RESEARCH ARTICLE

Trends in Broad Sense Heritability and Implications for Sugarcane Breeding in South Africa

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Abstract Relocation of South African Sugarcane Research Institute (SASRI) rain-fed research stations was due to urban encroachment and to increase representativeness of research farms. The relocation also coincided with the Recoverable Value (RV) payment system in 1998, which penalized growers for low sucrose content. After 12 years of trials, the large data set collected provided an opportunity to evaluate trends and progress. The objective of this study was to determine trends in broad sense heritability (H) over time and evaluate their implications on SASRI breeding strategies. Data were analysed using the mixed procedure of the Statistical Analysis System to estimate variance components used to calculate H. The coastal short cycle and midlands programs produced significant decrease in H for yield and marginal increase for sucrose content. The irrigated and coastal long cycle produced increase in H for yield. The breeding strategies resulting from the shift to RV payment system increased H for yield in irrigated and coastal long cycle probably due to stable populations for irrigated and increased efficiency for coastal long cycle. The coastal short cycle and midlands showed decreasing trends in H for yield probably due to intensive selection for sucrose content on populations with narrow genetic diversity. The H proved to be an effective parameter for evaluating breeding and selection strategies.

Keywords Variance components · RV payment system · Genetic gains - Selection strategies

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Introduction

Broad sense heritability (H) also referred to as degree of genetic determination or genetic repeatability refers to control of the phenotype of an individual by its genotype (Falconer [1989](#page-5-0); Allard [1960\)](#page-5-0). In clonally propagated crops such as sugarcane, after crossing, the progenies are propagated vegetatively. As a result, selections take advantage of H because recombination events are limited to segregation that occurs only at crossing. Therefore, a study of the trends in H across breeding cycles can be used to evaluate changes in breeding and selection populations as well as the effectiveness of breeding and selection strategies. H is also used to estimate genetic gains during selection (Allard [1960](#page-5-0)).

Broad sense heritability $(H) = V_G/V_P$, (1)

where V_G is the genotypic variance and V_P is the phenotype variance. V_{P} is generally made up of several components of variance representing genotype by environment interaction.

Since 1993, a series of events imposed changes on the South African Sugarcane Research Institute (SASRI) breeding and selection programs. The outcome of a plant breeding workshop held in August 1993 highlighted that few varieties were released from rain-fed breeding and selection programs compared to irrigated (Nuss [1998](#page-6-0)). The rain-fed research farms had variable soil properties within fields. Other research farms became unrepresentative because of urban encroachment. The sugar industry was divided into five agro-climatic regions which were used to create seven research stations (Table [1](#page-1-0)). At these research stations, genotypes from the coastal short cycle (T, U), coastal long cycle (G, K) and midlands (B, S) were combined in the pre-release trials.

Table 1 SASRI regional selection research stations (Nuss [2003](#page-6-0))

Research station	Code	Altitude (m)	Latitude	Harvest age	Conditions represented
Pongola	F	308	$27^{\circ}24'$	12 months	Northern irrigated areas
Empangeni	T	102	$28^{\circ}43'$	12 months	Coastal high potential
Gingindlovu	U	93	$29^{\circ}01'$	$12-15$ months	Coastal average potential
	G	93	$29^{\circ}01'$	18 months	Coastal average potential
Kearsney	K	241	$29^{\circ}17'$	18 months	Coastal hinterland
Bruyns Hill	B	1.012	$29^{\circ}25'$	24 months	Midlands humic soils
Glenside	S	997	$29^{\circ}25'$	24 months	Midlands sandy soils

The shift by millers to recoverable value (RV) payment system (Anonymous [2000](#page-5-0)) in 1998 also influenced the breeding and selection strategy. The RV payment system penalized growers for low sucrose content and resulted in increased demand for high sucrose content varieties. The shift forced breeders to implement intensive breeding and selection for high sucrose content. Intensive family selection for sucrose content among single stools deliberately advanced more seedlings from high sucrose families.

Of the nine series of trials completed by 2010, six were selected pre- and three post-RV from single stools. The data from these trials provided an opportunity to evaluate the impact of these changes on the breeding programs. The objective of this study was to determine the trends in H over time and evaluate their implications on SASRI breeding and selection programs.

Materials and Methods

Trial Sites

Data were collected from trial series planted from 1997 to 2008 and harvested from 1998 to 2010. Data were collected from early and late planted trials in Pongola and Malelane for the irrigated region (Parfitt [2000](#page-6-0)). Two sites, one at Pongola area and the other at Malelane were planted in March, to represent early season and three sites, two at Pongola and one at Malelane were planted in October to represent late season. For the coastal short cycle, three trials were established at Empangeni and two at Gingindlovu. At Empangeni one trial was planted early season (March) and the other late season (October). Two trials were planted at Kearsney (hinterland) and three at Gingindlovu (coastal long cycle). In the midlands, three trials each were planted at Glenside and Bruyns Hill areas. The trials for the hinterland, coastal long cycle and midlands programs were planted in October.

Populations

The coastal short cycle programs consisted of E, W, T and U populations. The E and W populations were selected from

crosses planted as seedlings at Mount Edgecombe and Shaka's Kraal research stations (respectively) near Durban and relocated to Empangeni and Gingindlovu research stations. The T and U populations were crossed and selected at Empangeni and Gingindlovu research stations, respectively. The genotype making up the coastal long cycle programs were from the L, M, G and K populations. Populations L and M were selected as seedlings from crosses planted at La Mercy and Mtunzini research stations, respectively. The G and K populations were crossed and selected at Gingindlovu and Kearsney research stations, respectively. The midlands region was made up of H, B and S populations. The H populations were selected from seedlings planted at Windy Hill Research Station. The B and S populations were crossed and selected at Bruyns Hill and Glenside research stations, respectively.

Experimental Design and Data Collection

All the trials were laid out as randomised block designs with three replications. Plot sizes were five rows by 8 m and spaced 1.2 m at Bruyns Hill, Glenside, Kearsney, Gingindlovu and Empangeni, and 1.4 m for irrigated trials. The genotypes in trials ranged from 24 to 36. At harvest, all millable stalks in the plots were cut by hand and weighed using a digital scale. From each plot, 12 stalks were randomly picked to provide a sample for estimating sucrose content. The sucrose content was measured in laboratory (Shoonees-Muir et al. [2009\)](#page-6-0) and expressed as estimable recoverable crystal (ERC % cane) using an empirical formula that accounts for losses via bagasse and molasses (waste products). The plot weights were divided by the plot area to estimate cane yield (Mg/ha). Sugar yield (ERC (Mg/ha)) was the product of cane yield by ERC % cane.

Data Analysis

The data were subjected to analyses of variance using the following linear mixed model where all variables were considered random:

$$
Y_{ijkl} = \mu + L_l + R(L)_{k(l)} + G_i + GL_{il} + GR(L)_{ik(l)} + C_j
$$

+ LC_{jl} + CR(L)_{jk(l)} + GC_{ij} + GL_{cjl} + E_{ijkl} (2)

where, Y_{ijkl} = observation for genotype i ($i = 1, 2, ..., g$), in Crop-year j ($j = 1, 2, ..., c$), in replication k ($k = 1, 2, ..., r$) nested within location l ($l = 1, 2, ..., l$); μ = overall mean; L_l = the random effect of the *l*th location; $R(L)_{k(l)}$ = the random effect of the kth replication nested within the lth location; G_i = the random effect of the *i*th genotype; $GR(L)_{ik(l)}$ = the random interaction effect between the *i*th genotype and the kth replication nested with the lth location; C_i = the random effect of the *j*th crop-year; LC_{il} = the random interaction effect between the lth location and the jth crop-year; $CR(L)_{ik(l)} =$ random interaction effect between the jth crop-year and the kth replication nested within the lth location; GC_{ii} = random interaction effect between the *i*th genotype and the *j*th crop-year; GLC_{ijl} = random interaction effect between the ith genotype, lth location and jth crop year; and E_{ijkl} = residual error. The genotypes, although selected were taken in this study to represent a random sample of several possible pre-release genotypes. Similarly, although the locations were chosen to represent sugarcane production environments, together with crop-years they represent a random sample of possible sugarcane growing environments being targeted. In sugarcane, yield and quality data in the first and second ratoon crops are measured from the same plots as the plant cane to facilitate the assessment for ratooning ability. As a result, the effects of years are confounded as each crop stage is grown in a different year. Therefore, the effects of years and crop stages are referred to as crop-years (Kang et al. [1987\)](#page-6-0).

The data were analysed using the mixed procedure of SAS (SAS Version 9.2 [2009](#page-6-0)). The estimates of variance components, their standard errors and probability tests were calculated using the COVTEST option in the model statement (Littell et al. [2008](#page-6-0)). The variance components were used to estimate variance of genotype means (V_k) for different combinations of locations, replications and cropyears within a location (Fehr [1987\)](#page-5-0):

$$
V_k = \frac{\sigma_E^2}{ljc} + \frac{\sigma_{GLC}^2}{lc} + \frac{\sigma_{GL}^2}{l} + \frac{\sigma_{GC}^2}{c}
$$
 (3)

where, σ_E^2 is the variance component for the residual term in the model; σ_{GLC}^2 is the variance component for the interaction between genotype, location and crop-year; σ_{GL}^2 is the variance component for the interaction between genotype and location and σ_{GC}^2 is the variance component for the interaction between genotype and crop-year.

From the above, it was possible to calculate H or genetic repeatability on a plot mean basis as:

$$
H = \sigma_G^2 / (\sigma_G^2 + V_k). \tag{4}
$$

The estimates of the standard errors (SE) for H were estimated using (Becker [1992\)](#page-5-0):

SE =
$$
\sqrt{\frac{2(1-H)^2[1 + H(k-1)]^2}{k(k-1)(n-1)}}
$$
(5)

where H is broad sense heritability, k is the number of observations per genotype and n is the number of genotypes.

The H for each of the programs was subdivided into two groups, the pre- and post-RV. The trends in H were analysed for the groups and compared among programs.

Results

Broad sense heritability (H) for all traits under study was calculated for all series for all programs (Tables 2, [3,](#page-3-0) [4](#page-3-0), [5,](#page-3-0) [6](#page-3-0)). The Standard Error (SE) was used to test whether the H values were significantly larger than zero. The SE of H was multiplied by 1.96 (*t*-statistic at $P = 0.05$ read from the T-tables). The product was added and subtracted from the mean H to produce confidence limits. When the confidence limits included zero in their interval, then the H value was similar to zero, and when the interval excluded zero, then the H values were significantly ($P < 0.05$) larger than zero. Our result showed that the H values for all the series across all the programs were significantly ($P < 0.05$) larger than zero.

The H for all the programs were subjected to analysis of variance and means for the programs (Table 2) compared using Tukey's adjustment (Freund and Wilson [2003](#page-6-0)). Anova comparisons among regions showed that for cane yield the coastal long cycle had significantly ($P < 0.05$) lower H than other regions (Table 2). The irrigated program produced significantly $(P<0.05)$ larger H than coastal programs. The coastal long cycle produced significantly $(P<0.05)$ lower H for sugar yield than other programs.

The H for ERC % cane in irrigated program was larger than that for cane and sugar yield (Table [3\)](#page-3-0). Cane and sugar yield produced larger fluctuations in H across series

Table 2 Broad sense heritability and their standard errors for cane yield (Mg/ha), ERC % cane and Sugar yield (Mg/ha) across breeding and selection programs

Program	Cane yield (Mg/ha)	ERC $%$ cane	Sugar yield (Mg/ha)
Irrigated	84.9 ± 4.1 ^{a†}	$90.6 \pm 2.7^{\circ}$	$79.3 \pm 5.4^{\circ}$
Coastal short cycle	$83.7 \pm 4.6^{\circ}$	$81.4 \pm 5.2^{\rm bc}$	$75.3 \pm 6.6^{\circ}$
Coastal long cycle	$69.4 \pm 7.9^{\rm b}$	$76.8 \pm 6.3^{\circ}$	58.4 \pm 9.7 ^b
Midlands	$83.8 \pm 4.6^{\circ}$	$84.0 \pm 4.6^{\circ}$	$75.7 \pm 6.5^{\circ}$

- Values followed by same letter in the column are not significantly different ($P<0.05$)

than ERC % cane. There were non-significant $(P > 0.05)$ differences between pre- and post-RV series but cane and sugar yield produced a six unit increase in H from pre- to post-RV. The populations for the irrigated program did not change from the pre- to the post-RV periods.

There were large and significant ($P < 0.05$) decrease in H from pre- to post-RV for cane and sugar yield in the coastal short cycle (Table 4). ERC % cane produced nonsignificant ($P > 0.05$) increase in H from pre- to post-RV. Genotypes in trials in pre- were derived predominantly from E and W populations while those in post- were derived from the T and U populations.

The post-RV H for coastal long cycle was larger than that of the pre-RV for all traits (Table 5). The H for ERC yield increased significant ($P < 0.01$) from pre- to post-RV while cane yield and ERC % cane produced non-significant

Table 3 Broad sense heritabilities (%) for cane yield (Mg/ha), sucrose content (ERC % cane) and sugar yield (Mg/ha) for the irrigated region across 12 series of breeding and selection cycles

Series	Cane yield (Mg/ha)	ERC $%$ cane	Sugar yield (Mg/ha)
G	84.4 ± 4.3	88.4 ± 3.3	73.0 ± 6.9
H	86.8 ± 3.7	92.4 ± 2.2	80.0 ± 5.4
T	71.9 ± 7.0	88.1 ± 3.4	66.5 ± 8.0
J	89.2 ± 3.0	90.2 ± 2.8	82.4 ± 4.7
K	79.4 ± 5.3	90.6 ± 2.6	73.5 ± 6.5
L	85.7 ± 3.9	94.9 ± 1.5	88.5 ± 3.2
M	90.6 ± 2.7	95.3 ± 1.4	86.6 ± 3.7
N	88.9 ± 3.0	90.9 ± 2.5	85.5 ± 3.8
Ω	86.9 ± 3.5	84.4 ± 4.1	78.0 ± 5.5
Pre	82.9 ± 4.6	90.8 ± 2.6	77.3 ± 5.9
Post	88.8 ± 3.1	90.2 ± 2.7	83.4 ± 4.4

Table 4 Broad sense heritabilities (%) for cane yield (Mg/ha), ERC % cane and sugar yield (Mg/ha) for the coastal short cycle regions

Series	Cane yield (Mg/ha)	ERC $\%$ cane	Sugar yield (Mg/ha)	Populations
G	91.4 ± 2.6	71.4 ± 7.3	79.1 ± 5.7	E, W, F, L, H
H	78.6 ± 5.8	81.3 ± 5.2	71.5 ± 7.3	E, W, F, L, H, M
T	88.9 ± 3.1	83.4 ± 4.5	81.1 ± 5.1	E. W. Z. F. W.
J	88.2 ± 3.4	80.0 ± 5.5	81.2 ± 5.2	E. W. F
K	92.0 ± 2.4	78.9 ± 5.8	84.7 ± 4.4	E, W, Z, L, M, F
L	88.1 ± 3.5	84.7 ± 4.4	82.2 ± 5.0	E, W, L, F, M
M	77.0 ± 6.3	80.6 ± 5.4	78.0 ± 6.0	T. U. F. L. M
N	73.8 ± 7.0	86.3 ± 4.0	51.0 ± 10.6	T. U. E. F
Ω	75.5 ± 6.6	85.8 ± 4.1	68.6 ± 8.0	T , U , L , M , E , W
Pre	87.9 ± 3.5	80.0 ± 5.5	80.0 ± 5.5	E, W
Post	75.4 ± 6.6	84.2 ± 4.5	65.9 ± 8.5	T, U

Bold letters represent populations that contributed more than 80% of the genotypes in the series

 $(P > 0.05)$ increase. ERC % cane produced larger H than cane and ERC yield. The genotypes that were in the pre-RV trials were largely derived from L and M populations while the genotypes that dominated the post-RV trials were derived from G and K populations.

The midlands programs produced significant ($P < 0.05$) decrease in H for cane yield from pre- to post RV (Table 6). Sugar yield and ERC % cane produced nonsignificant ($P > 0.05$) decrease and increase in H, respectively, from pre- to post-RV. The H values for cane yield and ERC % cane were larger than those for sugar yield. The genotypes tested in pre-RV trials were largely derived

Table 5 Broad sense heritabilities (%) for cane yield (Mg/ha), ERC % cane and Sugar yield (Mg/ha) for the coastal long cycle and hinterland regions

Series	Cane yield (Mg/ha)	ERC $%$ cane	Sugar yield Populations (Mg/ha)	
G	75.3 ± 6.8	51.4 ± 10.8		41.5 ± 11.7 L, M, E, F, H
H	59.0 ± 9.6	74.7 ± 6.8	59.0 ± 9.6	L, M
T	74.8 ± 6.7	80.5 ± 5.5	48.2 ± 10.9	L. M
J	51.9 ± 10.5	85.8 ± 4.1	45.5 ± 11.2 L, M, F, Z	
К	68.0 ± 8.1	75.9 ± 6.5		52.6 ± 10.4 L, M, E, H, W
L	72.8 ± 7.2	82.0 ± 5.1	62.5 ± 9.0	L, M, E, H, W
M	68.2 ± 8.4	91.0 ± 2.8	76.3 ± 6.7	G, E, H, L, M
N	79.5 ± 5.7	71.8 ± 7.4	76.5 ± 6.4	G. K. E. L. M. W
Ω	74.7 ± 6.7	78.4 ± 5.8	63.8 ± 8.7	G, K, H, L, M
Pre	67.0 ± 8.3	75.1 ± 6.7	51.6 ± 10.6	L, M
Post	74.1 ± 6.9	80.4 ± 5.5	72.2 ± 7.3	G, K

Bold letters represent populations that contributed more than 80% of the genotypes in the series

Table 6 Broad sense heritabilities (%) for cane yield (Mg/ha), sucrose content (ERC % cane) and sugar yield (Mg/ha) for the Midlands regions across 9 series of breeding and selection cycles

Series	(Mg/ha)	Cane yield ERC % cane	(Mg/ha)	Sugar yield Populations
G	83.2 ± 4.7	79.0 ± 5.7	75.5 ± 6.5	H, E, F, L, M, W
H	80.4 ± 5.5	75.2 ± 6.7	73.9 ± 6.9	$\mathbf H$
T	87.0 ± 4.3	83.8 ± 5.2	81.2 ± 5.9	H
J	88.3 ± 3.4	91.4 ± 2.6	77.2 ± 6.1	H
K	85.8 ± 3.9	87.8 ± 3.4	80.6 ± 5.2	H, F, CP
L	88.8 ± 3.2	80.5 ± 5.3	80.0 ± 5.4	H, L, M
M	81.8 ± 5.1	89.3 ± 3.2	79.8 ± 5.6	B, L, M
N	81.8 ± 5.1	89.4 ± 3.1	62.9 ± 8.8	B. S. W
Ω	76.9 ± 6.0	79.2 ± 5.5	70.6 ± 7.2	B, S, H, L, M
Pre	85.6 ± 4.1	82.9 ± 4.8	78.1 ± 6.0	H
Post	80.2 ± 5.4	86.0 ± 4.0	71.1 ± 7.3	B, S

Bold letters represent populations that contributed more than 80% of the genotypes in the series

from H populations while those in post-RV were derived from B and S populations.

Discussions

Broad sense heritability (H) is an important parameter that determines the efficiency of selection for vegetatively propagated crops. In vegetatively propagated crops such as sugarcane, the genotype of a plant is fixed after crossing because there is no opportunity for further segregation. Therefore, selection capitalises on the variability inherent from initial crossing. H is the proportion of genotypic variability to total variability in the population and indicates the ability to make genetic gains during selection. Therefore, H can be used to determine if the population has sufficient variability to identify superior genotypes. The magnitude of H determines the magnitude of gains from selection.

There were significant differences in H for cane yield among programs. The irrigated, coastal short cycle and midlands programs produced similar H of approximately 84 indicating the potential for high selection gains. The coastal long cycle, with an H of 69 that was significantly less than other programs indicated the limited potential gains to selection for cane yield. The irrigated program produced the largest H for sucrose content, 91, and was significantly larger than that of coastal programs indicating the potential high selection gains for sucrose content for the irrigated program. The coastal long cycle produced the least H for sucrose content, indicating the potential limited gains from selection. The large H for the irrigated region further validates the reason for the large gains in sucrose content already achieved where a significant number of varieties with very high sucrose content have been released recently. Varieties such as N24, N26, N30, N35 and N40 that produce very high sucrose content have been released from the irrigated areas. Generally, programs with larger H produced more released varieties. The irrigated and midlands programs have released the more varieties such as N25, N31, N44, N48, N49, N50, N52 and N53 while the coastal long cycle with the least H has released only two varieties, N47 and N51.

The selections strategy favouring high sucrose genotypes had an impact on H. The irrigated program, with high H for sucrose content indicated the potential of sustained selection gains for sucrose content. The increase in H for cane and sugar yield from pre- to post-RV indicated the potential for increasing selection gains for these traits. The coastal long cycle produced an increase in H for all traits. The results from the irrigated program indicated that it was possible to maintain high H over series for one trait while raising the values of other traits. The irrigated data could also be indicating that the sucrose content has reached the ceiling for H. The coastal long cycle indicated that even with programs starting with low H and low selection gains, the H of several traits can be increased simultaneously to achieve greater selection gains for multiple traits.

For coastal short cycle and midlands, an opposite trend occurred where the H for sucrose content marginally increased at the expense of significant decrease in H for cane and sugar yield. The significant decrease in H indicated reduced gains for the coastal short cycle which have manifested in non-significant differences among test genotypes and no promising varieties for release in recent selection series. Furthermore, the negative correlation between cane yield and sucrose content (Ahmed et al. [2010\)](#page-5-0) appears apparent where small increase in H for sucrose content lead to large decrease in that for cane yield. The manifestation of the negative correlation between cane yield and sucrose content indicates the lack of balance in the selection for these two traits. The greater selection pressure applied for sucrose content starting with family selection for seedlings may have been done at the expense of cane yield. The ideal situation would have been to select for high sucrose content among high yield families, a situation that appeared to prevail for the irrigated and coastal long cycles.

There was a drastic change in the composition of the genotype populations making up the varieties in the trials except for the irrigated region. The programs that experienced this change in populations also produced significant decrease or increase in H from pre- to post-RV. The irrigated program experienced no change in populations and produced increases in H for yield indicating the improved selection gains. The midlands and coastal short cycle experienced changes in population resulting in decrease in H for yield indicating probably potentially narrowing genetic diversity for yield in the post-RV populations. The need to balance the selection for yield and quality is required to reverse this trend in addition to diversifying the parent populations. The change in populations and strategies employed for the coastal long cycle increased H for all traits. However, the coastal long cycle started with very low H, probably close to unsustainable levels. Therefore, efforts to diversify the populations could also have resulted in increased H that eventually led to increased selection gains.

Cane and sugar yield produced larger increases and decreases in H across all programs. The large increases or decreases in H for cane yield could be a reflection of the sensitivity in cane yield to selection while the small changes for sucrose content indicate the opposite trend. Generally, the sensitivity could be influenced by the genetic diversity, negative associations and selection pressures imposed. Sucrose content is known to possess low genetic diversity because it is derived from the Saccharum officinarum species (Daniels and Roach [1987](#page-5-0); Berding and Roach [1987\)](#page-5-0) which is known to have a narrow

gene pool. Intensive selection for sucrose content is expected to produce more of S. officinarum type of genotypes that have narrow diversity for yield, thus lowering the genetic diversity for yield in those resulting populations. This situation could lead to low H for cane yield and the resultant low selection gains. The intensive selection for sucrose content was a response to the RV payment system.

The intensive selection for sucrose content favouring more of *S. officinarum* genome could potentially have reduced the genome content of S. spontaneum in post-RV compared to the pre-RV populations. Cytogenetic studies have shown that generally the sugarcane hybrids are made up of 80% of S. officinarum genome, 10% of S. spontaneum and 10% recombinants (D'Hont' et al. 1996; Grivet and Arruda 2001; Cuadrado et al. 2004). For example, variety R570 known to possess narrow adaptability has a chromosome constitution of 80:10:10 of S. officinarum, S. spontaneum and recombinants, respectively, while NCo376 has 70:20:10 (Ming et al. [2006\)](#page-6-0). The variety NCo376 was released in South Africa in 1955 and to date is the sugarcane cultivar with one of the longest commercial life (Wilson [1974\)](#page-6-0). Cultivar R570 is known to be restricted to specific more ideal growing areas. The cultivar NCo376 has been shown to be widely adaptable to several growing areas in South Africa (Nuss [2001](#page-6-0)), Zimbabwe (Zhou [2004](#page-6-0)), Swaziland, Malawi and Zambia and other countries. The shift in selection pressure towards high sucrose content could have reduced the S. spontaneum chromosome content thereby reducing adaptability.

Across the regional programs, population changes were associated with changes in H. In the irrigated regions, the populations remained unchanged resulting in non-significant changes to H. For the rain-fed programs, the changes in populations resulted in significant changes in H. These changes led to decrease in H for yield and an increase in H for sucrose content for the midlands and coastal short cycles. The coastal long cycle produced significant increase in H for yield and quality when the population changed. It appears that the changes in population could have positive or negative effects depending on the focus of the selection strategies and the baseline starting H. Starting with low H, for example, the coastal long cycle, a significant improvement occurred for both yield and quality. For programs that started with high H, intensive selection for sucrose content appeared to have the negative effect of reducing H for yield. A balanced selection strategy such as family selection for yield in the first stage followed by individual clonal selection within the best families (Stringer et al. [2011\)](#page-6-0) could reduce the declining H.

This study indicates that H is a parameter that can routinely be used to evaluate the breeding and selection strategies. Continuous monitoring of H could indicate strengths and deficiencies as well as progress from breeding strategies. The irrigated and coastal long cycle programs indicated that current breeding strategies were working well and enhancing the capacity to achieve genetic gains. Conversely, for the coastal short cycle and midlands, the strategies were bringing marginal non-significant benefits for sucrose content but large and significant negative effects on cane yield. The evaluation of H could have detected these trends earlier and provide for review of strategies that could have reversed such negative trends and allow for sustained progress in variety improvement.

Conclusions

Breeding and selection strategies influence parameters of populations over time and may bring desirable and undesirable results. The present study showed that it was possible to increase the H of multiple traits simultaneously. Unbalanced selection strategies that may put high pressure on one trait could lead to lower H for other traits particularly where negative correlations exist. Broad sense heritability as a parameter can be used to evaluate breeding and selection strategies over time as well as the productivity of breeding programs.

References

- Ahmed, A.O., A. Obeid, and B. Dafallah. 2010. The influence of character association on behaviour of sugarcane genotypes (Saccharum spp.) for cane yield and juice quality. World Journal of Agricultural Sciences 6(2): 207–211.
- Allard, R.W. 1960. Principles of plant breeding. New York, USA: Wiley.
- Anonymous. 2000. The RV payment system. South African Sugar Association Experiment Station. Information Sheet 11.8. 2 pages.
- Becker, W.A. 1992. Manual of quantitative genetics, 5th ed. Pullman, WA: Academic Enterprises.
- Berding, N., and B.T. Roach. 1987. Germplasm collection, maintenance and use. In Sugarcane improvement through breeding, ed. D.J. Heinz, 143–210. New York: Elsevier.
- Cuadrado, A., R. Acevedo, and M.D. Espina. 2004. Genome remodelling in three modern S. *officinarum* \times S. *spontaneum* sugarcane cultivars. Journal of Experimental Botany 55: 847–854.
- Daniels, J., and B.T. Roach. 1987. Taxonomy and evolution. In Sugarcane improvement through breeding, ed. D.J. Heinz, 7–84. New York: Elsevier.
- D'Hont', A., L. Grivet, and P. Feldmann. 1996. Characterisation of the double genome structure of modern sugarcane cultivars (Saccharum spp.) by molecular cytogenetics. Molecular and General Genetics 250: 405–413.
- Grivet, L., and P. Arruda. 2001. Sugarcane genomics: depicting the complex genome of an important tropical crop. Current Opinion in Plant Biology 5: 122–127.
- Falconer, D.S. 1989. Introduction to quantitative genetics. Essex, UK: Longman Scientific and Technical.
- Fehr, W.R. 1987. Principles of cultivar development: Theory and technique. New York, USA: MacMillan Publishing.
- Freund, R.J., and W.J. Wilson. 2003. Statistical methods. New York: Academic Press.
- Kang, M.S., J.D. Miller, P.Y.P. Tai, J.D. Dean, and B. Glaz. 1987. Implications of confounding of genotype \times year and genotype \times crop effects in sugarcane. Field Crops Research 15: 349–355.
- Littell, R.C., G.A. Milliken, W.W. Stroup, R.D. Wolfinger, and O. Schabenberger. 2008. SAS for mixed models, Second Edition ed. Cary, NC: SAS Institute Inc.
- Ming, R., P.H. Moore, and K.K. Wu. 2006. Sugarcane improvement through breeding and biotechnology. Plant Breeding Reviews 27: 15–118.
- Nuss, K.J. 1998. Aspects considered in the search for new farms for the experiment station. Proceedings of the South African Sugar Technologists' Association 72: 42–45.
- Nuss, K.J. 2001. The contribution of variety NCo376 to sugar production in South Africa from 1955 to 2000 and its value as a parent in the breeding programme. Proceedings of the South African Sugar Technologists' Association 75: 154–159.
- Nuss, K.J. 2003. Plant breeding crossing and selection programs. South African sugar association experiment station, 12. KwaZulu-Natal, South Africa: Mount Edgecombe.
- Parfitt, R.C. 2000. Genotype \times environment interaction among secondary variety trials in the Northern region of the South African sugar industry. Proceedings of the South African Sugar Technologists' Association 74: 245–248.
- SAS Version 9.2. (2009). SAS for windows, version 9.2. Cary, NC, USA: SAS Publishing
- Shoonees-Muir, B.M., M.A. Ronaldson, G. Naidoo, and P.M. Schorn. 2009. SASTA laboratory manual including the official methods. Mount Edgecombe, South Africa: Published by South African Sugar Technologists' Association.
- Stringer, J.K., M.C. Cox, F.C. Atkin, X. Wei, and D.M. Hogarth. 2011. Family selection improves the efficiency and effectiveness of selecting original seedlings and parents. Sugar Tech 13: 36–41.
- Wilson, J. 1974. Production of sugarcane in South Africa. South African Sugar Journal 58: 243–245.
- Zhou, M.M. 2004. Performance of varieties N14 and NCo376 in the South East Lowveld of Zimbabwe. Proceedings of the South African Sugar Technologists' Association 78: 137–147.