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Variability and prediction of energy nutritional traits in grains from maize genetic basis and their relationships with meteorological variables

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ABSTRACT - The purpose of this study was to evaluate whether there is variability in the energy and nutritional composition of maize grains among different genetic backgrounds and sowing dates and to determine whether there are relationships between energy nutritional traits and meteorological variables. In total, 773 grain samples from four maize genetic backgrounds, cultivated across ten sowing dates in the years 2021, 2022, and 2023, were evaluated. Descriptive statistics were calculated, and the principal component, correlation, multiple linear regression, and random forest analyses were performed. The contents of ash, ether extract, crude fiber, starch, amylose, and apparent metabolizable energy corrected for nitrogen balance varied among maize genetic backgrounds and sowing dates. At the study site, maize sown in January and February had the highest levels of starch, amylose, and apparent metabolizable energy corrected for nitrogen balance, and the lowest levels of ash, ether extract, and crude fiber. Single-, triple-, and double-cross hybrids had the highest contents of starch, amylose, and apparent metabolizable energy corrected for nitrogen balance, whereas open-pollinated varieties had the highest contents of ash, ether extract, and crude fiber. The contents of crude fiber, starch, amylose, and apparent metabolizable energy corrected for nitrogen balance in maize grains could be predicted using meteorological variables across all maize genetic backgrounds. Random forest models exhibited high predictive accuracy ($R^2 \geq 0.78$), with precipitation between female flowering and harvest emerging as the main meteorological variable associated with the contents of crude fiber, starch, amylose, and apparent metabolizable energy corrected for nitrogen balance (IncMSE ≥ 23.83%).

Keywords: energy nutritional composition, genetic variability, plant breeding, *Zea mays*

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1. Introduction

Maize (*Zea mays* L.) is the main energy source in rations for monogastric and ruminant animals. The contents of ash, ether extract, crude fiber, starch, amylose, and apparent metabolizable energy corrected for nitrogen balance in maize grains determine their nutritional value and influence feed efficiency in animals (Mehta et al., 2020; Guo et al., 2023). However, the nutritional composition of maize grains results from the interaction between genetic and environmental factors, which modulate grain quality and, consequently, animal performance. Maize genetic backgrounds, such as single-, triple-, and double hybrids, and open-pollinated varieties (populations maintained by natural pollination) influence the nutritional composition of the grains. For example, single and triple hybrids may have higher ash contents, with single hybrids tending to have higher ether extract contents and lower carbohydrate contents, while triple hybrids show the opposite pattern (Gonçalves et al., 2003). This compositional

variation among genetic backgrounds highlights the maize genetic diversity potential of maize genetic diversity for the development of genotypes adapted to different production contexts, considering nutritional, industrial, and environmental demands.

Meteorological conditions, especially during the reproductive stage, affect the energy content of maize grains. Variation in water availability among locations and sowing dates determines the physiological and metabolic processes involved in starch deposition and final grain quality (Martínez et al., 2017; Álvarez-Iglesias et al., 2021; Safian et al., 2022; Guo et al., 2023). Accumulated rainfall during the reproductive phase is one of the main factors that determine starch deposition, as water deficits compromise the activity of biosynthetic enzymes, reduce carbohydrate formation, and increase crude fiber content, thereby reducing digestibility (Yang et al., 2003; Chaves et al., 2009; Jeon et al., 2010). Despite these advances, studies that evaluate, in an integrated manner, the effects of genetic basis and meteorological variables on the energy composition of grains are still scarce, limiting the strategic use of this information in crop breeding and management.

In this context, understanding these complex interactions remains a major challenge, particularly due to the multivariate nature of the relationships between environmental conditions and plant performance. Recent advances in statistics and data science have enabled more precise approaches investigating these relationships. Models such as the stepwise multiple regression, and machine learning algorithms, such as random forest, have been successfully applied to model and predict agronomic and nutritional traits using environmental data (Maseko et al., 2024; Sun et al., 2025; Zelaya Arce et al., 2025). These tools help identify relevant environmental variables, estimate nutritional traits before harvest, and support field decision-making, such as the selection of appropriate sowing dates and genotypes for local conditions.

Understanding the variability in the nutritional composition of grains among genetic backgrounds and sowing dates, as well as identifying the meteorological factors that most influence this composition, is essential for the development of more efficient, economical, and sustainable production systems. This approach can also reduce laboratory testing costs, improve feed formulation, increase feed efficiency, and support crop adaptation to weather extremes. Therefore, our objectives were to evaluate whether there is variability in the energy nutritional composition of grains among maize genetic backgrounds (single hybrids, triple hybrids, double hybrids and open-pollinated varieties) and sowing dates, whether relationships exist between energy and nutritional traits and meteorological variables.

2. Material and methods

2.1. Location, dates, and years of the experiments

Maize genotypes were evaluated on ten sowing dates: September 21, 2021, October 20, 2021, November 20, 2021, December 20, 2021, January 30, 2022, September 6, 2022, October 14, 2022, November 24, 2022, December 30, 2022, and February 6, 2023 (years 2021, 2022, and 2023), at the experimental field of the Department of Plant Science of the Universidade Federal de Santa Maria. Except the September 21, 2021 sowing date, when 71 genotypes were sown, 78 maize genotypes, including single-, triple-, and double-cross hybrids and open-pollinated varieties, were sown on each of the other dates.

On each sowing date, maize genotypes were sown in single-row plots. Each plot consisted of a 5-m long row spaced 0.80 m between rows and 0.20 m between plants in the row, totaling 25 plants per plot. In this study, the genotypes were replicated on ten sowing dates. The area was harrowed and fertilized with 415 kg ha^{-1} chemical fertilizer, with the formula (NPK) 05-20-20. Nitrogen fertilization with urea (N - 46%) was split into two applications: 250 kg ha^{-1} at the V4 stage and 150 kg ha^{-1} at the V6 stage.

2.2. Assessment of the grain energy nutritional traits

At the harvest point, a 100-g sample of maize grains was collected from each genotype at each sowing date (773 samples), placed in a paper bag, and dried in a forced-air oven until reaching 13% moisture.

Subsequently, the grains were ground in a Retsch Mill (model ZM 200) fitted with a 1-mm sieve. The ground samples were then scanned using a FOSS NIRS DS2500 instrument (Adisseo Brasil Nutrição Animal) by near-infrared reflectance spectroscopy (NIRS). Based on the absorbance spectra generated for each sample, nutrient composition was determined using multivariate calibration for ground maize through the Precision Nutrition Evaluation (PNE) platform. Thus, ash (Ash), ether extract (EE), crude fiber (CF), starch (ST), and amylose (AML) contents were determined for each sample and expressed as g/100 g, whereas apparent metabolizable energy corrected for nitrogen balance (AMEn) was expressed as kcal/kg. Detailed information on the wet chemistry analyses used to calibrate the NIRS models can be obtained from Oviedo-Rondón et al. (2024).

2.3. Meteorological variables

The meteorological variables were obtained from the Instituto Nacional de Meteorologia (INMET) station, located 100 m from the experimental area. For each day, the hourly global solar radiation, in MJ m^{-2} $hour^{-1}$, the hourly maximum and minimum temperatures, in °C, and the rainfall, in mm, were obtained for the period between sowing and the harvest point of the genotypes, corresponding to each sowing date. For each day, the daily global solar radiation, in MJ m^{-2} $day^{-1,}$ was calculated by summing the hourly global solar radiation, in MJ m^{-2} $hour^{-1}$. Afterwards, for each genotype, on each sowing date, based on the daily global solar radiation, the accumulated global solar radiation was calculated for the following subperiods: Sowing to female flowering (RSFF, MJ m^{-2}) and female flowering to harvest (RFFH, MJ m^{-2}).

For each day, 24 hourly mean temperature values were calculated from the hourly maximum (Tmax) and minimum (Tmin) temperatures. Then, the mean daily air temperature (Tmed), in °C, was calculated by averaging these 24 hourly mean temperature values. Subsequently degree days (GD, in ^{o}C) were calculated according to the method proposed by Arnold (1960) using the following expression:

$$GD = Tmed - Tb,$$

in which Tmed = average daily air temperature, in ^{o}C and Tb = lower-base temperature (10 °C) . Tb is the temperature below which no plant growth occurs and if any growth occurs, it occurs at a significantly reduced rate. When Tmed ≤ Tb, GD was considered equal to zero. For each genotype, on each sowing date, the thermal sum was obtained by adding the GD values of each of the following subperiods: Sowing to female flowering (SSFF, °C day) and female flowering to harvest (SFFH, °C day). For each genotype, on each sowing date, the accumulated rainfall was calculated in each of the following subperiods: sowing to female flowering (PSFF, mm) and female flowering to harvest (PFFH, mm).

2.4. Statistical analysis

For each energy nutritional trait, on each sowing date, the following statistics were calculated: minimum, mean, maximum, and coefficient of variation. Afterwards, for each trait, on each sowing date and genetic basis, the average was calculated. The trait means between sowing dates regardless of genetic basis, between genetic basis on each sowing date, and between genetic basis regardless of sowing dates were compared using the Scott-Knott test at 5% significance. The principal component analysis was applied to group crops by harvest, genetic basis, sowing months and sowing dates in relation to energy nutritional traits and meteorological variables. For each maize genetic basis, Pearson linear correlation networks were developed between pairs of traits.

For each genetic basis, parameters of the stepwise multiple linear regression model with backward selection were estimated, considering the traits Ash, EE, CF, ST, AML, and AMEn as dependent variables and the meteorological variables (RSFF, RFFH, SSFF, SFFH, PSFF, PFFH) as independent variables. For each genetic and general basis, the random forest algorithm was used to estimate the importance of variables RSFF, RFFH, SSFF, SFFH, PSFF, and PFFH for predicting energy nutritional traits. The importance of the variables was estimated based on the percentage increase in the mean square error (IncMSE). The model was fitted with 500 trees (*ntree* = 500), selecting three random variables per node (*mtry* = 3) and activating the option to calculate the variable importance (*importance* = *TRUE*).

For each multiple linear regression and random forest model, the coefficient of determination (R^2), the root mean square error, the coefficient of determination of the leave-one-out cross-validation (R^2_{cv}), and the root mean square error of the leave-one-out cross-validation ($RMSE_{cv}$) were calculated, which generates the model with n-1 observations and evaluates it using the remaining observation. This procedure was repeated n times, excluding a different observation at each time. All statistical analyses were performed using R software (R Core Team, 2025).

3. Results

3.1. Variability of energy nutritional traits

The energy nutritional composition varied significantly between sowing dates (Table 1). The contents of ash (Ash), ether extract (EE), crude fiber (CF), starch (ST), amylose (AML), and apparent metabolizable energy corrected for nitrogen balance (AMEn) ranged between sowing dates, with overall mean of 1.121 g/100 g, 3.871 g/100 g, 2.438 g/100 g, 63.503 g/100 g, 31.582 g/100 g, and 3,292.62 kcal/kg, respectively. The content of each trait changed specifically depending on the environment, with emphasis on EE, whose highest value (4.029 g/100 g) was observed for the November 20, 2021 sowing date. However, this date did not provide maximum values for the other traits. Among the genotypes and sowing dates, grain yield ranged from 0.12 Mg ha^{-1} to 9.13 Mg ha^{-1}, with an average of 3.63 Mg ha^{-1}.

Table 1 - Minimum (Min), mean (Med), maximum (Max) contents and coefficient of variation (CV, %) of energy nutritional traits in grains of single, triple, and double cross hybrids and open-pollinated varieties sown on ten sowing dates in the years 2021, 2022, and 2023

Date	Ash				EE				CF			
	Min	Med	Max	CV	Min	Med	Max	CV	Min	Med	Max	CV
09/21/2021	0.890	1.114b	1.250	6.67	3.180	3.841c	4.710	5.97	1.870	2.256c	2.620	6.87
10/20/2021	0.980	1.158a	1.350	6.35	3.340	3.958b	4.590	5.99	1.860	2.337b	2.800	6.97
11/20/2021	0.940	1.129b	1.290	6.61	3.410	4.029a	4.830	6.78	1.900	2.297c	2.680	6.64
12/20/2021	0.860	1.074c	1.300	8.24	3.260	3.912b	4.540	7.43	1.950	2.278c	2.750	7.28
01/30/2022	0.920	1.107b	1.290	7.11	3.120	3.748c	4.260	7.26	1.920	2.240c	2.580	6.95
09/06/2022	0.890	1.100b	1.270	7.44	3.520	3.942b	4.710	5.91	2.250	2.633a	3.310	8.81
10/14/2022	0.960	1.171a	1.370	6.94	3.440	3.900b	4.460	5.56	2.330	2.666a	3.240	5.72
11/24/2022	0.950	1.166a	1.430	8.30	3.410	3.938b	4.620	5.65	2.310	2.663a	3.350	7.37
12/30/2022	0.940	1.112b	1.400	8.47	3.060	3.789c	4.550	7.14	2.170	2.636a	3.320	7.82
02/06/2023	0.910	1.077c	1.220	6.97	3.100	3.647d	4.750	7.82	1.870	2.352b	3.400	9.46
General	0.860	1.121	1.430	7.88	3.060	3.871	4.830	7.12	1.860	2.438	3.400	10.42
Date	ST				AML				AMEn			
	Min	Med	Max	CV	Min	Med	Max	CV	Min	Med	Max	CV
09/21/2021	62.310	64.664b	66.330	0.93	30.150	34.154a	37.140	4.64	3273.00	3358.620a	3406.00	0.77
10/20/2021	63.250	64.372c	65.520	0.78	28.290	31.422e	35.760	5.24	3291.00	3331.128b	3370.00	0.55
11/20/2021	63.690	64.618b	65.540	0.72	30.390	33.487b	36.410	3.76	3310.00	3352.538a	3384.00	0.61
12/20/2021	63.250	64.989a	66.180	1.00	29.160	32.943c	35.450	3.94	3264.00	3364.885a	3430.00	1.06
01/30/2022	62.600	64.311c	65.620	0.93	28.800	31.809e	35.320	4.09	3200.00	3359.141a	3422.00	1.49
09/06/2022	63.540	64.964a	66.830	1.24	27.180	31.437e	34.830	4.80	3294.00	3364.603a	3419.00	0.92
10/14/2022	60.110	61.299e	62.420	0.90	24.280	29.309g	34.090	6.24	3060.00	3176.051d	3267.00	1.35
11/24/2022	59.760	61.430e	63.460	1.06	24.470	28.913g	32.880	5.65	3059.00	3169.333d	3253.00	1.44
12/30/2022	58.960	61.365e	63.150	1.38	24.040	30.089f	34.210	5.67	3060.00	3183.385d	3269.00	1.47
02/06/2023	59.340	63.121d	66.250	2.67	26.920	32.483d	35.940	5.41	3065.00	3272.436c	3399.00	2.32
General	58.960	63.503	66.830	2.67	24.040	31.582	37.140	7.18	3059.00	3292.620	3430.00	2.78

*71 samples (09/21/2021); 78 samples (10/20/2021, 11/20/2021, 12/20/2021, 01/30/2022, 09/06/2022, 10/14/2022, 11/24/2022, 12/30/2022 and 02/06/2023); 383 samples (2021/2022); 390 samples (2022/2023); 773 samples (General).
Traits: ash (Ash, g/100 g), ether extract (EE, g/100 g), crude fiber (CF, g/100 g), starch (ST, g/100 g), amylose (AML, g/100 g), apparent metabolizable energy corrected for nitrogen balance (AMEn, kcal/kg).
Means not followed by the same letter in the column differ at the 5% significance level using the Scott-Knott test.

Among the maize genetic backgrounds (single, triple, and double cross hybrids, and open pollinated varieties), significant differences in grain composition were observed (Table 2). OPVs presented the highest Ash, EE, and CF contents, regardless of the sowing date. Meanwhile, single, triple and double cross hybrids showed the highest levels of AML, ST, and AMEn. In all genetic basis, an increase followed by a decrease in Ash, EE and CF contents was observed with the delay in the sowing date in each harvest (Table 2). For example, Ash content increased from seeding on September 21, 2021 to November 20, 2021, with subsequent reduction until January 30, 2022. Ash and CF contents were higher in the 2022/2023 harvest compared with the 2021/2022 harvest, while the highest ST, AML, and AMEn contents were observed in the 2021/2022 harvest. In all genetic basis, a reduction followed by an increase in ST, AML, and AMEn levels were observed with the delay in the sowing date, mainly in the 2022/2023 harvest.

Grain samples were grouped by crop, genetic background, sowing months, and sowing dates, capturing 56.0% of the total variability (Figure 1). The highest volumes of PSFF and PFFH occurred in the 2021/2022 harvest, compared with the 2022/2023 harvest. We observed the possibility of grouping the samples according to the sowing months occurred in the two harvests. Sowings in September, January, and February were associated with higher levels of AML, ST, and AMEn. The January and February sowings showed lower Ash, CF, and EE contents.

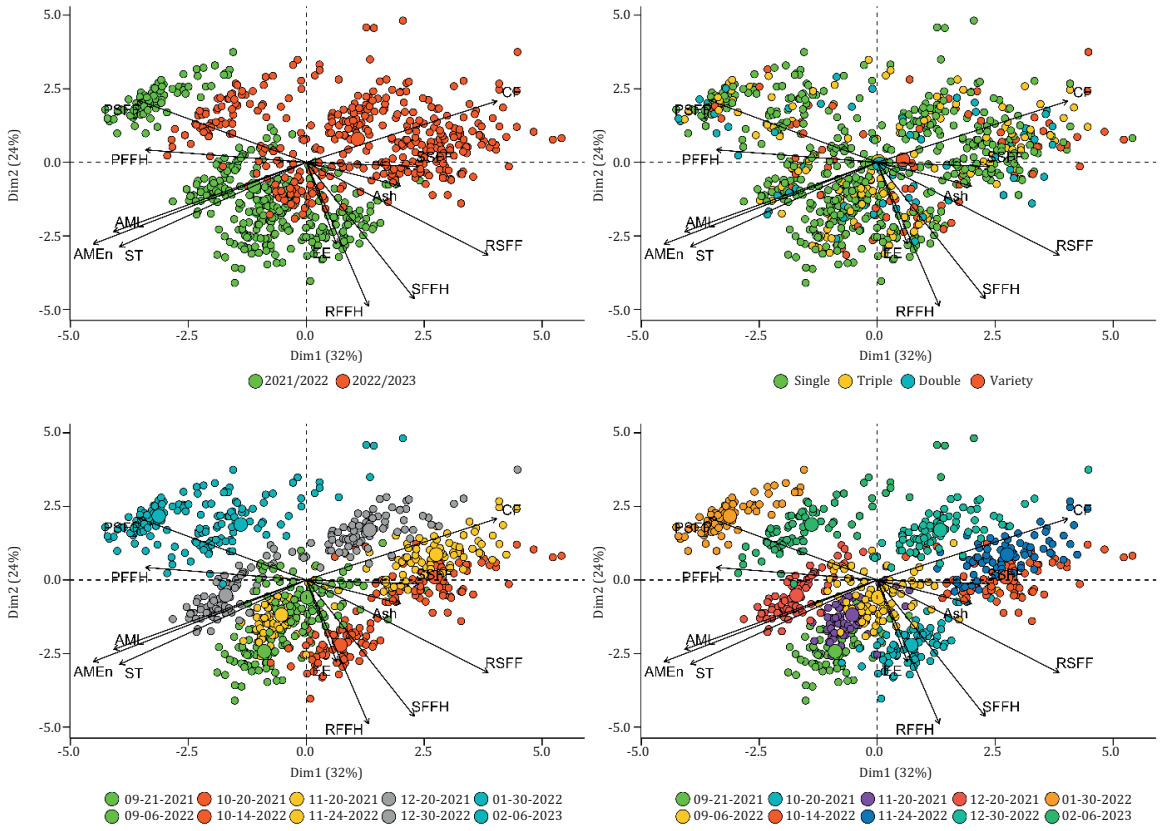


Figure 1 - Data variability (n = 773 samples) represented by two principal components stratified by crops (A), maize genetic basis (B), sowing months (C), and sowing dates for contents of ash (Ash), ether extract (EE), crude fiber (CF), starch (ST), amylose (AML), apparent metabolizable energy corrected for nitrogen balance (AMEn, kcal/kg), accumulated global solar radiation from sowing to female flowering (RSFF, MJ m^{-2}), accumulated global solar radiation from female flowering to harvest (RFFH, MJ m^{-2}), thermal sum from sowing to female flowering (SSFF, °C day), thermal sum from female flowering to harvest (SFFH, °C day), accumulated rainfall from sowing to female flowering (PSFF, mm), and accumulated rainfall from female flowering to harvest (PFFH, mm).

Table 2 - Mean contents and coefficient of variation (CV, %) of energy nutritional traits in grains of single-cross (SH), triple-cross (TH), and double-cross (DH) hybrids and open-pollinated varieties (OPV) sown on ten sowing dates in 2021, 2022, and 2023

Date	GB	Ash		EE		CF		ST		AML		AMEn	
		Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
09/21/2021	SH	1.107a	6.49	3.828a	6.58	2.236a	7.01	64.671a	0.89	34.545a	4.34	3360.804a	0.74
	TH	1.116a	7.55	3.830a	5.16	2.274a	6.58	64.834a	0.75	34.224a	3.11	3362.214a	0.67
	DH	1.140a	1.75	3.853a	4.32	2.287a	4.68	63.743b	1.95	33.347a	5.42	3335.667a	1.63
	OPV	1.141a	7.47	3.931a	4.13	2.333a	7.02	64.670a	0.62	32.086b	3.71	3348.375a	0.72
10/20/2021	SH	1.159a	6.59	3.939a	6.65	2.339a	7.68	64.271a	0.76	31.504a	6.33	3332.787a	0.55
	TH	1.149a	4.95	3.958a	3.85	2.299a	5.19	64.371a	0.75	31.489a	3.18	3331.000a	0.50
	DH	1.164a	5.32	4.020a	5.79	2.339a	7.22	64.746a	0.66	31.211a	2.47	3334.125a	0.62
	OPV	1.166a	8.84	4.009a	5.97	2.397a	5.21	64.594a	0.83	31.030a	2.93	3318.625a	0.50
11/20/2021	SH	1.128a	6.32	3.987b	6.89	2.301a	6.72	64.594a	0.81	33.636a	3.54	3354.745a	0.59
	TH	1.100a	8.40	3.978b	7.59	2.340a	8.08	64.618a	0.61	33.304a	4.91	3348.733a	0.68
	DH	1.145a	4.15	4.143a	4.31	2.232a	4.42	64.595a	0.58	33.986a	2.36	3364.250a	0.43
	OPV	1.174a	5.41	4.256a	3.33	2.263a	3.84	64.778a	0.42	32.460b	1.95	3335.000b	0.45
12/20/2021	SH	1.083a	8.78	3.866b	7.63	2.271a	6.50	64.882b	1.10	33.291a	3.35	3363.340a	1.15
	TH	1.033a	5.87	3.846b	6.24	2.287a	8.27	64.865b	0.51	32.730a	4.01	3365.000a	0.85
	DH	1.085a	2.96	4.176a	5.30	2.206a	8.47	65.491a	0.63	32.941a	2.85	3384.625a	0.54
	OPV	1.081a	10.93	4.040a	6.59	2.376a	7.92	65.354a	0.86	31.297b	4.52	3354.000a	1.19
01/30/2022	SH	1.116a	7.61	3.671b	8.01	2.262a	7.30	64.240a	1.06	31.909a	4.19	3347.319a	1.77
	TH	1.094a	6.56	3.766b	4.56	2.220a	5.68	64.254a	0.57	31.737a	3.74	3365.000a	0.70
	DH	1.075a	6.91	3.975a	3.67	2.149a	5.79	64.641a	0.51	32.413a	3.22	3394.125a	0.45
	OPV	1.105a	4.64	3.941a	4.00	2.243a	7.26	64.505a	0.92	30.755b	3.57	3382.625a	0.53
09/06/2022	SH	1.100a	7.58	3.892b	5.39	2.641a	9.21	64.970a	1.15	31.794a	5.11	3367.404a	0.88
	TH	1.087a	7.48	3.896b	3.35	2.629a	8.37	65.101a	1.29	31.456a	3.27	3365.467a	0.92
	DH	1.100a	7.64	4.026b	7.17	2.561a	5.36	64.900a	1.69	30.922a	3.12	3358.875a	1.22
	OPV	1.120a	7.33	4.239a	5.80	2.663a	10.65	64.735a	1.34	29.821b	2.43	3352.250a	0.92
10/14/2022	SH	1.165b	6.12	3.868a	5.62	2.658b	5.38	61.345a	0.86	29.690a	6.36	3188.085a	1.29
	TH	1.156b	8.62	3.881a	4.29	2.673b	4.87	61.232a	1.04	29.227a	3.96	3171.933a	1.15
	DH	1.165b	8.33	4.019a	6.61	2.593b	6.12	61.431a	0.82	29.064a	4.38	3165.750a	0.88
	OPV	1.244a	4.40	4.001a	5.28	2.774a	7.42	61.020a	0.95	27.473b	7.45	3123.375b	1.17
11/24/2022	SH	1.166a	8.05	3.944a	5.75	2.610a	6.46	61.468a	1.03	29.468a	5.05	3185.872a	1.27
	TH	1.136a	9.19	3.831a	4.04	2.778a	8.13	61.453a	0.92	28.131b	5.57	3146.800b	1.10
	DH	1.165a	6.73	3.987a	3.41	2.663a	6.60	61.110a	1.45	28.156b	4.34	3143.125b	1.24
	OPV	1.225a	8.67	4.054a	7.64	2.763a	7.72	61.484a	1.14	27.877b	6.38	3140.625b	1.92

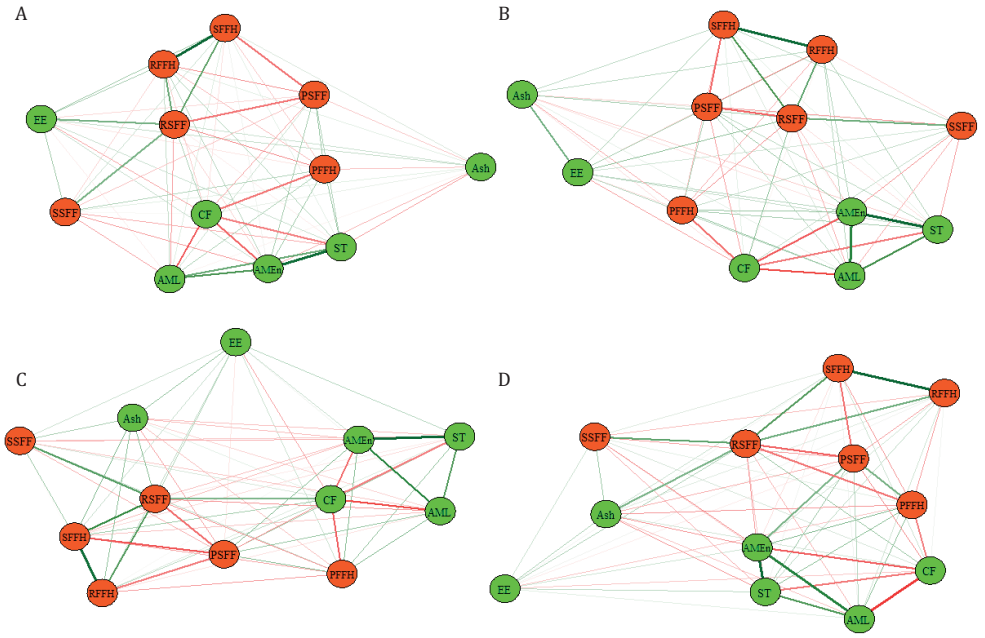
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Table 2 (Continued)

Date	GB	Ash		EE		CF		ST		AML		AMEn	
		Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
12/30/2022	SH	1.121a	8.33	3.755a	7.59	2.642a	7.17	61.346a	1.48	30.463a	5.04	3189.298a	1.32
	TH	1.075a	7.44	3.745a	5.89	2.664a	9.44	61.405a	1.35	29.781a	4.98	3173.667a	1.35
	DH	1.117a	7.86	3.921a	4.60	2.550a	5.07	61.483a	1.55	30.276a	5.23	3197.375a	1.85
	OPV	1.123a	11.27	3.946a	7.28	2.632a	10.60	61.280a	0.74	28.286b	7.69	3152.875a	1.92
02/06/2023	SH	1.089a	6.56	3.591b	7.78	2.393a	10.81	63.083a	2.62	32.688a	5.09	3272.426a	2.33
	TH	1.045a	7.19	3.618b	5.70	2.292a	6.19	63.154a	2.77	32.369a	6.47	3263.667a	2.39
	DH	1.069a	7.29	3.775a	5.41	2.204a	4.22	62.855a	3.09	32.504a	4.90	3262.625a	2.55
	OPV	1.075a	8.17	3.899a	9.61	2.376a	4.64	63.545a	2.71	31.476a	5.54	3298.750a	2.18
General	SH	1.123b	7.67	3.834b	7.44	2.436a	10.27	63.485a	2.63	31.893a	6.96	3296.070a	2.63
	TH	1.099c	8.07	3.835b	5.71	2.447a	10.92	63.520a	2.66	31.426a	7.16	3288.859a	2.88
	DH	1.121b	6.94	3.999a	5.68	2.384b	9.71	63.483a	2.91	31.358a	6.78	3291.280a	3.05
	OPV	1.145a	8.87	4.032a	6.53	2.482a	10.73	63.596a	2.76	30.256b	7.28	3280.650a	3.16

GB - genetic basis.
Traits: ash (Ash, g/100 g), ether extract (EE, g/100 g), crude fiber (CF, g/100 g), starch (ST, g/100 g), amylose (AML, g/100 g), apparent metabolizable energy corrected for nitrogen balance (AMEn, kcal/kg).
Means not followed by the same letter in the column differ at the 5% significance level using the Scott-Knott test.

The CF showed negative correlations with AML, AMEn, ST, and EE in all genetic basis, while AML, ST, and AMEn correlated positively with each other, as well as Ash and EE levels (Figure 2). The correlation analysis revealed that PFFH was negatively correlated with CF and positively correlated with AML, ST, and AMEn. In contrast, RSFF was positively correlated with EE and CF, with these relationships being more pronounced in single- and double-cross hybrids, respectively.



Red lines represent negative linear correlations between traits, while green lines indicate positive linear correlations. The line thickness reflects the correlation coefficient magnitude: thin lines correspond to weaker correlations, while thicker lines indicate stronger correlations.

Figure 2 - Pearson linear correlation network for single-cross (A), triple-cross (B), and double-cross (C) hybrids and open-pollinated varieties (D) between contents of ash (Ash), ether extract (EE), crude fiber (CF), starch (ST), amylose (AML), apparent metabolizable energy corrected for nitrogen balance (AMEn, kcal/kg), accumulated global solar radiation from sowing to female flowering (RSFF, MJ m^{-2}), accumulated global solar radiation from female flowering to harvest (RFFH, MJ m^{-2}), thermal sum from sowing to female flowering (SSFF, °C day), thermal sum from female flowering to harvest (SFFH, °C day), accumulated rainfall from sowing to female flowering (PSFF, mm), and accumulated rainfall from female flowering to harvest (PFFH, mm).

3.2. Influence of meteorological variables on the content of energy nutritional traits

Meteorological variables significantly explain the nutritional energy composition of maize grains (Table 3). The PFFH was the most relevant predictor, especially for ST, CF, and AMEn, being consistently selected in the best stepwise multiple linear regression models. This trend was consistent across genetic basis, with emphasis on single- and triple-cross hybrids and open-pollinated varieties. The regression models adjusted for the prediction of CF, ST, and AMEn presented the highest coefficients of determination ($0.31 \leq R^2 \leq 0.51$) and cross-validation ($0.25 \leq R^2_{cv} \leq 0.48$), with low values of the root mean square error (RMSE ranging from 0.17 to 0.22 g/100g for CF, 1.26 to 1.42 g/100 g for ST, and 65.26 to 73.61 kcal/kg for AMEn). In contrast, Ash and EE contents were less responsive to meteorological variables, with R^2 below 0.24. The models adjusted with the general data set showed high predictive performance, with R^2 greater than 0.40 for CF, ST, and AMEn. In single-cross hybrids, for example, a 10 MJ m^{-2} increase in RSFF, 10 mm in PSFF and PFFH, combined with a 10 °C reduction in SSFF, resulted in increases of 0.2953 g/100 g in ST content and 14.883 kcal/kg in AMEn.

Table 3 - Stepwise forward multiple linear regression for predicting the content of energy nutritional traits using meteorological variables for single, triple, and double cross hybrids and open-pollinated maize varieties sown on ten sowing dates in 2021, 2022, and 2023

Model	Ash	EE	CF	ST	AML	AMEn
			Single hybrids			
Intercept	1.08410	2.42824	3.03656	61.02132	34.17919	3241.48585
RSFF	-	0.00074	0.00013	0.00474	−0.00435	0.21467
RFFH	-	-	−0.00037	-	0.00588	-
SSFF	0.00008	-	-	−0.00942	-	−0.50468
SFFH	-	-	-	-	−0.00350	-
PSFF	-	0.00069	−0.00093	0.00601	-	0.31742
PFFH	−0.00015	0.00032	−0.00093	0.00936	0.00310	0.45153
R^2	0.05	0.27	0.39	0.43	0.30	0.43
R^2_{cv}	0.04	0.26	0.38	0.42	0.29	0.42
RMSE	0.08	0.24	0.19	1.26	1.85	65.26
$RMSE_{cv}$	0.08	0.25	0.20	1.27	1.87	65.88
			Triple hybrids			
Intercept	1.02160	3.31402	2.64340	62.38030	30.24880	3213.15578
RSFF	0.00007	0.00031	0.00026	0.00421	−0.00307	0.24597
RFFH	-	-	−0.00086	-	0.00835	-
SSFF	-	-	-	−0.00948	-	−0.57525
SFFH	-	-	0.00086	-	−0.00632	-
PSFF	-	-	-	0.00520	-	0.42786
PFFH	−0.00014	-	−0.00118	0.00833	0.00628	0.51140
R^2	0.11	0.13	0.46	0.39	0.37	0.51
R^2_{cv}	0.08	0.11	0.42	0.35	0.33	0.48
RMSE	0.08	0.20	0.20	1.32	1.79	66.17
$RMSE_{cv}$	0.09	0.21	0.20	1.36	1.84	68.12
			Double hybrids			
Intercept	0.97369	-	2.31257	60.33719	33.23160	3136.15163
RSFF	-	-	-	0.00472	-	-
RFFH	-	-	-	-	-	0.54774
SSFF	-	-	0.00040	−0.00897	−0.00401	-
SFFH	0.00021	-	-	-	-	−0.75906
PSFF	-	-	-	0.00711	-	-
PFFH	-	-	−0.00124	0.00975	0.00813	0.38415
R^2	0.19	-	0.46	0.40	0.25	0.46
R^2_{cv}	0.14	-	0.41	0.33	0.21	0.41
RMSE	0.07	-	0.17	1.42	1.82	73.47
$RMSE_{cv}$	0.07	-	0.18	1.50	1.88	76.53
			Open-pollinated variety			
Intercept	0.86756	3.61972	3.15513	59.79206	25.37945	3102.89767
RSFF	0.00016	0.00023	-	-	-	-
RFFH	-	-	−0.00021	0.00804	0.00242	0.58378
SSFF	-	-	-	-	-	-
SFFH	-	-	-	−0.00949	-	−0.79100
PSFF	-	-	−0.00103	-	-	-
PFFH	-	-	−0.00097	0.00747	0.00947	0.42489
R^2	0.19	0.06	0.31	0.40	0.22	0.49
R^2_{cv}	0.16	0.02	0.25	0.35	0.17	0.45
RMSE	0.09	0.25	0.22	1.35	1.93	73.61
$RMSE_{cv}$	0.09	0.26	0.23	1.41	2.00	76.36
			General			
Intercept	1.01892	2.66175	3.21676	61.05231	32.76465	3151.96782
RSFF	-	0.00061	0.00058	0.00460	−0.00382	0.10898
RFFH	0.00003	-	−0.00156	-	0.00614	0.30744

Continues...

Table 3 (Continued)

Model	Ash	EE	CF	ST	AML	AMEn
SSFF	0.00012	-	−0.00114	−0.00919	-	−0.24781
SFFH	-	-	0.00170	-	−0.00377	−0.40082
PSFF	-	0.00072	-	0.00618	-	0.21056
PFFH	−0.00017	0.00026	−0.00068	0.00925	0.00435	0.40613
R^2	0.09	0.22	0.43	0.41	0.32	0.47
R^2_{cv}	0.08	0.22	0.42	0.40	0.31	0.46
RMSE	0.08	0.24	0.19	1.30	1.87	66.44
$RMSE_{cv}$	0.08	0.24	0.19	1.31	1.88	66.95

R^2: adjusted coefficient of determination; R^2_{cv}: coefficient of determination of leave-one-out cross-validation; RMSE: root mean square error; $RMSE_{cv}$: root mean square error of cross-validation; -: variables not selected in the final stepwise regression model.
Content of ash (Ash), ether extract (EE), crude fiber (CF), starch (ST), and amylose (AML) and apparent metabolizable energy corrected for nitrogen balance (AMEn, kcal/kg), accumulated global solar radiation from sowing to female flowering (RSFF, MJ m^{-2}), accumulated global solar radiation from female flowering to harvest (RFFH, MJ m^{-2}), thermal sum from sowing to female flowering (SSFF, °C day), thermal sum from female flowering to harvest (SFFH, °C day), accumulated rainfall from sowing to female flowering (PSFF, mm) and accumulated rainfall from female flowering to harvest (PFFH, mm).
Parameter estimates for all multiple linear regression models were significant by the Student's t-test to 5%.

The random forest model performed better than the stepwise regression, especially for CF, ST, AML, and AMEn (Table 4). Among the meteorological variables, PFFH was the most important predictor, showing the highest percentage increase in mean squared error (IncMSE) across genetic backgrounds and in the general model. Overall, PFFH presented IncMSE of 47.48% for CF, 65.09% for ST, 48.02 for AML, and 62.65% for AMEn, highlighting its importance in predicting these traits. The PSFF variable also showed high importance, especially for CF (IncMSE 28.62%) and ST (IncMSE 46.34%). Across genetic backgrounds and traits, R^2 ranged from 0.61 (Ash in the general model) to 0.94 (AMEn in open-pollinated varieties). In the general model, the highest R^2 values were observed for CF (R^2 = 0.78), ST (R^2 = 0.91), AML (R^2 = 0.83), and AMEn (R^2 = 0.92), with a RMSE of 0.12 g/100 g, 0.50 g/100 g, 0.93 g/100 g, and 26.50 kcal/kg, respectively.

Table 4 - Relative importance of meteorological variables (% increase in mean square error, IncMSE) for predicting energy nutritional traits estimated by the random forest algorithm for single, triple, and double cross hybrids and open-pollinated maize varieties sown on ten sowing dates in 2021, 2022, and 2023

Variable	Ash	EE	CF	ST	AML	AMEn
			Single hybrids			
RSFF	8.66	29.29	19.21	25.03	35.59	24.86
RFFH	17.35	21.65	21.98	28.83	27.00	30.41
SSFF	7.45	18.27	17.47	32.43	22.57	31.00
SFFH	16.85	20.62	22.91	22.33	29.29	23.78
PSFF	17.25	12.68	26.16	38.19	31.48	38.20
PFFH	21.19	15.84	44.63	53.34	39.03	57.11
R^2	0.62	0.71	0.82	0.91	0.86	0.91
RMSE	0.05	0.15	0.11	0.50	0.83	26.26
R^2_{cv}	0.04	0.24	0.43	0.71	0.57	0.71
$RMSE_{cv}$	0.09	0.26	0.19	0.90	1.47	46.98
			Triple hybrids			
RSFF	12.99	13.37	10.89	12.46	15.62	12.41
RFFH	10.83	18.39	15.84	26.58	19.42	25.07
SSFF	3.16	3.96	10.38	20.51	13.97	22.61
SFFH	8.95	14.77	11.53	18.32	16.82	20.10
PSFF	8.96	8.57	14.61	25.09	22.55	24.78
PFFH	11.10	8.91	34.91	32.07	23.83	30.79

Continues...

Table 4 (Continued)

Variable	Ash	EE	CF	ST	AML	AMEn
R^2	0.67	0.65	0.82	0.91	0.85	0.93
RMSE	0.05	0.13	0.11	0.49	0.88	24.37
R^2_{cv}	0.03	0.04	0.43	0.66	0.49	0.74
$RMSE_{cv}$	0.09	0.23	0.21	0.99	1.62	48.74
			Double hybrids			
RSFF	0.86	6.46	11.44	9.66	18.09	12.01
RFFH	5.57	6.88	11.99	17.97	15.72	19.46
SSFF	−1.64	−0.26	8.78	14.56	11.37	14.94
SFFH	4.38	6.31	9.26	8.73	11.75	9.12
PSFF	2.01	8.70	13.45	19.77	24.89	26.88
PFFH	2.03	7.11	33.72	26.45	24.36	26.83
R^2	0.74	0.76	0.89	0.89	0.90	0.92
RMSE	0.04	0.11	0.08	0.60	0.66	27.42
R^2_{cv}	0.04	0.06	0.53	0.49	0.55	0.66
$RMSE_{cv}$	0.08	0.23	0.16	1.31	1.42	58.88
			Open-pollinated variety			
RSFF	15.12	8.41	6.82	9.98	13.95	10.73
RFFH	9.14	9.80	6.51	18.01	8.07	10.96
SSFF	2.88	3.96	2.96	16.46	12.01	22.52
SFFH	9.04	11.75	8.74	11.24	7.24	6.88
PSFF	5.25	6.96	10.28	22.48	13.76	21.19
PFFH	11.70	7.06	27.85	26.89	27.46	26.29
R^2	0.71	0.69	0.85	0.92	0.85	0.94
RMSE	0.05	0.15	0.10	0.50	0.85	26.08
R^2_{cv}	0.08	0.01	0.44	0.66	0.46	0.73
$RMSE_{cv}$	0.10	0.28	0.20	1.02	1.62	53.50
			General			
RSFF	18.06	36.57	18.32	29.88	37.22	30.13
RFFH	25.08	26.69	23.54	34.13	31.56	35.34
SSFF	17.34	20.03	20.40	32.07	27.40	30.51
SFFH	22.79	24.18	24.02	26.77	29.61	25.52
PSFF	19.25	20.96	28.62	46.34	36.25	49.61
PFFH	32.28	24.07	47.48	65.09	48.02	62.65
R^2	0.61	0.66	0.78	0.91	0.83	0.92
RMSE	0.06	0.16	0.12	0.50	0.93	26.50
R^2_{cv}	0.07	0.20	0.42	0.73	0.55	0.75
$RMSE_{cv}$	0.09	0.25	0.20	0.88	1.54	45.78

R^2: coefficient of determination, RMSE: root mean square error, R^2_{cv}: cross-validation coefficient of determination, $RMSE_{cv}$: cross-validation root mean square error.
Content of ash (Ash), ether extract (EE), crude fiber (CF), starch (ST), and amylose (AML) and apparent metabolizable energy corrected for nitrogen balance (AMEn, kcal/kg), accumulated global solar radiation from sowing to female flowering (RSFF, MJ m^{-2}), accumulated global solar radiation from female flowering to harvest (RFFH, MJ m^{-2}), thermal sum from sowing to female flowering (SSFF, °C day), thermal sum from female flowering to harvest (SFFH, °C day), accumulated rainfall from sowing to female flowering (PSFF, mm) and accumulated rainfall from female flowering to harvest (PFFH, mm).

4. Discussion

The results revealed the complexity of the interactions between environmental and genetic factors in determining the nutritional energy quality of maize grains. The variability of energy nutritional traits, influenced by years, sowing dates, and types of crossing, corroborates recent studies that highlight the need for multifactorial approaches in agronomic research (Alves and Cargnelutti Filho, 2017; Martínez et al., 2017; Zelaya Arce et al., 2025). Studies have observed variation in the nutritional energy composition of maize grains between sowing dates (Martínez et al., 2017), types of endosperm (Álvarez-Iglesias et al., 2021), soil water conditions (Safian et al., 2022; Guo et al., 2023), and biotechnology events (Vidal et al., 2024).

The observed linear relationships, such as the positive correlation between AMEn, ST, and AML, and the negative correlation between CF and AMEn, ST, and AML, were consistent with the consolidated knowledge on the composition of grains and their energy value (Alves and Cargnelutti Filho, 2017). The negative relationships involving CF may be explained by its lower digestibility and contribution to grain energy value. These interrelationships, observed across genetic backgrounds, suggest a robust physiological basis underlying the accumulation of these components in the grain.

Variation in trait levels between sowing dates may be associated with the occurrence of lower rainfall in critical phases of crop reproductive development, especially during flowering and grain filling (Safian et al., 2022; Guo et al., 2023). The PFFH was the main predictor for variation in energy nutritional contents, especially for ST, CF, and AMEn. This result corroborates studies that demonstrate the critical impact of water availability during the maize reproductive phases on biomass synthesis and the translocation of photoassimilates to the grains (Nicolas et al., 1985; Chaves et al., 2009; Guo et al., 2023). The correlation revealed a negative relationship between CF and PFFH, and a positive correlation between ST and PFFH. Water deficiency during this period can limit starch synthesis and increase the fiber proportion, directly impacting AMEn (Safian et al., 2022; Guo et al., 2023).

This indicates that lower PFFH reduces the quality of maize grains, since higher CF content reduces grain digestibility. The lower starch accumulation under lower PFFH may be related to the inhibition of endosperm cell division and the decrease in the number of endosperm cells (Nicolas et al., 1985). Lower PFFH may reduce photoassimilate supplementation by inhibiting photosynthesis and carbon metabolism, reducing starch and sugar accumulation in grains (Chaves et al., 2009). These results indicate the importance of synchrony between the maize development stage and environmental conditions to maximize the accumulation of energy nutritional traits of interest.

Previous studies have shown that water stress negatively affects the activity of enzymes involved in starch biosynthesis, resulting in reduced starch deposition in grains (Jeon et al., 2010; Yang et al., 2003). In maize, the reduction in precipitation in the period 15 to 30 days after pollination severely compromised the activity of these enzymes, being correlated with the decrease in starch content in the grains (Guo et al., 2023). Our results, by showing lower ST and AMEn contents on sowing dates with lower PFFH, reinforce this relationship, suggesting that water stress during the reproductive phase may have limited starch metabolism.

The predictive capacity of the models, with coefficients of determination (R^2) up to 0.51 for CF, ST, and AMEn in stepwise regression and up to 0.94 for ST in random forest, reinforces the viability of using predictive models to estimate the nutritional quality of maize based on meteorological data. The random forest model superiority in many scenarios, with greater predictive capacity and significant reduction in errors, demonstrates the potential of machine learning algorithms in analyzing complex data.

Our results provide insight into the factors associated with the nutritional and energy quality of maize grains, with emphasis on PFFH, regardless of the maize genetic background. Among the evaluated traits, ST, AML, CF, and AMEn showed greater sensitivity to meteorological variations, while Ash and EE were more stable. This information may help reduce costs and accelerate the evaluation of genotypes in breeding programs. Furthermore, such models inc may improve the accuracy of diet formulation for poultry and swine, which traditionally relies on mean reference values, without accounting for variability between genotypes and environments.

Selecting an appropriate sowing date and genotype is a strategic approach to optimizing the nutritional quality of maize. This study, which jointly evaluated the effects of different genetic backgrounds and growing seasons on the energy composition of maize grains, provides a basis for the development of genotypes adapted to environmental variability with and with high nutritional value. The models developed are specific to the conditions evaluated and may require adjustments before being applied to other agroclimatic regions. Future research should focus on the development and validation of these predictive models under different soil and climatic conditions.

5. Conclusions

There is variation in the contents of ash, ether extract, crude fiber, starch, amylose, and apparent metabolizable energy corrected for nitrogen balance in maize grains between genetic basis and sowing dates.

At the study site, sowings in January and February present the highest levels of starch, amylose, and apparent metabolizable energy corrected for nitrogen balance, and the lowest levels of ash, ether extract, and crude fiber. Single-, triple-, and double-cross hybrids have the highest contents of starch, amylose, and apparent metabolizable energy corrected for nitrogen balance, and open pollinated varieties have the highest contents of ash, ether extract, and crude fiber.

The contents of crude fiber, starch, amylose, and apparent metabolizable energy corrected for nitrogen balance in maize grains can be predicted from meteorological variables, in all maize genetic basis. Rainfall between female flowering and the harvest point is the main meteorological variable that determines the contents of crude fiber, starch, amylose, and apparent metabolizable energy corrected for nitrogen balance, regardless of the maize genetic basis.

Data availability

Data will be made available on request.

Author contributions

Conceptualization: Loro, M. V. and Cargnelutti Filho, A. **Data curation:** Loro, M. V. **Investigation:** Loro, M. V. and Cargnelutti Filho, A. **Software:** Loro, M. V. and Cargnelutti Filho, A. **Validation:** Loro, M. V. and Cargnelutti Filho, A. **Writing – original draft:** Loro, M. V. **Writing – review & editing:** Cargnelutti Filho, A.

Conflict of interest

The authors declare no conflict of interest.

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