REFEREED PAPER

REALISED SELECTION GAINS FOR CANE YIELD, SUCROSE CONTENT AND SUGAR YIELD AMONG SOUTH AFRICAN BREEDING PROGRAMMES

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Abstract

Realised selection gains provide a parametric evaluation of the potential of breeding programmes to produce genetic gains in their released varieties. The objective of this study was to determine the realised selection gains for cane yield, sucrose content and sugar yield, and evaluate their implication in variety improvement. The study was based on data collected from advanced variety trials at the South African Sugarcane Research Institute (SASRI). Data were analysed using the mixed procedure of Statistical Analysis System (SAS) to estimate least square means. Simple linear regression of least square means versus years of selection was used to test the significance of the trends. The Midlands programmes produced the highest gains followed by the coastal long cycle, while the coastal short cycle produced no gains. The gains for sugar yield from the Midlands programmes were derived from the additive gains from cane yield and sucrose content. The gains for the coastal long cycle and irrigated populations were derived from cane yield and sucrose content, respectively. The large gains for the Midlands were attributed to stable populations and low levels of eldana damage and smut disease resulting in two fewer traits at selection. The poorer performance of the coastal short cycle indicates the difficulty associated with breeding for 12 month crop varieties from populations initially designed for an 18 month crop. Development of coastal short cycle parents is expected to reverse the negative gains. Recurrent selection for cane yield (irrigated programme) and sucrose content (coastal programmes) is expected to increase realised selection gains for sugar yield.

Keywords: sugarcane, advanced variety trials, regional breeding programmes, genetic gains

Introduction

Assessment of delivery is important for determining the value to be derived from the investment in plant breeding programmes. Realised selection gains refer to the potential gains that will be attained over time from several cycles of breeding and selections. They indicate the potential of a breeding programme to deliver varieties at time of release that would increase genetic gains over time. The realised selection gains also indicate the potential or success of recurrent selection over time within breeding programmes (Lingle *et al*., 2010).

Previous studies to quantify the performance of sugarcane breeding programmes in Australia (Cox *et al*., 2005; Cox and Stringer, 2007) used complex computations of 30 year moving averages of commercial variety yield data. The trends of the 30 year moving averages were used to estimate genetic gains from the released varieties over time. While this approach has provided a good indication of the value of the Australian sugarcane breeding programmes, the scenario could be different for the sugar industry in South Africa. Variety adoption in South Africa is slow, largely because of the longer ratoon cycles. Studies by Burnquist *et al*. (2010) also attempted to quantify the benefits from breeding programmes, while studies by Donovan (1998, 1999) demonstrated the contribution of varieties to productivity. There has been no defined approach to determine the potential of breeding programmes to deliver sustained gains in yield over time.

The South African Sugarcane Research Institute (SASRI) operates seven regional breeding and selection programmes (Nuss, 1998). These programmes were established to develop varieties suited to each of the agro-ecological zones characterised by different environmental, soil, rainfall, age at harvest, pests and diseases (Table 1). The Midlands zone is characterised by high altitude and longer winters, and sugarcane is harvested at 24 months. The coastal areas are characterised by high and fairly well distributed summer rainfall and mild winter temperatures. The coastal long cycle combines the hinterland and coastal long cycle programmes where sugarcane is harvested at 15-18 months. In the coastal short cycle programmes, sugarcane is harvested at 12-15 months. The northern irrigated programme develops varieties suitable for 12 month harvest, and sugarcane is grown using irrigation.

To assess realised gains, data from the advanced variety trials were used because they represent varieties that are likely to be recommended for release. The objective of this study was to determine the trends in realised selection gains for cane yield, sucrose content and sugar yield across the regional breeding programmes, and to evaluate their implications in variety development.

Table 1. South African Sugarcane Research Institute regional selection research stations (Nuss, 2003).

Research station	Code	Altitude (m)	Latitude	Harvest age	Conditions represented
Pongola	F	308	27°24'	12 months	Northern Irrigated areas
Empangeni	T	102	28°43'	12 months	Coastal high potential
Gingindlovu	U	93	29°01'	12-15 months	Coastal average potential
	G	93	29°01'	18 months	Coastal average potential
Kearsney	K	241	29°17'	18 months	Coastal hinterland
Bruyns Hill	B	1012	29°25'	24 months	Midlands humic soils
Glenside	S	997	29°25'	24 months	Midlands sandy soils

Materials and Methods

Experiment designs and trial locations

Data were collected from advanced variety trial series planted from 1997 (establishment of new research stations) to 2009, and harvested from 1998 to 2010 (Table 2). Data were collected from five trials at Pongola (FV, FV2, NPV2), Malelane (NTV2) and Komati (NNV) for the irrigated programme (Parfitt, 2000). For the coastal short cycle, data were collected from five trials at Empangeni (TV, T1V, TV2) and Gingindlovu (UV, U1V). There were five trials for the coastal long cycle at Kearsney (KV, K1V) and Gingindlovu (GV, G1V, G2V). The six trials in the Midlands were at Glenside (SV, S1V, S2V) and Bruyns Hill (BV, B1V, B2V). Plot sizes were 5 rows by 8 m and spaced 1.2 m for the Coast, 1.0 m for Midlands and 1.4 m for irrigated trials. The number of genotypes in each trial ranged from 24 to 36.

Data collection

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 using standard laboratory procedures (Shoonees-Muir *et al*., 2009) and expressed as estimated 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 (t/ha). Sugar yield (ERC t/ha) was the product of cane yield by ERC % cane.

Table 2. Trial details for the breeding programmes.

Breeding programme	Number of cycles	Trial locations for each selection cycle	Crops harvested per trial series
Irrigated	13	Early trials = FV, NNV Late trials = FV2, NPV2, NTV2	Plant, first, second and third ratoon
Coastal short cycle	12	Empangeni = TV, T1V, TV2 Gingindlovu area = UV, U1V	Plant, first and second ratoon
Coastal long cycle	11	Gingindlovu area = GV, G1V, G2V Kearsney area = KV, K1V	Plant, first and second ratoon
Midlands	11	Humic soils = BV, B1V, B2V Sandy soils = SV, S1V, S2V	Plant, first and second ratoon

Data analysis

For each selection series, the data were subjected to analysis of variance using the Statistical Analysis System (SAS Institute, 2009). The following linear mixed model (Equation 1) was used to estimate the least square means. All the variables in model statement (except genotypes) were considered random:

$$Y_{ijkl} = \mu + L_l + R(L)_{k(l)} + G_i + GL_{il} + GR(L)_{ik(l)} + C_j + LC_{jl} + CR(L)_{jk(l)} + GC_{ij} + GLC_{ijl} + E_{ijkl} \quad \text{Eq 1}$$

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 lth location; $R(L)_{k(l)}$ = the random effect of the kth replication nested within the lth location; G_i = the fixed effect of the ith genotype; $GR(L)_{ik(l)}$ = the random interaction effect between the ith genotype and the kth replication nested with the lth location; C_j = the random effect of the jth crop-year; LC_{jl} = the random interaction effect between the lth location and the jth crop-year; $CR(L)_{jk(l)}$ = random interaction effect between the jth crop-year and the kth replication nested within the lth location; GC_{ij} = random interaction effect between the ith genotype and the jth crop-year; GLC_{ijl} = random interaction effect between the ith genotype, lth location and jth crop year; and E_{ijkl} = residual error. The least square means across sites and crop-years were transformed by expressing the values as a percentage of NCo376 (long-term control) to reduce the effect of year-to-year seasonal variation.

The transformed means (% NCo376) were used as the response variable, while the year of selection of planting the series of the trial was used as the predictor variable to perform simple linear regression analysis using SAS. The simple linear regression model used was:

$$Y_i = a + bx_i + e_i \quad \text{Eq 2}$$

where Y_i was the genotype means (% NCo376) for cane yield, sucrose content or sugar yield; a was the intercept for the ith series; b was the slope; x_i was the ith year of planting and also the predictor variable; e_i was the residual error.

Results

Irrigated
The cane yield for the irrigated programme trials produced non-significant (P>0.05) realised selection gains from 1997 to 2009 years of selection (Figure 1). The trend produced a weak and non-significant correlation (r=8.8, P=0.0578) between cane yield and year of selection. However, an increasing trend in selection gains for cane yield was evident. From 1997 to 2009, there was a 0.18% gain in tons cane per year. From Figure 1, there was consistent increase in gains to selection from 1997 up to 2005. A plateau appeared from 2006 to 2009. In this period, some very low cane yield genotypes are evident, while the number of high yield genotypes decreased.

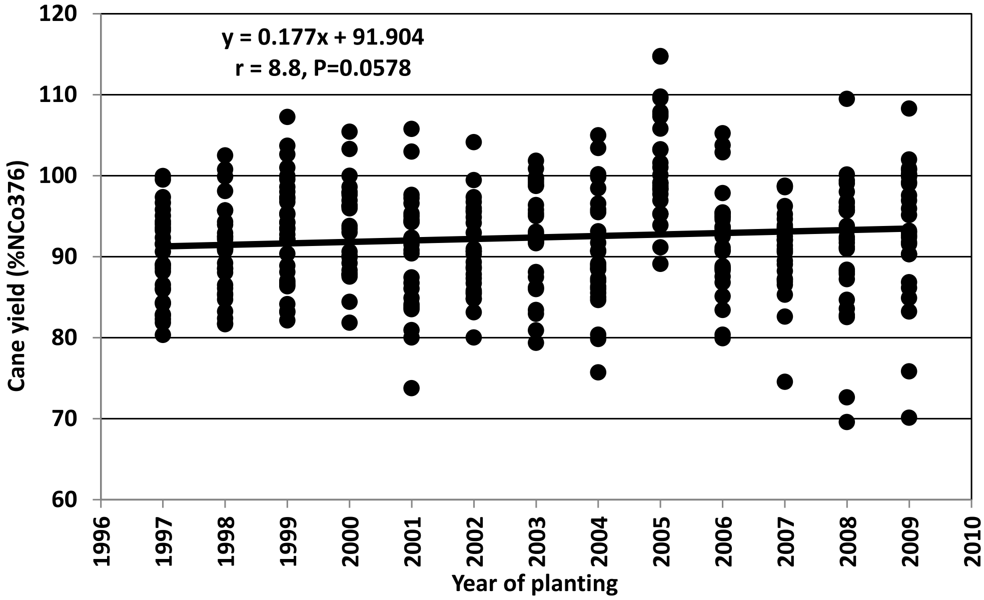

Figure 1. Trend in gains for cane yield for the irrigated programme.

Sucrose content of the genotypes increased by 0.70% per year (Figure 2). The trend produced a significant correlation (r=0.33, P<0.001) between the sucrose content and year of selection. The sucrose content peaked at 120% between 1997 and 2000. Sucrose content higher than 130% was recorded from 2001 to 2008. The high sucrose content from 2001 to 2009 was associated with large variability among the genotypes compared to the period 1997 to 2000. The range from 1997 to 2000 was between 90 and 120% while that from 2001 to 2009 was from 90 to 140% of the control (twice that of 1997 to 2000).

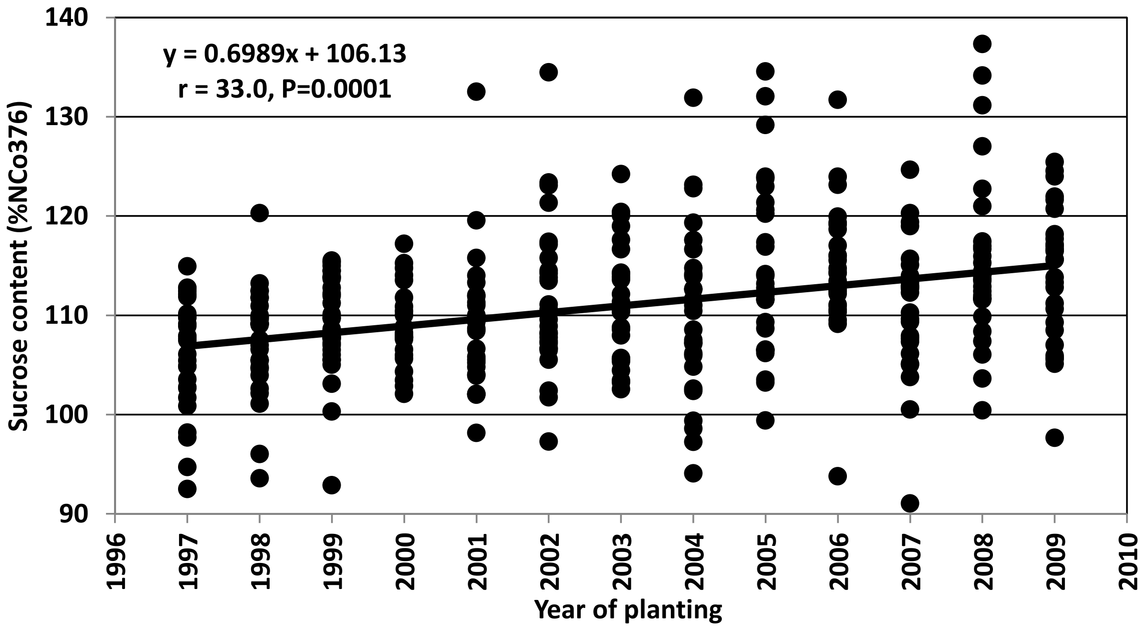

Figure 2. Trend in gains for sucrose content for the irrigated programme.

The sugar yield realised gains increased by 1.09% per year from 1997 to 2009 (Figure 3). The trend had high and significant correlation (r=37.9%, P<0.001) between sugar yield and year of selection. Very high values were observed in the 2005 genotypes. The genotypes in trials from 1997 to 2004 produced less than 120% sugar yield. From 2005 to 2009, some genotypes produced higher than 120% of the control.

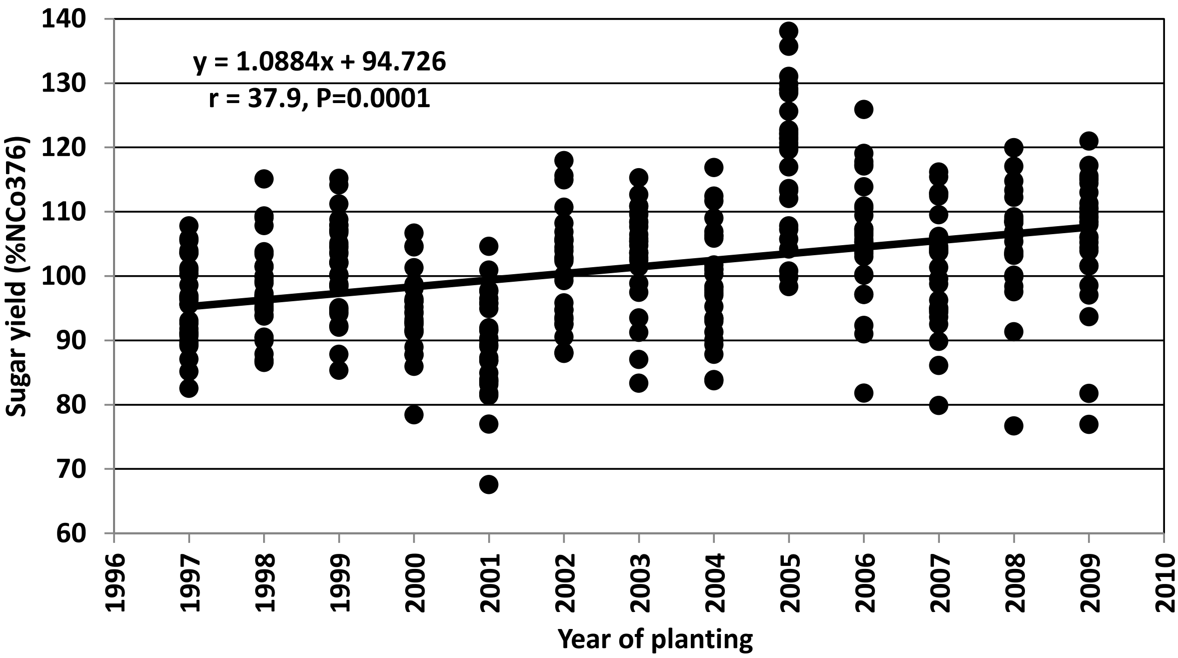

Figure 3. Trend in gains for sugar yield for the irrigated programme.

Coastal short cycle

The coastal short cycle programme had 0.32% per year gain in realised selection gains for cane yield (Figure 4). The correlation of the trend was significant (r=10.4%, P=0.041). From Figure 4, there is a decrease in cane yield from 1997 to 2001 and an increase from 2002 to 2008. Cane yield of the best genotypes decreased from 110% in 1997 to 100% of the control by 2000. In 2001, only two genotypes produce higher cane yield than the control. From 2002, the number of genotypes producing higher cane yield than the control increased, with some producing higher than 110%. This trend was associated with fewer genotypes producing less than 80% of the control.

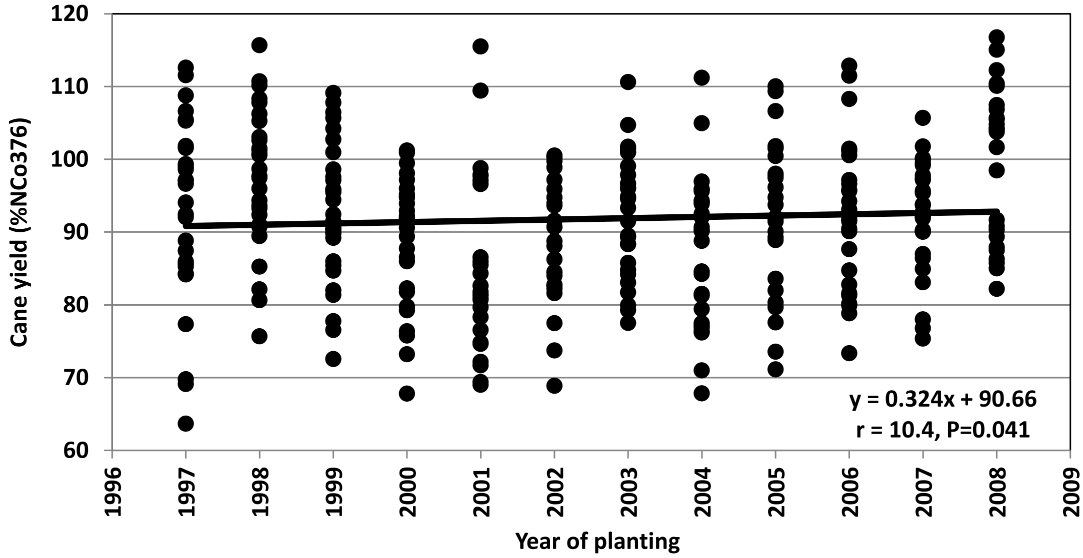

Figure 4. Trend in gains for cane yield for the coastal short cycle.

The realised gains for sucrose content decreased by 0.69% per year (Figure 5). The correlation of the trend was highly significant (r=-30.1%, P<0.001). The decreasing trend was associated with fewer numbers of genotypes producing high sucrose content. From 2006 to 2008, there was an increasing trend in sucrose content.

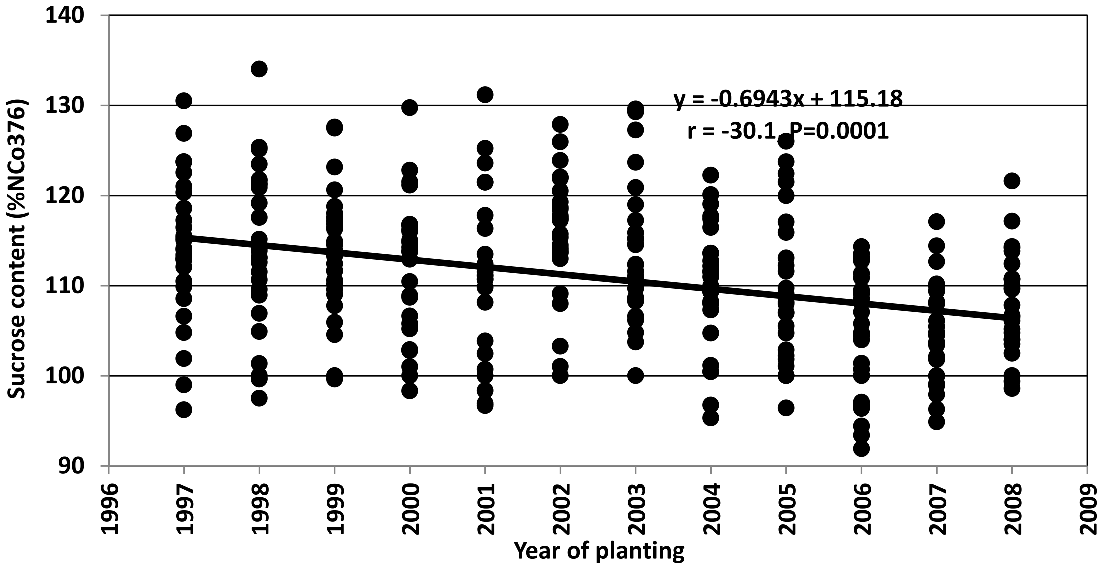

Figure 5. Trend in gains for sucrose content for the coastal short cycle.

The sugar yield had -0.50% per year decrease in sugar yield with advancing selection cycles (Figure 6). The trends produced significant correlation (r=-14.1%, P=0.0054). The number of genotypes producing higher than 130% sugar yield of the control also decreased consistently from 1997 to 2008. There was an increase in sugar yield to above 120% of the control in the period from 2006 to 2008. The sugar yield of lower yielding genotypes also decreased in this period.

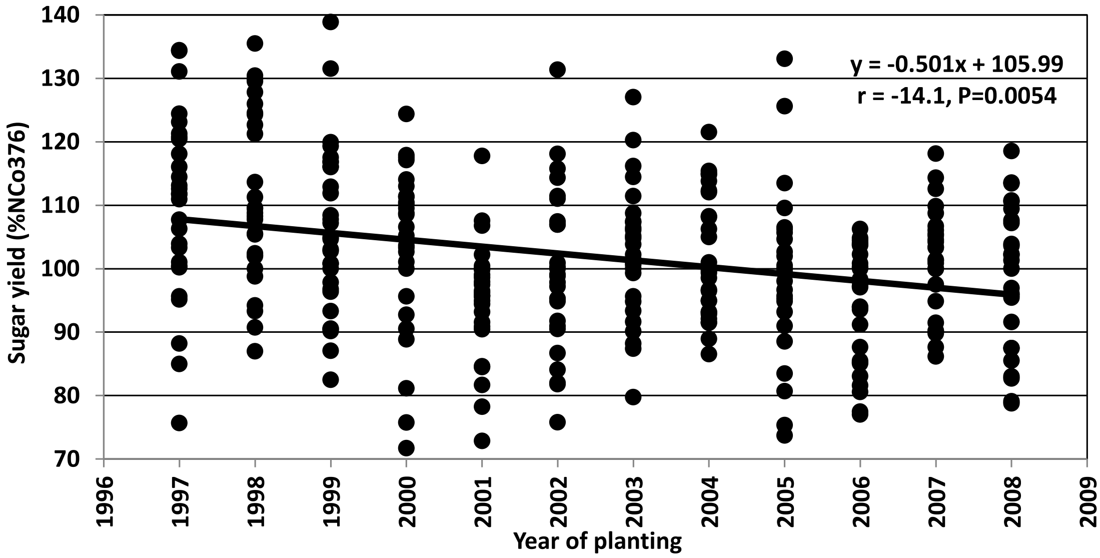

Figure 6. Trend in gains for sugar yield for the coastal short cycle.

Coastal long cycle

The coastal long cycle programmes had 1.76% per year realised gains for cane yield (Figure 7). The correlation of the trend was highly significant (r=45.4%, P<0.001). From 1997 to 1999, all genotypes produced less than 110%, while from 2000 to 2007, more genotypes produced higher than 110% with some exceeding 120%. The number of genotypes producing lower yield decreased with advancing selection cycles. From 1997 to 2000, a larger number of genotypes produced less than 80% while from 2001, very few genotypes produced less than 90%.

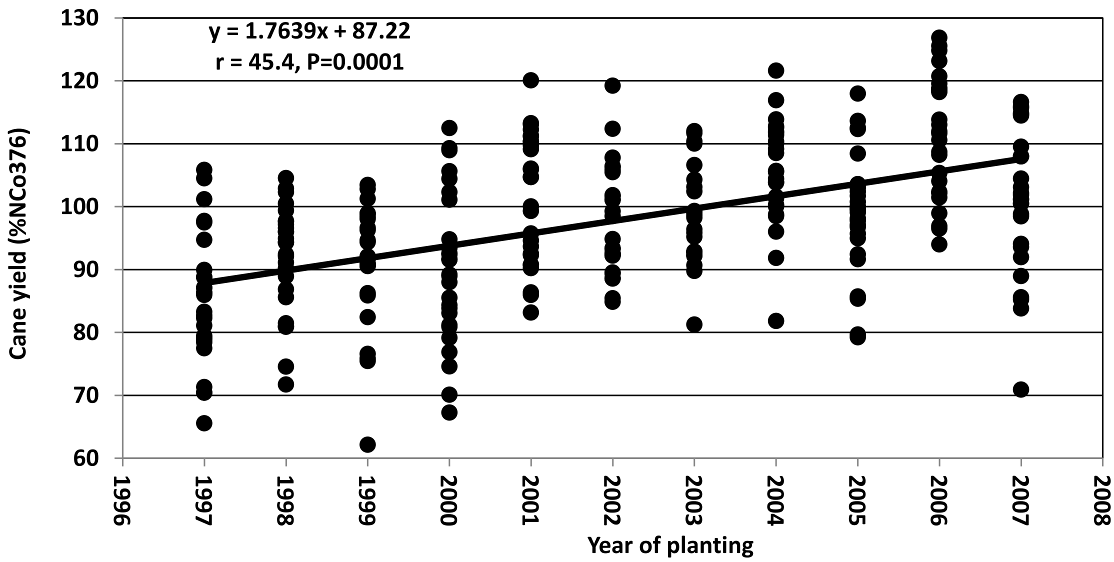

Figure 7. Trend in gains for cane yield for the coastal long cycle.

The sucrose content for the coastal long cycle had 0.0005% gains per year (Figure 8) and the correlation of the trend was not significant (r=0.0%, P=0.9969). The trend of the scatter was constant across years.

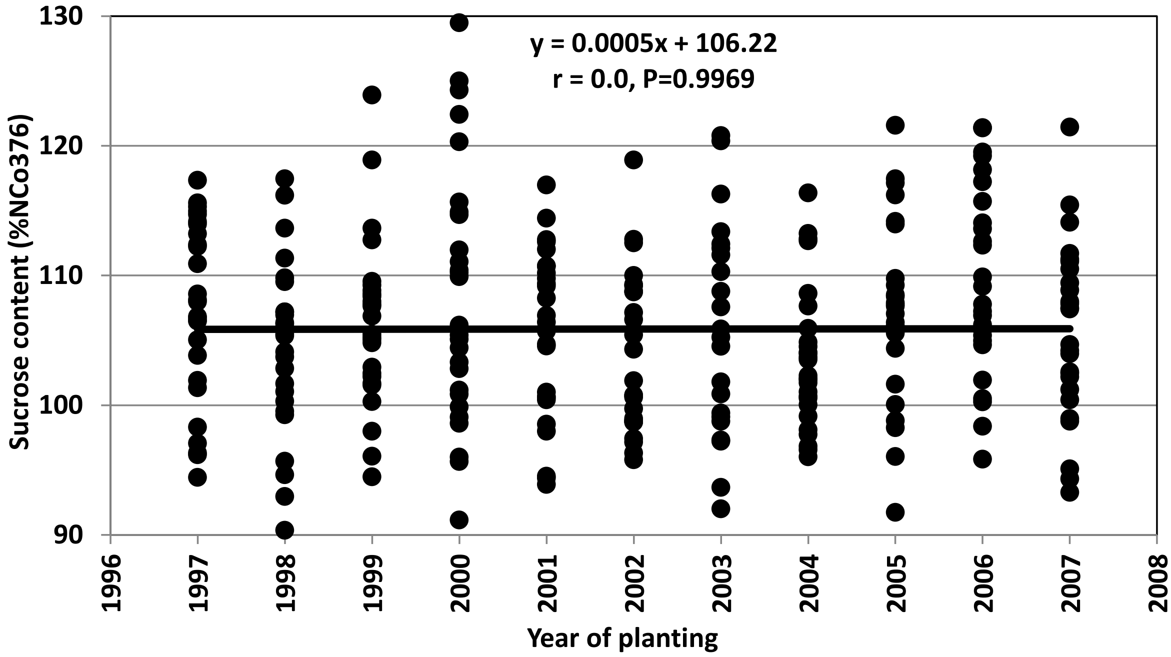

Figure 8. Trend in gains for sucrose content for the coastal long cycle.

The coastal long cycle sugar yield had 1.69% per year gains (Figure 9). The correlation of the trend was highly significant (r=41.1%, P<0.001). The increasing number of high sugar yield genotypes was associated with a decreasing number of low yield genotypes. From 2001 to 2003, there were genotypes that produced higher than 120% while from 2004 onwards, yield of up to 140% was produced from elite genotypes.

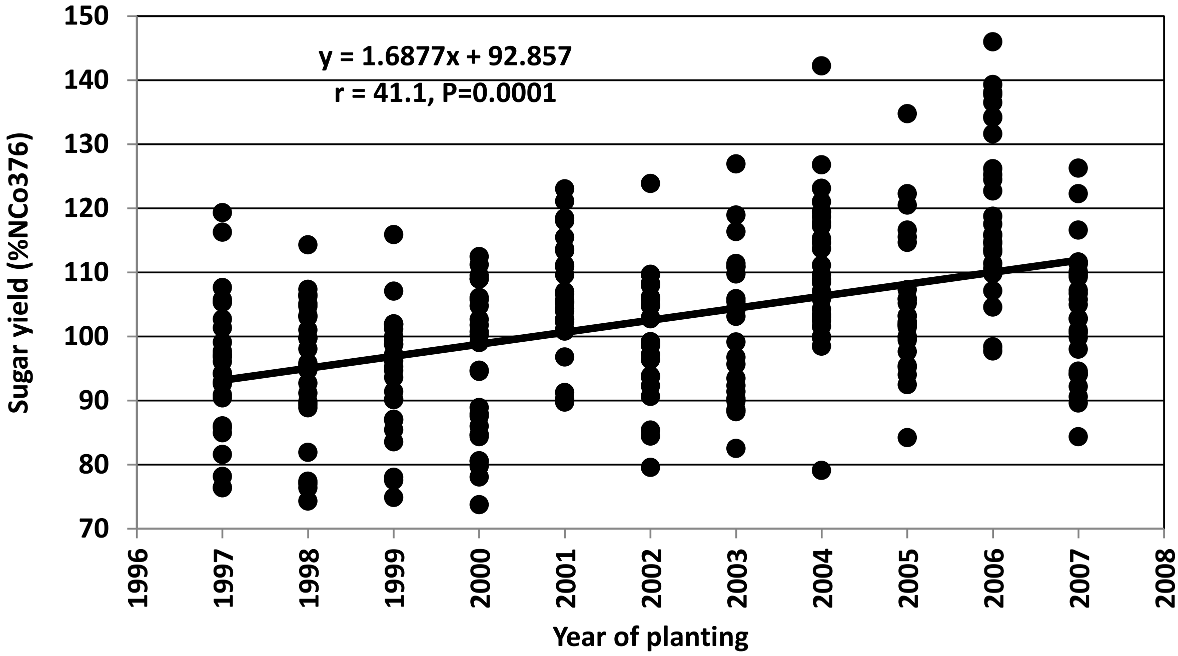

Figure 9. Trend in gains for sugar yield for the coastal long cycle.

Midlands

The Midlands programmes produced 1.85% gains per year for cane yield (Figure 10). The correlations of the trends were highly significant (r=48.6%, P<0.001). The increasing number of high yield genotypes was associated with decreasing numbers of low yield genotypes. In 2007, some genotypes produced 150% higher cane yield than the control.

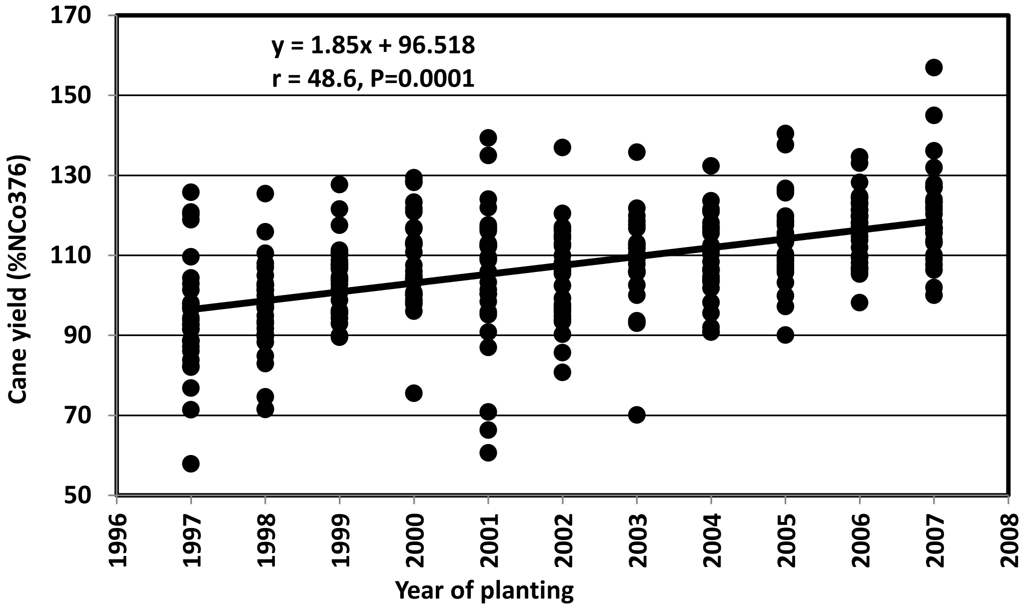

Figure 10. Trend in gains for cane yield for the Midlands programmes.

The sucrose content of the Midlands populations had 0.55% gains per year (Figure 11). The correlation of the trend was highly significant (r=29.5%, P<0.001). From 1997 to 2002, the sucrose content remained unchanged. From 2003 to 2007, the number of genotypes producing high sucrose content increased consistently and was associated with decreasing numbers of genotypes producing low sucrose content.

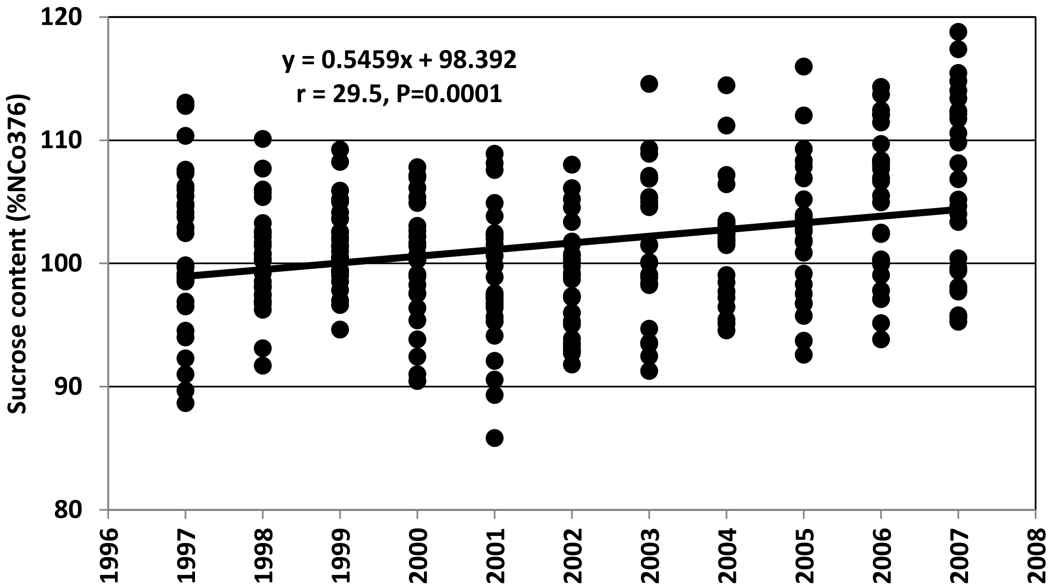

Figure 11. Trend in gains for sucrose content for the Midlands programmes.

The sugar yield of the Midlands programmes produced 2.57% gains per year (Figure 12). The correlation of the trend was highly significant (r=54.1%, P<0.001). The increase in the number of genotypes producing high sugar yield was associated with a decrease in the number of genotypes producing low sugar yield. The scatter plot was very narrow across the years, indicating the predictability of the trend. By 2007, the highest yield genotype produced more than 160% of the control.

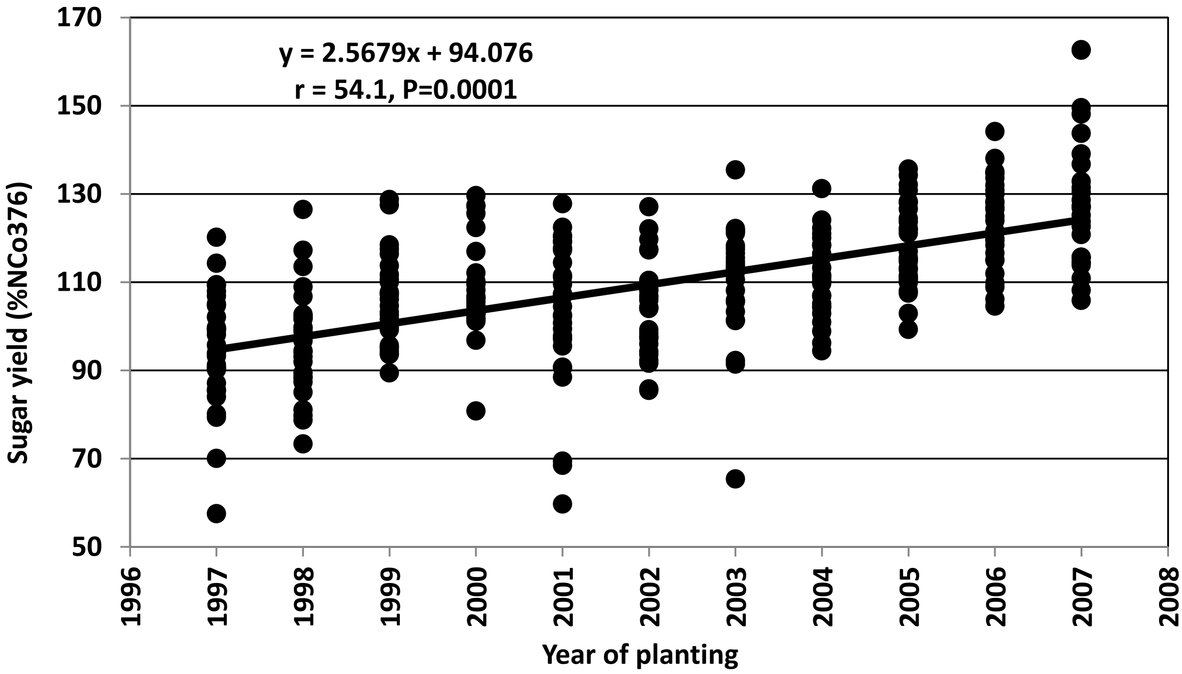

Figure 12. Trend in gains for sugar yield for the Midlands programmes.

Discussion

Realised selection gains provide a mechanism to evaluate the progress and potential of breeding programmes to produce genotypes that deliver genetic gains over time. From the four SASRI breeding programme groups, the Midlands breeding programmes produced the highest selection gains for sugar yield, followed by the coastal long cycle, while the coastal short cycle produced negative gains. The high selection gains for sugar yield from the Midlands programmes were largely derived from both high selection gains for cane yield and sucrose content. The coastal long cycle selection programmes achieved high selection gains for sugar yield that was attributed to high gains for cane yield. The high sugar yield selection gain in the irrigated programme was a result of the high selection gains for sucrose content. The coastal short cycle produced negative selection gains for sugar yield that were largely derived from large negative selection gains for sucrose content. These trends are reflected in the promising genotypes emanating from the respective breeding programmes. The irrigated programmes have produced promising released varieties that possess high sugar yield largely derived from high sucrose content, while the Midlands and coastal long cycle have produced high sugar yield from high cane yield. The coastal short cycle has produced no promising or released varieties in recent years. Therefore, the realised gains can reflect the potential of a breeding programme to produce varieties for release.

The trends in selection gains for the different breeding programmes were a reflection of the origins of the different parental genotypes used to initiate these breeding programmes. After the establishment of new research stations in 1997 (Nuss, 1998), various populations from previous stations were used to start the new breeding programmes. The irrigated breeding programme was not affected by the changes and therefore remained largely consistent and stable and therefore consistent gains, particularly in sucrose content, are evident. The Midlands programmes were relocated from an adjacent smaller farm to two programmes (sandy and humic soils) on larger farms. Their populations remained the same and therefore also remained largely continuous. The coastal long cycle programmes were started from programmes that were located close to the current sites. The Gingindlovu long cycle programme was from Mtunzini, 20 km from the present site, while the Hinterland programme was from LaMercy, 40 km from present site. Some level of continuity was present. The coastal short cycle programmes experienced the largest relocation distance, with the high potential research station relocated 150 km from the central field station (CFS) to Empangeni, and the Gingindlovu short cycle programme was started from scratch to address the need for 'eldana escape' as a form of resistance to the borer via early maturity among varieties. Varieties with an eldana escape form of resistance are expected to grow faster and mature earlier, before eldana damage causes significant yield loss. Previous studies by Zhou and Joshi (2012) reported low and decreasing broad sense heritabilities among these populations.

The coastal long cycle produced high realised gains for cane and sugar yield but no gains for sucrose content. The high gains for cane yield that contribute to the high gains for sugar yield indicate the major influence of cane yield in controlling sugar yield (Jackson, 2005). Previous research has indicated that, despite the early selection in some programmes around the world for sucrose content, the major contributor to sugar yield is cane yield. Further, the selection for eldana tolerance in these populations has resulted in lower sucrose content due to the negative association of sucrose content and fibre content (Gravois and Milligan, 1992). The high fibre content could have indirectly resulted in high biomass yield via high fibre and high cane yield. High fibre is known to be associated with reduced eldana damage and, generally, most resistance to eldana is likely to be linked to high fibre content. Further, the introgression programmes with high biomass genotypes in order to increase eldana resistance could also be contributing to high cane yield and low sucrose. Because the harvest age has remained constant after restructuring for the coastal long cycle populations, sustained gains from recurrent selection were expected.

The Midlands populations produced sustained gains for both cane yield and sucrose content, a more desirable combination that resulted in exceptionally high gains for sugar yield. Possible explanations for this trend are that after the transition in 1997, the Midlands populations were moved from a research station close to the current new research stations. Therefore the continuity allowed for sustained gains from previous selection efforts increasing the benefits from recurrent selection for both cane yield and sucrose content. Further, the Midlands programmes are in a region where the most prevalent disease is rust. Unlike other programmes, the Midlands programme has very low levels of eldana borer damage and smut disease. The reduced pressure of not selecting for eldana and smut resulted in increased gains for yield and sucrose content. The selection for eldana resistance results in high fibre content, which probably reduced the gains in sucrose content for the coastal long cycle. The Midlands, with two critical traits less to select for, has better gains to selection than the other programmes. Selecting for many traits is known to reduce potential gains of individual traits (Kang, 2006).

The results indicate potential opportunity to enhance the selection gains via transfer of parents across programmes as well as import of parents from other breeding programmes in other countries. To increase the yield gains in the irrigated programmes, utilisation of parents from the coastal long cycle and Midlands programmes could be a potential strategy. For the coastal short cycle, it appears these programmes would benefit from the transfer of parents from the coastal long cycle to enhance gains for yield. At the same time, imports from countries such as the USA could enhance the development of genotypes that possess the fast growth and early maturity required for eldana escape. The high cane yield and associated low selection gains for sucrose content in the coastal long cycles could be corrected by utilising the high sucrose content derived from the irrigated programme genotypes. Furthermore, considering that low sucrose content and high tonnage is suspected to be associated with the high fibre content for eldana resistance, further exploration of eldana resistance mechanisms not associated with fibre could also aid in enhancing potential gains for sucrose content in coastal long cycle.

The methodology described in this study can be applied to other crops and to other traits. For example, in the South African sugarcane breeding programmes, gains to breeding and selection for eldana resistance are suspected to be low because of the very few genotypes emerging with sufficient resistance. This analysis would provide insight into the ability and magnitude of realised gains. Further, such a study would also provide the breeders with potential strategies to correct or enhance the gains via approaches such as recurrent selection, introgression and the exploration of alternative but more durable resistance.

Conclusions

Realised gains can reflect the potential of a breeding programme to produce varieties for release. Relocation of breeding stations, as well as initiation of new breeding programmes, requires more effort in assembling the initial germplasm, as was the case with the coastal short cycle programmes. The selection for eldana tolerance is suspected to be contributing to high fibre, which indirectly leads to low sucrose content for the coastal long cycle programmes. The Midlands programme indicates the benefits of increased gains by selecting for two traits less (eldana and smut) compared to other programmes. The transfer of parents from Midlands and coastal long cycle (high cane yield) to coastal short cycle and irrigated (low cane yield) programmes is expected to increase gains for cane yield in these regions. High sucrose content parents from the irrigated programme can be transferred to other programmes. Potential for recurrent selection for cane yield and sucrose content is shown by the high selection gains for these traits in some programmes. The methodology described can be applied to other traits.

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