

Combining ability of sugarcane genotypes based on the selection rates of single cross families

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Abstract: *This study evaluated the genetic potential of parents used in sugarcane genetic breeding programs based on the performance of previously conducted single crosses. The average selection rate of each family, predicted using Best Linear Unbiased Prediction (BLUP) procedure, was used as a surrogate to the cross performance in the initial evaluation phase. Data analysis was performed using Griffing's method IV adapted for the available set of crosses to detail the general combining ability (GCA) and specific combining ability (SCA) effects. Significant GCA effects were detected, which demonstrated the possibility of selecting parents based on this parameter. SCA had a higher coefficient of determination than GCA. In conclusion, the selection rate is an effective indicator for evaluation of the combining ability of parents in the first selection stage of a sugarcane breeding program.*

Key words: *Saccharum, breeding, general combining ability, specific combining ability.*

INTRODUCTION

Sugarcane genetic breeding has become a decisive factor in sugar alcohol industry development in Brazil, with considerable selection gains over the years and regular release of new cultivars (Barbosa et al. 2012, Ramalho et al. 2012, Daros 2014, Iaia et al. 2014, Melo et al. 2014, Barbosa et al. 2015, Carneiro et al. 2015).

New sugarcane cultivars are obtained by vegetative propagation of selected genotypes, which are obtained by sexual reproduction of suitable parents. Selection is applied to all breeding stages, from parental choice to the final evaluation phase of the network trials. Individual selection is inefficient during the early stages due to the low heritability coefficients of most traits. Nevertheless, selection based on phenotypic evaluations of individual plants is commonly performed in the early stages of genetic breeding programs (Barbosa et al. 2005, Matsuoka et al. 2005).

Parental selection should fall on genotypes with the characteristics of interest and good cross performances to obtain populations with good performances and containing genes of interest. Parental crosses should be carefully planned, and crosses between related individuals should be avoided to reduce the occurrence of inbreeding depression and the narrowing of the genetic base (Matsuoka et al. 2005).

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The correct choice of parents for crosses depends on the goals and objectives of the genetic breeders, the characteristics of the parents in morphological and agronomic variables, and the progeny performance in previous crosses (Badaloo et al. 1999). The previous performances of the parents may be inferred by calculating the selection rate, which is the ratio between the genotypes selected from each cross and the number of genotypes in that cross. The average selection rate of a parent may be used as an indicator of its general combining ability (Badaloo et al. 1999).

The general combining ability (GCA) is used to estimate the average performance of genotypes in various hybrid combinations and is associated with additive allele effects and additive-by-additive epistatic effects. Conversely, the specific combining ability (SCA) is used to identify specific hybrid combinations that are better or worse than the expected abilities based on the GCA and is associated with gene dominance effects (Halauer et al. 2010).

Genetic variability of the germplasm collection is a basic need for a genetic breeding program. Knowledge of the genetic divergence among genotypes determines the success of hybridization from parental selection. Divergence between genotypes may be indirectly inferred using genealogy data, morphological and agronomic variables, or molecular markers. The SCA of a cross may also be used as an indicator of genetic divergence between parents for a given trait provided that the trait-controlling loci in question show dominance effects (Halauer et al. 2010). This study evaluated the genetic potential of sugarcane parents based on the GCAs estimates using the selection rates of previously generated single-cross families.

MATERIAL AND METHODS

Populations derived from 3043 single crosses (biparental crosses) involving 541 parents from the sugarcane genetic breeding program of the Inter-University Network for the Development of the Sugar Alcohol Industry (*Rede Interuniversitária de Desenvolvimento do Setor Sucoalcooleiro* – RIDESA) were used. The single cross progenies were assumed to be full-sib families, although contaminants may occur (Santos et al. 2014). The breeding program crosses were routinely conducted at the Serra do Ouro Flowering and Crossing Station, Murici, Alagoas state, Brazil. The seeds were sent to the federal universities (IFES) that composed the RIDESA (Barbosa et al. 2012). Sowing was performed in each IFES, and seedlings were produced. After a nursery growth phase, the seedlings were used to outline the first selection stage (termed stage T1) and installed in their own areas and experimental areas of associated sugar alcohol industries. In this stage, the best genotypes were selected by visual evaluation and measurements of some basic traits; then, the selected clones advanced to the next stage (termed T2). The average number of replications per family in experimental fields was 2.64.

The selection rate within each full-sib family evaluated in stage T1 was the basic variable used to evaluate the genetic value of a single cross in the present study. The contribution of each breeding program to the whole set of data used in this study (8045 data) is shown in Table 1. These data refer to crosses series RB 94 to RB 10 (1994 to 2010). The number of crosses series per breeding program varied from five (UFG and UFMT) to 17 (UFV). The variable corresponds to the ratios in percentages between the number of genotypes selected for stage T2 and the number of genotypes evaluated

Table 1. Number of original data per RIDESA Brazil breeding program and mean effects of selection rates predicted using the BLUP procedure (Intercept = 1.7702)

Breeding program	Number of data	BLUP – selection rate
Universidade Federal de Goiás – UFG	345	1.2817
Universidade Federal de São Carlos – UFSCar	1628	0.8788
Universidade Federal de Alagoas – UFAL	2497	0.2524
Universidade Federal do Paraná – UFPR	1033	-0.1072
Universidade Federal do Mato Grosso – UFMT	190	-0.1675
Universidade Federal de Pernambuco – UFRPE	124	-0.3334
Universidade Federal de Viçosa – UFV	1878	-0.8276
Universidade Federal Rural do Rio de Janeiro – UFRRJ	350	-0.9772
Total	8045	-

in stage T1. Only parents that participated in two or more crosses were analyzed to allow GCA estimation.

The selection rates of each cross were predicted using the Best Linear Unbiased Predictor (BLUP) method according to the model: $Y_{ijk} = \mu + \tau_i + \alpha_j + \rho_k + \varepsilon_{ijk}$; where, Y_{ijk} : selection rate (%) from the cross k , in the year j , in IFES i ; μ : effect of the mean (intercept), fixed, with $E(\mu) = \mu$ and $E(\mu^2) = \mu^2$; τ_i : effect of IFES (breeding program), random, with $E(\tau_i) = 0$ and $E(\tau_i^2) = \sigma_\tau^2$; α_j : effect of year j , random, with $E(\alpha_j) = 0$ and $E(\alpha_j^2) = \sigma_\alpha^2$; ρ_k : effect of cross k , random, with $E(\rho_k) = 0$ and $E(\rho_k^2) = \sigma_\rho^2$; ε_{ijk} : error (deviation) associated with the observation Y_{ijk} , random, with $E(\varepsilon_{ijk}) = 0$ and $E(\varepsilon_{ijk}^2) = \sigma_\varepsilon^2$. This procedure was adopted to minimize differences in the selection criteria of each program and other unmeasured effects between experiments. The predicted value of a specific cross ($\rho_k, k = 1, 2, \dots, 3043$) representing the adjusted average performance of its progeny in stage T1 was used to outline a partial diallel table. The use of the Restricted Maximum Likelihood (REML) mixed models method in sugarcane genetic breeding has been used for several authors (Barbosa et al. 2005, Barbosa et al. 2012, Silva et al. 2015).

Model I: Method IV proposed by Griffing (1956) was used for the combining ability analysis as follows: $Y_{ij} = \mu + g_i + g_j + s_{ij}$, wherein Y_{ij} is the BLUP value regarding the cross between parents i and j , μ is the overall mean, g_i and g_j are the general combining ability (GCA) effects of the i^{th} and j^{th} parents, respectively ($i < j = 2, 3, \dots, 541$), and s_{ij} is the specific combining ability (SCA) effect of the cross between the i - and j -order parents.

The estimates of the effects and their respective sums of squares were obtained using the least squares method. The model is described using matrix notation as follows: $Y = X\beta + \varepsilon$, wherein Y is the vector of observed means, X is the incidence matrix, β is the vector of parameters and ε is the vector of deviations from the model. Some restrictions, like the sum of estimates equal to zero, were added to obtain unique solutions for the vector β estimate.

The matrix X was constructed using the reduced model $Y_{ij} = \mu + g_i + g_j$. The parameter estimates were obtained by $\hat{\beta} = (X'X)^{-1}(X'Y)$. The sum of squares of the model was obtained by $SS_{Model} = \hat{\beta}(X'Y)$. SCA estimates were obtained by the differences between the observed value of each cross and predicted values by model based on GCA (\hat{g}_i and \hat{g}_j) (i.e., $S = Y - X\hat{\beta}$, wherein S is the vector of s_{ij} estimates). The sums of squares of the diallel analysis were obtained by $SS_{SCA} = Y'Y - SS_{Model}$ and $SS_{GCA} = SS_{Model} - C$; C is the sum of squares regarding the constant of the model. The analysis was performed using a specific script in the R environment (R Core Team 2014).

RESULTS AND DISCUSSION

Selection rate

The selection rate varied considerably between RIDESA member institutions depending on the purpose of each program, the experimental area, the material availability, the subjective evaluation of the breeder, and the year and site in which the materials were evaluated in stage T1. The average selection rate calculated from 8045 data points resulting from 3043 different crosses was 1.84% of genotypes selected per family, with a range from 0% to 90% and a 142.04% coefficient of variation, which shows a wide variation of selection rates among crosses and among experiments. Most values ranged from 0% to 5%, thereby generating a frequency distribution skewed to near-zero values; values higher than 10% were rare (Figure 1a). Applying the BLUP procedure to predict the genetic values of crosses proved efficient and generated a frequency distribution similar to the standard normal curve, with the higher frequency classes close to zero (Figure 1b).

The selection rate used in the present study to evaluate the genetic potential of the parents was a composite variable derived from different primary variables used in the T1 selection stage of the RIDESA sugarcane genetic breeding program. Conceptually, the selection rate may be considered a selection index because it encompasses several variables, including vigor, health, height, and stalk diameter, depending on the criteria adopted in each IFES. High selection rates are generated in crosses (families) with higher means and phenotypic variability when considering a single selection criterion and the same sample size. Populations with low means and variances generate low or null selection rates, whereas average rates occur in populations with a low mean and high variance, high mean and low variance or with both parameters with intermediate values.

The average selection rate per cross predicted using the BLUP method had values ranging from -0.692 to 4.734, with

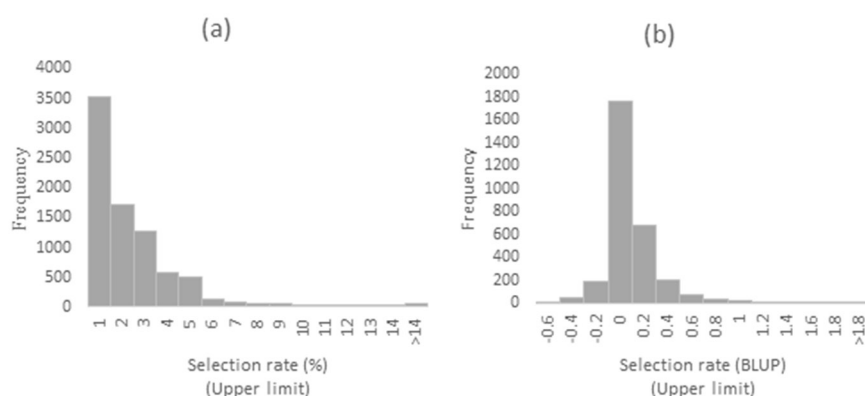


Figure 1. Histograms of the frequencies of selection rate values: a) original data (8045 values); b) mean values of 3043 crosses predicted using the BLUP procedure.

a 1.7702 intercept (Figure 1b). The effects of institutions ranged from -0.977 (Federal Rural University of Rio de Janeiro – UFRRJ) to 1.281 (Federal University of Goiás – UFG). These values showed the different selection intensities in T1 stage between institutions (Table 1).

Analysis of variance

The results from the analysis of variance performed according to the model by Griffing (1956) adapted for the available set of crosses are outlined in Table 2. A mean squared error on the same scale as the other mean squares was not available because the BLUP values used in the analysis were obtained at the level of means of crosses. Thus, the significance of the general combining ability (GCA) was tested using the F test with the mean square of the specific combining ability (SCA) as a denominator, which is a conservative test that is equivalent to considering the parental effects as random. The F test was significant at a 0.1% probability level for the GCA effect. The significance of the SCA was not tested using the F test for the aforementioned reason.

Table 2 also outlines the coefficients of determination for GCA (0.231) and SCA (0.769). These values indicate that 76.9% of the total data variation results from SCA and 23.1% from GCA. Although the significance of the mean squared SCA was not tested, the R² value demonstrated the importance of this effect for the determination of data variation compared with the GCA. These results demonstrate the possibility of parental selection for future crosses based on the GCA and the existence of specific complementation shown in particular crosses.

The results from the GCA and SCA analysis using diallelic models are usually interpreted regarding genetic effects; the GCA is predominantly associated with the additive effects and the SCA with the non-additive effects of the genes (Silva et al. 2002, Camacho et al. 2015). This interpretation seemed inappropriate in the present case because the variable was a composite variable and a large number of diverse primary variables were analyzed in the selection. The SCA shown using this model may at least partially result from the interaction between genotypes and the test environments.

General combining ability

The present study focused more on the GCA effects for both the reliability and its statistical significance; the SCA effects were estimated for a limited number of crosses compared to the total crosses possible if a full diallel was available.

Table 2. Analysis of variance using the model by Griffing (1956) for the selection rate (BLUP) in 3043 hybrid combinations involving 541 parents of the sugarcane genetic breeding program of RIDESA Brazil

Sources of variation	df	MS	R ²
GCA	540	0.0747***	0.231
SCA	2502	0.0537	0.769
Total	3042	-	-

*** Significant at 0.1% probability level by F test.

Estimates of the general combining ability effects for the 541 parents ranged from 0.454 to -0.353. These values showed that the best parent added 0.45 percentage points to the selection rate (predicted using the BLUP procedure) of crosses in which the best parent participated. Considering that the prediction intercept was 1.770, the best parent was 25.6% higher than the average of all parents. On the opposite end, the parent that contributed least to the crosses was 19.9% lower than the parental average. The GCA estimation method reported herein consists in modeling the concept introduced by Badaloo et al. (1999) in which the average selection rate of a parent is indicative of its GCA.

The 50 best genotypes regarding the GCA are outlined in Table 3. These parents are potentially the best based on the contribution of the highest positive values of the general combining ability effects. For these, the number of evaluated crosses per parent varied from two to 110 (Table 3). Among the 50 best parents, 29 participated of four or more crosses, allowing an acceptable accuracy for the estimates of GCA. Simulated study on the efficiency of partial circulant diallels showed good coincidence of the estimates of GCA with complete diallels, even with small number of crossings per parent (Veiga et al. 2000). A total of 1225 single crosses would be possible with these parents. The choice of crosses to be performed could consider other criteria, including genetic diversity and complementarity between parents, and specific characteristics according to the demands of each program. Some of the parents with the best GCAs outlined in Table 3 are commercial varieties cropped in Brazil, including RB855453, RB987935, SP832847, SP801816 and SP803280 (Chapola et al. 2013, Daros 2014). Only RB855453 was among the eight most planted varieties in 2011 (Barbosa et al. 2012).

Table 3. Estimates of general combining ability effects () and number of crosses (NC) for the 50 best sugarcane parents

Rank	Genotype	NC	GCA	Rank	Genotype	NC	GCA
1	RB7893	2	0.4538	26	RB945957	3	0.1761
2	RB945956	9	0.4227	27	RB855589	22	0.1742
3	RB977666	3	0.4206	28	SP775181	76	0.1734
4	RB951558	3	0.4179	29	RB00509	11	0.1725
5	B70710	4	0.3712	30	RB991555	8	0.1723
6	RB008304	6	0.3454	31	RB961	7	0.1722
7	RB99710	2	0.3299	32	SP801816	90	0.1703
8	JA6420	2	0.3118	33	RB957712	17	0.1669
9	RB865513	8	0.2922	34	RB00512	6	0.1657
10	CP82550	4	0.2889	35	RB951521	2	0.1640
11	RB855063	14	0.2781	36	RB971739	5	0.1611
12	IAC873396	18	0.2664	37	RB835487	4	0.1572
13	RB987965	2	0.2642	38	RB965908	3	0.1564
14	RB97327	2	0.2529	39	RB95549	5	0.1518
15	CB3822	8	0.2245	40	RB931546	2	0.1483
16	RB987935	9	0.2090	41	SP831483	3	0.1465
17	RB735200	11	0.2044	42	RB997810	2	0.1431
18	RB758516	4	0.2036	43	RB855453	26	0.1415
19	HJ5741	2	0.2008	44	CB654	2	0.1328
20	SP853877	16	0.1918	45	SP811663	9	0.1325
21	RB9358	2	0.1880	46	H566724	4	0.1320
22	CB4176	2	0.1869	47	RB997627	7	0.1295
23	SP832847	110	0.1839	48	RB961552	2	0.1293
24	RB971741		0.1783	49	SP803280	60	0.1280
25	RB975948		0.1762	50	RB865084	2	0.1235

Heterogeneity for GCA is of great relevance because the existence of genetic diversity among genotypes is important to generate genetic variability and obtain genetic gains on the variables selected in the T1 stage of the genetic breeding programs.

Specific combining ability

The estimates of SCA effects relative to the 3043 hybrid combinations ranged from 4.080 to -0.948 according to the model by Griffing (1956). This estimate had a noticeably higher value (4.080) and thus might be considered an outlier regarding the distribution of values concentrated below 2.0. This cross between parents RB945956 and IAC873396 had only 10 genotypes in the first selection stage in one of the environments; nine genotypes were selected for the following stages generating a selection rate of 90%.

As shown by the coefficient of determination (R^2), the SCA was high, with approximately 77% of the total variation of the BLUPs of selection (Table 2). Therefore, the extreme SCA values were noticeably higher in absolute values than the GCA values. Thus, selection may also be performed based on the SCA estimates.

A total of 146,070 hybrid combinations could be obtained using the 541 parents available. Only 3043 of these combinations were evaluated and used to perform the SCA predictions, which was a small percentage of the total that could be studied. Nevertheless, the number of crosses performed was high and might be considered a representative sample of the possible crosses. The genetic potential of the non-evaluated crosses could be estimated based on a reduced model that only analyzed the GCA of those parents (Reis et al. 2005).

SCA estimates enabled the identification of the most promising hybrid combinations to obtain families for genetic breeding programs. From a practical standpoint, crosses with high potential that were previously underexploited could be exploited using a larger sample. The following were the best hybrid combinations in terms of SCA: RB945956 with IAC87-3396, SP80-1816 with RB855063, RB72454 with RB721012, RB855063 with RB855127, RB008304 with RB92579, and RB955970 with SP91-1049.

Table 3 shows that some of the best parents in GCA are involved in the crosses with the highest SCAs. Parent SP83-2847 is noteworthy; this parent had a high GCA and participated in seven of the 45 best crosses. Similarly, parent SP77-5181 ranked 28th regarding the GCA values (Table 3) and participated in five crosses with good specific combining ability. Parent SP80-1816, which participated in six crosses with the best SCA, was also noteworthy.

The effect of SCA is associated with deviations from the mean cross compared to the expected outcome based on the GCA, which results from genetic complementation between parents. Thus, the selection of hybrid combinations with more favorable SCA estimates involving at least one parent with favorable GCA effects is recommended (Bressiani et al. 2002).

The genetic variability that exists between the parents noticeably indicates the possibility of successful selection. However, the selection rate variable, which is composed of other variables, hinders the comparison of the results obtained in this study with other studies because they are based on primary variables (i.e., each trait is individually evaluated), such as soluble solids (Brix), polarizable sugars (POL), tons of sugarcane per hectare (TCH) and stalk number (Bressiani et al. 2002, Silva et al. 2002, Bastos et al. 2003).

GCA has been mostly prioritized in parental selection complemented by SCA, which is also significant for various traits. Thus, it is best to use analyses based on primary variables when selecting individual traits to enable the identification of genotypes or hybrid combinations for the trait of interest. Conversely, the present study demonstrates the viability of using a composite variable to evaluate both parents and hybrid combinations. This procedure allows the use of data from previous cross performances of the parents in a single analysis, thereby enabling the planning of future crosses without conducting diallel crosses, which are labor-intensive and limit the number of parents that may be evaluated. In this case, GCA-based selection should be prioritized as an indicator of the genetic value of the parents. SCA-based selection can be performed within the evaluated set of crosses, and those with the greatest potential may be repeated using a more appropriate sample.

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