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Hybrid performance and heterosis in early segregant populations of Brazilian spring wheat

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Abstract

The objective of this study was to estimate the inbreeding depression and heterosis relative to the mid-parent and better parent for grain yield and yield components in a set of diallel crosses involving 10 wheat genotypes. Parents and F_1 and F_2 hybrids were evaluated under field conditions using a spaced plant scheme in a randomized block design with three replications. The heterosis, heterobeltiosis and inbreeding depression for agronomic traits were calculated. There was a negative correlation between the heterobeltiosis and grain yield per plant (GYP) inbreeding depression, indicating the presence of positive additive × additive epistatic interactions. The mean GYP values for the F_1 and F_2 progenies were 20 and 10% higher, respectively, compared with the parents, indicating that the hybrids were superior to the parents. The heterosis of the number of spikes per plant in the F_1 and F_2 generations can be a useful approach for the indirect selection of wheat plants with an improved grain weight and grain yield per plant. The study reveals good scope for isolation of pure lines from the progenies of heterotic F_1's as well as commercial exploitation of heterosis in spring wheat.

Keywords: *Triticum aestivum* L, diallel cross, choice of parents, hybrid vigor.
Abbreviations: PH, plant height; NSP, number of spikes per plant; KPS, kernels per spike; 100-KW, hundred-kernel weight; GYP, grain yield per plant; h^2, broad sense heritability; LSD, least significant differences; $CV_{\%}$, coefficient of variation; σ^2_G, genotypic variance; σ^2_E, environment variance; σ^2_P, phenotypic variance; H_{MP}, heterosis mid-parent; H_{BP}, heterosis better-parent or heterobeltiosis; ID, inbreeding depression; MP, mean performance.

Introduction

The wheat crop productivity in Brazil (average of 2.7 ton ha^{-1}; Conab, 2011) is relatively low when compared with world's largest wheat producers, such as the European Union (5.3 ton ha^{-1}) and China (4.7 ton ha^{-1}). The grain yield potential for wheat in Brazil increased by 44.9 kg ha^{-1} per year over the last 50 years, reflecting the extensive efforts of breeding programs (Rodrigues et al., 2007); this is one of the most dramatic genetic gains ever reported throughout the world. Parental selection represents the major step in the development of new high-yielding cultivars, and the efficient identification of superior hybrid combinations is a fundamental issue in wheat breeding programs (Gowda et al., 2010). The breeding value of genotypes is evaluated based on the analysis of hybrids. These data facilitate the choice of parental genotypes with a high probability of heterosis in their F_1 progeny (Krystkowiak et al., 2009; Rousselle et al., 2010). The performance of the hybrids is estimated in terms of the percentage increase or decrease of their performance over the mid-parent (heterosis) and better parent (heterobeltiosis) (Inamullah et al., 2006; Hochholdinger and Hoecker, 2007). From the perspective of the breeder, heterobeltiosis is more effective than heterosis, particularly in the breeding of self-pollinating crops, where the objective is to identify superior hybrids (Lamkey and Edwards, 1999). Both positive and negative heterosis is useful depending on the breeding objectives. Generally, positive heterosis is desired in the selection for yield and its components, whereas negative heterosis is desired for early cycling and low plant height (Lamkey and Edwards, 1999; Alam et al., 2004). Additive and non-additive effects have been reported for grain yield and its components in wheat in studies throughout the world (Krystkowiak et al., 2009). However, the selection of promising parents to obtain superior hybrids primarily depends on the predominance of the genes for the additive effect due to heterosis and heterobeltiosis (Gowda et al., 2010; Reif et al., 2007). This promotes a few loss of hybrid vigor (inbreeding depression) and facilitates an increase in the number of genotypic classes available for the selection of segregant populations (Menon and Sharma, 1995; Simon et al., 2004; Charlesworth and Willis, 2009). The predominance of additive genetic influences on non-additive effects has been reported in several studies, suggesting that this mechanism could be effectively used in the selection of promising crosses in conventional plant breeding (Joshi et al., 2004; Topal et al., 2004). The underlying genetic and molecular mechanisms of heterosis remain unknown. The prevailing genetic theories include dominance, over-dominance and epistasis (Hochholdinger and Hoecker, 2007; Birchler et al., 2010). Previous studies on wheat have reported extreme positive values of heterobeltiosis and heterosis (48 and 60%, respectively) for grain yield (Hussain et al., 2007; Bertan et al., 2009a; Gami et al., 2011). Since the discovery of male sterility controlled via cytoplasmic genes (Adugna et al., 2004) or chemical agents (Duvick, 1999; Parodi and Gaju, 2009), hybrid development has been considered to be promising approach to increasing the grain yield and stability of crop wheat (Rajaram, 1999; Gowda et al., 2010; Chen et al., 2011). The objective of this study was to determine the levels of heterosis, heterobeltiosis and inbreeding depression of different traits to identify desirable parents and develop high-yield wheat varieties for the use of hybrids in wheat breeding programs.

Results and Discussion

Mean performance and genetics variance

Significant differences were observed for the main effects of the hybrids (F_1 and F_2) and interactions (F_1 x F_2) for all traits that were tested (data not shown), which implied the existence of variability among the parents and crosses. This result is consistent with several recent studies (Joshi et al., 2003; Nazeer et al., 2004; Hussain et al., 2007). In this study, the coefficients of variation in both generations were between 0.52 and 11.97%, indicating a sufficient reliability of the tested inferences and a high level of experimental precision.

The estimated genotypic variances (σ^2_G) for parents and hybrids were significantly larger than zero for all five traits ($p \geq 0.01$) and consistently superior to the environmental variances (σ^2_E), indicating a small effect of the environment (Table 1). The parents and F_1 hybrids showed similar σ^2_G values for all traits with the exception of the plant height (PH), which is consistent with the results reported by Gowda et al. (2010). In autogamous plants, the F_2 generation manifests the highest genetic variability; this effect can be primarily observed in the number of grains per spike (KPS), which is the trait most commonly associated with the genetic progress regarding the grain yield of wheat in Brazil (Rodrigues et al., 2007). The estimates of the heritability (h^2) values were high, ranging from 0.74 to 0.99, demonstrating that the largest proportion of the phenotypic expression of traits in parents and hybrids is genetic. The mean heterosis was positive for all traits in both generations with the exception of the one hundred-kernel weight (100-KW) trait in the F_2 generation (Table 01). The highest estimates of the mean heterosis were observed for the grain yield per plant (GYP) in the F_1 (20.38%) and F_2 (10.46%) generations. Other authors have also observed an extent of heterosis for grain yield in the F_1 ranging from -55.2% to 32.8% (Akbar et al., 2007), -22.5% to 62.1% (Joshi et al., 2003) and -27.8% to 36.9% (Bertan et al., 2009b), suggesting the presence of genetic variability for the selection and exploitation of hybrid vigor. The mean heterobeltiosis was positive for the GYP in F_1 (7.09%), ranging from -28.73% to 40%. These results suggest the possibility of the commercial exploitation of hybrid wheat, as previously reported by several other studies (Hussain et al. 2007; Bao et al., 2009; Gowda et al., 2010).

Heterosis and heterobeltiosis effects

Generally the heterosis and heterobeltiosis is associated the non-additive effects (over-dominance and epistasis), although Topal et al. (2004) reported the largest contribution of additive effects for increase the efficiency of selection. The maximum values of heterosis for GYP were obtained with the BRS Guamirim *x* BRS 208 hybrid (F_1= 51.5% and F_2= 44.2%), and for this same trait, the highest heterobeltiosis was obtained with the BRS 208 *x* Abalone hybrid (F_1 = 40% and F_2 33.5%) (Table 3). BRS Guamirim, BRS 208 and Abalone presented the major values of heterosis for the mean performance for GYP in all crosses that they were involved and low estimates of inbreeding depression for GYP (Table 2), indicating the presence of additive gene action.

Table 1. Components of genetic variance (σ^2_G), environmental variance (σ^2_E), heritability (h^2), mean performance and ranges of heterosis, heterobeltiosis and inbreeding depression for five agronomic traits of 10 parents and 45 crosses of spring wheat in the F_1 and F_2.

Statistics	PH	NSP	KPS	100-KW	GYP
Parents					
σ^2_G	110.47**	2.57**	0.32**	1.56**	1.70**
σ^2_E	0.66**	0.15*	0.01*	0.16*	0.13*
h^2	0.99	0.95	0.98	0.91	0.93
LSD5%	4.11	1.95	0.45	2.02	1.81
CV%	2.38	7.25	3.21	2.28	10.26
F_1 hybrids					
σ^2_G	52.41**	1.01**	0.16**	1.20**	1.74**
σ^2_E	1.76**	0.16*	0.03*	0.05*	0.10*
h^2	0.97	0.86	0.86	0.96	0.95
LSD5%	7.81	2.39	0.97	1.27	1.86
CV%	3.86	7.61	5.87	1.23	7.8
F_2 hybrids					
σ^2_G	53.65*	0.80**	13.24**	0.04**	0.06**
σ^2_E	2.71**	0.28*	2.52**	0.01*	0.01*
h^2	0.95	0.74	0.84	0.98	0.92
LSD5%	9.70	3.13	9.35	0.10	0.44
CV%	4.81	9.82	11.97	0.52	5.07
Heterosis F_1					
mean	1.16	1.83	5.66	1.14	20.38
minimum	-10.43	-32.28	-33.8	-2.21	-9.2
maximum	12.8	21.87	37.60	5.32	51.51
Heterosis F_2					
mean	0.97	3.28	2.39	-0.36	10.46
minimum	-8.10	-19	-41.2	-14.6	-32.2
maximum	37.60	29.37	69. 60	3.24	44.23
Inbreeding depression					
mean	0.09	-2.41	2.94	1.48	8.2
minimum	-39.12	-32.21	-27.19	-0.46	-0.41
maximum	11.84	17.92	26.92	14.12	31.62
Heterobeltiosis F_1					
mean	-7.37	-4.36	-15.16	-1.55	7.09
minimum	-27.9	-44.58	-207.6	-7.31	-28.67
maximum	11.75	18.02	25.43	3.12	40.0
Heterobeltiosis F_2					
mean	-7.61	-2.94	-16.88	-3.01	-1.6
minimum	-32.21	-34.48	-190.7	-17.39	-47.09
maximum	14.33	23.44	43.43	0.75	33.49

$LSD_{5\%}$ - least significant difference at $\alpha_{5\%}$; CV% - coefficient of variation; PH – plant height. NSP – number of spikes per plant; KPS – kernels per spike; 100-KW –100-kernel weight and GYP – grain yield per plant; ** and * Significant values at 5% and 1% probability of error.

Large negative values of heterosis and heterobeltiosis were observed for certain hybrids that may have accumulated deleterious genes (Ilker et al. 2010), which causes difficulties for selection in wheat breeding programs. Breeders must prioritize the selection of hybrids with a lower loss of vigor in early generations to increase the genetic progress. In this study, 60% of the hybrids were superior with respect to the GYP in the F_1 and F_2 generations. Joshi et al. (2004) and Bertan et al. (2009a) evaluated wheat diallel and observed that less than 30% of the crosses showed superiority for the GYP in the F_1 and F_2 generations, suggesting that the existence of heterosis in the F_1 was accompanied by a loss of vigor with greater homozygosity. The estimates of heterosis

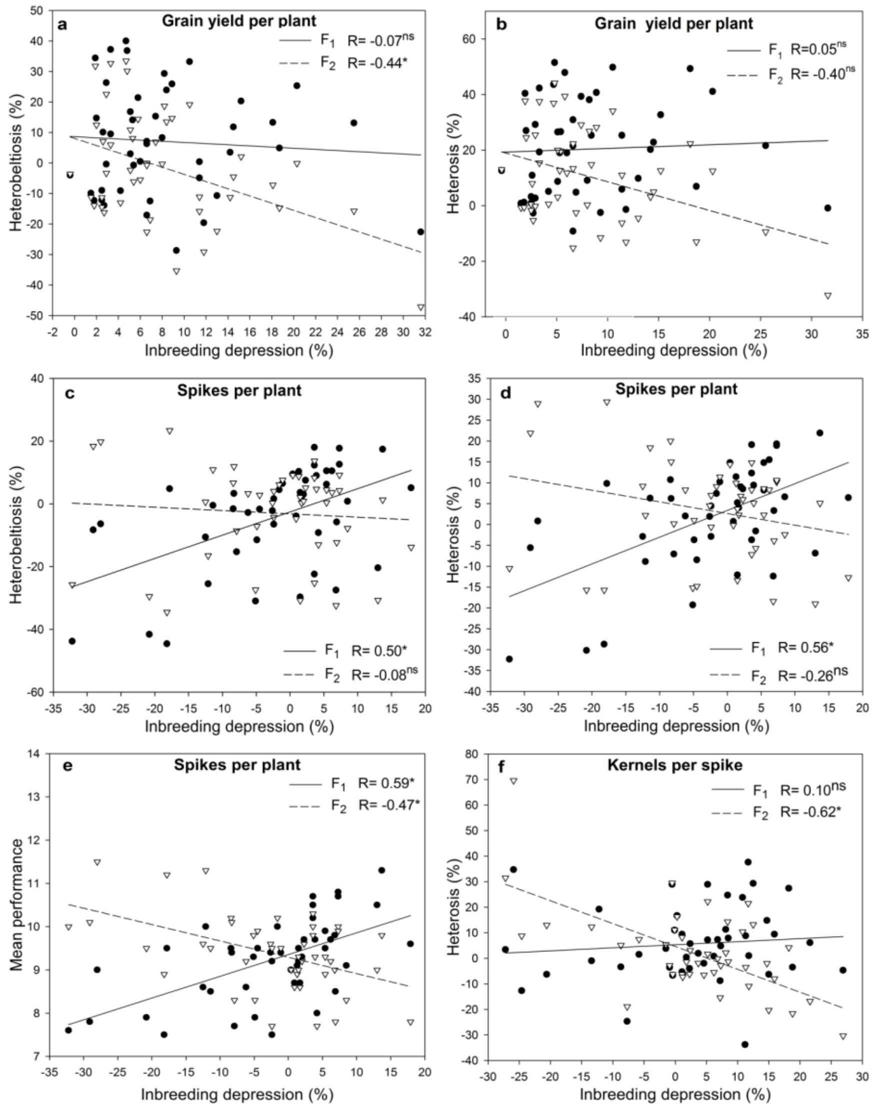

Fig 1. Correlations between mean performance, heterosis, heterobeltiosis and inbreeding depression of the traits: grain yield per plant, spikes per plant and kernels per spike of 45 spring wheat crosses in F_1 and F_2 generations. * Significant values at 5% probability of error by *t* test for DF - 2.

for 100-KW ranged from -2.2 to 5.3% and -14.5 to 2.9% in the F_1 and F_2 generations, respectively. Krystkowiak et al. (2009) also observed a small range of heterosis for kernel weight (-5.71 to 4.13%). The heterosis for KPS varied between -33.8 and 37.6% in the F_1 generation and between -41.2 and 69.6% in F_2. Among the evaluated components of the grain yield, KPS (26.9%) and NSP (-32.2%) were the largest and smallest values for inbreeding depression, respectively. NSP showed heterobeltiosis values ranging from -44.6 to 18% in F_1 and -34.5 and 23.4% in F_2. The hybrids BRS Guamirim *x* CD 115 (F_1= 18.0% and F_2= 13.7%), BRS Guamirim *x* Abalone (F_1= 12.3% and F_2= 8.3%) and BRS 208 *x* Abalone (F_1= 17.7% and F_2= 9.2%) showed positive heterobeltiosis for NSP. These results are in contrast with a study by Farooq and Shalig (2004) that reported only negative heterobeltiosis values for NSP. Qixin et al. (2008) concluded that the traits PH, 100-KW, KPS, NSP and GYP were not located in the same chromosomal region, which implies that heterosis and the performance of each trait can be controlled through different sets of loci, and therefore, the selection gain can be improved. The results of heterosis to PH ranged from -10.4 to 12.8% (F_1) and from -8.1 to 37.6% (F_2) (Table 1). Negative values of heterosis and heterobeltiosis are desirable for the reduction of plant height. In Brazil, the selection of plants of smaller stature is important for regions of high altitude (greater than 700 meters above sea level) with fertile soils and high rates of nitrogen use, where conditions are more favorable for plant lodging. The hybrid UTF 0605 x Pampeano showed the best levels of heterosis for PH with values of -27.9 (F_1) and -32.2 (F_2) (data not shown). In both generations, the values of heterosis and heterobeltiosis indicate that crosses between the UTF 0605 lineage and BRS Guamirim and BRS Figueira cultivars contribute to a reduction of the plant height. These results are also shown Table 2, where it appears that these parents have obtained low heterosis (0.44 to 3.48) and heterobeltiosis values for PH in the F_1 and F_2 generations.

Correlations between agronomic traits and genetics estimates

The heterosis of GYP in the F_1 generation was significant ($p \geq 0.05$) and positively associated with the mean performance of this trait in F_1 (0.64) and F_2 (0.58) (Table 4). Simiarly, the heterosis of GYP in F_2 was positively associated with the mean performance in F_1 (0.57) and F_2

Table 2. Mean values of heterosis, heterobeltiosis and inbreeding depression for five agronomic traits provided by the parents in diallel of spring wheat.

Parents*		PH	NSP	KPS	100-KKW	GYP
BRS Guamirim	F_1 *heterosis*	1.46	1.77	7.95	1.8	24.46
	F_2 *heterosis*	2.18	-1.28	9.66	0.13	14.37
	F_1	-6.23	-1.51	-3.62	-0.54	10.21
	F_2	-5.64	-3.49	-2.28	-2.17	1.22
	ID	-0.69	0.86	-1.49	1.64	7.71
UTF 0605	F_1 *heterosis*	2.15	-1	-3.78	2.03	22.26
	F_2 *heterosis*	3.48	3.12	0.39	-0.56	9.61
	F_1	-21.01	-9.49	-12.09	-1.27	0.64
	F_2	-19.91	-5.91	-8.1	-3.76	-9.71
	ID	-1.69	-4.63	-4.44	2.56	10.15
Fundacep 50	F_1 *heterosis*	3.71	3.43	7.23	3.12	25.82
	F_2 *heterosis*	2.2	6.36	-2.64	1.13	11.66
	F_1	-6.13	-2.1	-2.64	0	9.39
	F_2	-7.37	1.62	-11.2	-1.94	-2.84
	ID	1.4	-4.63	9.42	1.92	11.15
BRS 208	F_1 *heterosis*	0.36	5.99	13.45	0.97	27.2
	F_2 *heterosis*	-1.35	0.75	5.73	-0.43	17.74
	F_1	-5.79	1.5	-40.76	-1.87	16.89
	F_2	-7.19	-3.52	-42.58	-3.24	8.09
	ID	1.52	4.91	6.71	1.38	7.67
CD 115	F_1 *heterosis*	0.63	5.31	4.81	1.08	17.16
	F_2 *heterosis*	4.22	4.52	-3.48	-0.14	6.95
	F_1	-5.58	1.18	-27.24	-1.15	7.98
	F_2	-2.98	0.02	-31.17	-2.35	-1.32
	ID	-3.8	-0.99	7.76	1.2	8.56
BRS Louro	F_1 *heterosis*	2.04	4.32	2.97	1.19	15.48
	F_2 *heterosis*	2.75	9.22	-1.44	0.04	6.68
	F_1	-4.31	-0.56	-28.21	-1.04	5.27
	F_2	-3.75	3.98	-30.33	-2.17	-2.7
	ID	-0.74	-5.27	3.95	1.14	7.29
BRS Timbaúva	F_1 *heterosis*	1.94	6.99	6.05	0.41	25.22
	F_2 *heterosis*	-0.82	10.84	9.08	-0.57	17.85
	F_1	-6.74	1.21	-3.84	-1.75	14.85
	F_2	-9.26	4.85	-0.61	-2.71	8.19
	ID	2.74	-3.73	-3.66	0.97	5.67
Pampeano	F_1 *heterosis*	-2.46	2.34	-4.66	-0.53	7.57
	F_2 *heterosis*	-2.24	5.35	-13.74	-2.93	-1.44
	F_1	-9.13	-3.71	-22.71	-2.65	-9.8
	F_2	-8.9	-0.81	-30.29	-4.98	-17.13
	ID	-0.32	-3.4	9.61	2.41	8.51
Abalone	F_1 *heterosis*	1.14	6.31	9.46	1.15	28.38
	F_2 *heterosis*	-1.18	6.48	7.99	0.04	21.92
	F_1	-5.36	1.75	0.59	-1.05	17.97
	F_2	-7.44	1.97	-1.06	-2.13	12.09
	ID	2.29	-0.16	0.36	1.08	5.11
BRS Figueira	F_1 *heterosis*	0.65	-17.16	13.15	0.15	10.24
	F_2 *heterosis*	0.44	-12.53	12.32	-0.33	-0.78
	F_1	-3.37	-31.83	-11.04	-4.17	-2.49
	F_2	-3.7	-28.08	-11.21	-4.64	-11.92
	ID	0.22	-7.05	1.17	0.48	10.13

PH – plant height. NSP – number of spikes per plant. KPS – kernels per spike. 100-KW –100-kernel weight. GYP – grain yield per plant; ID- inbreeding depression. *Each value indicates the mean performance of the parent in all crosses involved

Table 3. Values of heterosis and heterobeltiosis for the grain yield per plant (GYP) observed in the 10 best crosses of diallel cross of spring wheat.

Better Crosses		F_1 hybrids (%)	F_2 hybrids (%)
Heterosis estimatives			
1 -	BRS Guamirim x BRS 208	51.51	44.23
2 -	BRS Timbaúva x BRS Figueira	49.85	34.13
3 -	UTF 0605x Fundacep 50	49.31	22.31
4-	UTF 0605x BRS Timbaúva	47.88	39.37
5 -	BRS 208 x Abalone	43.59	36.91
6 -	BRS Timbaúva x Abalone	42.25	37.54
7-	Fundacep 50 x BRS 208	40.69	28.15
8 -	CD 115 x Abalone	40.39	37.73
9 -	UTF 0605 x BRS 208	39.33	29.08
10 -	BRS Louro x Abalone	38.15	26.82
Heterobeltiosis estimatives			
1 -	BRS 208 x Abalone	40.00	33.50
2 -	BRS Timbaúva x Abalone	37.23	32.68
3 -	BRS Guamirim x BRS 208	36.78	30.21
4-	CD 115 x Abalone	34.39	31.84
5 -	BRS Timbaúva x BRS Figueira	33.15	19.18
6 -	BRS Louro x Abalone	29.34	18.73
7-	CD 115 x BRS Louro	26.28	22.62
8 -	Fundacep 50 x BRS 208	25.88	14.66
9 -	BRS 208 x BRS Timbaúva	23.91	13.54
10 -	UTF 0605x BRS Timbaúva	21.36	14.37

(0.69) ($p \geq 0.05$). There were positive and significant correlations of heterobeltiosis for GYP in F_1 and F_2 with the mean performance of both generations, indicating that indirect selection through heterosis and heterobeltiosis provides a superior selection for GYP. The mean NSP was significantly ($p \geq 0.05$) correlated with the heterosis of 100-KW (F_1= 0.52 and F_2= 0.41) and GYP (F_1= 0.61 and F_2= 0.53), indicating that the NSP can be used for indirect selection to increase grain yield potential. In the F_2 generation, the heterosis of GYP was positively associated with the mean performance of the NSP in both generations (F_1 and F_2=0.47), further confirming the importance of this trait for the efficient selection of GYP in wheat. The mean performances of the KPS, 100-KW and GYP in both generations were positively associated with the NSP heterobeltiosis in F_1 and F_2 with the exception of the KPS in the F_2 generation. This result indicates that NSP can be useful for the selection of genotypes with high yield and performance. In wheat, high heterosis for yield components determines the presence of heterosis for grain yield (Singh et al., 2004; Bao et al., 2009). These results are consistent with other studies suggesting that the absence of isolated genetic effects can explain the expression of grain yield (Gami et al., 2011; Nazeer et al., 2011). The associations between inbreeding depression and the mean performance of the traits NSP (-0.47) and 100-KW (-0.47) in the F_2 generation (Figure 1E) indicate a loss of vigor due to inbreeding ($p \geq 0.05$). In contrast, in the F_1 generation, the association between the NSP average and inbreeding depression (0.59) suggests that the selection for this trait might be hindered if the breeder prioritizes selection in the F_1 generation. This effect is supported by a positive association between heterosis (0.56) and heterobeltiosis (0.50) of NSP with inbreeding depression ($p \geq 0.05$) (Figures 1C and 1D), indicating that greater heterosis resulted in the highest inbreeding depression for this trait. The negative associations between inbreeding depression and heterosis for KPS (-0.62) (Figure 1F) and

Table 4. Correlations between the mean performance of five agronomic traits with heterosis and heterobeltiosis of F_1 and F_2 in a diallel of spring wheat.

Correlations		F_1 mean performance					F_2 mean performance				
		PH	NSP	KPS	100-KW	GYP	PH	NSP	KPS	100-KW	GYP
F_1 heterosis	PH	0.16	0.24	0.30	-0.11	0.02	-0.03	0.10	0.16	-0.15	-0.17
	NSP	0.01	0.60*	0.34	0.10	0.42*	0.31	0.05	0.32	0.12	0.12
	KPS	0.20	0.42*	0.48*	-0.07	0.30	0.31	0.27	0.41*	0.03	0.30
	100-KW	0.28	0.52*	0.12	0.63*	0.32	0.28	0.41*	0.31	0.51*	0.35
	GYP	0.17	0.61*	0.26	0.14	0.64*	0.10	0.53*	0.28	0.07	0.58*
F_2 heterosis	PH	-0.15	0.23	-0.03	0.02	0.03	0.32	0.19	-0.10	0.06	-0.11
	NSP	-0.31	0.14	0.00	0.18	0.28	0.08	0.47*	0.05	0.28	0.10
	KPS	-0.09	0.42*	0.10	0.09	0.33	-0.01	0.31	0.58*	0.18	0.41
	100-KW	0.06	0.40	-0.12	0.33	0.28	0.14	0.34	0.07	0.71*	0.34
	GYP	-0.19	0.47*	-0.07	0.12	0.57*	-0.16	0.47*	0.01	0.11	0.69*
F_1 heterobeltiosis	PH	0.69	0.47*	0.34	0.19	0.26	0.53*	0.48*	0.22	0.34	0.21
	NSP	0.27	0.51*	0.45*	0.58*	0.60*	0.16	0.01	0.31	0.44*	0.57*
	KPS	-0.03	0.07	0.13	-0.07	0.17	-0.03	0.13	0.24	0.01	0.22
	100-KW	0.02	0.08	0.11	0.60*	0.28	0.07	0.03	0.21	0.49*	0.28
	GYP	0.16	0.49*	0.27	0.36	0.59*	-0.01	0.19	0.28	0.46*	0.58*
F_2 heterobeltiosis	PH	0.50*	0.22	0.20	0.11	0.06	0.72*	0.38	0.10	0.31	0.06
	NSP	0.30	0.19	0.50*	0.54*	0.55*	0.26	0.33	0.37	0.42*	0.58*
	KPS	-0.12	-0.03	0.03	-0.13	0.05	-0.12	0.05	0.33	-0.05	0.12
	100-KW	0.10	0.16	0.20	0.39	0.25	0.19	0.23	0.31	0.71*	0.28
	GYP	0.15	0.35	0.30	0.31	0.52*	0.03	0.16	0.36	0.43*	0.66*

* Significant values at 5% probability of error by *t* test for DF - 2. PH – plant height. NSP – number of spikes per plant. KPS – kernels per spike. 100-KW –100-kernel weight. GYP – grain yield per plant.

heterobeltiosis for GYP (-0.44) (Figure 1A) in the F_2 generation showed that the higher heterosis and heterobeltiosis caused less inbreeding depression, thus increasing the changes associated with selecting superior hybrids. The absence of the loss of vigor potentially reflected an additive effect of the genes present in the parents that were evaluated (Sharma et al., 2003; Gowda et al., 2010). Thus, it is evident that wheat breeders should prioritize the selection of parents and genetically complementary crosses with the predominance of additive gene effects to increase the efficiency of the selection process.

Materials and Methods

Plant materials and experimental design

In the 2006 crop season, nine elite wheat cultivars (BRS Figueira, BRS Louro, Guamirim BRS, BRS Timbaúva, BRS 208, Pampeano, CD 115, Fundacep 50 and Abalone) and one line (UTF 0605) were chosen based on their yield potential and agronomical traits. The parents were crossed using a complete diallel mating design without reciprocals in a total of 45 hybrid combinations based on a manual crossing technique. In the same year, a sample of F_1 seeds from each cross was sown in a greenhouse to obtain the F_2 generation. The remaining seeds were maintained under controlled conditions. In the 2007 crop season, the F_1 and F_2 hybrids and the parent populations were sown in a complete randomized design with three replications. The experimental plots consisted of 20 plants for the F_1 hybrids and 40 plants for the parental and F_2 populations. A 30-cm spacing was used between the plants and rows.

Experimental conditions and crop management

The study was conducted during the 2007 crop season in the experimental area of the School of Agronomy at the Universidade Tecnológica Federal do Paraná (UTFPR), Campus Pato Branco, Paraná State, Brazil (26′10′ S; 52′41′W), at an altitude of approximately 760 m above sea level. The study area has a humid subtropical climate (Cfa, Köppen's classification). The soils in this area are LVdf2 – distroferric red latosols, with clayey texture and an alic and undulating profile (Bhering et al., 2008). Base fertilization consisted of applying 250 kg ha^{-1} NPK (8-20-20) and additional 50 kg ha^{-1} nitrogen at early tillering (Feekes-Large scale 2). For avoid interference from other factors in the expression of potential crop yield, pests, diseases and weed control were managed according to technical recommendations for wheat crops.

Agronomic traits measurement

The following morphological traits were evaluated: plant height (PH) obtained via the measurement of the culm length (cm) from the soil surface to the tip of the flower, excluding awns; the number of spikes per plant (NSP) obtained by counting the individual spikes of each plant; kernels per spike (KPS) obtained by counting the total number of kernels of each plant and dividing by the number of spikes; 100-kernel weight (100-KW) in grams; and the grain yield per plant (GYP), in grams, obtained by weighing the grain production of individually threshed plants.

Statistical analysis

The data were subjected to joint analysis of two generations to evaluate the random effects of generations and genotypes. In addition, the heterosis values were obtained from the mid-parent $H_{MP} = \frac{F_1 - MP}{MP} * 100$ and better-parent, called heterobeltiosis $H_{BP} = \frac{F_1 - BP}{BP} * 100$, where F_1 refers to the performance of the hybrids in the F_1 generation; MP refers to the mean performance of two parental inbreeds for the trait of interest; H_{BP} is the estimate of heterobeltiosis; and BP refers to the performance of better parent for the trait of interest (Eberhart and Gardner, 1966). Significance values of heterosis and heterobeltiosis were assessed using the "*t*" test at a 5% level of error probability. The calculation of the inbreeding depression considered the mean performance of the populations in both generations using the formula $ID = \frac{F_1 - F_2}{F_1} * 100$), where ID is the inbreeding depression or loss of vigor as a percentage, and F_1 and F_2 refer to the performance of the hybrids in the F_1 and F_2 generations, respectively, for the trait of interest. Analysis of variance (ANOVA) and genetics estimates were carried out according method 2 of Griffing (1956).

The genetic variance was obtained by dividing the mean squares of the genotypes (parents and hybrids) by the mean square error and by the number of replications using the formula $\sigma^2 G = \left(\frac{MSG}{MSE}\right) / r$. The broad-sense heritability was calculated by dividing the genotypic variance by the phenotypic variance according to the method of Melchinger et al. (1998) using the formula $h^2 = \frac{\sigma^2 G}{\sigma^2 p}$. Phenotypic variance is the sum of genetic variance (σ^2_G) and environmental variance (σ^2_E). The coefficient of variation (CV) was calculated by $CV_{\%} = 100 \times \sqrt{\sigma^2_{Error}} / \bar{x}$ where $\bar{x}$ the mean of trait and σ^2_{Error} is the error variance of trait.

The associations between the agronomic traits and genetics estimates of heterosis, heterobeltiosis and inbreeding depression calculated in this study were also evaluated using Pearson's correlations. All statistical analysis was performed using the Genes software (Cruz, 2006).

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