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# Unravelling the inheritance, $Q_{ST}$ and reproductive phenology attributes of the tetraploid tropical grass *Brachiaria ruziziensis* (Germain et Evrard)

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## Abstract

The autotetraploid forage Congo signal grass (*Brachiaria ruziziensis*) is an important component in the *Brachiaria* breeding programme. As with other tropical forage grass species, the association between flowering and seed yield components, the mode of inheritance and the effects of population structure on phenotypic breeding are lacking. Seventeen characteristics evaluated in 59 half-sib progeny of seven subpopulations were analysed using a mixed model methodology. According to the commonality analysis, the total seed yield (0.67) and number of days to flowering (0.22) had a greater influence on the filled-seed yield. The flowering synchrony, total number of panicles, filled-seed yield, green matter yield and dry matter yield presented statistically significant additive genetic variance between and within the subpopulations. The $Q_{ST}$ estimates ranged from 0.09 for the flowering synchrony index to 0.31 for the filled-seed yield. The effects of population structure and its use in breeding programmes are further discussed.

**Key words:** commonality — flowering — genetic correlation — heritability — population — structure — progeny test — seed yield — synchrony index

*Brachiaria ruziziensis* (syn *Urochloa ruziziensis* R. Germ. & Evrard Crins) is a diploid species ($2n = 2x = 18$) with a narrow distribution in Burundi and Rwanda, and it is a naturally occurring species in grasslands and in disturbed locations (Keller-Grein et al. 1996). Seven artificially induced tetraploid genotypes ($2n = 4x = 36$) were developed by Swenne et al. (1981) and successfully used for interspecific hybridization in Brazilian and Colombian in *Brachiaria* breeding programmes (Miles et al. 1996, Valle and Savidan 1996, 1996, Worthington and Miles 2015). Both ploidy levels in *B. ruziziensis* present sexual modes of reproduction that differ from most naturally polyploid modes, which are apomictic (Pagliarini et al. 2008). The study of Ferguson and Crowder (1974) demonstrated that the sexually diploid *B. ruziziensis* is highly self-incompatible. In addition, autotetraploid individuals present low levels of self-compatibility, but these levels may vary among individuals (Lutts et al. 1991).

Although the focus on sexual autotetraploid *B. ruziziensis* breeding has increased the plant's biomass yield and nutritional quality via hybridization with apomictic species (Simeão et al. 2016a), evaluations of seed yield are crucial for the selection of individuals that are reproductively viable and capable of producing hybrid cultivars that meet the market demand for seed. In Poaceae, seed yields are generally affected by several components and their interactions, including seed retention (Boelt and Studer 2010), which has not been a target for selection in non-domesticated grass forages species.

Information on the genetic variability and inheritance mode of seed yield and the genetic correlations between seed yield and other characteristics is lacking for most tropical grass forage species. Moreover, seed yield has rarely been considered a selection criterion in the early stages of breeding programmes. Similar information has been reported for important temperate species, such as switchgrass (Das and Taliaferro 2009) and alfalfa (Bolaños-Aguilar et al. 2000), for which breeding to improve seed yield is important because this characteristic is essential for improving the plant's ability to compete in the commercial market for grass cultivars (Fang et al. 2004).

There is limited information on forage grass seed production, and it is unclear why production results in fewer mature seeds than the number of ovules available for fertilization (Stür and Humphreys 1987, Studer et al. 2008). Moreover, information is lacking on inheritance in tropical forage grasses and the relationships among traits associated with seed yield, for which information on genetic parameters is essential. Genetic correlations are informative for the indirect selection and identification of correlated responses to selection, primarily when the genetic correlations are strong. However, the observed and predicted correlated responses may not be found under weak genetic correlations (Falconer and Mackay 1996). Genetic correlations between characteristics indicate relationships caused by genetic pleiotropic effects, including linkage disequilibrium, which may cause transient correlations. Analyses of commonality are analogous to path coefficients (Kloth 1998, Zeng et al. 2014) and more appropriate for use with general linear models because these analyses are better able to determine the unique and common contributions of predictor variables to dependent variables (Zeng et al. 2014). Analyses of commonality have been employed to evaluate *B. ruziziensis* to determine the causal relationships between filled-seed yield and other characteristics. The commonality parameter provides information on the variance explained by each of the measured characteristics and the common contribution from one or more additional characteristic (Capraro and Capraro 2001), and this information may be useful for selection and breeder decision-making.

In Brazil, efforts to obtain a segregating population and select the best individuals within this population in the breeding programme of *B. ruziziensis* have been intensified under the objective of improving hybrid cultivars. Breeding programmes begin by completely characterizing the founders of the segregating population according to seven autotetraploid individuals in the germplasm. Intraspecific breeding research must be undertaken to improve the decision-making and selection processes for identifying the best alternatives. One approach involves the use of population genetics theory to explain the potential genetic differentiation among the ancestral populations measured by $Q_{ST}$. $Q_{ST}$ is a quantitative genetic analog of Wright's $F_{ST}$ that uses

phenotypic traits and measures the amount of additive genetic variation among the population relative to the total genetic variance in the quantitative character (Holsinger and Weir 2009, Leinonen et al. 2013). Information on population structures has been used in fundamental (evolutionary biology, ecology and genetics, e.g. in Jungmann et al. 2010) and applied research (forestry management and conservation biology, e.g. in Pressoir and Berthaud 2004). However, population structure data are infrequently applied to breeding programmes, particularly in *B. ruziziensis*, for which the population structure is modified and likely broken as the breeding cycles progress.

Our data on *B. ruziziensis* breeding comply with all of the requirements described by Leinonen et al. (2013) for estimations of the parameter $Q_{ST}$. Specifically, this study is a breeding experiment that is conducted under standardized conditions and designed to evaluate half-sib progeny within subpopulations in which the within-subpopulation components of variance truly reflect the additive genetic variance.

Swenne et al. (1981) and Lutts et al. (1991) reported that tetraploid sexual *B. ruziziensis* was obtained by colchicination of diploid *B. ruziziensis* accessions collected in the Ruzizi plain (Burundi, Africa). Despite the geographic origin of the diploid individuals used in *B. ruziziensis* tetraploidy induction, the number of diploid individuals involved cannot be determined whether differences in local subpopulations occurred. Because the seeds received at Embrapa Gado de Corte, Brazil, were identified as seven different tetraploid accessions, our strategy was to define each autotetraploid accession as a representative of an ancestral subpopulation. Therefore, seven autotetraploid accessions were used as the basis of the breeding programme designed to obtain interspecific hybrids. In addition, to amplify their genetic variability and promote intraspecific selection within a hybrid population, we obtained 59 open-pollinated half-sib families from these seven individuals, and their progeny were experimentally evaluated according to the method of Simeão et al. (2016a). Accordingly, the seven original autotetraploid individuals were designated as the ancestral structural population. Each individual was classified as a subpopulation, and each progeny was connected to that ancestry and investigated.

The objectives of this study were to (i) assess the genetic variation and heritability of traits related to seed yield, (ii) determine the genetic correlations and commonality between seed yield and its components, (iii) determine the association between the phenological behaviour of flowering and seed yield and (4) estimate the population differentiation and its effect on *Brachiaria ruziziensis* breeding.

## Materials and Methods

Fifty-nine half-sib sexual and tetraploid progeny of *B. ruziziensis* were obtained by open pollination of seven original autotetraploid-induced accessions (R30, R38, R41, R44 R46, R47 and R50), which are treated here as the original subpopulations. The number of progeny per subpopulation varied around an average of eight. Simeão et al. (2016a,b) described in detail the methods used to generate and evaluate the 59 progeny studied here. Briefly, the experiment included 20 replications and one plant per plot (1.5 m × 1.5 m spacing), and the plants were sown in November 2012 in a randomized block design. The experiment was performed at Embrapa Gado de Corte in Campo Grande, Mato Grosso do Sul State, Brazil, 20°28′ latitude south, 55°39′ longitude west, altitude 530 m. The field soil is classified as Haplic Ferralsol (Rhodic) (FAO 2006). According to the Köppen climate classification, the region has a type Aw humid tropical climate with rainy summers and dry winters.

The characteristics regrowth capacity, as described by Figueiredo et al. (2012), green matter yield (GMY – in g per plant), total dry matter yield (DM yield – in g per plant) were evaluated on 22/01/2014 by clipping individuals at a height of 15 cm 21 days before the beginning of the phenological evaluation of flowering. Individuals were allowed to grow freely until seed harvest, and the nutritional characteristics were studied according to Simeão et al. (2016a).

The number of days to the first flowering (DTF) was counted for individual plants starting from the date of the last clipping on 22/01/2014, and the plants were considered to have flowered when three panicles per plant had started anthesis. The flowering evaluation occurred weekly over a period of 84 days.

The seed harvest occurred weekly over a period of 61 days starting on 03/04/2014 and ending on 02/06/2014. Individual plant mature panicles were clipped in the field and transported to the laboratory. The seeds were threshed, weighed to determine the total yield, aspirated and then weighed again to obtain the filled-seed yield. A 2-week overlap occurred between the last evaluations of flowering (Simeão et al. 2016b) and the start of seed harvest.

During seed harvest, the monthly rainfall was 42 mm, 100 mm and 54 mm and the mean minimum and maximum temperatures were 20°C/30°C, 16°C/26°C and 16°C/27°C for the months of April, May and June, respectively. The historical average monthly values for these months (1961 to 2014) for rainfall and temperature were 80 mm, 87 mm and 41 mm and 18°C/29°C, 16°C/27°C and 15°C/27°C, respectively.

**Calculating the overlap in flowering and seed harvest time via the synchrony index:** An index of synchronous flowering was calculated for each individual *i*, according to the expression presented by Mahoro (2002):

$$S_i = \frac{1}{2}\left(2 - \sum_{j=1}^{n}\left|y_{i,j} - \bar{y}_{i,j}\right|\right),$$

where $y_{i,j}$ is the ratio of newly opened flowers between the $(j-1)th$ census day and the $j$th day and the total number of flowers that opened during the season; $\bar{y}_{i,j}$ is the mean of all individuals; and $n$ is the last census day during flowering. The index varies from zero to one, and a larger $S_i$ indicates higher synchrony with other individuals (Mahoro 2002). The method for calculating the synchrony index proposed by Mahoro (2002) includes an opening rate that occurs on a specific day for each individual, and it is more suitable for distinguishing and quantifying differences between individuals along a relatively synchronous schedule. The mean number of flowering panicles per progeny, which is expressed as a percentage, was calculated as a function of the census period during which the individuals were flowering.

Because seasonal seed data (total and filled) and flower data were similarly obtained, the previously mentioned calculation method was employed to estimate the seed yield synchrony as a phenological event according Mahoro (2002).

**Estimation of genetic parameters:** A univariate analysis was performed using linear mixed models and the statistical model:

$$y = Xr + Za + Ts + e,$$

in which $y$ represents the data vector, $r$ represents the vector for replicate effects (fixed) added to the general mean, $a$ represents the vector of individual additive genetic effects (random), $s$ represents the vector of subpopulation effects (random), and $e$ represents the random residual vector. Capital letters represent the incidence matrices for the mentioned effects. Hypothesis testing in this analysis context was performed using the likelihood ratio test (LRT), which evaluates the difference between the deviances associated with the fit of two alternative models as described by Simeão et al. (2016a) using the same statistical considerations. The statistical analysis was performed using the Selegen – REML/BLUP software (Resende 2002, Resende et al. 2014, Simeão et al. 2016a), which provides statistical estimates of genetic parameters and breeding value prediction. The following parameters were estimated.

1 Narrow sense individual heritability:

$$h_a^2 = \frac{\sigma_a^2}{\sigma_y^2},$$

where $\sigma_a^2$ is the average additive genetic variation within subpopulations and can be estimated from within-subpopulation information (Holsinger and Weir 2009) and $\sigma_y^2$ is the total phenotypic variance between and within subpopulations.

2 Coefficient of determination of subpopulation effects:

$$h_{pop}^2 = \frac{\sigma_{pop}^2}{\sigma_y^2},$$

where $\sigma_{pop}^2$ is the genetic variation between subpopulations and can be estimated from the information between subpopulations (Holsinger and Weir 2009).

3 Total accuracy and $Q_{ST}$ (Resende et al. 2014):

$$r_{\hat{g}g} = [r_{\hat{g}gprog}^2(1 - Q_{ST})/(1 + Q_{ST}) + r_{\hat{g}gpop}^2 2Q_{ST}/(1 + Q_{ST}) + 0.75h_{aw}^2(1 - Q_{ST})/(1 + Q_{ST})]^{1/2}$$

where $r_{\hat{g}gprog}$ is the accuracy of progeny within the subpopulation effect, $r_{\hat{g}gpop}$ is the accuracy of the subpopulation effect, $h_{aw}^2$ is the within-progeny heritability, and $Q_{ST}$ is the coefficient of endogamy caused by differentiation among subpopulations (Lande 1992, Spitze 1993) and was estimated as follows:

$$Q_{ST} = \frac{\sigma_{pop}^2}{\sigma_{pop}^2 + 2\sigma_a^2}.$$

The fraction of the genetic variance that is among subpopulations relative to the total genetic variance was estimated as follows:

$$\rho_p = \frac{\sigma_{pop}^2}{\sigma_{pop}^2 + \sigma_a^2}.$$

4 Genetic correlations between characteristics (Falconer and Mackay 1996):

$$r_{a(x_1,x_2)} = \mathrm{cov}_{a(x_1,x_2)}/\sigma_{ax_1}\sigma_{ax_2},$$

where $\mathrm{cov}_{a(x_1,x_2)}$ is the additive genetic covariance between $x_1$ and $x_2$ and $\sigma_{ax_1}$ and $\sigma_{ax_2}$ are the additive genetic standard deviations for $x_1$ and $x_2$, respectively.

5 Commonality (Resende et al. 2014): The concept of commonality ($\mathrm{Com}(x_1, x_2)$) between two variables refers to a correlation coefficient penalized by the interaction between two variables. Its numerator is the common variance or covariance, and its denominator is the sum of the common variance with the specificity or interaction between two variables:

$$\mathrm{Com}(x_1, x_2) = \frac{Cov(x_1, x_2)}{Cov(x_1, x_2) + Var_{int}(x_1, x_2)}.$$

The variance of the interaction between two variables can be estimated by

$$\mathrm{Var}_{\mathrm{int}}(x_1, x_2) = \frac{\mathrm{Var}(\mathrm{x}_1) + \mathrm{Var}(\mathrm{x}_2)}{2} - \mathrm{Cov}(x_1, x_2),$$

Thus, $\mathrm{Var}_{\mathrm{int}}(x_1, x_2)$ is estimated as the average of the variances of the two variables minus the covariance between them. The commonality and the ordinary correlation are two alternative concepts of congruence or standardized (scaled) covariation, that is of correlation. In ordinary correlation, covariance is scaled (divided) by the geometric mean of the variances, that is:

$$\mathrm{Cor}(x_1, x_2) = \frac{\mathrm{Cov}(x_1, x_2)}{\sqrt{\mathrm{Var}(x_1)\mathrm{Var}(x_2)}}.$$

In the commonality, the covariance is scaled (divided) by the arithmetic average of the variances, that is:

$$\mathrm{Com}(x_1, x_2) = \frac{\mathrm{Cov}(x_1, x_2)}{\mathrm{Cov}(x_1, x_2) + Var_{int}(x_1, x_2)} = \frac{Cov(x_1, x_2)}{\frac{Var(x_1)+Var(x_2)}{2}}.$$

The commonality is lesser than or equal to the ordinary correlation and deviates from 1, to the extent that the interaction between the two variables increases. Thus, the commonality is a more conservative estimator of the association than is the ordinary correlation. Then, the commonality is a correlation measure free from interactions effects, scale and heterogeneity of variances, therefore being of great importance to breeding.

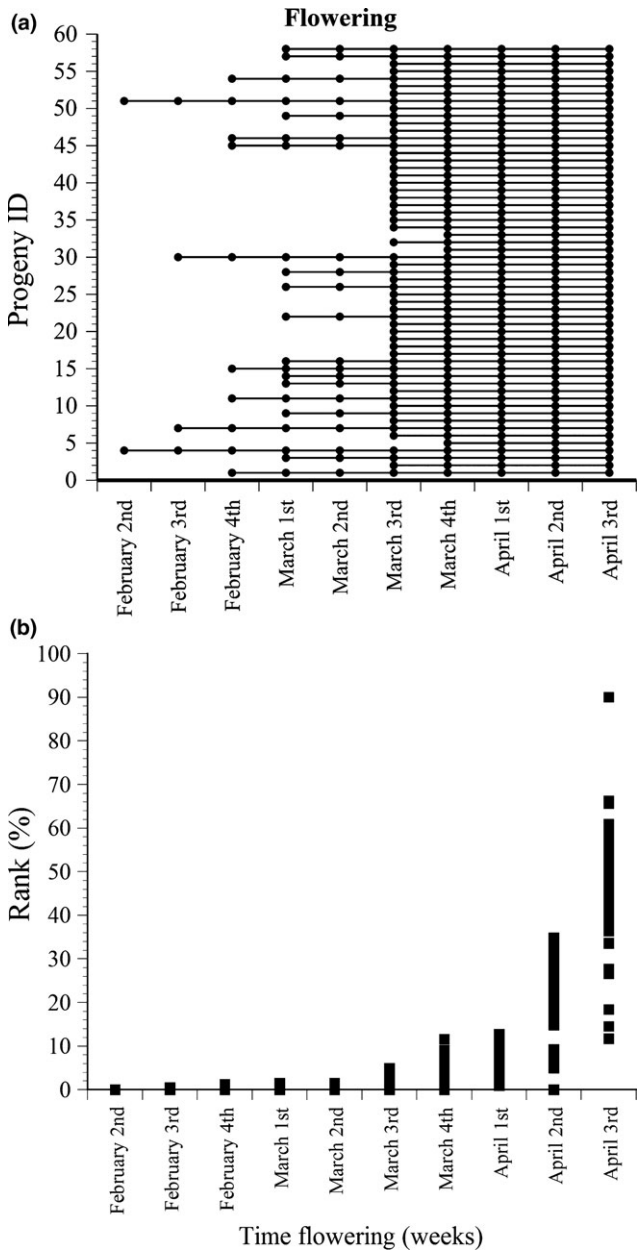


Fig. 1: Onset of flowering in 58 experimental progeny of *Brachiaria ruziziensis* tetraploid, in which each line represents each progeny and each dot represents the onset of one or more individual in that progeny, weekly (a) and rank of progeny flowering in weeks (b)

## Results

### Phenological aspects

In the *Brachiaria ruziziensis* tetraploid breeding population, flowering onset occurred throughout February and April; however, differences in onset and duration were observed between (Fig. 1a) and within the progeny. Three–five per cent of the progeny exhibited flowering onset on the third week in March, and by the fourth week, all progeny had at least one individual flower. Flowering onset was variable among the progeny. Two progeny flowered within 10 weeks, and 24 progeny

presented flowering onset after the sixth week. Of the 59 progeny studied, one entire progeny was flowerless and concomitantly seedless over the evaluation time. On average, 46 per cent of individuals in each progeny had flowered by the third week of April based on the rank of flowering (Fig. 1b). In addition, 0.2 per cent of individuals in each progeny were flowering at the first week, and 70% of individuals in each progeny were flowering at the last week of evaluation. In one progeny, 90% of individuals presented late flowering lately in the third week of April.

The flowering period overlapped with the start of the seed production and the harvest period on the second and third weeks of April. Seeds were harvested from April to the end of May. The onset of seed production ranged from four to 10 weeks for the mean number of progeny (Fig. 2a). The filled-seed yield was more variable among progeny, with intervals of production among individuals within progeny (Fig. 2b). Only one progeny produced filled seeds in the fifth week of May. Individuals within-progeny populations that produced filled seeds increased from a mean of 1% in 36 progeny in the first week of April to a mean peak of 36% among all 58 progeny in the first week of May, and this value decreased to 1% in only four progeny in the fifth week of May (Fig. 2c).

The synchrony index method was helpful for quantifying the synchronous between individual variation within the population and demonstrated the superposition of flowering between individuals (Fig. 3a). Sixty-seven per cent of individuals presented a large flowering synchrony index ($S_i > 0.8$ – Fig. 3a). However, 33% of flowering individuals were in relative asynchrony ($0.1 < S_i < 0.7$), and variation in this phenological trait was observed among individuals and progeny.

The synchrony index estimated for the seed yield, and filled-seed yield was 33% and 41%, respectively, and it showed moderate-to-low index peak values of 0.6 and 0.5, respectively (Fig. 3a). The filled-seed synchrony index presented low values ranging from 0.3 to 0.4 between subpopulations and from 0.2 to 0.5 among progeny. The correlation between the flowering synchrony index and filled-seed synchrony index was low and not significant ($r_a = 0.13$, $P > 0.05$, *Spearman's* rank correlation test) based on the progeny mean and per individual data. Individuals with a low flowering synchrony index presented a high seed-filled synchrony index (Fig. 3b), and the reciprocal was true as well.

### Phenological effects on seed yield and agronomic characteristics

According to the distribution classes based on the individual synchrony indices of flowering, the characteristics DTF, regrowth, crude protein (CP) and neutral detergent fibre (NDF) presented significant differences ($P < 0.05$, Tukey's test) among classes (Table 1). Individuals presenting a low (<0.4) flowering index synchrony were more precocious, which supported the results of the progeny flowering distribution (Fig. 1a). Because of the random distribution of their means among classes, CP, NDF and regrowth may not be directly associated with classes of flowering synchrony. The mean individual breeding value for total seed yield, regrowth, CP and NDF was statistically significant among the classes in the synchrony indices for filled-seed yield (Table 1). Total seed yield is associated with greater synchrony indices ($P < 0.05$) and a tendency to produce filled-seed; however, the results were not statistically significant. Similar to the results on classes of flowering synchrony indices, the averages for character regrowth, CP and NDF were randomly distributed among the filled-seed synchrony indices.

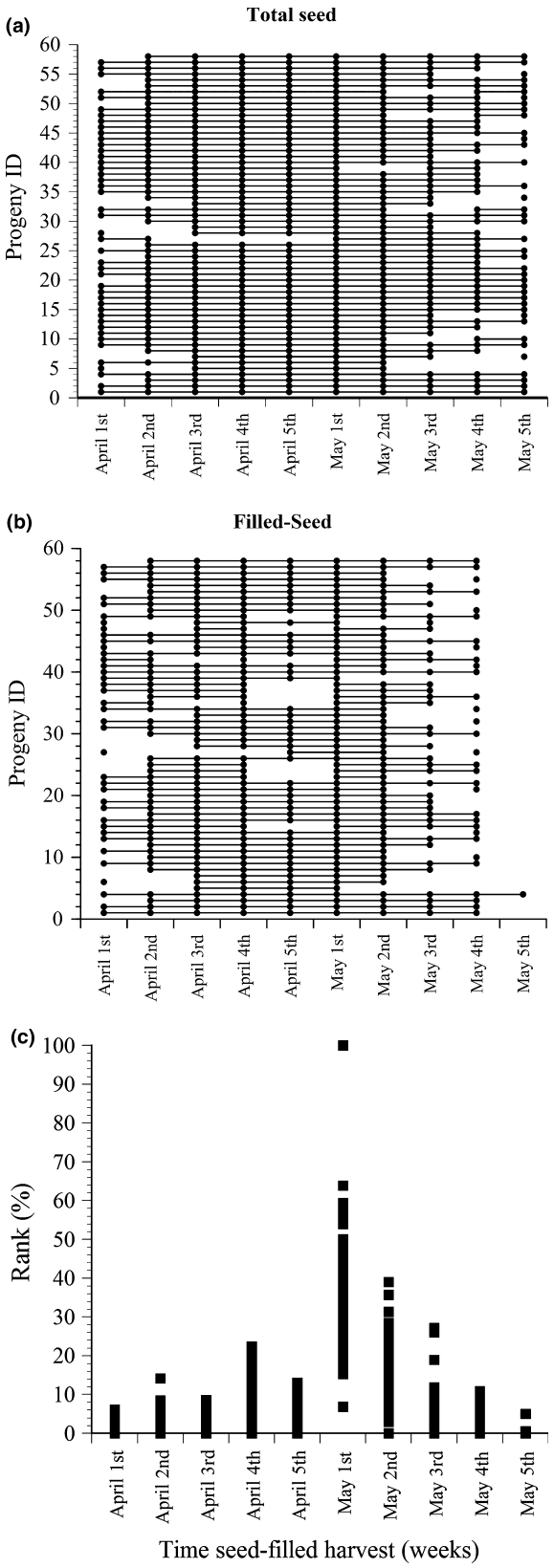


Fig. 2: Mean of total seed production weekly (a) and filled-seed (b) yield among 58 experimental progeny of *Brachiaria ruziziensis* tetraploid and rank of progeny filled-seed in weeks (c)

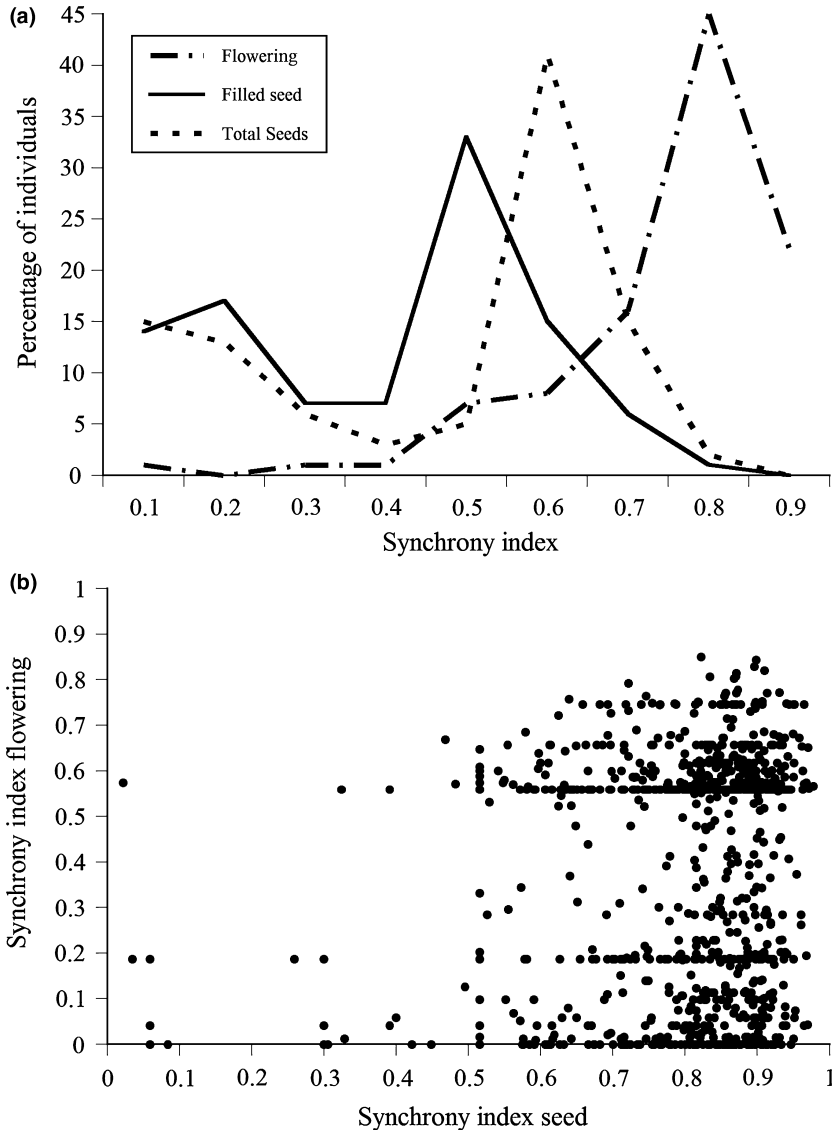


Fig. 3: Distribution of individuals per class of synchrony index for flowering, total seed and filled-seed yield (a), and relationship between synchrony indices of flowering and filled-seed yield for *Brachiaria ruziziensis* individuals (b)

Table 1: Classes of the synchrony index estimated for flowering (F) and filled-seed yield (S) and individuals mean breeding values in characteristics evaluated in the open pollinated progeny of tetraploid *B. ruziziensis*

| | DTF | | Number of panicles | | Total seeds (g) | | Filled seeds (g) | | Total DM yield (g) | | Regro-wth | | CP (g/kg) | | NDF (g/kg) | | IVOMD (%) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Synchrony index | F | S | F | S | F | S | F | S | F | S | F | S | F | S | F | S | F | S |
| 0.1 | 58 | 69 | 101 | 68 | 23 | 14 | 6 | 5 | 85 | 103 | 2 | 2 | 167 | 166 | 653 | 650 | 58 | 58 |
| 0.2 | 51 | 65 | 31 | 120 | 16 | 21 | 8 | 6 | 68 | 100 | 2 | 3 | 189 | 163 | 613 | 655 | 63 | 56 |
| 0.3 | 53 | 68 | 97 | 81 | 20 | 26 | 4 | 7 | 108 | 103 | 3 | 2 | 154 | 165 | 655 | 655 | 63 | 58 |
| 0.4 | 53 | 65 | 46 | 93 | 12 | 27 | 5 | 6 | 98 | 100 | 3 | 2 | 158 | 169 | 650 | 662 | 58 | 59 |
| 0.5 | 73 | 66 | 45 | 113 | 25 | 38 | 8 | 10 | 82 | 100 | 2 | 3 | 165 | 165 | 654 | 647 | 56 | 57 |
| 0.6 | 69 | 66 | 64 | 117 | 28 | 32 | 10 | 9 | 96 | 109 | 2 | 3 | 167 | 162 | 646 | 663 | 58 | 57 |
| 0.7 | 71 | 69 | 57 | 80 | 26 | 27 | 10 | 10 | 96 | 100 | 2 | 2 | 167 | 162 | 655 | 652 | 59 | 56 |
| 0.8 | 69 | 68 | 80 | 105 | 24 | 40 | 8 | 13 | 94 | 110 | 2 | 2 | 165 | 165 | 655 | 660 | 59 | 57 |
| 0.9 | 66 | 65 | 107 | 109 | 30 | 42 | 9 | 12 | 114 | 129 | 3 | 3 | 162 | 168 | 654 | 651 | 56 | 61 |
| P-value | ** | ns | ns | ns | ns | * | ns | ns | ns | ns | * | * | ** | ** | ** | ** | ns | ns |

**, * and ns – significant at 0.01 and 0.05 and not significant, respectively by Tukey′s test; DTF – Number of days to flowering; CP – Crude protein; NDF – Neutral detergent fiber; IVOMD – *in vitro* dry matter digestibility.

### Genetic characterization and $Q_{ST}$

Table 2 presents the estimates of the genetic parameters based on subpopulations and progeny tests of *B. ruziziensis* tetraploids. All of the characteristics exhibited considerably greater genetic variation within subpopulations than between subpopulations, based on the heritability magnitude (Table 2). The flowering synchrony index, total number of panicles, filled-seed yield,

Table 2: Estimates of the genetic parameters resulting the analyses using mixed linear models of phenotypic data associated with the phenology of flowering and seed yield, nutritional quality and agronomic traits for forage yield in progeny of *Brachiaria ruziziensis*

| Characteristics | $h_a^2$[1] | $h_{pop}^2$[2] | $\hat{r}_{\hat{g}gprog}$[3] | $\hat{r}_{\hat{g}gpop}$[4] | $\hat{r}_{\hat{g}g}$[5] | $Q_{ST}$[6] | Estimated mean | Phenotypic range | LRT[7] |
|---|---|---|---|---|---|---|---|---|---|
| Reproductive | | | | | | | | | |
| Flowering synchrony index | 0.21 | 0.04 | 0.66 | 0.73 | 0.80 | 0.09 | 0.8 | 0.1–0.9 | */* |
| Filled-seed synchrony index | 0.06 | 0.01 | 0.40 | 0.54 | 0.47 | 0.06 | 0.4 | 0.1–0.9 | ns/ns |
| Total number of panicles | 0.22 | 0.16 | 0.67 | 0.85 | 0.78 | 0.27 | 89.3 | 3–430 | */* |
| Total seed yield | 0.07 | 0.02 | 0.43 | 0.62 | 0.59 | 0.09 | 28.1 | 0.02–140.4 | ns/ns |
| Filled seed yield | 0.11 | 0.10 | 0.43 | 0.83 | 0.69 | 0.31 | 9.6 | 0.01–59.6 | **/** |
| Number of days to flowering | 0.23 | 0.01 | 0.67 | 0.47 | 0.71 | 0.02 | 68 | 21–84 | */ns |
| Nutritional quality | | | | | | | | | |
| Neutral detergent fiber (g/kg) | 0.01 | 0.01 | 0.15 | 0.66 | 0.56 | 0.52 | 653.6 | 487.4–910.2 | ns/ns |
| Acid detergent fiber (g/kg) | 0.09 | 0.03 | 0.51 | 0.74 | 0.64 | 0.15 | 332.9 | 218.5–722.9 | ns/ns |
| Cellulose (g/kg) | 0.18 | 0.01 | 0.64 | 0.56 | 0.73 | 0.03 | 193.8 | 117.3–262.7 | */ns |
| Lignin P (g/kg) | 0.20 | 0.02 | 0.66 | 0.63 | 0.75 | 0.04 | 97.6 | 39.8–302.3 | */ns |
| Crude protein (g/kg) | 0.11 | 0.02 | 0.55 | 0.65 | 0.64 | 0.07 | 164.1 | 104.5–218.4 | ns/ns |
| IVOMD[8] (%) | 0.02 | 0.01 | 0.30 | 0.50 | 0.37 | 0.09 | 56.9 | 6.6–76.2 | ns/ns |
| Agronomic | | | | | | | | | |
| Green matter yield (kg/plant) | 0.31 | 0.16 | 0.74 | 0.84 | 0.91 | 0.20 | 3.4 | 0.06–11.5 | */* |
| Dry matter yield (kg/plant) | 0.30 | 0.15 | 0.74 | 0.84 | 0.93 | 0.20 | 0.8 | 0.04–3.2 | */* |
| Regrowth | 0.11 | 0.04 | 0.54 | 0.78 | 0.68 | 0.17 | 3.4 | 0.5–5.0 | ns/* |

*, ** P < 0.005, 0.01; ns: not significant; [1]narrow sense heritability; [2]among population heritability; [3, 4 and 5]accuracy estimated on progeny selection, on population selection and total, respectively; [6]coefficient of endogamy among population; [7]likelihood ratio test for among progeny genetic variation/ among population genetic variation; [8]IVOMD – *in vitro* digestibility of dry matter.

GMY and DM yield presented genetic variance between and within subpopulations that was significantly higher than zero (P-value < 0.01) based on the LRT. These results confirmed the structure for many characteristics and the correct allocation of subpopulations. Other characteristics were not significantly different within subpopulations and between subpopulations (filled-seed synchrony index, total seed yield, DTF, acid detergent neutral – ADF, CP and *in vitro* digestibility of DM – IVOMD), indicating that the alleles for these characteristics are likely already fixed in the genetic material because of their evolutionary importance. Moreover, certain characteristics were exclusively significant within subpopulations (NDF, Cellulose – Cel and lignin via permanganate – Lig P) or between populations (regrowth). The narrow sense heritability within subpopulations varied from 0.11 to 0.31 for agronomic characteristics, from 0.01 to 0.20 for nutritional quality characteristics and from 0.06 to 0.22 for reproductive characteristics. The highest magnitudes of heritability among the subpopulations were observed for the total number of panicles, filled-seed yield, green matter yield and DM yield. The $Q_{ST}$ values ranged from 0.02 for DTF to 0.52 for NDF.

The $Q_{ST}$ values ranged from 0.09 to 0.31 when only the characteristics with significant genetic variation between and within populations were considered. According to the guideline proposed by Wright (1978) for interpreting $F_{ST}$ ($Q_{ST}$), the flowering synchrony index presented *little genetic* differentiation. The green matter yield, DM yield and regrowth presented *great genetic* differentiation (range 0.15 to 0.25), and total number of panicles and filled-seed yield, a *very great genetic* differentiation (above 0.25) between subpopulations. The proportion of genetic variation between subpopulations in relation to the total genetic variability indicates that the sources of variability within and between subpopulations must be considered when selecting for the total number of panicles ($\rho_p = 42\%$), filled-seed yield ($\rho_p = 48\%$), green matter yield ($\rho_p = 34\%$) and DM yield ($\rho_p = 33\%$). The total selective accuracy achieved for these characteristics increased when the between populations variability and individual trait accuracy were considered compared with selection based exclusively on within-subpopulation genetic variability or a mixture of progeny from all subpopulations. The contribution of the sub-population breeding value and accuracy to the individual breeding value is demonstrated in Table 3 for the characteristics in which the genetic variation between subpopulations was significant.

## Commonality and genetic correlation

Table 4 presents the results of the commonality and genetic correlations estimated for all 15 characteristics. A low magnitude of genetic correlation between the flowering and filled-seed

Table 3: Breeding value (BV) of the characteristics and accuracy among *Brachiaria ruziziensis* tetraploid subpopulations

| | Flowering synchrony index | | Number of panicles | | Filled-seed yield | | Green matter yield | | Total DM yield | | Regrowth | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Subpopulation | BV | Accuracy | BV | Accuracy | BV | Accuracy | BV | Accuracy | BV | Accuracy | BV | Accuracy |
| R30 | 0.8 | 0.63 | 76 | 0.82 | 11 | 0.78 | 332 | 0.80 | 91 | 0.79 | 2.5 | 0.70 |
| R38 | 0.7 | 0.79 | 147 | 0.88 | 6 | 0.87 | 538 | 0.88 | 141 | 0.88 | 2.6 | 0.83 |
| R41 | 0.8 | 0.50 | 76 | 0.73 | 14 | 0.66 | 387 | 0.72 | 102 | 0.71 | 2.4 | 0.58 |
| R44 | 0.8 | 0.83 | 70 | 0.90 | 10 | 0.89 | 313 | 0.90 | 85 | 0.89 | 2.3 | 0.86 |
| R46 | 0.8 | 0.72 | 94 | 0.86 | 8 | 0.83 | 397 | 0.85 | 106 | 0.84 | 2.5 | 0.76 |
| R47 | 0.8 | 0.81 | 88 | 0.89 | 8 | 0.88 | 480 | 0.89 | 128 | 0.88 | 2.6 | 0.84 |
| R50 | 0.7 | 0.83 | 71 | 0.89 | 10 | 0.88 | 291 | 0.89 | 81 | 0.89 | 2.3 | 0.86 |

Table 4. Commonality (above diagonal) and genetic correlations (below diagonal) among characteristics associated with flowering phenology, nutritional value and yield evaluated in the progeny of tetraploid *B. ruziziensis*

| Characteristics | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (1) Flowering synchrony index | – | −0.06 | −0.01 | 0.00 | 0.01 | −0.01 | −0.14 | 0.16 | −0.01 | 0.00 | −0.16 | 0.10 | 0.00 | 0.00 | 0.30 |
| (2) Filled−seed synchrony index | −0.07 | – | 0.00 | 0.00 | 0.00 | 0.01 | 0.03 | −0.16 | −0.10 | 0.02 | −0.03 | −0.06 | −0.01 | 0.00 | −0.02 |
| (3) Days to Flowering | −0.58* | 0.05 | – | −0.16 | 0.10 | 0.22 | 0.03 | 0.00 | 0.00 | −0.04 | 0.00 | 0.00 | −0.02 | −0.07 | −0.01 |
| (4) Number of panicle | 0.48* | −0.04 | −0.57* | – | 0.03 | −0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.20 | 0.40 | 0.00 |
| (5) Total seed yield | 0.16* | 0.03 | 0.11* | 0.14* | – | 0.59 | −0.03 | 0.00 | 0.00 | −0.08 | 0.00 | 0.00 | 0.02 | 0.07 | 0.03 |
| (6) Filled seed yield | −0.12* | 0.26* | 0.29* | −0.10* | 0.67* | – | 0.01 | −0.01 | 0.00 | −0.10 | 0.01 | 0.00 | 0.00 | 0.00 | 0.03 |
| (7) Crude Protein | −0.40* | 0.17* | 0.23* | 0.01 | −0.15* | 0.05 | – | −0.15 | 0.00 | 0.13 | 0.02 | −0.02 | 0.00 | 0.00 | 0.24 |
| (8) Neutral Detergent Fiber | 0.17* | −0.17* | −0.17* | 0.14* | −0.06 | −0.28* | −0.51* | – | 0.03 | −0.08 | 0.03 | 0.02 | 0.00 | 0.00 | 0.04 |
| (9) Acid Detergent Fiber | −0.03 | −0.18* | 0.24* | −0.06 | 0.39* | 0.40* | −0.15* | 0.08* | – | −0.04 | 0.68 | −0.03 | 0.00 | 0.00 | 0.04 |
| (10) *in vitro* Digestibility of DM | −0.02 | 0.14* | −0.21* | −0.01 | −0.30* | −0.26* | 0.13* | 0.36* | −0.83* | – | −0.07 | 0.01 | 0.00 | 0.00 | −0.19 |
| (11) Lignin P | −0.26* | −0.03 | 0.41* | −0.09* | 0.26* | 0.34* | 0.13* | 0.05 | 0.85* | −0.79* | – | −0.34 | 0.00 | 0.00 | 0.03 |
| (12) Cellulose | 0.35* | −0.12* | −0.30* | 0.16* | 0.23* | 0.09* | −0.47* | 0.09* | −0.03 | 0.17* | −0.49* | – | 0.00 | 0.00 | 0.03 |
| (13) Green Matter Yield | 0.48* | −0.25* | −0.28* | 0.47* | 0.38* | 0.01 | −0.46* | 0.30* | 0.22* | −0.16* | −0.01 | 0.39* | – | 0.47 | 0.00 |
| (14) Total DM Yield | 0.47* | −0.24* | −0.27* | 0.40* | 0.40* | −0.01 | −0.48* | 0.31* | 0.22* | −0.17* | −0.01 | 0.39* | 0.99* | – | 0.00 |
| (15) Regrowth | 0.46* | −0.04 | −0.19* | 0.21* | 0.33* | 0.24* | −0.31* | 0.08 | 0.32* | −0.31* | 0.13* | 0.25* | 0.51* | 0.49* | – |

Significant at 1% of probability by *t-Student* test; DTF –days to flowering, IVOMD – *in vitro* digestibility of dry matter.

synchrony indices and a negative correlation between flowering synchrony index and DTF corroborated the results presented above (Figs. 3b and 1a, respectively). The number of panicles was positively and significantly correlated with the flowering synchrony index and traits associated with biomass production; however, this value was negatively correlated with DTF. The genetic correlation between total seed yield and filled-seed yield was strong and positive (0.67), and this information is important when the parameter commonality is the focus. In general, high and low genetic correlation magnitudes did not imply high and low commonality between characteristics, respectively. The filled-seed yield presented a high magnitude of genetic correlation and commonality (0.59) with total seed yield and a moderate magnitude with DTF (0.22). However, the characteristics associated with biomass yield that demonstrated positive and significant correlations with filled-seed yield also were almost null for commonality. In terms of magnitude, a high degree of commonality was observed between the number of panicles and DM yield (0.40), between the ADF and lig P (0.68), and the green matter yield and total DM yield (0.47).

## Discussion

*Brachiaria ruziziensis* is a quantitative short-day flowering plant that exhibits vigorous flowering only after the autumnal equinox in the tropics (Hopkinson et al. 1996). The flowering phenology of *B. ruziziensis* tetraploid progeny was observed for at least 10 weeks after onset in February. In the last four census weeks, all of the families presented at least one individual flowering period, which was consistent with the greatest number of panicles in the vigorously flowering plants. However, considerable information is lost when the period of flowering and mean of panicle number are observed within a census period because the synchrony between individuals is not provided by either variable. Estimates of the synchrony index provide more important genetic information. Initially, the index variable is continuous among individuals, thus allowing for a parametric statistical approach (Mahoro 2002). Second, the index provides information on the overlap of flowering among individuals within and between populations, which increases the potential exchange of genes based on pollen availability for crossings. The mean flowering synchrony presented a high magnitude within subpopulations ($0.7 < S_i < 0.8$), indicating a greater number of individuals that were simultaneously contributing pollen.

However, a low magnitude was observed for the filled-seed synchrony index ($S_i = 0.4$, in mean), and heterogeneous seed development was observed during the period of production with peak values that occurred in the first weeks of May. Genetic, cytological, physiologic, or environmental factors may account for the filled-seed yield in forage grasses (Boelt and Studer 2010). Environmental factors have the most well-understood effect on grasses, particularly the cytological factor in *B. ruziziensis* tetraploid. *Brachiaria* species seed production is restricted to conditions that primarily occur at high tropical latitudes, and these species are controlled seasonally by photoperiodic flowering reactions (Hopkinson et al. 1996). Climatic conditions have a pronounced effect on fertilization, with high precipitation disrupting flowering and decreasing grass pollen dispersal (Boelt and Studer 2010). However, drought stress in the crop at anthesis promotes failures of seed set in *Brachiaria* (Hopkinson et al. 1996). Rainfall data during our evaluation revealed that the flowering peak in April was dryer and the seed production peak in May was wetter than the historical mean for

the same months. Therefore, we hypothesized that rainfall may not harm the pollen distribution but may harm the seed filling. However, additional studies on the environment effects on *B. ruziziensis* seed set are necessary.

Under experimental environment conditions, the seed set of tetraploid *Brachiaria ruziziensis* ranged from 13% to 46% among progeny within subpopulations and from 20% to 44% between subpopulations. A low percentage of seed set in *B. ruziziensis* may indicate an origin associated with induced polyploidy. Pagliarini et al. (2008) studied the meiotic behaviour of induced tetraploid accessions in *B. ruziziensis* and found that the mean of meiotic abnormalities ranged from 5.2% to 9.7% among subpopulations R30, R38, R41, R44 and R47, whereas this value reached 54% in R46. We found that the mean of seed set was 37% for R30, 20% for R38, 44% for R41, 36% for R44, 30% for R46, 23% for R47 and 36% for R50. Therefore, meiotic abnormalities in the subpopulation R46 did not affect its open-pollinated progeny seed set compared with the R38 and R47 progeny. As mentioned above, *B. ruziziensis* diploids are highly self-incompatible (Ferguson and Crowder 1974) and include autotetraploid individuals (Lutts et al. 1991); however, we did not test for compatibility among our progeny.

The number of days to flowering and the synchrony among individuals are associated with pollen availability during stigma maturity and affect random mating in low effective population sizes as well as seed-set efficiency. In the present study, flowering synchrony did not have a significant effect on the filled-seed yield, and the DTF effect was low but significant, which is similar to the results obtained by Studer et al. (2008) for heading date with the seed set of ryegrass. Moreover, important results for *B. ruziziensis* breeding were noted based on evidence of within-subpopulation significant genetic variability for DTF.

As stated by Boelt and Studer (2010), seed yield is a complex characteristic and is affected by environmental factors and a number components, including seed yield potential (e.g. number of reproductive tillers, number of spikelets per reproductive tillers); the utilization potential (e.g. seed set, seed weight); and the realization of seed yield potential, which is defined as the number of spikelets that form sellable seed. Seed yield is an important trait that determines whether a new *Brachiaria* variety can be profitably produced and distributed to farmers (Hopkinson et al. 1996, Worthington et al. 2016). Although it is relevant to seed trade, seed production in *Brachiaria* spp. is not the objective of selection but should be one of the selection criteria. Therefore, gaining insights into the genetic control, determining the correlations between seed yield and others characteristics and performing analyses to determine the contribution of predictor variables to dependent variables, such as commonality (Zeng et al. 2014), are essential to achieving simultaneous genetic gains among in multiple characteristics. Based on the genetic correlation and commonality analyses, *B. ruziziensis* tetraploid selection for seed yield does not affect the biomass yield, which is the main objective of forage breeding. The effects of the late flowering on the nutritional quality when higher filled-seed production is used as selection criteria must be investigated in the future.

Of the reproductive characteristics, the flowering synchrony index, number of panicles, filled-seed yield and NDF presented genetic variability and can be targeted by artificial selection in *B. ruziziensis* tetraploid breeding programmes. The narrow sense heritability among progeny for NDF was similar to that estimated by Ashraf et al. (2016) in ryegrass (*Lolium perenne* L.) using genomic data. The number of days to flowering and number of panicles in *B. ruziziensis* presented a lower magnitude of narrow sense heritability than that estimated for orchardgrass (*Dactylis glomerata* L. – Jafari and Naseri 2007, Araghi et al. 2014) and tall fescue (*Festuca arundinacea* Schreb. – Majidi et al. 2009). Genetic variability for filled-seed yield was distributed equally between and within subpopulations in which the total narrow sense heritability was 0.21. The magnitude of heritability for the filled-seed yield per plant was reduced compared with that for white clover (Annicchiarico et al. 1999), bromegrass (*Bromus riparius* – de Araújo and Coulman 2002) and orchardgrass (*Dactylis glomerata* – Majidi et al. 2015).

The analysis of interrelationships between the characteristics showed a strong negative genetic correlation ($r_a = -0.57$) between the number of panicles and NDF in *B. ruziziensis*, which is consistent with the results of Casler et al. (2014) in orchardgrass. The filled-seed yield presented a high magnitude of genetic correlations ($r_a > 0.29$) with NDF, total seed yield, and biomass production associated characteristics (GMY, DM yield and regrowth) in *B. ruziziensis* tetraploids. However, the commonality results indicated that only the characteristics NDF and total seed yield could be used as predictors of filled-seed yield. The other relevant commonality values were observed between the number of panicles and the DM yield (0.4) and between the green matter yield and DM yield (0.47).

### Use of $Q_{ST}$ information on breeding

The rationale stated by Holsinger and Weir (2009) for using the $F_{ST}$ can be extended to the $Q_{ST}$ because the $Q_{ST}$ is more than a descriptive statistic and measure of genetic differentiation and provides important insights that extend beyond evolutionary processes. $Q_{ST}$ information is generally published in comparison and as a reference to $F_{ST}$ when designing the type of selection criteria for populations (Pressoir and Berthaud 2004, Leinonen et al. 2013).

An important question is how to use $Q_{ST}$ information in breeding programmes when this information is available. Evidences suggests that within species, the $Q_{ST}$ varies widely among quantitative characteristics (McKay and Latta 2002), indicating that different characteristics experience different selection pressures, a result that our paper corroborates. Selection based on phenotypic quantitative data has the potential to use all information available between populations and within progeny. We compared the univariate selection of individuals within progeny using (and not using) the information of population structure. It was noteworthy that when the variation between subpopulations is greater than between progeny, the importance of the subpopulations increases (filled-seed yield) and results in the selection of almost all individuals of the best progeny in that subpopulation. This result was expected, considering the high accuracy caused by the greater precision and higher weight of subpopulation information in relation to progeny information. These higher weights are based on the high genetic variability between subpopulations and the greater amount of information used to evaluate subpopulations (number of replications × number of progeny) because progeny are only evaluated based on the number of replications.

The genetic variability available in experimental breeding populations is derived from the structuring of subpopulations and progeny and from Mendelian segregation effects within progeny. All three pieces of information can and should be capitalized on genetic improvement programmes, although such information cannot be used in genomewide association studies (GWAS) (Daetwyler et al. 2012) and genomewide selection (GWS) (Hill

2014) predictions, in which structuring should be eliminated when performing genomic estimations.

To our knowledge, this article seems to be among the first ones to fit the structure effects in a model for obtaining the estimates of breeding values and to increase the accuracy of selection. Nevertheless, the practical use the structuring of populations in applied plant breeding programmes should be common. The fitting of such structure effects in a model of genetic evaluation is straightforward and can be performed routinely. This will increase selection efficiency by fitting the structure between groups (or cluster or subpopulation) simultaneously to within group effects. One question could be raised concerning the correct allocation of subpopulations, although it is not an issue because the allocation can be statistically tested via the LRT as performed in this article, which confirmed the structuring for many characteristics and therefor the correct allocation of subpopulations.

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