

REFEREED PAPER

INTERPRETING SUGARCANE VARIETAL ADAPTABILITY TO TIME OF HARVEST

RAMBURAN S

*South African Sugarcane Research Institute, Private Bag X02, Mount Edgecombe,
4300, South Africa
Sanesh.Ramburan@sugar.org.za*

Abstract

The objectives of this study were to characterize varietal adaptability to time of harvest (TOH) under rainfed conditions, and to evaluate the appropriateness of multivariate analysis techniques to investigate factors driving genotype x environment (GxE) interactions. Two field trials consisting of the same seven varieties were planted alongside each other and harvested either early (May) or late (October) in the season for six ratoons. The GxE (trial x ratoon combination) interaction for cane yield (TCANE), estimated recoverable crystal percent (ERC) and ERC yield (TERC), was analyzed using the Additive Main Effects and Multiplicative Interaction (AMMI) model. Environmental covariates for temperature (TT), rainfall (RAIN), radiation (RAD) and a water stress index (WSI) were summarized within individual growth phases (establishment, stalk elongation, ripening). The GxE interactions were significant ($P < 0.001$) for all variables and the biplots showed that varieties N17, N19, and N27 were best suited to early harvesting while varieties NCo376, N29, N35 and N36 were suited best to late harvesting. Based on their correlations with biplot scores, the covariates were superimposed onto the AMMI biplots to allow for interpretations of GxE interactions. Higher TCANE of early harvests were associated with higher TT, RAD, and RAIN during stalk elongation. Higher ERC% of late harvests were associated with lower TT and higher water stress during stalk elongation and ripening. The interpretations corresponded to known knowledge of sugarcane growth and development, suggesting that the multivariate methods can be used to analyze more diverse GxE datasets.

Keywords: AMMI, environmental covariate, GxE, time of harvest

Introduction

Variety selection in the rainfed parts of the sugar industry is currently focused on adaptability to different yield potential conditions and harvest ages. In contrast, less emphasis is placed on time of harvest (TOH), which refers to the time in the milling season (April to December) when the crop is harvested. Past studies in the irrigated northern parts of the industry have demonstrated variety x TOH interactions (Parfitt, 2000; Thomas and Parfitt, 2000), and the current selection programme for that region is designed to accommodate such differences. However, in the southern rainfed regions, limited emphasis is placed on the differential responses of varieties to TOH, despite observed commercial differences. Knowledge of

adaptability of varieties to TOH in the rainfed regions is conventionally accumulated through commercial observation, and recommendations for older, established varieties can be made confidently. However, a range of new varieties have been released for the southern regions, and the adaptability of these varieties to TOH is currently unknown.

The effects of variety x TOH interactions on sugarcane productivity have been investigated in isolated studies. Gilbert *et al.* (2006) demonstrated highly significant differences in TOH and significant genotype x environment (GxE) interactions in three case studies with sugarcane in Florida. In Mauritius, Julien and Delaveau (1977) showed that dry matter partitioning in sugarcane was influenced to a greater extent by TOH than by location, while Nayamuth *et al.* (2005) proposed that varieties could be classified into three distinct maturity groups (early, mid, and late) based on their sucrose accumulation patterns. In Australia, Di Bella *et al.* (2009) found significant variety x TOH interactions for cane and sugar yields in ratoon crops at multiple locations. Studies on variety x TOH interactions have focused on variety characterisation and have also acted as decision aids for the design of sugarcane breeding programmes (Gilbert *et al.*, 2006). Few dedicated attempts, however, have been made to explain and interpret such interactions in relation to major environmental factors.

In South Africa, Donaldson *et al.* (2008) and Singels *et al.* (2005a) interpreted variety adaptability to TOH by focusing largely on single environmental variables and their influence on important crop development traits and biomass partitioning concepts used in crop modeling. Although contributing to fundamental physiological understanding and refinement of crop modeling, these studies focused on effects of environmental factors in isolation, and over a limited number of varieties. While their contribution to understanding crop adaptation cannot be disputed, the intensive measurements characteristic of such studies prevent replication over diverse environments and genotypes. A more generalized approach to understanding varietal adaptability to TOH may be to employ multi-environment trial (MET) data analysis techniques conventionally used in large-scale plant breeding studies. Such studies, which have historically been empirical in nature, are becoming increasingly analytical due to the availability/adaptation of statistical techniques that allow for interpretation of GxE patterns. The extent of physiological interpretation possible with such studies is highly dependent on the intensity of crop and environmental parameters measured within the MET dataset. Besides Jackson *et al.* (1995), no further attempts have been made to interpret sugarcane GxE interactions within a MET framework. The approach may allow for an evaluation of the relative contributions of environmental factors driving the variety x TOH interaction in sugarcane.

Multivariate methods such as the additive main effects and multiplicative interaction (AMMI) are routinely used to analyse GxE data (Gauch, 1992). Two dimensional biplots produced from AMMI analysis are characterised by variety and environment principal component (PC) scores. Such scores may be correlated to environmental covariates measured at the trial sites to help interpret environmental separation patterns and identify factors driving GxE interactions. Additionally, the effects of environmental factors on GxE interactions may also be examined through the use of factorial regression. Such methods have been employed to interpret varietal growth phase sensitivities to environmental factors in crops such as ryegrass (Van Eeuwijk and Elgersma, 1993), wheat (Voltas *et al.*, 2005),

barley (Voltas, *et al.*, 1999), and pearl millet (Van Oosterom *et al.*, 1996). Analysis of such sensitivities may identify specific growth phases (and environmental factors) responsible for production variability between early and late harvests of sugarcane in South Africa.

Recently, there has been much interest in trying to understand the factors driving GxE interactions in sugarcane for the purposes of improved selection and evaluation. No attempts have been made to interpret sugarcane GxE interactions using multivariate analysis techniques, and their appropriateness in this regard has not been evaluated. The objectives of this study were: (1) to characterise released varieties in terms of adaptability to TOH; (2) to identify the environmental factors and crop traits driving TOH variability; and (3) to evaluate the appropriateness of multivariate techniques to interpret sugarcane GxE interactions.

Materials and Methods

Field trials and weather variables

Two field trials were established on adjacent fields on the Empangeni research farm (28°43'S, 31°53'E, 102 masl) on the North Coast of the sugar industry. The two trials formed part of the South African Sugarcane Research Institute (SASRI) variety evaluation project and consisted of the same set of seven varieties, established in randomized complete block designs, with six replicates each. The treatments were comprised of new (N36, N35, N29, N27) and established (N19, N17, NCo376) varieties, whose relative adaptabilities to different harvest times were unknown. One trial was established in November 2000 and harvested annually in the late season (October/November) for six successive ratoons, while the other trial was established in March 2001 and harvested annually in the early season (April/May) for the same duration. Both trials were established on the same soil type with standardized nutrient and weed management.

At each harvest, nett cane plots (4 rows, 8 m long, spaced 1.2 m apart) were cut manually and weighed using a mechanical grab apparatus attached to a load cell to determine cane yield in tons/ha (TCANE). Plot samples of 12 stalks were taken from the trials at each harvest to determine the estimated recoverable crystal percentage (ERC). The tons ERC (TERC) was calculated as the product of ERC and TCANE. Other relevant variety traits determined at the plot level at each harvest included stalk population in stalks/ha, stalk mass in g/stalk, and stalk length in cm.

Daily weather data from an on-farm weather station were recorded during each crop cycle. The average duration of three growth phases: (i) crop establishment, (ii) stalk elongation and (iii) ripening, were estimated from previous observations (unpublished data¹), and the weather data within each phase were then summarized as environmental covariates. These covariates included average daily rainfall (RAIN) in mm, average daily solar radiation (RAD) in MJ/m²/sec, thermal time (TT) in heat units (base 10 °C), and a water stress index (WSI). The WSI (average daily values within each growth phase) was determined by calculating the total available moisture from soil depth and clay content (van Antwerpen *et al.*, 1994). This information was used in the Canesim crop growth model (Singels and Donaldson, 2000), which estimated the actual evapotranspiration (EVT_{act}) for each crop

¹MA Smit, South African Sugarcane Research Institute, Mount Edgecombe, South Africa, 2010.

cycle. The model was also run for each crop cycle as if fully irrigated to estimate potential evapotranspiration (EVT_{pot}) had there been irrigation. EVT_{pot} represented unstressed crop growth and the WSI was calculated as the ratio of $EVT_{act}:EVT_{pot}$, where a high WSI represented no moisture stress, while values closer to zero represented higher levels of stress.

In this study, an environment was considered as a trial and ratoon combination, resulting in a total of 12 environments, designated E1 to E6 (early season) and L1 to L6 (late season). Table 1 provides a summary of the daily averages for the environmental covariates for each crop cycle and illustrates how they originated. For example, RAIN1, RAIN2 and RAIN3 refer to average daily rainfall during establishment, elongation and ripening, respectively. Similar designations were used for the other covariates.

Table 1. Mean daily values of rainfall (mm) thermal time (heat units), radiation (MJm²/day), and water stress index (0-1), during three growth phases (establishment, elongation, ripening) of early and late harvests.

Covariate	Environments											
	Early harvests						Late harvests					
	E1	E2	E3	E4	E5	E6	L1	L2	L3	L4	L5	L6
Rainfall (mm)												
Establishment (RAIN1)	1.44	1.27	1.03	1.16	1.71	3.20	1.83	1.84	3.86	1.53	2.16	2.48
Elongation (RAIN2)	1.86	3.87	1.58	2.17	2.83	3.00	1.83	1.84	1.35	1.83	3.29	3.57
Ripening (RAIN3)	1.94	3.85	2.24	4.12	2.51	2.18	1.42	1.12	1.51	1.06	1.49	1.85
Thermal time (heat units)												
Establishment (TT1)	10.03	10.08	9.61	10.85	9.99	9.49	14.48	14.46	14.90	15.33	14.10	14.71
Elongation (TT2)	14.13	14.37	15.91	14.41	14.94	14.04	12.07	12.13	11.98	13.04	12.45	12.58
Ripening (TT3)	14.02	13.49	14.05	13.91	14.19	12.80	10.40	10.33	9.53	10.76	10.20	9.73
Radiation (MJ/m²/sec)												
Establishment (RAD1)	13.13	12.74	14.36	12.74	12.97	12.97	19.59	19.58	20.35	21.11	18.92	21.19
Elongation (RAD2)	19.27	17.96	21.66	18.90	21.73	20.32	14.29	14.36	14.77	15.50	15.12	15.05
Ripening (RAD3)	16.67	14.89	16.52	16.13	16.73	17.58	14.34	13.34	14.93	12.37	13.19	13.77
Water stress index (0-1)												
Establishment (WSI1)	0.45	0.39	0.61	0.45	0.70	0.80	0.44	0.37	0.58	0.44	0.53	0.53
Elongation (WSI2)	0.09	0.36	0.24	0.22	0.31	0.42	0.04	0.08	0.26	0.28	0.59	0.45
Ripening (WSI3)	0.06	0.82	0.37	0.59	0.40	0.55	0.21	0.14	0.30	0.18	0.31	0.45

AMMI analysis

The GxE interaction for TCANE, ERC and TERC was analysed using the AMMI model:

$$Y_{ij} = \mu + g_i + e_j + \sum \lambda_k \alpha_{ik} \delta_{jk} + R_{ij} + \varepsilon \quad (1)$$

where Y_{ij} is the value of the i^{th} genotype in the j^{th} environment; μ is the grand mean; g_i is the mean of the i^{th} genotype; e_j is the mean of the j^{th} environment; λ_k is the singular value for principal component (PC) axis k ; α_{ik} and δ_{jk} are the PC scores for axis k of the i^{th} genotype and j^{th} environment, respectively; R_{ij} is the residual and ε is the error term (Gauch, 1992).

AMMI analysis firstly involves a conventional analysis of variance (ANOVA) to investigate the effects of genotype, environment, and the GxE interaction. Thereafter, the matrix of residuals (matrix of genotype x environment means, with each cell having the respective genotype and environment means subtracted from it) is subjected to PCA. The responses of genotypes (rows) in different environments (columns) creates a multidimensional cloud of data points. PCA identifies the direction of greatest change (most variability) within this cloud and fits an axis through it. A second axis is then fitted at right angles to the first, accounting for the second largest amount of variation in the data cloud. Scores for each genotype and environment are then expressed relative to each of these interaction principal component axes (IPCA). PCA effectively reduces the dimensionality of the data so that the relationships between genotypes and environments can be easily investigated.

For each of the relevant variables (TCANE, TERC, ERC), AMMI2 biplots were produced to help visualise the TOH adaptability of varieties and to determine if these responses were consistent over seasons. The AMMI2 biplot is commonly used in the analysis of multi-environment trials and is characterised by the IPCA1 scores on the horizontal axis, and the IPCA2 scores on the vertical axis (Gauch, 1992). In these biplots, varieties and environments are depicted as points in a two dimensional space and their coordinates are defined by their IPCA1 and IPCA2 scores. Here, varieties and environments are represented by arrows and points, respectively. The distance from the origin of the biplot represents the amount of interaction that is exhibited by the respective variety or environment. The angles between two variety arrows correspond to their correlation. In general, acute angles between varieties represent positive correlations (similar responses to environments), right angles represent no correlation, and obtuse angles represent negative correlations (Voltas *et al.*, 1999). Similar interpretations hold true for environments. The magnitude of interactions between varieties and environments can be interpreted by their respective vector direction, where similar directions indicate positive interactions and vice versa (Gauch, 1992). The closer a variety is to an environment on the biplot, the greater is its interaction with that environment.

Interpretation of GxE interactions

In order to identify the most influential factors driving TOH variability, the environment IPCA scores were first correlated to each of the covariates to test the strengths of the relationships. Thereafter, the AMMI biplots were enriched with the environmental covariates. In this technique, the AMMI IPCA environmental scores were regressed against the covariates, and the derived regression coefficients then defined the positioning (IPCA1 and IPCA2 co-ordinates) of the covariates on the biplots (van Eeuwijk and Elgersma, 1993). When the covariates were superimposed onto the biplot (which effectively becomes a triplot), the adaptability of varieties to the different environments are interpreted as they are in a conventional biplot. The difference now is that the environmental characteristics (covariates) of the different environments can be simultaneously viewed. This allows for an interpretation of the environmental factors characterising the early and late environments, and which varieties showed responses to those factors.

In an attempt to explain the GxE interaction of TCANE relative to variety traits, a covariate-effect biplot was produced (Yan and Tinker, 2005). This biplot is produced through the principal component analysis of a trait x environment two-way table of correlation

coefficients between TCANE and the relevant trait in the relevant environment. A comprehensive description of this type of biplot is given by Yan and Tinker (2005). With this technique the correlation coefficients were used as a measure of the effects of the explanatory traits (POP, STKMS, STKLTH) on TCANE, and this helped determine the extent to which TCANE was influenced by different traits at different harvest times. All statistical analyses were conducted using Genstat® Version 12.1 statistical software (Anon, 2009) and biplots were produced using Canoco® for Windows Version 4.51 (Ter Braak and Smilauer, 2003).

Results

AMMI analysis

The AMMI2 analysis of variance indicated that environments, genotypes (varieties), and the GxE interactions were highly significant ($P < 0.001$) for all three variables (Table 2). Both the IPCA1 and IPCA2 axes were significant for the three variables, and although explaining only a small proportion of the total sums of squares, they did explain the majority of variation of the GxE interactions. For TCANE, IPCA1 and IPCA2 explained 56 and 23% of the GxE interaction, respectively. The relative proportions of the GxE interactions explained by IPCA1 (32%) and IPCA2 (29%) for ERC were more balanced, while the GxE interaction for TERC was explained by 53 and 22% by IPCA1 and IPCA2, respectively. When averaged over ratoons within trials, the AMMI means showed that early environments produced higher TCANE (Figure 1a) than late environments across all varieties except for N17. However, the late environments produced higher ERC than the early environments across all varieties and variety rankings did not change between the two harvest times (Figure 1b). The late environments produced higher TERC than the early environments across all varieties except for N35, and here, variety rankings differed between early and late harvesting (Figure 1c).

Table 2. AMMI2 analysis of variance for cane yield (TCANE), estimated recoverable crystal percentage (ERC) and tons ERC (TERC), including the first two interaction principal component analyses (IPCA) axes.

Source	df	SS	MS	%SS ^a	SS	MS	%SS	SS	MS	%SS
		TCANE			ERC			TERC		
Total	503	218310	434		2086.8	4.15		3611	7.18	
Genotype (G)	6	11674	1946 ^{**}	5.3	256.8	42.8 ^{**}	12.3	218	36.35 ^{**}	6.0
Environment (E)	11	154293	14027 ^{**}	70.7	1281	116.46 ^{**}	61.4	2307	209.74 ^{**}	63.9
GXE	66	10466	159 ^{**}	4.8	118.7	1.8 ^{**}	5.7	224	3.39 ^{**}	6.2
IPCA 1	16	5853	366 ^{**}	2.7	38.4	2.4 ^{**}	1.8	118	7.38 ^{**}	3.3
IPCA 2	14	2427	173 ^{**}	1.1	33.6	2.4 ^{**}	1.6	50	3.57 [*]	1.4
Residuals	36	2186	61		46.7	1.3		56	1.55	
Error	360	29534	82		378.6	1.05		609	1.69	

* and ** significance at $P < 0.05$ and $P < 0.001$, respectively

^a % of total sums of squares for each term or interaction

The AMMI2 biplot for TCANE, which captured 79% of the total GxE interaction, revealed two distinct non-overlapping clusters for the early and late season harvests (Figure 2a). These groupings were spread more explicitly across the IPCA1 axis. Varieties N17, N19 and N36 demonstrated clear adaptation to the late season harvests, while varieties N27, N29, N35 and NCo376 interacted positively with the early season harvest. The ERC biplot (Figure 2b) also showed TOH separation along the IPCA1 axis; however, significant spread was also observed along the second axis. Here, the varieties N29, N35 and N36, which are all characterised as high ERC varieties in the industry, were positively correlated with each other and were more strongly correlated to the early harvests. For the TERC biplot (Figure 2c), the first two axes accounted for 75% of the GxE interaction and also showed distinct clustering of the early and late harvests along the IPCA1 axis. Varieties N17, N19, and N27 showed similar responses to late season harvesting, while varieties NCo376, N29, N35 and N36 interacted positively with the early season.

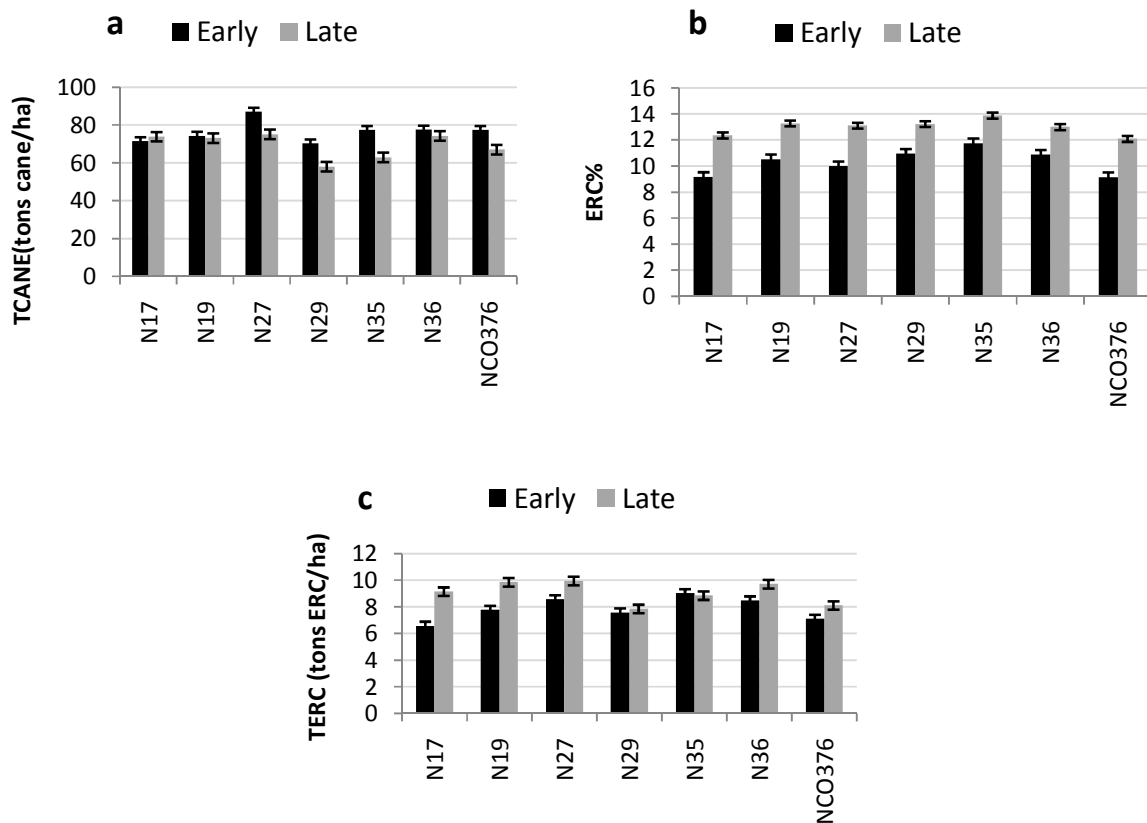


Figure 1. TCANE (a), ERC (b) and TERC (c) of seven varieties averaged over six ratoons when harvested either early or late in the season.

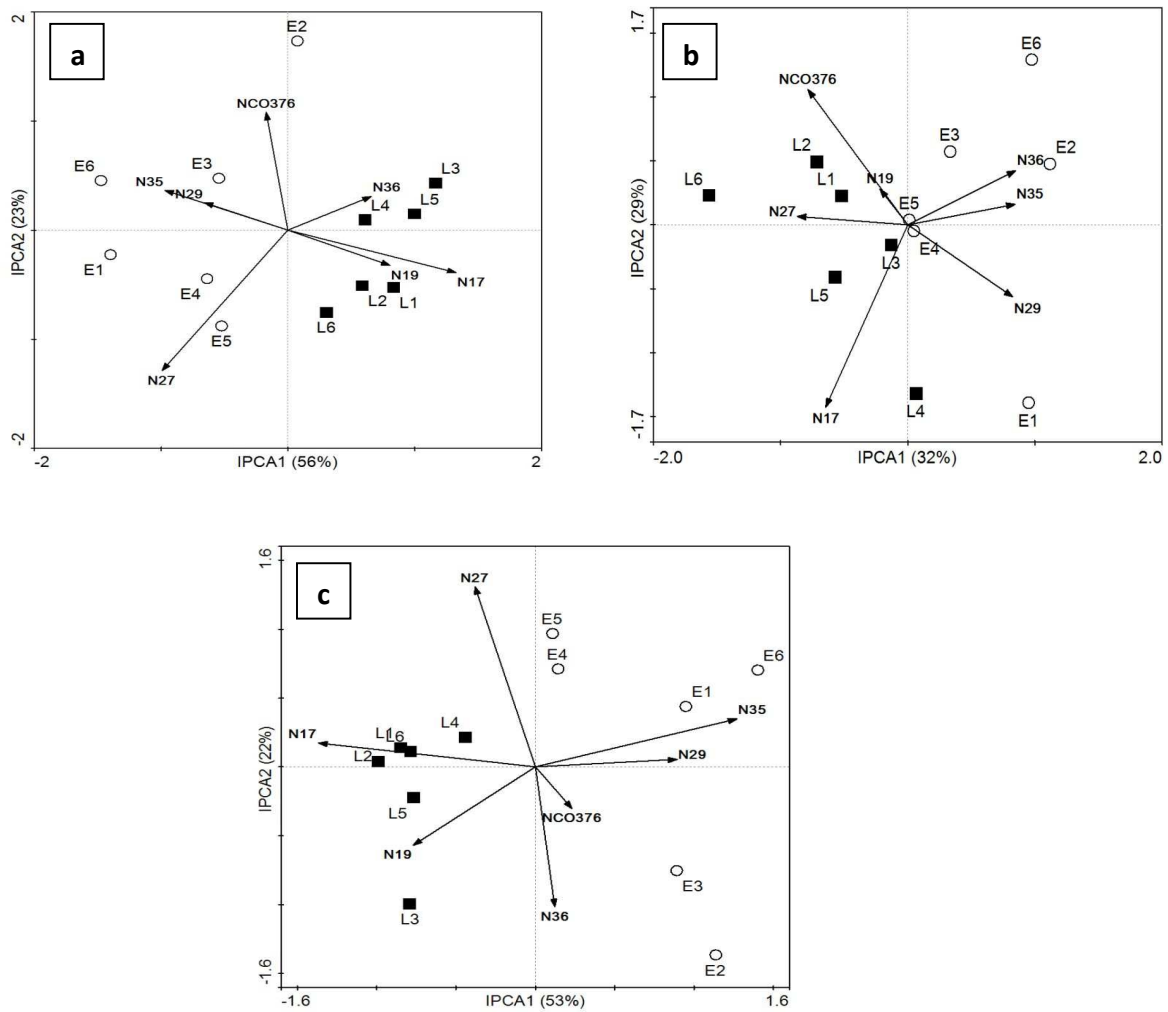


Figure 2. AMMI2 biplots for TCANE (a), ERC (b), and TERC (c). Varieties are represented by arrows while environments are represented by points. Early season harvests are represented by circles and late season harvests are represented by squares. (The percentage of the interaction explained by the IPCA axes are indicated in parentheses in the axis titles).

Interpretation of Gx E interactions

AMMI biplot enrichment

The AMMI2 biplot for TCANE, with environmental covariates superimposed is shown in Figure 3 (arrows omitted for easier visualisation). Biplots for ERC and TERC revealed similar covariate separation patterns and are therefore not shown. Figure 3 shows that most of the early environments were characterised by high temperatures and radiation during elongation and ripening (TT2, TT3, RAD2, RAD3), as well as high rainfall during ripening (RAIN3). In contrast, the late environments were characterised by higher TT, RAD and RAIN during the establishment phase (i.e. phase 1), and lower levels of these covariates during elongation and ripening.

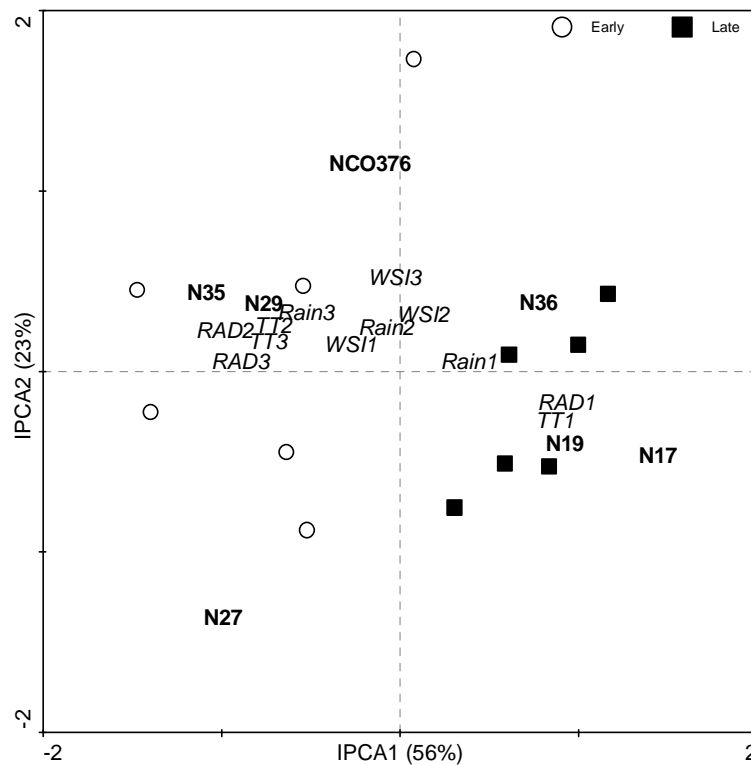


Figure 3. AMMI2 biplot for TCANE showing early (circles) and late (squares) environments and varieties (bold normal font), with environmental covariates (italic font) superimposed.

The lower ERC of early harvests may also be explained by the covariate separation patterns in Figure 3. High temperatures, radiation and rainfall during elongation typically stimulate vegetative growth, hence using up sucrose, resulting in lower ERC. Late environments, however, are characterised by lower levels of these covariates during elongation and ripening, which are known to cause stress induced improvements in ERC. The three WSIs did not follow the deviation patterns of the early and late environments as they were clustered toward the middle of the biplot. The rainfall and WSI during elongation and ripening were correlated, as high rainfall often implies less water stress (hence high WSI values). When correlated against IPCA scores (not shown), the covariates with the strongest correlations included radiation and temperature during all three growth phases. However, the WSI3 showed significant ($P < 0.05$) positive correlations to the IPCA2 scores for TCANE and ERC. The early environments showed greater deviation along the second axis compared to the late environments, suggesting that the early harvests were characterized by greater variation in water stress.

Effects of TOH on variety traits

The covariate effect biplot based on a trait x environment table of correlation coefficients explained 90% of the total variation in the table, suggesting that it was a good approximation of the table (Figure 4). In this biplot the length of a trait vector represents the magnitude of

its effects on TCANE. Interestingly, stalk population and stalk length had greater effects (only just) on TCANE than stalk mass. The near opposite directions of the population and stalk mass vectors indicate that these two variety traits had contrasting effects on TCANE. This does not imply that population and stalk mass were negatively correlated to TCANE. Both traits were in fact positively correlated to TCANE, but one (population) showed stronger correlations to TCANE in the early harvests while the other (stalk mass) showed stronger correlations to TCANE in the late season. Stalk length showed no strong correlation to either stalk mass or population (almost right angles), and was not correlated to either of the environment groups, suggesting that its effects on TCANE was not TOH dependant. The early and late harvests demonstrated a moderate degree of separation on the biplot, which were more distinct along IPCA2. The early harvests E1, E3, E4, E5 and E6 were positively correlated to population, suggesting that TCANE is influenced to a greater extent by stalk population in the early season than the late season. In contrast, the late harvests L2, L3, L4, L5 and L6 were positively correlated to stalk mass suggesting that TCANE is affected more by stalk mass in the late season than the early season.

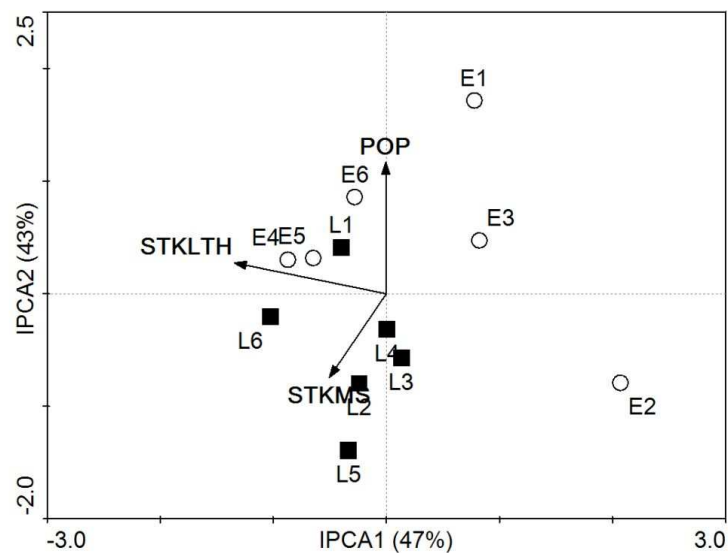


Figure 4. Trait x environment biplot based on a trait x environment two-way table of correlation coefficients between traits and TCANE in each environment. Stalk population (POP), stalk mass (STKMS) and stalk length (STKLTH) are represented by arrows while environments are represented by points. Early season harvests are represented by circles and late season harvests are represented by squares. (The percentage of the interaction explained by the IPCA axes are indicated in parentheses in the axis titles).

Discussion

In this study, the separation of varieties and environments on the AMMI2 biplots for all three relevant variables demonstrated explicit variety adaptation to TOH under rainfed conditions. Currently, most advanced selection trials along the coast are harvested late in the season, and

early season varietal adaptability is only evaluated post-release. These results suggest that future coastal selection trials may benefit from an equal splitting of the harvest times between the early and late season. However, the resource implications of such a split must be considered relative to the potential genetic gains.

The higher TCANE of the early harvests was attributed to greater exploitation of higher temperatures, radiation, and rainfall during stalk elongation and ripening, while the phases of stalk elongation and ripening in late harvests corresponded to periods with lower levels of these covariates. This synchronisation of phenology and environmental potential is proposed as a possible reason for differences in TCANE between early and late harvests. Donaldson *et al.* (2008) indicated that lower biomass production associated with late harvests were due to premature ripening of stalks in response to winter temperatures experienced the following year and that a feedback mechanism actually inhibits further structural growth, thereby limiting yields. Indeed, a feedback mechanism may very well be responsible at the physiological level, and the outcomes of this study may be explained using this concept. In fact, many of the responses observed in this study may be explained using concepts identified in other physiological studies (Singels *et al.*, 2005a; Singels *et al.*, 2005b; Donaldson *et al.*, 2008), and they correspond to what is generally known about sugarcane growth and development in the industry. This suggests that the multivariate techniques employed here (although only allowing for basic physiological interpretations from the available data) do have potential in future studies involving interpretations of GxE interactions. The approach may seem unnecessary for a study involving only 12 environments; however, when applied to more complex datasets comprising detailed crop and environmental parameters, this approach should yield more valuable interpretations that can inform selection and/or further physiological studies. Additionally, varieties chosen for detailed physiological studies are conventionally selected based on expert opinion, subjective information and anecdotal evidence. This type of study should be viewed as an objective way to characterize varieties to inform further physiological/crop modeling studies, and is conventionally considered as 'hypothesis generating', rather than 'hypothesis testing' research.

Rainfall and the water stress index were not correlated to IPCA1 or IPCA2 to the extent that temperature and radiation was, suggesting that significant variability between early and late harvests were not due to these former covariates. This may be due to the fact that the trials were located adjacent to each other and conducted simultaneously, thereby creating confounding effects of some environmental factors. For example, RAIN1 (average daily rainfall during establishment) for early harvest would have been similar to RAIN3 (average daily rainfall during ripening) for late harvests. This overlap of seasons and environmental factors between the two harvest times may have effectively nullified any real differences in rainfall or water stress. This highlights the need for diverse environments when studying GxE interactions. It is therefore acknowledged that the dataset used in this study was not ideal for interpretation of GxE interactions, as the experiments did not constitute a multi-environment trial (Gauch, 1992) *per se*. In fact, the experiments analysed in this study were designed to provide practical industry recommendations, yet the application of multivariate analysis techniques demonstrated how such experiments can be utilised to investigate and interpret growth and development in sugarcane. This represents an example of the benefits of post-release variety evaluation (Gilbert *et al.*, 2006). Despite the fact that the trials were

adjacent to each other and experienced overlapping climatic influences, the relative effects of temperature and radiation at different growth phases were clearly evident. This implies that application of this methodology to multi-environment trials using sites that vary substantially in their characteristics in the industry may reveal trends and mechanisms defining the adaptability of varieties to different conditions.

In this study, the duration of growth phases were estimated from stalk population and stalk height measurements done in previous studies, and were not based on actual measurements of phenology and development within the trials. It is acknowledged that this crude estimation is not ideal, especially when considering the effects of different seasons and responses of different varieties in terms of development. Most GxE interpretive studies of this nature have been conducted on determinate grain crops such as wheat and maize, where growth phase changes can be identified from visual observation (e.g. flag leaf appearance in wheat, or silking in maize). In sugarcane, such distinct growth phase switches are difficult to define, and may require detailed monitoring of different crop parameters for more accurate estimations. However, even when a crude estimation was used in this study, the biological interpretations from the analyses corresponded to known knowledge of sugarcane growth. Nevertheless, future studies of this nature should include more detailed crop measurements for accurate estimates of growth phases.

The covariate-effect biplot revealed positive correlations between stalk population and TCANE in four of the six early season harvests (Figure 4). This implies that early harvests were more dependent on the yield-population relationship, and selection for higher yield in the early season may be accelerated through selection of high stalk population varieties. This response may be linked to the effects of temperature on the duration of tillering in grasses. Lower temperatures increase the duration of tillering in other crops such as wheat, thereby resulting in greater tiller numbers at harvest (Ramburan and Greenfield, 2007). Hence, tillering and establishment of early harvests through winter may promote higher stalk populations in a similar manner. This may in turn be followed by favourable temperature and moisture conditions during spring, thereby limiting tiller mortality until harvest. Conversely, cane yields of late season harvests were more dependent on individual stalk mass, which implies that gains from selection for cane yield in the late season could be accelerated by selecting for higher stalk mass. The biplot also demonstrated the well-known negative correlation between POP and STKMS in sugarcane. These results indicate possible benefits of employing differential trait selection strategies for different harvest times in the industry. However, a more comprehensive study involving a greater number of relevant variety traits is needed.

Conclusions

This study demonstrated that varieties N17, N19 and N27 showed adaptability to late season harvesting, while varieties NCo376, N36, N35 and N29 demonstrated better adaptability to early season harvesting. Temperature and radiation were identified in this study as principal factors affecting TOH variability, while there are indications that rainfall and water stress have secondary effects. The multivariate techniques applied in this study allowed for a more comprehensive interpretation of GxE interactions in sugarcane. The results corresponded to

general knowledge of sugarcane growth and development in the industry, suggesting that the techniques may be appropriate for further GxE studies. However, the techniques may be more valuable when applied to datasets derived from METs conducted under a wider range of conditions. Further applications of these techniques will involve the inclusion of covariates derived from soil, climatic and management factors over diverse conditions.

REFERENCES

- Anon (2009). GenStat® Executable Release 12.1. Lawes Agricultural Trust, Rothamstead Experimental Station, Harpenden, U.K. Clarendon Press, London, UK.
- Di Bella LP, Stringer JK, Wood AW, Royle AR, and Holzberger GP (2009). What impact does time of harvest have on sugarcane crops in the Herbert River district (in Australia). *Sugar Cane Int* 27: 143-148.
- Donaldson RA, Redshaw KA, Rhodes R and van Antwerpen R (2008). Season effects on productivity of some commercial South African cultivars, I: Biomass and radiation use efficiency. *Proc S Afr Sug Technol Ass* 81: 517-527.
- Gauch Jr HG (1992). Statistical analysis of regional yield trials: AMMI analysis of factorial designs. Elsevier, Amsterdam.
- Gilbert RA, Shine JM, Miller JD, Rice RW and Rainbolt CR (2006). The effect of genotype, environment and time of harvest on sugarcane yields in Florida, USA. *Field Crops Res* 95: 156-170.
- Jackson P, McRae T and Hogarth M (1995). Selection of sugarcane families across variable environments II. Patterns of response and association with environmental factors. *Field Crops Res* 43: 119-130.
- Julien MHR and DeLaveau P (1977). The effects of time of harvest on the partitioning of dry matter in three sugarcane varieties grown in contrasting environments. *Proc Int Soc Sug Cane Technol* 16: 1755-1769.
- Nayamuth AR, Mangar M, Ramdoyal K and Badaloo MGH (2005). Early sucrose accumulation, a promising characteristic to use in sugarcane improvement programs. *Proc Int Soc Sug Cane Technol* 25: 421-429.
- Parfitt RC (2000). Genotype by environment interaction among secondary variety trials in the northern region of the South African sugar industry. *Proc S Afr Sug Technol Ass* 74: 245-248.
- Ramburan S and Greenfield PL (2007). The effects of chlormequat chloride and ethephon on agronomic and quality characteristics of South African irrigated wheat. *S Afr J Plant Soil* 24: 106-113.
- Singels A and Donaldson RA (2000). A simple model of unstressed sugarcane canopy development. *Proc S Afr Sug Technol Ass* 74: 151-154.
- Singels A, Smit MA, Redshaw KA and Donaldson RA (2005). The effect of crop start date, crop class and cultivar on sugarcane canopy development and radiation interception. *Field Crops Res* 92: 249-260.
- Singels A, Donaldson RA and Smit MA (2005). Improving biomass production and partitioning in sugarcane: theory and practice. *Field Crops Res* 92: 291-303.
- Ter Braak CJF and Smilauer P (2003). Canoco® for Windows Version 4.51. Biomteris Plant Research International, Wageningen, The Netherlands.

- Thomas DW and Parfitt RC (2000). The effect of early and late season harvesting on the ranking of 150 sugarcane clones from one cross. *Proc S Afr Sug Technol Ass* 74: 249-251.
- van Antwerpen R, Meyer JH and Johnston MA (1994). Estimating water retention of some Natal sugar belt soils in relation to clay content. *Proc S Afr Sug Technol Ass* 68: 75-79.
- Van Eeuwijk FA and Elgersma A (1993). Incorporating environmental information in an analysis of genotype by environment interaction for seed yield in perennial ryegrass. *Heredity* 70: 447-457.
- Van Oosterom EJ, Mahalakshmi V, Didinger FR and Rao KP (1996). Effect of water availability and temperature on the genotype-by-environment interaction of pearl millet in semi-arid tropical environments. *Euphytica* 89: 175-183.
- Voltas J, Van Eeuwijk FA, Sombrero A, Lafarga A, Igartua E and Romagosa I (1999). Integrating statistical and ecophysiological analyses of genotype by environment interaction for grain fill of barley I. Individual grain weight. *Field Crops Res* 62: 63-74.
- Voltas J, Lopes-Corcoles H and Borrás G (2005). Use of biplot analysis and factorial regression for the investigation of superior genotypes in multi-environment trials. *Europ J Agron* 22: 309-324.
- Yan W and Tinker NA (2005). An integrated biplot analysis system for displaying, interpreting, and exploring genotype x environment interaction. *Crop Sci* 45: 1004-1016.