Efficiency of indirect selection for green biomass production of *Urochloa ruziziensis*

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Abstract: *We aimed to measure the efficiency of visual selection of plant vigor for green biomass production of U. ruziziensis using single- and multitrait approaches to maximize the predictive accuracy of the genetic value. The green biomass production and plant vigor of 254 U. ruziziensis clones were measured over nine evaluation cuttings to determine the efficiency of these approaches for production improvement. Individual and multicutting analyses were performed under single-trait and multitrait approaches using mixed models. The efficiency of visual selection was assessed by measuring plant vigor based on direct and indirect genetic gains. Plant vigor showed a high genetic association with green biomass and could be selected for production, especially in the initial phases of breeding programs. The multitrait approach was superior to the single-trait approach in predicting the genetic value of the clones, and it can be used in U. ruziziensis breeding programs.*

Keywords: Brachiaria ruziziensis, *visual selection, mixed models, accuracy*

INTRODUCTION

Tropical forages of the genus *Urochloa* play a key role in raising Brazilian livestock, since these forages are used for direct grazing across an area of approximately 100 million hectares, which corresponds to approximately 90% of Brazilian cultivated pastures (Simeão et al. 2016). One of the species cultivated in Brazil, *Urochloa ruziziensis* (R. Germ. and C.M. Evrard) Crins (synonym *Brachiaria ruziziensis*), is a diploid species that can be sexually or clonally reproduced and has great potential as pasture due to its high nutritional quality and great value for pasture diversification (Pessoa-Filho et al. 2015).

The aim of the breeding programs is mainly to achieve a cultivar production capacity that is higher than those already on the market, since forage production is one of the most important traits to be considered in selection (Mauri et al. 2019). In forage crops, selection for green biomass production and other complex traits should be performed based on multiple cuttings. According to Souza Sobrinho et al. (2010), the number of cuttings necessary to assess the actual value of the traits with a coefficient of determination greater than 80% ranged between 7–8 for green biomass production. Thus, selection based on visual criteria, such as plant vigor, may be a good approach to identify forage mass production, as plant vigor has a strong association with forage production. In addition, selection based on visual criteria is a practical, fast, nondestructive,
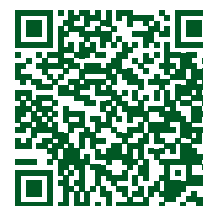
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and accessible method, which allows the evaluation of many genotypes (Silva et al. 2016). For crops such as *Urochloa decumbens*, red clover, and *Panicum virgatum* L., indirect preliminary selection for forage production has been shown to be as accurate as direct measurements for production (Costa et al. 2009, Riday 2009, Casler and Vogel 2014). For *Urochloa ruziziensis*, visual selection through plant vigor showed moderate to high efficiency in relation to direct selection strategies for green biomass production (Teixeira et al. 2020) and can be used especially in the early stages of breeding programs, where a large number of genotypes are evaluated.

Due to the complexity of the data derived from forage breeding programs, the statistical methods used need to be accurate, efficient and informative; they must also consider the spatial variation and temporal correlation between the repeated measures in addition to appropriately modeling the genetic effects over time (De Faveri et al. 2015). An approach that is used to address the complexity of the data generated in breeding programs is linear mixed models, which have been successfully used in animal, annual and perennial crop, and forage crop breeding programs (Andrade et al. 2016, Alves et al. 2018). An important aspect of linear mixed models is the ability to analyze the different traits evaluated during breeding programs via both univariate (single-trait) and multivariate (multitrait) models (Balsalobre et al. 2016).

Although the use of visual selection in the breeding of forage plants can be considered an accessible and low-cost method, its efficiency for the selection of superior genotypes for green biomass production via single-trait and multitrait approaches still needs to be investigated. Therefore, we aim to measure the efficiency of visual selection of plant vigor for green biomass production of *U. ruziziensis* and verify which approach maximizes the predictive accuracy of the genetic value.

MATERIAL AND METHODS

Data and experimental design

The experiment was conducted at the Embrapa Dairy Cattle Experimental Field (lat 21º 33' S, long 43º 06' W, alt 410 m asl) in Coronel Pacheco, Minas Gerais, Brazil. According to the Köppen classification, the climate of this region, with an annual mean temperature of 22.5 °C and mean rainfall of 1,600 mm, is of the Cwa type. The soil in the experimental area is classified as alic red-yellow Argisol (Santos et al. 2018).

A total of 254 *U. ruziziensis* clones derived from the breeding program of Embrapa Dairy Cattle, along with the cultivars Marandu (*U. brizantha*) and Basilisk (*U. decumbens*) as controls, were evaluated using a 16 x 16 lattice design with three replications. Single plant plots were spaced 1 m apart.

Two months after planting, a standardization cutting was performed, and nine evaluation cuttings were carried out (at 10 cm height in relation to the soil) on the following dates: 09/01/2013; 05/02/2013; 27/03/2013; 06/06/2013; 05/09/2013; 23/10/2013; 16/12/2013; 24/02/2014; 29/04/2014. Cuttings 1, 2, 3, 7, 8, and 9 were carried out in the wet season, while Cuttings 4, 5, and 6 were carried out in the dry season. The following traits were measured for each cutting: plant vigor (vigor), for which biomass yield, sanity and architecture before each cutting were considered using a score scale from 1 to 5: 1 – very poor; 2 – poor; 3 – fair; 4 – good; 5 – very good (Teixeira et al. 2020), and green biomass production (green biomass). The plots were cut and weighed on a portable digital scale (g plot^{-1}).

Statistical-genetic analyses

The data analyses were performed using a mixed-model methodology that included the estimation of fixed effects using the empirical best linear unbiased estimator (E-BLUE) and prediction of the random effects using the empirical best linear unbiased prediction (E-BLUP) with the solution of the system of equations according to Henderson (1975). The variance components were estimated using the residual maximum likelihood (REML) method (Patterson and Thompson 1971).

Initially, single-trait analyses per cutting were performed using the following model:

$$y = X_{\beta}\beta + X_b b + Z_g g + e \qquad [1]$$

where *y* is the vector of the phenotypic data for each cutting; β is the vector of fixed effects (intercept and replications); *b* is the vector of the random effects of blocks within replications, with $b \sim MVN(0, I_b\sigma_b^2)$; *g* is the vector of the random

effects of the clones, with $g \sim MVN(0, I_g \sigma_g^2)$; e is the vector of the residual errors, with $e \sim MVN(0, I_n \sigma_e^2)$; X_β is the incidence matrix for the fixed effects, and Z_b and Z_g are the incidence matrices for the random effects; and I is the identity matrix of the order appropriate for the respective random effect.

The multitrait analyses for the two traits in each cutting were performed according to the following model:

$$y = X\beta + Z_1 b + Z_2 g + e \qquad [2]$$

where y is a vector of the phenotypic data of the traits $y^t = [y_1, y_2]$; β is the vector of the fixed effects (intercepts and replications) for the traits; b is the vector of the random effects of blocks within replications for the traits, with $b \sim MVN(0, \sum_b)$; g is the vector of the random effects of the clones for the traits, with $g \sim MVN(0, \sum_g)$; e is the vector of the residual errors for the traits, with $e \sim MVN(0, \sum_e)$; and X is the incidence matrix for the fixed effects, and Z_1 and Z_2 are the incidence matrices for the random effects, respectively. An unstructured covariance structure (US) was assumed for the covariance matrices $\sum_b$, $\sum_g$ and $\sum_e$.

The multicutting analyses for each trait were performed using the model according to Smith et al. (2007):

$$y = X_\theta \theta + Z_b b + Z_g g' + \varepsilon \qquad [3]$$

where y is the vector of the phenotypic observations; θ is the vector of the fixed effects, which is comprised of the effects of replications, cuttings, and their interactions and are added to the intercept; b is the vector of the random effects of the blocks within repetitions of the cuttings, with $b \sim MVN(0, I_b \sigma_b^2)$; g is the vector of the random effects of the clones within the cuttings, with $g' \sim MVN(0, G)$; e is the vector of the residual errors, with $e' \sim MVN(0, R)$; and X_θ is the incidence matrix for the fixed effects, and Z_b and Z_g are the incidence matrices for the random effects, respectively.

In the multicutting analyses for green biomass production and plant vigor, different covariance structures were tested for the residual (R) and genetic (G) matrices, from simple structures such as compound symmetry to more complex structures such as US (Smith et al. 2007, De Faveri et al. 2015, Andrade et al. 2016). To choose the ideal structure for the R and G matrices, the Schwarz information criterion, which is also known as the Bayesian information criterion (BIC), was used. The best models were those with the lowest BIC values. The best structure for the R matrix was first chosen, and then, the best structure was identified for G by using the best structure identified for R (Smith et al. 2007, De Faveri et al. 2015, Andrade et al. 2016). The structures that resulted in convergence problems were removed from further analyses.

The covariance structure for R is $R = R_h \otimes I_n$, in which R_h is the residual covariance matrix that accommodates the temporal correlation between the cuttings and the possible presence of heterogeneity of variance between the cuttings for each plot, and I_n is the identity matrix of size $n \times n$, where n is the number of plots. The covariance structure for G is $G = G_h \otimes I_g$, where G_h is the genetic covariance matrix for cuttings, and I_g is an identity matrix of size $g \times g$, where g is the number of clones.

The multitrait and multicutting analysis for the two traits was performed according to the following model:

$$y = X\theta + Z_1 b + Z_2 g' + \varepsilon \qquad [4]$$

where y is the vector of the phenotypic data of the traits $y^t = [y_1, y_2]$; θ is the vector of the fixed effects, which are comprised of the effects of replications, cuttings, and their interactions; b is the vector of the random effects of the blocks within replications, with $b \sim MVN(0, \sum_b)$; g' is the vector of the random effects of the clones within the cuttings, with $g' \sim MVN(0, \sum_g)$; ε is the vector of the residual errors, with $\varepsilon \sim MVN(0, \sum_\varepsilon)$; and X is the incidence matrix for the fixed effects, and Z_1 and $+ Z_2$ are the incidence matrices and random effects. The covariance structures for the residual ($\sum_\varepsilon$) and genetic ($\sum_g$) effects that best fit the data were tested and chosen using the BIC.

In the single-trait [3] and multitrait [4] analyses for multiple cuttings, the E-BLUPs of all clones were estimated according to Smith et al. (2007): $E - BLUP = \sum_h w_h \widetilde{g_{1h}}$, where $\widetilde{g_{1h}}$ is the E-BLUP of clone i within cutting h, and w_h is the assigned weight of each cutting, with $w_h = 1/m$, where m is the number of cuttings. From the results of the single-trait [1] and multitrait [2] analyses for each cutting, the clone mean-based heritability was determined according to Cullis et al. (2006): $h^2 = 1 - \frac{\overline{v}_\Delta^{BLUP}}{2\overline{\sigma}_{g'}^2}$, where $\overline{v}_\Delta^{BLUP}$ is the variance of the pairwise mean prediction error of the effects of clones, and $\overline{\sigma}_{g'}^2$ is the mean genetic variance of the clones along the cuttings, which was obtained from the mean of the genetic

components for each cutting. The selective accuracy ($\hat{r}_{\hat{g}g}$) was estimated according to $\hat{r}_{\hat{g}g} = \sqrt{1 - \dfrac{\overline{PEV}}{\sigma^2_{g'}}}$, where $\overline{PEV}$ is the mean variance of the prediction error (Resende and Duarte 2007).

Efficiency of multitrait analysis and estimation of genetic and residual correlations

The relative efficiency (RE) of the multitrait approach over the single-trait approach was estimated according to Almeida Filho et al. (2016): $RE(\%) = \dfrac{\hat{r}_{\hat{g}g(m)} - \hat{r}_{\hat{g}g(s)}}{\hat{r}_{\hat{g}g(s)}} \times 100$, where $\hat{r}_{\hat{g}g(m)}$ and $\hat{r}_{\hat{g}g\ (s)}$ are the estimates of selective accuracy in multitrait and single-trait analyses, respectively.

To verify the association between the traits, the genetic ($r_{g(y_1y_2)}$) and residual ($r_{e(y_1y_2)}$) correlations were estimated by multitrait analysis (Falconer and Mackay 1996): $r_{g(y_1y_2)} = \dfrac{\sigma_{g_{y_1y_2}}}{\sqrt{\sigma^2_{g_{y_1}} \times \sigma^2_{g_{y_2}}}}$ and $r_{e(y_1y_2)} = \dfrac{\sigma_{e_{y_1y_2}}}{\sqrt{\sigma^2_{e_{y_1}} \times \sigma^2_{e_{y_2}}}}$, where $\sigma^2_{g_{y_1y_2}}$ and $\sigma^2_{e_{y_1y_2}}$ are the genetic and residual covariances, respectively, between the performance of the clones for traits y_1 and y_2; $\sigma^2_{g_{y_1}}$ and $\sigma^2_{g_{y_2}}$ are the genetic variances of traits y_1 and y_2, respectively, in the clones; and $\sigma^2_{e_{y_1}}$ and $\sigma^2_{e_{y_2}}$ are the residual variances of traits y_1 and y_2, respectively, in the clones.

Efficiency of indirect selection for green biomass

Based on the results obtained from the joint analyses of the single-trait and multitrait approaches, the 26 best clones (selection fraction of 10%) were selected for both traits to estimate the following parameters: I) Direct and indirect expected selection gain for green biomass and plant vigor when selection was performed according to plant vigor. For the estimates of direct and indirect gains, the absolute genetic selection (GS) gain was estimated by the E-BLUP mean of the 26 clones that were selected, and the relative genetic selection (GS%) gain was calculated by dividing the absolute gain by the overall mean. II) Spearman's correlation was calculated between E-BLUP values. Significance was verified using nonparametric bootstrapping with the boot package in R software (Cathy and Ripley 2019); III). The index of coincidence (IC%) was determined between the best clones (selection intensity of 10%) of the two traits, according to Hamblin and Zimmerman (1986): $IC = \dfrac{A - C}{B - C} \times 100$, where A is the number of coincident clones among the 26 best selected in each trait; B is the number of clones selected in Case 26; and C is the number of clones selected due to chance (in this case, 10% of B). All analyses were performed in R 3.3.2 with the ASReml 4.0 package (R Core Team 2016, Butler et al. 2017).

RESULTS AND DISCUSSION

The heritability and selective accuracy values were moderate to high for the two evaluated traits (Table 1). In all the evaluated cuttings, the highest estimates of these parameters were obtained for plant vigor in both prediction methods.

Table 1. Estimates of mean green biomass (GM), mean plant vigor (vigor), mean heritability of green biomass and vigor (h^2), and selective accuracy of green biomass and vigor ($\hat{r}_{g\hat{g}}$) in the single-trait and multitrait analyses and the relative efficiency of the multitrait analysis (*RE*) over nine evaluation cuttings of *U. ruziziensis*

Cuttings	Overall mean		Single-trait				Multitrait					
			Green biomass		Vigor		Green biomass			Vigor		
	GM	Vigor	h^2	$\hat{r}_{g\hat{g}}$	h^2	$\hat{r}_{g\hat{g}}$	h^2	$\hat{r}_{g\hat{g}}$	RE (%)	h^2	$\hat{r}_{g\hat{g}}$	RE (%)
1	1696.71	2.51	0.46	0.68	0.52	0.72	0.52	0.72	6.02	0.53	0.73	1.14
2	1087.64	3.12	0.55	0.74	0.69	0.83	0.65	0.80	8.21	0.69	0.83	0.09
3	1666.99	3.02	0.56	0.74	0.66	0.81	0.61	0.78	5.20	0.66	0.81	0.18
4	1124.88	2.72	0.53	0.72	0.62	0.79	0.58	0.76	5.47	0.62	0.78	-0.23
5	1153.98	2.67	0.56	0.75	0.61	0.78	0.59	0.77	2.07	0.62	0.79	0.30
6	1655.07	3.28	0.45	0.67	0.61	0.78	0.50	0.71	5.52	0.62	0.79	0.66
7	1759.34	3.18	0.23	0.48	0.49	0.70	0.42	0.65	35.96	0.50	0.71	1.10
8	1026.46	2.73	0.36	0.60	0.45	0.67	0.38	0.61	2.31	0.46	0.68	1.46
9	1186.12	3.06	0.29	0.54	0.56	0.74	0.43	0.66	21.63	0.56	0.75	0.31

The lower estimates for green biomass may be due to the large effect of the environment and genetic architecture, which are more complex (Gouveia et al. 2021). In general, there was an increase in the estimates of heritability and selective accuracy, especially for green biomass, in the multitrait approach. Moreover, increases in these estimates were more pronounced in Cuttings 7 and 9, which had lower reliability (Table 1).

For all cuttings, the genetic correlations between the traits were positive and strong, ranging from 0.80 (Cutting 8) to 0.96 (Cutting 1), which indicated the existence of a high association between the traits. The residual correlations were positive and ranged from 0.58 (Cutting 9) to 0.81 (Cutting 8), showing that the environment affected the traits in the same direction. The genetic correlation between the traits may be due to pleiotropy and/or linkage of the genes that control the traits (Falconer and Mackay 1996, Schaid et al. 2016). In the evaluation of the visual criteria, plant vigor showed a high association with green biomass and dry mass (Borges et al. 2012, Fonseca et al. 2020, Teixeira et al. 2020). The evaluation of plant vigor, which is easy, simple, and fast, may be less affected by the environment. Therefore, visual criteria are an interesting approach to enable indirect selection for forage production (Edvan et al. 2016, Dos Santos et al. 2018). The relative efficiency (RE) of the multitrait analysis for green biomass ranged from 2.31% to 35.96%, while for plant vigor, the RE was lower, with a range from 0.09% to 1.46% (Table 1). Thus, the genetic and residual correlations were beneficial to increasing the selection accuracy and heritability using a multitrait approach.

In the multicutting analyses, the choice of the covariance structure for genetic and residual effects was carried out based on the BIC to find a parsimonious model with goodness of fit. The ante-dependence (ANTE) matrix best fit the residual effects, and the heterogeneous first-order autoregressive (AR1H) structure best fit the genetic effects in the single-trait analyses for green biomass and plant vigor. In the multitrait analysis, the model that best fit the data had a first-order autoregressive (AR1) structure for the genetic and residual effects.

The clone mean-based heritability and selective accuracy provided by the joint analysis were high. Lower estimates were observed for green biomass than for plant vigor in the single-trait and multitrait analyses (Table 2). When comparing the two prediction methods, the multitrait analysis provided an increase in the estimates of these parameters for both traits, especially for green biomass, where the efficiency of the multitrait analysis was 8.47% higher than that of the single-trait analysis. The genetic correlation between the traits was positive and high (0.96), which demonstrates that an increase in plant vigor results in an increase in green biomass. The residual correlation was positive (0.54), which showed that the environment also affected the traits (Table 2).

The multitrait approach proved to be an important tool to maximize genetic gains and estimate heritability and selective accuracy. In this approach, the genetic and residual correlations between traits are used to estimate the genetic value. Therefore, the efficiency of the method may be related to the correlation between traits and heritability estimates (Ematné et al. 2018).

According to Piepho et al. (2008), the multitrait approach is more advantageous when the traits are highly correlated and have low to moderate heritability. In contrast, according to Bauer and Léon (2012), the advantage of the multitrait approach may be greater when the traits are negatively correlated, since selection based on multitrait analysis should provide opportunities for simultaneous gains in both traits, providing greater gains from selection. Thus, when the heritability estimates are similar, the traits that are favorably correlated and the values of genetic and residual correlations are similar, the adoption of the multivariate model may not provide an increase in the predictive accuracy of the genetic value (Volpato et al. 2019).

The estimates of direct and indirect genetic gains demonstrated that the multitrait approach was superior to the single-trait approach for both traits (Table 3). The largest increase was in green biomass, with an increase of 2.14% in

Table 2. Overall mean green biomass (GM) and plant vigor (vigor), genetic (r_g) and residual (r_e) correlations between traits, mean heritability of green biomass and vigor (h^2), selective accuracy of green biomass and vigor ($\hat{r}_{g\hat{g}}$) in the single-trait and multitrait analyses for multiple cuttings, and relative efficiency of the multitrait analysis (RE) in *U. ruziziensis*

Traits	Overall mean	r_g	r_e	Single-trait		Multitrait		
				h^2	$\hat{r}_{g\hat{g}}$	h^2	$\hat{r}_{g\hat{g}}$	*RE* (%)
GM	1373.70	0.96	0.54	0.63	0.80	0.76	0.87	8.47
Vigor	2.92			0.72	0.85	0.78	0.88	4.28

Table 3. Estimates of direct and indirect absolute genetic selection (GS) and relative genetic selection (GS%) gain of the top 26 best *U. ruziziensis* clones (selection fraction of 10%) in the single-trait and multitrait analyses for multiple cuttings for green biomass (GM) and plant vigor (vigor)

Genetic gain	Single-trait				Multitrait			
	Direct		Indirect		Direct		Indirect	
	GM	Vigor	GM		GM	Vigor	GM	
GS	353.86	0.51	278.12		383.22	0.57	369.31	
GS (%)	25.76	17.58	20.25		27.90	19.35	26.88	

Table 4. Spearman correlation between E-BLUPs and the coincidence index (IC%) between the best *U. ruziziensis* clones for green biomass (GM) production and plant vigor (vigor) in the single-trait (ST) and multitrait (MT) analyses for multiple cuttings

Correlation	GM-ST	Vigor-ST	GM-MT	Vigor-MT
GM-ST	1	0.87*	0.94*	0.90*
Vigor-ST	44	1	0.95*	0.98*
GM-MT	70	66	1	0.99*
Vigor-MT	44	83	74	1

* Significance by nonparametric bootstrapping.

the estimate of the direct gain. Moreover, the gain obtained by directly selecting for green biomass was higher than that obtained from indirect selection under both prediction methods. Selection based on plant vigor provided significant gains in green biomass, confirming the positive genetic correlation between these traits. In the multitrait analysis, the difference between direct and indirect gains was smaller. The indirect gain of the multitrait analysis for green biomass was higher than the direct gain under the single-trait analysis (Table 3), which demonstrated the greater efficiency of this approach, with more accurate and realistic estimates. These results are consistent with the estimates of heritability and selective accuracy (Table 2).

The Spearman correlation between E-BLUPs for green biomass and plant vigor in the single-trait and multitrait approaches ranged from 87% to 99% (Table 4). The lowest estimate of this parameter was between green biomass and plant vigor using the single-trait analysis, and the highest estimate was between green biomass and plant vigor using the multitrait analysis, thus corroborating the results of indirect genetic gain, since the indirect gain estimate was higher and the difference between direct and indirect gains was lower in the multitrait analysis. All correlations were significant by the nonparametric bootstrapping method. Moreover, the coincidence index between the best clones ranged from 44% to 83%. The coincidence between the best clones for green biomass and plant vigor was 44% in the single-trait approach, with 13 clones being among the top 26 best clones for both traits. In the multitrait approach, the coincidence index was 74%, where 20 clones coincided (Table 4).

The highest coincidences and correlations between the E-BLUPs of the traits occurred when using the multitrait analysis. These results are consistent with those found for direct and indirect gains, since the difference between direct and indirect gains was smaller in the multitrait analysis. Thus, the multitrait analysis was a better option for both indirect selection and direct selection because the absolute and relative genetic gain estimates were superior under this approach.

Therefore, there was a high genetic association of plant vigor with green biomass through visual selection. This is a useful tool in the breeding programs of *U. ruziziensis,* allowing indirect selection for green biomass, especially in the initial stages of the breeding programs. Moreover, the multitrait analysis provided a maximization of genetic gains and selective accuracy, proving that this approach is more efficient and informative with respect to plant vigor and green biomass, and it can be used in *U. ruziziensis* breeding programs.

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