REVIEW & INTERPRETATION

Insights into Genotype × Tillage Interaction Effects on the Grain Yield of Wheat and Maize

J. M. Herrera,* N. Verhulst, R. M. Trethowan, P. Stamp, and B. Govaerts

ABSTRACT

No tillage or zero tillage (NT) is the extreme form of reduced tillage; NT with residue retention is a main component of conservation agriculture. Using a literature survey and meta-analysis, this study aimed to (i) summarize the results of studies comparing the grain yield of wheat [*Triticum aestivum* L. and *Triticum turgidum* L. subsp. *durum* (Desf.) Husn. (syn. *Triticum durum* Desf.)] and maize (*Zea mays* L.) genotypes under contrasting tillage, (ii) identify sources of variation in the grain yield response of wheat and maize genotypes to tillage practices, and (iii) identify potential traits for NT breeding programs. Grain yield was compared under NT and conventional tillage (CT) for 112 wheat genotypes (44 spring, 60 winter, and eight durum wheat genotypes) across 12 locations and 24 yr and for 93 maize hybrids across six locations and 5 yr. Most of these studies showed slightly higher grain yields under CT for maize (+5%) and winter (+5%) and spring (+2%) wheat. In the few studies where selection had been conducted under NT, the effect of tillage on the grain yield was modified significantly by genotypes. Traits associated with the emergence of vigorous seedlings and resistance to a changed spectrum of diseases increase genotype performance under NT. There is a need to evaluate genotypes developed under NT and extend the research on genotype performance under NT to locations with reduced input use and, in addition to tillage, investigate other factors that differentiate conservation agriculture from conventional practice.

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Abbreviations: CA, conservation agriculture; CT, conventional tillage; G, genotype; G×T, genotype × tillage; MSE, mean square error; NT, no tillage or zero tillage; QTL, quantitative trait loci; RT, reduced tillage.

Conventional farming practice, based on intensive tillage (i.e., plowing to a depth of at least 0.15 m and seedbed preparation by harrowing or rototilling) and removal of residues from the soil surface, can result in serious soil degradation (Montgomery, 2007). Conservation agriculture (CA) has been promoted as an agricultural practice that increases agricultural sustainability and has the potential to mitigate greenhouse gas emissions (Dendooven et al., 2012) and it is based on minimal soil disturbance and the retention of crop residues for soil and water conservation (Hobbs et al., 2008). No tillage or zero tillage (NT) is the extreme form of minimum soil disturbance and compared to conventional practices, NT alters the soil environment in which the crop is growing. No tillage or zero tillage with retention of crop residues fulfills the principles of CA. Generally, NT improves topsoil structure compared to conventional practices and induces important changes in soil fauna and flora and subsequent disease pressure (Verhulst et al., 2010). It can be expected that changes in the soil environment have an impact on crop growth

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and development. Verhulst et al. (2011) found slower initial maize and wheat growth in NT compared to the conventional practice in the Mexican highlands; however, these differences narrowed later in the season. At the end of the season, grain yield under NT was equivalent to or higher than conventional practice (Govaerts et al., 2005; Verhulst et al., 2011). Additional improvements in grain yield may be attainable if genotypes better adapted to the CA soil environment can be developed. Most published studies, ranging from genotype evaluation to impacts of tillage management on grain yield, used genotypes developed under conventional tillage (CT). This does not reflect the significant increase in the adoption of NT, indicated by the fact that by 2008 the area under NT was 40.1, 47.6, 12.0, and 5.0 million ha in North America, South America, Oceania, and the rest of the world, respectively (Derpsch et al., 2010). In addition, in countries such as Australia there are an increasing number of breeders that conduct at least part of the selection of their materials under NT. The genotypes developed under CT may not necessarily adapt to the NT environment and therefore, newly specifically adapted genotypes may need to be developed (Trethowan et al., 2012). A better understanding of genotype (G) × tillage (G×T) interactions may be fundamental in the context of sustainably increase the global productivity of wheat and maize and planning selection programs to achieve that goal.

Fischer (2009) estimated that approximately 0.6% of the 1.1% annual wheat yield gain in Australia is from improved management and 0.5% is from improved genotypes and G × management interactions. Differences in crop management may give rise to G × management × environment interactions. Cooper et al. (2001) examined the magnitude of G × management × environment interactions for grain yield and grain protein concentration in multi-environment trials involving 272 advanced breeding lines. They reported that the G × management component of the three-way interaction (G × management × environment) was the largest source of variation for both grain yield and grain protein concentration. These findings not only indicate the importance of each component of the interaction to achieving high yields but also the potential to exploit such interactions to maximize grain yield under NT. However, little has been done through breeding to fully realize the yield potential of new germplasm under NT. From the potential interactions of genotypes with components of the farming system, the type of interaction most extensively studied for both wheat and maize is G×T (tillage practice). The identification and exploitation of G×T interactions may improve the rate of increase in grain yield, resulting in accelerated adoption of NT practices and sustainable increase in grain production. Therefore, there is a need to determine if G×T interactions change the performance of genotypes since the decision to screen and select germplasm using more than one tillage management depends on the magnitude of G×T interaction (Francis and Smith, 1985). A large G×T interaction indicates that specific genotypes should be developed for specific tillage management. Major G×T effects would also make it necessary to identify traits linked to the improved response under NT to facilitate genetic improvement. Some of these traits may have higher heritability than grain yield and their selection will improve the rate of genetic advance under NT conditions.

The objectives of this paper were to (i) summarize the results of existing studies comparing the grain yield of wheat and maize genotypes under contrasting tillage, (ii) identify sources of variation in the grain yield response of wheat and maize genotypes to tillage, and (iii) identify physiological traits linked to improved yield under NT that can be targeted by breeding programs.

MATERIALS AND METHODS

Literature Survey

A database of the effects of tillage practice on the grain yield of wheat genotypes was compiled by surveying peer-reviewed literature with the Web of Science (Thomson Reuters). Briefly, keyword searches covering the period of 1950 through November 2012 identified articles that reported effects of NT compared to CT on the grain yield of wheat (Table 1) and maize (Table 2) genotypes. Treatments that included a sequence of soil tillage, such as plowing and harrowing, and the removal of most of the plant residue from the previous crop were considered as CT. For suitable articles, further analysis was conducted with the forward and backward options of the citation map command. We included additional articles that considered physiological traits that may increase the performance of wheat and maize under NT (Table 3).

Crop Yields Analysis

A meta-analysis is a statistical treatment of a dataset derived from a literature review that obtains more information from existing data by pooling the results of smaller studies. Meta-analysis increases the statistical power, resolves uncertainty, improves estimates of effect size, and allows new questions to be asked after the initial design of the study. A meta-analysis was used in the present study to investigate grain yield differences of genotypes sown under NT relative to CT. Moreover, the meta-analysis was used to evaluate which tillage practice produced the highest grain yield of the same genotype and to assess differences in the grain yield of genotypes under NT and CT. Finally, the meta-analysis investigated the effect of environmental variables such as precipitation, temperature, and soil type on genotype response to tillage practice.

The data of certain reviewed articles were excluded according to the following parameters: (i) data presented did not allow objective assignment to tillage categories (e.g., Carr et al., 2003a, 2003b), (ii) type of wheat was not reported (e.g., Zamir et al., 2010), (iii) number of genotypes included in the study was less than five (e.g., Ciha, 1982), and (iv) segregating populations were reported rather than cultivars or advanced lines (e.g., Hwu and Allan, 1992). In total, 10 articles on wheat

and three articles on maize were included in the grain yield analysis from the 12 (Table 1) and 11 (Table 2) respective studies found in the literature survey.

For each observation included in the analysis, the mean grain yield under NT and CT was extracted from tables, text, and figures of each primary article and then entered into a database together with the categorical information described in Tables 1 and 2. In addition, the mean annual precipitation of each site was included. These categories were identified as potential sources of variation that could alter the response of genotypes to tillage system. For studies that included data from more than 1 yr, grain yield was averaged across years. For studies that included data from more than one site, values from each site were used in the meta-analysis. For each genotype included in the analysis, the grain yield difference between NT and CT was calculated as the grain yield under NT minus the grain yield under CT.

Statistical Analysis

Yield data from the selected publications were fitted to linear regression mixed models for the crop yield analysis. The grain yield under CT of each crop was set as a fixed effect while grain yield under NT nested within site was set as a random effect. Grain yield under NT and CT were taken as the response and independent variables of the regression model of each crop, respectively. The model was fitted by maximizing the restricted log-likelihood with the function lme belonging to the contributed R library nlme (Pinheiro and Bates, 2009).

A potential publication-bias effect on the relationship between the grain yield under NT and the grain yield under CT was evaluated by means of a funnel plot. The relationship between the NT and CT grain yield difference and the identification of each study was plotted for this assessment. Publication bias is based on the expectation that effect sizes will not be symmetrically distributed around the independent variable without showing a consistent increase or decrease funnel-like pattern.

The robustness of the predictions of the regression models were evaluated by means of a stratified 10-fold cross-validation approach (Witten et al., 2011) and a sensitivity analysis. For the 10-fold cross-validation approach the data set was divided into 10 parts and each part was

Table 1. Summary of 12 studies about genotype × tillage (G×T) effects on the grain yield of bread (hard red spring wheat [HRSW], soft white spring wheat [SWSW], hard red winter wheat [HRWW], winter wheat [WW], spring wheat [SW], and soft red winter wheat [SRWW]) and durum wheat (DW).

Study	Location (latitude)	Type	Sites	No. G†	First year‡	Years	Climate§	Soil type	Yield¶	Significant G×T?	Rank change?	In yield analysis?
Carr et al. (2003a, 2003b)	North Dakota (~46° N)	HRSW	1	5	1995	4	Dfb	Sandy loam	NT = CT > RT#; CT > RT > NT††	No	No	No
Ciha (1982)	Washington (~46° N)	SWSW	2	4	1979	2 + 1‡‡	Csb	Silt loam	NT ≥ CT	Yes	Yes	No
Cox (1991); Cox and Shelton (1992)	North Dakota (~47° N)	HRWW	4	14	1984	5	Bsk or Dfb	Clay loam	NT > CT	Yes	No	Yes
Dao and Nguyen (1989)	Oklahoma (~35° N)	HRWW	1	10	1983	5	Cfa	Silt loam	NT ≥ CT > RT	No	No	Yes
Hall and Cholick (1989)	South Dakota (~45° N)	HRSW	3	18	1985	2 + 1	Dfb or Dfa	Silt loam	NT = CT	Yes	Yes	Yes
Hwu and Allan (1992)	Washington (~46° N)	WW	1	5§§	1981	5	Csb	Silt loam	CT > NT	Yes	Yes	No
Joshi et al. (2007)	Varanasi, India (~25° N)	SW	1	12	2002	3	CWa	Alluvial	NT = CT	Yes	Yes	Yes
Kharub et al. (2008)	Karnal, India (~30° N)	SW	1	5	2002	2	BSh	Sandy loam	CT > NT	Yes	Yes	Yes
Kumudini et al. (2008)	Kentucky (~37° N)	SRWW	2	4	2003	3	Cfa	Silt loam	CT > NT	No	No	No
Thompson et al. (1987)	North Dakota (~47° N)	HRSW	1	10	1982	5	Dfb	Clay loam	CT > NT	Yes¶¶	Yes	Yes
		DW	1	9	1982	5	Dfb	Clay loam	NT = CT##	Yes	Yes	Yes
Weisz and Bowman (1999)	North Carolina (~35°N)	SRWW	2	12	1996	2	Cfa or Cfc	Clay loam Sandy loam	CT > NT	No	No	Yes
Zamir et al. (2010)	Faisalab, Pakistan (~31° N)	SW	1	4	2005	1	BWh	Not stated	NT > CT	No	No	No

†G, genotype.

‡Year the first trial of the study was started.

§Climate according to Köppen-Geiger (Kottek et al., 2006): Bsk, cold semiarid; Bsh, warm semiarid; BWh, warm desert; Cfb, temperate oceanic; Cfa, warm oceanic; Cfc, cool oceanic; Csb, temperate mediterranean; CWa, humid subtropical; Dfa, warm continental; Dfb, temperate continental.

¶CT, conventional tillage; NT, no tillage or zero tillage; RT, reduced tillage.

#For high and medium sowing densities.

††For low sowing densities.

‡‡Number of years that the experiment was conducted in each of the experimental sites.

§§Populations.

¶¶There was a significant G×T × year interaction effect.

##Results for durum wheat.

Table 2. Summary of 11 studies about genotype × tillage (G×T) effects on the grain yield of maize.

Study	Location (latitude)	Type†	Sites	No. G‡	First year§	Years	C¶	Soil type	Yield#	Significant G×T?	Rank change?	In yield analysis?
Anderson (1986)	Maryland (~39° N)	Hy	3 + 4	6 + 12	1982	3 + 2	Cfb	Silt loam Sandy loam	NT > CT	No††	No	Yes
Brakke et al. (1983)‡‡	Nebraska (~42° N)	Hy	2	169	1980	1	Bsk	Silt loam Sandy loam	CT > NT	Yes	Yes	No
Carter and Barnett (1987)	Wisconsin (~44° N)	Hy	4	15	1984	2	Dfb	Silt loam	CT > NT	Yes	No	Yes
Duiker et al. (2006)	Pennsylvania (~40° N)	Hy	1	5	2002	3	Cfb	Silt loam	NT = CT	No	No	No
Graven and Carter (1991)	Wisconsin (~44° N)	Hy	2	2	1986	3	Dfb	Silt loam	CT > NT	No	No	No
Hallauer and Colvin (1985)	Iowa (~42° N)	Hy	1	14	1979	5	Dfa	Fine loam	CT > NT	No	No	Yes
Karlen and Sojka (1985)	South Carolina (~34° N)	Hy	1	5	1983	1	Cfa	Fine loam	CT > NT	No	No	No
Kaspar et al. (1987)	Iowa (~42° N)	Hy	1	4	1980	2	Dfa	Fine loam	CT > NT	No	No	No
Newhouse and Crosbie (1986)	Iowa (~42° N)	Hy	2	60	1981	2	Dfa	Silt loam	CT > NT	No	No	No
Newhouse and Crosbie (1987)	Iowa (~42° N)	S_1	2 + 3	100	1981	2	Dfa	Silt and clay loam	CT > NT	Yes§§	Yes	No
Wall and Stobbe (1983)	Manitoba (~49 °N)	Hy	1	8	1980	2	Dfb	Sandy loam	CT > NT	No	No	No

†Hy, hybrids; S_1, S_1 lines;

‡G, genotype.

§Year the first trial of the study was started.

¶Climate according to Köppen-Geiger (Kottek et al., 2006): Bsk, cold semiarid; Cfb, temperate oceanic; Cfa, warm oceanic; Dfa, warm continental; Dfb, temperate continental.

#CT, conventional tillage; NT, no tillage or zero tillage.

††There was no significant G×T interaction effect except 1 yr at one location.

‡‡This was not exactly a study of G×T but there were genotypes were grown in two contrasting cropping systems that included CT and NT.

§§In one out of two populations tested.

Table 3. Traits with potential to increase the adaptation of genotypes to no-till or zero tillage.

Targeted response and trait	Reference
Emergence and establishment	
Longer coleoptiles	Erayman et al. (2006); Rebetzke et al. (2004, 2007); Trethowan et al. (2005)
Thicker coleoptiles	Rebetzke et al. (2004)
Emergence from depth	Joshi et al. (2007); Trethowan et al. (2005)
Homogeneous emergence	McMaster et al. (2002); Unger and McCalla (1980); Olesen et al. (2004)
Rapid growth	
Vigorous seedlings	Hall and Cholick (1989); Kharub et al. (2008); Liang and Richards (2012); Richards and Lukacs (2002); Trethowan et al. (2005)
Cold-tolerant seedlings	Boubaker and Yamada (1991); Cox (1991); Cox and Shelton (1992); Dell'Aquila and Spada (1994); Hund et al. (2007)
Greater kernel weight and embryo size	Ciha (1982); Liang and Richards (2012)
Greater specific leaf area	Liang and Richards (2012); Olesen et al. (2004)
Disease and pest resistance	
Broad disease resistance	Joshi et al. (2007); Simón et al. (2011); Trethowan et al. (2005)
Root rot resistance	Okubara et al. (2009); Paulitz et al. (2002)
Bacterial resistance	Mazzola (2004); Mazzola et al. (2004); Neal et al. (1973)
Cyst nematode resistance	Ogbonnaya et al. (2001a, 2001b)
Uptake and use of nutrients	
Deeper rooting	Manske and Vlek (2002); Qin et al. (2005); Reynolds et al. (2007); Watt et al. (2005)
Homogeneous root distribution	Qin et al. (2006); Reynolds et al. (2007)
Increased angle of seminal roots	Nakamoto and Oyanagi (1994)
Increased root elongation	Gahoonia and Nielsen (2004a, 2004b)
Reduced root gravitropism	Palta et al. (2011)
Adaptation and biomass partitioning	
Reduced tillering	Kumudini et al. (2008).
Higher winter survival	Cox (1991)
Optimized flowering	Araus et al. (2008); Kirkegaard and Hunt (2010); Thompson et al. (1987)
Optimized maturation	Chevalier and Ciha (1986); Kumudini et al. (2008)
Rate of leaf production	Dao and Nguyen (1989)
Integration into rotations	
Weed suppression	Bertholdsson and Brantestam (2009); Joshi et al. (2007); Olesen et al. (2004)
Faster stubble decomposition	Joshi et al. (2007)

removed in turn while a learning scheme was trained on the remaining nine-tenths. The error rate was determined based on the hold-out part and expressed as the average mean square error (MSE) of the entire cross-validation procedure. The sensitivity analysis was performed by removing one by one all the data originating from the same report and evaluating the effect this produced on the output. Deviation from a 1:1 ratio was additionally evaluated by means of MSE.

The dataset and R code (R Development Core Team, 2008) used for statistical analysis is available, on request, from the corresponding author.

RESULTS AND DISCUSSION

Genotype × Tillage Effects on Grain Yield

Wheat

Most studies that examined G×T effects on wheat were conducted in the United States (Table 1) and it is clear that more research in other agroecosystems is needed.

In the United States, significant G×T effects on the grain yield of spring wheat were reported for the Pacific Northwest by Ciha (1982), in North Dakota by Thompson et al. (1987), and in South Dakota by Hall and Cholick (1989). However, in other studies from North Dakota including reduced tillage (RT), NT, and CT treatments, no significant G×T, G × seeding rate, and G×T × seeding rate interactions were found for grain yield (Carr et al., 2003a, 2003b).

In U.S. winter wheat studies, Dao and Nguyen (1989) and Weisz and Bowman (1999) reported no significant G×T effect on grain yield in Oklahoma and in North Carolina, respectively. In the study by Dao and Nguyen (1989) the NT treatment was established at the first experimental year and therefore, the soil environment was probably not representative of a mature long-term NT soil. Similarly, no significant G×T interaction effect on grain yield was found in a study conducted at two locations in Kentucky from 2004 to 2006 (Kumudini et al., 2008). A significant G×T effect occurred in a 5-yr study at four locations in North Dakota (Cox, 1991; Cox and Shelton, 1992). There was no rank change, however, in the performance of the five top-yielding genotypes across the NT and CT environments and the significant G×T interaction was attributed to differential winter survival rather than tillage.

Only three studies outside the United States examined G×T interactions on spring wheat, all performed under subtropical to tropical conditions on the Indian subcontinent. Significant G×T for grain yield were found in the studies conducted in India at Varanasi (Joshi et al., 2007) and at Karnal (Kharub et al., 2008). In the latter study rotary tillage was also included together with four other tillage-planting systems (NT, CT, RT, and tilled raised beds). However, Zamir et al. (2010) reported no significant G×T for grain yield at Faisalabad (Pakistan).

In summary, in 7 out of 12 studies (58%) with spring and winter wheat, significant G×T interaction was reported. The percentage of reported significant G×T interactions was higher for spring wheat (71%) than for winter wheat (40%). In studies using spring wheat, the grain yield under NT was either higher than or equal to the grain yield under CT in 28 and 35% of the studies, respectively. In most winter wheat studies the grain yield was lower under NT (60%).

Maize

All studies that examined G×T effects on grain yield in maize were conducted in North America (the United States and one study in Canada) (Table 2).

Genotype × tillage interactions were significant in Manitoba (Canada) (Wall and Stobbe, 1983) and in Wisconsin (Carter and Barnett, 1987). However, in the latter study, the highest ranked hybrids under NT were the highest ranked hybrids under CT as well. Although an additional study was not specifically designed to test G×T interactions, Brakke et al. (1983) reported significant G × cropping system interactions in Nebraska where NT and CT treatments were part of the different cropping systems. In contrast, no significant G×T interactions were found in Iowa (Hallauer and Colvin, 1985; Kaspar et al., 1987), in South Dakota (Karlen and Sojka, 1985), and in Pennsylvania (Duiker et al., 2006). Karlen and Sojka (1985) attributed the lack of significant G×T interaction on the grain yield of maize to the fact that the maize hybrids were thinned to achieve the same population density under CT and NT. This is a strong indication that NT reduces seedling establishment, a yield component that is not easily compensated later in nontillering maize. In a detailed study in Maryland, Anderson (1986) also found no significant G×T effect on the grain yield of six maize hybrids in with the exception of one out of three locations (Beltsville).

Except for a recent study in Pennsylvania (Duiker et al., 2006), all other reports predate 1989. Since then, the planting density tolerance of hybrids has been a breeding target and seeding rates increased accordingly (Duvick, 2005). Unfortunately most of the fields used for the NT treatments were under CT until the year before the trial started (e.g., Carter and Barnett 1987; Kaspar et al., 1987; Duiker et al., 2006) and therefore the soil characteristics are probably not representative of a long-term NT field.

Most (82%) of the studies surveyed did not report significant G×T interactions, a value similar to winter wheat but lower than that for spring wheat.

Grain Yield Analysis of Genotype × Tillage Interaction Effects on Wheat and Maize

Several studies reported significant G×T effects on the grain yield of wheat and maize, without genotype rank change among different tillage managements (Cox, 1991; Cox and Shelton, 1992; Carter and Barnett, 1987). Such results suggest that significant G×T effects were due to

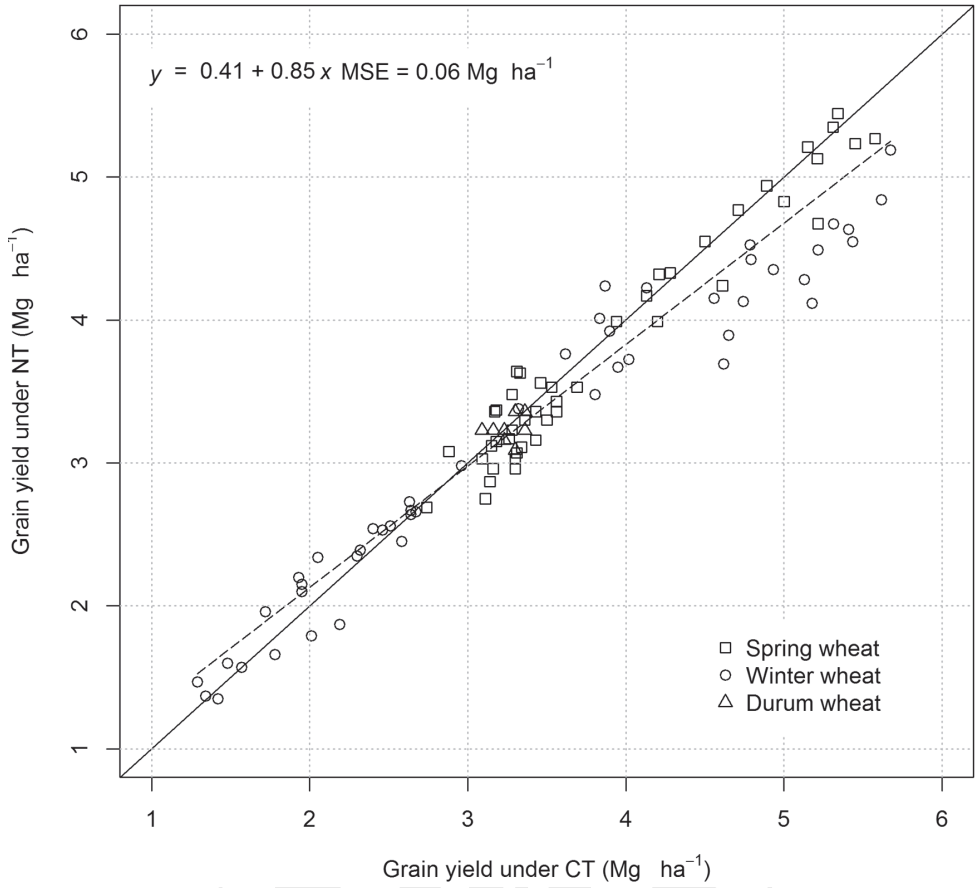

Figure 1. Relationship for grain yield under no tillage or zero tillage (NT) and conventional tillage (CT) for spring bread wheat, winter bread wheat, and durum wheat. The solid line indicates the 1:1 ratio while the dashed line indicates the predicted values according to a mixed effects regression model. Mean square error (MSE) is the average after a 10-fold cross-validation approach.

size effects without significant change in the relative performance of the genotypes. A meta-analysis can determine if this was an isolated output or a more general trend. We hypothesized that a lack of a relationship or a nonlinear relationship between the grain yields of the same genotypes grown under NT and CT would exist if the grain yield was broadly modified by G×T interactions. This hypothesis was tested for wheat and maize and the relationships are shown in Fig. 1 and 2, respectively.

For wheat, there was a highly positive and significant linear relationship for the grain yield of each genotype under NT and CT. The mixed model revealed no significant modification of the relationship by site and predicted a slope coefficient with a narrow confidence interval (0.85 ± 0.04). The 10-fold cross validation of the model suggested that wheat grain yield under NT can be predicted from the performance under CT with high accuracy (MSE = 0.06 Mg ha^{-1}) and that this model allowed better predictions than using a 1:1 relationship (MSE = 0.10 Mg ha^{-1}). No evidence of a publication bias was found based on the relationship between the NT – CT grain yield difference and the publication. However, the range of the NT – CT grain yield difference was higher in Weisz and Bowman (1999) than other reports. The sensitivity analysis revealed that removing the data included in the report by Weisz and Bowman (1999) slightly increased the slope (11%) while removing single-wise data included in the other reports did not change the value of this parameter by more than 5%. Therefore, the linear relationship between the grain yield of each genotype under NT and CT can be considered robust. Although the model suggests a relationship independent of the type of wheat, Fig. 1 indicates that small differences associated with wheat type may become evident if studies with more genotypes and sites are conducted. For spring wheat, the values were close to the 1:1 ratio, indicating that it was likely that high yielding genotypes under CT also yield well under NT. This was also observed for winter wheat at relatively low and intermediate grain yields. However, the relationship moved away from the 1:1 ratio for genotypes that yielded more than 4.5 Mg ha^{-1} under CT. At this range, a difference up to 1 Mg ha^{-1} between NT and CT was observed for the same genotypes. This indicates that genotypes with high yields under CT were not able to attain the same yield potential under NT.

For maize, a more scattered pattern was found for the grain yield of the same hybrids under CT and NT; however, as for wheat a significant linear relationship was found

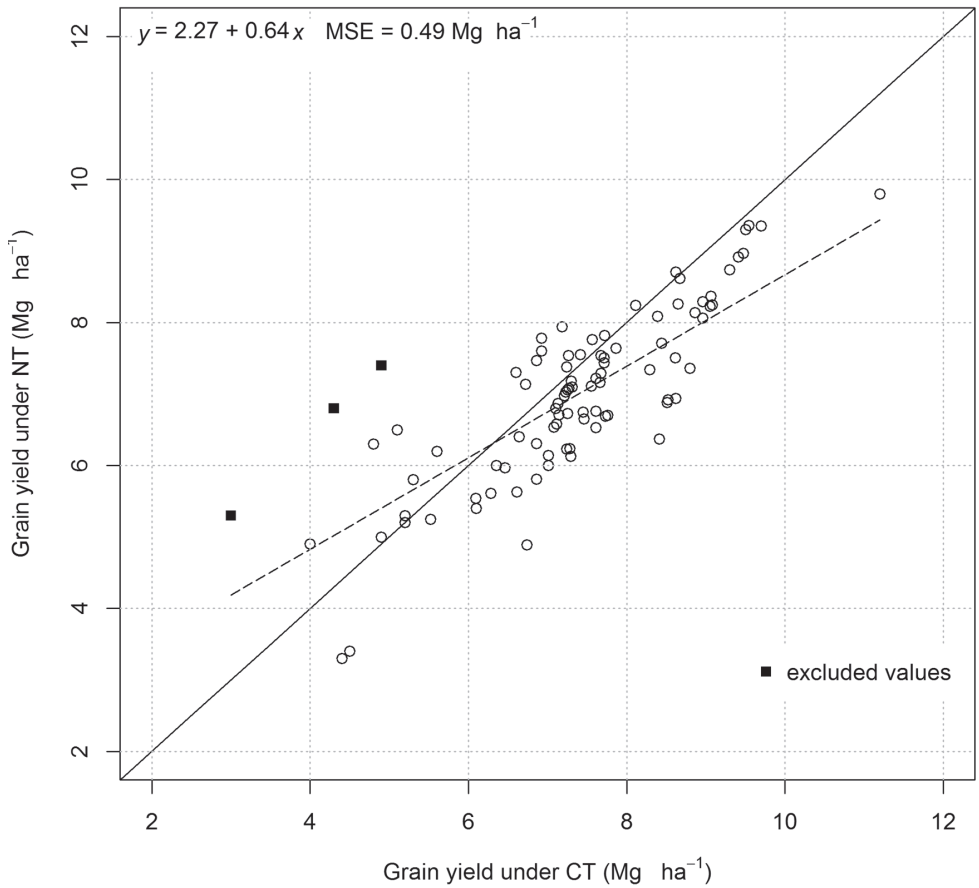

Figure 2. Relationship for grain yield under no tillage or zero tillage (NT) and conventional tillage (CT) for maize. The solid line indicates the 1:1 ratio while the dashed line indicates the predicted values according to a mixed effects regression model. Mean square error (MSE) is the average after a 10-fold cross-validation approach.

between the two variables (Fig. 2). Funnel and sensitivity analyses suggested a publication bias and a leverage effect by three hybrids out of 18 in the dataset of Anderson (1986). The difference in grain yield between NT and CT for these hybrids was 25% higher than for any other hybrids and was out of range compared to the rest of the data. Therefore, these observations were excluded from the analysis. The mixed model predicted a slope coefficient with a much wider confidence interval (0.64 ± 0.15) than found for wheat. Although the relationships in the figures represent all studies and sites, we verified each individual dataset for grouped data, and these potentially biased sources were discarded. The 10-fold cross validation of the model suggests that the model predicts maize grain yield under NT from performance under CT with an acceptable accuracy (MSE = 0.49 Mg ha^{-1}) and also that the model allowed better predictions than using a 1:1 relationship (MSE = 0.83 Mg ha^{-1}). In contrast to winter wheat, the relationship for maize was more linear at relatively high yield rather than low and intermediate grain yields.

The analysis of the relationships for spring wheat, winter wheat, and maize found that the highest yielding genotypes under NT were usually the highest yielding genotypes under CT. When interpreting these results, it should be noted that all the genotypes included were developed under CT.

Environmental Impact on Grain Yield at No Tillage or Zero Tillage and Conventional Tillage

In most studies the grain yield was higher under CT than NT for wheat (Thompson et al., 1987; Hwu and Allan, 1992; Weisz and Bowman, 1999; Kharub et al., 2008; Kumudini et al., 2008) and for maize (Brakke et al., 1983; Wall and Stobbe, 1983; Hallauer and Colvin, 1985; Karlen and Sojka, 1985; Newhouse and Crosbie, 1986; Carter and Barnett, 1987; Kaspar et al., 1987; Graven and Carter, 1991). In some studies higher grain yields under NT than CT were reported for wheat (Cox, 1991; Ciha, 1982; Zamir et al., 2010) while for maize only one report (Anderson, 1986) found higher grain yield under NT than under CT. The crop yield analysis revealed similar consequences of growing the same genotypes under NT and CT for spring wheat, winter wheat, and maize; the grain yields under NT were lower for spring wheat (–2%), winter wheat (–5%), and maize (–5%) compared to CT. In contrast, the grain yield of the durum wheat genotypes was similar under NT and CT.

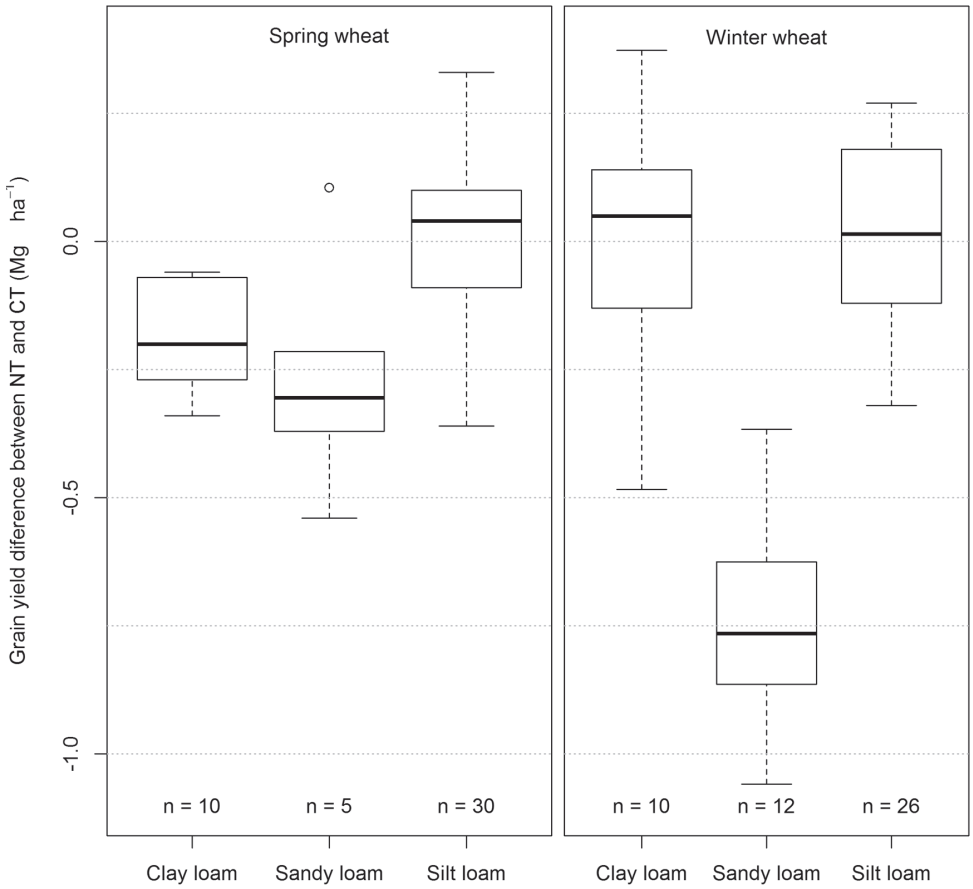

Figure 3. Box and whisker plots of grain yield (Mg ha^{-1}) difference for each genotype between no tillage or zero tillage (NT) and conventional tillage (CT) for spring and winter wheat as related to soil characteristics. The middle line represents the mean, and the outer horizontal lines of the boxes represent the upper and lower 25% quartiles. The ends of the error bars represent the 95% confidence intervals and the dots represent outliers.

Modern genotypes in contrast to old landraces often exhibit wide geographical adaptation as well as a broad adaptation to management practices (Reynolds et al., 2007). The identification of environments where genotype limits the performance of NT is fundamental to improving the productivity under such environments. The factors affecting the grain yield difference of the genotypes under NT and CT were investigated for spring and winter wheat but not for maize and durum wheat due to insufficient studies. The grain yield tended to be relatively lower for spring wheat and winter wheat in sandy loam soils compared to clay loam and silt loam soils, and this difference was significant between sandy loam and silt loam soils for winter wheat (Fig. 3). These results indicate lack of suitably adapted genotypes to NT in soils characterized by coarser texture. Alternatively, management of these soils to supply sufficient water and nutrients under NT may have been inadequate.

Differences in water availability were often used to explain differences in the performance of genotypes under NT and CT (Dao and Nguyen, 1989; Hall and Cholick, 1989; Cox, 1991; Carr et al., 2003a). Due to the limited number of studies, precipitation could not be considered as a continuous variable; it was therefore considered as a categorical variable. There was not a clear effect of annual precipitation on spring wheat yield differences between NT and CT for the genotypes included in the meta-analysis (data not shown). In contrast, a clear pattern was found for winter wheat; there was an increasing magnitude in the grain yield difference as precipitation increased (Fig. 4). This suggests that conservation of soil water is a critical factor explaining differences between NT and CT. With low precipitation CT has typically less soil water in the soil layer due to greater evaporation, which results in a patchier seedling emergence under CT than NT (Unger and McCalla, 1980; McMaster et al., 2002). This difference could be even higher since it is likely that the results of studies with CT not reaching minimum values of emergence were not reported. Similarly, by removing surface residue cover, snow catch was probably lower and resulted in lower soil moisture under CT. The resulting higher soil moisture under NT explains the higher grain yields of winter wheat at lower production (i.e., <2.75 Mg ha^{-1}) levels (Fig. 1). The results demonstrated that the grain yield of genotypes under NT was much lower than under CT at higher productivity levels. The variability observed

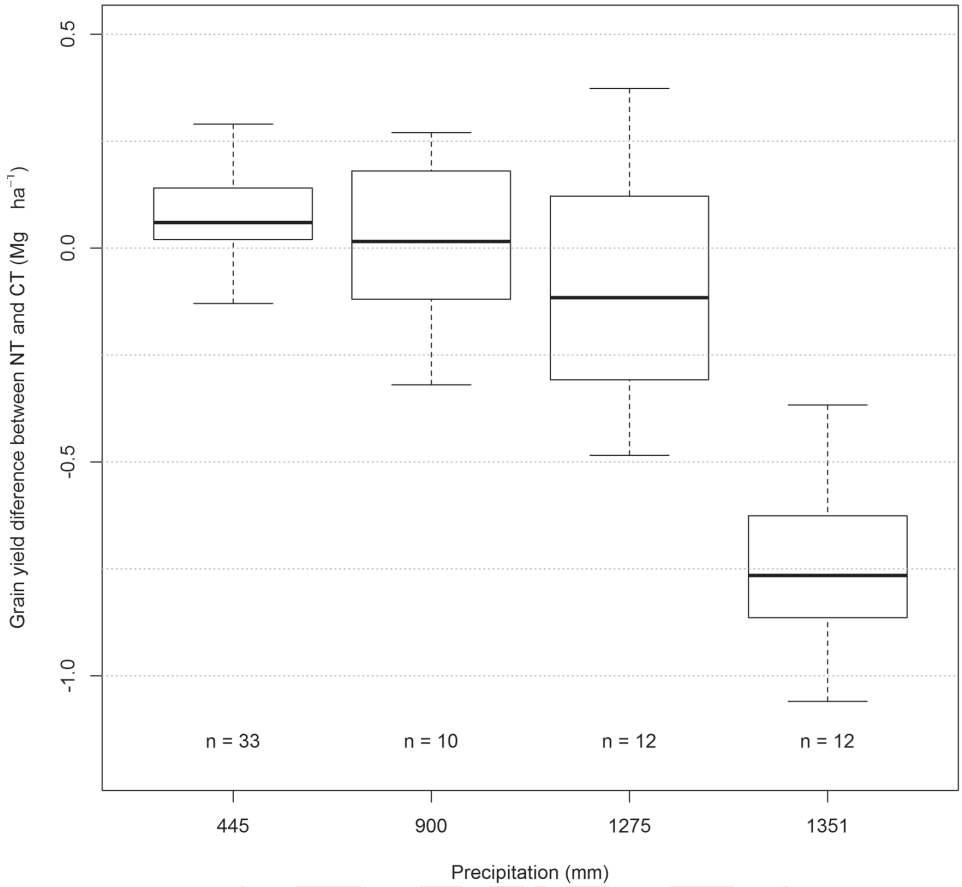

Figure 4. Box and whisker plots of grain yield (Mg ha^{-1}) difference for each genotype between no tillage or zero tillage (NT) and conventional tillage (CT) for winter wheat as related to annual precipitation. The middle line represents the mean, and the outer horizontal lines of the boxes represent the upper and lower 25% quartiles. The ends of the error bars represent the 95% confidence intervals.

in Fig. 3 and 4 also has important ramifications; even for winter wheat that showed a clear negative difference, the high variability in grain yield difference indicated that the lower grain yields under NT compared to CT can be greatly improved by growing better adapted genotypes.

Genetic Adaptation to No Tillage or Zero Tillage

Hwu and Allan (1992) conducted a study where selection under NT was conducted for wheat. The objective was to determine if selection under NT could be used to improve the adaptability of winter wheat to NT management. They studied five populations with genetic diversity for several traits in Washington. Each of the bulk populations was grown without artificial selection in a series of five planting and harvesting cycles. In two out of five populations, the NT-selected subpopulation performed significantly better than the CT-selected subpopulation when evaluated under NT. In their study, differentiation occurred only under NT, indicating that NT exerts a greater selection pressure than CT during genotype development. Their study also concluded that the original genetic diversity of the populations tested was sufficient to differentiate materials by divergent selection under CT and NT. Trethowan et al. (2012) studied the genetics of wheat adaptation to tillage management following a two-step approach. As the first step, significant G×T interactions were found in one out of two experimental sites in Mexico where a diverse set of cultivars was sown in two contrasting environments under two tillage systems (NT and CT). As the second step, a mapping population of 150 entries was derived using one of the genotypes identified in Mexico as a parent. These entries were evaluated in Australia under NT and CT. A quantitative trait loci (QTL) analysis of the mapping population identified several QTL associated with specific adaptation to tillage systems. These included normalized difference vegetation index traits that were associated with the screened early biomass production, indicating the importance of early plant vigor.

Sixty maize hybrids were evaluated (Newhouse and Crosbie, 1986) and 100 S_1 lines derived from two genetically diverse populations under CT and NT (Newhouse and Crosbie, 1987) at two locations in Iowa and included a third location in the last year of the trial. A significant G×T interaction among the S_1 lines derived from one out of the two original populations was found. Therefore, similar to wheat, significant G×T interactions were found in the only study in maize of selection under NT (Newhouse and Crosbie, 1987). A successful maize

selection program for a specific cropping system was reported in Germany (Burger et al., 2008), demonstrating that hybrids can be selected for an improved early vigor as needed to increase competitive ability in organic agriculture. This output is expected to result in relevant hybrids since the selected inbred lines can be superior to conventional hybrids (Walter Schmidt, KWS SAAT AG, personal communication, 2012).

The fact that for both wheat and maize G×T interactions were observed following selection of segregating populations under NT highlights the importance of parent selection in breeding for adaptation to tillage management.

Traits Influencing Grain Yield Under No Tillage or Zero Tillage

If cultivars are to be tailored to NT, it is fundamental that traits conferring adaptation are identified. It is likely that these traits will have higher heritability than grain yield alone and their targeted selection should increase rates of genetic gain under NT. Table 3 shows traits that were identified as potentially useful for improving the performance of wheat and maize genotypes under NT. Although traits in Table 3 were reviewed for NT, most of these traits are, based on the production environment, also selection targets for CT. Therefore, these traits could be additionally considered in a broader context of improving maize and wheat productivity.

Differences in emergence and initial growth were found in many studies comparing wheat performance under NT and CT (e.g., Ciha, 1982; Dao and Nguyen, 1989; Hall and Cholick, 1989; Karlen and Sojka, 1985). Weisz and Bowman (1999) reported a significant effect of tillage on plant density. Several traits associated with establishment and emergence (Trethowan et al., 2005) were identified as promising for NT including kernel weight and embryo size (Ciha, 1982; Liang and Richards, 2012), coleoptile length and thickness (Rebetzke et al., 2004, 2005, 2007; Trethowan et al., 2005; Erayman et al., 2006), emergence from depth (Trethowan et al., 2005; Joshi et al., 2007), rapid growth (Olesen et al., 2004), seedling vigor (Hall and Cholick, 1989; Richards and Lukacs, 2002; Trethowan et al., 2005; Erayman et al., 2006; Kharub et al., 2008; Liang and Richards, 2012), seedling temperature tolerance (Boubaker and Yamada, 1991; Cox, 1991; Cox and Shelton, 1992; Dell'Aquila and Spada, 1994; Hund et al., 2007), and early biomass and specific leaf area (Olesen et al., 2004; Liang and Richards, 2012). Most of these traits indicate that the emergence and establishment of vigorous seedlings must be a selection target for NT adapted genotypes, as NT can negatively affect the early germination due to denser soil, suboptimum soil contact, and lower soil temperature. The latter reduces early growth especially in maize.

The introduction of NT and the retention of crop residues can lead to a change in the disease and pest spectrum and previously unimportant diseases, such as yellow spot (*Pyrenophora tritici-repentis*), can become yield limiting. As the genetic control of such diseases is relatively simple the plant breeder should address such constraints in an integrated breeding program to increase crop performance under NT. However, none of the studies included in the literature review reported significant disease or pest effects on G×T interaction. Nevertheless, resistance to aboveground diseases (Trethowan et al., 2005; Joshi et al., 2007; Simón et al., 2011), belowground diseases (Neal et al., 1973; Paulitz et al., 2002; Mazzola, 2004; Mazzola et al., 2004; Okubara et al., 2009), or nematodes (Ogbonnaya et al., 2001a, 2001b) were suggested as target traits for production systems based on NT.

Tiller production was unaffected by G×T effects in several studies (Hall and Cholick, 1989; Weisz and Bowman, 1999; Carr et al., 2003a, 2003b). According to Hall and Cholick (1989), however, such interactions occur during early-season tiller production but are not found later in the season. Reduced tillering under NT compared to CT was reported by Chevalier and Ciha (1986) while increased tillering in NT compared to CT was reported by Zamir et al. (2010) and Kumudini et al. (2008). Zamir et al. (2010) associated the increased tillering with higher grain yield while Kumudini et al. (2008) suggested that increased tillering led to a reduction in harvest index and grain yield. However, it has to be considered that the advantage of an increased tillering capacity may depend on the environment. Additionally, the impact of tillering capacity on grain yield is influenced by patchiness of stands, winter kill (for winter wheat), and competition against weeds. Late tillering is always negative for grain yield, especially in spring wheat, as late tillers are always less productive. In contrast, early tillering genotypes will maximize the exploitation of a fertile environment with an adapted high seedling density. Therefore, high tillering capacity may be a selection target to optimize biomass under NT depending on the production environment. Selection of traits related to biomass accumulation may improve broad adaptability of wheat to different tillage practices since Thompson et al. (1987) reported that tall varieties were influenced more than semidwarf types by the tillage system.

According to Cooper et al. (2001), the source of G × management interaction effects on grain yield most extensively studied is phenology generated by varying the sowing date (e.g., Kirkegaard and Hunt, 2010). The influence of phenological traits on adaptation to NT was frequently mentioned as important in several reports. Examples are traits controlling rate of leaf production (Dao and Nguyen, 1989), days to heading and/or anthesis (Thompson et al., 1987; Araus et al., 2008; Kirkegaard and Hunt, 2010), and maturation time (Chevalier and Ciha, 1986; Kumudini et al., 2008). The

reports show contrasting effects; days to heading of durum and hard red spring wheat genotypes followed a similar trend among tillage systems (Thompson et al., 1987). Significant differences in days to heading between NT and CT were reported but without impact on grain yield (Kumudini et al., 2008) while rates of leaf production (Chevalier and Ciha, 1986) and days to anthesis (Dao and Nguyen, 1989) were modified by tillage. Therefore, phenological traits may be, based on the production environment, a selection target to improve adaptation to NT.

A major difference between NT and CT can be found in the soil environment. Recent studies demonstrated genotypic variation in cereal root systems in response to the differences in the soil environment (Watt et al., 2005) and P status (George et al., 2011) linked to tillage practice. Maize had more and finer roots under CT compared to NT (Qin et al., 2005, 2006). For winter wheat, no significant effect on root development has been reported (Qin et al., 2004). Similarly, Kharub et al. (2008) found significant differences in root density among tillage systems and genotypes in the early stages of crop growth but not at more advanced growth stages. The increased organic matter often found in the upper soil profile under NT compared to CT determines differences in the distribution of nutrients (Angers et al., 1997). Therefore, it may be important to target specific root traits through breeding such as rooting depth (Manske and Vlek, 2002; Watt et al., 2005; Reynolds et al., 2007), root distribution (Reynolds et al., 2007), angle of seminal roots (Nakamoto and Oyanagi, 1994), increased root elongation (Gahoonia and Nielsen, 2004a, 2004b), and reduced root gravitropism (Palta et al., 2011).

The effect of G×T on maize traits has been less studied than wheat. Some of the traits identified for wheat may be unique to species where tillers are a fundamental component determining grain yield. In contrast, in species such as maize where soil temperature during seedling has a significant impact on plant establishment and as result on grain yield, chilling tolerance may be a desirable target trait for NT. Significant G×T effects were found for grain moisture at physiological maturity (Carter and Barnett, 1987) whereas no significant G×T effect was found on the percentage of emerged plants (Carter and Barnett, 1987; Duiker et al., 2006), plant height (Kaspar et al., 1987; Duiker et al., 2006), biomass dry weight (Carter and Barnett, 1987), and stalk lodging (Carter and Barnett, 1987).

In relation to what the grain yield analysis revealed (Fig. 1 and 2), traits associated with disease and pest resistance, adaptation and biomass partitioning, and the integration into rotations may be important targets to attain stable higher grain yields (>4.5 Mg ha^{-1}) with winter wheat under NT. For maize, beside the traits identified for winter wheat, those associated with emergence and establishment and uptake and use of nutrients may be increasingly important to attain high yields under NT.

Research Gaps and Future Research Needs

Although only 12 G×T interaction studies for wheat and 11 for maize were identified in the literature, the effect of this type of interaction on grain yield has been the most studied. This suggests an urgent need to address the research gap on genotype interactions with other components of CA (e.g., rotation and residue management) thus improving our understanding of G × management interactions and the contribution of specific physiological traits for improved genotype adaptation to CA (Table 3).

There are conflicting reports of genotype responses to tillage systems, spanning from those that find no genotype differential effect to those that report a modified genotypic response to the tillage system (Table 1). There are not enough selection studies under NT to conclude whether breeding should be done independently for NT and CT systems. The analysis of the relationship of grain yield of the same genotypes under NT and CT (Fig. 1 and 2) corroborated the general absence of a tillage system effect on genotype performance. However, these analyses also suggest that differences among wheat types and between wheat and maize must be considered before drawing general conclusions.

Many studies failed to detect significant G×T interactions, which may reflect the small number of genotypes evaluated (e.g., Carr et al., 2003a; Kumudini et al., 2008; Zamir et al., 2010). Moreover, Trethowan et al. (2005) suggested that a lack of G×T interaction is because genotypes reported in the literature are usually developed under CT as this is common practice in most breeding programs (see Carena et al., 2009, too). In addition, cultivar performance trials are mostly conducted under CT even though there are an increasing number of farmers growing wheat and maize under NT. Clearly, there is a need to more extensively compare lines resulting from selection under NT and CT. By doing selection in parallel important questions may be answered: (i) whether tillage system should be considered when breeding wheat and maize and (ii) whether selection under NT results in higher yielding genotypes for both tillage systems. The results of the few studies where selection under NT has been considered for wheat (Hwu and Allan, 1992) and maize (Newhouse and Crosbie, 1987) suggest that selection under NT may identify high-yielding genotypes for NT systems. In addition, recent genetic studies showed a differential adaptation under NT compared to CT (Trethowan et al., 2012). Conducting selection under NT may allow introgression of traits associated with superior performance under NT such as resistance to soil borne diseases, which may also increase grain yield under CT.

Van Den Putte et al. (2010) conducted a meta-analysis on the effects of NT and CT on the grain yield of fodder and grain maize, potato (*Solanum tuberosum* L.), sugar beet (*Beta vulgaris* L.), spring and winter wheat, and spring and winter barley (*Hordeum vulgare* L.) at 47 European sites. They

found reduced grain yield in NT compared to CT and attributed this to inadequate crop rotation and to the use of lower inputs. Similarly, a literature review based on studies conducted in North America (Ogle et al., 2012) found that crop productivity, using the currently available genotypes, can be reduced with adoption of NT, particularly under wet (>800 mm yr^{-1}) climatic conditions. We also found, by means of a crop yield analysis, similar reductions for winter wheat with increased precipitation (Fig. 4). The differences in grain yield of genotypes under NT and CT were similar to the ones found by Van Den Putte et al. (2010) and Ogle et al. (2012) despite no pairwise comparison of the same genotype in these studies. The ranking from higher to lower reduction in the grain yield of genotypes grown under NT compared to CT was as follows: maize > winter wheat > spring wheat. Genotypes can have an important role in increasing grain yield under NT; even in the case of winter wheat, where the genotypes tended to have a reduced performance under NT compared to CT, the highly variable performance of genotypes showed that differences could be removed by choice of appropriate genotypes (Fig. 3).

In most studies, widely grown genotypes were not included and genotype selection was based on the expression of traits expected to contribute to a differential response under NT compared to CT. In addition to grain yield and yield components, the effect of G×T interaction on wheat has been studied for traits that can be grouped into traits related to the emergence and establishment, disease and pest resistance, uptake and use of resources, adaptation and biomass partitioning, and integration into rotations (Table 3). The final effect of a trait on grain yield can be highly site specific and management specific. Therefore, the scope to exploit specific traits to increase yield under NT may be much higher if the targeted physiological traits are first assessed in NT environments that are representative of farmer practice.

We found that a thorough description of NT, RT, CT, and agronomical management is generally missing in most studies. Generally, information on the history of the NT treatments is lacking. In addition, residue management is often not explained and it is well known that maintenance of residues on the soil surface under NT is fundamental (Verhulst et al., 2011). In this sense, it was important to conduct, besides the literature survey, a meta-analysis. The meta-analysis allowed to isolate results coming from studies where there were problems to generate representative conditions of the tested tillage practice (e.g., Fig. 2).

CONCLUSIONS

Among the management practices that may determine specific genotypic interactions under CA, the interaction with tillage is by far the most studied option. Although this interaction is the most studied, less than 25 studies have been published for wheat and maize. In addition, these studies were concentrated in only a few areas in the world (mainly northern United States) where higher levels of inputs than in developing countries are often used for cropping. The published studies do not cover all wheat types (e.g., durum wheat is underrepresented), which makes it difficult to make general inferences or to identify patterns of broad validity. In a strict sense, the inferences from the published studies may be regarded as genetically biased as almost all evaluated genotypes were bred under conventional practices and many NT treatments had only some characteristics of well-established NT environments.

Traits associated with the emergence of vigorous seedlings and resistance to a changed spectrum of diseases (e.g., yellow spot) increase genotype performance under NT. In the few studies where populations were selected under NT, the effect of genotype was modified by the tillage system suggesting that selection under NT should be considered in crop improvement programs. This consideration not only applies to genotype development but will also assist the identification of physiological traits that enhance crop performance under NT and overall wheat and maize improvement for other systems as well.

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