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Genetic inheritance and selection for multiple traits in segregating wheat populations

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Abstract – The objective of this work was to investigate genetic inheritance, selection gain, and simultaneous selection for multiple traits of interest in segregating wheat populations. Crosses were performed between genotypes 'Frontana', 'CD 1440', 'CD 105', and 'BRS Sabiá' and the F_1 and F_2 generations; the parents were sown in a field in 2020. From each plant, traits were obtained for germination in the spike, days from emergence to heading, plant height, number of tillers per plant, spike mass, number of spikelets per spike, grain mass per spike, number of grains per spike, and plant grain mass. In addition to the means, the following parameters were obtained: phenotypic, genetic, and environmental variances; broad-sense heritability; and selection gain. All traits showed quantitative inheritance controlled by many genes and influenced by the environment. In most traits, the segregated F_2 populations closely resembled the parents, notably for sprouting in the ear, influenced by the environment. Days from emergence to heading and plant height showed a high heritability and good selection gains, while yield components showed variability for advancements in selection. Simultaneous selection reduced the number of superior individuals, reinforcing the importance of using multivariate methodologies. Thus, the genetic progress depends on strategies that consider quantitative inheritance and adopt multivariate approaches to maximize gains.

Index terms: *Triticum aestivum*, plant breeding, quantitative inheritance.

Herança genética e seleção de múltiplas características em populações segregantes de trigo

Resumo – O objetivo deste trabalho foi investigar a herança genética, o ganho de seleção e a seleção simultânea de múltiplas características de interesse em populações segregantes de trigo. Os cruzamentos foram realizados entre os genótipos 'Frontana', 'CD 1440', 'CD 105' e 'BRS Sabiá' e as gerações F_1 e F_2; os genitores foram semeados em um campo em 2020. De cada planta, foram obtidas características quanto a germinação na espiga, dias da emergência ao espigamento, altura da planta, número de afilhos por planta, massa da espiga, número de espiguetas por espiga, massa de grãos por espiga, número de grãos por espiga e massa de grãos da planta. Além das médias, os seguintes parâmetros foram obtidos: variâncias fenotípica, genética e ambiental; herdabilidade em sentido amplo; e ganho de seleção. Todas as características apresentaram herdabilidade quantitativa controlada por muitos genes e influenciada pelo ambiente. Na maioria das características, as populações F_2 segregadas foram semelhantes aos genitores, principalmente para germinação na espiga, influenciada pelo ambiente. Dias da emergência ao espigamento e altura de planta exibiram alta herdabilidade e bons ganhos de seleção, enquanto os componentes de rendimento mostraram variabilidade para avanços na seleção. A seleção simultânea reduziu o número de indivíduos superiores, reforçando a

importância do uso de metodologias multivariadas. Assim, o progresso genético depende de estratégias que considerem a herança quantitativa e adotem abordagens multivariadas para maximizar ganhos.

Termos para indexação: *Triticum aestivum*, melhoramento de plantas, herança quantitativa.

Introduction

Traits controlled by many genes, such as most agronomically important traits in wheat, are strongly influenced by genotypic and environmental interactions, making it difficult to predict phenotypic traits and the identification of superior individuals (Raffo & Jensen, 2023; Yue et al., 2025). An effective selection for polygenic traits depends on the extent to which phenotypic variance reflects genetic variance, especially in complex environmental settings (Vieira et al., 2025).

The knowledge on genetic inheritance and estimation of selection gain in segregating populations for traits of interest are essential for the genetic progress and understanding of limitations imposed by the environment. Quantifying the genetic variation, environmental effects, and the possibility of combining traits of interest, in the same genotype, is strategic for maximizing long-term genetic improvement. This information allows of the choice of parents and the combination of superior traits, contributing to greater efficiency and progress in wheat breeding (Rutkoski et al., 2016; Shahi et al., 2022; Vieira et al., 2025).

The simultaneous selection for multiple traits presents additional challenges, due to their polygenic inheritance and sensitivity to environmental influences. Genomic prediction models for multiple traits, involving correlated secondary traits, offer support in determining the predictive capacity of success in plant breeding (Sandhu et al., 2021b; Shahi et al., 2022).

Plant breeding can combine classical methods with modern approaches to optimize selection for complex, low-heritability traits (Sandhu et al., 2021a). The genomic prediction for multiple traits, including plant physiological traits, improves prediction for complex traits such as grain yield (Shahi et al., 2022). Selection methods combined with genomic selection that optimize long-term selection gain and maintain genetic variability have been proposed for multiple traits recurrent selection programs (Atanda & Bandillo, 2024). To increase selection gains in quantitative inheritance traits and multiple traits selection, plant breeding programs increasingly rely on molecular marker-assisted selection strategies, the correct choice of selection methods for multiple traits, and periodic updating of these strategies (Vieira et al., 2025).

The objective of this work was to investigate the genetic inheritance, selection gain, and simultaneous selection for multiple traits of interest in segregating wheat populations.

Materials and Methods

The experiment was carried out at the Universidade Federal de Santa Maria, Frederico Westphalen Campus, in the municipality of Frederico Westphalen, in the state of Rio Grande do Sul, Brazil. Initially, contrasting parents for tolerance to germination in the spike were identified, and these parents showed other agronomic traits of interest. The selected parents were: the wheat cultivar 'Frontana', classified as resistant to moderately resistant; 'CD 1440', classified as resistant to moderately resistant; 'CD 105', classified as moderately susceptible; and 'BRS Sabiá' classified as moderately susceptible to susceptible to germination in the spike.

The selected parents were subjected to artificial crosses in a partial diallel, without considering reciprocals. The crosses were performed in 2019 in a greenhouse, from the emasculation of the female parent – removal of the anthers, the male part of the flower, before pollen is released –, to the pollination from 2 to 4 days later, performed with the male parent which was in the pre-anthesis stage.

After the crosses were performed, part of the seed from the F_1 generation were sown in pots, in a greenhouse, to obtain the F_2 generation, until the end of 2019. The F_1 and F_2 generations, together with the parents (P1 and P2) of all populations, were sown in a field. Each plot consisted of 4 lines of the F_1 generation, 14 lines of the F_2 generation, and 4 lines of each of the parents (P1 and P2) of each combination. The lines were 3 m long, with 34 cm spacing between lines, and 20 cm between plants positioned in a homogeneous area. The experiment was installed in the second half of May, 2020. The traits were obtained for each individual plant, as follows: days from emergence to

heading (DEH, days); plant height (PLH, cm), obtained by measuring the soil surface to the tip of the highest spike, excluding the awns; and the number of tillers per plant (NTP), obtained by counting the number of tillers on each plant.

At the physiological maturity, the spike of the main tiller of each plant was harvested for the germination in the spike test. The secondary spike of each plant of the parents (P1 and P2), generation F_1, and generation F_2 was harvested, from which the following trait measurements were performed: spike size (SPS, cm); spike mass (SPM, g); number of spikelets per spike (NSS); grain mass per spike (GMS, g); and number of grains per spike (NGS). The remaining spikes of each plant were harvested and threshed separately, and the trait plant grain mass (PGM, g) was obtained.

The spikes of the main tiller were immersed in pots with 1 L water, at room temperature for 8 hours. After the wetting period, the spikes were subjected to germination on germitest paper, in a germination chamber at 20ºC, for 7 days. Then, the germination was read, when scores from 1 to 11 were assigned, following the scale created by McMaster & Derera (1976), to obtain the traits of germination in the spike (GES).

After measuring the traits of F_1, F_2, P1 and P2 populations, the data were analyzed by determining the mean: $\overline{X} = \sum_{i=1}^{n} X_i / n$; the phenotypic variance $\sigma_P^2 = \sigma_{F2}^2$, where σ_{F2}^2 is the variance of F_2; the environmental variance $\sigma_E^2 = (\sigma_{P1}^2 + \sigma_{P2}^2)/2$ where σ_{P1}^2 is the variance of P1, and σ_{P2}^2 is the variance of P2; the genetic variance: $\sigma_G^2 = \sigma_P^2 - \sigma_E^2$, where σ_P^2 is the phenotypic variance, and σ_E^2 is the environmental variance; and the broad sense heritability $h_A^2 = (\sigma_G^2 / \sigma_P^2)x100$, where σ_G^2 is the genetic variance, and σ_P^2 is the phenotypic variance (Falconer & Mackay, 1996).

The gain selection was also obtained, as follows:

$$SLG = p \times I \times h_A^2 \times \sigma_G,$$

where: p is the parental control (considered equal to 1); i is the selection intensity (used 20%); h^2_A is the heritability in the broad sense; and σ_G is the genetic standard deviation.

For the calculation of the percentage selection gain, the SLG was divided by the original means of the F_2 generation and multiplied by 100. A selection intensity of 20% was considered, and for the traits days from emergence to heading, plant height, and germination in the spike, the individuals with the lowest values and those with the highest values were selected for the following traits: number of tillers per plant; spike size; plant grain mass; spike mass; number of spikelets per spike; grain mass per spike; and number of grains per spike.

The number of genes was calculated by

$$NOG = MaxF_2\text{-}MinF_2/8 \times \sigma^2_G,$$

where: $MaxF_2$ is the maximum value in F_2; $MinF_2$ is the minimum value in F_2; and σ^2_G is the genetic variance. In addition, the combined selection of all traits was determined. The analyses were performed using the Genes software (Cruz, 2016) and Microsoft Excel.

Results and Discussion

The parents were selected, mainly considering the divergence in tolerance to germination in the spike. In the analysis of the trait germination in the spike (GES) of the populations, for the different crosses (Table 1), the mean in F_2 tends to be closer to the parent most susceptible to GES, that is, this reduced genetic variability for tolerance to GES shows how difficult it is to expand it, with a view to selecting superior individuals. Ganeva et al. (2023) discuss the difficulty in selecting for GES because this trait shows low heritability of and is expressed by quantitative inheritance.

Tolerance to spike germination is quantitatively inherited and is highly influenced by environmental effects, associated with seed dormancy, physiological, hormonal, and genetic factors (Sohn et al., 2021; Hull et al., 2024; Matilla, 2024).

Regarding days from emergence to heading (DEH), a tendency for the mean in F_2 is shown to approach the parent with the lowest DEH for more divergent crosses (Table 1) ('Frontana' / 'BRS Sabiá', 'Frontana' / 'CD 105', and 'Frontana' / 'CD 1440'). For these same populations, more divergent for plant height (PLH), the same occurs, with the PLH in F_2 approaching the shortest parent. These results show the possibility of selecting individuals with lower DEH and PLH, even in populations obtained from crosses with parents with higher DEH and PLH, that is, for DEH and PLH, there are genes with some type of dominance effect for precocity and low plant height. Ding et al. (2023) shows that the phenotypic expression for DEH

is variable among wheat accessions in different years. They also conclude that precocity in wheat is due to the presence of genes that express complete or partial dominance effects.

Table 1. Means for the traits days from emergence to heading (DEH, days), plant height (PLH, cm), number of tillers per plant (NTP), spike size (SPS, cm), plant grain mass (PGM, g), spike mass (SPM, g), number of spikelets per spike (NSS), grain mass per spike (GMS, g), number of grains per spike (NGS), germination in the spike (GES, scale 1-11), and number of individuals (NOI) of the wheat (*Triticum aestivum*) parents (P1 and P2), mid-parent (P1+P2)/2, F_1 generation, and F_2 generation.

Population	Traits										
	DEH	PLH	NTP	SPS	PGM	SPM	NSS	GMS	NGS	GES	NOI
	CD 105 / BRS Sabiá										
P1	88.97	83.47	14.67	11.77	15.76	2.35	20.97	1.77	53.73	7.97	30
P2	86.00	87.14	19.43	12.94	18.86	2.53	20.46	1.94	59.29	9.11	28
(P1+P2)/2	87.49	85.31	17.05	12.36	17.31	2.44	20.72	1.86	56.51	8.54	-
F1	87.61	90.04	17.86	12.71	21.04	2.94	20.96	2.43	64.00	9.14	28
F2	86.87	83.17	17.39	11.18	19.43	2.30	19.24	1.77	50.72	8.48	200
Population	CD 1440 / BRS Sabiá										
P1	90.65	82.78	18.62	10.32	19.84	2.01	17.51	1.57	51.86	4.95	37
P2	86.83	86.43	19.17	12.59	21.30	2.66	20.00	1.96	64.17	8.73	30
(P1+P2)/2	88.74	84.61	18.90	11.46	20.57	2.34	18.76	1.77	58.02	6.84	-
F1	89.52	88.40	16.71	11.26	20.61	2.45	18.64	1.85	59.79	7.95	42
F2	88.00	84.34	14.86	11.31	19.87	2.41	19.57	1.82	53.29	8.30	193
Population	CD 1440 / CD 105										
P1	89.43	82.23	17.80	10.55	18.95	1.97	17.83	1.53	52.66	7.46	35
P2	88.89	82.58	15.45	12.32	16.82	2.46	21.39	1.92	54.08	8.42	38
(P1+P2)/2	89.16	82.41	16.63	11.44	17.89	2.22	19.61	1.73	53.37	7.94	-
F1	89.24	85.11	13.00	11.62	19.96	2.77	20.78	2.13	60.19	7.97	37
F2	92.26	84.96	16.87	11.09	18.61	2.27	19.46	1.65	50.29	8.23	207
Population	Frontana / BRS Sabiá										
P1	94.17	115.97	14.97	11.89	15.73	2.34	18.62	1.80	48.83	3.45	29
P2	86.39	85.96	16.79	12.26	19.04	2.51	19.93	1.95	60.25	9.39	28
(P1+P2)/2	90.28	100.97	15.88	12.08	17.39	2.43	19.28	1.88	54.54	6.42	-
F1	86.23	103.09	15.94	12.27	18.18	2.61	18.03	2.07	56.11	9.29	35
F2	87.16	100.35	14.54	11.99	17.32	2.44	18.64	1.78	49.95	7.82	193
Population	Frontana / CD 105										
P1	97.88	115.80	14.64	12.05	16.42	2.53	19.16	1.90	49.84	4.92	25
P2	87.31	80.33	14.75	10.92	16.46	2.45	20.42	1.91	55.75	8.58	36
(P1+P2)/2	92.60	98.07	14.70	11.49	16.44	2.49	19.79	1.91	52.80	6.75	-
F1	87.84	101.87	15.42	11.30	18.32	2.63	18.05	2.02	53.89	8.42	38
F2	88.49	94.87	14.58	10.73	16.88	2.36	17.78	1.78	48.22	8.62	187
Population	Frontana / CD 1440										
P1	96.77	117.69	18.12	12.22	15.92	2.33	19.15	1.76	50.73	4.73	26
P2	89.05	80.40	18.90	10.40	15.70	2.12	17.93	1.61	53.29	7.00	42
(P1+P2)/2	92.91	99.05	18.51	11.31	15.81	2.23	18.54	1.69	52.01	5.87	-
F1	88.44	98.03	15.69	10.56	17.44	2.54	17.97	1.96	52.19	7.25	32
F2	91.37	97.08	15.70	11.35	15.96	2.21	18.26	1.60	46.91	7.15	179

For number of tillers per plant (NTP), spike size (TDE), and number of grains per spike (NGS), a low variability was observed in F_2; for some crosses, the mean in F_2 was lower than those of both parents, that is, there was a transgressive segregation for lower NTP, TDE, and NGS, a factor that is not interesting for plant breeding (Table 1). For Swarup et al. (2021), genetic variability is essential for plant breeding. However, domestication, selection, and modern breeding have restricted the genetic variability of many crops. Research has shown concern about this in wheat (Sthapit et al., 2020; Liu et al., 2024; Wang et al., 2025).

Heterosis in F_1 (Table 1), a superior behavior of the F_1 generation in relation to the mean of the parents (Carvalho et al., 2008), was observed in the present study for the traits in practically all crosses. Plant grain mass (PGM), spike mass (SPM), grain mass per spike (GMS), number of grains per spike (NGS) and germination in the spike (GES) showed heterosis for all crosses. High heterosis may be indicative of greater amplitude of genetic variability in F_2 (Dharvesh et al., 2024; Tareque et al., 2025), but selection may be directed towards individuals in heterosis, and this is lost with the advancement of generations.

Continuing with the analysis (Table 2), we found that all the studied traits show quantitative inheritance, that is, they are controlled by several genes with environmental influence, this means that the greater is the number of genes responsible for the expression of the trait, the greater will be the effect of the environment. For the trait spike size (SPS), the greatest number of genes involved in determining it was observed (Table 2), reaching 13.92 genes for the 'CD 1440'/ 'CD 105' cross, in comparison with the other traits; and the proportion of environmental variance was greater than 40% for all the studied crosses, reaching 62.7% in the 'Frontana'/ 'CD 1440' cross (Figure 1), in comparison with the proportion of genetic variance. The number of spikelets per spike (NSS) also showed many genes involved in its determination, reaching 11.11 in the 'Frontana'/ 'CD 1440' cross, and an influence of the proportion of environmental variance of 59.5% in the 'CD 1440'/ 'CD 105' cross.

Sourdille et al. (2000) reported loci in the wheat genome with genes involved in the expression of the traits spike size and number of spikelets per spike. The broad-sense heritability for SPS and NSS reached a maximum of 54.35% and 58.73%, respectively. These values are high, according to the classification by Resende (2002), who considers heritability low when $h^2 < 15\%$, medium when it is between $15\% < h^2 < 50\%$, and high when $h^2 > 50\%$. Even so, the results are below those obtained by Mwadzingeni et al. (2017), who found heritability of 94.61% for SPS and 87.28% for NSS, in a study of a population of drought- and heat-tolerant lines. In the present study, the maximum gains obtained by selection were 10.72% for SPS and 10.85% for NSS (Table 2). These results show the difficulty in obtaining selection gains for these traits, due to the high effects of the environment on expression. Meier et al. (2022) found even lower selection gains of only 1.91% for SPS and 5.50% for NSS.

Even with a large number of genes involved in determining the traits, from 3.34 to 6.59 for the studied crosses, the traits days from emergence to heading (DEH) and plant height (PLH) showed a reduced effect of the environment in determining the phenotype, with a very low proportion of environmental variance, minimum of 9% for DEH in the 'Frontana'/ 'CD 1440' cross, and 13.2% for PLH in the 'Frontana'/ 'BRS Sabiá' cross, in comparison with the proportion of genetic variance (Figure 1). According to recent molecular marker association studies and quantitative trait loci mapping studies, the DEH genetic control is complex, with associated loci present on multiple chromosomes (Ding et al., 2023; Komura et al., 2024; Kim et al., 2025).

Regarding PLH, recent studies report that the genetic control of this trait in wheat is highly complex, with more than 20 loci associated with plant height distributed across different chromosomes (Zhang et al., 2025). In contrast, broad-sense heritability was high, according to the classification by Resende (2002), reaching 90.97% for DEH in the 'Frontana'/ 'CD 1440' population, and 86.77% in the 'Frontana'/ 'BRS Sabiá' population, with significant gains through selection for shorter cycle and lower plant height, of up to -10.72% for DEH, and 16.69% for PLH. Other studies have found high heritability in wheat, such as 96.9% for DEH and 97% for PLH (Desalew, 2024); Kefale & Menzir (2019) found 85% for PLH; Mwadzingeni et al. (2017) 76.26% for DEH and 86.33% for ALT. Meier et al. (2022) found 99.74% for DEH, with selection gains of 4.91%, and 90.74% for PLH, with selection gains of 15.84%. Therefore, even with many genes involved in the determination of DEH

Table 2. Phenotypic variance (σ^2_P), environmental variance (σ^2_E), genetic variance (σ^2_G), broad sense heritability (h^2_A, %), selection gain (SLG, %), number of genes (NOG) days from emergence to heading (DEH), plant height (PLH), number of tillers per plant (NTP), spike size (SPS), plant grain mass (PGM, g), spike mass (SPM), number of spikelets per spike (NSS), grain mass per spike (GMS), number of grains per spike (NGS) and, germination in the spike (GES) for the F_2 populations of wheat (*Triticum aestivum*).

Estimative	CD 105 / BRS Sabiá									
	DEH	PLH	NTP	SPS	PGM	SPM	NSS	GMS	NGS	GES
σ^2_P	41.63	71.36	42.28	2.11	76.94	0.29	6.34	0.28	151.05	3.93
σ^2_E	6.73	14.61	11.77	1.30	9.18	0.11	3.55	0.09	47.67	1.45
σ^2_G	34.90	56.75	30.51	0.80	67.76	0.18	2.78	0.17	103.38	2.48
h^2_A	83.83	79.52	72.16	38.08	88.07	62.39	43.95	66.67	68.44	63.11
SLG	-8.15	-10.72	41.23	7.53	61.59	20.17	7.32	25.39	21.56	-20.66
NOG	5.17	4.26	4.46	12.07	3.69	4.36	8.80	4.55	6.44	5.04
Estimative	CD 1440 / BRS Sabiá									
	DEH	PLH	NTP	SPS	PGM	SPM	NSS	GMS	NGS	GES
σ^2_P	28.32	67.42	24.01	2.15	71.80	0.37	6.69	0.25	151.52	2.84
σ^2_E	7.44	12.46	10.62	0.97	10.78	0.12	2.76	0.11	41.81	0.80
σ^2_G	20.88	54.96	13.39	1.18	61.02	0.25	3.93	0.14	109.71	2.04
h^2_A	73.72	81.52	55.75	54.35	84.98	67.96	58.73	56.54	72.40	71.57
SLG	-6.00	-10.78	27.75	10.22	55.13	24.49	10.85	22.54	22.70	-19.84
NOG	6.13	4.61	4.93	10.35	4.49	3.70	10.30	4.76	3.57	4.99
Estimative	CD 1440 / CD 105									
	DEH	PLH	NTP	SPS	PGM	SPM	NSS	GMS	NGS	GES
σ^2_P	48.80	63.47	33.31	1.43	67.49	0.28	5.29	0.21	155.15	2.11
σ^2_E	6.60	26.58	8.17	0.92	9.06	0.06	3.15	0.05	59.59	0.77
σ^2_G	42.20	36.89	25.14	0.50	58.44	0.21	2.14	0.16	95.56	1.34
h^2_A	86.47	58.12	75.46	35.38	86.58	77.12	40.42	75.83	61.59	63.45
SLG	-7.03	-8.03	40.26	5.30	60.27	24.05	6.68	27.62	19.98	-15.20
NOG	4.51	6.56	3.63	13.92	3.46	4.91	9.88	4.55	4.71	7.53
Estimative	Frontana / BRS Sabiá									
	DEH	PLH	NTP	SPS	PGM	SPM	NSS	GMS	NGS	GES
σ^2_P	81.31	195.02	26.26	3.03	71.83	0.34	8.89	0.22	140.02	4.77
σ^2_E	14.04	25.80	8.98	1.22	11.28	0.16	3.78	0.09	89.72	1.74
σ^2_G	67.27	169.23	17.28	1.81	60.55	0.19	5.11	0.14	50.29	3.03
h^2_A	82.73	86.77	65.82	48.82	84.30	54.31	57.44	61.18	35.92	63.53
SLG	-10.72	-16.69	35.53	10.72	64.55	18.70	13.83	22.68	11.26	-25.90
NOG	3.60	3.41	4.17	6.54	2.10	4.55	6.27	4.06	8.65	4.12
Estimative	Frontana / CD 105									
	DEH	PLH	NTP	SPS	PGM	SPM	NSS	GMS	NGS	GES
σ^2_P	51.77	198.32	33.19	1.70	50.77	0.32	5.42	0.23	128.26	1.57
σ^2_E	5.27	34.23	9.58	0.97	15.46	0.16	2.96	0.09	63.87	0.84
σ^2_G	46.49	164.09	23.58	0.73	35.31	0.16	2.46	0.15	64.40	0.73
h^2_A	89.81	82.74	71.10	42.74	69.55	50.01	45.38	62.28	50.21	54.37
SLG	-8.40	-16.69	44.38	7.57	44.56	16.79	8.51	23.09	16.62	-11.58
NOG	4.74	3.22	5.09	9.16	4.14	5.61	7.31	4.53	7.46	5.27
Estimative	Frontana / CD 1440									
	DEH	PLH	NTP	SPS	PGM	SPM	NSS	GMS	NGS	GES
σ^2_P	76.09	163.90	39.22	2.41	56.67	0.24	6.23	0.19	104.05	3.58
σ^2_E	6.87	42.30	19.08	1.51	15.11	0.09	2.97	0.07	57.98	2.00
σ^2_G	69.22	121.59	20.14	0.90	41.56	0.15	3.25	0.12	46.06	1.57
h^2_A	90.97	74.19	51.36	37.23	73.33	63.60	52.25	64.54	44.27	73.00
SLG	-10.44	-13.69	32.39	7.41	54.53	20.27	10.06	24.65	12.78	-28.67
NOG	3.34	4.75	4.52	10.29	3.42	5.13	11.11	5.05	8.21	4.78

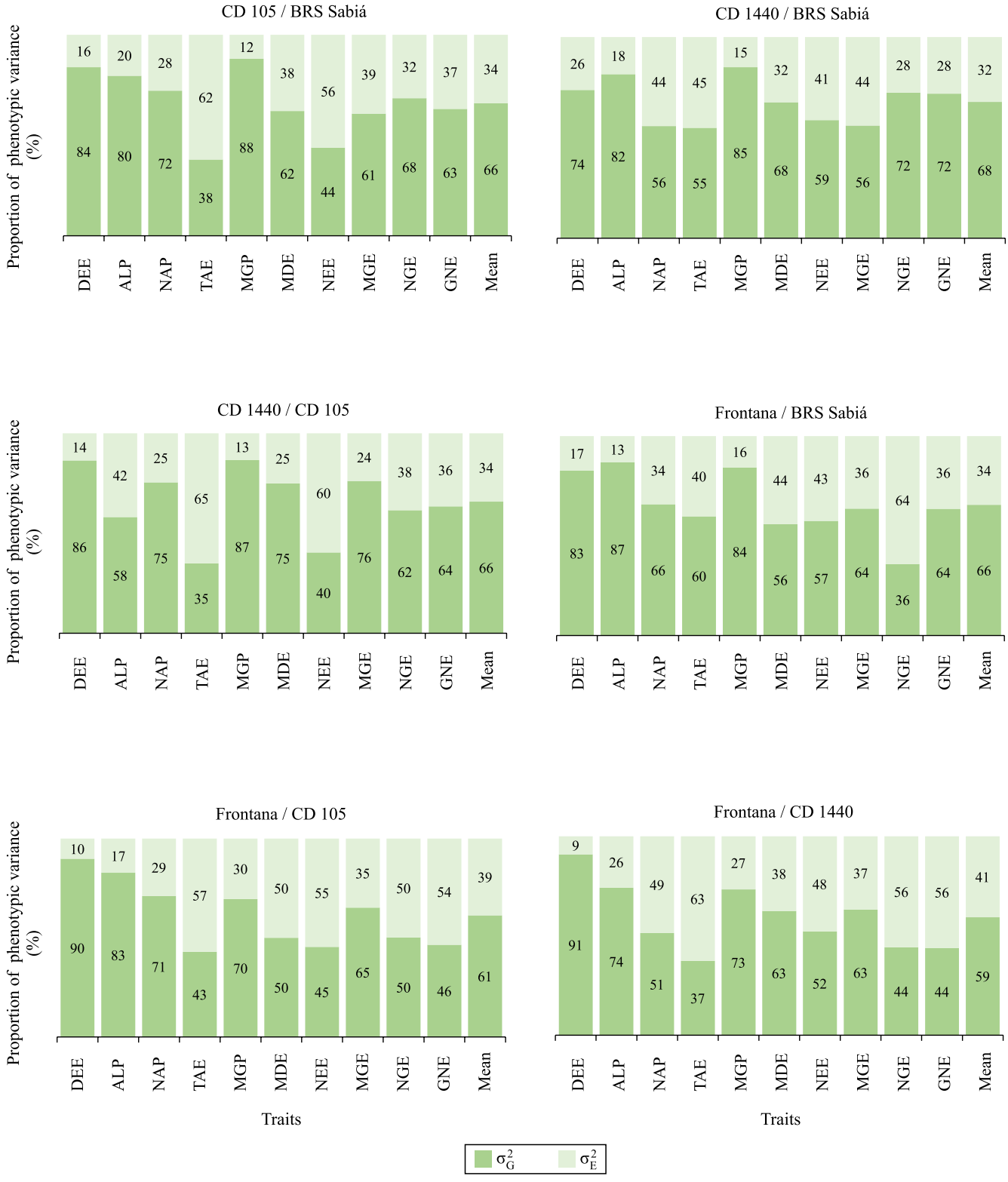

Figure 1. Proportion of the genetic (σ^2_G) and environmental (σ^2_E) variances, in the composition of phenotypic variance (σ^2_P) for the traits days from emergence to heading (DEH), plant height (PLH), number of tillers per plant (NTP), spike size (SPS), plant grain mass (PGM), spike mass (SPM), number of spikelets per spike (NSS), grain mass per spike (GMS), number of grains per spike (NGS), and germination in the spike (GES) in wheat F_2 populations of wheat (*Triticum aestivum*).

and PLH, with high heritability, we can expect more expressive selection gains.

Plant grain mass (PGM) also showed many genes involved in its expression; however the proportion of environmental variance was low, with 11.9 for the 'CD 105'/ 'BRS Sabiá' cross, 13.4% for the 'CD 1440'/ 'CD 105' cross, 15.0% for the 'CD 1440'/ 'BRS Sabiá' cross, and 15.7 for the 'Frontana'/ 'BRS Sabiá' cross, in comparison with the proportion of genetic variance. Thus, selection based on PGM can be efficient, even though it is a quantitative inheritance trait, since the observed broad-sense heritability varied from 69.55%, for the 'Frontana'/ 'CD 105' cross, to 88.07 for the 'CD 105'/ 'BRS Sabiá' cross, and the selection gains found in the present study were high, varying from 44.56%, for the 'Frontana'/ 'CD 105' cross, to 64.55 for 'Frontana'/ 'BRS Sabiá'.

The number of tillers per plant (NTP) trait is controlled by several genes, and recent studies using genome-wide association and functional analyses confirm its polygenic nature, with loci and candidate genes for tillering distributed across different regions of the wheat genome (Muhammad et al., 2021; Khan et al., 2022; Chachar et al., 2025). In the present work, the observed heritability ranged as follows: from 51.36%, with 2.39% selection gain for the 'Frontana'/ 'CD 1440' cross, to 72.16% with 41.23% selection gain for 'CD105'/ 'BRS Sabiá' cross, with selection gain of 41.23%. Even with significant selection gains found in this study, the trait does not seem to be complex for the selection process, since discrepant heritability were found in other studies for NTP, with 95.00% (Mangi et al., 2010) and 28.83 (Mwadzingeni et al., 2017).

The traits grain mass per spike (GMS) and number of grains per spike (NGS) showed interesting heritability for some populations, reaching 75.83% for GMS and 72.40% for NGS. However, heritability of 56.54% was found for GMS and 35.92% for NGS, that is, varying greatly depending on the studied cross. Significant selection gains of up to 27.70% were found for NGS in the 'CD 1440'/ 'CD 105' cross, and 22.70% for GMS in the 'CD 1440'/ 'BRS Sabiá' cross.

For germination in the spike (GES), a trait for which the contrasting parents were selected, heritability ranged from 54.37% to 73.00%, with a selection gain of -28.67% to -11.52%. The best selection gains were observed for crosses involving 'Frontana', a genotype with high tolerance to germination in the spike. However, in general, the proportion of environmental variance was high in relation to the proportion of genetic variance, ranging from 28.20% to 56.10%.

As we have seen previously, the selection for several traits simultaneously in wheat is a challenging task, due to the complexity of genetic inheritance. This challenge has been widely addressed in literature, particularly through the development of different methodologies for the improvement of multiple traits. Selection indices are among the most traditional and effective tools for combining multiple traits into a single value, and for guiding the choice of superior genotypes (Woyann et al., 2019; Rahimi & Debnath, 2023). Other approaches also support the breeder in managing this complexity, such as independent trait selection (Batista et al., 2021), trait assignment (Rahimi & Debnath, 2023), principal component analysis (Jolliffe, 2002), genomic selection (Escamilla et al., 2025), and factor analysis, combined with the multi-trait genotype-ideotype distance index (Olivoto & Nardino, 2021).

Considering the selection rate of 20% of the inferior plants for days from emergence to heading (DEH), plant height (PLH) and germination in the spike (GES), and 20% of the superior plants for number of tillers per plant (NTP), spike size (SPS), plant grain mass (PGM), spike mass (SPM), number of spikelets per spike (NSS), grain mass per spike (GMS), and number of grains per spike (NGS), we have a number of plants ranging from 43 to 61 superior plants for a trait in the different populations (Figure 2).

As two or more traits are combined in the same plant, the number of superior plants is drastically reduced and, for all populations, no plant was observed in the combination of 9 or 10 superior traits. For 7 and 8 combined traits, 0, 1, or 2 plants were verified, while for 5 and 6 combined traits, 0 ('Frontana'/ 'CD 105') to 13 ('CD 105'/ 'BRS Sabiá') superior plants were verified, depending on the population. With the combination of 2, 3 and 4 traits, a large variation appeared, from 7 ('Fontana'/ 'BRS Sabiá') to 49 ('CD 105'/ 'BRS Sabiá') superior plants.

These results confirm the difficulty in selecting several traits simultaneously. To obtain selection gains, the breeder can reduce selection pressure, as suggested by Woyann et al. (2019), who highlight that several methodologies can be used for the simultaneous selection of multiple traits in plant breeding programs.

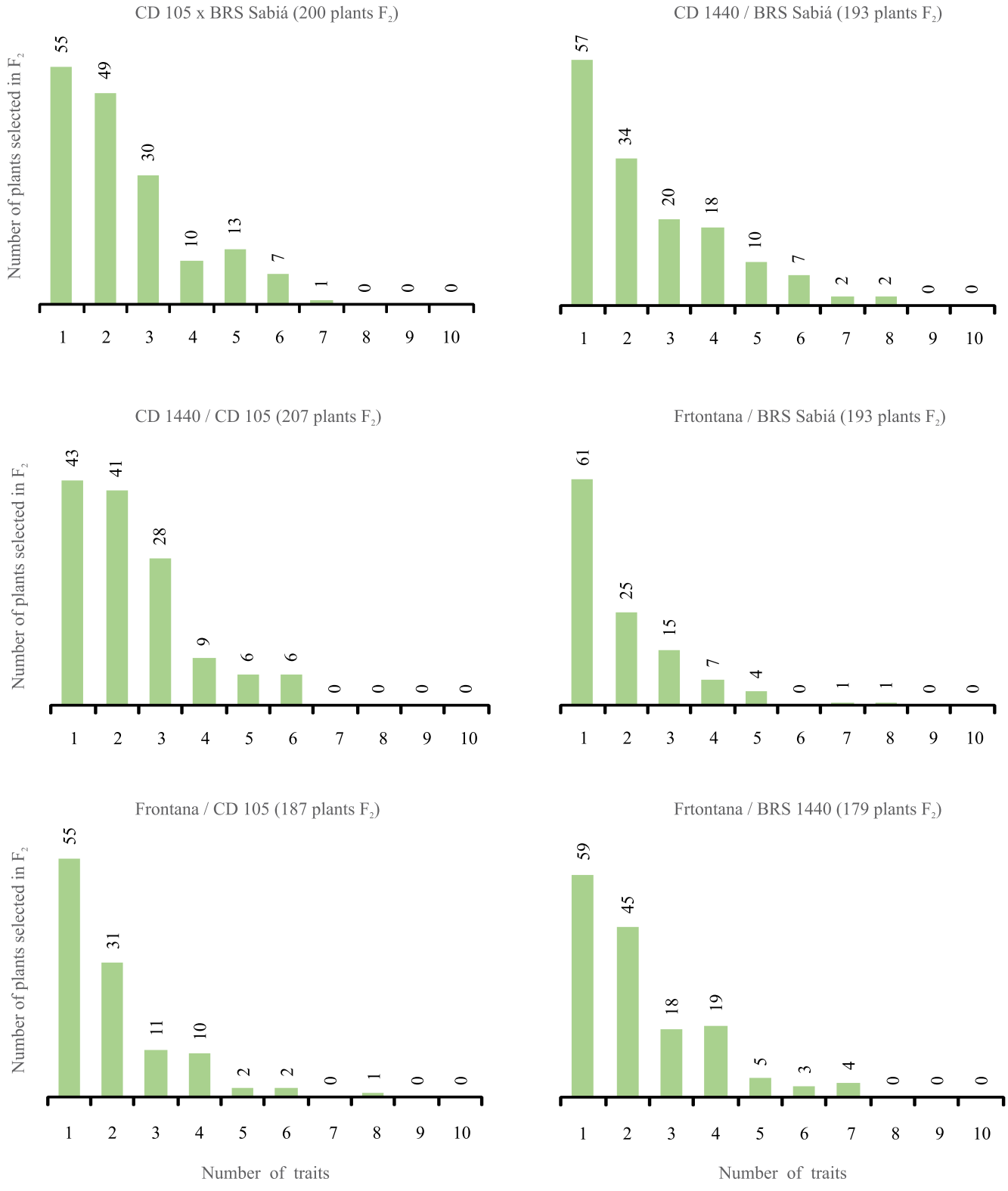

Figure 2. Combined selection in wheat (*Triticum aestivum*) F_2 populations for days from emergence to heading (DEH), plant height (PLH), number of tillers per plant (NTP), spike size (SPS), plant grain mass (PGM), spike mass (SPM), number of spikelets per spike (NSS), grain mass per spike (GMS), number of grains per spike (NGS), and germination in the spike (GES).

Conclusions

1. Segregation in the F_2 generation of wheat (*Triticum aestivum*) is close to the parents for most traits, especially for sprouting in the ear, which showed low reduction and strong environmental influence.

2. The traits of days from emergence to heading and plant height show high heritability and provide significant selection gains.

3. Traits comprising grain yield show significant variability in some crosses, allowing of relevant selective advances.

4. The simultaneous selection reduces the number of superior individuals, highlighting the need for multivariate methodologies in the selection process.

5. In order to maximize overall gain, the genetic progress depends on selection strategies that consider the complexity of genetic inheritance and the need for multivariate methods.

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Gabriel Pereira Pitana: conceptualization, investigation, methodology, writing – original draft; **Volmir Sergio Marchioro**: curation, investigation, methodology, supervision, validation, writing – review & editing; **Marcos Toebe**: conceptualization, data curation, methodology, formal analysis, funding, validation, writing – review & editing; **Maicon Nardino**: validation, writing – review & editing; **Joana Arsego Trombetta**: methodology, visualization, writing – original draft; **Cleiton Antônio Busatto**: methodology, visualization, writing – original draft; **Duana Cancian Garafini**: methodology, visualization, writing – original draft; **José Luiz Balansin Finatto**: methodology, visualization, writing – original draft; **Sidnei Teixeira Bairros**: methodology, visualization, writing – original draft; **Vanda Raul Dgedge**: methodology, visualization, writing – original draft.

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Declaration of use of AI technologies

No generative artificial intelligence (AI) was used in this study.

Conflict of interest statement

The authors declare no conflicts of interest.

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