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Scientific Article

Heterozygosity, adaptability, and phenotypic stability of sweet sorghum genotypes

Heterozigosidade, adaptabilidade e estabilidade fenotípica de genótipos de sorgo sacarino

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ABSTRACT - Sweet sorghum (*Sorghum bicolor* L.) is a promising energy crop for bioethanol production. This study aimed to investigate the influence of genetic structure on the adaptability and phenotypic stability of sweet sorghum lines and hybrids regarding the main agro-industrial traits, as well as selecting hybrids that associate high ethanol yield and yield stability in different growing environments. A total of 45 genotypes were evaluated in experiments conducted in a 5×9 triple alpha lattice design in three locations in the state of Minas Gerais, Brazil. The following traits were measured: fresh matter production, juice extraction percentage, total soluble solids content, tons of Brix per hectare, and ethanol production. Adaptability and phenotypic stability were assessed by the Wricke and Annicchiarico methods. Sweet sorghum adaptability and phenotypic stability depend on genotype genetic structure, with hybrids being more stable than parental lines. Additionally, H_{2x9} and H_{3x8} were the most promising hybrids.

Keywords: *Sorghum bicolor* (L.). Bioethanol. Homeostasis. Ecovalence. Reliability index.

RESUMO - O sorgo sacarino (Sorghum bicolor (L.)) é uma cultura energética promissora para a produção de bioetanol. O objetivo deste trabalho foi verificar a influência da estrutura genética na adaptabilidade e estabilidade fenotípica de linhagens e híbridos de sorgo sacarino quanto aos principais caracteres agroindustriais, bem como selecionar híbridos que associem elevado rendimento de etanol e estabilidade produtiva nos ambientes de cultivo testados. Foram avaliados 45 genótipos em experimentos conduzidos no delineamento alfa-látice triplo 5 x 9 em três localidades do Estado de Minas Gerais, Brasil. Foram mensurados os caracteres produção de massa verde, porcentagem de extração de caldo, teor de sólidos solúveis totais, toneladas de brix por hectare e produção de etanol. A adaptabilidade e a estabilidade fenotípica foram aferidas pelos métodos de Wricke e Annicchiarico. Observou-se que a adaptabilidade e estabilidade fenotípica em sorgo sacarino depende da estrutura genética dos genótipos, no qual os híbridos foram mais estáveis do que as linhagens parentais. Além disso, os híbridos H2x9 e H3x8 foram os mais promissores.

Palavras-chave: *Sorghum bicolor* (L.). Bioetanol. Homeostase. Ecovalência. Índice de confiabilidade.

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INTRODUCTION

Sweet sorghum (*Sorghum bicolor* [L.] Moench), a promising energy crop for bioethanol production, has a short cycle (120 days) and high production of biomass (> 50 t ha^{-1}), sugars in the stalk (13-24 ºBrix), and ethanol (3 thousand to 6 thousand L ha^{-1}) (REGASSA; WORTMANN, 2014; APPIAH-NKANSAH et al., 2019; UMAKANTH et al., 2019; FAGUNDES et al., 2021). It also requires fewer inputs and exhibits greater tolerance to abiotic stresses compared to other crops, such as maize and sugarcane (SOUZA et al., 2013; APPIAH-NKANSAH et al., 2019). Sweet sorghum's high tolerance to abiotic stresses, especially drought, has led to its cultivation in the semi-arid tropics of Asia, Africa, America, and Australia (AKBAR et al. 2019). However, the phenotypic performance of sweet sorghum genotypes is influenced by biotic and abiotic factors, resulting in some genotypes performing well in one environment but poorly in another (SOUZA et al., 2013; BERNAL; LIGARRETO; HERNÁNDEZ, 2014; RONO et al., 2016).

The impact of macroenvironmental factors on genotype performance can complicate recommendations to farmers for different growing conditions (ANNICCHIARICO, 1992). Therefore, it is essential to provide detailed information on candidate genotypes regarding their adaptability and stability. Studying adaptability and stability helps identify genotypes sensitive to positive environmental variations and those with a predictable response in specific environments or broad adaptability (ANNICCHIARICO, 1992). Various methods are available to analyze the adaptability and stability of genotypes when cultivated in diverse environments. The Annicchiarico method (ANNICCHIARICO, 1992) assesses the risk of adopting a cultivar compared to others under evaluation, summarizing the adaptability and stability of the genotypes using a recommendation reliability index. In contrast, the Wricke method (WRICKE; WEBER, 1986) estimates the ecovalence of each genotype by its relative contribution to genotype-by-environment interactions, exclusively measuring agronomic stability. These two methods are advantageous due to their ease of implementation and result interpretation.

Hybrid breeding for ethanol production is encouraged in sweet sorghum based on evidence of genes with non-additive effects (BUNPHAN et al., 2015; KUMAR et al., 2016; LOMBARDI et al., 2018; ROCHA et al., 2018). Multiple studies have demonstrated that hybrids yield 21% more ethanol than lines (FIGUEIREDO et al., 2015; KUMAR et al., 2016; ROCHA et al., 2018). Additionally, hybrids are believed to exhibit a higher degree of homeostasis, making them more stable and productive than lines, primarily due to their high heterozygosity (BECKER; LÉON, 1988).

Therefore, this study aims to evaluate the adaptability and phenotypic stability of sweet sorghum lines and hybrids concerning the main agro-industrial traits. It also seeks to explore the possibility of selecting hybrids that combine high ethanol yield and yield stability in various sweet sorghum growing environments.

MATERIALS AND METHODS

The experiments were conducted during the 2012/2013 crop year in three locations in the state of Minas Gerais, Brazil: Lavras (21°14' S; 45°00' W; 932 m), Nova Porteirinha (15°48'10" S; 43°18'03" W; 500 m), and Sete Lagoas (19°27' S; 44°14'49" W; 767 m). Sequential water balance (WB) was calculated for each location based on mean monthly rainfall and temperature, considering a soil available water capacity of 80 mm (Figure 1). The climate of Lavras, Nova Porteirinha, and Sete Lagoas was classified, according to Köppen, as Cwa, *Bsh*, and Cwa, respectively (ALVARES et al., 2013). Over the course of the experiment, total rainfall was 943.7, 318.1, and 381.5 mm, and the mean temperature was 22.4, 26.9, and 23.5 °C, respectively (Figure 1). The soils were classified as *Latossolo Vermelho-Amarelo* (Lavras and Nova Porteirinha) and *Latossolo Vermelho* (Sete Lagoas) according to the Brazilian Soil Classification System, corresponding to Oxisol.

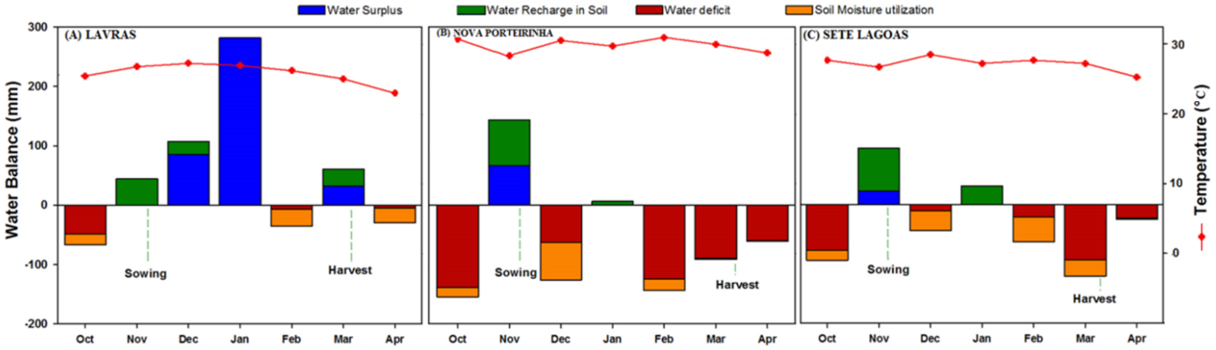

Figure 1. Water balance (mm) and mean temperature (°C) during the 2012/2013 crop year in Lavras (A), Nova Porteirinha (B), and Sete Lagoas (C), Minas Gerais State, Brazil.

The experiments were set up in a 5 × 9 alpha lattice design with three replications in November 2012. A total of 45 genotypes were evaluated, including 10 fertility restorer sweet sorghum lines (R_1: BR500R, R_2: BR501R, R_3: BR504R, R_4: BR505R, R_5: CMSXS633R, R_6: CMSXS634R, R_7: CMSXS642R, R_8: CMSXS643R, R_9: CMSXS644R, and R_{10}: CMSXS647R); three cytoplasmic non-sweet sorghum male-sterile lines (A_1: BR007A, A_2: BR008A, and A_3: CMSXS222A); 30 experimental hybrids (HE), resulting from partial diallel crosses between the lines A and R (H_{AxR}); and two commercial hybrids (HC) (HC_1: XBSW80007; HC2: XBSW80147). Each plot consisted of two 5-meter length rows spaced 0.70 meters apart. At sowing, 350 kg ha^{-1} of the fertilizer formulation 08-28-16 was applied in the plant furrows, with an additional 200 kg ha^{-1} of urea applied as topdressing when the plants reached the V_4-V_5 stage.

Weed control during the experiments included the application of an atrazine-based herbicide (3 Kg a.i. ha^{-1}) and mechanical weed removal when necessary. In Nova Porteirinha and Sete Lagoas, supplemental irrigation was applied. Harvesting was conducted manually, typically at 125 days after sowing.

The following traits were measured: fresh matter production (FMP, Mg ha^{-1}), determined by cutting plants with panicles and leaves from the plot at 5 cm above the soil surface, then weighing them using a digital hanging scale (Kg), and converting to Mg ha^{-1}; juice extraction (EXT, %), calculated as the ratio of the weight of juice extracted from eight randomly selected plants from the plot using a hydraulic press (minimum constant pressure of 250 kgf cm^{-2} for 1 minute in Lavras and Sete Lagoas) or a two-roll crushing mill in Nova Porteirinha; total soluble solids content (TSS, °Brix), measured with an automatic digital refractometer, with automatic temperature correction and a maximum resolution of 0.1 ºBrix; tons of Brix per hectare (TBH), calculated as the product of FMP × EXT/100 × TSS/100; yield of hydrated ethanol (ETH, L ha^{-1}), calculated as the product of RS × 10 × 0.6475 × 0.85 × FMP, where RS is the total content of reducing sugars (% juice) calculated using the equation RS = 3.641 - 0.0343 × (POL ÷ TSS × 100), and POL is sucrose content (% juice) measured with an automatic digital saccharimeter. ETH was evaluated only in Lavras and Sete Lagoas.

Individual analyses were performed for each location, with recovery of interblock information. The homogeneity of residual variances across locations was assessed using

Bartlett's test at the 0.01 significance level. Subsequently, multilocation analyses were performed based on the following statistical model:

$$y_{ijkl} = \mu + a_l + r_{i(l)} + b_{(il)j} + g_k + ga_{kl} + e_{ijkl},$$

where y_{ijkl} is the observation for the plot of block j within replication i in location l that received genotype k; μ is a constant associated with all observations; a_l is the effect of location l; $r_{i(l)}$ is the effect of replication i in location l; $b_{(il)j}$ is the effect of block j within replication i in location l, $b_{(il)j} \sim N(0, \sigma^2_b)$; g_k is the effect of the genotype k; ga_{kl} is the effect of the interaction of genotype k with location l; and e_{ijkl} is the experimental error associated with y_{ijkl}, $e_{ijkl} \sim N(0, \sigma^2_e)$. Both individual and multilocation analyses were performed using the lme4 package (BATES et al., 2015) in the R software (R CORE TEAM, 2019).

Experimental quality was assessed in each location by estimating the selective accuracy on a genotype-mean basis, reflecting the reliability of genotype selection based on phenotypic data. Genotype means were clustered using the Scott-Knott test at a 5% significance level with the ExpDes R package (FERREIRA; CAVALCANTI; NOGUEIRA, 2014). Adaptability and phenotypic stability were analyzed using the Wricke and Annicchiarico methods with the Genes software (CRUZ, 2013).

The Wricke (WRICKE; WEBER, 1986) method estimated the ecovalence (W_k), which measures the contribution of genotype k to the genotype × location interaction, using the following estimator: $W_k = r\Sigma(Y_{kl} - \bar{Y}_k - \bar{Y}_{.l} + \bar{Y}_{..})^2$, where Y_{kl} is the mean of genotype k in location l; $\bar{Y}_k$ is the mean of genotype k in all locations; $\bar{Y}_{.l}$ is the mean of location l for all genotypes; and $\bar{Y}_{..}$ is the overall mean. The percentage of the genotype × location interaction attributed to each genotype ($W_k\%$) was calculated as: $W_k\% = (W_k / \Sigma W_k) \times 100$.

The Annicchiarico (ANNICCHIARICO, 1992) method enables estimating a recommendation or reliability index (I_k) for a determined genotype from the estimator: $I_k = P_k - Z_{[1-\alpha]}S_k$, where P_k is the mean of relative performances of genotype k in all locations (in percentage); $Z_{[1-\alpha]}$ is the quantile $[1-\alpha]$ of the normal cumulative distribution function, in this case being pre-established at $\alpha = 0.25$; and S_k is the standard deviation of relative performances of genotype i in all locations.

Relative mid-parent heterosis (in percentage) of each hybrid was also estimated based on the mean of parental lines using the following estimator: $\left[\left[\bar{y}_{kk'} - \left(\frac{\bar{y}_k + \bar{y}_{k'}}{2}\right)\right] / \left(\frac{\bar{y}_k + \bar{y}_{k'}}{2}\right)\right] \times 100$, where $\bar{y}_{kk'}$ is the mean of the hybrid obtained from crossing lines R_k and $A_{k'}$; and $\bar{y}_k$ and $\bar{y}_{k'}$ are the means of lines R_k and $A_{k'}$, respectively.

Graphical representations were created using the ggplot2 R package (WICKHAM, 2016). All analyses were performed in the R environment (R CORE TEAM, 2019).

RESULTS AND DISCUSSION

Significant variations ($P \leq 0.01$) were observed among the genotypes and across the locations for all the traits evaluated. Genetic variation in sweet sorghum has also been documented in the literature (REGASSA; WORTMANN, 2014; ROCHA et al., 2018) and may be linked to the crop cycle and heterosis (SOUZA et al., 2016; LEITE et al., 2020). The variations seen among locations can be attributed to macroenvironmental factors (SOUZA et al., 2016), such as temperature and rainfall (RONO et al., 2016) (Figure 1). For instance, Nova Porteirinha, on average, exhibited higher TSS (14.6 °Brix), likely due to the higher temperatures recorded in that location (Figure 1), which favor the phenotypic expression of this trait (REGASSA; WORTMANN, 2014). Conversely, the juice extraction method used had a negative impact on EXT in that location.

The genotype by location interaction effect was significant for all the traits evaluated ($P \leq 0.05$), as also reported in the literature (BECKER; LÉON, 1988; RONO et al., 2016; EGGLESTON et al., 2018). This interaction can present both challenges and opportunities for genotype selection, recommendation, and the determination of superior genotypes for various locations (WRICKE; WEBER, 1986), underscoring the need for adaptability and stability analyses (LEITE et al., 2017; EGGLESTON et al., 2018). Studies on adaptability and stability in sorghum typically aim to identify genotypes that excel in specific sets of locations based on the evaluated traits (EUCULICA et al., 2019; CHAPARA et al., 2020) and/or according to the chosen analytical methods (WRICKE; WEBER, 1986; BECKER; LÉON, 1988; RONO et al., 2016; EUCULICA et al., 2019). Nevertheless, few studies have explored the impact of the genetic structure of the crop on stability (HAUSSMANN et al., 2000). In grain sorghum (HAUSSMANN et al., 2000), obtaining hybrids with a high degree of heterozygosity contributed to crop stability, aligning with reports that describe homeostatic functions as attributes of heterozygosity and genetic heterogeneity (ULICINI, 1973). Thus, it is expected that heterozygous genotypes exhibit greater stability than lines, regardless of the location evaluated.

The A lines demonstrated higher stability for the FMP, EXT, TBH, and ETH traits; however, they exhibited an elevated risk of recommendation and limited phenotypic expression (Figure 2). Regarding the R lines that displayed greater stability, phenotypic expression, and lower risk of recommendation, noteworthy ones include R_1 for the FMP trait, R_2, R_4, and R_6 for the EXT trait, R_5 and R_7 for TSS, and R_1, R_4, and R_5 for the MBH and ETH traits (Figure 2). In terms of stable hybrid combinations with minimal risk of recommendation and high phenotypic expression, notable hybrids are H_{2x9} and H_{3x9} for FMP, TSS, TBH, and ETH, as well as H_{3x8} and H_{2x7} for ETH (Figure 2). It is essential to emphasize that, on average, the experimental hybrids (HE) exhibited intermediate stability compared to the A and R lines, irrespective of the measured trait and the methods employed (Figure 2). This unexpected outcome underscores that the self-regulating capability leading to higher degrees of homeostasis is a trait of specific genotypes, and in hybrids, this stability originates from the parental lines (ULICINI, 1973). The parental lines, A and R, diverged concerning stability based on the method used (Figure 2). According to ecovalence estimates, the A lines, on average, displayed greater stability for all the traits evaluated. However, an opposite result was observed with the Annicchiarico method due to the low performance of those A lines (Figure 2). For TBH, for example, in the worst-case scenario, the R lines had a production that was 7.8% higher than the overall mean of the location, whereas the A lines had production 83.7% lower than the overall mean of the location, with 75% reliability. This discrepancy is because ecovalence estimates stability in the agronomic sense (LIN; BINNS; LEFKOVITCH, 1986), considering a cultivar stable if its response to the environment is parallel to the mean performance of the genotypes in different experiments, which can be either superior or inferior to the mean. In contrast, the Annicchiarico method measures adaptability and stability based on the genotype's superiority relative to the mean of each environment (WRICKE; WEBER, 1986).

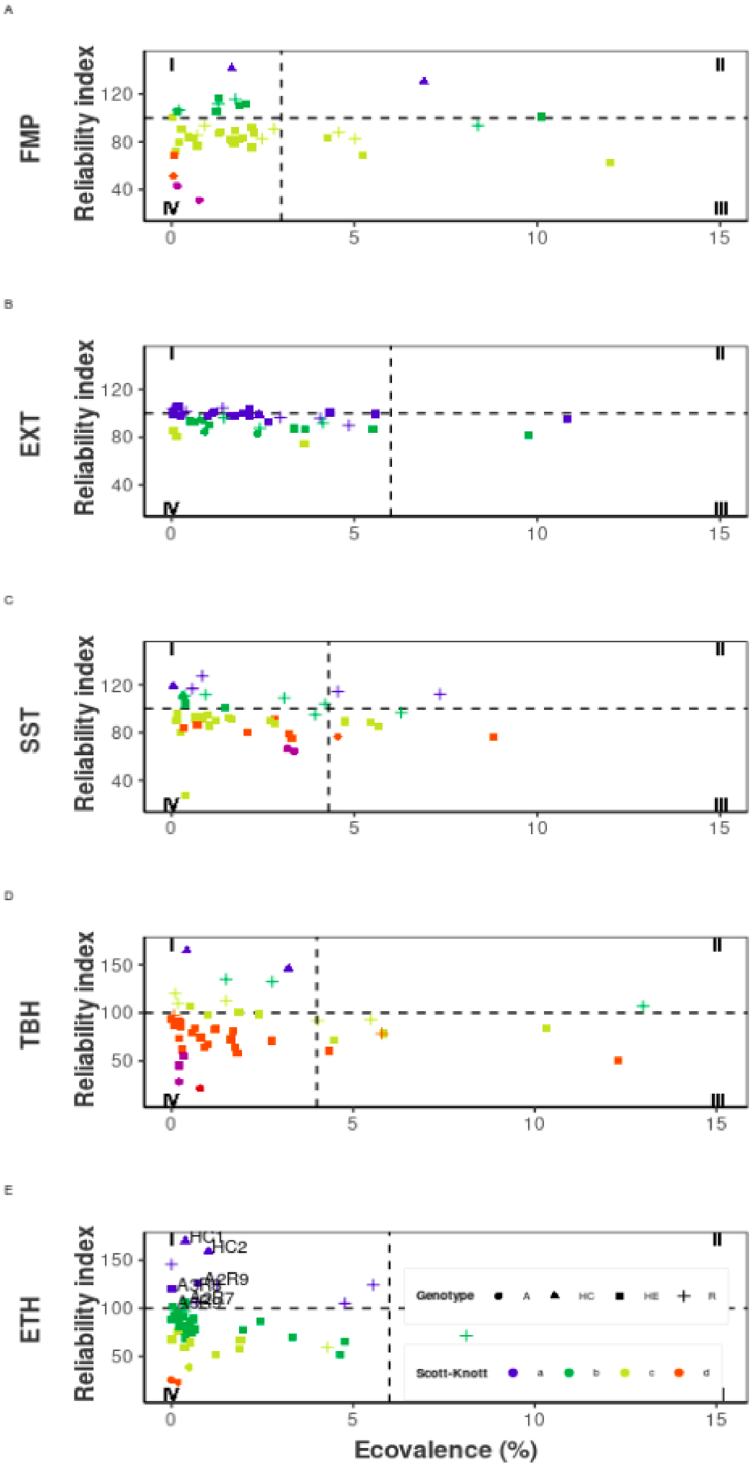

Figure 2. Reliability index estimates vs. ecovalence (%) and mean clustering by color, determined by Scott-Knott test ($P \leq 0.05$) for 45 sweet sorghum genotypes based on fresh matter production (FMP), juice extraction (EXT), total soluble solids content (TSS), metric tons of Brix per hectare (TBH), and ethanol production in liters per hectare (ETH). Genotypes are distinguished by different shapes according to their genetic structure: 'A' for A lines, 'R' for R lines, 'HC' for commercial hybrids, and 'HE' for experimental hybrids.

The A lines evaluated in this experiment are not typically grown as sugar crops and exhibited lower phenotypic expression for all measured traits, which was expected due to their short stature and early cycle. An analysis of the performance of hybrids compared to their male parent lines (R lines) becomes intriguing. On average, the hybrids demonstrated superior stability compared to the R lines but with a higher risk of adoption, primarily due to their lower performance, in alignment with other studies (BECKER; LÉON, 1988; SOUZA et al., 2013). The reduced performance of the hybrids can be attributed to the lower performance of the female parent lines. Nonetheless, certain hybrids were not only stable but also carried a minimal risk of recommendation, producing, in low-yield environments, up to 25% (H_{2x9} for ETH) more than the overall mean of the location, depending on the trait evaluated (Figure 2). This finding indicates the presence of specific genotypes with a higher degree of homeostasis (LIN; BINNS; LEFKOVITCH, 1986).

In contrast to the experimental hybrids (HE), the commercial hybrids (HC) displayed greater stability and a lower risk of adoption compared to the A and R lines (Figure 2), showcasing the role of heterozygosity and the genetic structure's effect on the phenotypic stability of sweet sorghum genotypes. Moreover, these observations underscore that stability also depends on the performance of the parental lines and their combining ability in various locations (ULICINI, 1973; BECKER; LÉON, 1988), which may be associated with the action of both additive and non-additive genes.

Estimates obtained based on the average of locations indicate that lines R_2 and R_9 exhibited positive heterosis, primarily for FMP, TBH, and ETH. While interactions between the A lines and locations were not detected, there is a slight variation in this effect, where line A_2 showed a positive value for all traits, especially for ETH. However, these lines did not simultaneously display good stability and a negligible risk of adoption (Figure 2). Nevertheless, these estimates suggest the possibility of more stable and adaptable hybrid combinations in response to environmental fluctuations (CRUZ; REGAZZI; CARNEIRO, 2014). Hybrid H_{2x9} displayed high stability and a low risk of adoption for all traits (Figure 3). This result is attributed to the substantial and positive magnitude of varietal heterosis and, particularly, the specific heterosis of this hybrid, leading to a higher degree of homeostasis derived from heterozygosity. Furthermore, the heterosis estimates also highlight hybrids originating from line A_3, such as hybrid H_{3x8} (Figure 3). This suggests that this line has deficiencies that are compensated for by the R lines, indicating genetic complementation and heterosis (CRUZ; REGAZZI; CARNEIRO, 2014), providing evidence of non-additive gene action in genotype stability (Figure 3).

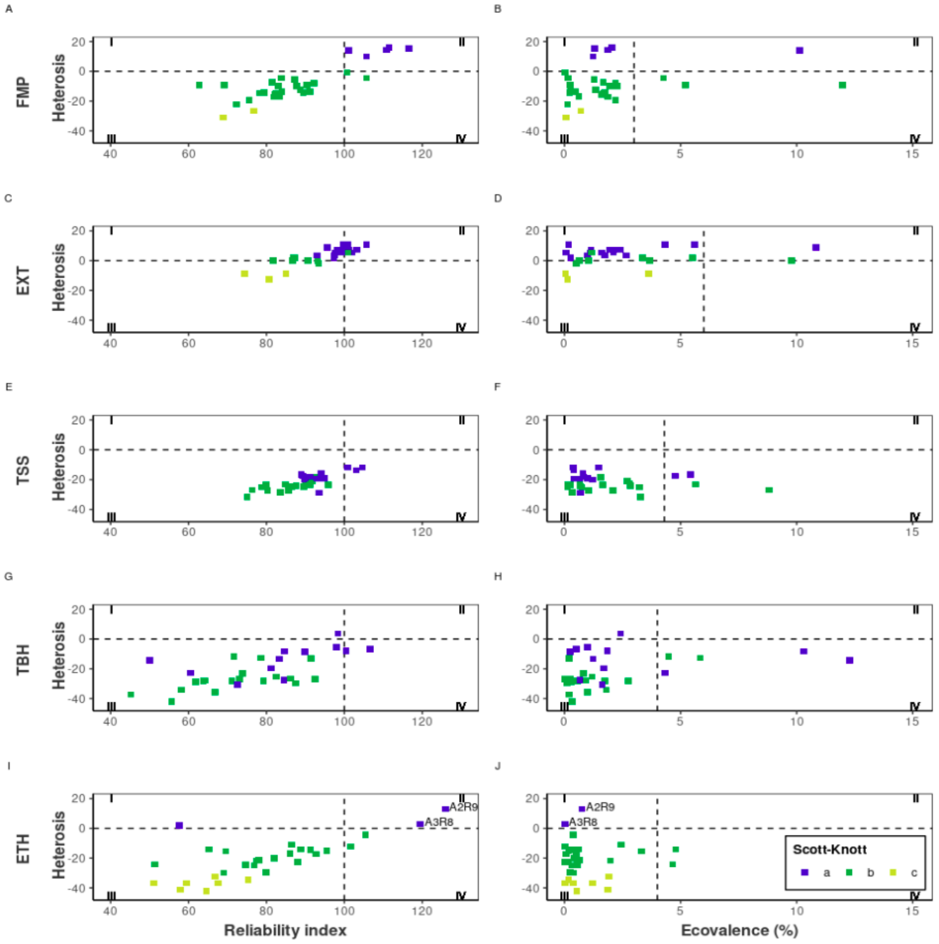

Figure 3. Heterosis estimates vs. reliability index estimates and vs. ecovalence, along with mean clustering by color, determined by Scott-Knott test ($P \leq 0.05$), for 30 sweet sorghum experimental hybrids based on fresh matter production (FMP), juice extraction (EXT), total soluble solids content (TSS), metric tons of Brix per hectare (TBH), and ethanol production (ETH).

The H_{2x9} and H_{3x8} hybrids were the only ones that combined high stability and minimal risk of adoption, especially for the most critical trait for the crop, ETH (Figure 3) This promising outcome can be attributed to the heterosis of these hybrids, which is linked to the action of both additive and non-additive genes, indicating that stability is associated with a high additive genetic potential and, more importantly, a high gene complementarity at loci controlling the trait between A and R lines. The mid-parent heterosis for ETH was primarily associated with the FMP and EXT traits (Figure 3). The limited heterosis for SST was a consequence of the A lines' lower performance, as they are characterized as juicy non-sweet lines. Therefore, the breeding of these lines, particularly the male-sterile (A) lines, is essential for obtaining more stable and superior hybrids.

CONCLUSION

Sweet sorghum adaptability and phenotypic stability are influenced by genotype genetic structure. Hybrids tend to exhibit greater stability when parent lines demonstrate high individual performance and/or substantial gene complementarity across distinct locations. Specifically, the hybrids H_{2x9} and H_{3x8} may be selected due to their combination of high performance and stability, and a low risk of adoption in the evaluated locations.

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