Revista Brasileira de Zootecnia

Genetic parameters, prediction of selection gains and genetic diversity in *Andropogon lateralis* Nees ecotypes

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How to cite: Silveira, D. C.; Sampaio, R.; Valentini, A.; Santos, W. M.; Longhi, J.; Nauderer, C.; Machado, J. M.; Mills, A.; Simioni, C.; Brunes, A. P.; Weiler, R. L. and Dall'Agnol, M. 2024. Genetic parameters, prediction of selection gains and genetic diversity in *Andropogon lateralis* Nees ecotypes. Revista Brasileira de Zootecnia 53:e20220097. https://doi.org/10.37496/rbz5320220097

Editors:
Luiz Fernando Brito
Tatiane Cristina Seleguim Chud

ABSTRACT - The objective of this study was to estimate the genetic parameters and predict selection of genetic gains and genetic diversity of 12 *Andropogon lateralis* ecotypes collected in the State of Rio Grande do Sul, Brazil. To estimate genetic parameters and predict selection gains, the REML/BLUP technique was applied. Genetic diversity among the ecotypes was evaluated by two clustering methods (optimization and hierarchical) and principal component (PC) analysis, the latter method also used to discard variables. The genetic parameters studied showed high potential for selection of important agronomic forage traits for livestock production. Results showed that the 12 *A. lateralis* Nees ecotypes exhibited high genetic variability for the studied forage characters and indicated parental prosperity for crosses within the genetic breeding program. Principal component analysis showed that number of total vegetative tillers, leaf:stem ratio, number of reproductive tillers, and leaf dry matter yield accounted for 80.6% of the observed variation in PC1. These variables are important characteristics for quantifying the dry matter production and nutritional value of forage plants, and they can help to discriminate amongst ecotypes. Ecotypes sourced from the Pelotas, Piratini, Passo Fundo, Bagé, and Montenegro regions showed superior forage production when evaluated by the BLUP methodology. Therefore, this group was identified as the most suitable for selection and crossing purposes. Tocher's cluster analysis grouped the ecotypes into five divergent groups. Principal component and UPGMA hierarchical methods were also efficient at separating the ecotypes.

Keywords: BLUP, genetic distance, multivariate analysis, REML

1. Introduction

In South America, natural pastures are the primary feed source for extensive livestock production systems and also provide a range of ecosystem services (Weyland et al., 2017; Jaurena et al., 2021). The species *Andropogon lateralis* Nees is particularly important due to its presence in the upper stratum of the natural grasslands of southern Brazil (Pampa and Atlantic Forest biomes) when they are managed under adequate grazing intensities the equivalent of 12 cm (Barros et al., 2022). The species is a clump-forming, perennial, C4 grass native to South America (Zanella et al., 2021) with gray-green

foliage and feathery inflorescences. It is well adapted to native South Brazil grasslands, is frost–tolerant, and can survive fires and trampling (Trindade and Rocha, 2001). *A. lateralis* Nees is a monoecious species that tends to allogamy and has variability in natural populations, especially stigma color and plant vigor (Norrmann and Quarin, 1991).

Previous research has shown that *A. lateralis* Nees is adaptable to the range of soil and climatic conditions in southern Brazil (Quadros et al., 2009; Machado et al., 2013; Santos et al., 2013; Confortim et al., 2017). The species exhibits high levels of phenotypic plasticity (Quadros et al., 2009), which favors its adaptive capacity to different management practices (Carvalho et al., 2009; Confortin et al., 2017; Zanella et al., 2021).

Within diverse grassland environments where *A. lateralis* Nees was present, the species provided grazing cattle with a high rate of ingestion of leaf blade material, which indicated grazing preference (Confortin et al., 2017). A recent study proposed a functional classification, which considered the association between the size of the bite taken and its relationship with the intake of nutrients in natural pastures of the Brazilian Pampa biome (Azambuja Filho et al., 2020). Results confirmed the high contribution of *A. lateralis* Nees to feed intake (Confortin et al., 2017; Azambuja Filho et al., 2020), this condition being characteristic of the high frequency of the species in the natural pastures of the Pampa biome, associated with the act of selectivity performed by the ruminant herbivore. The pasture structure allowed the animals to take larger herbage bites and the material ingested had a high neutral detergent fiber content (78.3%) and low levels of crude protein (5.8%) and *in vitro* digestibility (30.9%). The presence of species that produce large pieces of material with high fiber content in a complex mixed species pasture is complemented by forage species which grow smaller pieces with greater nutritional values (e.g., legumes) (Azambuja Filho et al., 2020).

A. lateralis Nees has been identified as a species worth including in genetic improvement programs for inclusion in native grazed pastures (Barros et al., 2022). However, current evaluations have been focusing on a restricted set of genetic parameters. Studies that can characterize genetic diversity are important for the conservation and use of genetic resources in breeding programs (Oliveira Neto et al., 2021). In native perennial species, when the objective is to select progenitors, the use of mixed models is a strategy to improve selection efficiency (Meier et al., 2021; Silveira et al., 2022; Silveira et al., 2023). The efficiency and success of a breeding program is directly related to the time required to obtain genetic gains (Hernández-Castro et al., 2021) and commercialize an improved cultivar for market release. Thus, the study and quantification of genetic diversity within a population, the associated variance components, and genetic parameters provide information for actions within the breeding program (Marostega et al., 2021). This provides essential tools for the efficient exploitation of genetic diversity of traits of commercial interest (Lustri et al., 2021).

Studies that provide information on genetic diversity and prediction of genetic parameters and gains through the selection of superior progenitors are vital to the success of a breeding program. Thus, the advances obtained with the evaluation of an important forage species, such as *A. lateralis* Nees, may aid the development of commercial cultivars with increased yield and persistence for intensive livestock production systems and/or in the recovery of degraded areas. Quantification of the diversity of native ecotypes can also contribute to the conservation of natural grassland areas in South America. Therefore, the objective of this study was to estimate the genetic parameters and predict gains and genetic diversity of ecotypes of *A. lateralis* Nees.

2. Material and Methods

The experiment was carried out in Porto Alegre, Rio Grande do Sul, Brazil (30°04'13.1" S, 51°08'26.3" W). *A. lateralis* Nees ecotypes were collected from 12 different physiographic regions of the state of Rio Grande do Sul, which differ in soil type, temperature, and annual rainfall distribution. Five plants of each of a total of 12 ecotypes were collected from Alegrete, Bagé, Caçapava do Sul, Capivari do Sul, Eldorado do Sul, Mariana Pimentel, Montenegro, Passo Fundo, Pelotas, Piratini, Soledade, and Tapes (Figure 1). These ecotypes were evaluated in a randomized block experiment with four replicates.
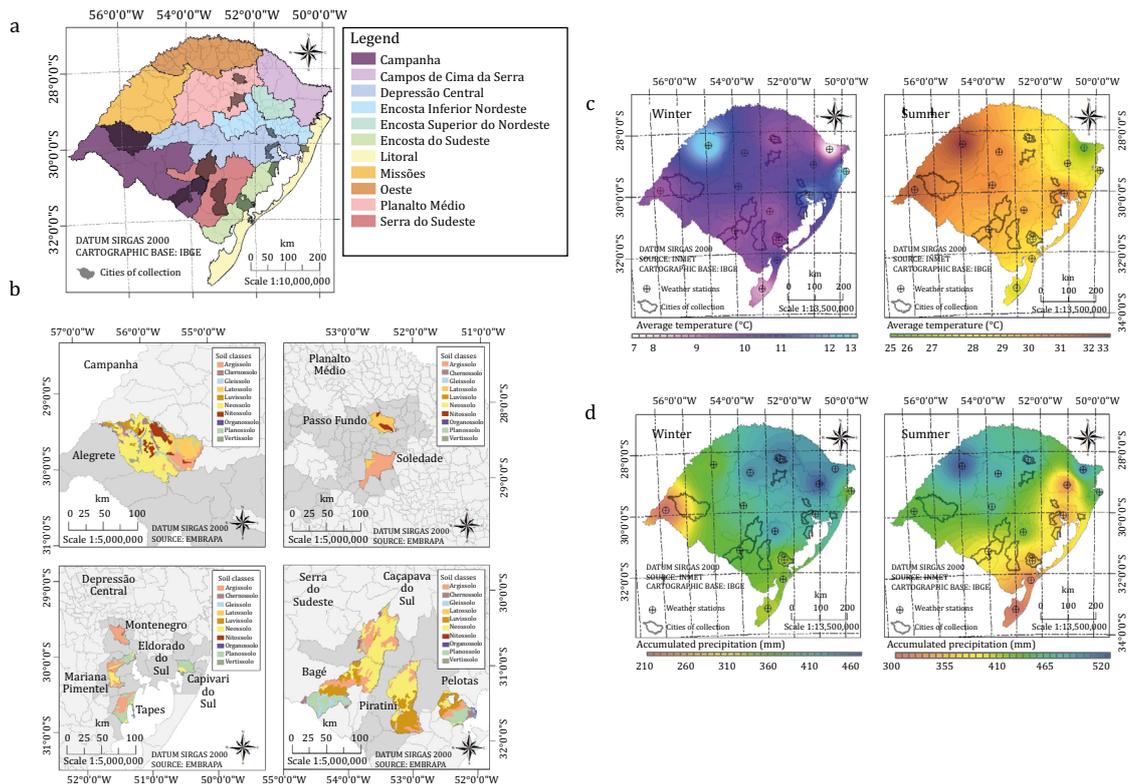
Figure 1 - Physiographic zones in Rio Grande do Sul state, Brazil (a), cities of collection (b), average winter and summer air temperature (c), and winter and summer rainfall (d).

The plants were kept in a greenhouse during autumn and winter. In spring, when plants had three to four tillers, they were transplanted into 2.8 L pots (22 cm high × 22 cm diameter) filled with a commercial substrate and transferred outside the greenhouse (Figure 2). On September 15th, 5.0 g N-P-K (05:20:20) fertilizer was applied to each pot. Thirteen days later, an additional 5.0 g of urea (45% N) was applied per pot. The evaluations were carried out during one active period of growth which encompassed autumn, spring, and summer (September 2011 to February 2012). In autumn, plants were placed in a greenhouse for acclimation. The average monthly minimum and maximum air temperature and rainfall during the experimental period are presented in Table 1. Pots were irrigated until soil saturation every seven days without precipitation to prevent water stress.

Herbage cuts were scheduled every 500 degree-days (°Cd), which is equivalent to the amount of thermal time required for the growth of three leaves (Machado et al., 2013). Base temperature was 10 °C. Thermal time was calculated by the equation: $Tt = \sum Tmd$, in which $\sum Tmd$ is the sum of the daily average temperatures in the interval between cuts. During the experimental period, seven herbage cuts were taken. Herbage was cut to a residual height of 12 cm.

At each evaluation, the number of vegetative and reproductive tillers of each plant were counted. Reproductive tillers were those where differentiation demonstrated the flowering induction of that stem. Plant height (cm) was measured with a graduated scale, from the soil surface to the extremity of the highest leaf of the plant. The experiment was concluded when there was a reduction in plant growth, possibly due to a reduction in photoperiod and temperature.

After cutting, samples were morphologically separated into leaf blades, stems, and dead material, then placed in a forced-air circulation chamber at 65 °C until constant weight. Variables quantified were accumulated total dry mass (TDM, g plant^{-1}), accumulated leaf dry matter (LDM, g plant^{-1}), accumulated stem dry matter (SDM, g plant^{-1}), total number of vegetative tillers (NVT), total number of reproductive tillers (NRT), number of total tillers (NTT), and plant height (PH, cm). The leaf:stem ratio (L:S) was calculated by dividing the LDM by SDM.

Figure 2 - Plots with *Andropogon lateralis* Nees plants.

Table 1 - Average monthly minimum (min) and maximum (max) temperature (°C) and rainfall (mm) during the experimental period (August 2011-March 2012) compared to 42-yr average (1970-2012)

Month	Temperature (°C, min-max)			Rainfall (mm)		
	2011	2012	40-yr average	2011	2012	40-yr average
Jan	-	20.2-31.3	18.5-28.7	-	165.8	23.8
Feb	-	22.4-33.6	16.2-25.9	-	136.6	20.7
Mar	-	18.8-30.3	16.7-25.9	-	120.2	20.2
Apr*	-	-	8.75-20.1	-	-	13.0
May*	-	-	12.2-20.3	-	-	13.7
Jun*	-	-	7.75-10.9	-	-	8.2
Jul*	-	-	9.66-16.3	-	-	13.7
Aug	11.4-20.0	-	10.5-18.5	147.8	-	15.0
Sep	12.0-23.5	-	8.82-14.8	52.8	-	11.4
Oct	15.9-25.8	-	15.1-22.0	124.4	-	18.4
Nov	17.1-28.8	-	10.5-20.9	14.8	-	18.3
Dec	18.4-29.6	-	17.6-24.9	53.0	-	22.6

* Plants were kept in a greenhouse.

Estimates of variance components and genetic parameters were obtained using SELEGEN-REML/BLUP software (Resende, 2016), following the REML/BLUP procedure. The genetic statistical model used considered a randomized block design in one location and one year, according to the model:

$$y = Xr + Zg + e \tag{1}$$

in which y is the data vector, r is the vector of replicate effects (assumed to be fixed), g is the vector of genotypic effects (assumed to be random), e is the error vector (random), and X and Z are the incidence matrices.

The mixed model equations for the prediction of r and g are equivalent to:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z \end{bmatrix} \begin{bmatrix} r \\ g \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix} \tag{2}$$

The significance of random effects was obtained through Deviance Analysis (ANADEV) by the REML (Restricted Maximum Likelihood) method, via LRT (Likelihood Ratio Test). The deviances were obtained as described by Resende (2016), using the model with and without the respective effects, subtracting the deviance obtained in the complete model from the model without the effect and compared with the Chi-square (χ^2) value with a degree of freedom. The block factor, considered as fixed effect, was tested by Snedecor's F test.

The genetic parameters determined by REML for phenotypic (σ_p^2), genotypic (σ_g^2), and environmental (σ_e^2) variance by the EM (Expectation-Maximization) algorithm are specified by the formulas:

$$\sigma_e^2\ [y'\,y - g'\,X'\,y - g'\,Z'\,y]\ /\ [N - r(x)] \tag{3}$$

$$\sigma_g^2\ [g'g + \sigma_e^2\ tr\ C^{22}]\ /\ N_g \tag{4}$$

$$\sigma_p^2 = \sigma_g^2 + \sigma_e^2 \tag{5}$$

Heritability in the broad sense (h_g^2) and selective accuracy ($\hat{r}_{gg}$), genetic variation coefficient (CV_g), residual variation coefficient (CV_{res}), and relative variation coefficient (CV_r) were estimated as:

$$h_g^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2} \tag{6}$$

$$\hat{r}_{gg} = (h_g^2)^{1/2} \tag{7}$$

$$CV_g\ (\%) = \frac{100\ \sqrt{\sigma_g^2}}{\overline{m}} \tag{8}$$

$$CV_{res}\ (\%) = \frac{100\ \sqrt{\sigma_e^2}}{\overline{m}} \tag{9}$$

$$CV_r\ (\%) = \frac{CV_g}{CV_{res}} \tag{10}$$

The genetic divergence among ecotypes was evaluated by three methods. Firstly, we applied the Tocher's optimization method (Rao, 1952), followed by a hierarchical method (Unweighted Pair-Group Method using Arithmetic Averages (UPGMA)), and finally, principal component analysis (PCA) was conducted. To quantify genetic divergence, the Mahalanobis genetic distance (D^2) matrix described by Resende (2007) was used. The predicted values were obtained from the variance and covariance matrix of these genetic values as $D_{ii'}^2 = {}^{\delta\prime}G^{\delta}$, in which $D_{ii'}^2$ is the Mahalanobis distance between genotypes i and i'; G is the matrix of genotypic variance and covariance; $^{\delta}$ [d_1, d_2, ... d_j], being $d_j = Y_{ij} - Y_{i'j}$; and Y_{ij} is the mean of the i-th genotype in relation to the j-th variable. We used PCA to eliminate observed variables that had less importance in the set of characteristics analyzed. The criterion of Jolliffe (1972, 1973) was applied. This criterion discards variables with greater weight in the last components of lesser importance. The criteria for discarding the main components were set at 80%.

All analyzes were performed using the SELEGEN-REML/BLUP genetic-statistical computational application (Resende, 2016) and GENES (Cruz, 2016) to obtain multivariate analyzes.

3. Results

The LRT demonstrated the significance (P<0.01) of the genetic effects, considering all forage characteristics. This analysis indicated that selection strategies for ecotypes can be adopted to obtain genetic gains. There was greater phenotypic ($\hat{\sigma}_p^2$) and genotypic ($\hat{\sigma}_g^2$) variance associated with PH, NTT, and NVT characteristics. Heritability in the broad sense (h_g^2) and average heritability of genotype (h_{mc}^2) of all eight characters studied were considered high (Table 2). These results demonstrated potential for genetic gains through selection of ecotypes and their use in future crosses.

Experimental precision, as quantified through selective accuracy (r_{gg}), ranged from 0.98 to 0.99, and these values were considered high. Based on these values, it can be concluded that the experiment adequately quantified high levels of variation among ecotypes, which indicated genetic variability and low experimental variation. The genetic variation coefficients (CV_g) for TDM, LDM, and NVT were 18.3, 21.0, and 42.1%, respectively. This parameter quantifies the magnitude of the genetic variation available for selection, with high values being desirable.

The five highest yielding ecotypes, which represented 41.6% of the germplasm evaluated, were selected by forage characteristics based on the BLUP methodology (Table 3). These ecotypes showed predicted breeding values higher than the general average for all parameters evaluated. In summary,

Table 2 - Verisimilitude values (LRT) of deviance analysis (ANADEV) and estimates of genetic parameters (individual REML) for characteristics quantified for 12 ecotypes of *Andropogon lateralis* Nees

Parameter	TDM	LDM	L:S	SDM
$DEV_{genotype}$	107.290	51.100	4.190	93.850
$DEV_{complete\ model}$	47.620	−67.710	−148.170	−71.170
LRT (χ^2)	59.670**	118.810**	152.360**	165.020**
$\hat{\sigma}_g^2$	3.005	0.921	0.321	2.466
$\hat{\sigma}_{res}^2$	0.357	0.016	0.002	0.011
$\hat{\sigma}_p^2$	3.362	0.938	0.323	2.477
h_g^2 (±SD)	0.894 (±0.386)	0.983 (±0.404)	0.994 (±0.407)	0.996 (±0.407)
h_{mc}^2	0.971	0.996	0.998	0.999
$\hat{r}_{gg}$	0.985	0.998	0.999	0.999
CV_g (%)	18.303	20.983	48.729	30.592
CV_{res} (%)	6.308	2.782	3.860	1.998
CV_r	2.901	7.541	12.623	15.313
Mean	9.471	4.575	1.162	5.133
Parameter	**NVT**	**NRT**	**NTT**	**PH**
$DEV_{genotype}$	233.780	147.400	236.940	245.730
$DEV_{complete\ model}$	155.420	93.430	170.050	190.050
LRT (χ^2)	78.360**	53.970**	66.890**	55.680**
$\hat{\sigma}_g^2$	56.027	10.295	58.590	68.767
$\hat{\sigma}_{res}^2$	3.546	1.236	5.430	9.403
$\hat{\sigma}_p^2$	59.573	11.532	64.021	78.169
h_g^2 (±SD)	0.940 (±0.395)	0.893 (±0.402)	0.915 (±0.390)	0.880 (±0.382)
h_{mc}^2	0.984	0.971	0.977	0.967
$\hat{r}_{gg}$	0.992	0.985	0.989	0.983
CV_g (%)	42.219	36.200	29.606	19.446
CV_{res} (%)	10.622	12.545	9.013	7.191
CV_r	3.975	2.886	3.285	2.704
Mean	17.729	8.864	25.854	42.645

$\hat{\sigma}_g^2$ - genotypic variance; $\hat{\sigma}_{res}^2$ - residual variance; $\hat{\sigma}_p^2$ - phenotypic variance; h_g^2 - individual heritability in the broad sense; SD - standard deviation; h_{mc}^2 - average heritability of genotype (range); $\hat{r}_{gg}$ - selective accuracy; CV_g - genetic variation coefficient; CV_{res} - residual variation coefficient; CV_r - relative variation coefficient; TDM - accumulated total dry mass; LDM - accumulated leaf dry matter; L:S - leaf:stem ratio; SDM - accumulated stem dry matter; NVT - total number of vegetative tillers; NRT - total number of reproductive tillers; NTT - number of total tillers; PH - plant height.
** Significant at P<0.01 by the Chi-square test (χ^2) with 1 degree of freedom.

Table 3 - Predicted genotypic effect (g), genotypic value (u+g), genetic gains (gain), and new average (X̄ new) for characters studied for ecotypes of *Andropogon lateralis* Nees

| Order	Ecotype	g	u+g	Gain	X̄ new	Order	Ecotype	g	u+g	Gain	X̄ new
	TDM (g plant⁻¹)						LDM (g plant⁻¹)				
5	Alegrete	0.21	9.68	1.24	10.71	10	Alegrete	−0.52	4.05	0.27	4.84
11	Bagé	−0.55	8.92	0.36	9.83	1	Bagé	1.66	6.24	1.66	6.24
7	Caçapava do Sul	−0.19	9.29	0.86	10.33	8	Caçapava do Sul	−0.25	4.33	0.46	5.03
2	Capivari do Sul	1.17	10.64	2.40	11.87	7	Capivari do Sul	−0.19	4.38	0.56	5.13
12	Eldorado do Sul	−3.96	5.52	0.00	9.47	12	Eldorado do Sul	−2.12	2.46	0.00	4.57
6	Mariana Pimentel	0.03	9.50	1.04	10.51	9	Mariana Pimentel	−0.46	4.12	0.36	4.93
3	Montenegro	0.78	10.25	1.86	11.33	2	Montenegro	0.85	5.42	1.26	5.83
9	Passo Fundo	−0.49	8.98	0.56	10.03	5	Passo Fundo	0.09	4.67	0.83	5.40
1	Pelotas	3.63	13.10	3.63	13.10	3	Pelotas	0.83	5.41	1.12	5.69
8	Piratini	−0.47	9.00	0.69	10.17	4	Piratini	0.71	5.29	1.01	5.59
10	Soledade	−0.55	8.92	0.45	9.92	6	Soledade	−0.04	4.54	0.69	5.26
4	Tapes	0.40	9.87	1.49	10.96	11	Tapes	−0.58	3.99	0.19	4.77
	L:S						SDM (g plant⁻¹)				
10	Alegrete	−0.39	0.78	0.09	1.25	5	Alegrete	0.51	5.65	1.42	6.56
1	Bagé	1.61	2.78	1.61	2.78	12	Bagé	−2.47	2.67	0.00	5.13
3	Caçapava do Sul	0.25	1.41	0.74	1.90	7	Caçapava do Sul	−0.18	4.95	1.03	6.16
9	Capivari do Sul	−0.30	0.86	0.14	1.30	3	Capivari do Sul	1.16	6.29	1.95	7.08
8	Eldorado do Sul	−0.28	0.89	0.19	1.36	11	Eldorado do Sul	−2.17	2.96	0.22	5.36
7	Mariana Pimentel	−0.13	1.03	0.26	1.42	6	Mariana Pimentel	0.25	5.38	1.23	6.36
6	Montenegro	−0.12	1.04	0.33	1.49	8	Montenegro	−0.29	4.84	0.86	5.99
4	Passo Fundo	−0.07	1.09	0.54	1.70	9	Passo Fundo	−0.82	4.31	0.67	5.81
5	Pelotas	−0.08	1.08	0.41	1.58	1	Pelotas	2.67	7.80	2.67	7.80
2	Piratini	0.36	1.53	0.99	2.15	10	Piratini	−1.43	3.70	0.46	5.60
11	Soledade	−0.40	0.76	0.04	1.20	2	Soledade	2.02	7.16	2.35	7.48
12	Tapes	−0.45	0.71	0.00	1.16	4	Tapes	0.75	5.88	1.65	6.78
	NVT (n)						NRT (n)				
7	Alegrete	−2.44	15.29	4.49	22	5	Alegrete	0.13	9.00	2.75	12
1	Bagé	16.51	34.24	16.51	34	12	Bagé	−3.51	5.36	0.00	9
10	Caçapava do Sul	−5.39	12.34	1.96	20	8	Caçapava do Sul	−1.81	7.05	1.25	10
6	Capivari do Sul	−0.47	17.26	5.64	23	2	Capivari do Sul	4.02	12.88	5.11	14
11	Eldorado do Sul	−8.84	8.89	0.98	19	9	Eldorado do Sul	−3.27	5.60	0.75	10
12	Mariana Pimentel	−10.81	6.92	0.00	18	10	Mariana Pimentel	−3.27	5.60	0.35	9
9	Montenegro	−3.43	14.30	2.78	21	11	Montenegro	−3.51	5.36	0.00	9
2	Passo Fundo	5.43	23.16	10.97	29	4	Passo Fundo	1.10	9.97	3.41	12
3	Pelotas	5.43	23.16	9.13	27	6	Pelotas	−0.84	8.03	2.16	11
4	Piratini	3.96	21.69	7.83	26	3	Piratini	2.32	11.18	4.18	13
5	Soledade	2.97	20.70	6.86	25	7	Soledade	−1.08	7.78	1.69	11
8	Tapes	−2.93	14.80	3.56	21	1	Tapes	6.20	15.06	6.20	15
	NTT (n)						PH (cm)				
8	Alegrete	−1.57	24.29	4.66	31	2	Alegrete	6.72	49.37	12.30	54.94
1	Bagé	8.45	34.30	8.45	34	11	Bagé	−11.19	31.46	1.09	43.73
10	Caçapava do Sul	−6.45	19.40	2.46	28	3	Caçapava do Sul	6.44	49.08	10.34	52.99
5	Capivari do Sul	4.30	30.15	6.45	32	9	Capivari do Sul	−3.40	39.25	3.12	45.76
11	Eldorado do Sul	−11.34	14.51	1.21	27	12	Eldorado do Sul	−11.97	30.67	0.00	42.64
12	Mariana Pimentel	−13.30	12.56	0.00	26	7	Mariana Pimentel	−1.56	41.08	4.94	47.58
9	Montenegro	−6.21	19.64	3.45	29	10	Montenegro	−4.90	37.75	2.32	44.96
2	Passo Fundo	7.23	33.08	7.84	34	6	Passo Fundo	1.08	43.72	6.02	48.66
4	Pelotas	5.27	31.13	6.98	33	8	Pelotas	−3.10	39.54	3.93	46.58
3	Piratini	6.98	32.84	7.55	33	5	Piratini	1.86	44.50	7.01	49.65
7	Soledade	2.59	28.44	5.55	31	4	Soledade	2.16	44.80	8.30	50.94
6	Tapes	4.05	29.91	6.05	32	1	Tapes	17.87	60.52	17.87	60.52

TDM - accumulated total dry mass; LDM - accumulated leaf dry matter; L:S - leaf:stem ratio; SDM - accumulated stem dry matter; NVT - total number of vegetative tillers; NRT - total number of reproductive tillers; NTT - number of total tillers; PH - plant height.

for TDM, LDM, L:S, and NVT, the ecotypes sourced from the Pelotas, Piratini, Passo Fundo, Bagé, and Montenegro regions were superior to the other ecotypes studied. Based on the most important forage traits, these five ecotypes can be used as potential progenitors in crosses to provide greater genetic gain for forage production in *A. lateralis* Nees.
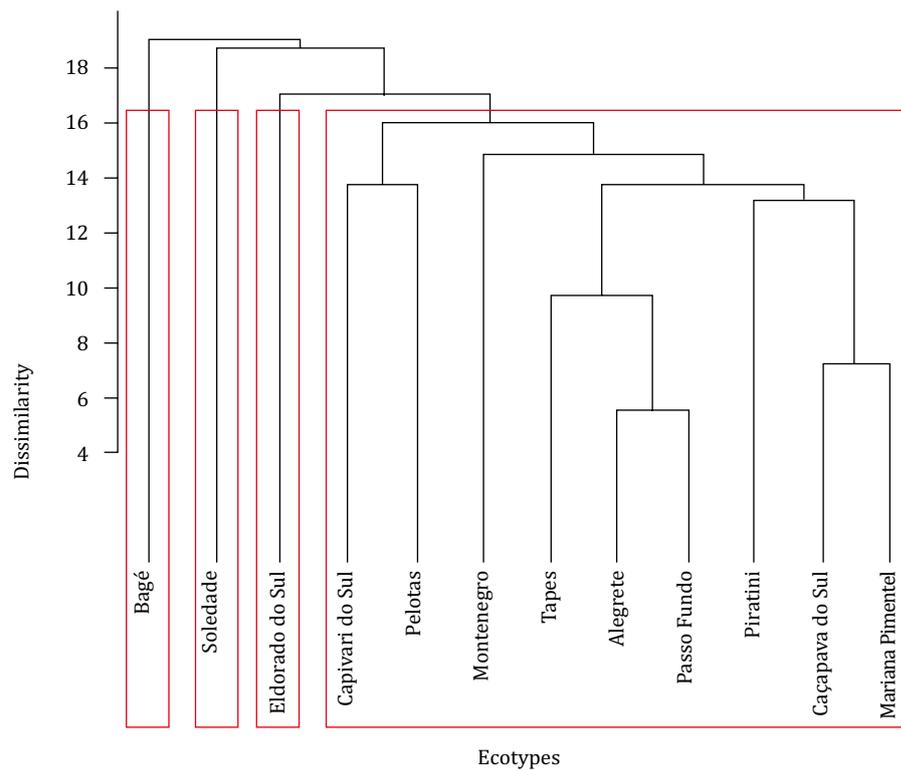
To verify the diversity among the ecotypes of *A. lateralis* Nees, we performed the cluster analysis aiming to identify and select progenitors based on the magnitude of the dissimilarity among the ecotypes. Thus, three types of clusters were used. Cluster analysis by Tocher's optimization method (Figure 3) showed the formation of five groups, with a higher concentration of ecotypes in group I (58.3%). This type of distribution reveals high genetic similarity among ecotypes within the group, and therefore, less variation.

For the crucial forage production traits (TDM, LDM, L:S, and NVT), group II had the highest average TDM (11.94 g plant^{-1}), followed by groups I, IV, and V with 9.51, 8.90, and 8.90 g plant^{-1} for both groups, respectively. Group IV had the highest average LDM (6.25 g plant^{-1}), followed by groups II (4.90), I (4.55), and V (4.54 g plant^{-1}). Group IV had the highest average L:S (2.78) and NVT (35 tillers plant^{-1}). The existence of variability in these traits allows the use of these ecotypes in breeding programs for the species. The greater the distance between ecotypes used as potential parents in future crosses may help explain subsequent heterosis.

The UPGMA evaluation method formed four groups (Figure 4). The highest concentration of ecotypes was in group IV, which accounted for 75% of the total variability of the studied germplasm. Group IV had the highest average TDM (10.1 g plant^{-1}), followed by groups I and II with an average of 8.90 g plant^{-1}. Group I had the highest mean LDM (6.25 g plant^{-1}), followed by groups IV (4.63 plant^{-1}) and II (4.54 plant^{-1}). Group I also had superior L:S (2.78), followed by groups IV (1.06) and III (0.98). Additionally, group I had the greatest NVT (35 vegetative tillers plant^{-1}), followed by groups II (21) and IV (17). Based on these results, the multivariate analysis by the hierarchical UPGMA indicated variability and made it possible to select promising parents in future crosses. This analysis showed (Figure 3) the Bagé and Soledade ecotypes to have greater genetic divergence (22.1), while the Alegrete and Passo Fundo ecotypes were more genetically similar (5.5). The cophenetic correlation matrix showed moderate correlation (r = 0.69), but lower distortion (3.13) and stress (17.7).
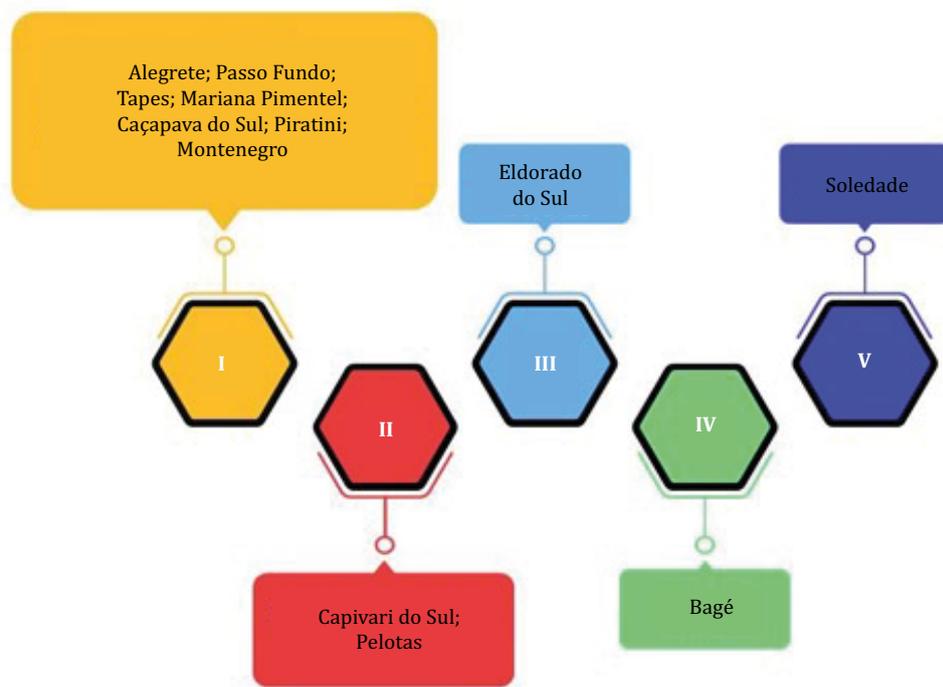
Figure 3 - Composition of groups formed by the graphical Tocher's optimization method in *Andropogon lateralis* Nees, based on the Mahalanobis genetic distance (D^2) matrix.

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Figure 4 - Dendrogram of dissimilarity among 12 ecotypes of *Andropogon lateralis* Nees, obtained by the UPGMA method, based on the Mahalanobis genetic distance (D^2) matrix.
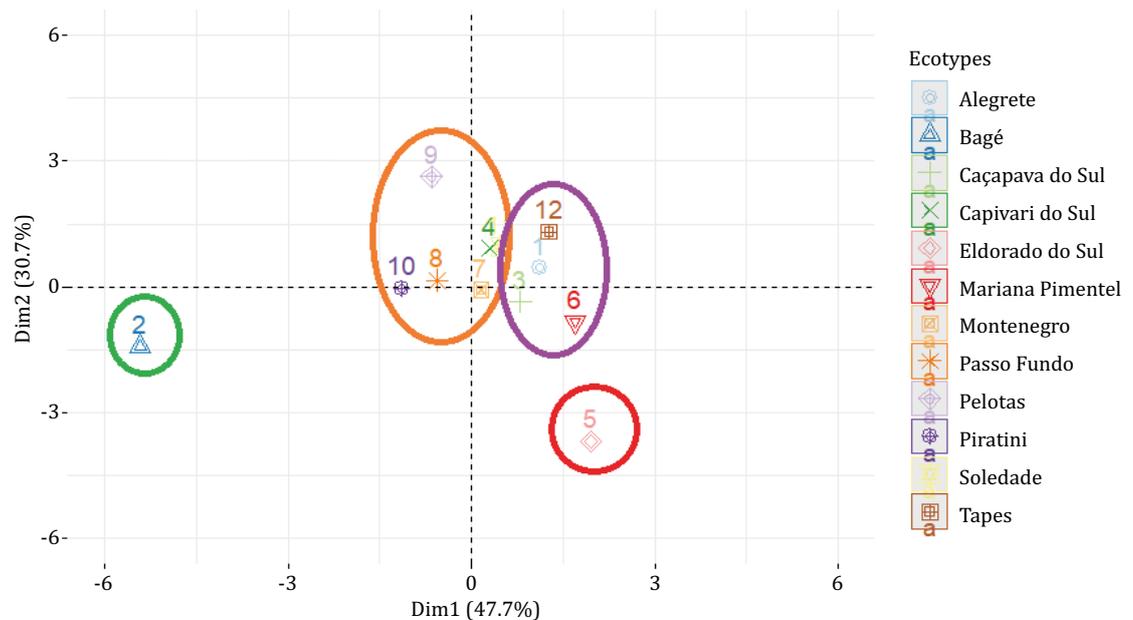
Orange circle: group I (Pelotas, Piratini, Passo Fundo, Montenegro, Capivari do Sul, and Soledade ecotypes), accounting for 50% of the genetic diversity; purple circle: group II (Alegrete, Caçapava do Sul, and Mariana Pimentel ecotypes), which accounted for 33% of genetic diversity; green circle: isolated group (Bagé ecotype); red circle: isolated group (Eldorado do Sul ecotype).

Figure 5 - Dispersion graph of the ecotypes in the first two principal components (PC).

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The forage characteristics distributed in the first two main components (PC1 and PC2) explained 78.5% of the total variation of the data (Figure 5; Table 4). The formation of four homogeneous and heterogeneous groups was observed through the PCA (Figure 5) and was similar to the grouping derived from the UPGMA method (Figure 4). Group I held 50% of the genetic diversity among the studied germplasm and was composed of the Pelotas, Piratini, Passo Fundo, Montenegro, Capivari do Sul, and Soledade ecotypes (orange circle). Group II had 33% of the variability and included the Tapes, Alegrete, Caçapava do Sul, and Mariana Pimentel ecotypes (purple circle).

The Bagé (green circle) and Eldorado do Sul (red circle) ecotypes formed isolated groups, which was similar to the pattern found via the Tocher (Figure 3) and UPGMA (Figure 4) methods. The characteristics NVT, L:S, NRT, and LDM, evaluated by PCA, accounted for 80.6% of the observed variation of PC1 (Table 4). In contrast, TDM, SDM, PH, and NTT represented 83.5% of observed variation within PC2. This reinforced the importance of these characteristics in the study of genetic diversity. The characteristics PH, NTT, and TDM accounted for 84.2% of the total variation in PC3. The other components (PC4, PC5, PC6, PC7, and PC8) suggested that PH, NRT, TDM, L:S, and NVT can be discarded from the study of genetic diversity.

Table 4 - Variables, principal components (PC), estimates of variances (eigenvalue λj), percentage of variance explained by components (importance %), and accumulated variance (accumulated %) of ecotypes of *Andropogon lateralis* Nees

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
TDM	0.57	31.65	16.70	5.11	0.42	39.32*	0.97	5.24
LDM	17.43	6.87	5.31	7.65	20.85	29.40	7.33	5.16
L:S	21.19	3.64	0.22	14.04	0.08	1.28	58.34*	1.20
SDM	3.65	28.27	7.23	2.95	28.28	14.88	10.44	4.29
NVT	21.98	2.63	3.04	11.75	0.51	4.69	0.52	54.88*
NRT	20.00	3.35	0.02	3.98	47.57*	0.63	22.35	2.09
NTT	11.17	11.45	21.93	19.75	1.37	8.80	0.03	25.51
PH	4.00	12.15	45.55	34.77*	0.91	0.99	0.01	1.62
λj	3.82	2.46	0.82	0.49	0.26	0.09	0.05	0.01
Importance (%)	47.73	30.72	10.28	6.14	3.21	1.13	0.62	0.18
Accumulated %	47.73	78.45	88.73	94.87	98.08	99.20	99.82	100.00

TDM - accumulated total dry mass; LDM - accumulated leaf dry matter; L:S - leaf:stem ratio; SDM - accumulated stem dry matter; NVT - total number of vegetative tillers; NRT - total number of reproductive tillers; NTT - number of total tillers; PH - plant height.
* According to the criterion of Jolliffe (1972).

4. Discussion

This study confirmed the effectiveness of quantified selection in relation to all the characteristics analyzed. Additionally, within the population under study, there is a significant level of genetic variability, which arises from the genetic variations observed among the evaluated ecotypes. Analysis of h_g^2 explains to what extent the genotype is expressed by the phenotype (Flôres Júnior et al., 2021). In our study, both h_g^2 were considered high (Table 2) according to Resende's (2015) criteria. Heritability is a genetic coefficient that expresses the relationship between genotypic and phenotypic variance. It is one of the most important genetic parameters for plant breeders and guides, in part, the progress of the genetic improvement program. The most important function of heritability in the genetic study refers to its predictive role, expressing the confidence of the phenotypic value as a guide for the genetic value or the degree of conformity between the phenotypic value and the genetic value.

The relative coefficient of variation (CV_r) quantifies the extent of genetic variation within the studied population (Silva et al., 2020). When the CV_r is close to or greater than 1, the available genetic variation is responsible for the estimated variation (Leite et al., 2016; Facchinello et al., 2021), which indicates a favorable situation in the selection process (Silveira et al., 2022). Indeed, selecting for traits of forage interest such as TDM, LDM, and NVT can prove to be effective in introducing agronomically important forage traits among different ecotypes of *A. lateralis* Nees (Table 2). The results reported here confirm

the pattern obtained in previous studies carried out with genus *Paspalum*, where TDM also made genotype discrimination possible (Pereira et al., 2012; Cavalcante et al., 2019). The TDM affects the rate of forage intake by grazing animals (Azambuja Filho et al., 2020), while ecotypes that exhibit superior LDM are important for plant breeding, because leaf blade material is preferred for intake by grazing livestock (Machado et al., 2019). This is confirmed by previous work that showed that cattle exhibited selective grazing preference for the intake of *A. lateralis* Nees leaf blades (Confortin et al., 2017). Ultimately, this variable will be directly associated with the nutritive value of the diet consumed by grazing animals (Hodgson, 1990). In the pastoral environment, NVT is directly related to primary production (forage production) (Machado et al., 2021) and contributes to the persistence of forage species (Volenec and Nelson, 1983; Sbrissia et al., 2010) and production of a diet of high nutritional value to animals, because it includes tillers in vegetative stage. Selective accuracy ($\hat{r}_{gg}$) supports the theory that selection for any of the characteristics studied would be effective within the set of ecotypes evaluated (Table 2). It represents the quality of the results obtained through statistical procedures and applied to assume genetic values (Cavalcante et al., 2019) and is associated with both selection precision and the correlation between predicted versus true genetic values of ecotypes (Pimentel et al., 2014). Therefore, it is an important genetic parameter for inclusion in plant breeding programs and will help accurately quantify the true genetic variability of the population being evaluated.

The findings of this study demonstrated that enhancing forage production in *A. lateralis* Nees can be achieved through direct selection based on the TDM trait. This particular trait is advantageous due to its ease of selection and shorter time requirement, thereby reducing the overall selection time. However, in cases where the TDM trait exhibits less favorable genetic parameters, indirect selection using LDM and NVT emerges as a promising strategy for augmenting forage production. By focusing on these alternative traits, which display a stronger correlation with forage production, it becomes possible to expedite genetic progress in *A. lateralis* Nees. Based on selection via BLUP, the Pelotas, Piratini, Passo Fundo, Bagé, and Montenegro ecotypes can be used as progenitors for genetic gain to increase forage production (Figure 3). Methodologies that allow evaluation of genetic parameters concomitantly with the prediction of possible genetic gains via selection, in combination with knowledge of the genetic control of the characteristics of interest, is fundamental to create more effective improvement strategies for plant breeders (Farias Neto, 2013; Lustri et al., 2021). Furthermore, a better genetic gain response for each characteristic can be obtained by choosing the most suitable selection pressure (Facchinello et al., 2021), without reducing genetic variability.

Using three different methods to estimate the genetic diversity, the Tocher method (Figure 3) was able to separate the 12 ecotypes evaluated into a greater number of groups compared with UPGMA (Figure 4) or PCA (Figure 5) methods. Differences in the distribution of groups are a determining factor in the choice of parents and the difference in heterotic potential (Sant'Anna et al., 2021). Understanding genetic diversity available within naturally occurring ecotypes is important for a number of purposes, particularly genetic conservation and potential species improvement for desirable traits (Namazzi et al., 2020). Furthermore, by gaining more knowledge about the biological and ecological factors that can affect the distribution of genetic diversity among, and within, populations of a given species over time and space are fundamental for the successful implementation of management and conservation strategies (Liddell et al., 2020). This information is especially important for grasses from the Pampa biome, such as *A. lateralis* Nees, which is present in the upper stratum of the natural grasslands in southern Brazil (Barros et al., 2022). Methods that increase our knowledge of the extent of existing diversity within a species, combined with the understanding of biological and ecological factors that govern ecotype distribution, form the fundamental basis for the formulation of solid strategies for germplasm conservation. This information may also help identify *in situ* conservation sites and contribute to the formulation of sampling strategies for conservation collections *ex situ*, which require in-depth knowledge of the diversity and genetic structure of the species present (Falk and Holsinger, 1991; Hogbin and Peakall, 1999).

Overall, Tocher's method gathers a large number of ecotypes in the first groups, mainly because it uses a single distance criterion, and the average within the groups is always lower than the average

among the groups (Vasconcelos et al., 2007). The use of this technique in genetic diversity studies is important because it identifies genetically different genotypes and not just groups (Pereira et al., 2019). Correct quantification of genetic diversity by the UPGMA and Tocher's method requires the most appropriate genetic dissimilarity matrix to be selected (Sant'Anna et al., 2021). Generally, in replicated experiments, the D^2 is most commonly used. Quantification of the distance between genotypes allows an overview of the phenotypic similarities, which allows the interpretation of possible dissimilarities existing within all evaluated characteristics (Łopatyńska et al., 2021). Of the hierarchical methods, the cophenetic correlation coefficient (Figure 4) identified which dissimilarity matrix was most appropriate. It also lowered the distortion and stress, which minimized the deformation of the dendrogram. The PCA method has previously been used to characterize accessions within germplasm banks for species including *Urochloa* (Namazzi et al., 2020), *Emmenopterys henryi* Oliv (Niu et al., 2021), *Passiflora* spp. (Jesus et al., 2022), *Pinus bungeana* (Tian et al., 2022), *Glycyrrhiza uralensis* (Dang et al., 2022), and *Zea mays* L. (Badu-Apraku et al., 2021). This technique allows the most important traits for diversity studies and promising genotypes for crosses to be identified (Oliveira Neto et al., 2021).

Clustering methods predict the possible heterosis to be obtained. As heterosis is the result of genetic divergence between parents and the occurrence of dominance effects, it is expected that the greater genetic distance between the parents will result in greater hybrid vigor in the F1 generation (Colombari Filho et al., 2010). This analysis has grouped ecotypes that exhibited similar forage characteristics. The results offer the opportunity to select within a group for maintenance and/or across groups to select genotypes that have higher productivity. In genetic diversity studies, the use of two or more methods should be encouraged and prioritized to test the consistency of the clusters identified. Different methodologies provide different types of information, and therefore the choice of method in the study of genetic diversity depends on the objective of the experiment. In general, the results of the clustering methods studied here were efficient in the characterization of genetic diversity among the ecotypes evaluated. The UPGMA method, Tocher's optimization method, and principal component analysis were complementary in the formation of groups.

It was evident that, due to its high genetic variability, a strategy for breeding in this species would be the selection and recombination of genotypes with the best agronomic characteristics. The results reported here are unique as there are currently no studies on genetic parameters for this species. There is also little published literature on seed production and genetic variability for *A. lateralis* Nees. Forage production is a quantitative character of a complex nature. It is a result of many individual factors, and their respective interactions. Our results also demonstrate there is high potential for selection of agronomically important forage characteristics by exploiting the naturally occurring genetic variation among existing ecotypes. Selection should not be based only on genetic divergence because it is necessary to consider the performance of each ecotype for its intended purpose and within its target environment. Therefore, the selection of parents must be based on high performance in traits of importance to the breeding program.

5. Conclusions

Genetic parameters estimated through REML indicated the presence of high genetic variability in *A. lateralis* Nees ecotypes and the potential for exploitation of heterosis. The high heritability and selective accuracy observed for forage characteristics offers potential for selection of superior ecotypes.

The Pelotas, Piratini, Passo Fundo, Bagé, and Montenegro ecotypes showed superior forage production using the BLUP methodology. Therefore, this group is the most suitable for selection and crossing purposes.

The NTT, L:S, NRT, and LDM accounted for 78.4% of the total observed variation in the first two principal components. These are important characteristics for yield and quality of the feed produced and species persistence, and help discriminate among ecotypes.

Tocher's cluster analysis grouped the ecotypes into five divergent groups. The principal components method and the UPGMA hierarchical method were also efficient at separating the ecotypes.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Conceptualization: Silveira, D. C.; Simioni, C. and Dall'Agnol, M. **Data curation:** Silveira, D. C. **Formal analysis:** Silveira, D. C. **Funding acquisition:** Weiler, R. L. and Dall'Agnol, M. **Investigation:** Sampaio, R.; Valentini, A.; Santos, W. M.; Longhi, J.; Nauderer, C.; Machado, J. M.; Simioni, C.; Brunes, A. P.; Weiler, R. L. and Dall'Agnol, M. **Methodology:** Simioni, C.; Weiler, R. L. and Dall'Agnol, M. **Project administration:** Dall'Agnol, M. **Supervision:** Dall'Agnol, M. **Visualization:** Brunes, A. P. **Writing – original draft:** Silveira, D. C.; Machado, J. M.; Mills, A.; Brunes, A. P. and Dall'Agnol, M. **Writing – review & editing:** Silveira, D. C.; Machado, J. M.; Mills, A. and Dall'Agnol, M.

Acknowledgments

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