Combining Ability of Biomass Sorghum Lines for Agroindustrial Characters and Multitrait Selection of Photosensitive Hybrids for Energy Cogeneration

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ABSTRACT

Sorghum [*Sorghum bicolor* (L.) Moench] biomass hybrids with high productivity and enhanced levels of lignin are seen as a promising alternative of feedstock for direct burning in ovens designed for cogeneration of electricity. The objective of this study was to estimate the genetic combing capacity of biomass sorghum lines and conduct multivariable selection of photosensitive biomass sorghum hybrids for use in cogeneration. Thirty-six photosensitive hybrids, the control BRS716, and 12 parental lines were evaluated in a seven-by-seven triple lattice design at two locations, and 12 characters were evaluated. There was superiority of additive effects on the genetic control of all the characteristics studied in both environments, less for female lines in the diallelic analysis of F₁ hybrids. The inclusion of parents in the estimates of combining capacities indicated predominance of dominance effects involved in the genetic control of the traits analyzed. The results demonstrate the action of epistasis of the dwarf genes present in the female lines for the biomass parameter and the false interpretation when these lines are included in the diallelic analysis. With the use of the index based on factor analysis and genotype–ideotype distance (FAI-BLUP index), four factors were established, which separated the characteristics of production and quality, as well as the two environments, resulting from the high hybrid × environment interaction. With the index, five hybrids with higher potential for burning (H5-5, H2-1, H1-1, H1-5, and H5-1) were selected. However, no hybrids obtained gains for the characteristics of production and quality, simultaneously, which indicates the need for genetic improvement of the parents used in the program.

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Abbreviations: ADF, acid detergent fiber; CEL, concentration of cellulose; CY, cellulose production; DBY, total dry biomass production; FAI-BLUP, index based on factor analysis and genotype–ideotype distance; FBY, production of fresh biomass; GCA, general combining ability; GCA × E, general combining ability × environments interaction; HEMI, concentration of hemicellulose; HUMI, moisture content; HY, hemicellulose production; LIG, acid detergent lignin; LY, lignin production; NDF, neutral detergent fiber; PH, plant height; SCA, specific combining ability; SCA × E, specific combining ability × environments interaction.

RECENTLY there has been a significant increase in interest in biomass as a renewable feedstock for bioenergy production. In addition to increasing energy security, it also increases climate security and generates sustainable development (Campi et al., 2016; Souza et al., 2017; Toklu, 2017; Wannasek et al., 2017). The estimate is that by 2050, bioenergies will supply 30% of the world's electricity demand, and the biomass could represent up to 18% of world primary energy (Lauri et al., 2014; Guo et al., 2015).

According to Foley et al. (2011), the allocation of crops for nonfood uses, including bioenergy, animal feed, seed, and other industrial products, affects the amount of food available for the human species globally. According to Rooney et al. (2007), bioenergy crops can potentially be produced in regions not conducive for food production and thus provide a way to minimize food use vs. fuel problems. In this context, sorghum biomass [*Sorghum*

bicolor (L.) Moench] is presented as one of the most promising crops (Rooney et al., 2007) and enters as an efficient alternative in the production of steam for industrialization or cogeneration of electricity (Gosse, 1996; Monti and Venturi, 2003; Zegada-Lizarazu and Monti, 2012; Campi et al., 2016; Toklu, 2017; Fernandes et al., 2018) and the production of second-generation ethanol (Amaducci et al., 2000; Sun and Cheng, 2002; Davila-Gomez et al., 2011; Castro et al., 2017).

Cogeneration is the technical term used in Brazil with reference to generating electricity in the sugar mills by burning the bagasse from sugarcane (Saccharum officinarum L.). Cogeneration is extremely important in the economic aspect of sugarcane mills. The electricity generated can be sold and distributed in the electrical grid, and the use of sorghum biomass can contribute to the profitability of these industries during the off-season of sugarcane. The energy content (caloric properties) was not directly measured in these experiments but was evaluated indirectly by the content of cellulose, hemicellulose, and lignin content.

The use of biomass for cogeneration of electricity or direct burning in boilers requires materials with low moisture content and high levels of lignin, cellulose, and hemicellulose (McKendry, 2002). According to May et al. (2013), the biomass cultivars must also be high yielding to promote sustainable energy production. High yields of sorghum biomass production can be achieved using photoperiod-sensitive cultivars (Rooney et al., 2007). Photosensitive sorghum cultivars remain vegetative during periods of long days with vegetative growth for 160 to 180 d when planted early during the long days of summer. This occurs because floral initiation and differentiation occurs when the daylength is less than 12 h and 20 min (Rooney and Aydin, 1999), resulting in higher biomass production per hectare compared with materials insensitive to photoperiod, with production cycles of 80 to 120 d (May et al., 2013). These photosensitive cultivars with high biomass production potential associated with high lignin content and low moisture stand out for cogeneration.

Photosensitive sorghum planted in long-day environments is a potential crop to produce high biomass yields with high-quality composition. This biomass sorghum is also highly efficient in water use and drought tolerant, has established production systems, is propagated by seed, is an annual crop with a short life cycle from planting to harvest, and has ample genetic diversity (Cosentino et al., 1996; Foti et al., 1996; Rooney et al., 2007; Campi et al., 2016). In addition, sorghum is a widely disseminated crop that can be exploited on a large scale and with wide adaptability to various climatic and soil conditions and with good adaptation to both tropical and temperate regions (May et al., 2013; Wannasek et al., 2017).

Sorghum is classified as a short-day species, with flowering induction occurring only during short days. The accessions introduced from Africa into the Americas, principally North America, ~200 yr ago would not flower during the long days of summer and did not set seed before autumn frosts killed the plants. A mutation from the dominant (wild type) to the recessive resulted in photoperiod insensitivity due to a loss of the function of the wild-type allele, Ma_1, what is now known as the maturity gene. Consequently, the genotypes with the homozygous recessive gene, ma_1ma_1, flower approximately 60 to 70 d after planting and are classified as photo-insensitive (Murphy et al., 2011). The germplasm and cultivars developed in the Americas are basically of the photo-insensitive type. Commercial photosensitive sorghum hybrids using $Ma1/ma1$ genes can only be produced in short-day environments with simultaneous flowering of the male and female parents. Normally, temperate environments do not have these conditions with adequate temperature for plant growth and development. However, in Brazil and other tropical environments south of the equator, there is a window of opportunity to produce commercial hybrid seed with March and April plantings. Embrapa follows a protocol for developing photosensitive hybrid cultivars in Brazil, by crossing photo-insensitive cytoplasmic male-sterile female A-lines with photosensitive male fertility restoring R-lines during a period of short days. These hybrids are heterozygous (Ma_1ma_1) for this maturity gene and are photosensitive. Stephens and Holland (1954) discovered cytoplasmic male sterility in sorghum followed by the introduction of hybrid grain and forage sorghum resulting in increased productivity (House, 1985).

The breeding programs for sorghum hybrids require three groups of lines, named A-, B-, and R-lines (House, 1985). A- and B-lines are isogenic, that is, they differ only by the type of cytoplasm. All A-lines have cytoplasmic male sterility, and they are used as the female parent in hybrid seed production. The isogenic B-line has normal cytoplasm and is used as the male parent in crosses with the isogenic A-line to produce A-line seed, both associated with recessive nuclear genes for restoration of fertility (Smith and Frederiksen, 2000). The R-line with dominant fertility restorer genes is used in a cross with a male-sterile A-line to produce fertile single-cross hybrids (House, 1985).

In sorghum, plant height is controlled by four dwarfing loci (Dw_1/dw_1, Dw_2/dw_2, Dw_3/dw_3, and Dw_4/dw_4) (Quinby, 1974). The isogenic strains (A and B) are characterized by short stature, determined by the combination of these dwarfing alleles, and are called four dwarfs when only recessive alleles are present at all four loci, or three dwarfs when only recessive alleles are present at three of the four loci (Quinby, 1974). In the sorghum breeding program of Embrapa, the parental lines are not divided by

heterotic groups, but by male sterility—Group I including sterile male lines (A-lines) and Group II including the male fertile lines (R-lines). When used as male-sterile parents in hybrid combinations, low-statured A-lines facilitate mechanized harvesting in seed production fields and reduce the need for labor, which consequently reduces production costs of hybrid seed.

The success of hybrid sorghum breeding programs is related to the development and identification of elite breeding lines regarding their overall and specific combining abilities. In this context, we have highlighted the use of diallel crosses, which allow for both the identification and selection of superior hybrid combinations and the selection of the best parental A- and R-lines. Elite lines can be intercrossed to generate segregating populations with potential to select for improved new elite lines. Diallelic crosses also provide information about the inheritance of the traits under analysis (Griffing, 1956), which are extremely important for the success of breeding programs (Cruz et al., 2012).

The selection of sorghum hybrids with high potential for the production of bioenergy requires good performance of these hybrids in different environments for characteristics associated with the productivity and quality of the biomass. Genetic improvement programs are designed to develop, evaluate, and select new genotypes that simultaneously meet the attributes of interest using selection indexes. Smith (1936) and Hazel (1943) suggested the first selection index for plant and animal breeding, respectively. Subsequently, several other indices have been proposed (Elston, 1963; Pešek and Baker, 1969; Mulamba and Mock, 1978). However, they present some obstacles that reduce the accuracy of the selection process and may lead to erroneous conclusions. Among the main limitations of the indices are the difficulty in assigning weights to the characters of interest and the presence of multicollinearity resulting from the correlation between these characters. In this context, Rocha et al. (2018) proposed a selection index based on factor analysis and genotype–ideotype distance (FAI-BLUP index) based on factor analysis that maximizes the genotype–ideotype relationship, allowing for genotype ordering based on multiple characters. In addition, this index waives the use of weights and presents no problems with multicollinearity, resulting in more balanced gains for the set of characters of interest.

In view of the above, the objective of this study was to estimate the combining ability of biomass sorghum lines and hybrids for agronomic and industrial characters and to carry out the multitrait selection of photosensitive hybrids.

MATERIALS AND METHODS

The lines used in this study are proprietary lines developed by the Embrapa sorghum improvement program. The six female male-sterile lines (A-lines) are photo-insensitive and three

dwarf and the six restorer lines (R-lines) are photosensitive (Fig. 1). These six restorer lines have not been evaluated for height expression in short day environments but are all tall (>4 m) in long-day environments. However, the male parents are taller than the female parents in the hybrid seed production plots. The 12 lines used in this study have shown promise in diverse hybrid combinations. It is worth mentioning that, our sorghum improvement program has not genotyped the lines with regard to the four genes controlling height. Likewise, the lines also have not been genotyped for the maturity genes.

These sorghum breeding lines were separated into two groups, Group I composed of six A-lines and Group II composed of six R-lines. These lines were crossed in a partial diallel scheme, in which Group I was used as the female line and Group II was used as male line to obtain 36 photosensitive hybrids (Table 1). The manual crosses to obtain the hybrids were conducted in the field during short days, in the experimental area of Embrapa Milho e Sorgo, located in Nova Porteirinha, Minas Gerais, Brazil. The female lines were planted on 5 May 2014, whereas the male lines were planted 10 d prior to the female lines to ensure coincidence of flowering. Each of the A-lines was composed of 50 plants, distributed in 5-m rows with 0.7 m between rows. Panicles obtained from each cross were harvested after physiological maturity for hybrid seed production.

The 36 hybrids and 12 parental lines, along with the commercial biomass hybrid BRS716, were evaluated in a triple lattice (7 × 7) design. The experiments were conducted at Embrapa Milho e Sorgo, located in Sete Lagoas (19°27′57″ S, 44°14′48″ W, at 761 m asl) and at Nova Porteirinha (15°48′09″ S, 43°18′02″ W, at 533 m asl), both in the state of Minas Gerais, during long days of the agricultural year 2014–2015. The specific conditions of climate during the period of these experiments are represented in Fig. 2. The soils of both areas were classified as a red-yellow latosol with medium texture.

Each experimental plot consisted of two 5-m rows with 0.70 m between rows, totaling an area of 7.00 m². The initial plant population used was 140,000 plants ha⁻¹. Four hundred and fifty kilograms per hectare of 08:28:16 N–P–K formulation was applied in the row at planting, and 200 kg ha⁻¹ urea was applied side-dressed 25 d after planting. The control of weeds and pests and other agricultural practices were performed as recommended for sorghum cultivation in the region (Borém et al., 2014).

The following agronomic and industrial traits were evaluated: plant height (PH, m), which is the mean height of the plot measured from the soil surface to the apex of the panicle; production of fresh biomass (FBY, t ha⁻¹), given by weighing all the plants in the plot area using a digital suspension scale and subsequently converted into production per hectare; moisture content (HUMI), in which a sample of the material was weighed by determining the green weight (PV), then packed in paper bags and taken to a forced ventilation oven at 65°C for 72 h, after which time at room temperature for 2 h and in sequence determined the dry weight (PS), and the HUMI was obtained by the equation HUMI = (PV − PS)/PV × 100; and the total dry biomass production (DBY, t ha⁻¹), obtained by the expression DBY = FBY × (100 − HUMI).

The analysis of the biomass composition was conducted at the Laboratory of Chemical Analysis of Plants (LAQP) at Embrapa Milho e Sorgo. A sample of the ground material was
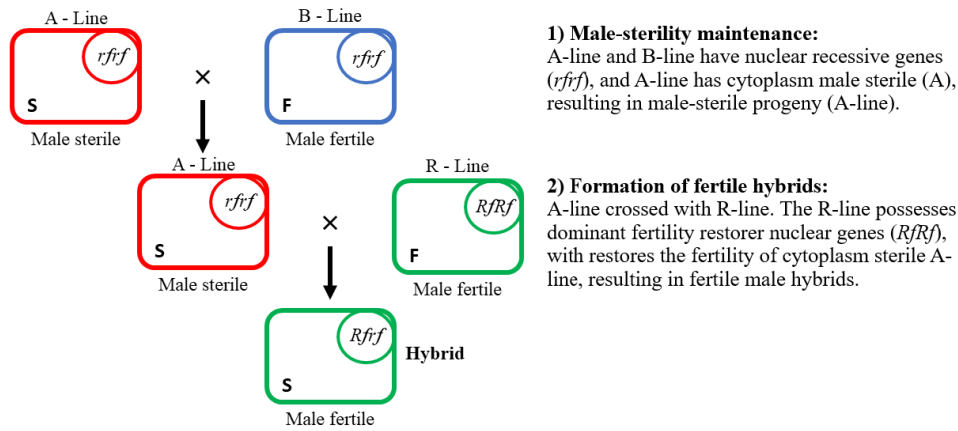
Fig. 1. Crossing scheme to maintain and produce the A-line and to produce the hybrids using cytoplasmic male sterility.

Table 1. Identification of 36 hybrids of the six-by-six diallel design.

Group I (R-lines)	Group I (A-lines)					
	CMSXS238A (1)†	CMSXS112A (2)	CMSXS156A (3)	CMSXS157A (4)	CMSXS222A (5)	CMSXS217A (6)
CMSXS7032R (1)	H (1-1)	H (2-1)	H (3-1)	H (4-1)	H (5-1)	H (6-1)
CMSXS650R (2)	H (1-2)	H (2-2)	H (3-2)	H (4-2)	H (5-2)	H (6-2)
CMSXS7039R (3)	H (1-3)	H (2-3)	H (3-3)	H (4-3)	H (5-3)	H (6-3)
CMSXS7041R (4)	H (1-4)	H (2-4)	H (3-4)	H (4-4)	H (5-4)	H (6-4)
CMSXS7042R (5)	H (1-5)	H (2-5)	H (3-5)	H (4-5)	H (5-5)	H (6-5)
CMSXS7043R (6)	H (1-6)	H (2-6)	H (3-6)	H (4-6)	H (5-6)	H (6-6)

† The values in parentheses refer to the six A-lines of Group I, six R-lines of Group II, and the 36 hybrids resulting from the crosses between these lineages. H, hybrid.
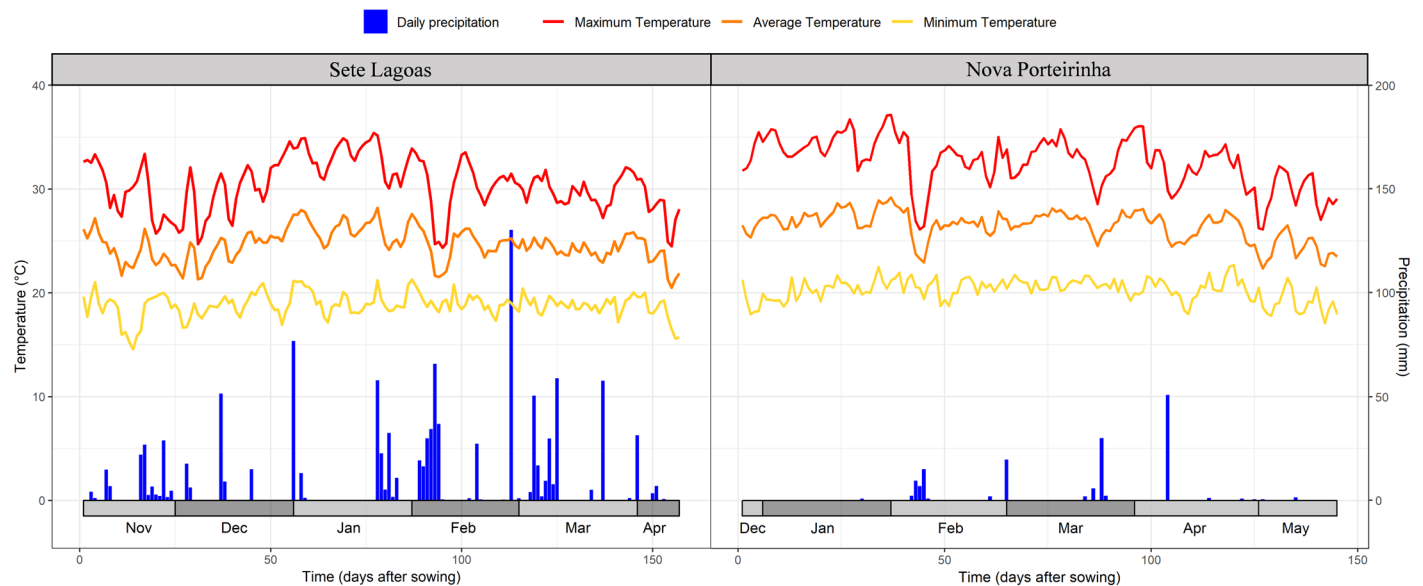

Fig. 2. Rainfall (mm) and minimum, average, and maximum temperatures (°C) collected during the field experiments in the agricultural year 2014–2015.

used to determine the percentages of neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (LIG) by the modified Van Soest and Wine (1963) method. The concentration of hemicellulose (HEMI) was obtained by the difference between the contents of NDF and ADF, and the concentration of cellulose (CEL) was determined by the difference between ADF and LIG (Guimarães et al., 2014).

Three new traits were proposed in this study, to express the burning efficiency of the materials: LY (lignin yield), CY (cellulose yield), and HY (hemicellulose yield). These traits represent the productivity of these components in tons per hectare and can be calculated according to the following equations:

$$LY = \% \ LIG/100 \times DBY$$

$$CY = \% \ CEL/100 \times DBY$$

$$HY = \% \ HEMI/100 \times DBY$$

The ANOVA for each location was based on the following linear mixed model:

$$y = X\tau + Z_h h + Z_l l + Z_b b + e$$

where **y** is the observation vector; **τ** is the fixed effects (replications) associated with the observation matrix **X**; **h** is the vector of random effects of the hybrids associated with matrix of the $\mathbf{Z_h}$ occurrence, where $\mathbf{h} \sim N\left(0, I\sigma_{\mathbf{h}}^2\right)$, with the incidence matrix **I** and the variance of hybrids $\sigma_{\mathbf{h}}^2$; **l** is the vector of random effects of the lines associated to the matrices of the $\mathbf{Z_l}$ occurrence, where $\mathbf{l} \sim N\left(0, I\sigma_{\mathbf{l}}^2\right)$, with the variance of lines $\sigma_{\mathbf{l}}^2$; **b** is the vector of random effects of blocks within replications associated to the matrix of the $\mathbf{Z_b}$ occurrence, where $\mathbf{b} \sim N\left(0, I\sigma_{\mathbf{b}}^2\right)$, with the variance of blocks within replications $\sigma_{\mathbf{b}}^2$; and **e** is the residual vector, where $\mathbf{e} \sim N\left(0, I\sigma_{\mathbf{e}}^2\right)$, with the residual variance $\sigma_{\mathbf{e}}^2$.

The combined analysis was made based on the following linear mixed model:

$$\mathbf{y} = \mathbf{X\tau} + \mathbf{Z_h}\mathbf{h} + \mathbf{Z_l}\mathbf{l} + \mathbf{Z_{he}}\mathbf{h}_e + \mathbf{Z_{le}}\mathbf{l_e} + \mathbf{Z_{be}}\mathbf{b_e} + \mathbf{e}$$

where **y** is the observation vector; **τ** is the vector of fixed effects (replications within environments) associated with observation matrix **X**; **h** is the vector of random effects of the hybrids associated with the observation matrix $\mathbf{Z_h}$, with $\mathbf{h} \sim N\left(0, I\sigma_{\mathbf{h}}^2\right)$; **l** is the vector of random effects of the lines associated with the $\mathbf{Z_l}$ observation, with $\mathbf{l} \sim N\left(0, I\sigma_{\mathbf{l}}^2\right)$; $\mathbf{h}_e$ is the vector of random effects of the interaction of the hybrids with environments associated with the matrix of the $\mathbf{Z_{he}}$ observation, with $\mathbf{h}_e \sim N\left(0, I\sigma_{\mathbf{he}}^2\right)$, with the variance of the interaction of hybrids with environments $\sigma_{\mathbf{he}}^2$; $\mathbf{l_e}$ is the vector of random effects of the interaction of lines with environments associated with the matrix with the $\mathbf{Z_{le}}$ observation, with $\mathbf{l_e} \sim N\left(0, I\sigma_{\mathbf{le}}^2\right)$, with the variance of the interaction of lines with environments $\sigma_{\mathbf{le}}^2$; $\mathbf{b_e}$ is the vector of random effects of blocks within environments associated with the $\mathbf{Z_{be}}$ observation, with $\mathbf{b_e} \sim N\left(0, I\sigma_{\mathbf{be}}^2\right)$, with the variance of the interaction of blocks within environments $\sigma_{\mathbf{be}}^2$; and **e** is the vector of residual effects, with $\mathbf{e} \sim N\left(0, I\sigma_{\mathbf{e}}^2\right)$.

The measure of accuracy (Ac), proposed by Mrode (2014), was estimated for each trait using $\mathrm{Ac} = \sqrt{1 - \left(\mathrm{PEV}/\sigma_{\mathrm{g}}^2\right)}$ for the above equation, where PEV (prediction error variance) is the mean variance of the difference between two genetic effects, and σ_{g}^2 is the genetic variance.

The diallel analysis for each environment was made based on the model of Bernardo (2010). The recommendations proposed by Möhring et al. (2011) were also used to separate the mean of hybrids and lines, and the variance attributed to the difference between the A-lines and R-lines. The mixed linear model used was

$$\mathbf{y} = \mathbf{X\tau} + \mathbf{Z_{g1}}\mathbf{g_1} + \mathbf{Z_{g2}}\mathbf{g_2} + \mathbf{Z_s}\mathbf{s} + \mathbf{Z_l}\mathbf{l} + \mathbf{Z_b}\mathbf{b} + \mathbf{e}$$

where **y** is the vector of observations; **τ** is the vector of fixed effects (replications, type of genotype [hybrid or line], and control) associated with incidence matrix **X**; $\mathbf{g_1}$ is the vector of random effects of general combining ability (GCA) of Group 1 associated with the matrix of the $\mathbf{Z_{g1}}$ observation, with $\mathbf{g_1} \sim N\left(0, I\sigma_{\mathbf{g1}}^2\right)$, with the variance of GCA of Group 1 $\sigma_{\mathbf{g1}}^2$; $\mathbf{g_2}$ is the vector of random effects of general combining ability (GCA) of Group 2 associated with the matrix of the $\mathbf{Z_{g2}}$ observation, with $\mathbf{g_2} \sim N\left(0, I\sigma_{\mathbf{g2}}^2\right)$, with the variance of GCA of Group 2 $\sigma_{\mathbf{g2}}^2$; **s** is the vector of random effects of specific combining ability (SCA) associated with the matrix of $\mathbf{Z_s}$ observation, with $\mathbf{s} \sim N\left(0, I\sigma_{\mathbf{s}}^2\right)$, with the

variance of the SCA $\sigma_{\mathbf{s}}^2$; **l** is the vector of random effects of the lines associated with the matrix of $\mathbf{Z_l}$ observation, with $\mathbf{l} \sim N\left(0, I\sigma_{\mathbf{l}}^2\right)$; **b** is the vector of random effects of blocks within replications associated with the matrix of $\mathbf{Z_b}$ observation, with $\mathbf{b} \sim N\left(0, I\sigma_{\mathbf{b}}^2\right)$; and **e** is the residual vector, with $\mathbf{e} \sim N\left(0, I\sigma_{\mathbf{e}}^2\right)$.

The combined diallelic analysis was performed using the following mixed linear model:

$$\mathbf{y} = \mathbf{X\tau} + \mathbf{Z_{g1}}\mathbf{g_1} + \mathbf{Z_{g2}}\mathbf{g_2} + \mathbf{Z_s}\mathbf{s} + \mathbf{Z_l}\mathbf{l} + \mathbf{Z_{g2e}}\mathbf{g_{1e}} + \mathbf{Z_{g2e}}\mathbf{g_{2e}}$$
$$+ \mathbf{Z_{se}}\mathbf{s_e} + \mathbf{Z_{le}}\mathbf{l_e} + \mathbf{Z_{be}}\mathbf{b_e} + \mathbf{e}$$

where **y** is the vector of observations; **τ** is the vector of fixed effects (replications, type of genotype [hybrid or line], and control) associated with the incidence matrix **X**; $\mathbf{g_1}$ is the vector of random effects of GCA of Group 1 associated with the matrix of the $\mathbf{Z_{g1}}$ observation, with $\mathbf{g_1} \sim N\left(0, I\sigma_{\mathbf{g1}}^2\right)$; $\mathbf{g_2}$ is the vector of random effects of GCA of Group 2 associated with the matrix of the $\mathbf{Z_{g2}}$ observation, with $\mathbf{g_2} \sim N\left(0, I\sigma_{\mathbf{g2}}^2\right)$; **s** is the vector of random effects of SCA associated with the matrix of $\mathbf{Z_s}$ observation, with $\mathbf{s} \sim N\left(0, I\sigma_{\mathbf{s}}^2\right)$; **l** is the vector of random effects of the lines associated with the $\mathbf{Z_l}$ observation, with $\mathbf{l} \sim N\left(0, I\sigma_{\mathbf{l}}^2\right)$; $\mathbf{g_{1e}}$ is the vector of random effects of the interaction of the GCA I with environments (GCA I × E) associated with the matrix of the $\mathbf{Z_{g1e}}$ observation, with $\mathbf{g_{1e}} \sim N\left(0, I\sigma_{\mathbf{g1e}}^2\right)$, where $\sigma_{\mathbf{g1e}}^2$ is the variance of the interaction of GCA I with environments; $\mathbf{g_{2e}}$ is the vector of random effects of the interaction of the GCA II with environments associated with the matrix of the $\mathbf{Z_{g2e}}$ observation, with $\mathbf{g_{2e}} \sim N\left(0, I\sigma_{\mathbf{g2e}}^2\right)$, where $\sigma_{\mathbf{g2e}}^2$ is the variance of the interaction of GCA II with environments; $\mathbf{s_e}$ is the vector of random effects of the interaction of the SCA with environments associated (SCA × E) with the matrix of the $\mathbf{Z_{se}}$ observation, with $\mathbf{s_e} \sim N\left(0, I\sigma_{\mathbf{se}}^2\right)$; $\mathbf{l_e}$ is the vector of random effects of the interaction of the lines with environments associated with the matrix of the $\mathbf{Z_{le}}$ observation, with $\mathbf{l_e} \sim N\left(0, I\sigma_{\mathbf{le}}^2\right)$; **b** is the vector of random effects of blocks within environment associated with the $\mathbf{Z_{be}}$ observation, with $\mathbf{b_e} \sim N\left(0, I\sigma_{\mathbf{be}}^2\right)$; and **e** is the residual vector, with $\mathbf{e} \sim N\left(0, I\sigma_{\mathbf{e}}^2\right)$.

For comparison purposes, the diallel model was also adjusted without the recommendations proposed by Möhring et al. (2011)—that is, parents and F$_1$s were considered in the calculation of GCA and SCA. The relative importance of additives effects, involved in the genetic control of the character evaluated in this study, was determined by the statistic θ, given by

$$\theta = \frac{\sigma_{\mathbf{g1}}^2 + \sigma_{\mathbf{g2}}^2}{\sigma_{\mathbf{g1}}^2 + \sigma_{\mathbf{g2}}^2 + \sigma_{\mathbf{s}}^2}$$

according to Baker (1978). The value of θ will be equal to 1 if $\sigma_{\mathbf{s}}^2 = 0$, will by equal to 0.5 if $\sigma_{\mathbf{s}}^2 = \sigma_{\mathbf{g1}}^2 + \sigma_{\mathbf{g2}}^2$, and will be <0.5 when $\sigma_{\mathbf{s}}^2 > \sigma_{\mathbf{g1}}^2 + \sigma_{\mathbf{g2}}^2$.

The FAI-BLUP index was used in the selection of hybrids, according to the R script provided by Rocha et al. (2018). All analysis of this work was performed with the use of software R (R Core Team, 2017). The analyses using mixed models were performed using the ASReml-R package (Butler et al., 2009).

RESULTS AND DISCUSSION

The deviance values (Supplemental Table S1) show a significant effect of hybrids ($P \leq 0.01$) on almost all the characteristics, except for FBY in Sete Lagoas, which was not significant ($P > 0.05$), indicating high variability among hybrids. Variability between hybrids is expected due to the divergence between the parents of the hybrids. The results of the joint analysis also show a significant effect of hybrids ($P \leq 0.01$) on almost all the characteristics, except for FBY, DBY, ADF, and CEL. A significant effect ($P \leq 0.01$) of the hybrid × environment interaction was observed for all the traits under analysis, indicating different responses of hybrids in the evaluated environments.

There was a highly significant difference ($P \leq 0.01$) between the group of lines (Lines), A-lines and R-lines, for all characteristics evaluated, except for HEMI in Sete Lagoas and LIG in Nova Porteirinha. Significant statistical differences between the lines in the joint analysis were also observed for all traits except for LIG and HEMI. Unlike the hybrids, line × environment interaction was significant only for characteristics related to biomass quality, except for HUMI, which was nonsignificant ($P > 0.05$). Thus, for the production characteristics the lines behaved in a similar way in both environments.

Accuracies varied from 0.77 (HEMI) to 0.95 (PH) in Sete Lagoas, from 0.81 (LIG and HEMI) to 0.95 (PH) in Nova Porteirinha, and from 0.63 (HEMI) at 0.95 (PH) in the joint analysis (Supplemental Table S1). According to Resende and Duarte (2007), these estimates of accuracy are classified as moderate (0.50 to 0.65) to very high (0.90 to 0.99). These results confirm the experimental quality of the trials for the traits evaluated. In general, the accuracy of the quality traits was lower than the accuracy of the production traits, with the lowest estimate for the HEMI variable in both environments. This characteristic, HEMI, is obtained by the difference from other variables, consequently accumulating the inaccuracies of the other characters.

It both environments and joint analysis, higher averages were observed for the hybrids, when the productions traits were analyzed (Supplemental Table S2), especially when compared with male-sterile parent strains (A-line). Regarding the quality traits, both the hybrids and the B-lines had higher mean values in both environments, except for HUMY and HEMI.

Figure 3 shows the relative contribution of each of the components of the phenotypic variance. In Sete Lagoas, it was observed for the characters evaluated that the phenotypic variance was, for the most part, explained by the genetic variance of the lines, being little influenced by the genetic variance of the hybrids and by the residual and block variance, which represented <20% of the total variation, with the exception of the HUMI and HEMI variables. The HEMI variable was the one that presented the greatest variation due to the residual variance, ~60%, which corroborates less accuracy due to the errors of measurement and/or sampling for this characteristic.

In Nova Porteirinha, similar behavior was observed for the characters related to production, in which the major contribution to the phenotypic variance was due to the genetic variance component of the lines. However, for the quality traits, the greatest contribution to the phenotypic variance was due to the genetic variance component of the hybrids. Also, in the joint analysis, the greater contribution to phenotypic variance of the production traits is mainly due to the variance between the lines, as well as in the individual location analysis. For the quality characteristics, however, the larger line × environment and hybrid × environment interactions for all variables are evident, which together with the genetic variance of the lines explain >70% of the phenotypic variations for all these variables except for HUMI and HEMI.

The variance components associated with GCA of Group I (A-lines) (Supplemental Table S3) were not significant ($P > 0.05$) for almost all the characteristics evaluated at Sete Lagoas, except for the characteristics HUMI and ADF. In Nova Porteirinha, the effects of GCA of the Group I lines were significant ($P \leq 0.01$) only for the traits FBY, LY, CY, HUMI, and LIG. The effects of GCA of the Group II lines (R-lines) were significant ($P \leq 0.01$) for all the characteristics at both Sete Lagoas and Nova Porteirinha. General combining ability estimates provide information on the frequency of favorable alleles with additive effects present in the parental lines (Cruz et al., 2012). Therefore, the variance associated with the additive genetic effects corresponds to the heritable fraction of the phenotypic variation, thus being responsible for the performance of the pure lines obtained when homozygosity is reached (Ramalho et al., 1988). The effects of SCA were significant ($P \leq 0.05$) only for PH and HUMI in Sete Lagoas and for NDF in Nova Porteirinha. This shows the small contribution of nonadditive effects of genes for heterosis in these hybrids for most of the traits.

In the combined analysis, both GCA of Group I and GCA of Group II were not significant for most of all the characteristics except for HUMI in Groups I and II and CY in Group II, which presented statistical significance ($P \leq 0.01$). The effects of SCA were not significant for all the characteristics ($P > 0.05$). There was no significant effect for the GCA I × E interaction for the characteristics evaluated, indicating that the A-lines exhibited the same behavior in both environments and that differential expression of their genes did not occur as was expected from the small genetic variance observed among the individuals in Group I. The GCA II × E interaction effects were significant for all the characteristics, except for CY and HUMI, indicating that the R-lines do not exhibit the same behavior of differential expression of their genes in both environments evaluated. This indicates
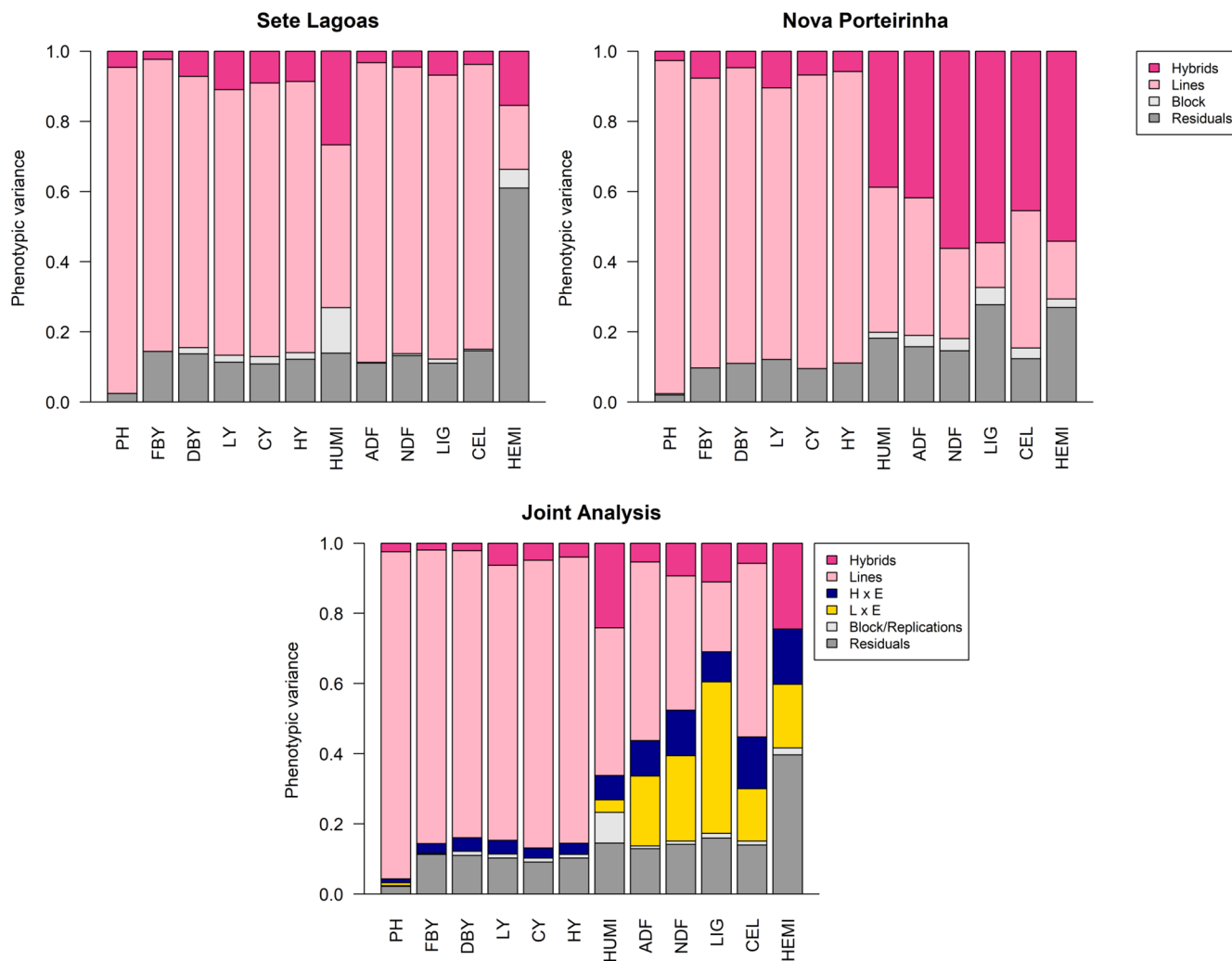
Fig. 3. Relative importance of the phenotypic variance components for 12 production and quality related characteristics (plant height [PH, m], production of fresh biomass [FBY, t ha⁻¹], production of dry biomass [DBY, t ha⁻¹], production lignin [LY, t ha⁻¹], cellulose production [CY, t ha⁻¹], hemicellulose production [HY, t ha⁻¹], moisture content [HUMI, %], neutral detergent fiber content [NDF, %], acid detergent fiber content [ADF, %], acid detergent lignin content [LIG, %], cellulose content [CEL, %], hemicellulose content [HEMI, %]), in the environments of Sete Lagoas, Nova Porteirinha, and in the joint analysis. H × E, hybrid × environment interaction; L × E, line × environment interaction.

that crosses may be made between these R-lines and selection of progeny to concentrate the favorable genes in one or a few lines for use to obtain superior hybrids.

Considering the relative importance (θ) of the additive effects (GCA I and GCA II) and nonadditive effects (SCA) of the genes in both environments (Supplemental Table S3), there was a superiority of additive effects in the genetic control of all the characteristics studied. This superiority is demonstrated by the highest relative importance (θ > 0.71) between GCA components (GCA1 + GCA2) and SCA. Values of θ equal to or close to unity indicate the absence of dominance in the control of the characteristic in question and were observed for the characteristics FBY, ADF, NDF, CEL, and HEMI at Sete Lagoas and CY in Nova Porteirinha. In the joint analysis, the superiority of the additive effects on the traits is evident, highlighting the values of θ equal to or close to unity for the DBY, LY,

CY, HY, HUMI, ADF, NDF, CEL, and HEMI traits, indicating an absence of dominance in the control of these characteristics. The SCA × E interaction in the joint analysis was nonsignificant ($P > 0.05$) for all the traits, indicating a consistency for the nonadditive effects in both environments, that is, the hybrids behaved in a similar way in both Sete Lagoas and Nova Porteirinha, except for PH and HUMI, which presented significant difference for the effect of the interaction SCA × E.

In diallel studies, Möhring et al. (2011) proposed that the effect of lines be separated in a new random effect, when the parents presented very contrasting behavior in relation to the hybrids. Figure 4 shows the influence of the phenotypic variance components studied, according to two diallel models for comparison purposes. The first model, proposed by Möhring et al. (2011), which was adopted in this study, only the F₁s are considered in the
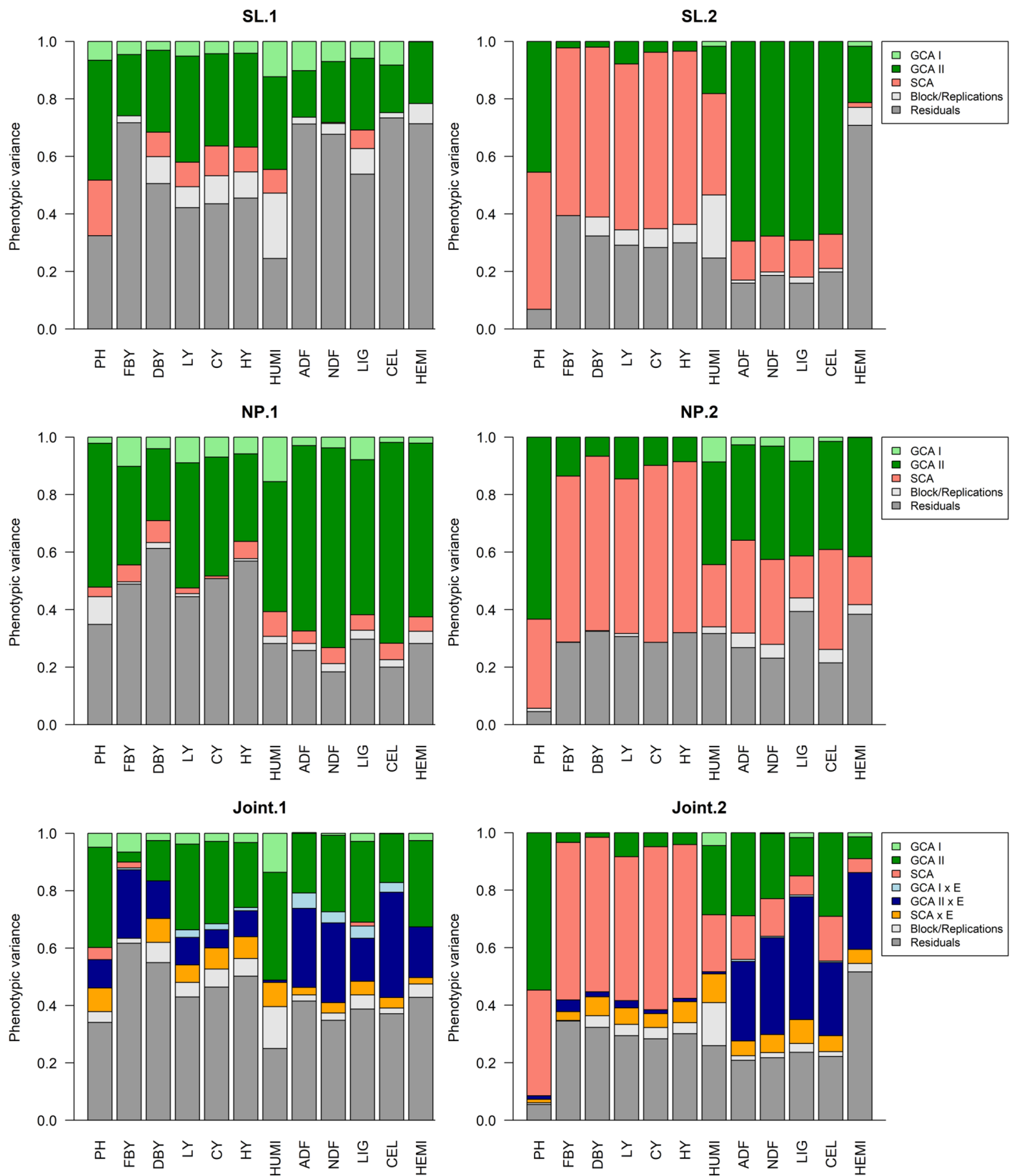
Fig. 4. Relative importance of the phenotypic variance components for 12 production-related traits(plant height [PH, m], production of fresh biomass [FBY, t ha⁻¹], production of dry biomass [DBY, t ha⁻¹], production lignin [LY, t ha⁻¹], cellulose production [CY, t ha⁻¹], hemicellulose production [HY, t ha⁻¹], moisture content [HUMI, %], neutral detergent fiber content [NDF, %], acid detergent fiber content [ADF, %], acid detergent lignin content [LIG, %], cellulose content [CEL, %], hemicellulose content [HEMI, %]) for the environments at Sete Lagoas (SL) and Nova Porteirinha (NP) and the joint analysis (Joint) of both environments, in diallel analysis considering only F₁s in the calculation of general (GCA) and specific combining ability (SCA) (1) and parental lines and F₁s in the calculation of GCA and SCA (2).

calculation of GCA and SCA and are represented by the graphs in Fig. 4 (Sete Lagoas [4.SL.1], Nova Porteirinha [4.NP.1], and joint [4.Joint.1]). The second model, proposed by Bernardo (2010), considers parents and F_1s in the calculation of GCA and SCA and is represented by the graphs in Fig. 4 (Sete Lagoas [4.SL.2], Nova Porteirinha [4.NP.2], and joint [4.Joint.2]). In the graphs representing the second model, it is possible to observe high phenotypic variation coming from SCA, mainly regarding the characteristics related to the production of biomass. When the first model is considered, the main component of the phenotype variation is that of the lines (GCA), whereas the contribution of the variance from SCA decreases drastically and, in some cases, is even null. Similar results were also observed in rice (*Oryza sativa* L.) (Garcia et al., 2008), cucumber (*Cucumis sativus* L.) (Olfati et al., 2012), and corn (*Zea mays* L.) (Garcia et al., 2008; Yao et al., 2013) when considering or not considering the parental lines in the diallel analysis.

Olfati et al. (2012) and Yao et al. (2013) have shown that methods including parents and hybrids in diallel analysis provide biased estimates of GCA and SCA variances. According to Garcia et al. (2008), the biased estimates of the variances of GCA and SCA in this case are due to the effect of epistasis, usually of an additive × additive nature, on the heterosis contribution of the hybrids when considering the parents in the diallel analysis. The variance of the effects of SCA is always positively influenced, that is, the resulting variance is greater than that observed, which might lead to an erroneous interpretation of the results. Thus, the heterosis observed in the analysis considering the parents and the hybrids in the present study is due to the epistatic effects and not to the effects of dominance, as expected.

Lombardi et al. (2018), Rocha (2016), and Durães (2014) in diallel studies on sorghum using the Griffing (1956) model, analyzing parents and F_1s, also observed high phenotypic variance due to the effects of SCA for plant height and production of fresh biomass and verified the presence of nonadditive gene effects in the determination of these variables but treated them as due to the effects of dominance. Jiang et al. (2017,) in more detailed studies of genetics in wheat, showed the importance of epistasis, mainly additive × additive in the heterosis calculation, in which it represented 50% of the genetic variation of heterosis, whereas the effects of dominance represented only 16% of the total variation. Thus, it is recommended for the study of gene action of agronomic and industrial traits of biomass sorghum via diallel analysis, especially when dwarf alleles are present, that the model proposed by Möhring et al. (2011) be used.

The parents of Group I (A-lines) have three pairs of dwarfism genes, facilitating the mechanical harvesting of the hybrid seed, since these strains are used as the female

parent. These dwarf alleles act indirectly on the genes that determine the characteristics related to the production of biomass in these lines (Li et al., 2015). Thus, these genes may be the main cause of the overestimation of the SCA effects when the parents are included in the diallel analysis. The height of sorghum plants is controlled by four independent genes: *Dw1/dw1*, *Dw2/dw2*, *Dw3/dw3*, and *Dw4/dw4* (Quinby, 1974).

The combination of these genes determines the height of the plant, so that short sorghum plants have genotype with all four recessive alleles (4 dwarf) or only one of the loci with a dominant allele (3 dwarf). In this case, the plants normally range in height from 0.90 to 1.20 m. The genotypes of sorghum with two pair of dwarf genes (2 dwarf) (*Dw1__*, *Dw2__*, *dw3 dw3*, and *dw4 dw4*) are of medium height (1.80 to 2.20 m) (Parrella et al., 2010). Tall sorghum genotypes have only one dwarf (*Dw1__*, *Dw2__*, *Dw3__*, and *dw4 dw4*), or no dwarf genes (*Dw1__*, *Dw2__*, *Dw3__*, and *Dw4__*). Thus, these genes when in a recessive homozygous state prevent the manifestation of other genes involved in determining biomass–related traits (Li et al., 2015), such as lower biomass production and, consequently, lower production of LY, CY, and HY. It is noteworthy that when these three dwarf A-lines are crossed with tall lines, the hybrids manifest heterosis and are as tall as or taller than the tallest parent, which in diallel analysis including the parents may be misinterpreted as being due to the dominance effect or even overdominance.

Table 2. Correlation of hybrid performance with mid parent performance and general combining ability (GCA) effects.

| Trait† | Sete Lagoas | | Nova Porteirinha | |
	Hybrid vs. mid-parent‡	Hybrid vs. GCA§	Hybrid vs. mid-parent	Hybrid vs. GCA
PH	0.20ns¶	0.83**	0.35*	0.86**
FBY	−0.05ns	0.79**	0.63**	0.86**
DBY	−0.04ns	0.78**	0.62**	0.77**
LY	0.02ns	0.83**	0.67**	0.89**
CY	−0.01ns	0.79**	0.60**	0.88**
HY	−0.05ns	0.81**	0.62**	0.82**
HUMI	0.64**	0.85**	0.55**	0.90**
ADF	0.30ns	0.79**	0.48**	0.93**
NDF	0.34*	0.80**	0.65**	0.94**
LIG	0.41*	0.77**	0.74**	0.91**
CEL	0.31ns	0.78**	0.51**	0.93**
HEMI	0.31ns	0.72**	0.75**	0.90**

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† PH, plant height (m); FBY, production of fresh biomass (t ha⁻¹); DBY, production of dry biomass (t ha⁻¹); LY, production lignin (t ha⁻¹); CY, cellulose production (t ha⁻¹); HY, hemicellulose production (t ha⁻¹); HUMI, moisture content (%); NDF, neutral detergent fiber content (%); ADF, acid detergent fiber content (%); LIG, acid detergent lignin content (%); CEL, cellulose content (%); HEMI, hemicellulose content (%).

‡ Hybrid performance vs. mid-parent performance.

§ Hybrid performance vs. GCA-predicted hybrid performance.

¶ ns, not significant.

Table 2 shows the correlations between mid-parent performance and hybrid performance. In Sete Lagoas, a significant correlation ($P \leq 0.01$) was observed only for the traits HUMI, NDF, and LIG, and in Nova Porteirinha, all the characters presented significant correlations, with it being possible to highlight LIG and HEMI, which were the highest values ($\rho = 0.74$ and $\rho = 0.75$, respectively). Correlations between the performance of the hybrids and their GCA were high and significant ($\rho > 0.72$) for all traits and in both environments. Correlations between hybrid performance and parent average performance were smaller for all traits compared with correlations between hybrids performance and GCA. These results indicate that the genic effects were predominantly additive for all traits, and similar results were found by Fischer et al. (2010) in triticale (×*Triticosecale* Wittmack) studies.

Four factors (Table 3), highlighted in bold, were formed for the set of characters evaluated in both environments, Sete Lagoas and Nova Porteirinha, using factor analysis. The first factor (FA1) grouped the production characteristics (PH, FBY, HUMI, DBY, LY, CY, and HY) evaluated in the Sete Lagoas environment. The second factor (FA2) was composed of the variables of production (PH, FBY, DBY, LY, CY, and HY), whereas the third factor (FA3) was composed of the variables related to biomass quality for burning (HUMI, ADF, NDF, CEL, and HEMI), both trait sets evaluated in the Nova Porteirinha environment. The fourth factor (FA4) was formed by the quality traits (ADF, NDF, LIG, CEL, and HEMI) evaluated in the Sete Lagoas environment.

These results corroborate the significant effects of the hybrid × environment interaction (Supplemental Table S1) for the characters evaluated. The estimates of commonality obtained by factor analysis varied from 0.70 to 0.99, indicating that the four common factors explain at least 70% of the variation of each trait under analysis.

Table 3 shows the participation of each quality and production trait in each factor of both environments. Thus, for the identification of hybrids with higher productive potential and high quality, independent of the evaluated environments, the FAI–BLUP index was used based on these four factors. Using this index, five hybrids with greater potential were selected, being the hybrids H5-5, H2-1, H1-1, H1-5, and H5-1, in this order. When compared with the commercial control hybrid (BRS716), all presented higher genetic gain for the PH characteristic in both Sete Lagoas and Nova Porteirinha (Tables 4 and 5). Also, considering the characteristics related to quality, greater genetic gains were observed for the experimental hybrids than for the commercial control.

Table 3. Summary of the factor analysis (FA) for 12 traits evaluated for biomass sorghum at Sete Lagoas (SL) and Nova Porteirinha (NP).

Environment	Character†	FA1	FA2	FA3	FA4	Commonality
SL	PH	0.62‡	−0.01	−0.46	−0.37	0.73
	FBY	0.79	−0.41	−0.19	0.24	0.88
	HUMI	−0.64	−0.11	0.31	0.57	0.84
	DBY	0.92	−0.22	−0.28	−0.13	0.99
	ADF	0.18	0.07	−0.09	−0.94	0.93
	NDF	0.17	0.07	−0.17	−0.96	0.98
	LIG	0.28	0.07	−0.35	−0.84	0.91
	LY	0.85	−0.16	−0.33	−0.37	0.99
	CEL	0.08	0.05	0.01	−0.96	0.92
	CY	0.89	−0.19	−0.26	−0.31	0.99
	HEMI	0.12	0.04	−0.38	−0.75	0.73
	HY	0.89	−0.21	−0.31	−0.23	0.98
NP	PH	0.36	−0.51	−0.48	−0.28	0.70
	FBY	−0.08	−0.71	0.40	0.48	0.91
	HUMI	−0.22	0.23	0.61	0.47	0.70
	DBY	0.12	−0.98	−0.02	0.11	0.98
	ADF	0.29	−0.18	−0.90	−0.15	0.95
	NDF	0.29	−0.16	−0.92	−0.18	0.99
	LIG	0.26	−0.29	−0.90	−0.08	0.96
	LY	0.25	−0.84	−0.46	0.04	0.98
	CEL	0.29	−0.10	−0.90	−0.21	0.96
	CY	0.25	−0.88	−0.38	−0.01	0.99
	HEMI	0.28	−0.08	−0.82	−0.24	0.81
	HY	0.20	−0.93	−0.23	0.03	0.96

† PH, plant height (m); FBY, production of fresh biomass (t ha⁻¹); DBY, production of dry biomass (t ha⁻¹); LY, production lignin (t ha⁻¹); CY, cellulose production (t ha⁻¹); HY, hemicellulose production (t ha⁻¹); HUMI, moisture content (%); NDF, neutral detergent fiber content (%); ADF, acid detergent fiber content (%); LIG, acid detergent lignin content (%); CEL, cellulose content (%); HEMI, hemicellulose content (%).

‡ In bold are the traits grouped in the formation of the four factors.

Table 4. Genetic gain for 12 characteristics of biomass sorghum of selected hybrids using the index based on factor analysis and genotype–ideotype distance (FAI-BLUP index) at Sete Lagoas.

Hybrid	PH	FBY	HUMI	DBY	ADF	NDF	LIG	LY	CEL	CY	HEMI	HY
	m	t ha⁻¹	%	t ha⁻¹	——————— % ———————			t ha⁻¹	%	t ha⁻¹	%	t ha⁻¹
H5-5	16.07	2.45	−7.39	15.85	2.16	2.41	7.47	27.00	1.81	20.04	2.07	21.17
H2-1	1.70	15.00	0.94	14.23	−0.10	0.55	3.42	20.07	0.06	14.92	1.26	18.40
H1-1	6.79	16.18	−5.69	32.81	4.18	2.47	−0.52	32.20	4.31	41.17	−0.85	32.15
H1-5	10.33	10.79	−9.80	35.29	0.72	1.17	4.92	45.21	0.72	38.70	1.44	40.63
H5-1	8.78	0.54	−2.80	5.65	3.85	3.04	7.36	14.43	3.32	10.52	0.89	7.56
BRS716	−1.61	28.30	−2.64	45.33	−4.87	−3.95	−5.96	33.51	−5.40	33.67	−1.11	41.32

† PH, plant height; FBY, production of fresh biomass; DBY, production of dry biomass; LY, production lignin; CY, cellulose production; HY, hemicellulose production; HUMI, moisture content; NDF, neutral detergent fiber content; ADF, acid detergent fiber content; LIG, acid detergent lignin content; CEL, cellulose content; HEMI, hemicellulose content.

Table 5. Genetic gain for 12 characteristics of biomass sorghum of selected hybrids using the index based on factor analysis and genotype–ideotype distance (FAI-BLUP index) at Nova Porteirinha.

Hybrid	PH	FBY	HUMI	DBY	ADF	NDF	LIG	LY	CEL	CY	HEMI	HY
	m	t ha⁻¹	%	t ha⁻¹	——————— % ———————			t ha⁻¹	%	t ha⁻¹	%	t ha⁻¹
H5-5	10.18	4.49	−8.96	18.55	1.79	1.57	1.35	21.04	2.66	22.33	0.86	19.78
H2-1	8.09	23.98	0.47	22.45	6.05	3.92	13.01	43.16	4.56	31.10	−0.21	23.11
H1-1	14.12	5.41	−6.30	16.14	−0.24	−0.66	−0.52	18.12	−0.73	18.17	−0.81	16.83
H1-5	4.15	−6.24	−10.78	9.72	8.79	7.46	16.39	28.97	7.06	17.55	4.80	15.16
H5-1	7.86	1.14	−1.91	5.54	4.33	4.51	9.16	14.36	3.79	9.22	4.52	10.17
BRS716	1.37	22.92	−2.03	25.15	1.48	2.08	8.00	36.48	0.23	27.12	2.77	28.87

† PH, plant height; FBY, production of fresh biomass; DBY, production of dry biomass; LY, production lignin; CY, cellulose production; HY, hemicellulose production; HUMI, moisture content; NDF, neutral detergent fiber content; ADF, acid detergent fiber content; LIG, acid detergent lignin content; CEL, cellulose content; HEMI, hemicellulose content.

However, for the production-related characters (FBY, DBY, LY, CY, and HY), the control was superior to most selected hybrids, at both Sete Lagoas and Nova Porteirinha. However, it should be noted that none of the selected hybrids obtained simultaneous gains for the quality and production characteristics in both environments. These results illustrate the need to improve both the quality and production traits of the parental lines to obtain superior hybrids.

Considering the predominance of additive effects for most of the agronomic and industrial traits of biomass sorghum, a breeding strategy would be to develop new male-sterile strains through biparental crosses between the six B-lines in normal cytoplasm, isogenic to the A-lines used in this study, totaling 15 crosses. The GCA is directly related to the additive effects that are due to different alleles present in the lines. New A-lines (male-sterile) could be obtained by intercrossing their respective B isogenic lines (male-fertile) to increase the number of favorable alleles, improving the male-sterile germplasm. The stacking of alleles for the traits of interest is expected to promote an increase of the GCA of these new lines, which are expected to result in superior hybrids for both yield and quality. Due to the difficulty and long process in the synthesis of new male-sterile lines in a sorghum breeding program, this would be a faster and more efficient strategy for the breeders.

The backcrossing of selected F_3 progeny to an A-line for the male-sterile conversion process can be initiated before the finalization of selection of a completely homozygous B-line progeny. Backcrossing continues as the B-line progeny is finalized and used as the recurrent parent. The same scheme was proposed by Parrella et al. (2016) and Leite (2018) in sorghum to obtain parents with higher sugar production potential. The male-sterile progenies under development in the BC_3 generation will be used to obtain experimental hybrids using a group of testers R-lines. The resulting experimental hybrids can then be evaluated in the field in different locations for agronomic and industrial traits, and A-lines with greater GCA and SCA for the characters of interest can be selected to compose the bank of male-sterile A-lines in the sorghum breeding program of Embrapa Milho e Sorgo. The same procedure should be performed with the R-lines, aiming at pyramiding the desirable genes in a smaller number of parents.

Supplemental Material

Supplemental material is available online for this article.

Conflict of Interest

The authors declare that there is no conflict of interest.

Acknowledgments

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