SHORT NON-REFEREED PAPER

EVALUATING ADDITIVE AND NON-ADDITIVE GENETIC EFFECTS FOR BRIX CONTENT IN SUGARCANE BREEDING POPULATIONS

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Abstract

Currently, sugarcane breeding programmes directly exploit additive genetic effects by selecting genotypes with high trait values for crossing. There is limited indirect exploitation of non-additive effects using family selection. Additive genetic effects reference the breeding values, narrow-sense heritability and General Combing Ability (GCA), while non-additive effects predict heterosis, dominance, epistasis and Specific Combing Ability (SCA) used to identify superior crosses. The objective of this study was to evaluate the magnitude of additive and non-additive genetic effects and their implications on breeding for Brix content in sugarcane. Data for Brix content were collected from genotypes within replicated family plots that were planted in 12 trials at Bruyns Hill, Pongola, Gingindlovu and Glenside research stations, and analysed using Statistical Analysis System (SAS) mixed models. Female variance was significant ($P<0.05$) in eight trials, while male variance was significant ($P<0.05$) in three trials suggesting larger maternal effects than paternal effects. Female x male interaction variance was significant ($P<0.05$) in six trials suggesting non-additive genetic influence. The proportion of parents (6.2%) that produced significant additive variance was higher than that of crosses (2.4%) with significant non-additive variance. Female and male variance was 13 to 100% larger than female x male interaction variance in 9 out of 12 trials, suggesting predominance of additive effects. There were 30 genotypes with low additive values, compared to eight with high additive values that produced crosses with significant non-additive variance suggesting the presence of heterosis. Additive effects can be used to produce parents with high breeding values, and non-additive effects to evaluate parent cross-combinations at crossing potentially maximising the exploitation of heterosis in sugarcane breeding for Brix content.

Keywords: Sugarcane breeding, brix content, Additive effects, Non-additive effects, Heterosis

Introduction

Sugarcane is an outcrossing plant with high levels of inbreeding depression when plants are self-pollinated, and heterosis, when outcrossed (Zhou, 2020). Commercial sugarcane varieties are complex interspecific hybrids with a complex genetic make-up, which makes it difficult to predict the potential of genotypes as parents for crossing (Mbuma *et al*., 2018; 2020). One of the challenges in sugarcane breeding is determining the genetic control of traits of economic importance. The genetic effects are partitioned into additive and non-additive effects (Hogarth 1977).

Additive genetic effects reference narrow-sense heritability, mid-parent values breeding values, and General Combining Ability (GCA) used to assess the potential of genotypes as parents (Oakey *et al.*, 2007). Non-additive genetic effects reference Specific Combining Ability (SCA), which is used to identify superior crosses and is associated with heterosis, epistasis,

dominance and other gene interactions. Sugarcane breeding programmes directly exploit additive genetic effects by utilising genotypes that produce progenies with high trait values for crossing, with limited or indirect exploitation of non-additive genetic effects. Mishasha *et al*. (2018) reported high and positive correlations (*r* = 0.86 to 0.99) among Brix, sucrose and ERC% cane suggesting Brix can be used to provide adequate estimates of sucrose content. The objective of this study was to determine the magnitude of additive and non-additive genetic effects for hand-refractometer Brix, as a proxy for sucrose content in sugarcane breeding.

Materials and Methods

The crosses used for this study were made in the South African Sugarcane Research Institute (SASRI) glasshouse at Mount Edgecombe (29.7°S, 31.03°E, 96 m above sea level) Durban, South Africa. Brix% data were collected from stage 1 (mini-lines) trials planted at Pongola (FML15, FMLL18, FMLE19, FMLE20, FMLL20 and FMLF20), Gingindlovu (UML15), Glenside (SML15 and SML17) and Bruyns Hill (BML18, BML19 and BMLF19) research stations.

The trials were laid out as randomised complete block designs, with three replicates per family. At crop maturity Brix was measured from one stalk of each of the first 20 genotypes per family plot, by using a hand-held refractometer. A refractometer determined sugarcane Brix content by measuring the refractive index of sugarcane juice. The stalk was cut at the centre and sugarcane juice was squeezed from the centre cut-end of the stalk onto the refractometer, and a reading was obtained. The hand-held refractometer was calibrated after each reading, using distilled water.

Data were analysed using the following linear mixed models on Statistical Analysis System (SAS) software (SAS institute, 2015).

$$Y_{ijkl} = \mu + R_i + F_j + M_k + FM_{jk} + G(RFM)_{ijkl} \qquad \text{Equation 1}$$

Where Y_{ijkl} is the observation from the ith genotype in the jth female, kth male in the ith replication. μ is the overall mean, R_i is the random effects of the ith replication, F_j is the random effect of the jth female, M_k is the random effect of the kth male, FM_{jk} is the random interaction effect of the jth female by the kth male and $G(RFM)_{ijkl}$ is the residual error.

Results and Discussion

Statistical analysis of data produced estimates of female, male and female by male interaction and residual variance (Table 1). The female and male variances represent additive genetic effects, and female x male interaction variance represent non-additive genetic effects. The female variance was significant $P<0.05$ for trials FML15, FMLE19, FMLL20, FMLF20 UML15, SML15, BML18 and BML19. The male variance was significant $P<0.05$ for FMLE20, UML15 and SML7. The female variance was larger than the male variance for FML15, FMLL18, FMLE19, FMLL20, FMLF20, SML14, BML18, BML19 and BMLF19, but lower for FMLE20, UML15 and SML17. The female x male interaction variance was significant for FML15, FMLL18, FMLL20, SML15, BML18 and BMLF19. The female and male variance was larger than the female x male interaction variance for FML15, FMLE19, FMLE20, FMLF20, UML15, SML15, SML17, BML18 and BML19, but lower in FMLL18, FMLL20 and BMLF19. The residual variance was highly significant ($P<0.001$) across all trials and larger than female, male and female x male interaction variances. The R^2 values were low, ranging from 0.13 (FMLE19 and BMLF19) to 0.32 (SML17). The coefficient of variance (CV%) values ranged from 2.49 (FMLE19) to 20.39 (FMLE20). SML15 (22.21) produced the highest Brix mean, and FMLE19 (12.64) had the lowest Brix mean from the trials planted in the irrigated and rainfed regions.

The higher and significant female variance than the male variance suggested larger maternal effects, where the larger genetic contribution to progenies is from females than from males. In South Africa, a significant proportion of crosses is made up of poly-crosses, where the source of pollen is unknown potentially confounding the contribution of male parents to the progenies. There was a high ratio of additive variance to non-additive variance suggesting a predominance of additive effects for the genetic control of sugarcane Brix. The significant female x male interaction variance suggests non-additive genetic control of sugarcane Brix content. Currently, sugarcane breeding programmes use genetic and breeding values for parent selection; however, the significant female x male interaction variance suggests that using additive genetic effects (genetic and breeding values) limits the exploitation of the full genetic potential of sugarcane.

Table 1. Additive (female, male) and non-additive (female x male) variances for the Brix of trials planted in irrigated and rainfed regions

			Irrigated			
Effect	**FML15**	**FMLL18**	**FMLE19**	**FMLE20**	**FMLL20**	**FMLF20**
Female	1.25±0.61*	0.29±0.20	0.45±0.16**	0.28±0.36	0.47±0.23*	2.08±0.54***
Male	0.00±0.00	0.00±0.00	0.00±0.00	0.92±0.92**	0.00±0.00	0.63±0.50
F x M	1.09±0.46**	0.75±0.20***	0.05±0.07	0.32±0.32	0.48±0.21*	0.02±0.19
Residual	9.7±0.28***	5.57±0.12***	6.19±0.16***	6.69±0.15***	3.15±0.07***	10.22±0.21***
GCA/SCA	1.15	0.39	9.00	3.75	0.98	135.5
R^2	0.22	0.28	0.13	0.23	0.24	0.17
CV%	18.34	12.61	2.49	20.39	8.70	18.41
Mean±SD	16.98±3.11	18.70±2.36	12.64±2.49	12.68±2.59	20.41±1.77	17.37±3.20
			Rainfed			
Effect	**UML15**	**SML15**	**SML17**	**BML18**	**BML19**	**BMLF19**
Female	0.51±0.25*	1.26±0.49**	0.81±0.58	0.34±0.12**	0.47±0.15***	0.19±0.13
Male	1.50±0.58**	0.00±0.00	2.40±1.03**	0.05±0.09	0.00±0.00	0.004±0.03
F x M	0.00±0.00	0.35±0.16*	0.39±0.40	0.23±0.10*	0.08±0.07	0.22±0.11*
Residual	7.52±0.23***	3.79±***	8.20±0.23***	3.02±0.06***	3.27±0.08***	2.75±0.06***
GCA/SCA	0.00	3.6	8.23	1.70	5.88	0.88
R^2	0.21	0.28	0.32	0.18	0.15	0.13
CV%	14.82	8.76	13.53	7.95	9.04	8.37
Mean±SD	18.51±2.74	22.21±1.95	21.18±2.86	21.88±1.74	19.99±1.81	19.79±1.66

*Significant at P<0.05, **Significant at P<0.01, ***Significant at P<0.001,
F x M means female by male interaction
GCA – General combining ability (Additive genetic effects)
SCA – Specific combining ability (non-additive genetic effects)
R^2 – Coefficient of determination
CV – Coefficient of variation
SD – Standard deviation

The parent genotypes and crosses producing significant additive and non-additive genetic values in cross-combinations, are shown in Table 2, where P<0.10 was considered the significant threshold. Trials UML15, SML17, BML19, FMLE19, FMLE20 and FMLF20 produced no combinations of genotypes with significant non-additive genetic effect. However, genotypes 02U1215, 88W1323, 04U1274, 05U0645, 03U0907, 04G0014, 3U1030, 05K1501 (UML15), 01S1681, 85L1056, 00B1941, MO, MP (SML17), 97B0456, 97B0197, 98B0532, N48, 97B0707, 06B0362, 00B1056, 97B0272, N37 (BML19), HOCP9654, N26, 96F0701,99F3567, 00F0637 (FMLE19), 87W0042, 97F1586, 97F0771, 76F2547, 96E0708, 94F3188 and 79F0779 (FMLE20), N40, 01F2810, 96F1290, 95L0828, 03F2441, CP78304, 00F0884, 08F1635, N53, Q155, 02F0645, MO and 07F4417 (FMLF20) produced significant (P<0.10) additive values. Genotypes 03F2264, N49 (FML15), 98S0290, 06B1567, 03S0282, 06S1476 (SML17), 95H0426, 06S1834, 01B0586 and 90H0482 (BML18) produced significant additive genetic values. None of the genotypes with significant additive values produced significant non-additive values in cross-combinations. Genotypes with non-significant additive values produced crosses with significant non-additive genetic values. A low proportion of parents, 93F0373, 90F0556, 89F1649 (FMLL18), 93F3950, 88F0280, 93F1235 and N26 (FMLL20) with

significant additive values produced crosses (89F1649 x 76E0537, 90F0556 x MO, 93F0373 x MP, 93F3950 x 96F1387, 88F0280 x MO, 93F1235 x 91M1603, N26 x MP) with significant non-additive genetic values. BMLF19 had no genotypes and crosses with significant additive and non-additive values.

A higher proportion of genotypes with non-significant additive values produced significant non-additive values in cross-combinations, which suggested that genotype combinations were more important than genetic and breeding values. Genotypes with significantly higher additive values in FML15, UML15, SML15, SML17, BML18, BML19, FMLE19 and FMLE20 produced crosses with non-significant, non-additive values further emphasizing the importance of genetic combinations between genotypes (Zhou, 2020). Currently, most sugarcane breeding programmes use genetic values and breeding values (Mbuma et al., 2018; 2020) to select parents, with limited exploitation of non-additive genetic effects. Results suggest the possibility of using breeding values to select parents, and non-additive genetic effects to evaluate genotype cross-combinations, potentially maximising the exploitation of heterosis for Brix content.

Table 2. Genotypes and crosses that produced significant additive variance (female and male) for Brix

Trial	Parent genotype	Crosses
FML15	03F2264[a], N49*	04F1991 x 06B2039*
UML15	02U1215***, 88W1323*, 04U1274[a], 05U0645***, 03U0907*, 04G0014[a], 03U1030[a], 05K1501*	-
SML15	98S0290***, 06B1567*, 03S0282[a], 06S1476[a]	04S1130 x 96H0220[a] 06S0746 x 06B0925*
SML17	01S1681*, 85L1056*, 00B1941*, MO*, MP*	-
BML18	95H0426*, 06S1834*, 01B0586[a], 90H0482**	97B0272 x MO*
FMLL18	93F0373*, 90F0556[a], 89F1649[a]	89F1649 x 76E0537***, 90F0556 x MO*** 93F0373 x MP**, CP721312 x MP* 99F2394 x MO*, 96F0269 x 87F3580* 86F0423 x 95F3255*, 86F0466 x MO* 86F0423 x 84F2753*, 92F2332 x MO* 75F2673 x 90H0482*, N36 x 94L1760* Q155 x 87F2019*, N41 x MO[a] N40 x 87F3580[a], 95L1458 x 92F2332[a]
BML19	97B0456***, 97B0197***, 98B0532*, N48*, 97B0707*, 06B0362[a], 00B1056[a], 97B0272**, N37[a]	-
FMLE19	HOCP9654**, N26*, 96F0701*, 99F3567*, 00F0637[a]	-
FMLE20	87W0042*, 97F1586*, 97F0771[a], 76F2547[a], 96E0708[a], 94F3188[a] 79F0779[a]	-
FMLL20	93F3950**, 88F0280* 93F1235[a], N26[a]	93F3950 x 96F1387**, 88F0280 x MO* 93F1235 x 91M1603*, N26 x MP* 98F1268 x MP[a]
BMLF19	-	-
FMLF20	N40**, 01F2810***, 96F1290**, 95L0828***, 03F2441***, CP78304***, 00F0884**, 08F1635***, N53***, Q155*, 02F0645 [a], MO*, 07F4417[a]	-

[a]Significant at P<0.1*Significant at P<0.05, **Significant at P<0.01, ***Significant at P<0.001

Conclusions

The higher and significant female variance indicated a larger genetic contribution to progenies from the female, rather than the male, parents. The study suggested Brix content in sugarcane

populations is mainly controlled by additive genetic effects. The significant female x male interaction variance indicated the influence of non-additive genetic effects. Genotypes with non-significant additive genetic effects produced crosses with significant non-additive genetic effects, which suggests that the combinations among genotypes ware more important than genetic or breeding values for producing superior crosses. The results suggest the possibility of using additive genetic effects for parent selection, and non-additive genetic effects to evaluate the crosses potentially maximising the exploitation of heterosis.

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