adopted by CIMMYT breeding programs for the last decades. It involved selection at two locations annually, namely Cd. Obregon Sonora in Northern Mexico during the winter crop cycle (F_2 and F_4 generations in this case) and Toluca in the Central Mexican Highlands during the summer crop cycle (F_3 and F_5 generations in this study). In terms of selection methods, a selected bulk was used in the F_2 (of the initial 1800 seeds sown, variable number of selected plants were bulked together to generate seed for the next generation) and F_3 (of the initial 1000 seeds sown, variable number of selected plants were bulked together to generate seed for the next generation). In both these generations, the number of plants selected was very similar for each stream. In the F_4 generations (600 seeds initially sown), selected plants were threshed individually to produce single-plant-derived F_5 families. From then on, the derived lines (by then mostly fixed genetically) were increased and handled in bulk without selection.

At the end of the selection process, between ten and 25 lines were selected under CT and between ten and 22 under ZT, in each of the 16 crosses, producing a total of 234 lines selected under CT and 250 under ZT. The resulting F_7-F_9 generations were evaluated in different testing environments as described below.

2.2. Performance evaluation of resulting lines from two selection streams

The 484 genotypes produced from both selection streams were evaluated in yield trials conducted over three winter growing seasons (November to May), from 2012/13–2014/15, at the CENEB (Campo Experimental Norman E. Borlaug) near Ciudad Obregon, Sonora (lat. 27.33 N, long. 109.09 W, 38 masl). The station is characterized by an arid climate with highly variable rainfall. Annual reference evaporation is approximately 1800 − 2000 mm (Verhulst et al., 2011d) and average annual rainfall is 308 mm (1993–2015) of which about 45 mm fall during the growing season. Mean annual temperature is 23.5 °C with monthly mean temperatures ranging from 16 °C in January to 31 °C in July (1993–2015). According to the World Reference Base the soil is classified as Hyposodic Vertisol (Calcaric, Chromic). It is characterized by low soil organic matter (SOM $< 12\ g\ kg^{-1}$ soil) and slight alkalinity (pH 8) (Verhulst et al., 2009).

The yield trials were conducted in three different testing environments. Those included ZT (in plots managed following CA practices for four previous years) and CT (most common practice on station and in farmers’ fields in the region), both with full irrigation. An additional testing environment consisted of a conventionally tilled treatment with reduced irrigation (RI). In the CT treatment, plots were tilled after harvest and before sowing and new planting beds were formed every year before sowing. Crop residues were incorporated through tillage (Supplementary Fig. 1). In the ZT treatment, residue was retained (Supplementary Fig. 2), soil was not tilled or moved and the planting beds were reshaped if necessary by a superficial intervention that did not disturb the area in which seed was deposited.

Soil analysis carried out with samples taken in the first year of testing (March 11, 2013) showed differences between soils under CT and ZT management. Dry sieving aggregate size was significantly larger in CT plots, with mean weight diameter (MWD) of 1.59 mm, compared to ZT plots with 1.33 mm (Supplementary table. 1). Contrastingly, wet sieving resulted in significantly larger aggregate size under ZT, MWD 0.44 mm, compared to 0.33 and 0.31 mm with CT and RI, respectively (Supplementary table 1). This shows that aggregates were more stable in ZT than CT. Infiltration ability, measured as time to pond (Govaerts et al., 2006) was significantly larger in ZT plots than in CT plots, with on average 22.5 and 13.1 s, respectively (Supplementary table 1). Small differences were also observed in penetrations resistance, though those were not statistically significant. Under ZT conditions resistance was slightly higher in depths 7.5 cm, 37.5 cm, and 52.5 cm, while it was slightly larger under CT at the depths of 22.5 mm (Supplementary Fig. 3). Chemical soil properties showed some differences between CT and ZT as well; in the first 5 cm of the soil, electrolytic conductivity was significantly higher in tilled than in non-tilled soils, while soil organic matter was significantly higher in ZT than in CT (Supplementary table 2).

The experiment was set-up as an incomplete block alpha lattice design with three replications for each testing environment. Alpha lattices are incomplete block designs (sometimes balanced) that have the property that incomplete blocks group together into “super-blocks” that are complete (are resolvable) (Edmeades et al., 1997; Patterson and Williams, 1976). Within each replication, genotypes were arranged randomly in three incomplete blocks of 160 and 170 genotypes. Plot size was 3.84 m^2, consisting of two beds (0.8 m width each) of 2.4 m length. Wheat was sown in two rows per bed with 0.27 m between rows. In the ZT environment, a planter with double cutting discs ensured minimal soil disturbance. All treatments received a pre-seeding irrigation. Full irrigation treatments (CT and ZT) received three to four auxiliary irrigations accumulating to approximately 520 mm per season (total of pre-seeding plus in-crop). The reduced irrigation received only a single auxiliary irrigation at heading, a total of approximately 240 mm per season. In all testing environments, water was applied using furrow irrigation.

At the start of the season, 59 kg N ha^{-1} and 23 kg P ha^{-1} were applied as band application at the center of each double row in all environments. The second N fertilization was applied as urea at first node banded in the furrow. Both full irrigation treatments received 150 kg N ha^{-1}, and the reduced irrigation treatment 100 kg N ha^{-1}. Wheat was sown on separate days in the three agronomic systems. In 2012 sowing dates were November 21 (CT), 22 (ZT), and December 5. In 2013 sowing was carried out between December 2 and 4, and in 2014 between November 20 and 22. The experiment was harvested between mid of April and beginning of May. During the summer season *Sesbania* sp. was grown as a rotation cover crop.

Pest, disease and weeds were controlled as necessary to ensure those factors would not influence the outcome of the experiment. No pathogens specific to ZT were observed so pest and disease control was the same across environments.

2.3. Data collection

Weather data was collected at a weather station situated at approximately 2 km from the experiment. During the growing season, plant growth was assessed using the normalized difference vegetative index (NDVI), measured with a GreenSeeker™ Handheld Optical Sensor Unit (Trimble Ag, USA; Verhulst et al. (2011b)). The sensor was passed approximately 0.8 m above the crop canopy with the sensing head centered over the bed. 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 second at maximum growth (NDVI2), around flowering. The first measurement represents early vigor, while the second is a proxy for maximum biomass accumulation. The other data collected included days to heading (DH) and plant height (PHT) and grain yield (GY) per ha was measured by harvesting the complete plot at the end of the growing season.

2.4. Statistical analyses

The statistical analyses included both individual analysis by environment (year by testing environment combination), and combined analysis across environments, using a mixed models framework. The durum wheat lines were classified into two groups derived from selection streams SELCT and SELZT. For the individual analyses, the linear model was the following (Eq. 1).

$$Y_{ilm} = \mu + C_l + G_i(C_l) + R_m + \varepsilon_{ilm} \tag{1}$$

where Y_{ilm} is the response of the i^{th} line ($i = 1, 2, \ldots, I$) in the l^{th} selection stream($l = 1, 2, \ldots, L$) and the m^{th} replication ($m = 1, 2, \ldots, R$), μ stands for the overall mean, C_l is the effect for the l^{th} selection stream, $G_i(C_l)$ is the effect of the i^{th} line in the l^{th} selection stream, R_m is the effect of the $Y_{ilm} = \mu + C_l + G_i(C_l) + R_m + \varepsilon_{ilm} m^{th}$ replication, and ε_{ijk} is the error assumed to be normally and independent distributed $(0,\sigma^2)$.

The terms selection streams and lines were declared as fixed terms while the replications were taken as random effects. From this model the least squares means (BLUEs) were calculated, as well as the contrast between the two selection streams.

For the combined analyses across environments, the environment and the genotype × environment interaction terms were added to Eq. 1 resulting in model given by Eq. 2.

$$Y_{ijlm} = \mu + E_j + R_m(E_j) + C_l + G_i(C_l) + (E_j \times G_i(C_l)) + \varepsilon_{ijlm} \tag{2}$$

where the new terms E_j and $(E_j \times G_i(C_l))$ are the effects of the j^{th} environment and the environment × line interaction, respectively. All terms were considered as fixed terms, except the $R_m(E_j)$ which was taken as random. Also the least square means and contrasts, as in the individual analyses, were computed. In both cases, the corresponding linear models were implemented in PROC Mixed of SAS using REML to estimate the variance components.

2.4.1. The site regression model and its biplot

The site regression model fits the combined effects of the environments and the genotype within environments × environment interaction; in this particular case the terms that are estimated together are $[E_j + G_i(C_l)]$. Then the model is given in (Eq. 3)

$$\bar{Y}_{ij} = E_j + \sum_{k=1}^{t} \lambda_k \alpha_{ik} \gamma_{jk} + \bar{\varepsilon}_{ij} \tag{3}$$

where λ_k is the singular value for the k^{th} component, α_{ik} are the eigenvectors associated with the i^{th} line and the k^{th} component, and γ_{jk} are the eigenvectors associated with the j^{th} environment and the k^{th} component.

The results of the SREG can be presented in a graph biplot where durum lines from the two selection streams and the environment scores of the first two terms are represented by vectors in a space, with starting points at the origin and endpoints determined by the scores. Usually the environmental and durum wheat lines scores of the first and second bilinear terms are plotted. The distance between two durum line vectors (end points) indicates the amount of interaction between the durum lines. The cosine of the angle between two line (or environment) vectors approach the correlation between the lines (or environments) with respect to their interaction. Acute angles indicate positive correlation, with parallel vectors (in the same directions) representing a correlation of 1. Obtuse angles represent negative correlations, with opposite directions indicating a correlation of -1. Perpendicularity of directions indicates a correlation of 0. The relative amounts of interaction for a particular durum wheat line over environments can be obtained from orthogonal projections of the environmental vectors on the line determined by the direction of the corresponding durum wheat line vector. Environmental vectors having the same direction as the durum line vectors have positive interactions (that is, these environments favored these durum lines); however, vectors in the opposite direction have negative interactions.

2.4.2. Heritability

Broad-sense heritability at an individual environment was calculated as

$$h^2 = \sigma_g^2/(\sigma_g^2 + \frac{\sigma_e^2}{nreps})$$

where σ_g^2 and σ_e^2 are the genotype and error variance components, respectively, and *nreps* denotes the number of replicates. For the combined analyses, the heritability was calculated as

$$h^2 = \sigma_g^2/(\sigma_g^2 + \frac{\sigma_{ge}^2}{nenvs} + \frac{\sigma_e^2}{(nenvs \times nreps)})$$

where the new term σ_{ge}^2 is the genotype × environment interaction variance component and *nenvs* is the number of environments in the analysis.

3. Results

3.1. Growing conditions

Annual rainfall was variable during the testing period (2012–2015), ranging from 273 to 422 mm and occurring mainly during July to September (Fig. 1). Rainfall during the growing season (sowing to harvest) was 18, 47 and 85 mm in the 2012–2013, 2013–2014 and 2014–2015 growing seasons, respectively. Mean annual temperature during the experiment was 24.2 °C (range 23.7 °C – 24.7 °C), slightly higher than the long-term average of 23.5 °C. Minimum temperatures during January to March were elevated in 2014 and 2015.

3.2. Trait performance

Coefficients of variations (CV) were relatively low for all traits. Across years and testing environments, CVs were lowest for DH (2.7 %), 4.2% for PHT and NDVI2, and highest for GY (9.1 %) and NDVI2 (10.1 %). Heritability was in general high. Across years and testing environments, it ranged between 0.86 and 0.94 for all traits (NDVI1: 0.86, NDVI2: 0.88, PHT: 0.94, DH: 0.94, YLD: 0.87).

Correlations between traits were calculated across years, separately for selection streams and testing environments (Supplementary table 3). In general, these correlations were moderate to low. The strongest associations were observed between DH and NDVI2 in testing environments CT and RI, with r-values between 0.61 and 0.69. All correlations between measured traits and yield were low; the maximum value was $r = 0.42$, between NDVI2 and yield in CT testing environment and SELZT lines. Values larger than $r = 0.5$ were observed also for associations between NDVI2 and PHT in CT, and NDVI2 and DH in ZT, in both cases among the SELZT lines. All other values were smaller than 0.5.

3.2.1. NDVI1

Early vegetative growth measured as NDVI1 was highest in CT testing environment, followed by RI and ZT. Highest values were measured in 2013 with 0.5 and lowest values in 2015 with 0.2 (Fig. 2). Lines selected under ZT had consistently higher NDVI1 values than those selected under CT, in all testing environments in all years. The difference ranged between 0.004 and 0.015. The difference was significant in almost all cases, with the exception of CT testing environment in 2013.

3.2.2. NDVI2

Highest maximum growth, with NDVI values of up to 0.82, was observed in all years in the CT testing environment (Fig. 3). Lowest growth was measured under ZT in 2014 with values as low as 0.65. Differences between selection environments were marginal, ranging

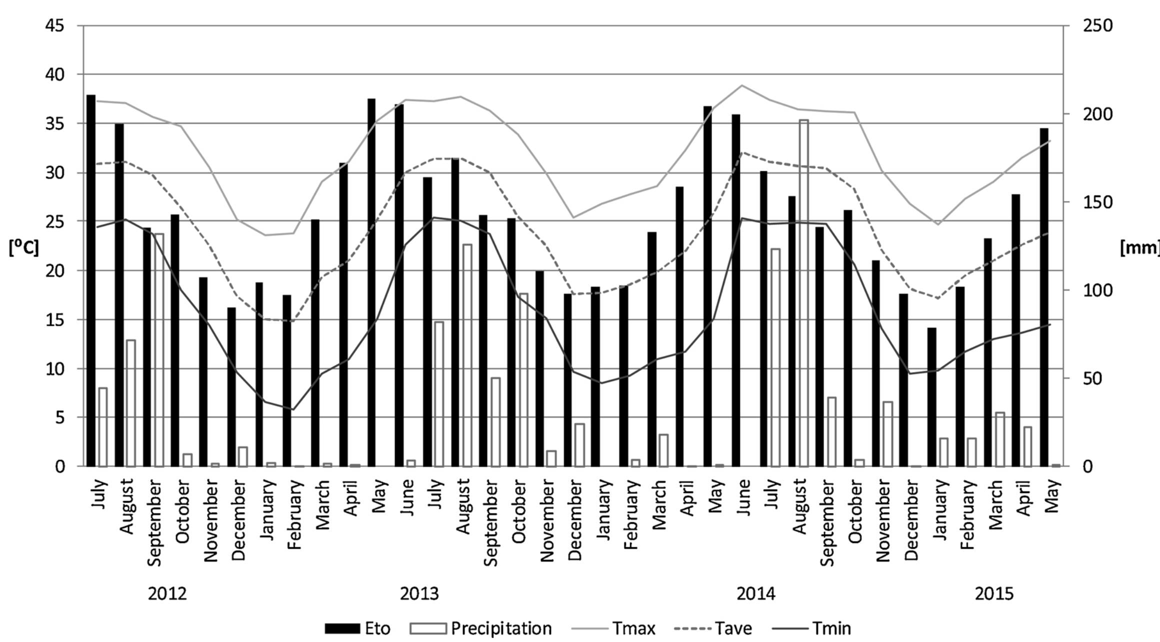

Fig. 1. Monthly climate conditions for the growing season July 2012 to May 2015 at the experiment station near Ciudad Obregon. Minimum (Tmin) and maximum (Tmin) temperatures are monthly average temperatures. Tave: average temperature, Et0: reference evapotranspiration.

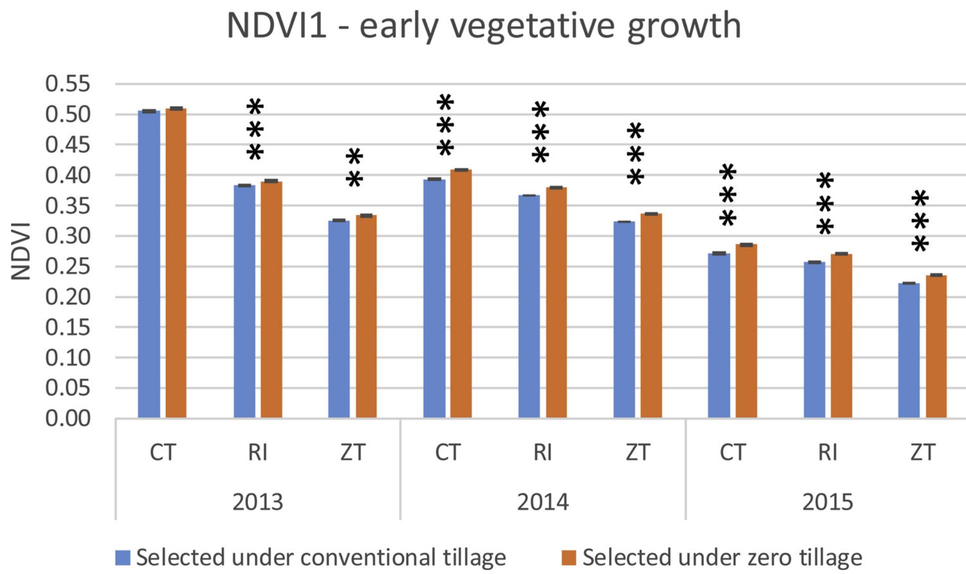

Fig. 2. Mean values for NDVI1 with standard errors, significant differences between genotypes selected under CT and ZT per test environments (CT: conventional tillage, RI: reduced irrigation conventional tillage, ZT: zero tillage) and year are indicated with *(p < 0.05), **(p < = 0.001), ***(p < = 0.0001).

between 0.001 and 0.004 and only significant under RI in 2014.

3.2.3. Days to heading

Days to heading ranged from 70.3–81.1 days over testing environments, selection environments, and years (Fig. 4). The smallest differences between testing environments and selection environments were observed in 2013. When tested under reduced irrigation conventional till, genotypes that were selected under ZT headed on average after 79.0 days and genotypes selected under CT after 79.1 days. When evaluated under conventional till with full irrigation DH was 79.8 and 80.2 for genotypes selected under CT and ZT, respectively. When tested in ZT conditions, DH was slightly later, 80.8 days for genotypes selected under CT and 81.1 days if selected under ZT. In 2014 plants tended to head earlier than in 2013 and differences between testing environments were larger. Genotypes selected under CT and under ZT had average days to heading of 73.1 and 73.0 when tested under RI, of 75.5 and 75.2 when evaluated under CT and of 79.4 and 79.3 when tested under ZT, respectively. While in the first two years latest heading was observed with ZT testing environment, in 2015 plants grown under CT headed the latest. Differences between selection streams were significant for testing environment CT and ZT in 2013 and 2014 and for RI in 2014 and 2015.

3.2.4. Plant height

Plant height ranged from an average of 77.8 cm under DR in 2013 to 89.9 cm in CT in the same year (Fig. 5). Plants in well-watered treatments grew tallest in 2013 and stayed shortest under RI treatment in the same year, leading to differences in height to up to 12 cm. In the remaining years, differences between well-watered and reduced irrigation treatments were smaller. In 2014, genotypes grown in well-watered treatments grew between 83.8 and 84.6 cm tall, while under RI they were approximately 4 cm shorter (80 cm). In 2015, plant height was very similar, around 82 cm under RI and CT testing environments. With ZT in the same year, genotypes grew around 2 cm taller. Differences in height between genotypes selected under CT and ZT were marginal, ranging between 0.1 and 0.7 cm. They were significant in all years for testing environment ZT and in years 2013 and 2014 for testing environment CT.

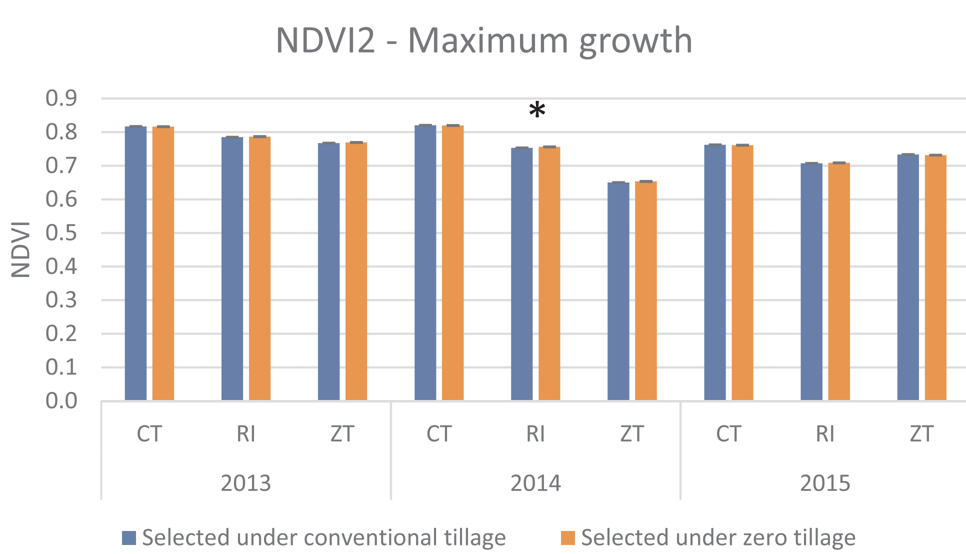

Fig. 3. Mean values for NDVI2 with standard errors, significant differences between genotypes selected under CT and ZT per test environments (CT: conventional tillage, RI: reduced irrigation conventional tillage, ZT: zero tillage) and year are indicated with *(p < 0.05), **(p < = 0.001), ***(p < = 0.0001).

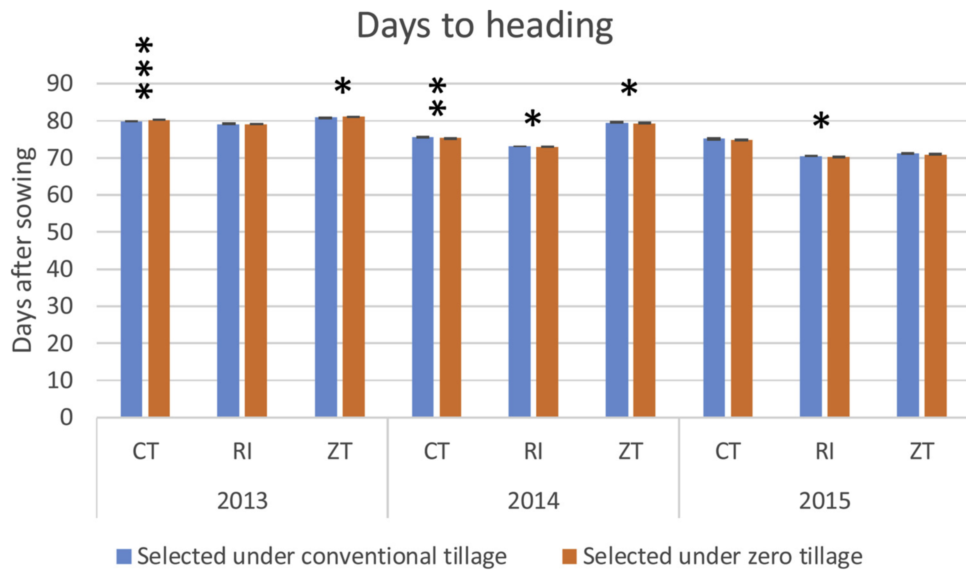

Fig. 4. Mean values for days to heading with standard errors, significant differences between genotypes selected under CT and ZT per test environments (CT: conventional tillage, RI: reduced irrigation conventional tillage, ZT: zero tillage) and year are indicated with *($p < 0.05$), **($p \le 0.001$), ***($p \le 0.0001$).

3.2.5. Yield

Grain yield was highest in the ZT testing environment in all three years, ranging between 5.1 and 6.6 t ha^{-1} (Fig. 6). Yield in the ZT testing environment was 0.11, 0.65 and 0.42 t ha^{-1} higher than in CT in 2013, 2014 and 2015, respectively. Differences between genotypes selected under ZT and CT were small, with a maximum of 92 kg in 2013. Grain yields under RI were lowest in 2013 (3.1 t ha^{-1}). In that year the difference between yield under RI and well-watered treatment was largest, with yield under RI being less than half of that under well-watered treatment. In 2014, grain yield under RI was 4.2 t ha^{-1} compared to 5.3 t ha^{-1} (CT) and 5.6 t ha^{-1} (ZT). Smallest differences were observed in 2015, where yield was around 400 kg ha^{-1} less under RI (4.3 t ha^{-1}) than with CT (4.7 t ha^{-1}). Yield in ZT was highest with up to 5.2 t ha^{-1}. The difference between selection streams was only significant in 2013 in testing environments CT and ZT.

3.3. Effects of selection environments

The generalized linear mixed model revealed significant effects of year as well as interaction between year and selection environment. Therefore, analyses for the effect of selection environment were carried out separately for each testing environment and year combination (Supplementary tables 4–8).

Genotype within selection environment had significant effect for all traits in all environments, with the exception of NDVI2 in CT in 2014. As described above, differences in trait levels between genotypes selected under ZT and CT were altogether very small. The largest number of significant selection environment effects was detected for NDVI1. During this early stage of plant development, genotypes selected under ZT had higher NDVI values, i.e. faster, more vigorous development, in all years and for all testing environments. This difference was significant in all cases but in testing environment CT in 2013 ($p = 0.061$) (Fig. 2).

Later during plant development, this effect decreased. At maximum

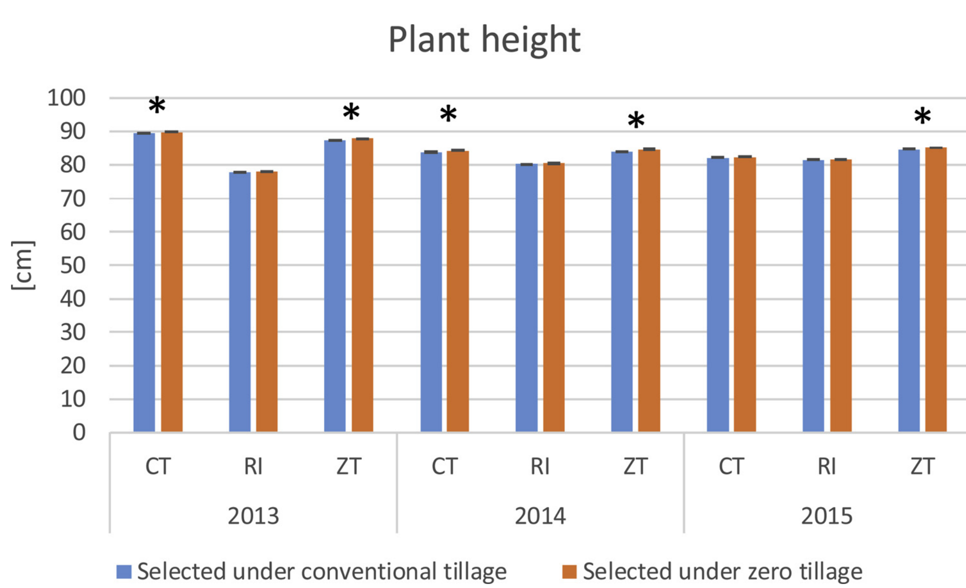

Fig. 5. Mean values for plant height with standard errors, significant differences between genotypes selected under CT and ZT per test environments (CT: conventional tillage, RI: reduced irrigation conventional tillage, ZT: zero tillage) and year are indicated with *($p < 0.05$), **($p \le 0.001$), ***($p \le 0.0001$).

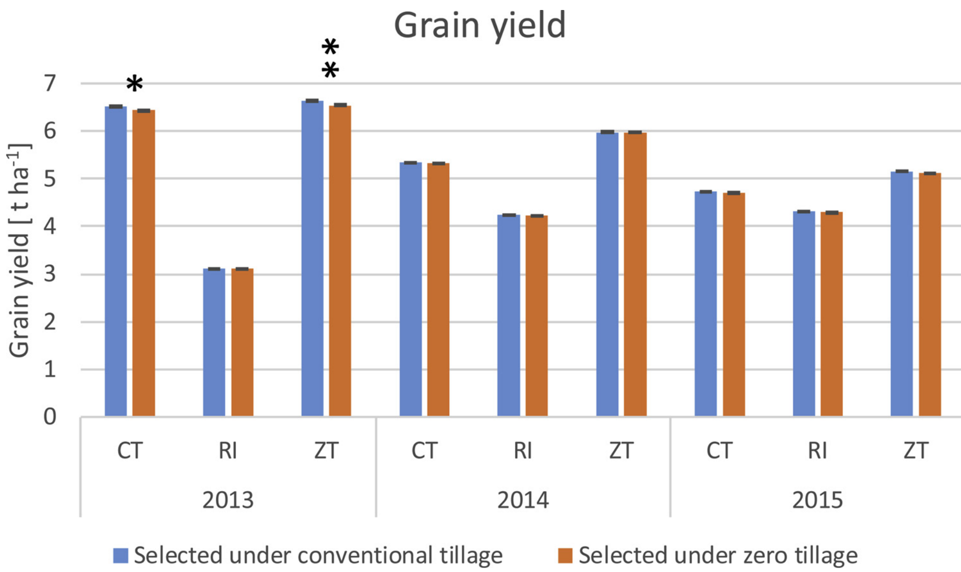

Fig. 6. Mean values for grain yield with standard errors, significant differences between genotypes selected under CT and ZT per test environments (CT: conventional tillage, RI: reduced irrigation conventional tillage, ZT: zero tillage) and year are indicated with *(p < 0.05), **(p < = 0.001), ***(p < = 0.0001).

vegetative development, selection environment had very little influence on accumulated biomass levels. Only under RI in 2014 plants selected under ZT showed higher biomass than plants selected under CT (0.756 vs 0.753) (Fig. 3).

For DH, differences between the genotypes from the two selection streams ranged between 0.1 and 0.4 days. Significant effects were detected in all testing environments. In 2013, under full irrigation, ZT selected plants headed slightly later than CT selected ones. In 2014, ZT selected genotypes headed slightly earlier in all testing environments. In 2015 the same effect occurred, but was only significant under RI (Fig. 4).

Plant height was consistently greater for plants selected under ZT. The differences were small but significant in testing environment ZT in all three years and in testing environment CT in 2013 and 2014. Differences in PHT were not significant under reduced irrigation (Fig. 5).

Yield was consistently numerically higher in genotypes selected under CT, independent of the testing environment. The differences between selection environments, however, were very small, with a maximum of 92 kg ha^{-1}. The effect of selection environment was only significant in testing environment CT and ZT in 2013 (Fig. 6).

The biplots of the site regression model analyses showed no clear separation of genotypes from the two selection streams for YLD (Fig. 7), NDVI2, PHT, and DH (Supplementary Figs. 4–6). For grain yield, the first two components explained a sizeable proportion of the total variation (74.5%). Years were clearly separated from each other. Highest and most stable yields were observed in lines derived from both selection streams; 372 (ZT), 451 (CT), 461 (CT), 481 (ZT), 400 (ZT), and 338 (ZT). No clear trend in favor of any of the two selection streams was apparent.

For NDVI1 (Fig. 8) the results show a separation between years. As opposed to grain yield, the density of genotypes derived from SELZT was larger on the right side of the biplot, indicating higher NDVI values for early vigor in genotypes from this selection stream. The best lines were 194, 199, 195, 101, 239, all derived from SELZT. The biplots also indicate that, in general, the difference between testing environments within a year was smaller than the difference between years. This indicates that the same genotypes perform well across different agronomic systems. This effect was most consistent for NDVI1 and yield. For DH the environment RI in 2015 was closer to RI 2013 than CT or ZT in 2015, indicating larger differences in terms of interaction with genotypes between the agronomic systems in that year. For plant height, the difference between agronomic systems was slightly larger in 2013 than in other years, however, all environments remained in the same quadrant. In the case of NDVI2 no consistent performance of either year or agronomic environment were observed.

4. Discussion

All genotypes were tested under ZT with full irrigation and under CT with full as well as reduced irrigation. Early vegetative growth was largest under CT with full irrigation and smallest under ZT. The reduced growth, as assessed by NDVI, can be explained by differences in N dynamics and resulting availability (Grahmann et al., 2018). Additionally, higher soil bulk density as described in a study by Verhulst et al. (2011c) and the residue cover (Wuest et al., 2000) could constrain seedling establishment. Residue on the soil surface also alters the microclimate. Cutforth and McConkey (1997) describe how standing stubble reduces wind speed, temperature and solar radiation near the soil surface. This alteration may also lead to slower initial crop growth and lower NDVI values. By mid to end season, plants in ZT compensated the initial slow growth, which was observed in several earlier studies (e.g. Riley, 1998; Verhulst et al., 2011a). This resulted in NDVI2 values only slightly, and not significantly, higher in CT compared to ZT.

Grain yield decreased under reduced irrigation by about 50 % in 2013. In the two following seasons, yield difference between full and reduced irrigation was less. In those years, there was more rainfall during the growing season than in 2013. This probably increased yield under reduced irrigation. Additionally, the rainfall could have caused excess water in the testing environments with full irrigation, reducing yield. However, the yield reduction under full irrigation in 2014 and 2015 compared to 2013 is more likely because minimum temperatures during early plant development and flowering time were elevated in those years. A yield reduction under such conditions is frequently observed in the Yaqui valley (Lobell and Ortiz-Monasterio, 2007).

Under full irrigation, grain yield was higher in ZT than in CT. This shows how well the crop compensated slower initial growth and confirms observations made for durum wheat varieties developed by CIMMYT between 1970 and 2009 by Honsdorf et al. (2018). In that study, 13 genotypes were tested in six seasons and yields under ZT were higher on average. Higher yields under ZT might be due to better water availability over longer periods and reduced stress between irrigations. In addition, cooler temperatures due to residue cover might benefit the plants in this environment. Verhulst et al. (2011b) suggest that slower

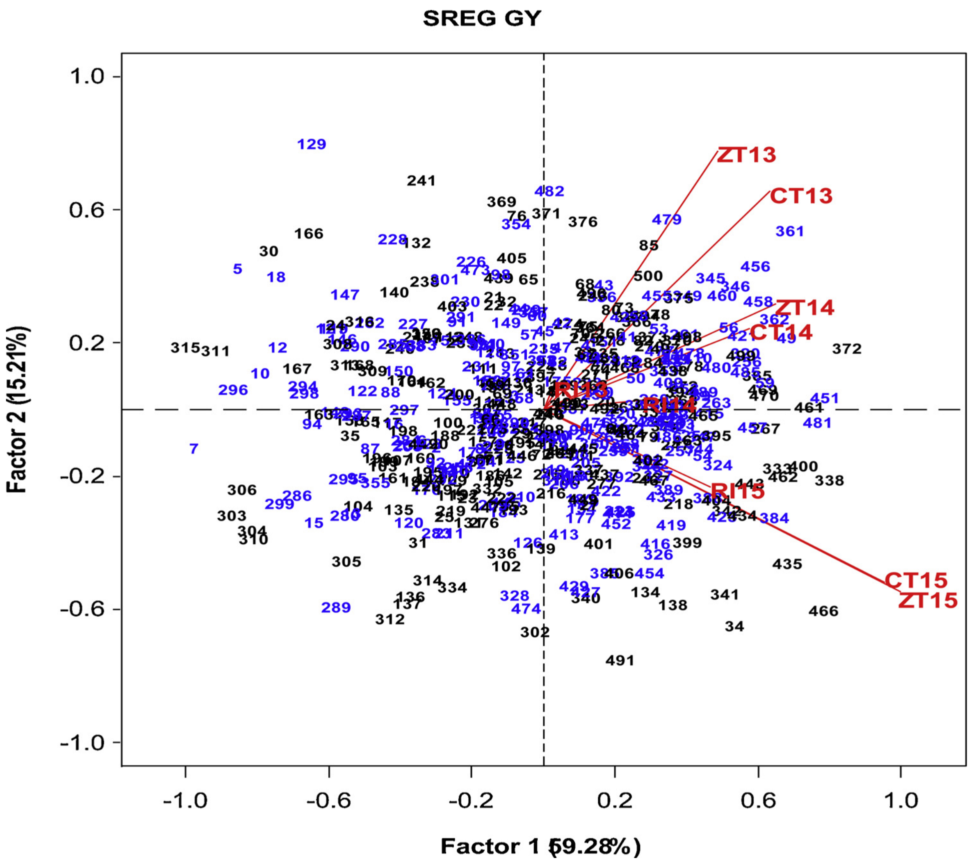

Fig. 7. Biplot of the site regression model for grain yield, blue numbers (in the online version of the figure) indicate genotypes selected under CT, black numbers selected under ZT. Red lines indicate testing environment and test year, CT: conventional tillage, DR: reduced irrigation conventional tillage, ZT: zero tillage.

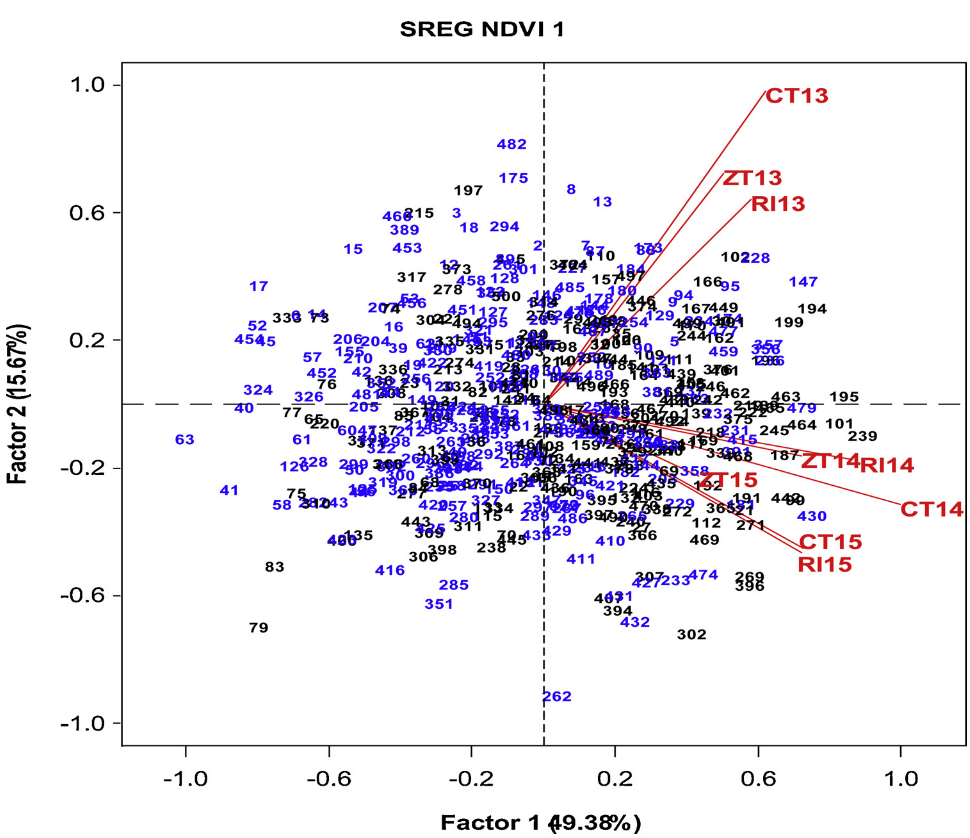

Fig. 8. Biplot of the site regression model for NDVI1, blue numbers (in the online version of the figure) indicate genotypes selected under CT, black numbers selected under ZT. Red lines indicate testing environment and test year, CT: conventional tillage, DR: reduced irrigation conventional tillage, ZT: zero tillage.

initial growth under ZT/CA conditions might lead, under the specific conditions found in the Yaqui valley, to more timely and efficient resource use for crop growth.

Several authors discussed the need to breed crops adapted to specific production systems. The rationale behind this quest for production system-specific cultivars is based on the hypothesis that different management practices pose different stresses to the plants and that specific mechanisms bred into genotypes that mitigate these stresses could ultimately improve yield. This is discussed for ZT and CA systems (e.g. Carena et al., 2009; Maich and Di Rienzo, 2014) as well as for organic farming systems (e.g. Kirk et al., 2012; Wolfe et al., 2008). Important traits frequently mentioned as useful for adaptation to CA are early vigor to cope with high residue loads and higher bulk density as well as resistances to diseases that survive on crop residues (Joshi et al., 2007). However, Carena et al. (2009) point out that breeding for specific production systems causes a significant increase in costs. It could also conceivably affect the wide-adaptation of resulting germplasm, which is an attribute of critical importance for a globally oriented program such as CIMMYT's. Therefore, before starting a breeding program for a specific production system, it is recommended to quantify and characterize the interaction between genotypes and production system (e.g. zero tillage, organic management) in order to assess the suitability and worthiness of breeding specifically for such a system. In this context, it is important to note that the existence of merely “quantitative” interactions that do not result in cross-over scenarios, even if statically significant, cannot be considered a justification for system-specific breeding. The only interactions that could warrant such an initiative are those “qualitative” ones that result in crossovers in performance of a genotype across different systems (Baker, 1988). This kind of study and approach is also recommended before adopting new production methodologies, in order to avoid failures of the systems, due to an inappropriate variety.

The interaction between CIMMYT-bred, widely-adapted durum wheat genotypes and tillage treatment was previously investigated. In the above-mentioned study, Honsdorf et al. (2018) did not observe significant G × T for most traits, with the exception of NDVI2 (maximum growth) under reduced irrigation. Genotypes performed equally well under both tillage systems. While from that study it could be concluded that separate breeding programs to address adaptation to ZT were not justified, it is important to note that all genotypes used in that study were exclusively selected under CT, with no selection pressure that would result in a potential specific adaptation to ZT conditions. Therefore, it is reasonable to hypothesize that if breeding populations were subjected to selection under ZT, from the beginning and all through the segregating phase, some progenies would be selected that have a noticeable specific adaptation to ZT conditions. This hypothesis of “engineering” or “breeding in” genotype by tillage interactions through selection under ZT has not been tested to our knowledge. Trethowan et al. (2012) pointed out that it is important to develop materials under ZT in order to breed useful traits into selected progenies that would provide adaptation to the tillage conditions. However, no decisive experimental evidence was provided identifying those traits or that supported the hypothesis that selection under ZT would result in specific adaptation to ZT.

In the present study, early vegetative growth was consistently higher in genotypes selected under ZT than in genotypes selected under CT in all testing environments. This difference was small though significant in all cases but CT testing environment in 2013. The selection environment ZT with standing and laying crop residues on the soil surface, as it is typical in viable CA systems, exposes seedlings to more difficult germination, emergence and early development conditions. Also, the ZT conditions are known to modify the micro-climate (soil and air temperature, wind speed, solar radiation…) around emerging seedlings and during their initial growth (Cutforth et al., 2002; Cutforth and McConkey, 1997), which could contribute to explaining why plants selected under such conditions would have more early vigor than those exposed to the initially more favorable conditions of conventionally tilled soils. The conditions present in the selection environment put higher pressure on the plants during early development and made the environment suitable for selection for this trait. This is especially useful in the case of durum wheat, which is notably slower in crop establishment compared to bread wheat or barley. Differences in early vigor of individual plants in segregating populations were more visible under these conditions and made selection more straightforward. Early vigor is considered an important trait in CA, to improve slower initial growth observed in that system (Verhulst et al., 2011a). The trait is also important in dry environments, where it can improve yield through rapid development of maximum leaf area (El Hafid et al., 1998) and greater ground cover. The results showed selection under ZT/CA has the potential to improve early vigor under ZT as well as under CT conditions. However, in absolute numbers early vigor was still considerably lower in ZT than in CT testing environments. It is conceivable, however, that if parental lines with outstanding early vigor characteristics are used more systematically in crosses, selection under ZT/ CA may facilitate further improvement of early vigor and drive a breeding program towards the generalization of this useful attribute.

Maximum growth was not significantly different between populations selected under ZT and CT, with the exception of RI treatment in 2014. However, the difference was minimal and therefore not of practical relevance. While difference in early plant development are common, they narrow later in the season. This might be the reason why selection under different tillage practices did not result in differences for this trait.

Because ZT/CA conditions tend to allow moderately taller plants to thrive with less likelihood of lodging, one could reasonably be concerned that selection under ZT/CA could result in the selection of taller plants that would otherwise lodge in CT systems, thereby biasing the selection towards plants that would not be competitive in CT systems. In light of the results of the present study, plant height was slightly greater in ZT selected genotypes, with this slight difference observed only in well-watered testing environments in most years. However, the average differences, while significant, were small, in the order of a few centimeters and could not be considered of concern. This is supported by the lack of any significant lodging observed while testing this material under CT over the three years. Furthermore, Berry et al. (2004) describe that stem and root anchorage strength are more important factors for lodging resistance than reduction of height.

Because ZT/CA tends to result in greater soil water content (due to residue retention and improvement of soil structure) over the season, plants tend to stay greener longer. This could favor the selection of later plants that often have better appearance under conditions of prolonged water availability and therefore drive breeders to select plants that would otherwise be too late under CT or under conditions of harsh terminal conditions (terminal drought or heat), where earliness is usually an advantage. In the present study, small but significant differences due to selection environment were observed for DH, but these differences were not consistent. Additionally, the magnitude of the average differences observed between the two selections streams, when significant, was much reduced and all material selected had a heading date well within the range for wide adaptation to most of CIMMYT's target environments, even when tested under CT conditions. Furthermore, there was no decrease in yield under reduced irrigation (water stress) related to selection under ZT, laying to rest the concern that selection under ZT could affect performance under water-stressed conditions through the selection of later types.

Yield was significantly higher in SELCT genotypes under both CT and ZT with full irrigation in 2013. The difference was about 90 kg ha^{-1}. In all other years and treatments, there was no significant effect of selection stream on average grain yield.

The results show that for the conditions in which the trials were carried out - high input and irrigated - the selection environment was of no significant consequence on the ultimate performance of progenies in any of the testing environments. In fact, the importance of the agronomic management was more important than the selection environment. The CA testing conditions consistently led to higher yields, irrespective of the selection environment, likely due to the longer periods with sufficient plant available water between irrigations.

While CIMMYT promotes CA as a vehicle for sustainable intensification of wheat and maize systems, most of the farmers that use CIMMYT germplasm still use some form of tillage. Therefore, adaptation to a wide range of production systems is necessary. CIMMYT varieties are known for their wide adaptation (Braun et al., 1996) and this seems to be sufficient to provide adequate performance in very different tillage systems. This was also shown by Honsdorf et al. (2018), where breeding progress and yield were very similar under ZT and CT conditions for durum and bread wheat lines. The plant material used in the crosses for the selection experiment had this wide adaptation, leading to good performance in both tillage systems. Overall, CIMMYT's wheat material has the ability to perform well in many different stress situations, and the difference between tilled and non-tilled soil might not be the greatest challenge if other stresses are managed well.

Taken together, the results of the present study suggest that breeders within CIMMYT's durum breeding program can freely choose to conduct their selection in segregating populations under either ZT/CA or CT conditions, without negative consequences in terms of yield performance of resulting progenies in either system. This is an important result of significant relevance to CIMMYT's global mandate, as it suggests the lack of need for separate breeding programs/efforts to address the needs of production systems where CA and ZT are prevalent or increasing in area. This is also important from a resource allocation standpoint, demonstrating that the current breeding effort is likely to address needs of durum wheat areas under CA without the need to allocate resources to breeding for specific adaptation to these systems. Finally, this is important for any breeding program with a global reach or with very wide target environments, as those programs have to adopt breeding strategies based on wide adaptation and not on specific adaptation to narrowly representative conditions (Braun et al., 1996). Wide adaptation is defined herein as a proxy for yield stability at the highest level, i.e., the capacity of a genotype to have a relative superior performance under a wide range of growing conditions (including of different production systems, such as ZT/CA and CT). Having the insurance that breeding for wide adaptation will not be adversely affected by selection pressures prevailing under the ZT/CA conditions we have implemented is an important strategic result, enabling globally oriented breeding programs using CIMMYT-derived germplasm, to take advantage of the logistical and soil-improving benefits of working under CA should they elect to do so. Whereas these results, essentially the neutrality of selection under ZT/CA in relation to performance of progenies, cannot be generalized beyond the ZT/CA conditions that prevailed across the present study and should be considered valid only for the CIMMYT germplasm base, they provide a likely hypothesis that should be tested in other ZT/CA conditions/germplasm pool combinations.

5. Conclusion

The selection experiment was carried out with plant material produced by crosses that were representative of those regularly made in CIMMYT's durum wheat breeding program and selected using the shuttle breeding scheme between Ciudad Obregon and Toluca, which is an essential part of CIMMYT's strategy to breed for wide adaptation. Applying these standard practices, we did not find relevant effects of selection under a given tillage system on the breeding process and final yield of the progenies. The zero tillage environment with crop residues on the soil surface was especially suited for the selection for early vigor.

We conclude that, within the germplasm pool handled in CIMMYT's durum wheat breeding program, selection can be conducted under either tillage conditions without affecting negatively the performance of resulting progenies. The neutrality of selection under zero tillage/conservation agriculture in relation to performance of progenies is a likely hypothesis that should be tested in other zero tillage/conservation agriculture conditions and germplasm pool combinations.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.fcr.2019.107675.

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