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# Wheat Yield Improvements in Brazil: Roles of Genetics and Environment

Elesandro Bornhofen, Matheus Henrique Todeschini, Matheus Giovane Stoco, Alana Madureira, Volmir Sergio Marchioro, Lindolfo Storck, and Giovani Benin\*

## ABSTRACT

Several studies have shown a significant increase in wheat (*Triticum aestivum* L.) grain yield (GY) worldwide during the 20th century as a result of genetic and environmental improvement. The objective of this study was to measure the genetic gains achieved in a wheat breeding program maintained by the Central Cooperative of Agricultural Research (COODETEC) in Brazil through the annual evaluation of lines in multi-environment trials. The dataset was composed of 836 advanced trials and was evaluated in 40 representative locations to assess the value for cultivation and use (VCU) regions in the south, southeast, and central-west areas of the country from 2004 to 2013. Each trial consisted of 25 treatments (lines + checks) in a randomized complete block design with three replicates. A linear mixed model was fitted to predict the genetic values of each genotype per year and a restricted maximum likelihood algorithm to estimate the variance components. These genetic values were used to compute the genetic gain over the years. The overall estimated genetic gain of the breeding program was 61.59 kg ha<sup>-1</sup> yr<sup>-1</sup> (1.68% yr<sup>-1</sup>) for GY, although it was partially counterbalanced by the estimated negative environmental effects. The genetic gain per VCU region ranged from 31.38 (VCU 4) to 115.33 kg ha<sup>-1</sup> yr<sup>-1</sup> (VCU 1). After accounting for the environmental changes over years, the yield gain was 39.40 kg ha<sup>-1</sup> yr<sup>-1</sup> (1.10% yr<sup>-1</sup>), ranging from -0.82 (VCU 3) to 3.35% yr<sup>-1</sup> (VCU 1). The assessment of Brazilian cultivars released between 1998 and 2014 showed genetic gains in GY of 34.8 kg ha<sup>-1</sup> yr<sup>-1</sup> (1% yr<sup>-1</sup>), demonstrating that the efforts of Brazilian research institutions to develop cultivars have produced additive results. The implications of genetic gain estimates on breeding programs are discussed.

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**Abbreviations:** BLUP, best linear unbiased predictor; COODETEC, Central Cooperative of Agricultural Research; GY, grain yield; LRT, likelihood ratio test; REML, restricted maximum likelihood; VCU, value for cultivation and use.

**W**HEAT (*Triticum aestivum* L.) plays a unique role in the global economy, given its direct use as food for human consumption and its wide geographic cultivation. In Brazil, domestic wheat production meets approximately half of the demand, characterizing the country as one of the largest importers in the world. Wheat production is of major importance in the southern region, where >90% of all Brazilian wheat is harvested on nearly 2 million ha. Therefore, breeding programs are constantly developing stable and high-yielding cultivars to reduce costs and increase the competitiveness against international wheat production.

Since the 1970s, an approximate annual gain of 43 kg ha<sup>-1</sup> yr<sup>-1</sup> has been recorded in terms of grain yield (GY) for Brazilian wheat cultivars, considering only the cultivated area and production data records (Conab, 2017). In the same period, the improvement in US wheat yield was ~26 kg ha<sup>-1</sup> yr<sup>-1</sup> (USDA-NASS, 2017). However, US wheat production has been shifting into more marginal environments. Not only does the magnitude of these values account for the absolute participation of plant breeding, but it also incorporates

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environmental enhancement by improving agricultural management practices and high-tech inputs.

Wheat breeding programs in Brazil generally perform field trials for the assessment of lines in four values of cultivation and use (VCU) regions. These four regions represent mega-environments with contrasting environmental variables and are useful in the execution of regionalized trials, required for the registration, protection, and recommendation of new cultivars (Diário Oficial da República Federativa do Brasil, 2008). Climatic scenarios of these regions oscillate from cold and humid (VCU 1, southern) to hot and dry (VCU 4, Brazilian Cerrado), demanding an extensive trial network. Because of the high cost of the multienvironment trials, it is extremely important to obtain high-quality information. Many authors demonstrate that it is possible to use these data to perform meta-analyses and measure the genetic gains in a variety of crop species (Oury et al., 2012; Qin et al., 2015; Balota et al., 2017; Laidig et al., 2017).

The estimation of the genetic gain is essential for breeding programs and demonstrates the effective performance of plant breeding in promoting an annual increase in traits of interest. Breeding programs must be periodically evaluated (Brescghello et al., 2011; Do Vale et al., 2012), and this assessment allows us to measure the success of the adopted breeding strategies (Condón et al., 2009). The evaluation of genetic gains in Brazilian breeding programs is available for soybean [*Glycine max* (L.) Merr.] (Lange and Federizzi, 2009), common beans (*Phaseolus vulgaris* L.) (de Faria et al., 2013), rice (*Oryza sativa* L.) (Atroch and Nunes, 2000; Brescghello et al., 2011), and maize (*Zea mays* L.) (Storck et al., 2005). However, similar studies regarding wheat are scarce. Cargnin et al. (2008) reported a genetic gain of 48 kg ha<sup>-1</sup> yr<sup>-1</sup> in wheat yields under irrigated conditions of the Brazilian Cerrado; however, Cargnin et al. (2009) found a genetic gain of 37 kg ha<sup>-1</sup> yr<sup>-1</sup> in dryland conditions. Related studies are available but only report the results of a small set of commercial cultivars (Rodrigues et al., 2007; Beche et al., 2014).

Despite the genetic gains achieved after 1970s, there are studies pointing out decreases in annual wheat GY gains in recent years in Brazil (Cargnin et al., 2008; Beche et al., 2014) and other regions of the world (Graybosch and Peterson, 2010). The lack of gains by lines annually evaluated in breeding programs must be treated with caution, and new strategies must be implemented to support constant gains. Notwithstanding, measuring gains in new lines over years is not a routine practice among breeders, at least not directly. In addition, it is necessary to quantify the effect of environmental changes over time and to what extent such changes can influence genetic gains. In this sense, data obtained from VCU trials might be useful for achieving environmental and genetic gains in GY in a variety of climate conditions. Additionally,

climate change is a growing concern for food security. Studies have documented that climate change affects the development and productivity of field crops (Liu et al., 2010). In lower latitudes, high temperatures significantly reduce wheat GY, as they reduce the grain-filling period (Tahir et al., 2006) and can affect the progress rate. In this context, dividing larger geographic regions into smaller subareas for estimating genetic gain may provide advantageous information (Lange and Federizzi, 2009; de la Vega and Chapman, 2010; Crespo-Herrera et al., 2017).

The objective of this study was to investigate the genetic gain and environmental effects on wheat GY in multienvironment trials using a historical data record of four large geographic regions. The genetic gain of wheat commercial cultivars released by Brazilian research institutions was assessed, and the variance components across Brazilian crop areas were also estimated.

## MATERIAL AND METHODS

### Field Trials

A dataset of 836 advanced wheat trials performed in 40 locations between 2004 and 2013 (Fig. 1) from the wheat breeding program of the Central Cooperative of Agricultural Research (COODETEC) was used for this study. It consisted of 771 inbred lines and 58 commercial cultivars used as checks (Table 1). This dataset was obtained after removing 209 trials with low average GY (<2500 kg ha<sup>-1</sup>) due to detrimental conditions in the wheat fields (e.g., drought, frost damage at flowering, lodging, and prolonged rainfall before harvest).

Each experiment was arranged in a randomized complete block design with three replications. The plots consisted of six 5-m rows spaced 0.20 m apart. All of the experiments were performed with 25 treatments, consisting of advanced lines and commercial cultivars (checks, four or five per experiment). The check cultivars were derived from different breeding programs, are well accepted by farmers, and are generally grown in large crop areas. These cultivars frequently change across VCU regions and crop seasons but tend to be common across trials in a given VCU region and year. The sowing rate was 350 seeds m<sup>-2</sup>. The crop management was performed according to the recommendations for the crop, published annually by RCBPTT (2008). The edges were discarded at harvest, and GY was recorded from equal areas in all plots. Each plot was mechanically harvested, and GY was estimated in kilograms per hectare after grain moisture correction to 13% (wet basis).

The average number of trials per year was 21.4, ranging from 2 (VCU 4, 2011) to 66 (VCU 2, 2010) (Table 1). A total of 62,700 plots were evaluated (average of 1608 plots yr<sup>-1</sup>). The average number of lines tested per year was 95 (81.5%), varying from 13 (VCU 4, 2004) to 164 lines (VCU 2, 2011) and 22 commercial cultivars as checks (18.5%).

### Statistical Analysis

The imbalanced characteristic of the dataset was due the fact that, each year, novel lines were selected on the basis of preliminary tests and included for evaluation in VCU trials, whereas lines that were already determined as low performance were

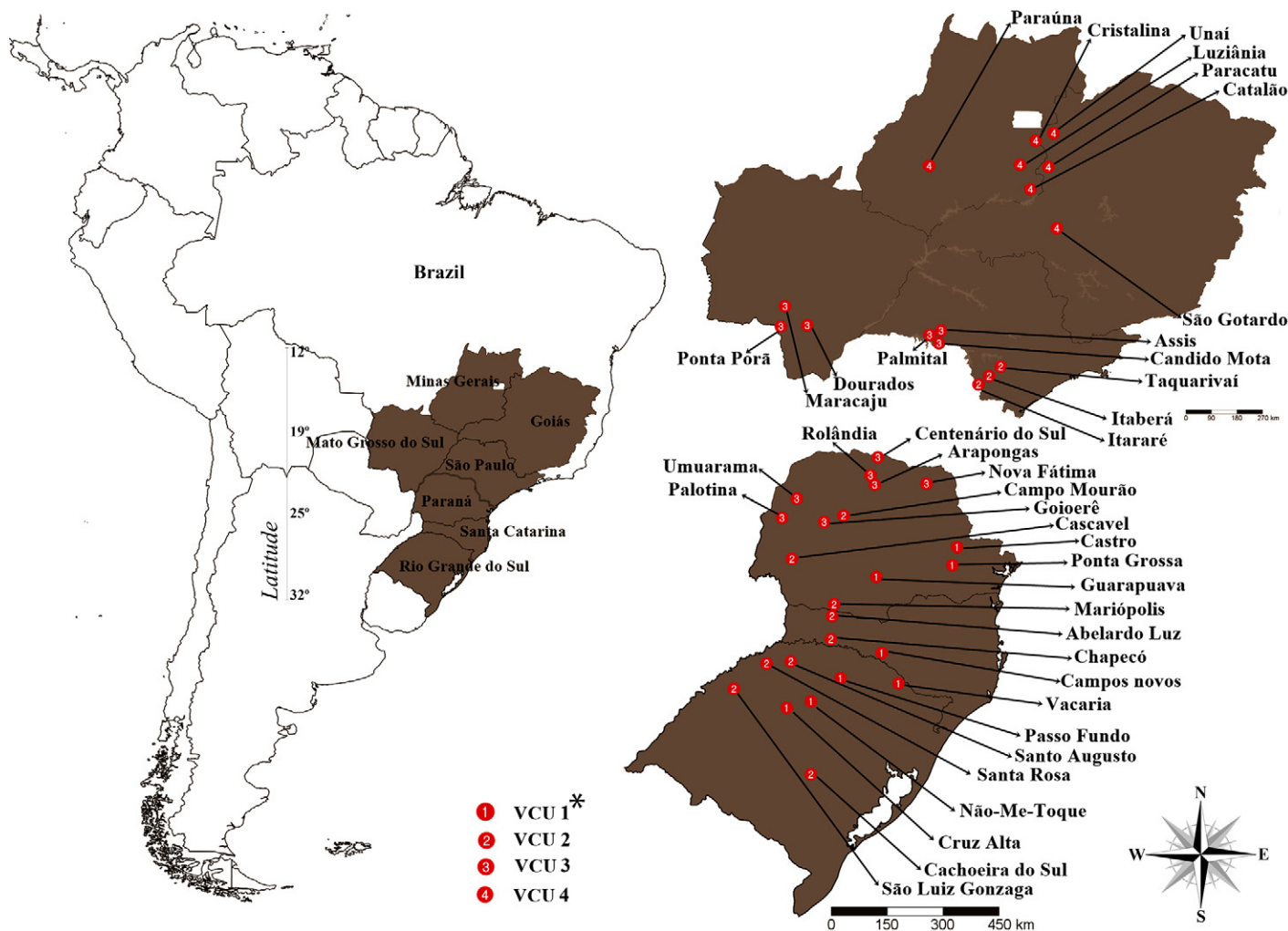


Fig. 1. Geographic location of the 40 sites of the Central Cooperative of Agricultural Research (COODETEC) spring wheat multi-environment trials in Brazil. The dataset used in this study is from the period between 2004 and 2013. \*VCU, value of cultivation and use.

removed. The fraction of the lines with high GY potential remained under testing for >1 yr. To handle this situation, the REML-BLUP (restricted maximum likelihood–best linear unbiased predictor) approach was used. This procedure was adopted to predict the genetic values, free from interaction and error effects. Then, the genetic value of each genotype was used to calculate the genetic gain per VCU region.

All sites were initially analyzed in each year using the following matrix model:

$$\mathbf{y} = \mathbf{X}_r + \mathbf{Z}_g + \mathbf{W}_i + \mathbf{e} \quad [1]$$

where  $\mathbf{y}$  is the data vector;  $\mathbf{r}$  is the effect of replicates vector (assumed to be fixed) added to the grand mean, taking into account the effects of site and replications within site;  $\mathbf{g}$  is the genotypic effect vector (assumed to be random);  $\mathbf{i}$  is the vector of genotype  $\times$  environment interaction effects (random); and  $\mathbf{e}$  is the error vector (random). Capital letters ( $\mathbf{X}$ ,  $\mathbf{Z}$ , and  $\mathbf{W}$ ) refer to incidence matrices corresponding to the respective effects. The estimates of variance components by REML were computed inside every year and VCU region. Each parameter estimated was averaged by the number of years, and the results were added in a table with the respective standard deviation. The analyses were performed using Selegen software (Resende, 2016).

A deviance analysis was used to test the model significance. The deviances were obtained from the analysis with and without genotype and genotype  $\times$  location interaction effects (saturated  $\times$  reduced model). These differences were compared to the  $\chi^2$  value with one degree of freedom, at 1 (6.63) and 5% (3.84) error probabilities. The lack of significance of the hypothesis for the tested effect was rejected when the likelihood ratio test (LRT)  $> \chi^2$ . The accuracy of selection ( $A_c$ ) was measured using Eq. [2] (Henderson, 1984):

$$A_c = \left[ 1 - \left( \text{PEV} / \hat{\sigma}_g^2 \right) \right]^{0.5} \quad [2]$$

where PEV represents the prediction error variance and  $\hat{\sigma}_g^2$  is the genotypic variance. The correlation between genotypic values across locations ( $r_{gl}$ ) was estimated using Eq. [3]:

$$r_{gl} = \sigma_g^2 / (\sigma_g^2 + \sigma_{int}^2) \quad [3]$$

where  $\sigma_{int}^2$  is the variance due to the genotype  $\times$  location interaction. The broad-sense heritability ( $h_g^2$ ) was obtained by Eq. [4]:

$$h_g^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{int}^2 + \sigma_e^2) \quad [4]$$

where  $\sigma_e^2$  is the residual variance between plots. The heritability of the genotypic mean ( $h_{mg}^2$ ) was obtained by Eq. [5]:



**Table 1. Summary of the Central Cooperative of Agricultural Research (COODETEC) wheat breeding program dataset used in this study from 2004 to 2013.**

Trial	Year	Nt†	Np†	Nl†	Nc†	$\bar{Y}†$ kg ha <sup>-1</sup>
VCU‡ 1	2004	18	1,350	71	22	3,671.5
	2005	6	450	59	9	3,620.9
	2006	9	675	70	20	3,235.1
	2007	11	825	38	10	3,527.4
	2008	25	1,875	68	21	4,200.9
	2009	16	1,200	38	10	3,253.4
	2010	29	2,175	82	26	4,070.9
	2011	30	2,250	82	27	3,899.7
	2012	20	1,500	73	15	3,119.9
	2013	28	2,100	70	17	4,902.4
Total		192	14,400	417§	45§	
VCU 2	2004	15	1,125	79	27	3,587.4
	2005	9	675	98	25	3,008.8
	2006	20	1,500	122	27	3,478.7
	2007	21	1,575	98	17	3,015.2
	2008	48	3,600	135	31	3,269.4
	2009	26	1,950	118	17	2,901.1
	2010	66	4,950	163	35	4,174.5
	2011	37	2,775	164	30	3,770.7
	2012	48	3,600	148	22	3,819.3
	2013	25	1,875	89	26	4,375.0
Total		315	23,625	717§	56§	
VCU 3	2004	17	1,275	77	26	3,116.8
	2005	19	1,425	119	28	3,106.7
	2006	16	1,200	122	27	3,009.2
	2007	29	2,175	98	17	3,249.0
	2008	34	2,550	135	31	3,412.6
	2009	33	2,475	118	17	3,031.5
	2010	47	3,525	163	34	3,237.4
	2011	34	2,550	164	30	3,077.4
	2012	24	1,800	148	22	2,899.5
	2013	NA	NA	NA	NA	NA
Total		253	18,975	681§	55§	
VCU 4	2004	6	450	13	12	5,471.8
	2005	6	450	34	13	5,048.8
	2006	13	975	83	25	5,244.4
	2007	12	900	98	17	4,045.5
	2008	4	300	70	19	5,401.6
	2009	11	825	97	16	4,652.1
	2010	15	1,125	143	33	5,141.7
	2011	2	150	41	6	6,291.0
	2012	3	225	34	13	4,438.3
	2013	4	300	65	20	5,284.7
Total		76	5,700	443§	50§	
Overall mean		21.4	1,607.7	94.5	21.5	
Overall total		836	62,700	771	58	

† Nt, number of trials; Np, number of plots; Nl, number of lines; Nc, number of checks;  $\bar{Y}$ , average grain yield; NA, data not available.

‡ VCU, value of cultivation and use.

§ The total of Nl and Nc diverge from the sum of the column once some lines and checks are evaluated for more than one crop season.

$$h_{mg}^2 = \sigma_g^2 / [\sigma_g^2 + \sigma_{int}^2 / b + \sigma_e^2 / (nb)] \quad [5]$$

where  $n$  is the number of plots and  $b$  is the number of blocks. The determination coefficient of interaction ( $c_{int}^2$ ) was obtained from Eq. [6]:

$$c_{int}^2 = \sigma_{int}^2 / (\sigma_g^2 + \sigma_{int}^2 + \sigma_e^2) \quad [6]$$

The genotypic values for the average of environments ( $\hat{\mu} + \hat{g}$ ) were estimated in each year of evaluation to obtain the genetic progress in the breeding program per VCU region. The genetic values predicted by the BLUP property are free from any interaction with the environment and consist of the prediction of genetic values ( $\hat{g}$ ) of each genotype (random) adjusted to the fixed effects ( $\hat{\mu}$ ) for an unequal amount of genotype information across the locations.

The year 2004 was chosen as a reference year to estimate the genetic gain and to remove noise due to the year effect by applying an appropriate statistical method. The choice was made according to the environmental conditions during the crop season (i.e., an absence of large-scale events of stress). As described by Brisson et al. (2010) and Oury et al. (2012), the corrected genotype mean yield is given by Eq. [7]:

$$yc_j^{Ai+1} = y_j^{Ai+1} + d_{AiAi+1} \quad [7]$$

where  $y_j^{Ai}$  is the genotype mean  $j$  in the  $Ai$  year;  $y_j^{Ai+1}$  is the genotype mean  $j$  in the following year;  $yc_j^{Ai+1}$  is the corrected genotype mean  $j$ ; and  $d_{AiAi+1}$  is obtained by Eq. [8]:

$$d_{AiAi+1} = \left[ \sum_{j=1}^{n_{AiAi+1}} (y_j^{Ai} - y_j^{Ai+1}) \right] / n_{AiAi+1} \quad [8]$$

where  $n_{AiAi+1}$  is the number of eligible genotypes in the year  $Ai$  and  $Ai + 1$ . For the year  $Ai + 2$ , the following expression returns the corrected mean:

$$yc_j^{Ai+2} = y_j^{Ai+2} + d_{Ai+1Ai+2} \quad [9]$$

where

$$d_{Ai+1Ai+2} = \left[ \sum_{j=1}^{n_{Ai+1Ai+2}} (y_j^{Ai+1} - y_j^{Ai+2}) \right] / n_{Ai+1Ai+2}$$

and in the same manner for years after  $Ai$ . The genetic difference ( $\Delta G$ ) for a biennium is measured by Eq. [10]:

$$\Delta G^{AiAi+1} = \overline{yc}^{Ai+1} - \overline{yc}^{Ai} \quad [10]$$

where  $\overline{yc}^{Ai+1}$  is the overall mean of the corrected genotype's performance in the year  $Ai + 1$ , and  $\overline{yc}^{Ai}$  is the overall mean of the corrected genotypes performance in year  $Ai$ . Since 10 yr were evaluated, nine values of  $\Delta G$  were estimated.

The average genetic difference in each biennium was estimated by the method of generalized least squares described by Cruz (2006), following Eq. [11]:

$$\mathbf{Y} = \mathbf{X}\beta + \epsilon \quad [11]$$

where  $\mathbf{Y}$  is a vector composed of the values of  $\Delta G$ ,  $\mathbf{X}$  is a vector of ones,  $\beta$  is a vector ( $1 \times 1$ ) to be estimated and represents the average genetic gain, and  $\epsilon \sim N(\Phi, \mathbf{V}\sigma^2)$  where  $\Phi$  is zero mean and  $\mathbf{V}\sigma^2$  is the covariance.  $\beta$  is estimated by solving Eq. [12]:

$$\hat{\beta} = \hat{\mu}_{\Delta G} = (\mathbf{X}'\mathbf{V}^{-1}\mathbf{X})^{-1} \mathbf{X}'\mathbf{V}^{-1}\mathbf{Y} \quad [12]$$

where  $\mathbf{V}$  is the variance-covariance matrix between the estimated genetic differences. The components of this matrix are obtained as follows:

$$\hat{\mathbf{V}}(\Delta G_{ij}) = \left( \frac{2}{n_{ij}} - \frac{1}{n_{ii}} - \frac{1}{n_{jj}} \right) \sigma^2 \quad [13]$$

$$\text{COV}(\Delta G_{ij}, \Delta G_{kl}) = \left( \frac{1}{n_{ii}} - \frac{n_{ijk}}{n_{kl}n_{ij}} \right) \sigma^2 \quad [14]$$

$$\text{COV}(\Delta G_{ij}, \Delta G_{kl}) = 0 \quad [15]$$

where  $n_{ii}$  is the number of genotypes tested in the  $i$ th year;  $n_{ij}$  is the number of genotypes tested in the years  $i$  and  $j$ , and so on. The same model was applied to the environmental gain ( $\hat{\mu}_{\Delta E}$ ) using the differences between biennia ( $d_{AiAi+1} + d_{Ai+1Ai+2} + \dots + d_{Ai+8Ai+9}$ ) in the  $\mathbf{Y}$  vector, and this time, the components of the  $\mathbf{V}$  matrix were obtained as follows:

$$\hat{\mathbf{V}}(\Delta E_{ij}) = \frac{2}{n_{ij}} \sigma^2 \quad [16]$$

$$\text{COV}(\Delta E_{ij}, \Delta E_{ik}) = \frac{n_{ijk}}{n_{ki}n_{ij}} \sigma^2 \quad [17]$$

$$\text{COV}(\Delta E_{ij}, \Delta E_{kl}) = 0 \quad [18]$$

The genetic and environmental gain (%) was obtained by the following expressions:

$$G_{\text{gain}(\%)} = 100\hat{\mu}_{\Delta G} / \hat{\mu}_{\Delta G} + \hat{\mu}_{\Delta E} \quad [19]$$

$$E_{\text{gain}(\%)} = 100\hat{\mu}_{\Delta E} / \hat{\mu}_{\Delta G} + \hat{\mu}_{\Delta E} \quad [20]$$

The total gain was calculated by summing both the genetic and environmental gains. The aim of this approach was to assess the genetic and nongenetic trends across years. It is important to emphasize that, if the number of common lines in two consecutive years is high, the bias due to the accumulation of correction errors can be moderate (Brisson et al., 2010). This statistical routine is updated from the classical methodology that has been used in this type of meta-analysis in Brazil since the work published by Vencovsky et al. (1988) and is implemented in the Genes software (Cruz, 2013) that was used in the analyses. Additionally, the genotype maintenance and replacement rates throughout the analyzed historical data record were computed according to Cruz (2006).

Cultivars used as checks represent genotypes from the main wheat breeding institutions and companies in Brazil cultivated by farmers in large areas over the last two decades. Data from 47 commercial cultivars evaluated in a representative set of environments were analyzed. The observational median of the number of plots for each cultivar was  $\sim 250$  during the entire period. The genetic values of those cultivars were used to measure the genetic gain in GY related to the overall performance of wheat breeding in Brazil. First, the predicted genotypic performance ( $\hat{\mu} + \hat{g}$ ) of each cultivar per year was

computed. A  $p \times n$  matrix was designed, and the missing data were inputted using the singular value decomposition procedure of GGE Biplot software (Yan, 2001). The noise due to the year effect was then removed as described previously (Oury et al., 2012), in which the average of the differences in the common cultivars in every biennium was used to correct GY. A linear regression was performed using the year of cultivar release as the independent variable. We did not include VCU 4 in this analysis because of the irrigation in the field trials. The results were plotted using the graphics software SigmaPlot version 11 (Systat Software, 2008).

## RESULTS

### Deviance and Variance Components

The standard deviation of heritability in the broad sense ( $h_g^2$ ) indicates the significant genotypic effects that occurred for all VCU regions (Table 2). The LRT showed the significant effects of genotype for the VCU regions and the 10 yr of evaluation in 77.5% of cases. Nonsignificant effects of genotype  $\times$  environment interactions were found for VCU 3 in 2005 and in many years for VCU 4. A highly significant interaction effect in the other years indicates the differential ranking of genotypes among sites and implies the existence of at least one contrasting environment.

With the exception of VCU 3, all other environments had a variance of the interaction component ( $\hat{\sigma}_{\text{int}}^2$ ) that was greater than the genetic variance ( $\hat{\sigma}_g^2$ ) (Table 2). Consequently, low estimates of broad sense heritability ( $h_g^2$ ) were observed. The genotypic CV varied between 6.77 (VCU 4) and 9.59% (VCU 1). The residual CV was low and varied between 8.69 (VCU 3) and 10.18% (VCU 4). The genotypic accuracy of selection, which measures the correlation between predicted and observed values, ranged from 0.64 (VCU 4) to 0.80 (VCU 1). VCU 1 exhibited the highest genotypic CV (9.59%), indicating a greater occurrence of genetic variability in this region, unlike VCU 4. The highest average GY was recorded in VCU 4 (5219.38 kg ha<sup>-1</sup>), and the lowest average in VCU 3 (3126.70 kg ha<sup>-1</sup>). The genotypic correlations ( $r_{g|}$ ) varied among the VCU regions (0.31 in VCU 2 to 0.51 in VCU 3). In addition, VCU 3 showed the lowest  $\hat{\sigma}_{\text{int}}^2 / \hat{\sigma}_g^2$  ratio (0.95), whereas VCU 2 showed the highest value (2.22).

### Estimated Grain Yield Changes and Genotype Replacement Rates

The estimated overall genetic gain of the wheat breeding program was 61.59 kg ha<sup>-1</sup> yr<sup>-1</sup> (Table 3). However, this gain was partially counterbalanced by the negative effects of environment ( $-22.19$  kg ha<sup>-1</sup> yr<sup>-1</sup>). Hence, the observed total gain was 39.40 kg ha<sup>-1</sup> yr<sup>-1</sup>. The overall genetic gain corresponds to 1.10% yr<sup>-1</sup>. In VCU 4, composed of the Brazilian Cerrado, 31.38 kg ha<sup>-1</sup> yr<sup>-1</sup> of genetic gain was found in terms of GY, which was

**Table 2. Estimated variance components for grain yield (GY), and deviance analysis for the genotypic and genotype × environment (G × E) interaction effects. The trials were performed between 2004 and 2013 in several locations in Brazil.**

Individual REML‡	Value for cultivation and use (VCU) regions†			
	VCU 1	VCU 2	VCU 3	VCU 4
$\hat{\sigma}_g^2$	137.92 ± 62.6 (32.9%)§	64.17 ± 36.9 (21.1%)	86.87 ± 39.6 (35.2%)	137.49 ± 85.8 (21.9%)
$\hat{\sigma}_{int}^2$	159.65 ± 69.8 (37.0%)	142.86 ± 83.9 (47.0%)	82.97 ± 32.5 (33.7%)	199.54 ± 89.6 (31.8%)
$\hat{\sigma}_e^2$	133.86 ± 51.8 (37.1%)	97.09 ± 33.8 (31.9%)	76.70 ± 27.2 (31.1%)	290.76 ± 137.2 (46.3%)
$\hat{\sigma}_p^2$	431.43 ± 115.9	304.12 ± 10.4	246.54 ± 33.6	627.80 ± 196.6
$h_g^2$	0.32 ± 0.06	0.20 ± 0.04	0.35 ± 0.06	0.22 ± 0.07
$h_{mg}^2$	0.66 ± 0.19	0.50 ± 0.17	0.63 ± 0.13	0.43 ± 0.10
$c_{int}^2$	0.37 ± 0.12	0.45 ± 0.12	0.34 ± 0.11	0.31 ± 0.09
$r_{gl}$	0.46 ± 0.17	0.31 ± 0.11	0.51 ± 0.14	0.41 ± 0.14
Ac	0.80 ± 0.14	0.69 ± 0.14	0.79 ± 0.08	0.64 ± 0.14
CV <sub>g</sub> (%)	9.59 ± 3.03	6.84 ± 1.83	9.24 ± 2.12	6.77 ± 2.00
CV <sub>e</sub> (%)	9.61 ± 1.79	8.73 ± 1.20	8.69 ± 1.65	10.18 ± 2.45
$\hat{\sigma}_{int}^2/\hat{\sigma}_g^2$ ratio	1.15	2.22	0.95	1.45
Average GY (kg ha <sup>-1</sup> )	3750.21	3540.00	3126.70	5219.38

Year	Likelihood ratio test¶							
	VCU 1		VCU 2		VCU 3		VCU 4	
	G	G × L	G	G × L	G	G × L	G	G × L
2004	76.7**	267.8**	72.4**	421.3**	26.4**	387.2**	14.8**	54.3**
2005	11.3**	34.27**	0.7ns	158.9**	0.0ns	0.0ns	12.6**	65**
2006	13.5**	253.0**	11.9**	801.5**	8.16**	52.4**	23.4**	192.9**
2007	38.1**	184.3**	10.5**	98.35**	83.9**	117.0**	0.0ns	525.4**
2008	61.9**	339.0**	28.47**	400.5**	44.4**	193.1**	0.0ns	0.0ns
2009	72.8**	116.7**	46.1**	215.0**	91.0**	174.1**	1.0ns	134.1**
2010	172.3**	117.7**	129.5**	395.0**	190.0**	105.6**	5.1*	47.9**
2011	25.3**	129.5**	13.7**	410.8**	7.6**	33.1**	0.0ns	0.0ns
2012	0.9ns	305.6**	23.4**	134.9**	10.5**	261.6**	0.0ns	0.0ns
2013	61.9**	160**	18.5**	113.5**	NA	NA	0.0ns	0.0ns

\*,\*\* Significant at the 0.05 (3.84) and 0.01 (6.63) probability levels, respectively, according to the  $\chi^2$  test with 1 df.

† Average of the estimates for 10 (VCU 1, 2, and 4) and 9 yr (VCU 3) ± the standard deviation across years. The values of variance components are shown divided by 1000 for easy presentation.

‡  $\hat{\sigma}_g^2$ , genotypic variance;  $\hat{\sigma}_{int}^2$ , variance of G × E interaction;  $\hat{\sigma}_e^2$ , residual variance;  $\hat{\sigma}_p^2$ , individual phenotypic variance;  $h_g^2$ , broad-sense heritability of individual plots (i.e. total genotypic effects + standard deviation);  $h_{mg}^2$ , heritability of the genotypic mean, assuming total survival;  $c_{int}^2$ , coefficient of determination for the GEI effects;  $r_{gl}$ , correlation between genotypic values across sites; Ac, accuracy of genotype selection; CV<sub>g</sub> (%), genotypic CV; CV<sub>e</sub> (%), residual CV;

§ Parenthetical values indicate the percentage of the observed phenotypic variance ( $\hat{\sigma}_p^2$ ).

¶ G, genotype; L, location; ns, nonsignificant; NA, data not available.

**Table 3. Grain yield gain due to genetic and environmental terms per value for cultivation and use (VCU) region and for the entire Central Cooperative of Agricultural Research (COODETEC) wheat breeding program. Data were obtained from multienvironment trials conducted in four VCU regions in Brazil between 2004 and 2013.**

Description of the gain	Grain yield progress					
	Genetic		Environmental		Total	
	kg ha <sup>-1</sup>	%	kg ha <sup>-1</sup>	%	kg ha <sup>-1</sup>	%
Grain yield gain per VCU region						
VCU 1	115.33	3.14	7.75	0.21	123.09	3.35
VCU 2	47.96	1.34	30.80	0.86	78.76	2.20
VCU 3	51.67	1.66	0.86	-77.26	2.20	-25.59
VCU 4	31.38	0.57	-50.08	-0.92	-18.70	-0.35
Overall gain of the breeding program						
Total	61.59	1.68	-22.19	-0.58	39.40	1.10

also counterbalanced by negative environmental effects, resulting in a negative total gain ( $-18.70 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ). In 2007 and 2012, the average GY for VCU 4 was low, contributing to the negative environmental effect. The northern region of Paraná stands out in VCU 3 (Fig. 1), but droughts can occasionally occur, as they did in 2008 and 2012, resulting in low GY ( $<1550 \text{ kg ha}^{-1}$ ) and a low rate of environmental improvement (Table 3). Gains in GY due to the environmental component were detected only in VCU 1 and 2, amounting to 7.75 and  $30.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ , respectively.

A high replacement rate (52%) was detected in the breeding program, varying from 45 (VCU 3) to 60% (VCU 4) (Table 4). High values of genotype replacement imply that a high number of new lines were included for evaluation relative to the total number of lines being evaluated (new lines + selected lines from the last crop season). On average, 30% of the genotypes were evaluated in two consecutive crop seasons (genotype maintenance rate), varying between 23 (VCU 4) and 38% (VCU 3).

### Cumulative Genetic Gain and the Performance of Commercial Breeding

Figure 2 shows the accumulated genetic progress in the historical data records examined in this study. The gains obtained by the breeding program in VCU 1 were greater than others, and although there was a linear increasing trend across years (Fig. 2), the trend was flat over the last three crop seasons. In VCU 2, the gains tended to stagnate until the 2008–2009 crop season, and genetic gains after 2009–2010 were then observed. However, the GY stagnation is clear in VCU 3 after 2007–2008. Although VCU 4 had the lowest genetic gain, it still showed a linear increase. Finally, when focused on the commercial cultivars, the genetic gain was estimated at  $34.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$  for GY between 1998 and 2014 (Fig. 3), representing  $1\% \text{ yr}^{-1}$ .

## DISCUSSION

### Experimental Precision and Climate

The residual CV and the moderate to high values of accuracy of selection (Resende and Duarte, 2007) indicated, in general, a high experimental accuracy of the trials. VCU 4, which is composed of both high-altitude and low-latitude environments, had the highest average GY (Table 2). This is partially explained by irrigation applied to the experiments that is necessary in the Brazilian Cerrado, where wheat is grown during the dry season.

Wheat production in Brazil is considered risky due to the environmental variability and adverse climatic conditions frequently observed in winter. Wheat is frequently affected by frost at flowering time, hailstorms, and water stress, which all negatively affect GY. Between 2004 and 2013, 20% (209) of the field experiments presented average GY  $<2500 \text{ kg ha}^{-1}$  as a consequence of adverse environmental conditions, which is an indication of the risk level of wheat production in Brazil. The 836 trials had an overall average GY of  $3909.07 \text{ kg ha}^{-1}$ ,  $\sim 42\%$  above the Brazilian average. However, GY varied according to the geographical region. With the exception of VCU 4, there is an increase in GY toward the south (higher latitude) due to the decrease in temperature and increase in the length of phenological development stages, including grain filling.

### Variance Components across VCU Regions

Overall, VCU 1 had high estimates of genetic variance, genotypic CV, broad-sense heritability, and average GY (Table 2), which led to increased genetic gain in this region (Table 3, Fig. 2). In VCU 4, the genetic variance accounted for 21.90% of the total variation and, in combination with relatively low experimental precision, resulted in the lowest genetic gain estimate ( $0.57\% \text{ yr}^{-1}$ ). According to Gourdji et al. (2012), although there are many tradeoffs between high GY potential and stress adaptation, it should be feasible to accomplish both goals once hot environments are covered in the experimental network. Hence, it

**Table 4. Genotype substitution rates during 10 yr of value for cultivation and use (VCU) trials carried out by the Central Cooperative of Agricultural Research (COODETEC) wheat breeding program.**

Biennium	Genotype replacement rate					Genotype maintenance rate				
	VCU region									
	1	2	3	4	Mean	1	2	3	4	Mean
	%									
2005–2004	66	55	63	70	64	17	32	28	24	25
2006–2005	60	64	58	82	66	30	24	26	14	24
2007–2006	48	42	42	58	47	22	34	34	27	29
2008–2007	66	59	59	58	61	28	32	32	22	29
2009–2008	2	31	31	57	30	52	44	44	31	43
2010–2009	79	66	65	68	69	17	26	26	25	24
2011–2010	43	44	39	2	32	40	39	41	26	36
2012–2011	48	49	2	68	42	31	31	69	19	37
2013–2012	53	49	NA†	79	60	31	21	NA	16	22
Mean	52	51	45	60	52	30	31	38	23	30

† NA, data not available.



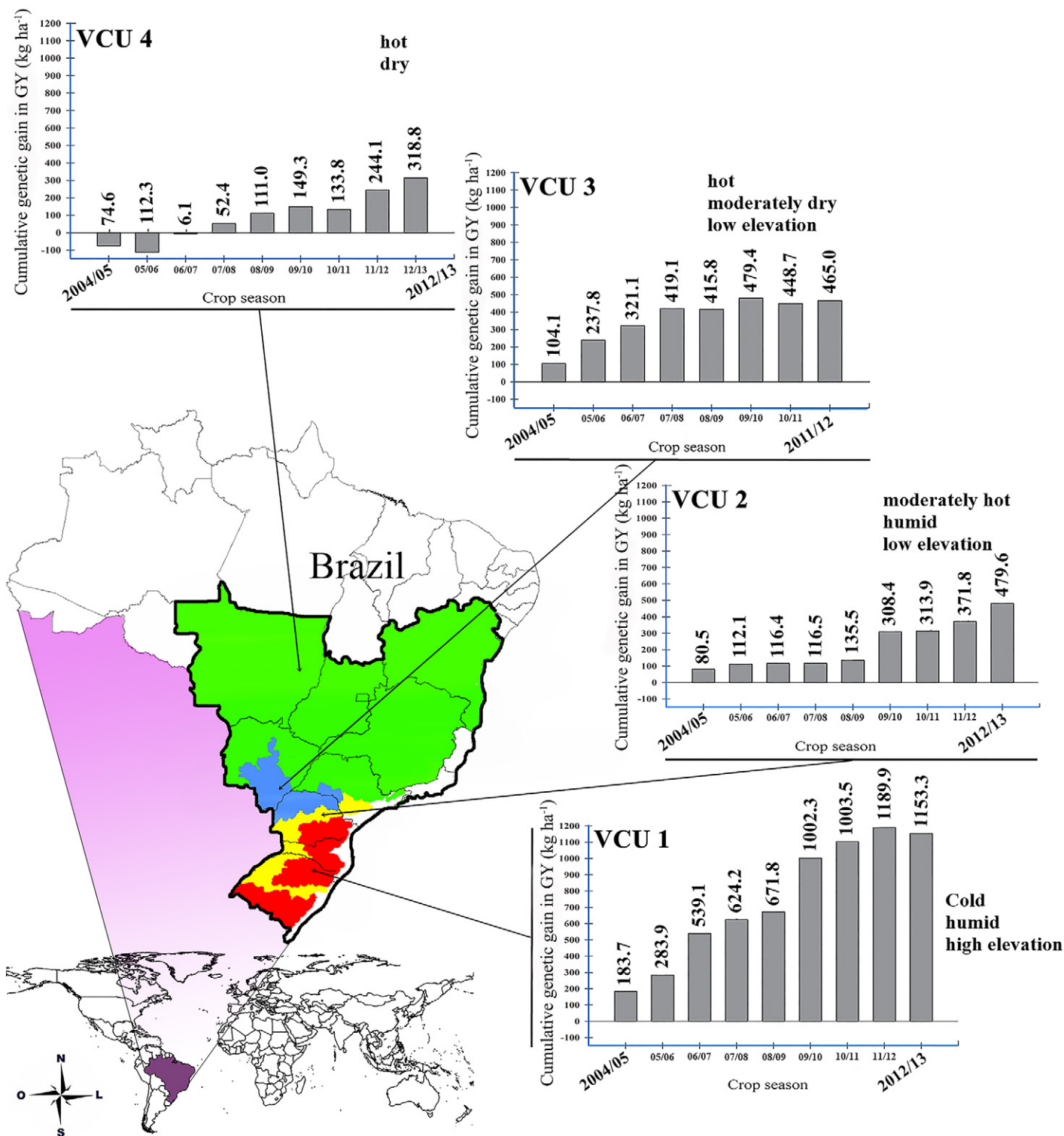


Fig. 2. Estimate of the cumulative genetic gain of wheat grain yield (GY) over 10 yr (2004–2013). Data were obtained from multienvironment trials conducted in four values of cultivation and use (VCU) regions in Brazil.

is possible to optimize genetic gain in VCU 4 by including sites that are more discriminant-effective (high genetic variance) and representative of the mega-environment for more efficient genotype selection, as reported for other crops (Blanche and Myers, 2006; Zhe et al., 2010).

Genotypic correlation ( $r_g$ ) varied among the different VCU regions. As it increases, there is a concomitant

decrease in the interaction variance and a better predictability of genotype behavior across locations. In this sense, studies measuring the necessity of reduction of test locations in VCU 3 and the insertion of more locations in VCU 2 are highly recommended, since the genotypic performance in the latter region is less predictable, and the interaction variance is pronounced (46.97%) related

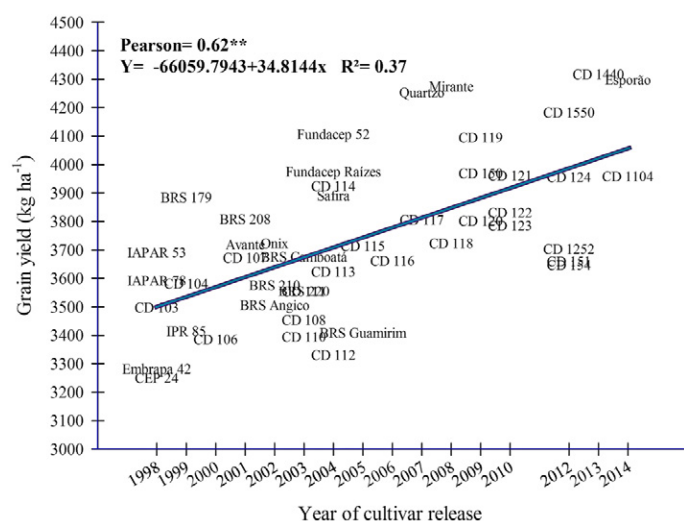


Fig. 3. Linear regression showing the relationship between grain yield for 47 Brazilian wheat cultivars and the year of release (1998–2014). The data were obtained from multienvironment trials conducted between 2004 and 2013, and the analyses were performed after the exclusion of the interaction and year effects. \*\* Significant at the 1% level ( $p \leq 0.01$ ), confirmed by *t* test.

to the genotypic variance (21.10%) (Table 2). In maize, Mendes et al. (2012) reported values ranging from 0.6 to 0.25 for a group of favorable and unfavorable environments, respectively. In addition, the low magnitude of the  $\sigma_{\text{int}}^2/\sigma_g^2$  ratio found in the VCU 3 (0.95) indicates high repeatability of the genotypic information. Variability of this ratio among geographic regions was reported by de la Vega and Chapman (2010) for sunflower (*Helianthus annuus* L.) in Argentina.

## Performance of the Breeding Program and the Environmental Effect

The genetic gain of  $1.68\% \text{ yr}^{-1}$  observed in the breeding program evaluated in this study is considered high (Table 3), although the cumulative genetic gains seem to reach a plateau in the last three to four crop seasons (Fig. 2). Other studies have shown genetic gains in multienvironment trials of  $1.44$  (Brescghello et al., 2011) and  $1.99\% \text{ yr}^{-1}$  (Do Vale et al., 2012) in rice and  $0.72\% \text{ yr}^{-1}$  in common beans (de Faria et al., 2013). In wheat, Crespo-Herrera et al. (2017) showed the genetic gain in the international elite spring wheat trials to be  $0.53$  and  $1.67\% \text{ yr}^{-1}$  relative to local checks and a widely grown cultivar, respectively. Wu et al. (2014) reported  $1\% \text{ yr}^{-1}$  in China, and Laidig et al. (2017) estimated  $0.65\% \text{ yr}^{-1}$  in Germany. The results obtained in the present study are as high as those achieved in typical wheat-producing countries. However, a negative influence of the environmental component was observed for the overall estimate of GY progress ( $-0.58\%$ ). Environmental losses over years was also reported by Oury et al. (2012) in French wheat. In the present study, the estimates of year effect are highly reliable since, on average, 30%

of the lines were maintained under evaluation for  $>1$  yr (Table 4). Despite the observed negative effects, the balance (genetic minus environmental) showed a GY increase of  $1.10\% \text{ yr}^{-1}$  ( $39.40 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ).

VCU 3 and VCU 4 are characterized as moderately dry and dry regions, respectively. Both environments are characterized by the presence of hot weather during the wheat growing period (da Cunha et al., 2006). The overall performance of the GY progress in VCU 3 and VCU 4, although demonstrating positive genetic gains, was negatively influenced by environmental conditions ( $-2.48$  and  $-0.92\% \text{ yr}^{-1}$ , respectively), and the resultant GY gains were negative (Table 3). According to Gourdjji et al. (2012), studies evaluating the progress of cultivar development in hot environments are scarce. Cargnin et al. (2008) observed genetic progress of  $48 \text{ kg ha}^{-1} \text{ yr}^{-1}$  in irrigated wheat in the Brazilian Cerrado from 1976 to 2005, with a positive environmental effect ( $23.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ). The environmental gains observed by these authors are likely due to the long-term historic records analyzed (30 yr), capturing the improvement that occurred in the region due to the enhancement of production systems since the 1970s (e.g., liming and fertilization).

The temporal stability of genotypic performance over time is conditioned by the variability of environmental factors from one year to another. This source of variation is frequently superior to the spatial variation in multienvironment trials (Malosetti et al., 2013). The environmental component positively affected GY gains in only VCU 1 and 2 (Table 3). This scenario indicates the existence of environmental improvement due to climatic variables and/or by anthropic action, by means of management practices such as high-precision mechanization and the use of inputs. Hence, the partition of the genetic and environmental components is important since, apart from providing accurate information, it allows inferences in both directions.

Breeding programs need to be dynamic, meaning that they must replace the tested lines annually at a sufficient rate so that only the superior genotypes remain for evaluation in  $>1$  yr. On average, the genotype renovation rate was  $52\% \text{ yr}^{-1}$  (Table 4). Values lower than this were reported by Cargnin et al. (2008) ( $33\%$ ) and Cargnin et al. (2009) ( $35\%$ ) in wheat and Atroch and Nunes (2000) ( $46\%$ ) in rice. Also in rice, Do Vale et al. (2012) reported an average renovation rate of  $29\%$  and emphasized that, in modern lines, the differences in GY are becoming narrower, favoring a high-maintenance rate across years.

Gains obtained in VCU 1 were higher than in the other VCU regions (Table 3, Fig. 2). In VCU 2, it is possible to note a stagnation tendency until 2008–2009 for the cumulative genetic gain in GY (Fig. 2). In VCU 3, the stagnation occurred after the 2007–2008 crop season. In this region, the environmental effect contributed to

the reduction in GY in the evaluated period, apart from being the region with the lowest GY average. Initially, the COODETEC wheat breeding program was mainly directed to release superior genotypes for Paraná state, based on CIMMYT germplasm. However, since the beginning of the 2000s, efforts have been directed towards obtaining cultivars adapted to the coldest regions of the country (high latitude) using the national wheat germplasm, which have superior plant health attributes. This change in direction has led to impressive gains in VCU 1, demonstrating the effectiveness of the breeding strategies used. However, new strategies should be considered to continue increasing annual gains in VCU 3.

The genetic improvement for heat tolerance provides a potential adaptation response, enabling the GY increase in crop areas normally exposed to heat stress (Gourdji et al., 2012). VCU 4 presented the lowest total genetic gain ( $0.57\% \text{ yr}^{-1}$ ) even though it exhibited an ascending pattern (Fig. 2). This is partly because some of the annually tested lines are high-performance materials from the south region (i.e., they are not adapted to that environment). The occurrence of gains associated with high average GY in irrigated environments confirms the viability of the crop expansion to the Brazilian Cerrado, which has been taking place in recent years. In this region, a GY of  $\sim 6 \text{ t ha}^{-1}$  is commonly obtained in field conditions. Additionally, the release of adapted cultivars such as BRS 264 and BRS 254 significantly contributed to the increase of production in the Brazilian Cerrado. Overall, the genetic contribution in Brazilian hot regions has been significant, providing subsidies to the expansion of the “tropical wheat” and to face warm environments projected for the next decades.

### Are Genetic Gains of Brazilian Wheat Stagnating?

Similar to other crops, new varieties are released each year, and the best performers are cultivated in large areas by farmers over a relatively long-term period. Breeding programs use these cultivars as controls in VCU trials. The  $1\% \text{ yr}^{-1}$  ( $34.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) of genetic gain for GY observed between 1998 and 2014 is a measure of the research efforts on breeding better wheat varieties (Fig. 3). Rodrigues et al. (2007) investigated wheat cultivars released over years in Brazil and found a genetic gain of  $44.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$  between 1940 and 1992. In a similar study, Beche et al. (2014) reported a genetic gain of  $29 \text{ kg ha}^{-1} \text{ yr}^{-1}$  from 1940 to 2009. However, both studies considered a small sample of cultivars of 7 and 10, respectively. In addition, Beche et al. (2014) reported a reduction of genetic progress in the last decade, a fact that was not observed in the present study.

In a worldwide scenario, numerous studies reported the situation of wheat breeding in recent historical data records. It is noteworthy that, although there are reports of the

narrowing wheat genetic basis and GY stagnation in some regions (Brisson et al., 2010), the annual gains vary around  $1\% \text{ yr}^{-1}$ . Among some of the major cereal producers, there are reports of gains in the order of  $0.7\% \text{ yr}^{-1}$  in Canada (Thomas and Graf, 2014),  $0.45\% \text{ yr}^{-1}$  in the European Union (Cormier et al., 2013),  $0.7\% \text{ yr}^{-1}$  in Russia (Morgounov et al., 2013), from 0.8 to  $1.3\% \text{ yr}^{-1}$  in the United States (Graybosch and Peterson, 2010), and  $0.81\% \text{ yr}^{-1}$  in China (Zhou et al., 2007). In an extensive study (919 environments and 69 countries) with CIMMYT wheat, Sharma et al. (2012) reported a gain of  $27.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$  ( $0.65\% \text{ yr}^{-1}$ ) from 1995 to 2009. Thus, challenges exist in maximizing the efficiency of wheat production in a sustainable manner, since food production will not need to double by 2050, but roughly remain at historical rates (Hunter et al., 2017).

Annual gains reported in this study apparently disqualify the possibility of GY stagnation in Brazilian wheat. However, there is a need for in-depth studies on the negative effects of environment on GY in hot climate regions of the country and a constant assessment of breeding program performances. According to Laidig et al. (2017), a critical point in VCU trials vs. on-farm cultivation is the extent to which performance progress achieved in VCU trials is transformed into on-farm progress. On-farm progress in terms of GY continues through years; on the other hand, the average GY is still relatively low, varying around  $2.3 \text{ t ha}^{-1}$ . This suggests the necessity for improvements in agricultural practices, high-quality inputs, and restricting the GY gap observed between high- and low-tech farmers. Finally, wheat breeders need to continue improving traits of interest by the introgression of favorable alleles, with a focus on disease resistance (Underdahl et al., 2008) that reflects GY stability.

### CONCLUSION

Because of the drastically projected scenario for global environmental changes in the upcoming decades, it is crucial to investigate and report the trends for wheat GY in the primary producer regions around the world. In the breeding program evaluated, a genetic gain for GY was identified in the four VCU regions, especially in VCU 1, with  $115.53 \text{ kg ha}^{-1} \text{ yr}^{-1}$  ( $3.14\% \text{ yr}^{-1}$ ). The overall genetic progress of the breeding program was  $61.59 \text{ kg ha}^{-1} \text{ yr}^{-1}$  ( $1.68\% \text{ yr}^{-1}$ ). Nonetheless, the periodic evaluation is critical to identify stagnation tendencies. The gain for well-established commercial cultivars released between 1998 and 2014 was  $34.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ , equivalent to  $1\% \text{ yr}^{-1}$ , characterizing the current status of genetic gain and the efforts of institutions aiming to improve the crop and transform the country into a self-sufficient wheat producer. The environmental effect appears to be a determinant of GY improvement, with unfavorable influence evidenced in the hot and dry conditions of VCU 3 and 4 and positive effect on VCU 1 and 2.



## Conflict of Interest

The authors declare that there is no conflict of interest.

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