Contribution of Additive and Dominance Effects on Agronomical and Nutritional Traits, and Multivariate Selection on *Urochloa* spp. Hybrids

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ABSTRACT

A tropical forage breeding program contains several peculiarities, especially when it involves polyploid species and facultative apomixis. *Urochloa* spp. are excellent perennial forages, and the identification of superior genotypes depends on the selection of many characteristics under complex genetic control, with high cost and time-consuming evaluation. Therefore, the use of tools such as multivariate analysis and diallel analyses could contribute to improving the efficiency of breeding programs. Thus, the objectives were to estimate (i) the contribution of additive and nonadditive effects on agronomical and nutritional traits in a population of interspecific hybrids of *Urochloa* spp., originated from a partial diallel between five apomictic and four sexual parents, and (ii) the accuracy of multivariate index selection efficiency. Genetic variability was detected between the parents, crosses, and hybrids for all the traits. There was no clear trend of the importance of the additive and nonadditive genetic effects on agronomical and nutritional traits. Furthermore, the predominant component of genetic variance changed depending on the characteristic. Moreover, there was no parent or cross that was outstanding for all traits simultaneously, showing the high variability generated from these crosses. The Mulamba and Mock index associated with principal components analysis allowed a more significant gain only for agronomic characteristics. However, the per se index, at the univariate level, promoted a more balanced response to selection for all traits.

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Abbreviations: BLUP, best unbiased linear predictor; CP, crude protein; CSBLUP, selection of individual phenotypes combined with information about the progeny; DEN, density of regrown tillers; FGW, field green weight; GCA, general combining ability; HS-IND, selection between progenies and individual selection; IVD, in vitro organic matter digestibility; %L, percentage of leaves; LDM, leaf dry matter; LIG.S, lignin in sulfuric acid; LRT, likelihood ratio test; L:S, leaf/steam ratio; MMI, Mulamba and Mock index; NDF, neutral detergent fiber; NIRS, near–infrared reflectance spectroscopy; REG, plant regrowth capacity; SCA, specific combining ability; TDM, total dry matter; VEL, regrowth speed.

Grasslands are the most economical source of livestock feed in dairy and beef production (Jank et al., 2014). In tropical regions, forage grasses such as *Urochloa* spp. and *Panicum maximum* Jacq. are the first planted pastures (Almeida et al., 2011), covering millions of hectares. Due to reproduction through apomixis and to a shortage of commercial cultivars of certain species, such as *U. decumbens* (Stapf) R. Webster (syn. *Brachiaria decumbens*), with a single cultivar available, pastures constitute extensive monocultures with their associated risks (Sluszz, 2012). It is thus necessary to generate new sources of variability either by introducing exotic

genotypes or by hybridization whenever possible. Considering the genus *Urochloa* in Brazil, Embrapa (Empresa Brasileira de Pesquisa Agropecuaria) maintains a germplasm bank with ∼450 accessions of thirteen different species. Four of these species have commercial importance [*U. brizantha* (Hochst. ex A. Rich.) R. Webster, *U. decumbens*, *U. ruziziensis* (Hochst. ex A. Rich.) R. Webster, and *U. humidicola* (Rendle) Morrone & Zuloaga). *Urochloa ruziziensis* is a diploid sexual species, whereas *U. brizantha*, *U. decumbens*, and *U. humidicola* are apomictic species with different levels of ploidy. For these last three species, the diploid genotypes found in nature are sexual, whereas the accessions of higher ploidy are obligatorily apomictic (Resende et al., 2008).

To accomplish the hybridization in *Urochloa* spp., chromosomal duplication of diploid sexual individuals (Swenne et al., 1981; Simioni and Valle, 2009) was used in crosses to overcome the apomixis barrier, thus creating new hybrids in the process of forage cultivar development. Sexual tetraploids of *U. ruziziensis* were crossed to natural tetraploids of *U. brizantha* and *U. decumbens* to obtain interspecific hybrids (*Urochloa* interspecific breeding program of Embrapa), whereas sexual tetraploids of *U. decumbens* were crossed to a natural tetraploid commercial cultivar of *U. decumbens* 'Basilisk' (*U. decumbens* intraspecific breeding program of Embrapa) (Lutts et al., 1991; Souza-Kaneshima et al., 2010; Mateus et al., 2015; Matias et al., 2016). Hybridization allowed the introgression of traits of interest such as high forage quality of *U. ruziziensis* with resistance to pasture spittlebugs present in some *U. brizantha*, and tolerance to acid soils and to low soil fertility of *U. decumbens* as well (Resende et al., 2008; Jank et al., 2014).

The improvement of forage is usually time consuming and costly because it involves several steps that differ from other plant species, such as evaluations with grazing animals. Forages in themselves are not the final product desired, but the substrate for the synthesis of animal protein (Jank et al., 2011). Thus, obtaining new cultivars from a partial diallel scheme involves hybridization between elite apomictic and superior sexual parents, evaluation of full or half-sibs, identification of the mode of reproduction (apomictic or sexual), evaluation of value of cultivation and use (VCU) under cuts and under grazing to establish animal performance (Hanna and Bashaw, 1987; Jank et al., 2011, 2014; Barrios et al., 2013).

An ideal forage plant should produce large quantities of dry matter, especially of leaves; good regrowth ability, which allows more grazing cycles throughout the year; and high nutritional value regarding the content of protein and less fiber and lignin content, which allows for good digestibility (Resende et al., 2008). Although selection on a single trait provides for higher genetic progress, its use may be detrimental due to the occurrence of unwanted correlations between the traits of interest under improvement (Bauer and Léon, 2008). Thus, multivariate methods, such as principal component analysis, allow for multivariate patterns of interest to be shown graphically, assisting in the simultaneous selection of agronomic and nutritional characteristics.

In a breeding program, it is necessary to estimate genetic parameters to assist the plant breeder in establishing the best strategy of hybridization, selection, and germplasm organization considering traits of interest. Estimation of genetic parameters and correlations have been described in the literature for *U. decumbens* (Mateus et al., 2015; Matias et al., 2016) and *U. humidicola* (Figueiredo et al., 2012). However, studies on genetic parameters such as additive and dominance variance, as well as general and specific combining ability (SCA) in interspecific hybrid populations, are not yet available in the literature.

The objectives were to estimate (i) the contribution of additive and nonadditive effects on agronomical and nutritional traits in a population of interspecific hybrids of *Urochloa* spp., originated from a partial diallel between five apomictic and four sexual parents, and (ii) the efficiency of using different multivariate selection indices.

MATERIAL AND METHODS
Plant Material
A population of 1000 interspecific hybrids of *Urochloa* spp., composed by genetic background of *U. ruziziensis*, *U. decumbens*, and *U. brizantha* from 20 full-sib progenies, was originated from a partial diallel between five elite tetraploid apomictic male genitors (*U. brizantha* cultivar 'Marandu', *U. brizantha* cultivar 'Paiaguás', *U. decumbens* cultivar 'Basilisk', the interspecific commercial hybrid Mulato II and the accession B140 of *U. brizantha*) with four sexual elite tetraploid hybrids used as female genitor, obtained in the interspecific breeding program of Embrapa (BS9, BS15, 336-T1, and 336-T2). The characteristics of each genitor are highlighted in Table 1.

Experimental Design
The plant material was evaluated in the experimental field of Embrapa Beef Cattle in Campo Grande, Mato Grosso do Sul, Brazil (20°27′ S, 54°37′ W, 530 m asl). This region has two well-defined seasons: a dry one (May to October) and a wet one (November to April), characterizing the Aw climate on the Köppen's climate classification (Alvares et al., 2013). The field had ∼3300 m² and was set to support two experimental subdesigns:

1. The first subdesign involved the 20 progenies of full sibs in a randomized complete block design with 10 blocks. Each plot had five different hybrids from the same cross (Fig. 1), thus each progeny was represented by 50 hybrids totaling 1000 hybrids individually. Additionally, a plot of five clonal plants of each parent (total of nine parents, Table 1) were placed in each of the 10 blocks, totaling 45 additional parental plants per block. As a whole,

450 parental plants were evalutated in this trial (Fig. 1). However, these genotypes were only accounted as a check on the second subdesign described below.

2. The second experimental subdesign was superimposed on the first and evaluated the hybrid per se (e.g., HB-01, HB-02, ..., HB-1000), considering each different hybrid in an augmented block design (Federer, 1961). For environmental effect, the nine parents were used as checks in each block (Resende et al., 2007), represented by dark gray rectangles. In this second subdesign, each plot was represented only by one plant (i.e., 1000 plots of hybrids and 450 plots of parents were added, used as checks). In other words, each hybrid was evaluated individually, since they represent different hybrid combinations from heterozygous parents (Fig. 1), therefore the same number of blocks (10) were maintained, with one plant per plot and no replication for the hybrids, spaced 1.5 × 1.5 m between plants with an area of 2.25 m^2 per plot. The parents, added in

Table 1. Descriptions of genitors that were used to obtain the progenies of full-siblings.

| Species	Characteristics
Apomictic genitors	
U. brizantha (cv. Marandu)	High productivity and intolerance to flooding
U. brizantha (B140)	High productivity
U. brizantha (cv. Paiaguás)	High productivity (especially in the dry season)
U. decumbens (cv. Basilisk)	Medium-high productivity, tolerance to drought, and tolerance to toxic Al
Urochloa spp. (Mulato ll)	High productivity and intolerance to flooding
Sexual genitors	
Four hybrids of sexual *Urochloa* spp. (BS09, BS15, 336-T1m and 336-T2)	Good seed production and high productivity
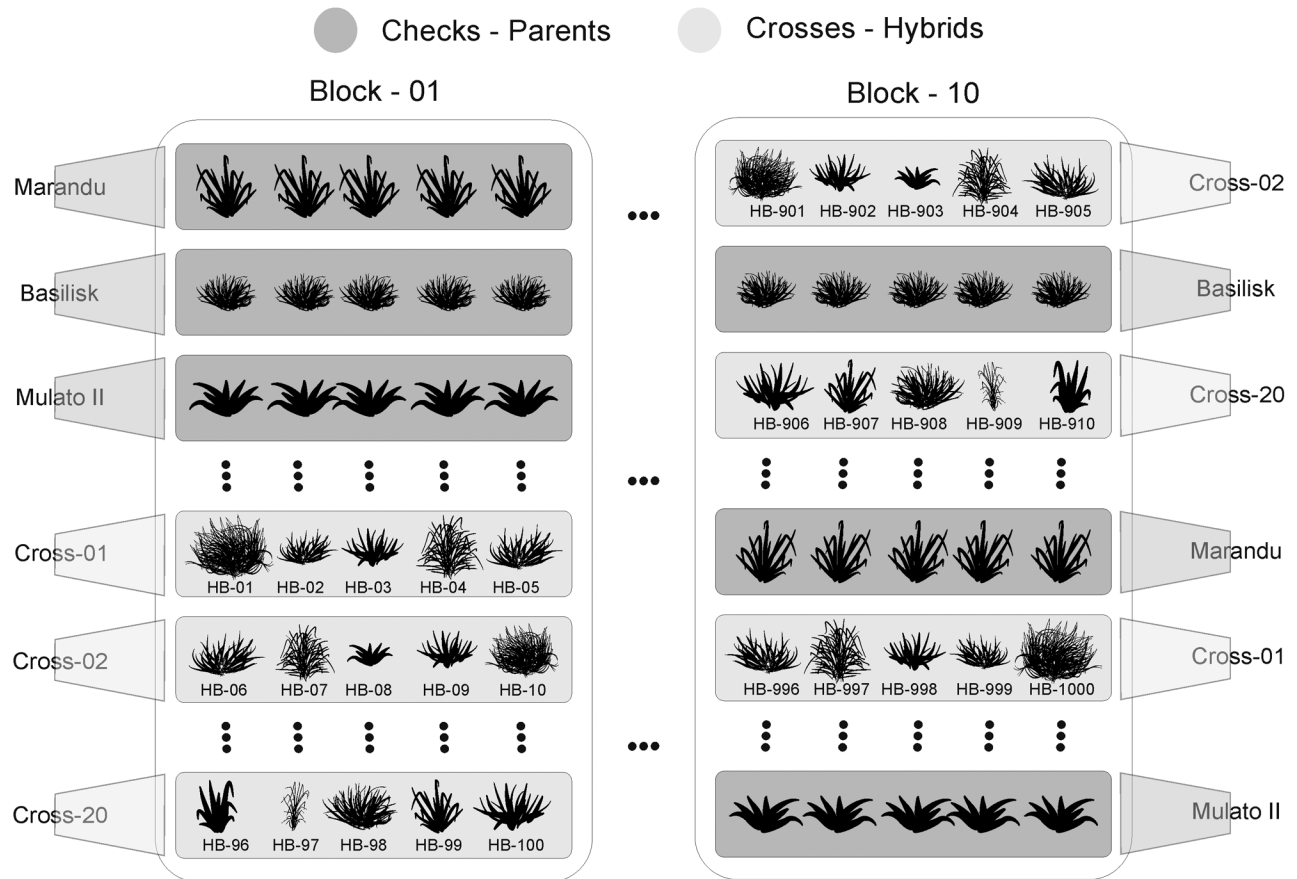
Fig. 1. Scheme of two experimental subdesigns for the evaluation of interspecific *Urochloa* hybrids from crosses between apomictic and sexual tetraploid heterozygous parents. The progenies are randomized and repeated in all 10 blocks (e.g., Cross-01, Cross-02, ..., Cross-20, represented in light gray rectangles) defining the random complete block design (Subdesign 1). Each plot in the block is composed of five different hybrids from a single cross, totaling 50 hybrids per progeny. These 50 full-sib F$_1$ hybrids and progenies segregate in the plot. Thus, there is no hybrid per se replication, and there are 1000 different hybrids in the experiment (HB-01, HB-02, ..., HB-1000). Subdesign 2 evaluated hybrids per se and had an augmented block design, due to the inclusion of checks (the nine parents) in each one of the blocks. Therefore, five clonal cuttings of each parent were placed in each of the 10 blocks, totaling 45 additional plots per block in Subdesign 1 and 450 plots in Subdesign 2. Each plant in Subdesign 2 was represented by only one plant (i.e., 1000 plots of hybrids and 450 plots of parents [checks]). The checks were only accounted for statistical analysis of Subdesign 2.

each block as checks, were used only to estimate the environmental effect of the statistical design.

Phenotypic Data

The evaluation involved seven cuts from 2013 to 2014, with intervals of 48 d: 29 Apr. 2013 (Cut 1), 3 June 2013 (Cut 2), 28 Oct. 2013 (Cut 3), 17 Dec. 2013 (Cut 4), 13 Feb. 2014 (Cut 5), 16 Apr. 2014 (Cut 6), and 3 June 2014 (Cut 7).

Phenotypic Analysis
Agronomic Characteristics

The agronomic traits were evaluated for each plant individually through seven cuts, considering Cuts 1, 4, 5, and 6 as representing the rainy season and Cuts 2, 3, and 7 the dry season. The biomass of each plant (field green weight [FGW], kg ha^{-1}), cut 10 cm above the soil surface, was weighed in the field using a dynamometer. A subsample of ~200 g was taken for plant morphological separation (leaves, stems, and dead material) and estimation of the dry matter, leaf dry matter (LDM, kg ha^{-1}), total dry matter (TDM, kg ha^{-1}), leaf/stem ratio (L:S), and the percentage of leaves (%L).

The final plant regrowth capacity (REG) was estimated 7 d after cutting, obtained by the combination between scores for the density of regrown tillers (DEN) and regrowth speed (VEL), according to the methodology described by (Figueiredo et al., 2012). The scores for DEN were 1 = <20%, 2 = 20 to 40%, 3 = 40 to 60%, 4 = 60 to 80%, and 5 = >80% of regrown tillers, and the scores for VEL were 1 = low, 2 = medium, and 3 = high.

Nutritional Characteristics

The traits related to the nutritional value of the forage were evaluated in Cuts 3 and 4. A sample of green forage was obtained through simulation of grazing. This technique consists of manually removing a mass of ~80 g forage in each plant, simulating harvesting by the animal. Subsequently, this sample was dried, ground, and sent to the laboratory for analysis using near-infrared reflectance spectroscopy (NIRS; Marten et al., 1989). The parameters considered were crude protein (CP), in vitro organic matter digestibility (IVD), neutral detergent fiber (NDF), and lignin in sulfuric acid (LIG.S).

The calibration of the NIRS was performed previously by comparing the results obtained in the wet chemical analyses and the spectrum read from these same samples in the NIRS for several nutritional characteristics. For this purpose, a regression equation was estimated for each nutritional characteristic, using a set of samples of tropical forage grasses (*Urochloa* spp. and *Panicum maximum*) for this purpose (647 samples for CP, 613 for IVD, 631 for NDF, and 147 for LIG.S). Estimates of the coefficient of determination were 0.99 (CP), 0.96 (IVD), 0.95 (NDF) and 0.96 (LIG.S), showing a good fit of the model for the prediction of nutritional characteristics (data not shown).

Statistical Analysis
Diallel Analysis (Progenies of Full-Sibs)

Fitting the Model with All Cuttings. For the analysis of phenotypic data, equations of mixed models were used, testing the random effects by the likelihood ratio test (LRT) and the

fixed effects by Wald F test (Paula, 2013) using the software R with the support of the ASReml-R (Butler et al., 2009) package. Thus, to obtain the variance components and estimates of genetic parameters of the parents and crosses, the data were subjected to analysis via the restricted maximum likelihood method and best unbiased linear predictor (REML/BLUP) (Resende, 2000), according to the following model:

$$\mathbf{y}_{cdfg} = \mu + \mathbf{q}_c + \mathbf{t}_d + \mathbf{u}_f + \mathbf{v}_g + \mathbf{x}_{f \times g} + \mathbf{z}_{f \times c}$$
$$+ \mathbf{w}_{g \times c} + \mathbf{k}_{f \times g \times c} + \varepsilon_{cdfg} \quad [1]$$

in which **y** is the vector of phenotypic data, μ is the vector of the fixed effect of the general mean, **q** is the vector for the fixed effect of cuts with $c = \{1, 2, …, 7\}$, **t** is the vector of random block–level effect into cuts with $\mathbf{t} \sim N(0, \mathbf{I}\sigma_t^2)$ where **I** is the identity matrix, σ_t^2 is the variance component of the blocks, and $d = \{1, 2, …, 10\}$, **u** is the vector of the random effect of general combining ability (GCA) of apomictic parents with $\mathbf{u} \sim N(0, \mathbf{I}\sigma_{APO}^2)$ where σ_{APO}^2 is the variance component of the apomictic parent and $f = \{1, 2, …, 5\}$, **v** is the vector of the random effect of GCA of the sexual parents with $\mathbf{v} \sim N(0, \mathbf{I}\sigma_{SEX}^2)$ where σ_{SEX}^2 is the variance component of the sexual parent and $g = \{1, 2, …, 4\}$, **x** is the vector of the random effect of SCA between the parents with $\mathbf{x} \sim N(0, \mathbf{I}\sigma_{APO \times SEX}^2)$ where $\sigma_{APO \times SEX}^2$ is the variance component of the interaction between parents, **z** is the vector of the random effect of the interaction of the apomictic parent with cuts with $\mathbf{z} \sim N(0, \mathbf{I}\sigma_{APO \times c}^2)$ where $\sigma_{APO \times c}^2$ is the variance component of the interaction of the apomictic parent with cuts, **w** is the vector of the random effect of the interaction of the sexual parent with cuts with $\mathbf{w} \sim N(0, \mathbf{I}\sigma_{SEX \times c}^2)$ where $\sigma_{SEX \times c}^2$ is the variance component of the interaction of the sexual parent with cuts, **k** is the vector of the random effect of the interaction cross with cuts with $\mathbf{k} \sim N(0, \mathbf{I}\sigma_{APO \times SEX \times c}^2)$ where $\sigma_{APO \times SEX \times c}^2$ is the variance component of the interaction of the cross with cuts, and ε is the error vector with $\varepsilon \sim N(0, \mathbf{I}\sigma_{E_1}^2)$ where $\sigma_{E_1}^2$ is the residual variance coefficient from Eq. [1] or [2]. The components of variance were tested by deviance analysis (ANADEV) using the LRT, and the significance was verified by the χ^2 test with 1 df. The LRT replaces the ANOVA and the F test of the ANOVA in cases of models with unbalanced data (Sturion and Resende, 2010).

Fitting the Model by Cutting. For the estimation of variance components considering each cut, Eq. [1] was modified to remove the effect of cut and interactions with cuts, keeping only the random effect of blocks (**t**), apomictic parent (**u**), sexual parent (**v**), and cross (**x**), as follows:

$$\mathbf{y}_{dfg} = \mu + \mathbf{t}_d + \mathbf{u}_f + \mathbf{v}_g + \mathbf{x}_{f \times g} + \varepsilon_{dfg} \quad [2]$$

Genetic Component Evaluation. Using genetic variance equations adapted to tetraploid species (Lynch and Walsh, 1998), we calculated the genetic components of variance for the all cuts together and each cut (harvest) separately. The approximate additive variance was estimated by the equation $\sigma_A^2 = 4\sigma_{APO}^2$. This additive variance is approximate, since this species is a polyploid, so 1/36th of the dominance variance is present in the σ_{APO}^2 component, which we, however, assumed as zero. The relative dominance variance was calculated by the interaction component

APO×SEX, given by $\sigma_D^2 = 9/2\left(\sigma_{APO \times SEX}^2 - 2\sigma_{APO}^2\right)$, assuming that the trigenetic and quadrigenetic effects are equal to zero. The proportion of each variance was obtained by the division concerning the phenotypic variance $\sigma_{P.1}^2 = \sigma_A^2 + \sigma_D^2 + \sigma_{E_1}^2/cb$, where $\sigma_{E_1}^2$ is the residual variance coefficient from Eq. [1] or [2], c is the number of cuts (accounted only for Eq. [1]), and b is the number of blocks. The selection at the progeny level was simulated through the ranking of the effect of the apomictic parents, sexual parents, and cross BLUPs from Eq. [1]. The narrow-sense heritability was calculated by $h_{GCA}^2 = \sigma_A^2/\sigma_{P.1}^2$.

Individual Analysis (Hybrids)

The variance components and estimates of the genetic parameters of individual hybrids in an augmented block design (Federer, 1961) were performed including type (check and hybrids), assisting in the correction of the block and cut effects according to the following model:

$$\mathbf{y}_{abcdg} = \boldsymbol{\mu} + \mathbf{m}_a + \mathbf{p}_b + \mathbf{q}_c + \mathbf{s}_d + \mathbf{t}_g + \mathbf{u}_{g \times c} + \boldsymbol{\varepsilon}_{abcdg} \quad [3]$$

where $\mathbf{y}$ is the vector for phenotypic data, $\boldsymbol{\mu}$ is the vector for the general mean fixed effect, $\mathbf{m}$ is the vector for the fixed effect of type (check or hybrid), $\mathbf{p}$ is the vector the fixed check effect with $b = \{1, 2, \ldots, 9\}$, $\mathbf{q}$ is the vector for the fixed cut effect with $c = \{1, 2, \ldots, 7\}$, $\mathbf{s}$ is the vector or the random block level within cut effect $\mathbf{s} \sim N\left(0, \mathbf{I}\sigma_s^2\right)$ where σ_s^2 is the variance component of blocks and $d = \{1, 2, \ldots, 10\}$, $\mathbf{t}$ is the vector for the random hybrid effect with $\mathbf{t} \sim N\left(0, \mathbf{I}\sigma_g^2\right)$ where σ_g^2 is the variance component of hybrids and $g = \{1, 2, \ldots, 1000\}$, $\mathbf{u}$ is the vector of the random hybrid by cut interaction effect with $\mathbf{u} \sim N\left(0, \mathbf{I}\sigma_{g \times c}^2\right)$ where $\sigma_{g \times c}^2$ is the variance component of interaction of hybrids with cuts, and $\boldsymbol{\varepsilon}$ is the error effect with $\boldsymbol{\varepsilon} \sim N\left(0, I\sigma_{E_2}^2\right)$ where $\sigma_{E_2}^2$ is the residual coefficient of the variance of Eq. [3].

The hybrid heritability at the means level, in the second model, was calculated by $h^2 = \sigma_g^2/\sigma_{P.2}^2$, for $\sigma_{P.2}^2 = \sigma_g^2 + \left(\sigma_{g \times c}^2/c\right) + \left(\sigma_{E_2}^2/c\right)$, where $\sigma_{E_2}^2$ is the residual coefficient of the variance of Eq. [3]. Selective accuracy $(\hat{r}_{\hat{g}g})$ was estimated by the square root of the hybrid heritability. Similarly described above for progenies selection, the selection of individual hybrids from Eq. [3] was made by the rank of the hybrid BLUPs and the check best linear unbiased estimates (BLUEs).

Multivariate Analysis

In our study, FGW, regrowth ability, CP, and fiber content were the four traits that together could represent the main traits in forage performance. Then, these four traits were used to verify the multivariate pattern of the hybrid, and a principal component analysis was conducted using the hybrid BLUPs in Eq. [2], followed by the construction of a *biplot* graph with the first two principal components. Each observation was identified in accordance to the cross to which it belonged. This plot had the purpose of assisting in the selection of hybrids with greater FGW, REG, CP, and lower NDF. The R packages *prcomp* and *ggfortify* (Ginestet, 2011) were used to fit this analysis and graphics.

The Mulamba and Mock index (MMI; Mulamba and Mock, 1978) was used for multivariate selection of hybrids, given by

$$\mathrm{MMI}_{PC_i} = \left(P_{PC1_i} + P_{PC2_i}\right)/2$$

where P_{PC1_i} is the position i of the hybrid in the rank of the first principal component (PC1); P_{PC2_i} is the position i of the hybrid in the rank of the second principal component (PC2). The response to selection was estimated for a selection intensity of 1% (10 superior hybrids).

For the comparison between the multivariate selection using principal components and verification of the direct and indirect effects of this selection, the MMI based on the relative positions of the ranking of hybrids for the same four traits (FGW, REG, CP, and NDF) was performed according to

$$\mathrm{MMI}_{Uni_i} = \left(P_{PVC_i} + P_{REB_i} + P_{PB_i+} + P_{FDN_i}\right)/4$$

The correlations between agronomic and nutritional characteristics were estimated by the BLUP of the hybrids in Eq. [3] using the Pearson method $r_{g_{(x,y)}}$ using the function *correlation* from R package *Agricolae* (Mendiburu, 2014). Although a formal test of correlation significance has not yet been established, the significance of the correlation was verified using an approximate Student's t test (Steel and Torrie 1997), considering $n - 2$ df, where n is the number of hybrids.

RESULTS

Genetic Variability in the Populations

Statistical differences between the apomictic parents were identified ($p < 0.01$ and 0.05) regarding GCA for VEL and LDM (Table 2). On the other hand, the sexual parents showed differences in GCA for DEN, REG, CP, and NDF ($p < 0.01$ and 0.05). Concerning the effect of crosses (SCA), there was a significant difference ($p < 0.01$ and 0.05) for FGW, TDM, VEL, REG, CP, and NDF, indicating that there are combinations of apomictic and sexual parents that can be more advantageous in the breeding program.

Field green weight, TDM, and REG are traits with a balance between additive and nonadditive variation. Field green weight presented practically 50% of each genetic effect (additive and dominant) when all the cuts were evaluated together (Table 2). Density of regrown tillers, VEL, LDM, CP, NDF, and IVD are predominantly additive traits, with proportions varying from 20 to 90%, whereas LIG.S showed only dominance effect of 53% (Table 2). Leaf/stem ratio and %L showed no relevant genetic effect when all the cuts were evaluated together. These results are only an inference about the genetic behavior of these traits in this population. The narrow-sense heritability for progeny selection ranged from 0 to 84% depending on the trait (Table 2).

When cuts were considered individually (Supplemental Table S1), genetic effects varied with the seasons. Field green weight and TDM showed an increase in the dominance effect between Cuts 3 and 5 (October 2013–February 2014). Plant regrowth showed greater dominance effect on Cuts 1 to 4 and greater additive effect on Cuts 5 to 7. Neutral detergent fiber and IVD showed more dominance on Cut 3 and greater additive effect on Cut 4. Density of regrown tillers, %L, L:S, and LIG.S showed

greater dominance effect, whereas VEL, LDM, and CP had a greater additive effect across all the cuts.

When using Eq. [3], for all traits except L:S ($p > 0.05$), genotypic differences were found among hybrids (Table 3, $p > 0.01$ and 0.05). When evaluating them individually, disregarding the effect of progenies, estimates of heritability between hybrids means were of greater magnitude: 81, 77.9, 62.2, 74, and 67.5% for FGW, TDM, VEL, REG, and CP, respectively. Also, selective accuracy was higher at the individual level, with values >70% for most traits, which indicates high experimental precision and good fit of Eq. [3], according to the limits set by Resende and Duarte (2007). The ideal plot size for progenies of *U. ruziziensis* was ~3 m^2 (Dias et al., 2014), or a line of 3 m with six plants (Souza Sobrinho et al., 2010, 2011). In this experiment, plots with five plants and 2.25 m^2 $plant^{-1}$ were used, which is more than commonly reported for evaluation of progenies. This spacing could have positively influenced the experimental accuracy of Eq. [3], allowing for some isolation of hybrids and less competition between plants.

Correlations among Agronomic and Nutritional Traits

The traits most positively related to each other were FGW × TDM (0.99), FGW × REG (0.55), DEN × REG (0.73), VEL × REG (0.69), FGW × NDF (0.29), and FGW × LIG.S (0.33) (Table 4). Although DEN and VEL have strong correlations with REG (~0.70), these two characteristics have weak correlation with each other (~0.14) (Table 4)

The correlations of CP and IVD with most of the other traits were negative and nonsignificant even though they are positively correlated (0.50). The high contents of fiber and lignin negatively affected digestibility as expected, and a negative correlation was observed between CP and NDF (−0.42), NDF and IVD (−0.31), and LIG.S and IVD (−0.26) (Table 4).

Selection of Parents, Crosses, and Hybrids

The selection of the best parents and crossings was made by the ranking of the genotypic value of estimates of GCA and SCA (Table 5). Cultivar Basilisk was the apomictic

Table 2. Deviance analysis (ANADEV) for apomictic parents (σ^2_{APO}), sexual parents (σ^2_{SEX}), cross effect ($\sigma^2_{APO \times SEX}$) and its interaction with cuttings ($\sigma^2_{APO \times SEX \times c}$), additive variance ($\sigma^2_A$), dominant variance ($\sigma^2_D$), narrow-sense heritability (h^2_{GCA}), and general mean ($\overline{X}$) for agronomic and nutritional value traits based on the evaluation of *Urochloa* spp. hybrids in seven cuts. Significance was determined by the likelihood ratio test.

						Trait						
Component	FGW†	TDM	DEN	VEL	REG	LDM	%L	L:S	CP	NDF	IVD	LIG.S
σ^2_{APO}	4,381.84ns‡	5,777.55ns	0.00ns	0.01*	0.00ns	3,709.61*	0.00ns	0.15ns	0.10ns	0.13ns	0.22ns	0.00ns
σ^2_{SEX}	0.11ns	0.04ns	0.02*	0.00ns	0.05*	3,886.82ns	14.93*	1.97ns	0.21**	0.21*	0.37ns	0.00ns
$\sigma^2_{APO \times SEX}$	12,264.92**	13,894.79**	0.00ns	0.01**	0.01**	1,145.56ns	0.00ns	0.40ns	0.11**	0.18*	0.20ns	0.00ns
$\sigma^2_{APO \times SEX \times c}$	3,206.05ns	5,727.73ns	0.00*	0.00ns	0.01**	0.00ns	19.01*	0.37ns	0.00ns	0.20*	0.34ns	0.00ns
σ^2_A	17,527.35	23,110.19	0.00	0.03	0.02	14,838.43	0.00	0.61	0.41	0.50	0.90	0.00
σ^2_D	15,755.58	10,528.64	0.00	0.00	0.02	0.00	0.00	0.42	0.00	0.00	0.00	0.01
σ^2_A (%)	46.45	58.88	35.56	83.69	40.98	69.62	0.00	18.65	78.46	62.56	53.15	0.00
σ^2_D (%)	41.76	26.82	0.00	0.00	38.03	0.00	0.00	12.86	0.00	0.00	0.00	53.20
h^2_{GCA}	0.46	0.59	0.36	0.84	0.41	0.70	0.00	0.19	0.79	0.63	0.53	0.00
$\overline{X}$	1,084.82	1,369.41	2.98	1.54	1.60	443.96	62.86	2.92	15.44	63.34	72.33	2.07

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† FGW, field green weight (kg ha^{-1}); TDM, total dry matter (kg ha^{-1}); DEN, density of regrown tillers; VEL, regrowth speed; REG, regrowth capacity; LDM, leaf dry matter (kg ha^{-1}); %L, percentage of leaves; L:S, leaf/stem ratio; CP, crude protein (%); NDF, neutral detergent fiber (%); IVD, in vitro organic matter digestibility (%); LIG.S, lignin in H_2SO_4 (%).

‡ ns, nonsignificant.

Table 3. Deviance analysis (ANADEV) for *Urochloa* spp. interspecific hybrid effect (σ^2_g). Selective accuracy ($\hat{r}_{gg}$), heritability between hybrid means (h^2), and general mean ($\overline{X}$) for agronomic and nutritional value traits based on the evaluation in seven cuts. Significance was determined by the likelihood ratio test.

						Trait†						
Component	FGW	TDM	DEN	VEL	REG	LDM	%L	L:S	CP	NDF	IVD	LIG.S
σ^2_g	144,522.40**	162,654.20**	0.08**	0.07**	0.22**	33,837.46**	41.72**	0.00ns‡	1.47**	2.48**	5.98**	0.04**
$\hat{r}_{gg}$	0.90	0.88	0.71	0.79	0.86	0.75	0.56	–	0.82	0.70	0.71	0.65
h^2	0.81	0.78	0.51	0.62	0.74	0.56	0.31	0.00	0.68	0.49	0.51	0.42
$\overline{X}$	1,540.61	1,790.55	3.57	1.81	2.29	767.86	66.92	2.57	15.75	64.41	73.32	2.17

** Significant at the 0.01 probability level.

† FGW, field green weight (kg ha^{-1}); TDM, total dry matter (kg ha^{-1}); DEN, density of regrown tillers; VEL, regrowth speed; REG, regrowth capacity; LDM, leaf dry matter (kg ha^{-1}); %L, percentage of leaves; L:S, leaf/stem ratio; CP, crude protein (%); NDF, neutral detergent fiber (%); IVD, in vitro organic matter digestibility (%); LIG.S, lignin in H_2SO_4 (%).

‡ ns, nonsignificant.

parent that provided greater green weight gains and, at the same time, reduced the fiber content, and may give rise to hybrids with better nutritional value. Regarding the sexual parents, the hybrid 336-T1 was the most frequent among the best crosses and was responsible for gains in protein and less fiber content in the progenies. For FGW,

REG, CP, and NDF, there was no clear pattern among the parents or a better combination of crosses for all these traits simultaneously.

Comparing the effects of the parents (Table 5) with the effects of the 10 best hybrids in the population (Table 6), it was observed that the effect of the individual is far superior

Table 4. Correlation estimates between agronomic and nutritive value traits in *Urochloa* interspecific hybrids. Significance was determined by the *z* test.

Trait†	TDM	DEN	VEL	REG	LDM	%L	L:S	CP	NDF	IVD	LIG.S
FGW	0.99*	0.40*	0.49*	0.55*	0.51*	0.03ns‡	−0.17*	0.00ns	0.29*	−0.19*	0.33*
TDM		0.39*	0.49*	0.54*	0.51*	0.02ns	−0.16*	−0.01ns	0.30*	−0.19*	0.33*
DEN			0.14*	0.73*	0.20*	0.19*	0.08*	0.12*	−0.07*	−0.05ns	0.08*
VEL				0.69*	0.33*	0.14*	−0.05ns	−0.14*	0.21*	−0.11*	0.24*
REG					0.39*	0.29*	0.04ns	−0.08*	0.09*	−0.13*	0.20*
LDM						0.25*	−0.23*	−0.15*	0.20*	−0.17*	0.18*
%L							0.38*	0.00ns	−0.02ns	0.01ns	0.02ns
L:S								0.03ns	−0.14*	0.04ns	−0.10*
CP									−0.42*	0.50*	−0.08*
NDF										−0.31*	0.37*
IVD											−0.26*

* Significant at the 0.05 probability level.

† FGW, field green weight (kg ha⁻¹); TDM, total dry matter (kg ha⁻¹); DEN, density of regrown tillers; VEL, regrowth speed; REG, regrowth capacity; LDM, leaf dry matter (kg ha⁻¹); %L, percentage of leaves; L:S, leaf/stem ratio; CP, crude protein (%); NDF, neutral detergent fiber (%); IVD, in vitro organic matter digestibility (%); LIG.S, lignin in H_2SO_4 (%).

‡ ns, nonsignificant.

Table 5. General combining ability (GCA) estimates of apomictic parents and sexual parents, and specific combining ability (SCA) estimates of the five best and five worst *Urochloa* spp. crosses for different agronomic and nutritional value traits.

	Apomictic parents†			
Rank	VEL	GCA	LDM	GCA
1	B140	0.13	Basilisk	74.44
2	Basilisk	−0.02	B140	45.51
3	Marandu	−0.02	Marandu	−20.85
4	Mulato II	−0.04	Mulato II	−47.23
5	Paiaguás	−0.05	Paiaguás	−51.87
$\overline{X}$ ‡		1.54		443.96

	Sexual parents§							
Rank	DEN	GCA	REG	GCA	CP	GCA	NDF	GCA
1	336-T2	0.08	BS15	0.12	336-T1	0.52	336-T2	−0.51
2	BS15	0.06	336-T2	0.11	BS09	0.05	336-T1	−0.11
3	336-T1	0.04	336-T1	0.05	336-T2	−0.04	BS15	0.15
4	BS09	−0.18	BS09	−0.30	BS15	−0.52	BS09	0.46
$\overline{X}$		2.98		1.60		15.44		63.34

	Urochloa spp. crosses							
Rank	FGW¶	SCA	REG	SCA	CP	SCA	NDF	SCA
1	B140 × 336-T1	119.38	B140 × BS15	0.22	Mulato II × BS09	0.34	B140 × 336-T2	−0.36
2	Basilisk × BS09	93.81	Marandu × 336-T2	0.08	B140 × 336-T2	0.32	Mulato II × 336-T1	−0.32
3	Mulato II × 336-T2	93.12	B140 × BS09	0.08	Marandu × BS15	0.20	Mulato II × BS09	−0.32
4	Basilisk × BS15	72.85	Mulato II × 336-T2	0.08	Basilisk × BS15	0.19	Basilisk × 336-T1	−0.25
5	Paiaguás × 336-T2	68.49	B140 × 336-T1	0.05	Mulato II × 336-T1	0.18	Paiaguás × 336-T2	−0.20
16	Marandu × 336-T1	−92.65	Marandu × 336-T1	−0.04	Paiaguás × BS09	−0.22	Mulato II × 336-T2	0.14
17	Basilisk × 336-T2	−103.25	Mulato II × BS15	−0.05	Basilisk × BS09	−0.22	Marandu × 336-T2	0.18
18	Paiaguás × BS15	−121.45	Paiaguás × BS15	−0.14	Marandu × 336-T2	−0.24	B140 × BS09	0.21
19	Paiaguás × BS09	−122.17	Mulato II × BS09	−0.14	Mulato II × 336-T2	−0.24	Basilisk × BS09	0.41
20	Mulato II × 336-T1	−158.24	B140 × 336-T2	−0.14	B140 × BS15	−0.63	B140 × 336-T1	0.72
$\overline{X}$		1084.82		1.60		15.44		63.34

† VEL, regrowth speed; LDM, leaf dry matter (kg ha⁻¹).

‡ $\overline{X}$, general mean.

§ DEN, density of regrown tillers; REG, regrowth capacity; CP, crude protein (%); NDF, neutral detergent fiber (%).

¶ FGW, field green weight (kg ha⁻¹).

to the effect of the cross. However, although there are hybrids with great agronomic and nutritional potential in the population, there was no hybrid that combined all features simultaneously when using the univariate selection intensity of 1% (Table 6).

The SCA was significant for some of the main traits. However, no crosses were superior for all traits at the same time (Table 2). Therefore, a multivariate selection at the individual level for FGW, REG, CP, and NDF was used (Fig. 2). The first two principal components explained ~75% of the total multivariate variation observed among hybrids.

There was no clear pattern such as the clustering of a superior cross (Fig. 2). Although no multivariate pattern defines the best cross for all the traits at the same time, there are some hybrids with high potential, with higher FGW, REG, and CP and lower NDF. These are written in red in Fig. 2 with lower values for the first and second principal components, simultaneously. These hybrids were selected with the help of MMI_{PC} and correspond to hybrids 1357 (336-T1 × B140), 1954 (336- T1 × Mulato II), 2002 (336-T2 × Mulato II), 1908 (BS15 × Mulato II), 1871 and 1897 (BS09 × Mulato II), 1620, 1579 (336-T1 × BRS Paiaguás), and 1623 and 1629 (336-T2 × BRS Paiaguás) (Table 7).

The 10 best hybrids selected by MMI_{Uni} for the traits FGW, REG, CP, and NDF (Table 7) are shown in blue in the lower part of Fig. 2. Those hybrids are 1419 (336-T2 × B140), 1366 (336-T1 × B140), 1764 (336-T1 × Basilisk), 1954, 1964, and 1984 (336-T1× Mulato II), 2012 (336-T2 × Mulato II), 1863 (BS09 × Mulato II), 1546 (BS15 × BRS Paiaguás), and 1623 (336-T2 × BRS Paiaguás). Some of these hybrids are not among the 10 best for each one of the traits at the same time (Table 6), which was expected, because these are the best hybrids in a multivariate context, representing, in general, a desirable hybrid. Thus, only hybrids 1954 and 1623 were identified using both strategies of building indices.

Gains of 817.5, 411.5, and 921.8 kg ha⁻¹ in FGW are expected for selection of the 10 best hybrids by MMI_{PC}, MMI_{Uni}, and univariate selection, respectively (Table 7). The MMI_{PC} and MMI_{Uni} indices were coincident on the selection gain for REG, promoting an increase of ~0.4 relative to the population average, which amounts to ~ 65% of the gain by direct univariate selection. Selection using indices presented some differences, however: MMI_{Uni} allowed higher relative gain than univariate selection for CP and NDF of 63 and 50%, respectively, whereas MMI_{PC} had 27% better gain for CP and a decrease of 2% for NDF (Table 7).

The direct univariate selection of the best 10 hybrids had gains ranging from 1 to 60% (Table 8). Interestingly, the indirect gains of selection followed the correlations between the traits (Table 4). Direct and indirect gains were similar when selecting the 1% best hybrids for FGW

Table 6. Genotypic value (GV) of the best 10 Urochloa spp. hybrids.

Rank	FGW	GV	TDM	GV	DEN	GV	VEL	GV	REG	GV	LDM	GV	%L	GV	L:S	GV	CP	GV	NDF	GV	IVD	GV	LIG.S	GV
1	HB-1620	1753.89	HB-1620	1807.96	HB-1215	0.57	HB-1371	0.56	HB-1566	1.16	HB-1797	637.75	HB-1245	7.69	–	–	HB-1089	0.00	HB-1773	–4.37	HB-1683	5.15	HB-1563	–0.51
2	HB-1357	1253.53	HB-1897	1181.85	HB-1207	0.55	HB-1372	0.56	HB-2002	1.13	HB-1897	629.27	HB-2035	7.21	–	–	HB-1744	2.20	HB-1173	–3.08	HB-1479	5.03	HB-1773	–0.44
3	HB-1897	1186.26	HB-1743	1170.68	HB-1552	0.54	HB-1353	0.50	HB-1954	1.13	HB-1885	447.11	HB-1385	7.12	–	–	HB-1730	2.20	HB-1524	–2.92	HB-1488	4.28	HB-1685	–0.36
4	HB-1255	1128.18	HB-1558	1083.58	HB-1419	0.49	HB-1319	0.44	HB-1301	1.08	HB-1128	400.60	HB-1231	6.96	–	–	HB-1589	2.17	HB-1512	–2.92	HB-1577	4.22	HB-1429	–0.34
5	HB-1743	1103.18	HB-1255	1070.22	HB-1566	0.49	HB-1366	0.44	HB-1623	0.96	HB-1785	396.80	HB-1394	6.90	–	–	HB-1983	2.14	HB-1416	–2.67	HB-1582	4.10	HB-1997	–0.33
6	HB-1954	1083.64	HB-1785	1059.89	HB-1427	0.48	HB-1520	0.44	HB-1348	0.96	HB-1747	353.95	HB-1177	6.70	–	–	HB-1991	2.12	HB-1441	–2.61	HB-1588	4.01	HB-1798	–0.32
7	HB-1785	1006.09	HB-1797	1030.22	HB-1629	0.48	HB-1716	0.44	HB-1366	0.95	HB-1928	327.43	HB-1591	6.61	–	–	HB-1752	2.09	HB-1230	–2.55	HB-1674	3.99	HB-1191	–0.31
8	HB-1372	960.75	HB-1617	995.75	HB-2028	0.48	HB-1063	0.44	HB-1452	0.92	HB-1428	322.79	HB-1784	6.57	–	–	HB-1997	2.06	HB-1407	–2.42	HB-1961	3.93	HB-1981	–0.30
9	HB-1908	956.76	HB-1372	991.44	HB-1511	0.47	HB-1311	0.44	HB-1552	0.92	HB-1943	303.97	HB-1547	6.35	–	–	HB-1784	2.02	HB-1419	–2.42	HB-1374	3.88	HB-1416	–0.30
10	HB-2002	954.71	HB-1885	965.37	HB-1147	0.46	HB-1811	0.44	HB-1111	0.85	HB-1546	301.67	HB-1794	6.22	–	–	HB-1665	2.00	HB-1421	–2.32	HB-1970	3.83	HB-1094	–0.28
$\bar{X}$‡		1540.61		1790.55		3.57		1.81		2.29		767.86		66.92		2.57		15.75		64.41		73.32		2.17

† FGW, field green weight (kg ha^{-1}); TDM, total dry matter (kg ha^{-1}); DEN, density of regrown tillers; VEL, regrowth speed; REG, regrowth capacity; LDM, leaf dry matter (kg ha^{-1}); %L, percentage of leaves; L:S, leaf/stem ratio; CP, crude protein (%); NDF, neutral detergent fiber (%); IVD, in vitro organic matter digestibility (%); LIG.S, lignin in H_2SO_4 (%).
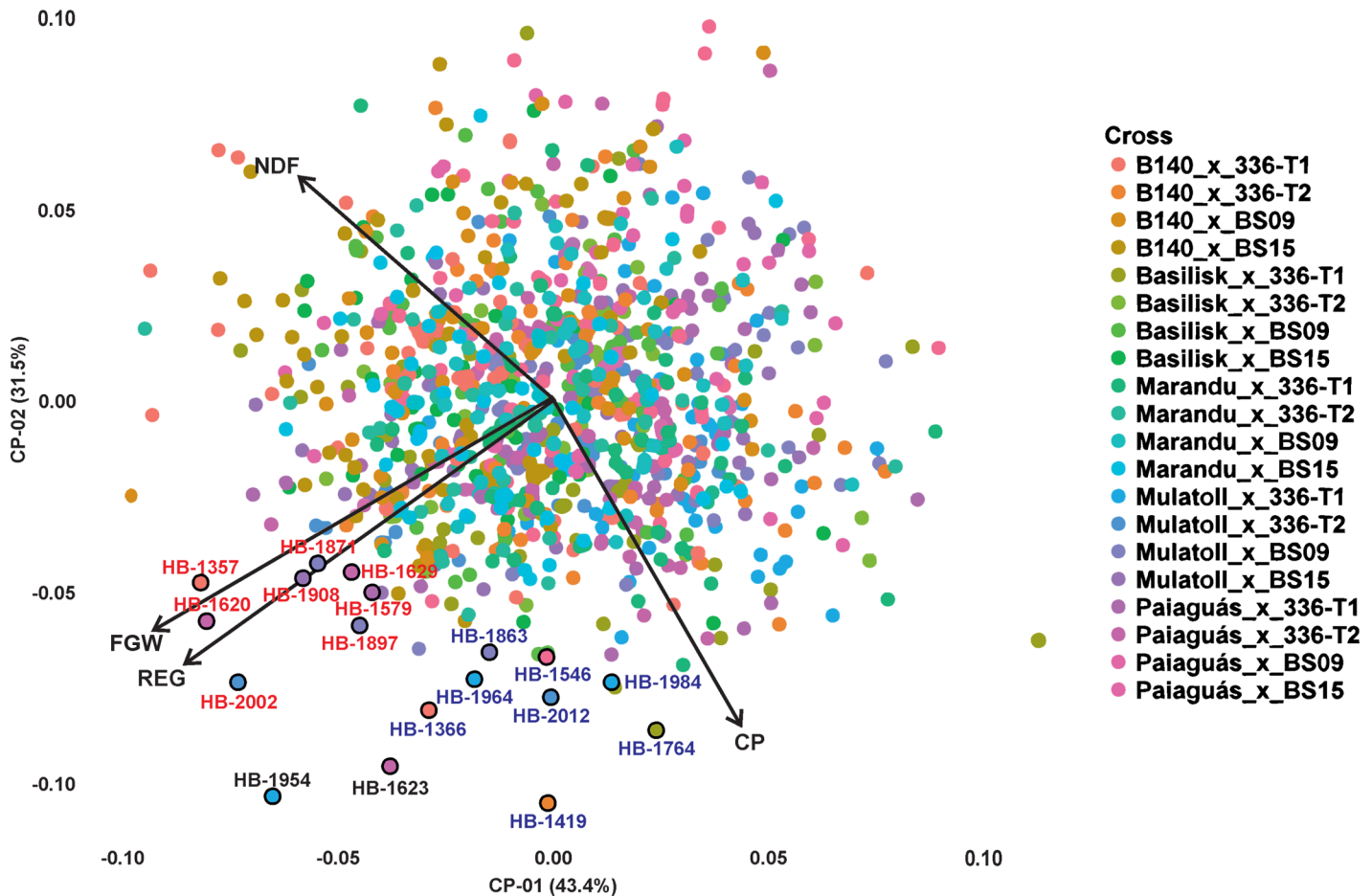
‡ $\bar{X}$, general mean.

Fig. 2. Biplot of the principal component multivariate analysis of 1000 interspecific hybrids of *Urochloa* spp., from a partial diallel between five tetraploid apomictic parents (*U. brizantha* 'Marandu', *U. brizantha* accession B140, *U. brizantha* 'BRS Paiaguás', *U. decumbens* 'Basilisk', and *Urochloa* spp. Mulato II) with four tetraploid sexual interspecific hybrids (BS9, BS15, 336-T1, and 336-T2) for field green weight (FGW, kg ha⁻¹), regrowth scores (REG), percentage crude protein (CP), and percentage neutral detergent fiber (NDF). The axes represent the first (CP-01) and second (CP-02) principal components. Hybrids written in blue were the best hybrids selected by MMI$_{Uni}$.

and TDM, as well as when selecting for CP and IVD. Univariate direct selection for FGW promoted a reduction of −0.915% in the performance of the population for IVD, whereas the univariate selection for IVD reduced the performance of the population for FGW by −10,508%.

DISCUSSION
Diallel Analysis and Selection Methods

Significant genetic variability among the hybrids is a fundamental principle in plant breeding to perform selection for a particular trait of agronomic interest (Pandolfi Filho et al., 2016). In reciprocal recurrent selection schemes, the SCA between the parents is used to select the best crosses, whereas the GCA indicates the additive genetic potential of a parent to produce good hybrids (Comstock et al., 1949; Oliboni et al., 2013). This combined information allows the selection of parents to be recombined to produce hybrids for the next cycle of selection and intercrossing, to gradually accumulate favorable alleles with a slow reduction in variability (Bernardo, 2010).

Breeding of *Urochloa* spp., particularly of *U. decumbens* and *U. brizantha*, involves recombination solely between sexual parents, since apomixis prevails in this genus (Worthington and Miles, 2015). Thus, a selection scheme called recurrent selection for SCA has been used (RS-SCA; Miles, 2007), in which an elite apomictic parent is used as a tester on a group of sexual plants. Modifications of this scheme resemble a reciprocal recurrent selection scheme since, to promote crosses, a group of apomictic individuals from a population are used as pollen donors to a sexual group of individuals from another population (Worthington and Miles, 2015). Such a scheme is typically associated with a system of partial diallel crosses to obtain hybrids and genetic information on the population in each cycle of reciprocal recurrent selection. Furthermore, the parents are not taken to homozygosity before the next cycle of crossings, since these are polyploids with self-incompatibility issues (Lapointe and Miles, 1992; Valle and Savidan, 1996).

This interspecific tetraploid population presented higher additive variability than that observed in a

Table 7. Genotypic value (GV) of the 10 best *Urochloa* spp. hybrids selected by the Mulamba and Mock index (MMI) using the first two principal components (MMI$_{PC}$), mean genotypic value of the selected hybrids by principal components (GV.PC), mean genotypic value of selected hybrids using MMI based only in phenotypic information (GV.MM), mean genotypic value of selected hybrids by univariate analysis (GV.Uni), broad-sense heritability estimate (h^2), selection gain by MMI$_{PC}$ considering 1% of selection intensity (SG.PC), selection gain by phenotypic MMI$_{Uni}$ considering 1% of selection intensity (SG.MM), selection gain by univariate analysis considering 1% of selection intensity (SG.Uni), relative selection gain given by SG.CP/ and SG.Uni (rSG.PC), relative selection gain given by SG.MM and SG.Uni (rSG.MM), and general mean ($\overline{X}$).

Selection method	FGW‡	TDM	DEN	VEL	REG‡	LDM	%L	L:S	CP‡	NDF‡	IVD	LIG.S
MMI$_{PC}$												
HB-2002	954.71	874.99	0.33	0.38	1.13	0.00	0.00	0.00	0.52	0.12	–1.59	0.26
HB-1954	1083.64	924.72	0.43	0.38	1.13	0.00	0.00	0.00	1.70	–0.04	1.44	–0.01
HB-1620	1753.89	1807.96	0.08	–0.05	0.15	0.00	0.00	0.00	0.04	0.22	–0.05	–0.01
HB-1357	1253.53	931.12	0.25	0.40	0.56	0.00	0.00	0.00	0.27	1.00	–1.97	–0.03
HB-1908	956.76	839.45	0.25	0.40	0.51	0.00	0.00	0.00	0.33	0.37	–1.94	0.27
HB-1897	1186.26	1181.85	–0.05	0.19	0.22	629.27	1.44	0.00	0.15	–0.87	–1.54	0.09
HB-1871	937.62	845.44	0.19	0.18	0.38	0.00	0.00	0.00	0.54	0.67	–0.40	0.05
HB-1623	741.01	749.57	0.40	0.31	0.96	0.00	0.00	0.00	1.49	–0.92	2.16	–0.07
HB-1629	667.64	651.08	0.48	0.19	0.70	184.95	2.09	0.00	–0.25	–0.52	1.03	0.06
HB-1579	563.55	601.18	0.28	0.44	0.65	146.62	1.99	0.00	0.98	0.51	0.78	0.12
GV.PC	1009.86	940.74	0.26	0.28	0.64	96.08	0.55	0.00	0.58	0.05	–0.21	0.07
SG.PC	817.53	733.16	0.13	0.18	0.47	53.46	0.17	0.00	0.39	0.03	–0.10	0.03
MMI$_{Uni}$												
HB-1419	574.27	466.83	0.49	0.19	0.68	0.00	0.00	0.00	1.61	–2.42	2.85	–0.12
HB-1623	741.01	749.57	0.40	0.31	0.96	0.00	0.00	0.00	1.49	–0.92	2.16	–0.07
HB-2012	511.44	585.50	0.16	0.19	0.38	0.00	0.00	0.00	1.21	–1.85	1.34	0.04
HB-1366	470.19	361.33	0.18	0.44	0.95	0.00	0.00	0.00	1.24	–0.86	1.31	–0.12
HB-1964	523.00	574.90	0.27	0.19	0.59	0.00	0.00	0.00	1.25	–0.96	1.47	–0.04
HB-1863	499.87	442.51	–0.04	0.32	0.54	0.00	0.00	0.00	0.67	–1.44	0.56	–0.03
HB-1764	141.36	129.86	0.27	0.07	0.43	0.00	0.00	0.00	1.82	–2.28	3.16	–0.03
HB-1546	284.19	254.93	0.25	0.06	0.54	301.67	5.21	0.00	0.98	–1.58	1.34	–0.11
HB-1954	1083.64	924.72	0.43	0.38	1.13	0.00	0.00	0.00	1.70	–0.04	1.44	–0.01
HB-1984	254.37	196.12	0.23	0.05	0.33	81.22	1.31	0.00	1.47	–1.84	0.66	–0.08
GV.MM	508.34	468.63	0.26	0.22	0.65	38.29	0.65	0.00	1.34	–1.42	1.63	–0.06
SG.MM	411.52	365.23	0.13	0.14	0.48	21.31	0.20	0.00	0.91	–0.69	0.82	–0.02
GV.Uni	1138.70	1135.70	0.50	0.47	1.01	412.13	6.83	0.00	2.12	–2.83	4.24	–0.35
SG.Uni	921.83	885.11	0.26	0.29	0.75	229.32	2.12	0.00	1.43	–1.38	2.14	–0.15
rSG.PC	0.89	0.83	0.53	0.60	0.64	0.23	0.08	0.00	0.27	–0.02	–0.05	–0.21
rSG.MM	0.45	0.41	0.53	0.47	0.65	0.09	0.10	0.00	0.63	0.50	0.38	0.16
h^2	0.81	0.78	0.51	0.62	0.74	0.56	0.31	0.00	0.68	0.49	0.51	0.42
$\overline{X}$	1540.61	1790.55	3.57	1.81	2.29	767.86	66.92	2.57	15.75	64.41	73.32	2.17

† FGW, field green weight (kg ha⁻¹); TDM, total dry matter (kg ha⁻¹); DEN, density of regrown tillers; VEL, regrowth speed; REG, regrowth capacity; LDM, leaf dry matter (kg ha⁻¹); %L, percentage of leaves; L:S, leaf/stem ratio; CP, crude protein (%); NDF, neutral detergent fiber (%); IVD, in vitro organic matter digestibility (%); LIG.S, lignin in H_2SO_4 (%).

‡ Traits used for direct selection in MMI.

population of diploid *U. ruziziensis* (Simeão et al., 2016c), or *Panicum virgatum* L. (Bhandari et al., 2010) or *Panicum maximum* (Resende et al., 2004). Most of the traits evaluated presented more addictive effect, so the selection and use of parents with higher GCA are reasonable (Mendes et al., 2015). It must be considered, however, that there was no statistically significant variability between sexual and apomictic parents for several traits (Table 2). Thus, the indications are of sexual parents BS15 and 336-T2 for higher REG, 336-T1 for higher CP, and 336-T2 for lower NDF.

The FGW and the TDM are volume-related characteristics of forage on pasture, which are used for estimating the potential forage on offer and the definition of carrying capacity (Santos and Corrêa, 2009). These traits showed high variability of nonadditive origin in the case of this population, and only SCA was significant. In this case, the selection should be based on the performance of the best cross (e.g., B140 × 336-T1 to improve FGW, Table 5). This result is the opposite of what was observed in *U. humidicola*, in which there was significant difference between the sexual parents for GCA and no significant interaction (SCA) between sexual and apomictic parents for FGW and TDM (Figueiredo, 2015). In *U. ruziziensis*, significant additive variability was also observed for FGW

and TDM, with narrow-sense heritability of 0.31 and 0.30, respectively (Simeão et al., 2017). These values of heritability are lower than observed for the same traits in this interspecific population of *Urochloa* spp., with FGW = 0.46 and TDM = 0.59 (Table 2).

The absence of the effect of crosses (SCA) for some of the traits was expected (Table 2), since this population comes from interspecific crosses between polyploid heterozygous species, so that there are many sources of variation within and among progenies, to the point of not being able to clearly discriminate parents or ideal combinations. The genetic composition of the hybrids within the progenies is variable, and some may show high hybrid vigor whereas others have much lower vigor within the same progeny, which can contribute to the nonsignificance of the effect of crosses for many traits (Figueiredo, 2015). Then, the best and worst hybrids are distributed among all progenies, and it is not possible to identify the best progeny. Factorial statistical models usually promote a good fit of data from partial diallel. However, the incorrect specification of parameters in the construction of complex model reduces the absorption of variability and consequently affects GCA and SCA (Ogut et al., 2014). It is possible that the number of parameters used in Eq. [1] could also have influenced the lack of significance of the parents and crosses.

Estimates of the proportions of the additive variance and dominance were considered of moderate to high magnitude for FGW, TDM, REG, CP, and NDF in the progenies evaluated (Table 2). In progenies of half-sibs, it has been reported that for traits with lower heritability estimates, greater gain is expected when selecting the parents. However, for broad-sense heritabilities of more substantial magnitude, combined selection methods are indicated, such as selection between progenies and individual selection (HS-IND), as well as those that are based on the selection of individual phenotypes combined with information about the progeny (CSBLUP) (Resende et al., 2013). In this population, however, the selection of parents is not indicated, since there are only four parents, which could quickly increase inbreeding of the population (Han and Casler, 1999). Studies on the effect of selection on the inbreeding in populations of *Urochloa*, however, have not yet been conducted to confirm this assumption. In this case, for univariate selection, the evaluation and use of the CSBLUP, HS-IND, or individual selection methods are indicated.

Traits such as FGW, REG, CP, IVD, NDF, and Lig.S are the most important in forage breeding since they tend to correlate well with animal production, indicating a plant with good quantity and quality of forage (Sousa et al., 2007; Montagner et al., 2012). The results did not point to a single parent or crossing that could deliver all these characteristics at the same time (Table 5), but there are hybrids in the population that in a multivariate context fall within this ideotype (Fig. 2). The nonstandardization of

complementarity of the parents, in a multivariate context, supports the idea of maintaining all parents and recombination of the sexual parents associated with selection at the hybrid level (individual selection). Selected hybrids should be evaluated on their reproductive system, and if they are sexual, they should be used as parents in crosses; if they are apomictic, they can follow the next steps of the breeding program (Jank et al., 2014).

Traits Correlations

There were positive correlations between FGW and TDM with structural characteristics such as NDF and Lig.S. On the other hand, FGW and TDM exhibited a negative correlation with CP and IVD, thus the higher the weight of a plant, the higher its fiber and lignin content and lower its protein. A similar pattern was observed between the REG, FGW, and TDM, with positive correlation of ~50% and low or no correlation of REG with CP, IVD, NDF, and Lig.S. These results were unlike those observed in *U. decumbens* (Matias et al., 2016) and *U. ruziziensis* (Simeão et al., 2016a), in which the increase in weight and regrowth promotes an increase in fiber and lignin for dealing with structural components of the cell wall (Van Soest, 1995; Mauri et al., 2015). It indicates that, for this population, higher regrowth capacity should not promote changes in protein, fiber, and lignin. Furthermore, since the regrowth potential depends on the density and speed of growth, with a positive correlation of ~70%, the selection for REG by itself is recommended, since it should automatically increase VEL and DEN

It is interesting to note that when performing selection for CP, which has higher heritability, one strategy is indirectly selecting for digestibility without drastically reducing the FGW and TDM (Table 8), due to the lower correlation between these traits (Table 4). These observations contrast with those for *U. humidicola* (Figueiredo et al., 2012) and *U. decumbens* (Matias et al., 2016), where a high negative correlation between CP and FGW jeopardized the selection of one in favor of the other. One possibility is that the presence of alleles from *U. ruziziensis* of high nutritional value (Euclides and de Medeiros, 2003), and from *U. brizantha* and *U. decumbens* that involve good agronomic production (Jank et al., 2014), allowed for a balance or independence of these groups of contrasting traits. Therefore, these results indicate that hybrids with high FGW, REG, and CP and low NDF and LIG.S can be identified. Thus, through multivariate analysis, such as the principal components or multivariate indices, it should be possible to find desired ideotypes for selection of a potential cultivar (Jain and Patel, 2016).

Correlation between agronomic and nutritional characteristics similar to this experiment have been estimated for a population of *U. ruziziensis* (Simeão et al., 2016c), where the concentration of fiber and cellulose were found

Table 8. Selection gain for nutritional traits considering 1% selection intensity. Values along the diagonal (in bold) indicate direct selection gains (10 superior hybrids selected in the univariate analysis, Table 6). Values above and below the diagonal are indirect selection gains.

Trait†	Selection intensity											
	FGW	TDM	DEN	VEL	REG	LDM	%L	L:S	CP	NDF	IVD	LIG.S
	%											
FGW	**59.84**	47.24	2.22	8.97	16.34	9.23	−0.10	0.00	0.63	0.55	−0.92	2.52
TDM	56.29	**49.43**	0.98	6.04	10.01	17.09	−0.32	0.00	−0.79	0.65	−1.01	3.11
DEN	12.81	10.10	**7.15**	3.23	24.25	2.65	0.28	0.00	−0.41	−0.20	−0.03	−0.97
VEL	18.41	15.54	−1.32	**16.19**	15.86	0.00	0.00	0.00	−1.52	0.59	−0.59	1.52
REG	19.51	14.54	5.51	9.79	**32.52**	1.76	0.23	0.00	−0.15	0.27	0.00	−0.08
LDM	37.91	34.39	1.27	6.32	11.38	**29.86**	0.42	0.00	−0.44	0.30	−0.59	2.26
%L	−5.26	−1.40	1.75	0.15	7.85	−2.15	**3.17**	0.00	1.64	−0.58	0.40	−1.03
L:S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	0.00	0.00	0.00	0.00
CP	−10.52	−7.54	−0.32	−6.20	−9.69	−7.63	−0.17	0.00	**9.09**	−0.83	1.03	−1.79
NDF	−14.88	−14.57	−0.57	−4.37	−8.85	−1.99	−0.40	0.00	2.37	**−2.15**	0.84	−3.19
IVD	−10.51	−9.86	−0.98	−1.84	−7.77	−3.82	−0.54	0.00	4.48	−0.51	**2.92**	−1.87
LIG.S	−22.66	−19.21	−0.61	−6.50	−8.27	−6.98	−0.61	0.00	0.91	−1.07	0.34	**−6.72**

† FGW, field green weight (kg ha⁻¹); TDM, total dry matter (kg ha⁻¹); DEN, density of regrown tillers; VEL, regrowth speed; REG, regrowth capacity; LDM, leaf dry matter (kg ha⁻¹); %L, percentage of leaves; L:S, leaf/stem ratio; CP, crude protein (%); NDF, neutral detergent fiber (%); IVD, in vitro organic matter digestibility (%); LIG.S, lignin in H_2SO_4 (%).

to be inversely proportional to CP concentration. It follows the principle of plant physiology that growth or maturity brings about the deposition of cell wall structures and reduces energy reserves (Van Soest, 1995). However, for legumes such as *Arachis* (perennial peanut), there were positive correlations of CP with LIG.S, NDF, and TDM (Simeão et al., 2016b), indicating that biomass is directly related to the concentration of CP and nutritional value in forage legumes (Phelan et al., 2014).

The strong correlation between FGW and TDM allows for early selection of forage biomass (Borges et al., 2011). The selection of hybrids with greater digestibility provides high CP content in the population (Torres et al., 2016). Understanding the correlations between the traits and determining the forage ideotype assists in selection of superior hybrids in breeding programs. Direct selection for a characteristic can also promote indirect and disadvantageous selection of other characteristics; for example, direct selection for CP and IVD led to the reduction of FGW and TDM (Table 8). Also, the selection to reduce Lig.S could lead to a reduction in FGW and TDM (Table 8). In this case, selection in a multivariate context becomes an interesting alternative.

Multivariate Selection and Choice of Potential Cultivars

Multivariate selection in forages is intended to select commercial ideotypes or to characterize germplasm banks, as previously described in *P. maximum* (Martuscello et al., 2015), *Pennisetum glaucum* (L.) R. Br. (Kumari et al., 2017), *U. humidicola* (Assis et al., 2014), and *U. brizantha* (Olivera et al., 2014). In a multivariate analysis involving principal components, it is possible to identify groups of crosses that present desirable commercial standards in progenies (Beheshtizadeh et al., 2013; Legesse et

al., 2013). In this study, however, there was no pattern to define a better parent or multivariate cross. Nonetheless, it was possible to individually select hybrids that approached the commercially desirable ideotype (Fig. 2). The variability observed within the same progeny was expected, since it contained both the best and the worst hybrids at the same time.

In the literature, there are approaches for multivariate selection by different techniques, such as the canonical analysis used by Martuscello et al. (2015) to select hybrids of *P. maximum* adapted to the conditions of the Agreste region in Alagoas, Brazil. The authors selected genotypes with high leaf production, height, and L:S and intermediate values of volumetric density of forage. Multiplicative multivariate indices were used to select tetraploid *U. ruziziensis* genotypes to simultaneously tackle greater regrowth after cutting, dry matter, and CP concentration (Simeão et al., 2016a). In *Arachis* spp., the MMIs were used to select genotypes with higher dry matter content in the dry season and the wet season, less fiber content, and the highest concentration of protein in the stem (Simeão et al., 2016b).

In this work, using the MMI_{PC} index to accomplish selection in an interspecific population of *Urochloa* spp., the gains compared with univariate selection were higher for agronomic characteristics and lower or negative for the nutritional ones (Table 7). On the other hand, although the use of the MMI_{Uni} index did not result in higher gains for agronomic characteristics (SG.MM in Table 7) as observed for MMI_PC (SG.PC in Table 7) (e.g., 411.52 and 817.53 kg ha⁻¹ for FGW, respectively), at least it did not promote the reduction of the ones for nutritional value, as observed for digestibility where the SG.PC was −0.1 and SG.MM was 0.82. Thus, the MMI_{Uni} is perceived as a more balanced index between agronomical and nutritional traits, with gains in both groups of traits. This is due to the fact that

principal component analysis reorganizes the contribution of each trait to capture the most variability in the first component (Marques and Marques, 2005); in our case, the first two components represented mostly the variability associated with agronomic characteristics that are privileged with more significant gains than nutritional traits in MMI_{PC} (Table 7). The MMI_{Uni} considered each trait individually and thus provided a higher balance of multivariate gain than MMI_{CP}. Therefore, the use of the traits directly in the MMI to perform multivariate selection is indicated.

CONCLUSIONS

This study sought to obtain a better understanding of the inheritance of the most important traits and selection criteria for *Urochloa* hybrids to help the plant breeder in choosing a selection method to obtain new commercial hybrids. There was no clear trend in the importance of additive and nonadditive effects on agronomical and nutritional traits. Furthermore, the predominant component changed regarding the trait. Understanding the genetic behavior of the main traits, as well as the correlations between traits, should facilitate the choice of the best selection criteria. This information is also expected to contribute to the definition and construction of multivariate indices to identify superior hybrids. The MMI, per se, at the univariate level, promoted a more efficient response to selection for all traits.

Conflict of Interest

The authors declare that there is no conflict of interest.

Supplemental Material Available

Supplemental material for this article is available online.

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