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BIOLOGY

Canonical correlations between high and low heritability wheat traits via mixed models

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ABSTRACT: *Canonical correlation analysis based on genotypic correlations allows determining the associations between groups of traits and carrying out the direct or indirect selection of superior genotypes. This study investigated the existence of linear and multivariate relationships between high and low heritability traits via canonical correlation analysis based on genotypic correlations. The experiment was conducted at the Professor Diogo Alves de Melo Experimental Field at the Universidade Federal de Viçosa, in Viçosa, MG. 90 wheat cultivars were evaluated under a 9 × 10 alpha-lattice design, with three replications and plots consisting of four rows of three meters spaced at 0.20 meters. Canonical groups were established between spike height and plant height, days for heading, number of spikelets per spike, and number of grains per spike (Group I) and, spike weight, spike grain mass, 100-grain mass, hectoliter weight, and grain yield (Group II). There was dependence between the established groups, which allowed the investigation of the relationships between traits based on their genotypic values. The traits cycle and plant height can be used for indirect selection of genotypes superior in hectoliter weight and grain yield, which are important factors for industries and farmers.*

Key words: *Triticum aestivum L., genotypic and multivariate correlation, indirect selection, REML/BLUP.*

Correlações canônicas entre caracteres de trigo de alta e baixa herdabilidade via modelos mistos

RESUMO: *As análises de correlações canônicas baseadas nas correlações genotípicas, permitem determinar associações entre grupos de caracteres e realizar a seleção direta ou indireta de genótipos superiores. Objetivou-se com este trabalho investigar a existência de relações lineares e multivariadas entre caracteres de alta e baixa herdabilidade via análise de correlações canônicas com base nas correlações genotípicas. O experimento foi conduzido no Campo Experimental Professor Diogo Alves de Melo da Universidade Federal de Viçosa, em Viçosa, Minas Gerais. 90 cultivares de trigo foram avaliadas sob o delineamento alpha-lattice 9 × 10, com três repetições e parcelas constituídas por quatro linhas de três metros espaçadas a 0.20 metros. Os grupos canônicos foram estabelecidos entre altura de espiga e planta, dias para o espigamento, número de espiguetas por espiga e número de grãos por espiga (Grupo I) e, peso de espiga, massa de grãos da espiga, massa de 100 grãos, peso hectolitro e produtividade de grãos (Grupo II). Houve dependência entre os grupos estabelecidos, o que permitiu a investigação das relações entre os caracteres com base em seus valores genotípicos. Os caracteres ciclo e altura de plantas podem ser utilizados para a seleção indireta de genótipos superiores em peso hectolitro e produtividade, fatores estes importantes para indústrias e produtores.*

Palavras-chave: *Triticum aestivum L., correlação genotípica e multivariada, seleção indireta, REML/BLUP.*

INTRODUCTION

The Brazilian wheat chain has 7,810.8 thousand tons in production, 2,723.9 thousand hectares in sown area, and 12,547.8 thousand tons in internal consumption referring to the 2021/2022 harvest. To meet the internal consumption demand in 2022, Brazil will import about 6.200 thousand tons of wheat (CONAB, 2021). The dependence on wheat imports to supply domestic demand highlights the need for advances in breeding programs for the development of superior genotypes.

With the search for breeding programs for genotypes that have the greatest number of favorable attributes, the elucidation of the nature and magnitude of the associations between traits is fundamental.

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MARTIN et al. (2013), studying the cause-and-effect relationships in dual-purpose wheat, obtained satisfactory results from the path analysis, indicating an adequate adjustment in the decomposition of correlations. However, path analysis may not be the most suitable option due to the limitation of having only one dependent variable.

Canonical correlation analysis is an interesting alternative, as it makes it possible to evaluate relationships between traits gathered in two distinct groups. In this way, it is possible to determine associations between groups and carry out the direct or indirect selection of superior genotypes (CRUZ et al., 2012). Although, the use of canonical correlations has been reported in the literature (CARVALHO et al., 2015), few studies are based on the use of genotypic values for investigation of associations between traits. (MEZZOMO et al., 2021). This should be prioritized, in view of the reduction of noise provided by the effect of the environment and the possibility of success and progress in improvement (CRUZ et al., 2012).

Used in several species, the REML/BLUP (Restricted Maximum Likelihood/Best Linear Unbiased Prediction) method presents greater precision in the estimation of genetic parameters, variance components, and in the prediction of genetic values, being recognized as a standard mixed model methodology for such estimates (RESENDE, 2016). Thus, the determination of cause-and-effect relationships between traits based on genotypic correlations is important, as it allows the practice of indirect selection, especially for traits whose measurements are difficult or expensive.

The objective of this research was to estimate the genetic parameters via REML, determine genotypic linear associations via BLUP, and investigate the cause-and-effect relationships between agronomic traits of wheat with high heritability (morphology, cycle and height) × low heritability (production and yield components) via analysis of canonical correlations based on the genotypic values of 90 wheat cultivars.

MATERIALS AND METHODS

Field experiment and plant material

An experiment was conducted from June to October 2020, in the experimental field Professor Diogo Alves de Mello (20º45’14” S; 42º52’55” W; 648 m), subtropical Cwa climate with dry winter, belonging to the Departamento de Agronomia, Universidade Federal de Viçosa, Viçosa, Minas Gerais. Ninety wheat cultivars recommended for the Center-South region of Brazil were evaluated in a 9 × 10 alpha-lattice design (PATTERSON & WILLIAMS, 1976), with three replications. The plots were composed of four rows of 3 m spaced at 0.20 m, adopting a population density of 350 seeds m^{-2}.

Management

At sowing, the base fertilization was carried out with 300 kg ha^{-1}of the formula 08-28-16 (nitrogen, phosphorus and potassium). In coverage, 90 kg ha^{-1} of nitrogen were distributed in the form of urea (45% N), divided into two phases: tillering, phase 20 to 29 of the scale by ZADOKS et al. (1974); and booting, phase 40 to 46 of the scale by ZADOKS et al. (1974). The experiment was conducted with sprinkler irrigation to meet the crop’s water requirements. The other cultural management were carried out in compliance with the technical recommendations for the cultivation of wheat (EMBRAPA, 2020).

Traits evaluated

The number of days for heading (DH, days) was evaluated when at least 50% of the plants in the plot had fully exposed spikes [stage 54 to 59 on the scale of ZADOKS et al. (1974)]. Five representative plants of each plot were used to measure the average spike height (SH, cm) and plant height (PH, cm) with the aid of a ruler graduated in centimeters. Five representative spikes were collected from each plot to obtain the average spike weight (SW, g), average number of spikelets per spike (NSS, units), average number of grains per spike (NGS, units), average grain mass per spike (GMS, g) and average 100-grain mass (HGM, g). After physiological maturation, the plots were manually harvested to determine yield (GY, kg ha^{-1}), adjusting the humidity to 13% in all plots. The hectoliter weight (HW) was determined according to a specific scale from the Dalle Molle brand, measured in kg 100 L^{-1}.

Statistical Analysis

Data were subjected to analysis of deviance for estimation of genetic parameters, genotypic values, and confidence intervals via REML/BLUP methodology, as follows (RESENDE, 2006):

$y = X_r + Z_g + e$,

where y is the data vector; *r* is the vector of repeat effects (assumed to be fixed) added to the overall average; *g* is the vector of genotypic effects (assumed to be random) [g~NID(0,σ_g^2)], where σ_g^2 is the matrix of genotypic variances; and *e* the vector of errors or (random) residuals [e~NID(0, σ_e^2)], where σ_e^2 is the matrix of residual variances; and X and Z are incidence matrices for said effects.

Genotypic values were used to estimate Pearson's linear correlation coefficients between all pairs of traits, as follows:

$$\hat{r}_{g_{xy}} = \frac{Cov_g\,(x, y)}{\sqrt{\sigma_g^2(x)\sigma_g^2(y)}}$$

where $\hat{r}_{g_{xy}}$ is the Pearson's linear correlation coefficient between two random variables; Cov_g is the genotypic covariance; σ_g^2 is the genotypic variance; and *x* and *y* are any two random variables.

Deviance analysis and the estimation of Pearson's linear correlation coefficients were performed using the R software version 4.0.2 (R CORE TEAM, 2020), using functions from the metan 1.12.0 package (OLIVOTO & LÚCIO, 2020).

In the analysis of canonical correlations, the variables were divided into two groups. The first group was established in order to gather morphological variables, cycle, and plant height (high heritability). Thus, Group I contained the variables spike height (SH), plant height (PH), days for heading (DH), number of spikelets per spike (NSS), and number of grains per spike (NGS). The second group gathered traits related to grains yield, which, in turn, are strongly influenced by the environmental effect and there are many genes that act the trait, having low heritability. Thus, Group II contained the variables spike weight (SW), grain mass per spike (GMS), 100-grain mass (HGM), hectoliter weight (HW), and grain yield (GY).

Each group was submitted to a diagnosis of multicollinearity, with condition number (CN) and variance inflation factor (VIF) used as indicators of severity levels, according to MONTGOMERY et al. (2012). After detecting moderate to strong multicollinearity, the variables that most contributed to this problem were excluded (SH in Group I and SW in Group II).

The first canonical correlation between the linear combination of variables from groups I and II was given by (CRUZ et al., 2012): $r_1 = \sqrt{\lambda_1}$, on what λ_1 corresponds to the eigenvalue of the matrix $R_{11}^{-1}R_{12}R_{22}^{-1}R_{12}'$, where R is the matrix of genotypic correlations. The first canonical pair was given by $X_1 = a'X$ and $Y = b'Y$, where a is the first eigenvector associated with the first eigenvalue of $R_{11}^{-1}R_{12}R_{22}^{-1}R_{12}'$; and b is the first eigenvector associated with the first eigenvalue of $R_{22}^{-1}R_{12}R_{11}^{-1}R_{12}'$. The other canonical correlations and canonical pairs were estimated using the eigenvalues and eigenvectors of the expressions described, with the aid of the GENES software (CRUZ, 2016). The significance of the hypothesis that all canonical correlations are null was evaluated by the test of χ^2 associated with 16 degrees of freedom (DUNTEMAN, 1984).

RESULTS AND DISCUSSION

There was significance of the effect of genotype ($P < 0.01$) for all traits evaluated (Table 1). For most of the traits, the estimated variance components showed a greater contribution of genotypic variation in phenotypic variation to the detriment of residual variation. This indicates that the variability between genotypes for the traits is predominantly genetic, which suggested the possibility of studying the relationships between traits based on their genotypic values. Average heritability estimates ranged from 0.71 (NGS) to 0.94 (DH), indicating the possibility of obtaining high gain in breeding programs whose selection is based on this set of character. The residual variation coefficients (CVr) ranged from 2.52 (HW) to 13.41% (SW) and can be considered of low magnitude. Accordingly, the high estimates obtained for accuracy (0.84, NGS to 0.97, DH) indicate a good experimental precision (RESENDE & DUARTE, 2007). Although traditionally used to assess experimental quality, only the residual coefficient of variation is not suitable for such inference (RESENDE & ALVES, 2020). These authors emphasized that the inference of the quality of genotypic assessments should be based on accuracy. The genotypic variation coefficient (CVg), responsible for quantifying the share of the genotypic variation in the total variation, ranged from 2.91 (HW) to 25.21% (GY). The reason CVg/CVr ranged from 0.94 (SH) to 2.36 (DH). Estimates of this parameter superior to the unit are desired and indicated chances of success on gains in the selection process for the set of traits evaluated (CASAGRANDE et al., 2020).

The genotypic correlations between the evaluated traits are shown in figure 1. PH was positively correlated with SH and DH, while it was negatively correlated with GY and NGS. BECHE et al. (2014) also reported a negative association between plant height and grain yield, relating greater plant height with the occurrence of lodging and a decrease in the harvest index. DH showed negative correlations with most traits (HGM, HW, GY, SW and GMS), corroborating the results of MANSOURI et al. (2018), who also found significant associations in the opposite direction between the character days for heading and characters related to yield. GMS and SW were positively correlated with HGM, NSS and NGS, showing significant association between the yield components. HW showed positive correlations

Table 1 - Likelihood Ratio Test, variance components and genetic parameters of 90 wheat genotypes for the traits spike height (SH), plant height (PH), days for heading (DH), number of spikelets per spike (NSS), spike weight (SW), number of grains per spike (NGS), grain mass per spike (GMS), 100-grain mass (HGM), hectoliter weight (HW) and grain yield (GY).

Parameters	---------------------Traits---------------------				
	SH	PH	DH	NSS	SW
$\hat{\sigma}_g^2$	80.8093	89.5174	25.1242	1.5245	0.1161
$\hat{\sigma}_r^2$	34.1424	41.4778	4.5201	1.2698	0.1191
$\hat{\sigma}_p^2$	120.7869	137.0017	29.7636	2.9175	0.2371
$\hat{h}^2$	0.6690	0.6534	0.8441	0.5225	0.4896
$\hat{h}_m^2$	0.8670	0.8569	0.9421	0.7651	0.7348
$\hat{h}$	0.9311	0.9257	0.9706	0.8747	0.8572
CV_g	10.7925	10.0931	7.5860	6.9772	13.2459
CV_r	7.0152	6.8703	3.2176	6.3678	13.4179
CV_g/CV_r	1.5384	1.4690	2.3576	1.0956	0.9871
Mean	83.2925	93.7407	66.0740	17.6963	2.5725
p-value	6.73E-29**	3.58E-27**	1.01E-54**	7.03E-16**	3.41E-14**
Parameters	NGS	GMS	HGM	HW	GY
$\hat{\sigma}_g^2$	28.6548	0.0792	0.1590	4.5601	1191365.0
$\hat{\sigma}_r^2$	32.0181	0.0715	0.0535	3.4380	265014.4
$\hat{\sigma}_p^2$	62.2648	0.1540	0.2199	8.2532	1477876.0
$\hat{h}^2$	0.46021	0.5147	0.7231	0.5525	0.8061
$\hat{h}_m^2$	0.7132	0.7553	0.8868	0.7790	0.9104
$\hat{h}$	0.8445	0.8691	0.9417	0.8826	0.9541
CV_g	10.5560	14.4914	10.8625	2.9036	25.2026
CV_r	11.1583	13.7621	6.2990	2.5212	11.8866
CV_g/CV_r	0.9460	1.0529	1.7244	1.1516	2.1202
Mean	50.7106	1.9431	3.6709	73.5457	4330.8770
p-value	9.89E-13**	8.38E-16**	3E-33**	5.41E-18**	1.37E-35**

** Significant at 1% probability by Chi-Square test: $\chi^2_{1\%}$= 6.63;

[1] $\hat{\sigma}_g^2$, genotypic variance component; $\hat{\sigma}_r^2$, residual component variance;$\hat{\sigma}_p^2$, phenotype variance component; $\hat{h}^2$, individual heritability; $\hat{h}_m^2$, average heritability; $\hat{h}$, selective accuracy; Cvg (%), genotypic variation coefficient; CVr (%), residual variation coefficient.

with HGM and GY, which suggests that these traits can be used as an indirect selection criterion for increasing hectoliter weight. Finally, GY had negative correlations with DH, SH and PH.

In studies of the relationship between agronomic traits of wheat, we should give priority to the estimates of genotypic correlations over phenotypic correlations, since this contains the effect of variations provided by the environment. Thus, genotypic correlations allow an accurate understanding of the true associations between traits.

Canonical correlation analysis (Table 2) shows that all the canonical pairs were significant at 1% probability. This fact shows that the groups considered are not independent and that intergroup associations can be established. The first pair indicated that the increase in NGS also entails an increase in GMS. Although the number of grains, usually presents negative correlations with the mean grain mass (ARECHE & SLAFER, 2006), this relationship does not reflect significant competition between grains for assimilates during the filling period (FERRANTE et al., 2015). In addition, number of grains tends to show great plasticity, being extremely responsive to genetic and environmental factors (SLAFER et al., 2014). This evidence explains the direct relationship between the increase in the number of grains with the increase in the grain mass per spike found in this work.

The second canonical pair evidence relationships in the opposite direction between DH and, HW and HGM (Table 2). Contrary to what was reported by MEZZOMO et al. (2021), these results indicated that earlier cultivars have higher values for hectoliter weight and 100-grain mass. Thus, the cycle

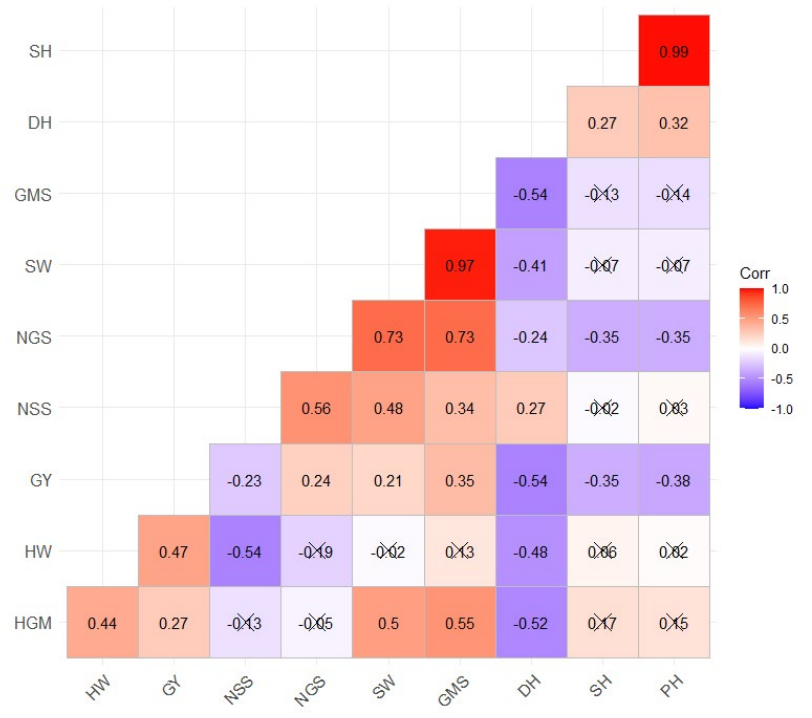

Figure 1 - Pearson's genotypic correlation coefficients between the traits spike height (SH), plant height (PH), days for heading (DH), number of spikelets per spike (NSS), spike weight (SW), number of grains per spike (NGS), grain mass per spike (GMS), 100-grain mass (HGM), hectoliter weight (HW) and grain yield (GY). Crosses indicate non-significant correlations and non-crosses indicate significative correlation by t-test the 5% of probability.

can be used as an indirect criterion for the selection of genotypes with greater hectoliter weight, a trait that is considered a quality criterion by the industries, since it is associated with flour yield. Given the high influence of the environment on this trait (ROSSI et al., 2013), these results can be explained by the fact that plants with a lower cycle are less susceptible to the incidence of biotic and abiotic stresses.

The third canonical pair indicated opposite relationships between PH and GY (Table 2), suggesting that smaller plants are the most productive. According to VELU et al. (2017), the relationship between short plant and high grain production is explained by the pleiotropic effect of the Rht1 (Rht-B1b) and Rht2 (Rht-D1b) genes. For ÁLVARO et al. (2008a), the decrease in plant height provided by genetic improvement over the years contributed to the reduction of competition for carbohydrates between the periods of elongation and ear development, resulting in the obtainment of plants with heavier and more productive ears.

The fourth canonical pair showed relationships in the same direction between NSS and GY, suggesting that the increase in the number of spikelets per spike also leads to an increase in productivity. This result may be associated with the high correlation between the number of spikelets per spike and the number of grains per spike reported in this research. ÁLVARO et al. (2008b), evaluated the gains in traits determining yield in Spanish and Italian durum wheat varieties and concluded that the increase in the number of spikelets per spike also contributes to the increase in grain yield. According to GUO et al. (2018) the number of spikelets per spike, together with other components such as spike size and spike weight, number, and weight of grains per spike, contributed to the final yield. Thus, the development of productive varieties depends on the knowledge of the relationships of the spike morphological traits. MA et al. (2019) highlighted that the number of spikelets per spike can be influenced by population density, nitrogen availability, temperature, and light intensity.

Table 2 - Estimates of correlations and canonical pairs between the traits plant height (PH), days for heading (DH), number of spikelets per spike (NSS), number of grains per spike (NGS) (Group I) and grain mass per spike (GMS), 100-grain mass (HGM), hectoliter weight (HW) and grain yield (GY) (Group II).

-----Canonical coefficients from Group I-----				
Traits	-----Canonical pairs-----			
	1	2	3	4
PH	0.0756	-0.2677	0.7166	0.8233
DH	-0.1768	0.9014	-0.5356	0.5603
NSS	0.0143	0.3175	0.8961	-1.0656
NGS	0.9621	0.0982	-0.4422	1,0330
-----Canonical coefficients from Group II-----				
Traits	-----Canonical pairs-----			
	1	2	3	4
GY	0.1029	-0.2218	-0.7269	-0.9308
HW	-0.0535	-0.5679	-0.2760	1,0983
HGM	-0.5919	-0.4883	0.7910	-0.7838
GMS	1.1577	0.0375	0.1867	0.5402
r	0.93**	0.72**	0.51**	0.30**

**Significant at 1% probability by Chi-Square test: $\chi^2_{1\%}$= 6.63.

The last pair also shows an association in the same direction between NGS and HW, indicating that the increase in the number of grains per spike leads to an increase in hectoliter weight. According to MEZZOMO et al. (2021), the hectoliter weight can be used as an indirect selection criterion for the increase of physiological traits, such as the intracellular concentration of carbon dioxide (CO_2). This would lead to an increase in the CO_2 diffusion capacity, associated with a higher photosynthetic rate of plants. Thus, there would also be a greater grain production per plant, which explains the positive relationship reported between NGS and HW found in this work.

The association in the opposite direction reported between the traits NGS and HGM, indicated that the increase in the number of grains per spike implies a reduction in the 100-grain mass. According to BUSTOS et al. (2013), the simultaneous increase in the number and mass of grains increases the chances of reducing the trade-off between these components and, consequently, leads to increased productivity. CRUZ et al. (2012) defined the nature of associations between traits in two causes: transient, given by genes linked in the same chromosome and; therefore, liable to be broken as a result of sexual recombination between superior individuals; and permanent, caused by the phenomenon of pleiotropy, in which a gene is responsible for the expression of two or more characters.

The knowledge of the genotypic correlations between traits is extremely important, especially in the intermediate stages of a breeding program, as this information allowed us to trace the most efficient strategies for selecting superior genotypes (BHUTTO et al., 2016). When there are traits of low heritability, whose measurements are difficult or expensive, an alternative is the practice of indirect selection based on traits that are easy to measure and with high correlation with the variable in which we want to obtain gains (CRUZ et al., 2012). However, knowledge of these associations alone is not enough, it is necessary to decompose such estimates into information that establishes cause and effect relationships, so that the interpretation of relationships and biological phenomena was performed accurately (CARVALHO et al., 2017). The results reported in the present allow the practicing of indirect selection in wheat breeding programs. The increase in hectoliter weight and 100-grain mass, for example, can be carried out based on the selection of precocious plants. Shorter plants with a high number of spikelets per spike will be the most productive (MANSOURI et al., 2018).

CONCLUSION

The predominant existence of genetic variability allowed the study of relationships between characters based on genotypic values. There was dependence between the groups of established characters, which enabled the study of the cause-and-effect relationships between the characters in view of the practice of indirect selection. The traits cycle and plant height (high heritability) can be used for the indirect selection of superior genotypes in hectoliter weight and productivity (low heritability), which are important factors for industries and producers, respectively.

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DECLARATION OF CONFLICT OF INTEREST

The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analysis, or interpretation of the data; in the writing of the manuscript, and in the decision to publish the results.

AUTHORS' CONTRIBUTIONS

All the authors contributed equally to the conception and writing of the manuscript. All authors revised the manuscript and approved the final version.

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