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# **Retrospective analysis of the relationships among the test environments of the Southern Queensland sugarcane breeding programme**

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**Abstract** Repeatability of aspects of genotype by environment (G $\times$ E) interactions is an important factor to be assessed in designing more efficient selection programmes. Sugar yield data from multi environment trials (METs) which were part of the sugarcane breeding programme in southern Queensland were analysed. Data were obtained from 71 environments consisting of trials planted from 1986 to 1989. Retrospective analysis on these data was conducted to assess the repeatability of the clone by environment (CxE) interactions over locations and years. This analysis focussed on identifying similarities among test environments in the way they discriminated among clones for sugar yieId. Analyses of variance and pattern analyses on environments over years based on standardised data were conducted. The pattern analyses were done sequentially according to the accumulated data sets over years. Squared Euclidean distances among environments were averaged over data sets and years before pattern analyses across the data sets were conducted. A graphical methodology was developed to present the results of the cumulative historical analysis. CxE interactions of a magnitude which affected selection decisions were present in each data set studied. Pattern analyses on cumulative data sets identified environmental groupings that were based on geographical positions. Each location generated a different pattern of discrimination among the clones. These results emphasised the importance of clone by location (CxL) interactions in southern Queensland and the need to concentrate more on testing across locations than on ratooning ability within a location. The classifications identified similarities among ratoon crops within a location, differences among locations and differences between ratoon

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crops and their plant crop (PC). This suggested that some aspects of  $C \times L$  and clone by crop-year  $(C \times Y)$  interactions were repeatable across years. The potential applications of these results to increase efficiency of the sugarcane breeding programme, such as the possibility of applying indirect selection among environments generating similar discrimination among clones, are discussed.

Key words  $G \times E$  interactions Retrospective analysis Pattern analysis  $\cdot$  Multi environment trials  $\cdot$  Sugarcane

Abbreviations *G*×*E* Genotype-by-environment interactions · *METs* multi-environment trials · *CxE* clone-by-environment interactions  $\cdot$  *C×L* clone-by-location interac $tions \cdot PC$  plant crop  $\cdot$  *C*×*Y* clone-by-crop-year interactions  $\cdot$  C $\times$ L $\times$ Y clone-by-location-by-crop-year interactions  $\cdot$  *SYT* substation yield trials  $\cdot$  *BSES* Bureau of Sugar Experiment Stations

## **Introduction**

Test environments used to select genotypes must be appropriate samples of the crop production areas targeted by the crop breeding programme (Donald 1962; Hinson and Hanson 1973; Nyquist 1991; Cooper et al. 1993a). However, for such reasons as limited resources, politics, convenience and difficulties in obtaining appropriate land in an area the selection of test environments for crop breeding programmes is often not ideal (Hamblin et al. 1980). Another complication is that "representative" sites are difficult to define and therefore to choose, especially if the target environments are highly variable (Nix 1980; Muchow et al. 1991; Cooper et al. 1993a).

The case for retrospective analysis

Genotype by environment (GxE) interactions complicate the selection of high yielding genotypes, particularly when

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they result in a change in the rank of genotypes across environments (Haldane 1947; Allard and Bradshaw 1964). A lack of knowledge of the causes and repeatability of GxE interactions reduces confidence in the effectiveness of selection for specific adaptation expressed in these interactions. Exploiting GxE interactions by defining optimal test environments or structuring target environments will only be possible when the aspects of environments responsible for the interactions are repeatable (Baker 1988; Cooper et al. 1993a). Distinguishing between repeatable and non-repeatable interactions is a complicated process. Allard and Bradshaw (1964) considered interactions caused by weather variation in different years to be unpredictable. However, if the interactions are due to differences in soil types, and therefore associated with locations, they should be considered to be repeatable and predictable.

Large numbers of METs are routinely conducted as part of a crop breeding programme. Data collected from these METs are a readily available source of information that can be used to assess the repeatability of certain types of GxE interactions. Assuming that the crop breeding programme is conducted routinely for a number of years, the data collected from the METs over time would provide a large sample of the target environments over years. The presence of common standards which are maintained in the METs allows linking of data sets across years (Fox and Rosielle 1982b; Eisemann et al. 1990; Cooper et al. 1990). This has increased the value of the MET data as a source of information that can be utilised and developed into an historical database. The historical database allows a retrospective analysis of the repeatability of certain types of GxE interactions. This greatly expands the sample of environments considered in the analysis of genotypic adaptation. Therefore, many questions which cannot be addressed in 1 year of METs can be investigated using the larger database.

Many of the statistical techniques which have been developed to analyse historical databases (DeLacy et al. 1990) are developments of pattern analysis techniques originally developed for two way data sets. The availability of both the historical MET database and appropriate analytical methodology for their analysis is a strong impetus for retrospective analysis of the METs. Some retrospective analyses of historical databases have been reported. Lin and Butler (1988) and Lawrence and DeLacy (1988) used their databases to identify important test sites. Peterson and Pfeiffer (1989) and Peterson (1992) assessed the relationships among test sites, while Brennan et al. (1981), Brennan and Sheppard (1985) and Lawrence and DeLacy (1988) suggested an appropriate core set of test environments.

## Problems with retrospective analysis

A common problem with the analysis of MET data collected over years is that the genotypes tested change over years. In addition, sites may be missing in 1 or more years of experiments. As a result, data obtained from METs are unbalanced. One option is to analyse the data by extracting subsets of genotypes that are balanced over years. This process, which may result in data sets consisting of only common standards, removes much of the useful information. The number of standards used in the METs is generally not large and these also change over years. Methodology for the analysis of variance which deals with such unbalanced data has been developed (Patterson and Thompson 1975; Patterson and Silvey 1980). However, analysis of variance is relatively uninformative when investigating specific aspects of GxE interactions, as it cannot describe the form of the genotypic responses (Baker 1990; DeLacy et al. 1990).

Recently, multivariate methods have been developed to accommodate such problems. Classification and ordination of environments across years for such data sets can be done by averaging squared Euclidean distance values among environments across years (DeLacy and Lawrence 1988; Lawrence and DeLacy 1988; DeLacy et al. 1990). Relationships among test sites across years can also be estimated by factor analysis (Peterson and Pfeiffer 1989; Peterson 1992) based on an average of all pairwise correlations among test sites studied across years. Investigation of the relationships among environments using pattern analysis must be related to plant breeding objectives. A proximity measure which compares the environments based on their phenotypic or genotypic correlations is preferred (Fox and Rosielle 1982a; DeLacy et al. 1990). This relates the grouping of environments to the theory of indirect selection (Cooper et al. 1993b).

### Application of retrospective analysis to sugarcane

The problems associated with clone by environment  $(C \times E)$ interactions for commercial characters of sugarcane are widely recognised (Kang and Martin 1987). In Queensland, these problems resulted in the development of five separate sugarcane breeding programmes across the state (Mirzawan et al. 1993a). With respect to the commercial characters of sugarcane in Queensland, clone-by-location (CxL) interactions are more important than clone-by-cropyear  $(CXY)$  and clone-by-location-by-crop-year  $(CXL\times Y)$ interactions (Hogarth and Bull 1990; Bull et al. 1992; Jackson and Hogarth 1992; Mirzawan et al. 1993a,b). Therefore, it has been argued that, to increase response to selection, greater emphasis should be placed on sampling more locations than on testing clonal ratooning ability within a location (Jackson 1992). Studies based on pattern analysis of sugarcane MET data indicated that crop classes within the same locations showed similar discrimination among clones compared to that observed at different locations (Jackson and Hogarth 1992; Mirzawan et al. 1993a,b). For sugarcane, different locations are considered to reflect differences in soil type, weather and management situations. If the soil factor is a major determinant of CxL interactions, it would be expected to generate repeatable interactions. The repeatability of the large CxL interactions reported for sugarcane in Queensland should be assessed in larger data sets.



Fig. 1 The southern sugarcane production regions in Queensland showing the five locations used for the multi-environment trials (METs): Bundaberg, Bingera, Millaquin, Maryborough and Moreton

The Bureau of Sugar Experiment Stations (BSES) conduct METs every year and the same sites are used from year to year. Therefore, it is possible to test the similarities among test sites used, not only for the particular year studied but also across planting years. IfCxL interactions were found to be repeatable over years, this may lead to recommendations on what is a more appropriate sample of locations for the target crop production system. An optimal balance of testing across locations and crop classes within locations could be defined.

This paper reports a retrospective analysis of the sugar yield adaptation of sugarcane clones in the METs of the B SES sugarcane breeding programme in Southern Queensland (Fig. 1). The application of the results of this study to increase the efficiency of the sugarcane breeding programme is discussed.

#### **Materials and methods**

#### Data sets

Data on tonnes of sugar yield per hectare (TSH) for the 1986-1989 planting years of the substation yield trials (SYT) conducted by the BSES were used for this study (Table 1). The data set used was explained in detail by Mirzawan et al. (1993b). Briefly, the data set was compiled from sugar yield evaluation experiments of two independent sets of clones for the 1987, 1988 and 1989 planting years and one set of clones for the 1986 planting year. The number of clones including standards in each experiment, ranged from 54 to 81. Data were collected up to the second ratoon (R2) for the 1986 and 1987 planting years, and up to the first ratoon (R1) in the 1988 and 1989 planting years. Of the five sites used for the experiments (Fig. 1), the three sites in the Bundaberg area (Bundaberg, Millaquin and Bingera) and the Maryborough site were irrigated. The Moreton site was rainfed.

At each site, the clones were evaluated in a randomised complete block experiment with two replicates. Each clone was planted in a one-row plot. Plot length ranged from 12 to 15 m and the inter-row spacing ranged from 1.42 to 1.50 m. Two stalk samples per plot were taken for determination of commercial cane sugar percentage (CCS) before final harvest. Sugar yield data were derived as the product of cane yield and CCS. Crop-year data in each location were treated as different environments.

Meteorological data on rainfall and maximum and minimum temperatures were compiled for each experimental location. Whenever data from a location or for a year were not available, the long term average from the closest location was used. Data from the Bundaberg station were used for Millaquin, since the distance between those experimental locations was less than 10 km.

#### Analysis of variance

The relative sizes of the sources of variation were assessed as a ratio of CxE interactions on clone (C) variance components estimated from the expected mean squares of the analysis of variance. A completely random model was used in the analysis of variance as reported in Mirzawan et al. (1993a).

#### Pattern analysis

Prior to pattern analysis, the data were standardised by subtracting from each value its corresponding environment mean and dividing by the corresponding environment standard deviation (Fox and Rosielle 1982a; DeLacy et al. 1990; Cooper et al. 1993b). The association among test environments was investigated by applying classification and ordination methodologies to standardised TSH data. Changes of environmental groupings and positions in the multidimensional space over years were observed in the sequence of accumulating data sets derived by the increasing number of planting years studied (Fig. 2).

The environments were classified using the agglomerative hierarchical clustering procedure with squared Euclidean distance (SED) as the dissimilarity measure and incremental sum of squares (ISS) as the grouping strategy (Ward 1963; Wishart 1969; Burr 1968, 1970). The method of environment classification for unbalanced data suggested by Delacy and Lawrence (1988) and DeLacy et al. (1990) was used. With this method, the SED values among environments obtained from each planting year were averaged over sets within and across years before the classification was done.

The data for the classifications were arranged sequentially on a planting year basis (Fig. 2). The initial data set (1986 planting year) was analysed first. The 1987a data set was then added and a second analysis conducted on the average SED matrix over the two sets. Data sets from the subsequent planting years were sequentially accumulated in this way, so that all the data from the seven available sets (4 planting years, two sets in 3 years) studied were included in the retrospective analyses. Seven cumulative data sets were analysed (Table 1). A separate classification of the environments was done on those seven data sets as they were generated. This cumulative analysis enables investigation of the interactions among clones, locations and crop years by observation of any changes over time of the environmental groupings due to the addition of the new data sets.

A principal coordinate analysis (PC'A) (Gower 1966, 1967) of the environments was conducted on the same seven data sets used for the classification. Changes in the association among the environ-

Table 1 The number of clones, crops and locations for the substation yield trials in Southern Queensland from 1986 to 1989 together with their corresponding variance components and standard errors for the clone  $(V<sub>C</sub>)$ , the interactions between clone and location

 $(V_{C\times L})$ , clone and crop year  $(V_{C\times Y})$ , clone, location, and crop year  $(V_{C \times L \times Y})$ , the total of the three interaction variance components  $(V_{C \times E}^{\sim}$  clone-by-environment interaction variance component) and the ratio of  $V_{C\times E}$  on  $V_C$ 



<sup>a</sup> a and b indicate different sets of clones planted in the same year

 $<sup>b</sup>$  The two and three crops considered were plant crop (P), first ratoon (R1), and second ratoon (R2)</sup>



Fig. 2 Flow chart to describe the cumulative pattern analysis of the historical database. ( $i = 1..y$  number of years,  $j = 1..s$  number of data sets within a year)

ments across planting years identified by the PC'A were portrayed by the proximity plots. Each new proximity plot, showing the cumulative relationship among locations, was superimposed on the plot derived from the cumulative analysis of the previous year's data. This gives a graphical display of how the relationships among the locations, for their ability to discriminate among the clones, change over time as more data are accumulated. In addition, the final year's data set (1989b) was analysed separately and the proximity plot for these data was superimposed on the proximity plot from the cumulative analysis of all previous data (1986-1989a). This procedure allows an assessment of how the clone discrimination at the locations sampled in a particular year relates to that observed at those locations in the historical database.

## **Results**

## Analysis of Variance

Results of the analyses of variance indicated that, based on the ratio of CxE on C variance components, three (1986, 1987b, 1988a) out of seven data sets studied showed larger variation for C×E interactions than for C variation (Table 1). Two data sets (1987a, 1988b) showed similar variation between CxE interactions and C, and the remaining two data sets (1989a, 1989b) showed less variation for CxE interactions relative to C variation. These results suggested that CxE interactions were present in most of the data sets studied and that their magnitude was sufficient to affect selection.

# Classifications and principal coordinate analysis

Classification of environments generally grouped environments within a location before these grouped with environments from other locations (Figs. 3a-d). This reflects the strong influence of  $C \times L$  interactions relative to  $C \times Y$ 

interactions. Within a location, the ratoons grouped together before they grouped with their respective plant crop (PC), except for the Millaquin location in the 1986 data set. This reflects the incidence of CxY interactions and identifies a change in relative genotypic performance between plant and ratoon crops.

On the basis of the classification of the 1986 data, Bundaberg and Bingera grouped together and were separated from Maryborough, Millaquin and Moreton (Fig. 3a), while Maryborough and Millaquin grouped together before they grouped with Moreton. However, as information from more planting years was accumulated, Maryborough and Moreton grouped together and were separated from Bundaberg, Bingera, and Millaquin (Figs. 3b, c, d). Among the latter three locations, there were changes in grouping associations with the accumulation of subsequent years of data sets in the analysis. These changes in location groupings over years may reflect changes in environmental conditions over the planting years studied or the influence of the change over time in clones screened at these sites.

The cumulative classifications of the locations strongly reflected their geographical positions (Fig. 1) but did not reflect the differences in soil types among and within those regions. The three locations, Bundaberg, Millaquin and Bingera, are geographically close to each other in the northern part of the southern Queensland sugarcane growing region (Fig. 1). Since Maryborough and Moreton are located approximately 100 and 250 km, respectively, south of Bundaberg, differences in climatic and edaphic conditions associated with latitude are expected.

The first three vectors of the PC'A accounted for 21-25%, 16-18%, and 11.5-12% of the total variation, respectively. In the first two principal axes, environments within the same locations were closely associated (Fig. 4). The proximity of the environments on the first two principal axes strongly reflected the grouping of environments from the classifications. Therefore, environmental differences associated with these axes were considered to summarise the CxL interactions.

The relative positions of the locations in the proximity plots were consistent as data were accumulated over years (Fig. 4). This suggested that there was little change over the period of the study in the way these environments discriminated among the clones relative to the effects of CxL interactions. The distribution of environments belonging to different locations on the first two vectors of the PC'A indicated that every location contributed a different form of discrimination among clones in the MET programme. This conformed with the finding that CxL interactions were the largest source of CxE interactions for these data sets, as reported in previous studies (Mirzawan et al. 1993b) Therefore, for this selection stage, it is important to retain all of the locations as experimental sites.

The environment groupings derived from the last planting year data set (1989b) were different from those derived from the accumulated data sets of the 1986-1989a planting years (Figs. 5a, b). In the latter data set the Bundaberg (a, b) and Millaquin (d, e) environments were grouped to-





b Cumulative analyses: 1986 - I987B



c Cumulative analyses: 1986 - 1988B data

Cumulative analyses: 1986 - 1989B data

Fig. 3 a-d Dendrograms for the cumulative classification of 15 environments based on standardised tonnes of sugar yield per hectare (TSH) data of the sugarcane clones planted in 1986 until 1989. Abbreviations for the environments are listed in Table 1

gether and separated from the grouping of Maryborough (j, k) and Bingera (g, h) (Fig. 5b). These groupings did not reflect geographical distances among the environments. Changes in the relative positions of the environments from the 1989b data set were observed when the proximity plot from this analysis was superimposed on the plot from the cumulative analysis of previous data (1986-1989a) sets (Fig. 5c). The absence of Moreton environments in the 1989b data set may have contributed to these differences. In the 1989b data set, the discrimination among the clones at Maryborough (j, k) differed from the long term discrimination at Maryborough. It was repositioned toward the long term discrimination at Moreton (M, N, O). The discrimination at Bundaberg in 1989b (a, b) was similar to the long term discrimination at Bingera (G,H), while that at Bingera (g, h) was similar to the long term discrimination produced at Bundaberg (A, B, C).



**Fig. 4** a-d Proximity plots of the first two vectors from the cumulative principal coordinate analysis (PC'A) on 15 environments based on standardised tonnes of sugar yield per hectare (TSH) data of the sugarcane clones planted in 1986 until 1989. *Arrows* indicate changes of PC' scores of environments when extra information was added. The environments considered were Bundaberg PC *(A,a),* R1 *(B,b),* R2 *(C,c);* Millaquin PC *(D,d),* R1 *(E,e)*, R2 *(F,f)*; Bingera PC *(G,g),* R1 *(H,h),* R2 *(I,i);* Maryborough PC *(J,j),* R1 *(K,k),* R2  $(L, l)$ ; and Moreton PC  $(M, m)$ ; R1 (N,n); R2 *(0,o).* The *boundaries* around environments delineate those environments from the same locations

## Meteorological information

Rainfall data from the experimental locations indicated similarities of total rainfall pattern over years among the locations in the Bundaberg region (Bundaberg and Bingera) and at Maryborough. Moreton, however, was much wetter (Fig. 6).

Maximum temperature during the day at Maryborough was slightly higher than that observed for Bundaberg or Moreton, particularly during the spring and summer (Fig. 7a). Throughout the year, maximum and minimum temperatures at Moreton were the lowest of the three locations (Figs 7a, b). The minimum temperature throughout the year was generally similar at Bundaberg and Maryborough. Different patterns of differences between the maximum and minimum temperatures were observed for all three locations (Fig. 7c). The Bundaberg region had the smallest differences between maximum and minimum temperatures throughout the year, while Maryborough and Moreton had similar differences from July to December but differed from January to June. The locations did differ in their meteorological characteristics, and this may have contributed to the geographical grouping of the test environments. In addition, interactions with other factors which were not measured would complicate the situation.

# **Discussion**

The incidence of strong CxE interactions was emphasised in the analyses of variance, classifications and the PC'A of the MET data sets studied. There were stronger commonalities among crop years within a location than among locations for each planting year. These results were in agreement with the previous reports from Jackson and Hogarth



Fig. S a-e Dendrograms for the classifications (a and b) and proximity plots of the first two vectors from the PC'A on environments (e) based on cumulative analysis of standardised tonnes of sugar yield per hectare (TSH) data of the 1986 to 1989a data sets *(uppercase letters)* and individual 1989b data set *(lowercase letters).* Arrows indicate changes of PC'scores for environments when extra information was added. Codes for environments are listed in Fig. 4. The *boundaries* around environments delineate those environments from the same locations



Fig. 6 Total annual rainfall  $(mm)$  for the locations of sugarcane substation yield trials in south-east Queensland during the years 1986 to 1991

(1992) in north Queensland and Bull et al. (1992) and Mirzawan et al. (1993a, b) in southern Queensland.

The retrospective analyses identified changes in the associations among environments, which corresponded with environmental changes that occurred during the course of the experiments. The environment classifications grouped Bundaberg and Bingera separately from Millaquin in the 1986 and 1987 planting years. However, when data from

the 1988 planting year were added to the analysis, the Bingera environments grouped with Millaquin and were separated from Bundaberg. Results of the PC'A confirmed this change in association among environments over years. Changes in the ordinate positions for the Bingera environments occurred from the 1986 to 1987 planting years and these stabilised from 1988 onwards. This coincided with a known change in soil type associated with the location for



Fig. 7 a-c Maximum temperature (a), minimum temperature (b) and the difference between maximum and minimum temperatures (e) expressed as monthly mean temperature throughout the year for the Maryborough, Moreton and the Bundaberg region

the Bingera experiments. The sites used for experiments changed from red earth in 1986 to forest soil in 1987 and onwards. These results indicate that this change in experimental procedure influenced the discrimination among the clones observed in the METs. Other changes in relative discrimination among the clones in each environment over planting years were considered small relative to that observed at Bingera. This was indicated by the stable positions of the environments on the proximity plots as the data were accumulated over years.

The different positions of environments shown by the proximity plots indicated differences among locations in the way they discriminated among clones. This indicated the importance of sampling a number of locations for se-

lection among clones for TSH. However, since CxY interactions were not as important as CxL interactions for sugar yield, this suggests that it is possible to reduce the number of environments (crop years) within a location.

Consistency of the importance of CxL interactions relative to those of CxY interactions was also reflected in the classification and ordination analyses over all data sets studied. Therefore, it is concluded that some of the CxL interactions are repeatable, as discussed by Allard and Bradshaw (1964). The tendency of the ratoons within a location to group together before grouping with their plant crop indicated that some of the  $C \times Y$  interactions were also repeatable. Unlike Jackson (1992), who suggested that testing in only a plant crop may be satisfactory in the early stages of selection, these results indicate that it is important to gain some information on ratooning ability in the SYT stage of the sugarcane breeding programme.

The differences in environmental groupings between accumulated data sets and an individual data set (Fig. 5) indicated that different relationships among environments relative to the longer term perspective can result from analysis when a small data set is used. Hence the use of small data sets in the analysis may result in misleading conclusions about the relationships among locations. The degree of discrepancy between the discrimination of locations in the current data set (1989b) and its long-term average (1986-1989a) can be observed by inspecting their current positions in the cumulative proximity plots formed from analysis of the historical data set. This technique will allow plant breeders to place the discrimination obtained from current data in context with a long term perspective gained from running many years of METs.

The groupings of locations obtained from the cumulative classifications strongly reflected the geographical distance between the locations. Bundaberg, Millaquin and Bingera are located in the Bundaberg region which is the northern part of the southern Queensland region targeted by the breeding programme (Fig. 1). Soil type differs markedly between Bundaberg, Millaquin and Bingera. However, all three locations grouped together and were separated from Maryborough and Moreton. Maryborough and Moreton differ in soil type, Maryborough with yellow podzolic and reddish-bronze krasnozem soils, while the Moreton site has a peat soil. Maryborough is in the central and Moreton is in the southern part of the southern Queensland region. Different management practices can be expected between Moreton and the other locations (Bundaberg region and Maryborough) due to the use of irrigation in the latter environments.

The available meteorological information did not give an obvious explanation for the geographical grouping of the locations. Differences in the pattern of maximum and minimum temperature over the crop season were identified. However, whether these contributed to the CxL interactions for sugar yield is not known. With the data sets available, it is not possible to explain the basis of the geographical grouping of the locations. More studies specifically investigating the important environmental characteristics responsible for the CxE interactions are suggested.

The historical analysis developed in this study provides a framework for using the plant breeder's experience gained from running many years of METs in judging the relevance of current experiments. For example, where a particular year generates a different pattern of interactions among clones in comparison to the long term trend, the plant breeder can adjust the selection pressure applied to the breeding populations to accomodate the atypical years. In this way the historical analyses enable adjustments to selection in the current year of METs. This adjustment is possible, since indirect response to selection among environments may be inferred from the environmental associations obtained from the retrospective analysis. In addition, the opportunity for exploiting indirect selection among environments may be investigated. For example, it is possible to test whether selection in Moreton is effective for indirect selection in Maryborough. The geographical groupings of locations used in this study provide a basis for investigation of the important environmental factors responsible for the CxE interactions for sugar yield.

The influence of the unbalanced data in the current database requires further study. Some locations considered in the analysis were not present each year. Moreton, as the high-yielding location, was present in three data sets in the 2 planting years (1986 and 1987), while Bundaberg data were absent in 1987 (two data sets). This contrasts with the other locations, which were present in all seven data sets. The conclusions from this study can be tested further as the historical database is expanded.

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