



Genetic analysis for brix weight per stool and its component traits in sugarcane (*Saccharum officinarum*)*#

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Abstract: Brix weight per stool (BW) of sugarcane is a complex trait, which is the final product of a combination of many components. Diallel cross experiments were conducted during a period of two years for BW and its five component traits, including stalk diameter (SD), stalk length (SL), stalk number (SN), stalk weight (SW), and brix scale (BS) of sugarcane. Phenotypic data of all the six traits were analyzed by mixed linear model and their phenotypic variances were partitioned into additive (*A*), dominance (*D*), additive×environment interaction (*AE*) and dominance×environment interaction (*DE*) effects, and the correlations of *A*, *D*, *AE* and *DE* effects between BW and its components were estimated. Conditional analysis was employed to investigate the contribution of the components traits to the variances of *A*, *D*, *AE* and *DE* effects of BW. It was observed that the heritabilities of BW were significantly attributed to *A*, *D* and *DE* by 23.9%, 30.9% and 28.5%, respectively. The variance of *A* effect for BW was significantly affected by SL, SN and BS by 25.3%, 93.7% and 17.4%, respectively. The variances of *D* and *DE* effects for BW were also significantly influenced by all the five components by 5.1%~85.5%. These determinants might be helpful in sugarcane breeding and provide valuable information for multiple-trait improvement of BW.

Key words: Genetic analysis, Brix weight (BW), Component traits, Sugarcane (*Saccharum officinarum*)

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INTRODUCTION

For plant breeders, yield in crops is one of the most important and complex traits. Continued improvement of yield remains the top priority in most breeding programs (Cox *et al.*, 1994). Brix weight per plant in sugarcane depends on various growth and component traits, which is the final outcome of a combination of different yield components, such as stalk diameter (SD), stalk length (SL), stalk number per stool (SN), stalk weight (SW) and brix scale (BS) (Hogarth, 1971b). Many component analyses have

been performed for complex traits based on morphological and physiological characterizations (Zhou *et al.*, 1984; Bull *et al.*, 1992; Luo *et al.*, 2004). It could be more effective that yield components were selected to increase yield because of lower heritability for yield and higher heritability for yield components (Hogarth, 1971a). However, yield is correlated with yield components in complicated ways (Risch, 2000; Darvasi and Pisanté-Shalom, 2002). Therefore, it is imperative to reveal the genetic relationship between yield and its component traits, and their interaction to various environments.

Traditionally, multiple linear regression and path analysis techniques are applied for analyzing the relationship between the complex trait and its component traits (Samonte *et al.*, 1998; Wu *et al.*, 2004). However, partial regression and path coefficients

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depend on the selected variables in a model, and all these approaches were with limitations due to the disturbance of the other related variables (Wen and Zhu, 2005). Subsequently, several approaches based on the normal conditional distribution theory were proposed for analyzing a complex trait and its multiplicative component traits (Jobson, 1991; Sparnaaij and Bos, 1993; Piepho, 1995). However, these approaches only can analyze the data from single environment and do not take into account the phenotypic data of multiple environments simultaneously; in addition to partition the phenotypic variances due to different components (Wu *et al.*, 2004). Zhu (1994; 1995) proposed several methods in a framework of mixed linear model for analyzing quantitative traits. The unconditional methods can analyze the data derived from multiple environments and partition the phenotypic variance into various genetic components (Zhu, 1994), and can deal with complex traits excluding the disturbance of related traits (Zhu, 1995). These methods have been employed to study the genetic basis of quantitative traits in mice, rice and cotton (Zhu and Weir, 1996; Yan *et al.*, 1998a; 1998b; Ye *et al.*, 2003). In previous studies, conditional analysis method was mainly used to measure the epigenetic effects of the causal components on the dynamic variability of developmental behavior (Atchley and Zhu, 1997; Cao *et al.*, 2001). Recently, this approach was extended to make inference on contribution of multiple components to a complex target trait (Wu *et al.*, 2004; Wen and Zhu, 2005).

In this study, we analyzed two-year data for brix weight per stool (BW) and its five component traits from an incomplete diallel cross of 5×6 in sugarcane using Zhu (1994; 1995)'s methodologies. Unconditional analysis method was employed to investigate the genetic basis of inheritance and genetic correlations among these traits, and the conditional analysis approach was used to measure the contribution ratios for various component traits to BW in sugarcane. Our findings may provide a better understanding of genetic inheritance and the relationship among these traits in sugarcane.

MATERIALS AND METHODS

Materials and field experiment

Five female parents: (1) Yuetang 81/3254, (2)

Yuetang 85/177, (3) Yuetang 72/426, (4) Yuetang 79/177 and (5) Yuetang 80/101, and six male parents: (6) ROC16, (7) ROC20, (8) ROC22, (9) ROC23, (10) ROC24 and (11) ROC25, were used to generate 30 crosses of F₁ population. These parents and their F₁s were planted at the experimental station of Zhanjiang Sugarcane Research Center, Guangdong, China in 2000 and 2001, respectively. All the materials were evaluated in a randomized complete block design with three replicates. Plot size was three rows 4 m in length with a between-row spacing of 1 m and an intra-row spacing of 0.2 m. Standard cultural practices were followed throughout the growing season. A 20-plant sample was collected from each plot before harvest to measure the stalk diameter (SD, cm), stalk length (SL, cm), stalk number per stool (SN), stalk weight (SW, kg) and brix scale (BS, %). Brix weight per stool (BW, kg) was calculated by $BW=SN \times SW \times BS$.

Statistical analysis

The genetic model for agronomic traits with genotype×environment (GE) interaction effects (Zhu, 1994; 1995) was employed to study the inheritance of each trait investigated. Unconditional genetic analysis (Zhu, 1994) was conducted based on phenotypic values, which can be partitioned in a matrix form of mixed linear model as:

$$y = Xb + U_A e_A + U_D e_D + U_{AE} e_{AE} + U_{DE} e_{DE} + e_\varepsilon = Xb + \sum_{u=1}^5 U_u e_u \sim MVN(Xb, V = \sum_{u=1}^4 \sigma_u^2 U_u U_u^T + \sigma_\varepsilon^2 I), \quad (1)$$

where y is the vector ($n \times 1$) of phenotypic values with mean Xb and variance V ; b is the vector ($p \times 1$) of fixed effects; X is the known incidence matrix ($n \times p$) relating to the fixed effects; e_u ($u=1,2,3,4,5$) is the vector ($q_u \times 1$) of the u -th random factor, $e_u \sim (0, \sigma_u^2 I)$; e_A , e_D , e_{AE} , and e_{DE} refer to additive, dominance, additive×environment interaction and dominance×environment effects, respectively; U_u is the known coefficient matrix relating to the random vector e_u , U_u^T is the transpose matrix of U_u ; e_ε is the vector ($n \times 1$) of the residuals random effects with $e_\varepsilon \sim N(0, \sigma_\varepsilon^2 I)$. The covariance between two traits y_1 and y_2 can be expressed by

$$\text{Cov}(\mathbf{y}_1, \mathbf{y}_2^T) = \sum_{u=1}^4 \sigma_{u_1/u_2} \mathbf{U}_u \mathbf{U}_u^T + \sigma_{5_1/5_2} \mathbf{I}. \quad (2)$$

The estimates of fixed effects (\mathbf{b}) were obtained by the generalized least squares estimation method. The random genetic effects (\mathbf{e}_u) were predicted by the adjusted unbiased prediction (AUP) method (Zhu and Weir, 1996).

Considering that a trait \mathbf{y}_C is one component of a target complex trait \mathbf{y}_T , the conditional variable $\mathbf{y}_{T|C}$ for the phenotypic value of the target trait \mathbf{y}_T conditioned upon the phenotypic value of component trait \mathbf{y}_C can also be partitioned as (Zhu, 1995):

$$\begin{aligned} \mathbf{y}_{T|C} &= \mathbf{X}\mathbf{b}_{T|C} + \mathbf{U}_A \mathbf{e}_{A_{T|C}} + \mathbf{U}_D \mathbf{e}_{D_{T|C}} + \mathbf{U}_{AE} \mathbf{e}_{AE_{T|C}} + \\ &\mathbf{U}_{DE} \mathbf{e}_{DE_{T|C}} + \mathbf{e}_{\varepsilon_{T|C}} = \mathbf{X}\mathbf{b}_{T|C} + \sum_{u=1}^5 \mathbf{U}_u \mathbf{e}_{u_{T|C}} \sim \quad (3) \\ &MVN(\mathbf{X}\mathbf{b}_{T|C}, \mathbf{V} = \sum_{u=1}^4 \sigma_{u_{T|C}}^2 \mathbf{U}_u \mathbf{U}_u^T + \sigma_{5_{T|C}}^2 \mathbf{I}), \end{aligned}$$

with all the parameters and variables defined similar to those in Eq.(1).

Both unconditional and conditional variances and covariances were estimated by a minimum norm quadratic unbiased estimation (MINQUE) method (Zhu and Weir, 1994). The Jackknife resampling method was used to estimate the standard errors of genetic variances and correlation coefficients (Miller, 1974; Zhu and Weir, 1994). For data analysis, all of these methods were implemented in the quantitative genetic analysis software package QGA Station 1.0 (<http://ibi.zju.edu.cn/software/QGA.htm>).

RESULTS

Trait performances

The performances of two types of parents, female and male, and their F₁s for each of the studied traits are summarized in Table 1. Females had larger SD and SW but smaller SN and BW than males, and showed approximately the same SL and BS as males. Means of F₁s were no larger than those of parents for most of the traits, but similar to the best parent for SN. The trait performances indicated that variations of these traits should be affected by genotypic effects. In addition, means of each trait were different across the

two years (2000 and 2001), indicating that the variations of these traits should be affected by genotype×environment interaction effects.

Table 1 Means of two types of parents and their F₁s for each trait

Year	Genotype	SD (cm)	SL (cm)	SN	SW (kg)	BS (%)	BW (kg)
2000	Females	2.53	247.53	2.73	1.24	0.1964	0.6613
	Males	2.40	237.44	3.15	1.08	0.2076	0.7051
	F ₁ s	2.37	230.53	3.19	1.00	0.2021	0.6416
2001	Females	2.65	244.00	2.63	1.32	0.1889	0.6518
	Males	2.50	248.00	3.03	1.21	0.1968	0.7139
	F ₁ s	2.43	235.29	3.01	1.06	0.1973	0.6253

Components of heritability

For the genetic model with *GE* interaction effects, the total heritability $h^2=(V_G+V_{GE})/V_P$ can be partitioned into the general genetic heritability $h_G^2=V_G/V_P$ and the *GE* interaction heritability $h_{GE}^2=V_{GE}/V_P$ (Zhu, 1997). The general heritability, which is applicable to multiple environments, is the ratio of variances accumulated heritable general genotypic effects (V_G) to the phenotypic variance (V_P). The *GE* interaction heritability, which is only applicable to specific environment, is the ratio of variances accumulated heritable *GE* interaction effects (V_{GE}) to the phenotypic variance (V_P). The estimated components of heritability for the six traits are presented in Table 2.

Table 2 Estimated proportion of variance component to phenotypic variance for each trait

Proportion	SD (cm)	SL (cm)	SN	SW (kg)	BS (%)	BW (kg)
V_A/V_P	0.145**	0.093**	0.437**	0.114**	0.250**	0.239**
V_D/V_P	0.358**	0.444**	0.240**	0.527**	0.199**	0.309**
V_{AE}/V_P	0.052*	0.030	0.009	0.000	0.070*	0.000
V_{DE}/V_P	0.273**	0.342**	0.000	0.233**	0.366**	0.285**
V_ε/V_P	0.172*	0.091**	0.314**	0.126**	0.115**	0.167**

* and ** indicate that the proportions of variance are detected at the significance levels of 0.05 and 0.01, respectively. V_A , V_D , V_{AE} , V_{DE} , V_ε and V_P are the variances of additive, dominance, additive×environment interaction, dominance×environment interaction, residual and phenotypic effects, respectively

The results revealed that all these traits in sugarcane might be influenced by three factors i.e. general genetic effects, *GE* interaction effects and the residual effects. For the genetic factors, SN was mainly controlled by general genetic effect, while the

other five traits were controlled by both general genetic and GE interaction effects. These results indicated that SN could stably inherit, but the genetic effects of the remaining traits were sensitive to the environments. As for the genetic components, the variance of dominance effects was larger than that of additive effects for all traits except for SN. In breeding practice, it is possible to increase SN in sugarcane by selection in early generations, while the remaining traits could be improved through heterosis in hybrid sugarcane by selection in later generations.

Phenotypic correlation and its components

Since the phenotypic variance (V_P) and covariance (C_P) can be partitioned into components of G , GE and residual effects, phenotypic correlation between two traits (1 and 2) can also be partitioned into the corresponding components of correlation:

$$r_P = \frac{h_{G(1)}h_{G(2)}r_G + h_{GE(1)}h_{GE(2)}r_{GE} + \sqrt{(1-h_{G(1)}^2-h_{GE(1)}^2)(1-h_{G(2)}^2-h_{GE(2)}^2)}r_\epsilon}{\sqrt{V_{P(1)}V_{P(2)}}}$$

where $r_P = C_P / \sqrt{V_{P(1)}V_{P(2)}}$, $r_G = C_G / \sqrt{V_{G(1)}V_{G(2)}}$, $r_{GE} = C_{GE} / \sqrt{V_{GE(1)}V_{GE(2)}}$ and $r_\epsilon = C_\epsilon / \sqrt{V_{\epsilon(1)}V_{\epsilon(2)}}$ are the phenotypic, the general genotypic, the GE interaction genotypic and the residual correlation coefficient between two traits, respectively (Zhu, 1997). All estimated correlation coefficients of various genetic effects among six traits are listed in Table 3.

All the phenotypic and genetic correlations among these traits, except for genetic correlation between SL and SN, were at both the 5% and 1% levels of significance. Therefore, it would be a feasible way to improve one trait through improving its related trait. The BW would be improved by increasing its five component traits due to the positive genetic correlations between BW and them. However, simple phenotypic correlation coefficient cannot measure the direct relationship between two traits due to the presence of residual effect. For example, residual correlation coefficients between three component traits (SD, SN and BS) and BW were significant, which indicated that larger values on the three traits would accompany with higher BW due to the residual effects.

Genetic correlations exclude the residual effect and all were significant except for those between SL and SN. The results showed that the genetic correlation coefficients were similar to the corresponding phenotypic correlation coefficients. It was implied that the phenotypic correlation mainly attributed to the genetic correlation between two traits. All the genetic correlation coefficients were in the same sign but higher in magnitude than the corresponding phenotypic correlations. Thus, the heritable amount of correlation between two traits would be provided by genetic correlation coefficients. However, genetic correlation coefficients were affected by the GE interaction effects, which were unstable across the environments.

Table 3 Estimated correlation coefficients among six traits investigated in sugarcane

Pairs of traits	r_P	r_{G+GE}	r_ϵ	r_A	r_D	r_{AE}	r_{DE}
SD-SL	0.598**	0.599**	0.622**	0.244*	0.761**	-0.686**	0.705**
SD-SN	-0.470**	-0.409**	-0.695**	-0.933**	-0.512**	0.589**	0.000
SD-SW	0.883**	0.886**	0.876**	1.000**	0.924**	0.000	0.820**
SD-BS	-0.210**	-0.250**	0.032	-1.000**	0.118	0.190	-0.113
SD-BW	0.254**	0.346**	0.195 ⁺	-0.971**	0.644**	0.000	0.838**
SL-SN	-0.146**	-0.073	-0.520**	0.482**	-0.538**	-0.648**	0.000
SL-SW	0.759**	0.777**	0.620**	0.338**	0.892**	0.000	0.850**
SL-BS	-0.141**	-0.155**	-0.020	-0.580**	-0.068	-0.875**	0.026
SL-BW	0.495**	0.591**	-0.164	0.591**	0.558**	0.000	0.838**
SN-SW	-0.415**	-0.372**	-0.638**	-0.737**	-0.497**	0.000	0.000
SN-BS	0.246*	0.315*	0.001	0.481*	0.353*	-0.297*	0.000
SN-BW	0.577**	0.538**	0.744**	0.983**	0.278*	0.000	0.000
SW-BS	-0.192**	-0.224**	0.045	-0.922**	-0.088	0.000	-0.042
SW-BW	0.404**	0.476**	-0.013	-0.651**	0.666**	0.000	1.000**
BS-BW	0.364**	0.383**	0.253*	0.431**	0.403**	0.000	0.385 ⁺

⁺, * and ** indicate that the correlation coefficients are detected at the significant levels of 0.10, 0.05 and 0.01, respectively. r_P , r_{G+GE} , r_ϵ , r_A , r_D , r_{AE} and r_{DE} are the correlation of phenotypic, genotypic, residual, additive, dominance, additive×environment interaction, dominance×environment interaction, respectively

General genetic correlations do not take into account the *GE* interaction effect, which is heritable and can be expected in various environments. General genetic correlation consists of additive correlation and dominance correlation. It was found that all the additive correlation coefficients were significant at 5% significance level. Two traits, SD and SW, showed negative additive correlations with BW, indicating that larger additive effect values on SD or SW could be accomplished by lower additive effect values on BW. For the remaining three component traits, larger values could be accomplished by higher BW due to positive additive correlation coefficients. Significant positive dominance correlations between BW and its component traits were detected, suggesting that simultaneous improvement of BW and its components could be obtained by their hybrids.

The *GE* interaction correlation was heritable but unstable, which could be applied for specific environment. All additive×environment interaction correlation coefficients between BW and its component traits were zero, indicating that all additive correlations were stable across environments. All dominance×environment interaction correlations except for that between SN and BW were significant, indicating that these dominance correlations were sensitive to the environments. Although there existed negative additive correlations between SD (or SW) and BW, the indirect selections in early generations could be influenced by positive dominance correlations. Significant dominance correlations between BW and its component traits were recorded, suggesting that high BW and its components could be obtained by hybrids.

Contribution ratios of conditional traits

Since, simple correlation cannot exclude the disturbance effect of other related traits, the conditional variance analyzing approach was employed to study the effects of closely related traits for dissecting the complex relationships and to reveal the net contribution of each causal trait to the resultant trait (Wu et al., 2004; Wen and Zhu, 2005). Since conditional variable $y_{T|C}$ is independent of y_C , conditional random effects $e_{u|TC}$ contain extra genetic variation without the influence of the given component trait y_C on the target trait y_T . The proportion of $\sigma_{u|TC}^2 / \sigma_{uT}^2$ could uncover the contribution of genetic effects without

the influence of the given component trait y_C on the target trait y_T . Define $CR_u = 1.0 - \sigma_{u|TC}^2 / \sigma_{uT}^2$ as the contribution ratio measuring the contribution proportion of the u -th genetic variation of the given component trait y_C to the target trait y_T . The estimates of contribution ratios for phenotypic values per each component trait to various genetic effects on BW in sugarcane are presented in Table 4.

Table 4 Estimated contribution ratios for each component trait to BW in sugarcane

Component traits	SD (cm)	SL (cm)	SN	SW (kg)	BS (%)
CR_A	-0.219**	0.253**	0.937**	-0.308**	0.174**
CR_D	0.422**	0.290**	0.051**	0.381**	0.153**
CR_{AE}	0.000	0.000	0.000	0.000	0.000
CR_{DE}	0.520**	0.608**	0.074**	0.855**	0.149**
CR_ϵ	0.038**	0.027**	0.553**	0.000	0.064**
CR_P	0.224**	0.293**	0.346**	0.270**	0.133**

** indicates that significant contribution is detected at the level of 0.01. CR_A , CR_D , CR_{AE} , CR_{DE} , CR_ϵ , and CR_P are the contribution ratios of causal trait to additive, dominance, additive×environment, dominance×environment, residual and phenotypic effects of BW, respectively

Most contribution ratios were at 1% significance level, indicating that these effects on the resultant traits were influenced by phenotypic values on given casual traits in some extent. For example, the phenotypic variation of BW was affected by the phenotypic variation of SD with the contribution ratio of 22.4%. Some contribution ratios were not significant, indicating that these variations of BW were not affected by the casual traits. For example, the CR_{AE} for SD to BW was zero, indicating that the AE interaction variation of BW was slightly influenced by SD. There were two contribution ratios, CR_A for SD to BW and CR_A for SW to BW, with negative values because the conditional variance was larger than the unconditional variance of BW. It was suggested that the additive variation of BW could be larger when the influence of SD or SW are excluded.

As regard to the additive variance of BW, the contribution of SN (93.7%) was the largest among all the five component traits. Three traits, SL, SN and BS, showed positive contributions to BW, while the remaining two traits displayed negative contributions. The variances of *D* and *DE* effects of BW were largely contributed by SD, SW, SL and BS, but slightly contributed by SN with CR_A at 5.1% and

7.4%, respectively. The variance of *AE* effect of BW was independent of all five component traits. Among phenotypic variations on BW, 22.4%, 29.3%, 34.6%, 27.0% and 13.4% were explained by the five component traits, respectively.

DISCUSSION

Sugarcane is one of important crops. Breeders are now paying much more attention to improve BW in sugarcane than before. However, the understanding of genetic basis of BW and its related traits remains unsolved. Although the genetic parameters for most characters in sugarcane were estimated in previous studies but most of these estimates lacked precision due to the limitation of statistical methods (Hogarth, 1971a; 1971b; Lin *et al.*, 1993; Gallacher, 1997). In this study, the genetic variance components of BW and its five component traits of sugarcane were estimated by mixed linear model approaches (Zhu, 1994; Zhu and Weir, 1996). We found that BW and its five components were mainly influenced by additive, dominance, and dominance \times environment interaction effects. Additive effect was more prominent than dominance effect on SN, which was reversed on the remaining five traits. In breeding practice, additive effect could be a useful practice in early generations while dominance effect could be used in hybrid sugarcane, for selection of traits.

Genotype \times environment interaction is an important component affecting quantitative traits and determines the stability of crop varieties across different locations and years (Yan *et al.*, 1998b). Understanding the genetic mechanism of complex traits across various environments is crucial to identify the genetic basis of these traits, and is also of great significance to biologists and breeders for trait selection. In the present investigations, it was observed that all the traits except SN were affected by dominance \times environment interaction effects, suggesting that hybrid heterosis could be expected in special environments. More studies in special environments can reveal the genetic bases of these traits in sugarcane.

In crop breeding, genetic correlation is considered to be a general theoretical method for indirect selection (Ram *et al.*, 1997). Although genetic correlations can be used in measuring the relationship

between pair-wise traits, they can provide information about the additive and dominance correlations only (Zhou *et al.*, 1984; Luo *et al.*, 2004). Our results showed that additive, dominance, additive \times environment, and dominance \times environment correlations existed extensively among BW and its component traits in sugarcane. Additive correlations between BW and its two component traits (SD and SN) were more important than other genetic correlation components, suggesting that indirect selections of SD or SN might improve BW in sugarcane breeding. Dominance correlations were also important among BW and its component traits, so breeding for hybrid sugarcane could be expected to improve BW and its component traits. In addition, dominance \times environment interaction correlations between BW and its all component traits except for SN were positive, suggesting that simultaneously improving BW and its related component traits could be obtained in sugarcane hybrid crosses in special environments. Therefore, we may conclude that indirect selection could be effectively applied in sugarcane breeding in regard to the understanding of correlation of different genetic components. Breeders could simultaneously improve pair-wise traits possessing high additive correlation coefficient. Dominance correlation could be used in hybrid sugarcane breeding to improve related trait-pairs. In summary, it may be helpful for breeders to understand the mechanisms of genetic correlation among various complex quantitative traits.

BW of sugarcane is the final outcome of a combination of different component traits. Although the relationships between BW and its component traits in sugarcane have been extensively explored (Hogarth, 1971b), little has been reported about the genetic basis of these traits due to the lack of sophisticated analytical tools. We applied a simple approach of correlation analysis to evaluate the relationships between BW and its five component traits. It was determined that BW was significantly correlated with its five component traits. However, simple correlation analysis between two traits may confound the effects of other related traits and thus provide biased estimates of the true correlations (Wen and Zhu, 2005). To dissect the complex relationships and to reveal the net contributions of single component trait to BW in sugarcane, the conditional analyzing approach was applied (Wen and Zhu, 2005) in the present study.

This method is considered to be a properly statistical approach to account for dependencies among variables, and measure the direct influence of one trait to another. Our findings revealed that each component trait of BW in sugarcane contributed more than 13.3% to the phenotypic variation, i.e. 5.1%~42.2% of dominance variation, and 7.4%~85.5% of dominance \times environment interaction variation on BW. Similarly, 25.3%, 93.7% and 17.4% of additive variations on BW were explained by SL, SN and BS, respectively. These genetic correlation mechanisms of quantitative traits may provide information to improve effectively BW by means of enhancing its component traits in sugarcane.

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