Theor Appl Genet (1994) 87:627–640

THEORETICAL AND APPLIED GENETICS



# Quantitative analysis of the effect of selection history on sugar yield adaptation of sugarcane clones

**B. L. Srivastava[1], M. Cooper[2], R. T. Mullins[3]**

[1] Indian Institute of Sugarcane Research, Lucknow-226002, India
[2] The Department of Agriculture, The University of Queensland, Brisbane, Queensland 4072, Australia
[3] Bureau of Sugar Experiment Stations, 50 Meiers Rd, Indooroopilly, Queensland 4068, Australia

Received: 8 December 1992 / Accepted: 17 May 1993

**Abstract.** An objective of the CSR sugarcane breeding programme in Australia was to assess the scope for broadening the genetic base of the commercial sugarcane germ plasm through interspecific hybridization with *Saccharum spontaneum* clones. The contribution of both selection history and *S. spontaneum* to sugar yield and its components was investigated in the germ plasm pool assembled. The analysis was conducted on a data-set of 256 clones, consisting of parents and full-sib families generated from 32 biparental crosses, tested in six environments. The minimum number of generations back to *S. spontaneum* ancestor in the clone's pedigree was used as a germ plasm score. The geographical origin and selection history of each parent and their use in the biparental crosses were used to develop a selection history score for parents and offspring. The variation for seven attributes, cane yield, commercial cane sugar %, sugar yield, stalk number per stool, stalk weight, fibre % and ash % juice was partitioned according to the germ plasm and selection history scores. Significant ($P<0.05$) clone variation and clone × environment interaction for all attributes was present. The germ plasm scores accounted for a significant ($P<0.05$) component of the clone variation for all of the attributes except cane yield. There was an increase in sugar yield with an increase in the minimum number of generations back to a *S. spontaneum* clone. The selection history groups accounted for a high proportion of the variation among parental clones for all of the attributes except cane yield. This suggested that parents were the outcome of strong selection pressure for the commercial cane attributes. However, the selection history groups for the offspring produced by random mating of parents did not account for a high proportion of the variation for the attributes.

Using the mixture method of classification we partitioned the 256 clones into five groups for patterns of performance for the seven attributes across the six environments. The five groups emphasized major differences in the patterns of performance for the seven attributes across environments. The distribution of germ plasm and selection history scores in each of the five groups indicated that their patterns of performance were associated with selection history and minimum generations to *S. spontaneum*. Therefore, both the analysis on selection history and germ plasm scores (extrinsic classification) and the analysis on the mixture method of classification (intrinsic classification) emphasized the influence of selection history on the sugar yield of sugarcane.

**Key words:** Sugarcane – *Saccharum spontaneum* – Sugar yield – Selection history – Pattern analysis

Communicated by G. Wenzel
*Correspondence to:* M. Cooper

## Introduction

Advances in sugar yield from sugarcane have been achieved during recent decades. Present day sugarcane cultivars are complex interspecific hybrids having *Saccharum officinarum* as a principal component. The involvement of *S. spontaneum* and other wild species in the development of commercial sugarcane has been detailed by Price (1963), Stevenson (1965), Simmonds (1976), Roach (1977), Sreenivasan et al. (1987) and Roach and Daniels (1987). However, relative to the diversity that actually exists, most of the current commercial

sugarcane varieties have only a limited range of wild cane species in their lineage (Arceneaux 1965; Price 1965; Ethirajan et al. 1982; Roach 1989; Symington 1989). Considerable genetic variation exists among commercial varieties of sugarcane due to their hybrid nature, heterozygosity and high polyploidy. Hogarth (1971) and Hogarth et al. (1981) reported that genetic variance for the yield of cane in commercial breeding populations has not been exhausted. However, the availability of the maximum possible commercial potential of the original noble cane (*S. officinarum*) and wild canes in the immediate parents of the current commercial varieties is unlikely (Symington 1989).

An objective of the CSR sugarcane breeding programme at Macknade (Queensland, Australia) was to assess the scope for broadening the genetic base of the commercial sugarcane germ plasm through interspecific hybridization with *S. spontaneum* clones.The long-term process of broadening the genetic base of sugarcane will provide genetic variation for further improvement of quantitative traits and sources of resistance to biotic and abiotic stresses (Roach 1989). Inadequate understanding of the quantitative aspects of sugar yield and its components and how they are influenced by selection history may pose problems in selecting adapted clones from the breeding programme. An enhanced understanding of the contribution of the component species to high sugar yield in current commercial sugarcane clones would assist the process of broadening the genetic base accessed by sugarcane breeding programmes. The positive contribution of *S. spontaneum* in the pedigree of commercial sugarcane clones has been reported by Berding and Roach (1987) and Roach (1989). Therefore, a more quantitative analysis of the influence of *S. spontaneum* on the sugar yield and adaptation of sugarcane clones is justified. One approach for such an analysis is to field-test a range of various germ plasms having quantified differences in the contribution of *S. spontaneum* to their pedigree. This is the approach adopted in the current study.

Large data sets are commonly generated from multi-environmental experiments for parental evaluation in the early stages of selection programmes. Pattern analysis methodology (Williams 1976) has been widely applied to the study of these large data sets (DeLacy and Cooper 1990). The study of major differences in patterns of performance among groups of genotypes has been shown to be useful as a preliminary analysis to rationalize and simplify any detailed investigation of the responses of individual genotypes (Byth et al. 1976; Hayward et al. 1982; Basford and Mc Lachlan 1985; Bull and Hogarth 1990; Fox et al. 1990). The selection of adapted clones or groups of clones is influenced by the presence and nature of clone by environment interactions within the target production environments (Cooper et al. 1993). Clone by environment interaction has been shown to affect selection in sugarcane (Ruschel 1977; Ramdoyal et al. 1986; Tai and Miller 1986; Bull and Hogarth 1990; Hogarth and Bull 1990; Jackson and Hogarth 1992).

Basford and McLachlan (1985) developed a grouping method to deal with three-way data sets that includes the case where multiple attributes are measured on clones in different environments. In the present study, just such a data set was investigated. Sixty-four parents, with known pedigree and selection history, were intercrossed in a bi-parental progenies design (Kearsey 1965) to generate 32 full-sib families from each of which 6 progeny were sampled. Seven attributes were measured on the progeny and parents in six environments. The influence of *S. spontaneum* and selection history on the patterns of performance for the seven attributes was investigated.

The influence of selection history and *S. spontaneum* on the adaptation of sugarcane clones was investigated by classifying the clones in two complementary ways and comparing the classifications. First, the clones were allocated into groups based on the selection history and minimum number of generations back in their pedigree to a *S. spontaneum* clone. The partitioning of variation among clones was then investigated in terms of these selection history and pedigree groupings. This is referred to as an extrinsic classification since information independent of the data set is used to group the clones. Second, the clones were classified into groups using the three-way clustering method of Basford and McLachlan (1985). This is referred to as an intrinsic classification since the data set is directly used to group the clones. Correspondence between the extrinsic and intrinsic classifications was investigated.

## Materials and methods

*Parental and offspring population*

A random sample of 64 clones was taken from germ plasm available to the CSR breeding programme. The collection from which the sample was taken included material from other breeding programmes around the world. The 64 clones were intercrossed in a bi-parental progenies design (Kearsey 1965) to produce 32 full-sib families. A random sample of 6 full-sib clones was taken from each family. The $6 \times 32$ progeny, together with the 64 parents provided the 256 clones that were studied. The pedigree of each parent was determined (Table 1) to measure the minimum number of generations back to a *S. spontaneum* clone. This measure was used as a germ plasm score (GS) (Table 2). The selection history of each parent clone and their offspring was determined to give each clone a selection history (SH) score (Table 2). To quantify the influence of selection history, the parental clones were placed into groups based on their geographical origin and the offspring into groups according to the use of locally adapted or imported clones as parents (Table 3).

**Table 1.** Pedigree for the 32 female and male clones that were intermated to produce the experimental population

| Family number | Parents | | Grandparents | |
|---|---|---|---|---|
| | Female | Male | Female | Male |
| 1 | CP38-34 | MQ67-588 | CO-421 × CP27-156 | Azul × MQ63-427 |
| 2 | BN61-1338 | MQ72-441 | CP48-117 × SN39-3821 | Akbar × MQ66-52R |
| 3 | MQ63-527 | Vesta | BM × BT | POJ-2878 × MQ31-228 |
| 4 | BN68-8051 | MQ63-423 | CP51-21 × LF47-2777 | BT × BM |
| 5 | CO-961 | MQ72-2130 | POJ-2878 × CO-449 | HQ-409 × SES-528 |
| 6 | N52-219 | MQ68-8310 | NCO-339 × NM-214 | Korpi × MQ63-83R |
| 7 | MQ68-624 | MQ61-1197 | Akbar × MQ63-522R | Q-50 × Unknown |
| 8 | CO-270 | BN67-7520 | B37-47 × CO-206 | LF46-1902 × CP50-11 |
| 9 | MQ72-5151 | Apollo | HQ-409 × Sumatra-1 | F36-819 × Unknown |
| 10 | HQ-409 | MQ69-83R | Noble | NG57-225 × SES-100A |
| 11 | R-565 | MQ66-1635 | H32-8560 × R-397 | CO-281 × LF47-2777 |
| 12 | CP57-526 | MQ64-253 | CP52-114 × US54-24-9 | Trojan × MQ36-2717 |
| 13 | Trojan | MQ72-3192 | CO-270 × MQ27-1124 | HQ-409 × SES-528 |
| 14 | MQ72-2188 | MQ60-754 | Chittan × Glagah W.T. | MQ55-2635 × Unknown |
| 15 | Kruos | MQ72-212 | CP52-68 × SN39-3821 | Triton × MQ69-61R |
| 16 | TS68-577 | CO-775 | F-152 × F-159 | POJ-2878 × CO-371 |
| 17 | H64-8510 | BN63-3003 | H58-1566 × H55-1241 | CP53-19 × Polycross |
| 18 | MQ69-42R | BN59-8432 | MQ66-184R × MQ27-1104 | MQ37-1325 × Unknown |
| 19 | MQ64-522 | F-150 | Vidar × F-134 | NCO-310 × PT43-52 |
| 20 | MQ72-4128 | MQ54-1301 | NG57-225 × Sumatra-1 | Trojan × Vesta |
| 21 | Demos | MQ72-5150 | CO-270 × MQ33-371 | Badila × MOL-5904 |
| 22 | MQ72-4143 | MQ64-575 | Oramboo × MOL-5801 | Vidar × M44-147 |
| 23 | Cassius | MQ72-5121 | Trojan × H49-104 | NG57-225 × Tabongo |
| 24 | N55-805 | MQ64-30 | NCO-310 × CO-301 | Vidar × M44-147 |
| 25 | MQ75-900 | TS64-375 | MQ62-260 × LF47-2777 | TSF-153 × TSF-152 |
| 26 | MQ72-607 | F-151 | CO-270 × MQ68-46317 | NCO-310 × PT43-52 |
| 27 | CO-440 | MQ72-489 | CO-360 G.C. × CO-361 | Comus × Polycross |
| 28 | MQ74-720 | CP53-19 | Trojan × MQ72-3068 | F36-819 × CP48-126 |
| 29 | MQ64-219 | Cyclops | Trojan × H51-4336 | CO281 × MQ27-1124 |
| 30 | Cadmus | H48-4646 | CO-281 × MQ33-157 | H37-1933 × Unknown |
| 31 | Triton | TS65-28 | CO-270 × Eros | TS56-377 × TS56-2668 |
| 32 | BN65-5634 | MQ73-641 | CP52-68 × SN39-3821 | Apollo × MQ69-45R |

BT, Badila × Tabongo cross; BM, Badila × Mandalay cross
The underlining of a clone in a pedigree denotes a *S. spontaneum* clone

*Environments and experimental layout*

The 256 clones were grown in six environments generated at one location (CSR Macknade Experiment Station, latitude 18.5° S, Longitude 145.0° E) in a split plot design with two replicates. The environments consisted of three successive plantings of the clones over 3 years (1982–1984). Plant crop and first and second ratoon were evaluated for the 1982 planting, plant crop and first ratoon for the 1983 planting and only the plant crop for the 1984 planting. The six environments were randomized within replicates and clones were randomized within environments. Crops were sampled, harvested and ratooned during October, 1983, 1984 and 1985. Pregerminated bud shoots were transplanted. Consequently, there were no missing plots in the plant crop. Plant size consisted of one row having 6 stools 0.5 m apart with an inter-row spacing of 1.42 m. To reduce the influence of competition and edge effects only the 4 central stools from each plot were sampled. Measurements on seven attributes, sugar yield as tonnes of sugar per hectare (TSH), sugar content as commercial cane sugar (CCS), cane yield as tonnes of canes per hectare (TCH), average weight of single stalk (SWT), stalk number per stool (SNO), fibre % cane (FIB) and ash % juice (ASH) were taken.

General characteristics of the environments which were noted include water stress during January and February of 1983 and December and January of 1985. High rainfall and temperature occurred during April and May of 1983. The low CCS observed for 1984 may have been because of growth stimulated by heavy rainfall. While there was no direct assay, ratoon stunting disease may have influenced clone performance in 1985.

*Analysis of variance*

The data from a split block design with two replicates were analysed using the following model

$$y_{ijk} = m + b_k + c_i + (\varepsilon 1)_{ik} + e_j + (\varepsilon 2)_{jk} + (ce)_{ij} + (\varepsilon 3)_{ijk} \quad (1)$$

where, $y_{ijk}$ is the observation on clone $i$ in environment $j$ of block $k$, $m$ is the grand mean, $b_k$ is the effect of block $k$, $c_i$ is the effect of the clone $i$, $(\varepsilon 1)_{jk}$ is the interaction effect of clone $i$ and block $k$ (error 1), $e_j$ is the effect of environment $j$, $(\varepsilon 2)_{jk}$ is the interaction effect of environment $j$ and block $k$ (error 2), $(ce)_{ij}$ is the interaction effect between clone $i$ and environment $j$ and $(\varepsilon 3)_{ijk}$ is the interaction effect of clone $i$, environment $j$ and block $k$ (error 3).

**Table 2.** Germ plasm (GS) and selection history (SH) scores for the 64 parents and 32 full-sib offspring families

| Family number | Female parent | | Male parent | | Offspring | |
|---|---|---|---|---|---|---|
| | GS | SH | GS | SH | GS | SH |
| 1 | 3 | 2 | 3 | 9 | 4 | 3 |
| 2 | 4 | 5 | 2 | 8 | 3 | 2 |
| 3 | 2 | 7 | 4 | 9 | 3 | 1 |
| 4 | 5 | 5 | 2 | 7 | 3 | 2 |
| 5 | 4 | 3 | 1 | 7 | 2 | 3 |
| 6 | 4 | 9 | 2 | 8 | 3 | 3 |
| 7 | 2 | 8 | 5 | 9 | 3 | 1 |
| 8 | 2 | 3 | 5 | 5 | 3 | 4 |
| 9 | 1 | 7 | 5 | 6 | 2 | 1 |
| 10 | 5 | 9 | 1 | 7 | 2 | 1 |
| 11 | 4 | 4 | 3 | 9 | 4 | 3 |
| 12 | 2 | 2 | 4 | 9 | 3 | 3 |
| 13 | 3 | 9 | 1 | 7 | 2 | 1 |
| 14 | 1 | 7 | 4 | 9 | 2 | 1 |
| 15 | 4 | 5 | 3 | 9 | 4 | 2 |
| 16 | 5 | 4 | 4 | 3 | 5 | 4 |
| 17 | 4 | 1 | 5 | 5 | 5 | 4 |
| 18 | 2 | 8 | 5 | 5 | 3 | 2 |
| 19 | 5 | 9 | 4 | 4 | 5 | 3 |
| 20 | 1 | 7 | 4 | 9 | 2 | 1 |
| 21 | 3 | 6 | 1 | 7 | 2 | 1 |
| 22 | 1 | 7 | 3 | 9 | 2 | 1 |
| 23 | 4 | 6 | 1 | 7 | 2 | 1 |
| 24 | 4 | 4 | 4 | 9 | 5 | 3 |
| 25 | 2 | 8 | 3 | 4 | 3 | 3 |
| 26 | 3 | 9 | 4 | 4 | 4 | 3 |
| 27 | 5 | 3 | 3 | 9 | 4 | 3 |
| 28 | 2 | 8 | 5 | 2 | 3 | 3 |
| 29 | 4 | 9 | 3 | 9 | 4 | 1 |
| 30 | 3 | 9 | 5 | 1 | 4 | 3 |
| 31 | 3 | 6 | 4 | 4 | 4 | 3 |
| 32 | 4 | 5 | 2 | 8 | 3 | 2 |

**Table 3.** Clone groups according to selection history (SH) for the parents and offspring

| Group number | Source or selection history |
|---|---|
| Parents | |
| 1 | Hawaii, USA |
| 2 | Canal point, Florida, USA |
| 3 | Coimbatore, India |
| 4 | Natal, East Africa |
| 5 | Broadwater, NSW, bred Macknade, Australia |
| 6 | Macknade, Queensland, commercial varieties |
| 7 | Macknade, first cross interspecies hybrid |
| 8 | Macknade, second cross interspecies hybrid |
| 9 | MQ parents excluding 6, 7 and 8 |
| Offspring | |
| 1 | Cross between locally selected clones |
| 2 | Cross between a locally selected clone and one selected for NSW environments |
| 3 | Cross between a locally selected clone and an imported clone |
| 4 | Cross among imported clones |

All effects are assumed to be randomly distributed, uncorrelated normal variates, with a common variance and zero mean (Eisenhart 1947). Expectations for mean squares were derived as indicated by Schultz (1955). Variance components were estimated by equating mean squares to the expected mean squares and solving for the variance components. The approximate standard error of the variance component was estimated by the procedure outlined by Anderson and Bancroft (1952). As pointed out by Jackson and Hogarth (1992) the assumption of uncorrelated errors in sugarcane trials which involve measurements on plant and rantoon crops within locations is unlikely to be valid. Therefore, variance components should be interpreted with the failure of this assumption in mind.

The main-effect variation among clones was subjected to further partitioning on two bases. First, it was partitioned into sources due to parents and progeny. This was used to test whether there was a contrast in the expression of the attributes between the parents and progeny. Second, the main-effect variation within the parent and progeny groups was further partitioned into among and within group components for both germ plasm score and selection history. This was used to test whether there was significant variation for the seven attributes associated with the GS and SH groupings.

*Three-way classification*

The $256 \times 7 \times 6$ clone by attribute by environment matrix was subjected to the three-way mixture method of clustering developed by Basford and Mclachlan (1985). A truncation level was determined by monitoring the increase in the log likelihood of the optimal group solution between the two and ten group levels. The distribution of germ plasm score groups and selection history groups from the pedigree analysis in the groups identified by classification was investigated at the adopted truncation level. The association between the pedigree and classification groupings was investigated as a contingency table as outlined in Snedecor and Cochran (1980).

## Results

*Analysis of variance*

There was significant ($P < 0.05$) variation for clones and clone by environment (C × E) interaction for all seven attributes (Table 4). Main-effects differences among environments were significant ($P < 0.05$) for tonnes of cane per hectare, tonnes of sugar per hectare, commercial cane sugar, stalk weight and fibre %. The variance component for C × E interaction was generally smaller than the main-effect differences among clones and experimental error (Table 5). The size of the C × E interaction component relative to the clone variance component ranged from a maximum of 25% for sugar yield to a minimum of 8% for stalk number.

There was a significant ($P < 0.05$) difference between parents and offspring for tonnes of sugar per hectare, commercial cane sugar, stalk weight, fibre and

**Table 4.** Degrees of freedom, mean squares and significant level for the combined analysis of variance for seven attributes – cane yield (TCH), commercial cane sugar (CCS), sugar yield (TSH), stalk number (SNO), stalk weight (SWT), fibre percentage (FIB) and ash percentage of juice (ASH)–measured on 256 sugarcane clones tested in six environments

| Source | *df* | Attribute | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | TCH (t ha$^{-1}$) | CCS (%) | TSH (t ha$^{-1}$) | SNO (number stool$^{-1}$) | SWT (KG) | FIB (%) | ASH (%) |
| Block | 1 | 1 415.97 | 142.06 | 24.26 | 1.53 | 0.155 | 17.63 | 0.105 |
| Clones (C) | 255 | 4 878.83** | 50.76** | 111.36** | 36.35** | 0.842** | 65.60** | 0.036** |
| Error 1 | 255 | 623.64 | 3.03 | 14.09 | 2.36 | 0.037 | 2.59 | 0.002 |
| Environment (E) | 5 | 177 210.42** | 415.57** | 2253.36** | 96.93 | 22.776** | 452.80* | 0.632 |
| Error 2 | 5 | 9 255.69 | 65.29 | 166.61 | 36.58 | 0.325 | 46.28 | 0.128 |
| C × E | 1275 | 613.04** | 4.18** | 14.14** | 2.35** | 0.050** | 3.80** | 0.003** |
| Error 3 | 1275 | 465.98 | 2.57 | 10.63 | 1.89 | 0.029 | 2.57 | 0.002 |

** and * denote significance at the 1% and 5% probability levels, respectively

**Table 5.** Components of variance for clones, C × E interaction, error 1 and error 3 and their standard errors for seven attributes – cane yield (TCH), commercial cane sugar (CCS), sugar yield (TSH), stalk number (SNO), stalk weight (SWT), fibre percentage (FIB) and ash percentage of juice (ASH) – measured on 256 sugarcane clones tested in six environments

| Source of variation | Attribute | | | | | | |
|---|---|---|---|---|---|---|---|
| | TCH (t ha$^{-1}$) | CCS (%) | TSH (t ha$^{-1}$) | SNO (number stool$^{-1}$) | SWT (kg) | FIB (%) | ASH (%) |
| Clones | 342.34 ± 36.25 | 3.84 ± 0.37 | 7.79 ± 0.83 | 2.79 ± 0.27 | 0.065 ± 0.006 | 5.15 ± 0.48 | 0.003 ± 0.0003 |
| Error 1 | 26.28 ± 9.67 | 0.08 ± 0.05 | 0.58 ± 0.22 | 0.08 ± 0.04 | 0.002 ± 0.001 | 0.01 ± 0.004 | 0.000 ± 0.0000 |
| C × E | 75.53 ± 15.24 | 0.80 ± 0.10 | 1.91 ± 0.36 | 0.23 ± 0.06 | 0.011 ± 0.001 | 0.62 ± 0.09 | 0.001 ± 0.0001 |
| Error 3 | 465.98 ± 18.44 | 2.58 ± 0.10 | 10.63 ± 0.42 | 1.89 ± 0.08 | 0.029 ± 0.001 | 2.57 ± 0.10 | 0.002 ± 0.0001 |
| (CE/C)%[a] | 22 | 21 | 25 | 8 | 16 | 12 | 21 |

[a] (CE/C) % gives the C × E interaction variance component as a percentage of the clone component of variance

ash % (Table 6). The attributes commercial cane sugar, tonnes of sugar per hectare and stalk weight were higher for parents than offspring, and the converse was observed for fibre and ash (Table 7).

The clone variance component was greater than that for C × E interaction for all attributes when the parents and progeny were considered separately (Table 8). However, for some attributes there were slight differences between the parents and offspring in the ratio of the C × E interaction component of variance on the clone component. For tonnes of cane per hectare, stalk weight and fibre, the ratio was greater in the parents, while the ratio was greater in the progeny for commercial cane sugar and stalk number. The ratio was similar in both parents and progeny for tonnes of sugar per hectare and ash.

*Germ plasm (S. spontaneum) groups*

When the parents and progeny were considered separately, the GS groups accounted for a significant ($P<0.01$) proportion of clone variation for all attributes except cane yield (Table 6). However, there was also significant ($P<0.01$) variation within the GS groups. From the partitioning of sums of squares, the majority of the variation for the attributes was observed to be within the GS groups. Since the partitioning of variation was similar for the grouping of both parents and offspring on GS score, they were considered together. There were definite trends in the expression of the seven attributes with increasing GS (Fig. 1).

Germ plasm group 1 expressed the highest tonnes of cane per hectare (Fig. 1a), stalk number (Fig. 1d), fibre percentage (Fig. 1f) and ash percentage (Fig. 1g). These attributes decreased with an increase in the minimum generations to a *S. spontaneum* clone. The opposite of this was observed for commercial cane sugar (Fig. 1b), tonnes of sugar per hectare (Fig. 1c) and stalk weight (Fig. 1e).

*Selection history groups*

When the parents and offspring were considered separately, the SH groups accounted for a significant

**Table 6.** Clonal main-effect variance partitioned according to parents versus offspring (P v O) and among (Amg) and within (W/n) germ plasm (GS) and selection history (SH) groups for seven attributes – cane yield (TCH), commercial cane sugar (CCS), sugar yield (TSH), stalk number (SNO), stalk weight (SWT), fibre percentage (FIB) and ash percentage of juice (ASH)–measured on 256 sugarcane clones tested in six environments

| Partition variation measure[a] | *df* | Attribute | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | TCH (t ha$^{-1}$) | | CCS(%) | | TSH (t ha$^{-1}$) | | SNO (number stool$^{-1}$) | | SWT (kg) | | FIB (%) | | ASH (%) | |
| | | SS% | MS | SS% | MS | SS% | MS | SS% | MS | SS% | MS | SS% | MS | SS% | MS |
| CLONES | 255 | 100 | 4878.83** | 100 | 50.76** | 100 | 111.36** | 100 | 36.34** | 100 | 0.842** | 100 | 65.60** | 100 | 0.036** |
| P v O | 1 | 1 | 9892.70 | 4 | 498.22** | 3 | 935.66** | 0 | 34.52 | 6 | 13.657** | 0 | 22.97** | 0 | 0.018** |
| W/n P and O groups | 254 | 99 | 4859.10** | 96 | 49.00** | 97 | 108.11** | 100 | 36.35** | 94 | 0.791** | 100 | 65.77** | 100 | 0.036** |
| Offspring | 191 | 100 | 5658.55** | 100 | 42.93** | 100 | 114.83** | 100 | 32.34** | 100 | 0.760** | 100 | 65.74** | 100 | 0.031** |
| Partitions of the offspring population | | | | | | | | | | | | | | | |
| Amg GS groups | 3 | 0 | 666.40 | 6 | 823.15** | 6 | 437.93** | 9 | 183.42** | 9 | 4.470** | 7 | 302.90** | 15 | 0.286** |
| W/n GS groups | 188 | 100 | 5738.21** | 94 | 29.52** | 94 | 109.67** | 91 | 29.93** | 91 | 0.701** | 93 | 61.95** | 85 | 0.027** |
| Amg SH groups | 3 | 1 | 3881.59 | 18 | 502.23** | 4 | 277.87** | 6 | 139.43** | 7 | 3.201** | 4 | 179.25** | 10 | 0.198** |
| W/n SH groups | 188 | 99 | 5686.91** | 82 | 35.58** | 86 | 112.23** | 94 | 30.63** | 93 | 0.720** | 96 | 63.92* | 90 | 0.028** |
| Parents | 63 | 100 | 4687.5** | 100 | 129.82** | 100 | 178.88** | 100 | 83.17** | 100 | 1.754** | 100 | 132.23** | 100 | 0.103** |
| Partition of the parent population | | | | | | | | | | | | | | | |
| Amg GS groups | 4 | 3 | 2029.97 | 63 | 1290.25** | 29 | 805.63** | 41 | 530.11** | 37 | 10.191** | 32 | 660.90** | 39 | 0.634** |
| W/n GS groups | 59 | 97 | 4868.37** | 47 | 51.15** | 71 | 136.39** | 59 | 52.87** | 63 | 1.182** | 68 | 96.38** | 61 | 0.067** |
| Amg SH groups | 8 | 26 | 9542.11* | 79 | 811.39** | 51 | 718.30** | 51 | 331.77** | 51 | 7.035** | 32 | 430.09** | 57 | 0.466** |
| W/n SH groups | 55 | 74 | 3981.49** | 21 | 30.68** | 49 | 100.42** | 49 | 47.01** | 49 | 0.985** | 58 | 88.90** | 43 | 0.051** |

** and * denotes significance at 1% and 5% probability levels, respectively

[a] SS% denotes the percentage of the clone main-effect sum of squares accounted for by each partition and MS is the mean squares for the partition

**Table 7.** Mean values of seven attributes – cane yield (TCH), commercial cane sugar (CCS), sugar yield (TSH), stalk number (SNO), stalk weight (SWT), fibre percentage (FIB) and ash percentage of juice (ASH) – measured separately on parents and offspring in six environments

| Attributes | Generation | |
|---|---|---|
| | Parents | Offspring |
| TCH (t ha$^{-1}$) | 76.64 | 72.49 |
| CCS (%) | 13.53 | 12.60 |
| TSH (t ha$^{-1}$) | 10.36 | 9.08 |
| SNO (number stool$^{-1}$) | 5.25 | 5.50 |
| SWT (kg) | 1.097 | 0.943 |
| FIB (%) | 14.76 | 14.99 |
| ASH (%) | 0.2742 | 0.2814 |

($P < 0.05$) proportion of the variation among clones for all attributes except cane yield of the offspring (Table 6). There was significant ($P < 0.01$) variation within both the parent and offspring groups for all attributes. For the offspring there was a greater percentage of the clone sum of squares within the offspring groups than among the groups. This contrasted with the parents, where a large percentage of the sum of squares was among the selection history groups for all attributes except tonnes of canes per hectare and fibre %. This suggests that the selection history groups (Table 3) defined for the parents strongly reflected variation for commercial cane attributes that have been under strong selection pressure. The high within-group sum of squares for the offspring may have been a consequence of random pairing of the parents that may have mixed up many of the genetic complements developed by the selection to produce the parents.

### *Three-way, three-mode classification*

Classification of the clones was truncated at the five group level. The patterns of performance for the five groups of clones over the six environments emphasized the strong influence of clone main-effect variation relative to C × E interaction for each attribute (Fig. 2). Inspection of the group performance plots for each attribute suggested that there were strong inter-relations between the attributes among the groups. Group 1 expressed consistently low values for tonnes of canes per hectare, tonnes of sugar per hectare, stalk number, stalk weight and fibre. This group contrasted markedly with the other four for tonnes of canes per hectare. Group 2 expressed the highest values for stalk number, fibre and ash, whereas it showed the lowest value for commercial cane sugar; group 3 had high values for commercial cane sugar, tonnes of sugar per hectare and stalk number; group 4 had the highest value for com-

**Table 8.** Clone and C × E interaction components of variance for the parent and offspring generations for seven attributes – cane yield (TCH), commercial cane sugar (CCS), sugar yield (TSH), stalk number (SNO), stalk weight (SWT), fibre percentage (FIB) and ash percentage of juice (ASH) – measured on 256 sugarcane clones tested in six environments

| Component of variance | Attribute | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | TCH (t ha$^{-1}$) | | CCS (%) | | TSH (t ha$^{-1}$) | | SNO (number stool$^{-1}$) | | SWT (kg) | | FIB (%) | | ASH (%) | |
| | Parent | Offspring | Parent | Offspring | Parent | Offspring | Parent | Offspring | Parent | Offspring | Parent | Offspring | Parent | Offspring |
| Clone | 155.76 (34.88)[b] | 406.80 (48.38) | 5.15 (0.95) | 3.20 (0.37) | 6.46 (1.32) | 8.15 (0.98) | 3.32 (0.61) | 2.45 (0.28) | 0.069 (0.013) | 0.059 (0.007) | 5.24 (0.97) | 5.17 (0.56) | 0.0041 (0.0008) | 0.0023 (0.0003) |
| C × E | 49.37 (21.63) | 77.95 (17.27) | 0.77 (0.11) | 0.77 (0.12) | 1.44 (0.49) | 1.53 (0.39) | 0.20 (0.07) | 0.25 (0.07) | 0.017 (0.002) | 0.008 (0.001) | 1.06 (0.13) | 0.48 (0.11) | 0.0007 (0.0001) | 0.0005 (0.0001) |
| (CE/C)%[a] | 32 | 19 | 15 | 24 | 22 | 19 | 6 | 10 | 24 | 13 | 20 | 9 | 17 | 22 |

[a] (CE/C) % gives the size of the C × E interaction variance component as a percentage of the clone variance component

[b] Standard errors of the variance components are in parentheses

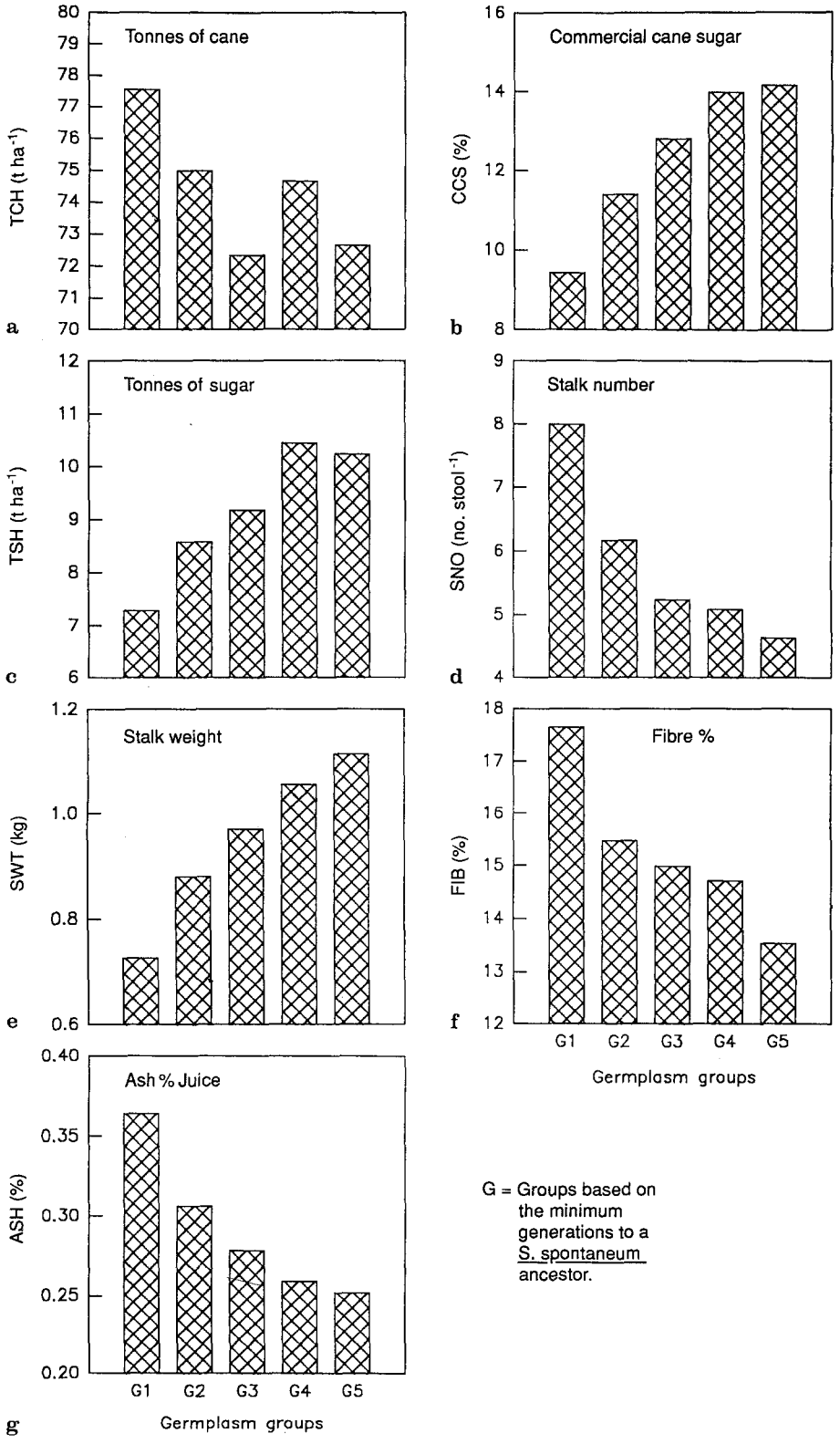


**Fig. 1a–g.** Germ plasm groups for seven attributes measured on 256 clones in six environments

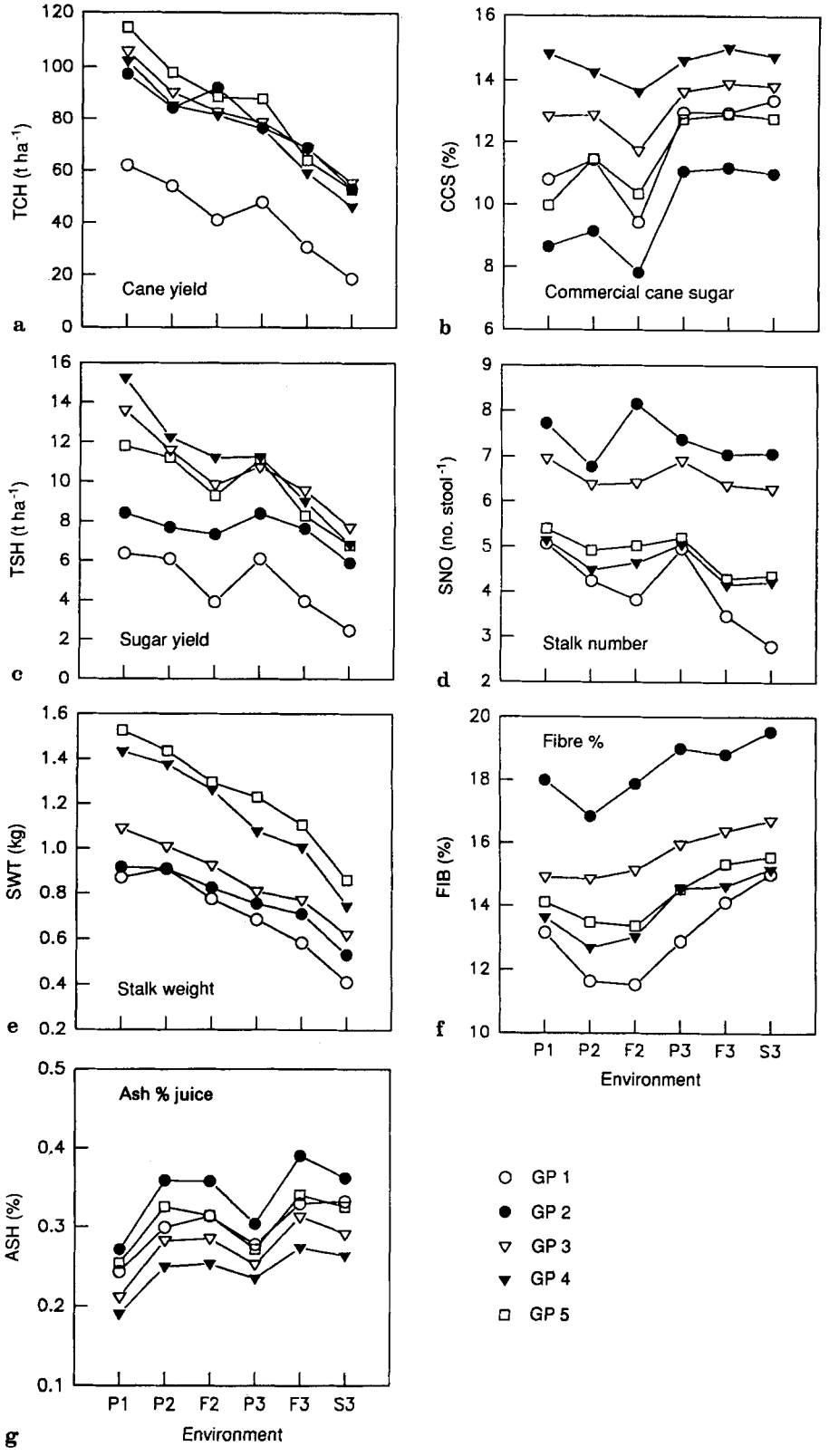


**Fig. 2a–g.** Clone group (GP) patterns of performance for seven attributes, at the five group truncation level, identified by the mixture method of classification on seven attributes measured in six environments

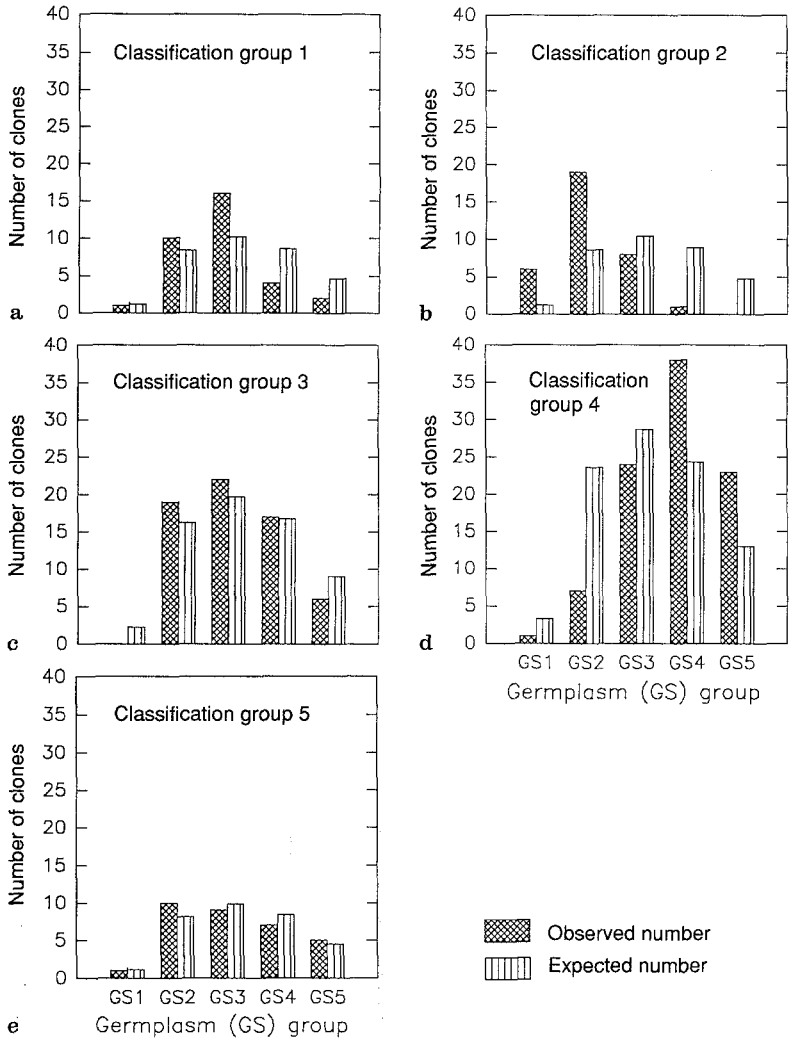


**Fig. 3a–e.** Observed and expected clone numbers for the distribution of germ plasm groups among each of the five intrinsic groups, identified by the mixture method of classification

mercial cane sugar, expressed high values for tonnes of sugar per hectare and stalk weight and had low values for stalk number, fibre and ash; group 5 had the highest value for stalk weight, had a high value for tonnes of sugar per hectare and low to intermediate values for commercial cane sugar, stalk number, fibre and ash.

### *Comparision of the intrinsic and extrinsic classifications*

The chi-square values for the contingency table comparison between the intrinsic classification groups and the extrinsic selection history (SH) and pedigree (GS) groups were highly significant ($P < 0.01$) in each case. Therefore, clones with similar germ plasm scores and selection history tended to group together in the intrinsic classification. The observed and expected numbers of each germ plasm (Fig. 3) and selection history (Figs. 4, 5) groups were compared for each of the five groups derived by the intrinsic classification. Since the selection history scores differed for parents and progeny (Table 3) the two groups were considered separately.

From the intrinsic classification group 2 had a higher than expected frequency of clones with a low germ plasm score (GS1, GS2) (Fig. 3), which indicated that this group consisted of clones with a strong influence of *S. spontaneum*. This corresponded with the expression of low values for commercial cane sugar and stalk weight and high values for stalk number, fibre and ash (Fig. 2), characteristics to be expected when there is a strong influence of *S. spontaneum*. In contrast, group 4 had a higher than expected frequency of clones with high germ plasm score (GS4 and GS5, Fig. 3). This corresponded with high values for tonnes of sugar per hectare, commercial cane sugar and stalk weight and low values for stalk number, fibre and ash (Fig. 2). These are the characteristics expected for clones with a reduced influence of *S. spontaneum*.

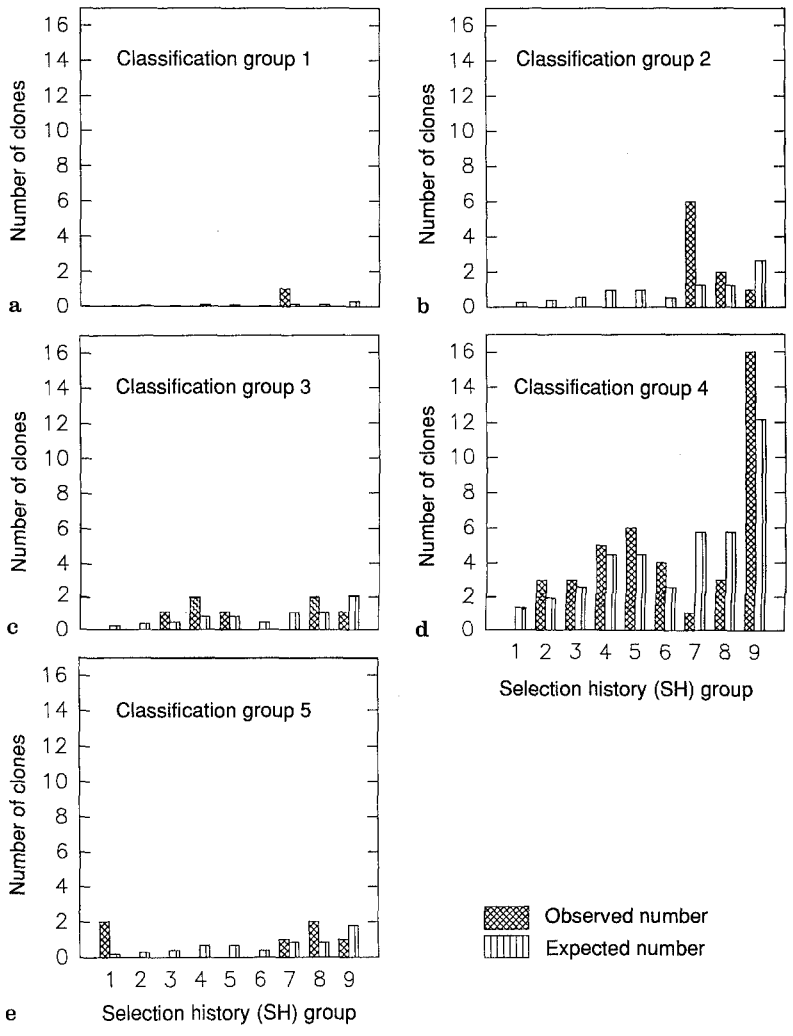


**Fig. 4a–e.** Observed and expected number of parental clones for the distribution of selection history groups among each of the five intrinsic groups, identified by mixture method of classification

The intrinsic classification partitioned the majority of the parents into the largest group, group 4 (Fig. 4). All the selection history categories except SH1 were represented in this group. Generally, there was a higher than expected frequency of selected parents and a lower than expected frequency of first and second cross interspecies hybrids (SH7 and SH8, Table 3). In contrast to group 4, in group 2 there was a higher than expected frequency of first and second cross interspecies hybrids and a lower than expected frequency of the other selection history groups. This corresponded with the expected influence of *S. spontaneum* from the distribution of the germ plasm score groups (Fig. 3) and the patterns of performance for the attributes (Fig. 2).

While there were only four selection history groups for the offspring (Table 3), they were partitioned among all five groups identified by the intrinsic classification (Fig. 5). There were deviations from the expected numbers in the selection history groups among the five groups. For group 2, there was a greater than expected frequency of the SH1 offspring, which were crosses between locally selected clones. This corresponded with a greater influence of *S. spontaneum* (Fig. 3) and a distinct set of patterns of performance for the seven attributes (Fig. 2). In group 4, there was a lower frequency of offspring from the locally selected clones (SH1) and a higher than expected frequency of offspring from parents that included at least 1 imported clone (Fig. 5).

## Discussion

There was significant ($P < 0.01$) variation among clones for the seven attributes measured. While significant C × E interaction was expressed for all of the attributes, this component of variation was generally smaller than main-effect variation among clones. Ramdoyal (1986),

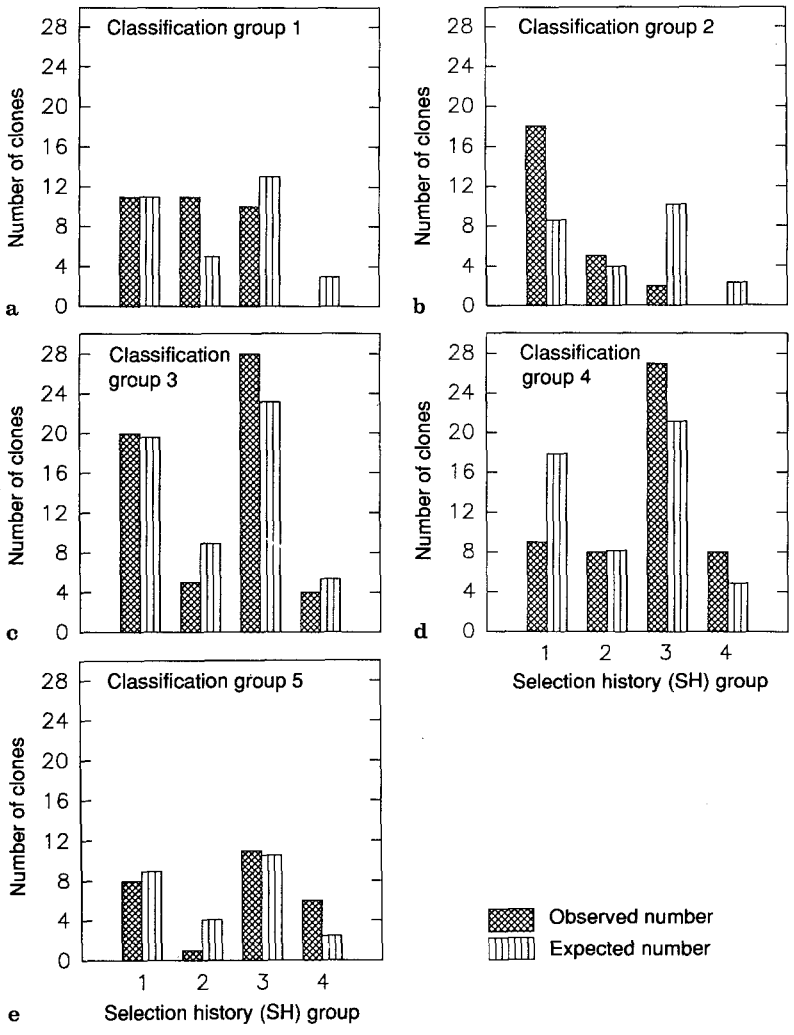


**Fig. 5a–e.** Observed and expected number of offspring clones for the distribution of selection history groups among each of five intrinsic groups, identified by mixture method of classification

Tai and Miller (1986) and Bull and Hogarth (1990) reported C × E interaction of a sufficient size to affect selection in sugarcane. The higher values of C × E interaction relative to main-effect variation among clones that has been reported in other studies may have been because more highly selected clones were used (Tai et al. 1982). The smaller values for C × E interaction in this study may also be in part due to our sampling a less diverse set of environments. However, the 3 years sampled were considered to be diverse.

The germ plasm groups based on the minimum generations back to a *S. spontaneum* clone accounted for a significant ($P < 0.01$) component of the clone variation for all attributes except tonnes of canes per hectare. The larger effect of *S. spontaneum* on commercial cane sugar, stalk weight and stalk number other than on tonnes of canes is in agreement with the observations of Roach (1986) regarding the contrasting expression of these attributes in the progenitor species. Therefore, differences among the clones in the contribution of *S. spontaneum* to their lineage was apparently influential upon variation for all characters except tonnes of canes per hectare. This finding should have broad applicability to sugarcane since the population studied included selected clones as well as clones derived from recent attempts to broaden the genetic base of sugarcane through hybridization involving *S. spontaneum*. In addition, there was a mixture of selected and non-selected germ plasm: the parents were the product of selection while the offspring were not.

There was a strong association between the level of expression of all characters and the minimum number of generations back to *S. spontaneum* in the pedigree of the clones. As the number of generations increased there was a reduction in tonnes of canes per hectare, stalk number, fibre and ash % and a complementary increase in commercial cane sugar, tonnes of canes per hectare, tonnes of sugar per hectare and stalk weight

(Fig. 2). Similar observations regarding changes in the means for yield components of cane and juice quality have been reported by Mullins and Roach (1985).

For the selection history groups, there was a higher proportion of the clone sum of squares among the groups for the parents than among those for the offspring. This may be attributed to the fact that the clonal selection which went into developing the parents for a range of different environments started from different gene pools. The production of the offspring in this study involved mixing the products of these different selection programmes. Partitioning of variation within the population for the seven attributes on the basis of selection history and minimum generations to *S. spontaneum* indicated that these criteria accounted for a major proportion of the clonal variation for most of the attributes.

Intrinsic classification of the 256 clones into five groups on the variation for the seven attributes measured in six environments identified groups of clones that differed markedly in the expression of the seven attributes. These clonal groups were associated with clonal differences in selection history and the minimum number of generations back to the *S. spontaneum* clone. Group 2, for example, possessed clones that demonstrated a stronger influence of *S. spontaneum*, and the expression of the attributes for this group reflected the influence of the *S. spontaneum* germ plasm. Therefore, the results of the intrinsic three-way classification provided an extremely effective summary of the results of the clonal evaluation. The five clonal groups highlight the major differences in patterns of performance for the seven attributes. Interpretation of these groups in terms of the extrinsic information on selection history and contribution of *S. spontaneum* provided a quantification of the influence of these pedigree characteristics on the variation in adaptation of the clones for these attributes.

The intrinsic and extrinsic classification both indicate that selection history and the contribution of *S. spontaneum* to the clone's pedigree influence adaptation for sugar yield and its components. This supports the comments of Roach (1989) that the number of nobilizing generations a clone has gone through is influential on its adaptation. He argued that clones which had undergone less nobilization would be more suitable for harsher subtropical environments. Accessing new sources of germ plasm which would improve the adaptation of a crop is critical to the long-term success of any breeding programme. The influence of *S. spontaneum* on the adaptation of sugarcane clones suggests that the wider use of this source of the germ plasm is worth investigation. The introduction of genetic variation through a new cycle of nobilization using diverse clones of *S. officinarum* and *S. spontaneum* and other wild species should be considered to be a component of any attempt to broaden the genetic base of sugarcane breeding programmes. In addition, an enhanced understanding of the influences of both sources of germ plasm from *S. spontaneum* and other wild relatives and selection history on the relationships between sugar yield and quality attributes in breeding populations would assist in directing the process of introgression of new germ plasm from wild relatives into current breeding populations.

*Acknowledgements.* The authors thankfully acknowledge support from CSR Ltd. for the experimental component of this work and the Australian International Development Assistance Bureau for funding the study programme of B. L. Srivastava.

## References

Anderson RL, Bancroft TA (1952) Statistical theory in research. McGraw-Hill, New York

Arceneaux G (1965) Cultivated sugarcanes of the world and their botanical derivation. Proc Int Soc Sugar Cane Technol 12:844–854

Basford KE, McLachlan GJ (1985) The mixture method of clustering applied to three-way data. J Classif 2:109–125

Berding N, Roach T (1987) Germplasm collection, maintenance and use. In: Heinz DJ (ed) Sugarcane improvement through breeding. Elsevier Sci Publ, New York, pp 143–210

Bull JK, Hogarth DM (1990) The implications of genotype × environment interaction for evaluation of sugarcane families II. Alternative methods of analysis. In: Kang MS (ed) Genotype by environment interaction and plant breeding. Louisiana State University, Baton,Rouge La., pp 347–363

Byth DE, Eisemann RL, DeLacy IH (1976) Two-way pattern analysis of a large data set to evaluate genotypic adaptation. Heredity 37:215–230

Cooper M, DeLacy IH, Eisemann RL (1993) Recent advances in the study of genotype × environment interactions and their application to plant breeding. In: Imrie BC, Hacker JB (eds) Focused plant improvement: towards responsible and sustainable agriculture. (Proc 10th Aust Plant Breed Conf.) Organising Committee, Canberra, pp 116–131

DeLacy IH, Cooper M (1990) Pattern analysis for the analysis of regional variety trials. In: Kang MS (ed) Genotype by environment interaction and plant breeding. Louisiana State University, Baton Rouge, La., pp 301–333

Eisenhart C (1947) The assumptions underlying the analysis of variance. Biometrics 3:1–37

Ethirajan AS, Natrajan BV, Nagrajan R (1982) Parental diversification for improved sugarcane varietal production. Maharastra Sugar 75:9–12

Fox PN, Skovmand B, Thompson BK, Braun HJ, Cormier R (1990) Yield and adaptation of hexaploid spring triticale. Euphytica 47:57–64

Hayward MD, DeLacy IH, Tyler BF, Drake DW (1982) The application of pattern analysis for the recognition of adaptation in a collection of *Lolium multiflorium* populations. Euphytica 31:383–396

Hogarth DM (1971) Quantitative inheritance studies in sugarcane. I. Estimation of variance components. Aust J Agric Res 27:93–102

Hogarth DM, Bull JK (1990) The implications of genotype × environment interactions for evaluation of sugarcane families I. Effect on selection. In: Kang MS (ed) Genotype × environment interaction and plant breeding. Louisiana State University, Baton Rouge, La., pp 335–346

Hogarth DM, Wu KK, Heinz DJ (1981) Estimating genetic variance in sugarcane using a factorial cross design. Crop Sci 21:21–25

Jackson PA, Hogarth DM (1992) Genotype × environment interactions in sugarcane. I. Pattern of response across sites and crop years in north Queensland. Aust J Agric Res 43:1447–60

Kearsey MJ (1965) Biometrical analysis of a random mating populations, a comparison of five experimental designs. Heredity 20:205–235

Mullins RT, Roach BT (1985) Genetic origins of ash in sugarcane juice. In: Egan BT (ed) Proc Aust Soc Sugarcane Technol. Australian Society of Sugar Cane Technologists, Queensland, pp 43–51

Price S (1963) Cytological studies in *Saccharum* and allied genera. VIII. $F_2$ and $BC_1$ progenies from 112 and 136 chromosome *S. officinarum* and *S. spontaneum* hybrids. Bot Gaz 125:186–190

Price S (1965) Interspecific hybridisation in sugarcane breeding. Proc Int Soc Sugar Cane Technol 12:1021–1026

Ramdoyal K, Domaingue FHF, Fong-Sam-Pin, Julien MHR (1986) Inter-relationships between different crops of a cane cycle and their impact on selection strategies in sugarcane. Proc Int Soc Sugar Cane Technol 1:447–453

Roach BT (1977) Utilization of *S. spontaneum* in sugarcane breeding. Proc Int Soc Sugar Cane Technol 1:43–57

Roach BT (1986) Evaluation and use of sugarcane germplasm. Proc Int Soc Sugar Cane Technol 1:492–503

Roach BT (1989) Origin and improvement of the genetic base of sugarcane. In: Egan BT (ed) Proc Aust Soc Sugarcane Technol. Australian Society of Sugar Cane Technologists, Queensland, pp 34–47

Roach BT, Daniels J (1987) A review of the origin and improvement of sugarcane. In: Proc Copersucar Int Sugarcane Breed Workshop. Copersucar Technol Centre, Piracicaba-SP Brazil, pp 1–31

Ruschel R (1977) Phenotypic stability of some sugarcane varieties (*Saccharum* spp.) in Brazil. Proc Int Soc Sugar Cane Technol 1:275–281

Schultz EF (1955) Rules of thumb for determining expectations of mean squares in analysis of variance. Biometrics 11: 123–135

Simmonds NW (1976) Sugarcane. In: Simmonds NW (ed) Evolution of cultivated plants. Longman, London New York, pp 104–108

Snedecor GW, Cochran WG (1980) Statistical methods, 7th edn. The Iowa State University Press, Ames

Sreenivasan TV, Ahloowalia BS, Heinz DJ (1987) Cytogenetics. In: Heinz DJ (ed) Sugarcane improvement through breeding. Elsevier Sci Publ, New York, pp 211–253

Stevenson GC (1965) Genetics and breeding of sugarcane. Longmans, London

Symington WM (1989) Commercial potential of Macknade nobilizations for yield, sugar content and stress tolerance. In: Egan BT (ed) Proc Aust Soc Sugar Cane Technol. Queensland, pp 48–53

Tai PYP, Rice ER, Chew V, Miller JD (1986) Genotype by Environment interaction for cold tolerance in sugarcane. Proc Int Soc Sugar Cane Technol 1:454–462

Tai PYP, Miller JD (1982) Phenotypic stability analysis of sugarcane cultivar performance tests. Crop Sci 22: 1179–1183

Williams WT (1976) Pattern analysis in agricultural Science. CSIRO, Elsevier, Amsterdam