Theoretical and Applied Genetics 39, 1—10 (1969)

Quantitative Genetics of Sugarcane

II. Correlation Analysis of Continuous Characters in Relation to Hybrid Sugarcane Breeding

A. H. D. BROWN[1], J. DANIELS[1] and B. D. H. LATTER[2]

Agricultural Experiment Station, South Pacific Sugar Mills Ltd., Lautoka, Fiji[1],
and Division of Plant Industry, CSIRO, Canberra[2]

Summary. 1. A study has been made of the genetic, clonal and environmental correlations existing among commercially important characters in a sugarcane breeding population of interspecific hybrid origin.

2. In general, there is a close correspondence between genetic correlation coefficients measuring the extent of association at the level of family means, and clonal correlations measuring genotypic relationships at the level of clone means. Greater weight has therefore been given to the numerical estimates of the clonal correlations, in view of their greater accuracy, and the possibility that atypical family groups may unduly influence the genetic correlations.

3. Many significant environmental correlations, generally of a low order of magnitude, have been detected. These have been found to fall naturally into a pattern based on the operation of factors causing differences from plot-to-plot in either growth rate or the process of ripening.

4. A wide variety of genetic relationships cannot be explained in terms of these same two physiological processes. The signs of the clonal correlation coefficients for these particular associations fall very clearly into a pattern identical with that distinguishing the wild species from *Saccharum officinarum*.

5. The cytological basis for this partial retention of original parent species associations is almost certainly the segregation of whole chromosomes from the wild species as intact units, with little possibility of gene exchange or recombination with chromosomes from *S. officinarum*.

6. The magnitudes of the observed clonal correlations in general indicate ample scope for independent genetic manipulation of traits from wild and noble canes, provided selection pressure is maintained on all those of commercial importance. However, the interrelationships involving number of stalks per plot, stalk cross-sectional area and fibre percent fresh weight, are somewhat more restrictive.

7. Attention is drawn to the need for a more extensive sampling of the genetic variation available within the wild species *S. spontaneum*, *S. robustum* and *S. sinense*.

1. Introduction

The theory of quantitative genetics provides the basis for an interpretation not only of analyses of variation shown by individual quantitative characters, but also of analyses of *covariance* describing the way in which a number of characters vary conjointly in a population. This information may be used in the prediction of correlated responses to directional selection, in the detection of unfavourable genetic associations existing in a given breeding population, and in the construction of selection indices (ROBINSON et al., 1951; JOHNSON et al., 1955).

It has been the practice in studies of hybrid sugarcane populations to derive only phenotypic correlation coefficients, despite the fact that these may be misleading whenever different mechanisms are operative at the genetic and environmental levels. BROWN (1965) has discussed one such example, viz. the correlation between sugar and fibre. Commercial acceptability in sugarcane is determined by a wide range of characters showing continuous variation, and it is of particular importance to the breeder that the relationships existing among these characters be well understood. This paper reports the results of such a study of the Fiji breeding population (BROWN et al., 1968), made possible by the use of high-speed computing facilities. In particular, attention is given to the origin and extent of unfavourable genetic associations existing in this typical commercial hybrid breeding population.

2. Material and Methods

The experimental material consisted of 141 hybrid sugarcane clones, each derived from crosses made as part of the normal breeding programme in Fiji. There are represented three full-sib progeny from each of 47 families, with four replicate plots per clone. The first paper of this series (BROWN et al., 1968) gives details of the origin of the clones, the experimental design, the 42 characters under study, the breeding behaviour of the population, and the heritability and repeatability estimates for individual characters. In the present paper the characters are given identical numbers and designations.

The basic analysis of covariance is comparable with the analysis of variance presented in the previous paper. Table 1 sets out the expectations of the mean products in the analysis, in terms of environmental, intra-family and inter-family components of covariance. Estimates have been derived of four distinct parameters measuring the genetic, clonal and environmental correlations, and the standardized genetic covariance (Table 2). The *genetic correlation* is derived solely from the between full-sib family

Table 1. *The analysis of covariance table*

Source of variation	d.f.	Mean product	Expectation
Sub-blocks	11		
Families	46	F	$\text{cov}_e + 4\ \text{cov}_i + 11.8\ \text{cov}_f$
Blocks × families	92	I	$\text{cov}_e + 4\ \text{cov}_i$
Residual	414	E	cov_e

components of variance and covariance, and will therefore include some contribution due to non-additive genetic effects (FALCONER, 1960). A *clonal correlation* provides a measure of the relationship between two characters in terms of their 'true' clone means, and may therefore include non-heritable effects transmitted during asexual reproduction. The *environmental correlation* reflects the influence of environmental factors on joint variation displayed within clones.

Table 2. *Parameters characterizing the relationship between variables x_1 and x_2*

Parameter	Definition	Notes
Genetic correlation	$\frac{\text{cov}_f(1,2)}{\sigma_f(1)\cdot\sigma_f(2)}$	
Clonal correlation	$\frac{\text{cov}_c(1,2)}{\sigma_c(1)\cdot\sigma_c(2)}$	$\text{cov}_c = \text{cov}_f + \text{cov}_i$ $\sigma_c^2 = \sigma_f^2 + \sigma_i^2$
Environmental correlation	$\frac{\text{cov}_e(1,2)}{\sigma_e(1)\cdot\sigma_e(2)}$	
Standardized genetic covariance	$\frac{2\ \text{cov}_f(1,2)}{\sigma_p(1)\cdot\sigma_p(2)}$	$\sigma_p^2 = \sigma_f^2 + \sigma_i^2 + \sigma_e^2$

The term *standardized genetic covariance* is used here to describe a measure of joint variation which is specifically involved in prediction formulae for correlated responses to directional selection (FALCONER, 1960). It corresponds to the expression $h_1\, r_g\, h_2$, where h_1^2, h_2^2 denote the heritabilities of two characters and r_g denotes the genetic correlation existing between them.

The standard errors of all statistics have been estimated by means of large sample formulae given by MODE and ROBINSON (1959). The accuracy of the experiment was such that a genetic correlation greater in absolute magnitude than 0.5 could be detected unless the heritability of one of the characters concerned was particularly low. Greater resolution was obtained in the estimation of clonal correlations, values of 0.30 and less frequently being judged statistically significant.

3. Results

From the matrix of possible covariance analyses, sub-sets have been chosen for detailed study because of their specific biological interest. Only a selection of the results will be presented here, dealing in turn with: (a) the effect of statistical transformations on estimates of the three types of correlation coefficient; (b) the relationships of all characters with yield and sucrose percent fresh weight, the two traits of most direct concern in the determination of commercial yield of sucrose per acre; (c) relationships with sucrose percent dry weight, a variable which provides a direct measure of the efficiency of sucrose storage; (d) important associations involving reducing sugars percent fresh weight, fibre percent fresh weight and starch; and finally (e) a discussion of analyses of some measures of within-plot variability.

Scale transformations

In the first paper of this series a table was given of those variables with distributions showing pronounced asymmetry, with details of their coefficients of variation on the scale of measurement and appropriate logarithmic transformations. Correlation analyses involving these seven variables have shown the scale transformations to have relatively unimportant effects on the numerical estimates obtained. Table 3 sets out comparisons which are typical of those observed throughout this study.

In the analyses to be presented in this paper, transformations have been used for all variables with a skewed distribution of family means, the nature of the change in scale being indicated in the Tables. Approximate normality can therefore be assumed in making predictions of direct and correlated responses to selection. In each case of scale transformation, the signs of the derived correlation coefficients are identical with those which would be obtained from the untransformed scales.

Components of sucrose per acre

The most useful overall measure of the commercial potential of a genotype is the quantity of sucrose produced per unit area. Figure 1 sets out the conventional breakdown of sucrose per acre into two components, yield of cane per acre (x_{16}) and sucrose percent fresh weight (x_{27}), and indicates those *primary* variables directly influencing the level of these two major components. It is our intention to concentrate attention initially on those characters for which measurements were taken directly in the experiment, and then to consider the derived variables calculated numerically from the primary observations. Mathematical relationships can then readily be distinguished from more fundamental associations.

The relationships involving the six primary variables in Figure 1 are set out in detail in Table 4. Before proceeding to discuss the numerical estimates, an important general point should be made here with regard to the utility of the genetic and clonal correlations. In some instances, as with stalk numbers

(x_{17}) and total sugars (x_{22}), the two correlations differ appreciably in magnitude (Table 4), and we shall in general give more weight to the measure of the clonal relationship in such cases, for two quite different reasons.

Firstly, the precision of the clonal correlations is considerably greater than that of the genetic correlations, as judged from their respective standard errors. Secondly, a genetic correlation may be unduly influenced by atypical progeny groups, being derived solely from between-family components of variance and covariance (BROWN et al., 1968). Figures 2 and 3

Table 3. *The effects of changes of scale on estimates of genetic parameters*

Variable	Scale	Correlations with Sucrose % D.W. (x_{29})†		
		Genetic	Clonal	Environmental
Mean leaf area (x_{10})	x	+.52 ± .34	+.02 ± .10	−.09 ± .05
	log x	+.54 ± .35	+.03 ± .10	−.08 ± .05
Yield grade (x_{15})	x	−.20 ± .28	−.13 ± .12	+.03 ± .05
	− log (14.5 − x)	−.23 ± .27	−.18 ± .12	+.01 ± .05
Stalks per plot (x_{17})	x	−.83* ± .22	−.49* ± .08	+.05 ± .05
	log x	−.88* ± .25	−.49* ± .08	+.07 ± .05
Reducing sugars (x_{26})	x	−.56* ± .21	−.46* ± .08	−.44* ± .04
	log (2.5 + 10 x)	−.57* ± .22	−.47* ± .08	−.41* ± .04
Starch content (x_{21})	x	−.30 ± .25	−.22* ± .10	+.00 ± .05
	log x	−.31 ± .22	−.24* ± .10	+.02 ± .05
Leafhopper count (x_5)	x	+.43 ± .27	+.21 ± .13	+.08 ± .05
	log (1.6 + x)	+.25 ± .24	+.15 ± .12	+.10 ± .05

† The transformation − log (70 − x) has been used for x_{29} whenever the covariable has been transformed.

* Significantly greater than zero in absolute value.

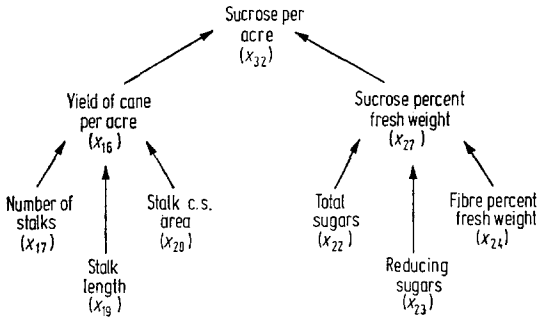


Fig. 1. Primary variables with a direct influence on yield of sucrose per acre. The primary variables in this study (x_1—x_{24}) are those actually measured, as opposed to those derived numerically (x_{25}—x_{42}). Specific gravity, the remaining major component of sucrose per acre, did not show significant genetic variation in this population

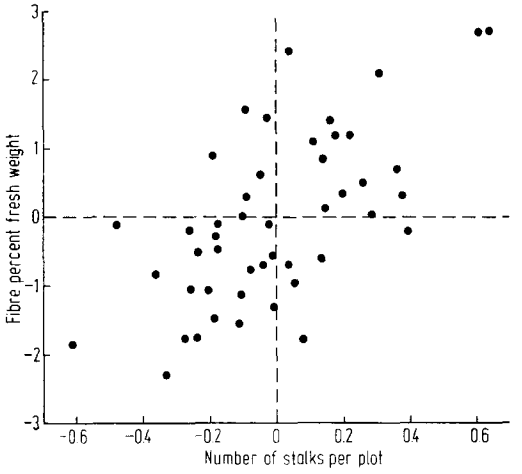
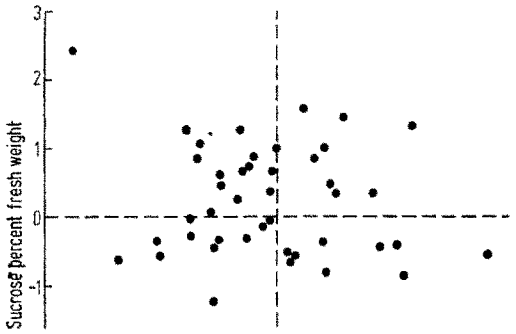


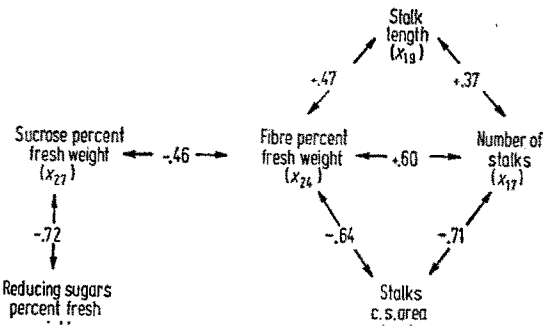
Fig. 2. Relationship between fibre percent fresh weight (x_{24}) and number of stalks per plot (x_{17}), plotted in terms of observed full-sib family means

Table 4. *Relationships among primary variables directly involved in the determination of sucrose per acre. Above diagonal: upper-genetic, lower-clonal correlations. Below diagonal: environmental correlation*

	Stalk number (x_{17}) [log x]	Stalk length (x_{19})	Stalk c.s. area (x_{20})	Total sugars % extract (x_{22})	Reducing sugars % extract (x_{23})	Fibre % fresh fresh wt. (x_{24})
Stalk number (x_{17}) [log x]		+.51 ± .27 +.37* ± .09	−.59* ± .28 −.71* ± .06	−.79* ± .34 −.21 ± .11	+.43 ± .38 +.13 ± .10	+.90* ± .22 +.60* ± .07
Stalk length (x_{19})	+.39* ± .04		−.29 ± .31 −.17 ± .10	−.16 ± .25 −.06 ± .11	+.12 ± .28 +.02 ± .11	+.40 ± .24 +.47* ± .08
Stalk c.s. area (x_{20})	−.02 ± .05	+.25* ± .05		+.52 ± .31 +.17 ± .10	−.03 ± .37 +.03 ± .10	−.93* ± .19 −.64* ± .06
Total sugars % extract (x_{22})	+.21* ± .05	+.21* ± .05	+.07 ± .05		−.59* ± .20 −.54* ± .08	−.80* ± .20 −.49* ± .08
Reducing sugars % extract (x_{23})	−.02 ± .05	+.02 ± .05	+.00 ± .05	−.40* ± .04		+.21 ± .34 +.02 ± .10
Fibre % fresh wt. (x_{24})	+.17* ± .05	+.15* ± .05	−.04 ± .05	+.20* ± .05	−.31* ± .04	

* Significantly greater than zero in absolute value.





given that stalk number and stalk length are the important components of yield. It appears that ample opportunity exists for genetic improvement in yielding ability while maintaining fibre at a commercially acceptable level. The *partial* clonal correlation between sucrose percent fresh weight (x_{27}) and yield (x_{16}), with fibre level held constant, can be calculated to be essentially zero (−.004).

Of the derived variables (x_{25}—x_{42}), dry matter per plot (x_{33}), juice per plot (x_{34}) and volume of cane per plot (x_{35}) can be seen from Table 6 to be virtually identical with yield itself (x_{16}). The variables x_{33} and x_{34} both involve x_{16} in their derivation (cf. Table 3 of Brown et al., 1968), and variables showing positive clonal correlations with yield, viz. dry matter percent fresh weight (x_{31}) and fibre percent fresh weight (x_{24}), are also involved.

The indices of leaf area per plot (x_{41}) and leaf weight per plot (x_{42}) are also closely correlated with yield (Table 6), due primarily to the fact that stalk number (x_{17}) is involved in the derivation of both variables. It is this component which has the highest coefficient of variation (Brown et al., 1968). Of the other variables concerned, viz. x_{13}, x_{14}, x_{18} and x_7, leaf weight (x_7) and leaf length (x_{14}) can be seen from Table 6 to be positively correlated with yield, the clonal correlations being +.29 and +.24 respectively.

Characters related to sucrose content

Tables 7 and 8 set out the significant clonal relationships involving sucrose percent fresh weight (x_{27}) and sucrose percent dry matter (x_{29}) respectively. Of the associations involving sucrose percent fresh weight, that with stalk number has previously been discussed (Figures 3, 4), and the correlations with reducing sugars (x_{26}) and fibre (x_{24}) have been presented in Figure 4.

The observed relationship between sucrose and total sugars, both expressed on a fresh weight basis (x_{27}, x_{25}), can be seen from Table 7 to be extremely close. In view of the fact that total sugars and reducing sugars are genetically *negatively* correlated (Table 4), selection on the basis of total sugars can be expected to achieve the breeder's objectives of increasing sucrose and decreasing reducing sugar

that a positive environmental correlation exists between sucrose percent *dry* weight (x_{29}) and dry matter percent fresh weight (x_{31}), though it is of a very low order. The clonal correlation in this case is of *opposite* sign to the environmental correlation and it is pertinent to discuss the probable nature of the genetic and environmental variation involved in this and similar instances.

From the environmental correlations presented in Tables 4, 6, 7 and 8, and others calculated in the course of this study, it is apparent that environmental conditions favouring *increased yield of cane* (x_{16}) are responsible for increases in stalk number (x_4, x_6, x_{17}), stalk length (x_{19}) and stalk cross-sectional area (x_{20}). Node length (x_{39}) also tends to be increased, as does leaf weight (x_7) and leaf width (x_{13}). In this 9 months old crop such conditions led to higher values of total dry matter percent fresh weight, due to increases in both sucrose percent fresh weight (x_{27}) and fibre percent fresh weight (x_{24}). Sucrose percent *dry* weight (x_{29}) and reducing sugars percent fresh weight (x_{26}) appear not to be affected.

On the other hand, environmental conditions favouring *increased sucrose percent dry weight* (Table 8) lead to an *increase* in dry matter percent fresh weight (x_{31}) which is associated with *decreases* in fibre percent fresh weight (x_{24}) and in reducing sugars percent fresh weight (x_{26}). These particular relationships are those to be expected from plot-to-plot variation in environmental factors affecting the process of *ripening*, which involves the cessation of growth and subsequent channelling of assimilates into sucrose storage (Hatch and Glasziou, 1963).

It therefore appears that the observed environmental correlations can be accounted for satisfactorily in terms of factors influencing either growth rate or the process of ripening. However, many of the *genetic* relationships obviously cannot be explained in terms of corresponding genotypic effects on these two basic processes. Conspicuous examples are:

(i) the negative clonal correlation (−.64 ± .06) between fibre percent fresh weight (x_{24}) and stalk cross-sectional area (x_{20}) with no detectable environmental correlation (Table 4);

(ii) the negative genetic relationship between stalk

Table 7. *Characters showing statistically significant clonal correlations with sucrose % fresh weight (x_{27})*

No.	Character	Correlations with sucrose % fresh wt.		
		Genetic	Clonal	Environmental
x_4	Stalks per plot: [log x]	−.84* ± .29	−.25* ± .11	−.03 ± .05
x_{17}	Stalks per plot: [log x]	−.78* ± .33	−.23* ± .10	+.19* ± .05
x_{22}	Total sugars % extract	+.99* ± .01	+.98* ± .01	+.98* ± .01
x_{23}	Reducing sugars % extract	−.69* ± .16	−.67* ± .06	−.56* ± .03
x_{24}	Fibre % fresh wt.	−.76* ± .21	−.46* ± .08	+.22* ± .05
x_{25}	Total sugars % fresh wt.	+.99* ± .01	+.98* ± .01	+.98* ± .01
x_{26}	Reducing sugars % fresh wt. [log x]	−.78* ± .14	−.72* ± .06	−.56* ± .03
x_{28}	Sucrose % juice	+.99* ± .01	+.98* ± .01	+.99* ± .01
x_{29}	Sucrose % dry wt.: [− log (70 − x)]	+.94* ± .05	+.85* ± .03	+.79* ± .02
x_{30}	Sucrose % total sugars; [− log (100 − x)]	+.88* ± .08	+.83* ± .04	+.71* ± .02
x_{31}	Dry matter % fresh wt.	+.22 ± .41	+.24* ± .10	+.79* ± .02
x_{42}	Leaf weight per plot	−.40 ± .26	−.24* ± .11	+.20* ± .05

* Significantly greater than zero in absolute value.

Table 8. *Characters showing statistically significant clonal correlations with sucrose % dry weight (x_{29})*

No.	Character	Correlations with sucrose % dry wt.		
		Genetic	Clonal	Environmental
x_4	Stalks per plot: [log x]	−.82* ± .25	−.38* ± .09	−.04 ± .05
x_8	Leaf moisture	+.84* ± .38	+.36* ± .09	+.02 ± .05
x_{11}	Leaf potassium % dry wt.	+.62* ± .22	+.28* ± .10	+.08 ± .05
x_{12}	Early yield grade (ratoons)	−.38 ± .23	−.29* ± .11	+.08 ± .05
x_{14}	Leaf length	†	−.28* ± .09	−.10 ± .05
x_{16}	Yield per plot	−.54* ± .23	−.40* ± .09	+.05 ± .05
x_{17}	Stalks per plot: [log x]	−.88* ± .25	−.49* ± .08	+.07 ± .05
x_{19}	Stalk length	−.31 ± .23	−.33* ± .10	+.07 ± .05
x_{20}	Stalk cross-sectional area	+.74* ± .23	+.46* ± .08	+.08 ± .05
x_{21}	Starch: [log x]	−.31 ± .22	−.24* ± .10	+.02 ± .05
x_{22}	Total sugars % extract	+.95* ± .05	+.85* ± .03	+.76* ± .02
x_{23}	Reducing sugars % extract	−.47* ± .23	−.45* ± .08	−.41* ± .04
x_{24}	Fibre % fresh wt.	−.95* ± .08	−.82* ± .03	−.36* ± .04
x_{25}	Total sugars % fresh wt.	+.96* ± .04	+.87* ± .03	+.78* ± .02
x_{26}	Reducing sugars % fresh wt.: [log x]	−.60* ± .22	−.48* ± .08	−.40* ± .04
x_{27}	Sucrose % fresh wt.	+.94* ± .05	+.85* ± .03	+.79* ± .02
x_{28}	Sucrose % juice	+.88* ± .09	+.75* ± .05	+.71* ± .02
x_{30}	Sucrose % total sugars: [− log (100 − x)]	+.72* ± .16	+.60* ± .07	+.52* ± .04
x_{31}	Dry matter % fresh wt.	−.15 ± .43	−.27* ± .10	+.28* ± .05
x_{33}	Dry matter plot per	−.54* ± .24	−.42* ± .09	+.09 ± .05
x_{34}	Juice per plot	−.49* ± .24	−.36* ± .10	+.07 ± .05
x_{35}	Volume of cane per plot	−.49* ± .25	−.35* ± .10	+.07 ± .05
x_{36}	Specific gravity	†	−.46* ± .19	−.08 ± .05
x_{38}	Mean node volume	+.31 ± .36	+.23* ± .09	+.07 ± .05
x_{39}	Mean node length	−.50* ± .18	−.40* ± .09	+.01 ± .05
x_{41}	Leaf area per plot: [log x]	−.54 ± .31	−.43* ± .09	+.06 ± .05
x_{42}	Leaf weight per plot	−.39 ± .24	−.42* ± .09	+.10 ± .05

* Significantly greater than zero in absolute value.
† No estimate possible because of negative or near-zero variance component between families.

(x_{14}), yield (x_{16}), stalk length (x_{19}), stalk cross-sectional area (x_{20}) and starch (x_{21});

(v) the clonal correlation between dry matter percent fresh weight (x_{31}) and sucrose percent dry weight (x_{29}) is negative (−.27) whereas the corresponding environmental correlation is positive (+.28), as previously noted (Table 8).

Almost all these genetic relationships are in accord with the character patterns responsible for the contrast between wild and "noble" canes. By compari-

son with the noble canes, the wild species typically produce many thin stalks of high fibre content per unit land area, with leaves of low moisture content. They are of high yield in terms of cane per unit area, but their sucrose content is low and starch content frequently relatively high. The cytological basis for a partial retention of these parental character associations is well understood, and will be discussed in the final section of this paper.

Note in particular the contrast between sucrose expressed on a fresh weight basis (Table 7) and on a dry weight basis (Table 8), in the detection of genetic relationships. Sucrose percent dry weight (x_{29}) appears to be the more valuable character for this purpose, and is much less affected by the factors responsible for environmental correlations between characters, apart from those influencing sucrose storage.

An unexpected genetic association with sucrose percent dry weight is that of leaf potassium level (x_{11}), expressed on a dry weight basis (Table 8). It is possible that this is simply a chance result, the estimates of genetic and clonal correlations being roughly three times their respective standard errors. However, it is well known that K^+ or other univalent cations are required as cofactors for a wide variety of enzymes, catalyzing apparently unrelated chemical reactions (Evans and Sorger, 1966). Though there is no evidence of potash deficiency in this experiment (the clone means ranging from 1.35 to 1.89%), it is possible that the ability of some genotypes to achieve high levels of sucrose storage may be dependent on above-average concentrations of K^+.

Characters associated with reducing sugars, fibre or starch

The level of reducing sugars percent fresh weight (x_{26}) has been shown to be inversely related to that of sucrose percent fresh weight (x_{27}), due to both genetic and environmental effects (Table 7, Figure 4). The only other genetic associations involving reducing sugar level detected in this study were those reflecting this same phenomenon. The clonal correlation between reducing sugars percent fresh weight and dry matter percent fresh weight (x_{31}) is only $-.44 \pm .09$, because of the non-significant clonal correlation between reducing sugars and fibre (Table 4).

Many of the important associations involving fibre percent fresh weight (x_{24}) have already been discussed (Tables 4, 6, 7, 8). As might be anticipated, leaf moisture (x_8) is negatively correlated with fibre, the clonal correlation being $-.53 \pm .07$, and the environmental correlation $-.10 \pm .05$. Leaf potassium (x_{11}) also shows a significant clonal correlation of $-.37 \pm .10$ with fibre. Three further clonal correlations are of particular interest from the point of view of original parental species associations. Leaf width is negatively correlated with fibre, leaf length positively correlated, and stalk weight also negatively correlated, the clonal correlation coefficients being $-.23 \pm .09$, $+.29 \pm .09$ and $-.26 \pm .09$ respectively. Here again the genetic relationships can be seen to be of a very low order, but the signs of the correlations are those to be anticipated from residual parental associations.

The significant clonal correlations shown by starch (x_{21}) are of interest from the same point of view. In order of absolute magnitude the clonal correlations are $+.43 \pm .09$ with stalk number (x_{17}); $+.35 \pm .10$ with yield (x_{16}); $+.32 \pm .09$ with fibre percent fresh weight (x_{24}); $+.27 \pm .10$ with dry matter percent fresh weight (x_{31}); $-.24 \pm .10$ with sucrose percent dry matter (x_{29}); $-.23 \pm .10$ with leaf moisture (x_8); $-.21 \pm .10$ with leaf width (x_{13}); $+.21 \pm .09$ with leaf length (x_{14}); and $-.20 \pm .10$ with stalk weight (x_{37}). Again these relationships are all of a low order, but the sign of each is consistent with the view that genes from the wild species are primarily responsible for high starch levels.

Measures of within-plot variability

In the first paper of this series, it was pointed out that measures of within-plot variability may themselves be considered as variables which might show significant genotypic variation, and which might also possibly be genetically related to other characters involved in the study. It was shown that within-plot variability in nodes per stalk, stalk length and stalk cross-sectional area was under genotypic control, and these variables were therefore included in the present correlation analysis.

In each case the measure of within-plot variability proved to be genetically related to the corresponding plot mean value, the clonal correlations between plot mean and variance being $+1.04 \pm .11$, $+.73 \pm .21$, and $+.92 \pm .05$ respectively for nodes per stalk, stalk length and stalk cross-sectional area. Little additional genetic information could therefore be expected from the variability measures. The corresponding environmental correlations, after allowing for independent sampling variation in both the means and the plot variances, were $+.29 \pm .05$, $+.21 \pm .05$, and $+.51 \pm .05$. These correlations are directly related to the skewness of the overall distribution of plot mean values, positive skewness being obvious to the eye only in the case of cross-sectional area (Brown et al., 1968). It is of some interest from a statistical point of view to see that a close genotypic relationship may exist between mean and variability, which may not readily be detected from the shape of the frequency distribution of the plot mean values.

4. Discussion

The environmental and genetic relationships emerging from this study can be understood on the basis of three main generalizations.

1. The many significant *environmental* correlations can be accounted for satisfactorily in terms of factors influencing either *growth rate* or the process of *ripening*. The various relationships fall into a consistent pattern if one considers environmental conditions favouring increased yield of cane on the one hand, and those favouring increased sucrose percent dry matter on the other, as representative of effects on these two basic physiological processes.

2. Many of the *genetic* relationships cannot be explained in terms of the same two basic processes. The clonal correlation coefficients observed in these instances are, with two exceptions, of a low order of magnitude (less than 0.5 in absolute value), and the signs of the clonal correlations fall very clearly into a pattern indicating partial preservation of *original parental species associations*. The two character combinations with exceptionally high clonal correlations are stalk number and stalk cross-sectional area (−.71), and fibre and stalk cross-sectional area (−.64).

3. The variables x_1-x_{24} in this study are the primary experimental observations recorded. The remainder have been derived arithmetically from these, and many high genetic and environmental correlation coefficients are readily understood from the mathematical relationships involved (BROWN et al., 1968). In a number of instances, a single component with a high coefficient of variation has been seen to determine the genetic relationships of a derived variable almost completely.

Of these three generalizations, that involving the retention of many of the original species associations is of particular interest. It is the objective of the commercial sugarcane breeder to combine the economically desirable features of both the noble canes and their wild relatives, and the usual procedure of successive backcrossing to the *S. officinarum* group is thought to involve the manipulation of chromosomes from the wild species virtually as intact units (PRICE, 1965). One of the objectives of the quantitative genetic analysis of this dynamic commercial breeding population has therefore been the measurement of the degree to which variables are *genetically independent*, in spite of cytological behaviour which restricts gene exchange and recombination between chromosomes derived from different species (BROWN et al., 1968).

A representative measure of the clonal correlation between two characters of commercial importance which fall into this category, is that between yield of cane per plot (x_{16}) and sucrose percent dry weight (x_{29}), viz. $-.40 \pm .09$. Such a figure must on the whole be taken as encouraging, in that 84% of the genetic variation shown by the two characters is *independent*, though an obvious necessity exists for selection pressure to be maintained on each of the two variables. On the other hand, the relationships involving stalk number, stalk cross-sectional area and fibre percent fresh weight (Figure 4), with clonal correlations of absolute value in the range .60—.71, are somewhat more restrictive. It appears likely that pleiotropic effects of genes dictated by purely structural considerations may be to some extent involved here, but it is nevertheless clearly desirable to consider breeding procedures capable of achieving a greater degree of gene exchange between wild and noble canes.

One possibility is the increase of recombination by the induction of chromosome breakage, a proposal which has been discussed by PRICE and WARNER (1959) in some detail. A second procedure, which seems assured of at least a measure of success, involves a more extensive sampling of the genetic variation available within the wild species, particularly *S. spontaneum*. ARCENEAUX (1965) and PRICE (1965) have pointed out that modern commercial varieties rest on a very narrow genetic base. Only one or two gametes have been sampled from a very small number of clones of *S. spontaneum*, *S. robustum* and *S. sinense*. There is considerable variation in biochemical characters within *S. spontaneum*, and some high sucrose and low starch clones have been recorded (PANJE and RAO, 1954; 1956). These clones have not yet been utilised, and it is possible that they may not transmit some of the unfavourable associations reported in this paper.

The approach should then be to introduce into hybrid breeding populations a larger and more useful sample of wild chromosomes by means of conventional nobilization programmes using a wide array of wild clones, and also by deliberate pre-nobilization recombination and selection within the wild species themselves. In the following paper of this series, an experiment designed to evaluate the potential for sucrose selection in *S. spontaneum* will be described and some of the operational difficulties inherent in such a programme will be discussed.

Acknowledgments. We are indebted to the Colonial Sugar Refining Company Limited for permission to publish these data.

Zusammenfassung

1. Genetische, klonale und Umweltkorrelationen wurden an wirtschaftlich wichtigen Merkmalen einer aus interspezifischen Kreuzungen stammenden Zukkerrohr-Zuchtpopulation untersucht.

2. Im allgemeinen besteht eine gute Übereinstimmung zwischen den genetischen Korrelationskoeffizienten, denen die Familienmittelwerte zugrunde liegen, und den klonalen Korrelationen, die auf Grund der genotypischen Beziehungen der Mittelwerte der Klone errechnet werden. Mit Rücksicht auf ihre größere Genauigkeit und auf die Möglichkeit, daß atypische Familiengruppen die genetischen Korrelationen beeinflussen können, ist den numeri-

schen Schätzungen der klonalen Korrelationen größeres Gewicht beigelegt worden.

3. Es wurden viele signifikante Umweltkorrelationen, in der Regel geringer Größenordnung, aufgefunden. Sie bilden ein natürliches Muster, das auf der Wirkung von Faktoren beruht, die Unterschiede von Parzelle zu Parzelle in bezug auf die Wachstumsrate oder den Reifungsprozeß verursachen.

4. Eine große Anzahl von genetischen Beziehungen kann aber nicht auf der Basis eben dieser beiden physiologischen Prozesse erklärt werden. Die Vorzeichen der klonalen Korrelationskoeffizienten für diese besonderen Beziehungen passen sehr klar in ein Muster, das mit dem identisch ist, das die Wildarten von *Saccharum officinarum* unterscheidet.

5. Die cytologische Basis für diese teilweise Aufrechterhaltung von Merkmalsbeziehungen der ursprünglichen Elternarten ist mit ziemlicher Sicherheit die Spaltung ganzer Chromosomen der Wildarten als intakter Einheiten mit geringer Möglichkeit eines Genaustausches oder einer Rekombination mit Chromosomen von *S. officinarum*.

6. Die Stärke der beobachteten klonalen Korrelationen deutet im allgemeinen auf ein großes Ausmaß unabhängiger Verteilung der genetischen Grundlagen von Merkmalen wilden und veredelten Zuckerrohrs hin, vorausgesetzt, daß der Selektionsdruck auf die wirtschaftlich wichtigen Merkmale erhalten bleibt. Bei der Anzahl der Stengel je Parzelle, dem Stengelquerschnitt und dem Faseranteil am Frischgewicht sind die Beziehungen jedoch etwas mehr eingeschränkt.

References

1. Arceneaux, G.: Cultivated sugarcanes of the world and their botanical derivation. Proc. int. Soc. Sug. Cane Technol. **12** (1965). — 2. Brown, A. H. D.: Correlation between brix in juice and fibre in commercial hybrid sugarcane populations. Proc. int. Soc. Sug. Cane Technol. **12** (1965). — 3. Brown, A. H. D., J. Daniels and B. D. H. Latter: Quantitative genetics of sugarcane. I. Analysis of variation in a commercial hybrid sugarcane population. Theoret. Applied Genet., **38**, 361—369 (1968). — 4. Evans, H. J., and G. J. Sorger: Role of mineral elements with emphasis on the univalent cations. Ann. Rev. Plant Physiol. **17**, 47—76 (1966). — 5. Falconer, D. S.: Introduction to Quantitative Genetics. Edinburgh: Oliver and Boyd 1960. — 6. Hatch, M. D., and K. T. Glasziou: Sugar accumulation cycle in sugar-cane. II. Relationship of invertase activity to sugar content and growth rate in storage tissue of plants grown in controlled environments. Plant Physiol. **38**, 344—348 (1963). — 7. Johnson, H. W., H. F. Robinson and R. E. Comstock: Genotypic and phenotypic correlations in soybeans and their implications in selection. Agron. J. **47**, 477—483 (1955). — 8. Mode, C. J., and H. F. Robinson: Pleiotropism and the genetic variance and covariance. Biometrics **15**, 518—537 (1959). — 9. Panje, R. R., and J. T. Rao: Studies in *Saccharum spontaneum*. Selection of material from amongst variants of Indian spontaneums. Proc. 2nd Bienn. Conf. Sug. Cane Res. and Devel. Workers in India, Jullunder, 1954. — 10. Panje, R. R., and J. T. Rao: Studies in *Saccharum spontaneum*. Geographical distribution of the starch character in Indian spontaneums. Proc. int. Soc. Sug. Cane Technol. **9**, 757—764 (1956). — 11. Price, S.: Interspecific hybridization in sugarcane breeding. Proc. int. Soc. Sug. Cane Technol. **12** (1965). — 12. Price, S., and J. N. Warner: The possible use of induced mutations for sugarcane improvement. Proc. int. Soc. Sug. Cane Technol. **10**, 782—791 (1959). — 13. Robinson, H. F., R. E. Comstock and P. H. Harvey: Genotypic and phenotypic correlations in corn and their implications in selection. Agron. J. **43**, 282—287 (1951).

A. H. D. Brown
Dept. of Agronomy
University of California
Davis, Calif. 95616
USA

J. Daniels
Agricultural Experiment Station
South Pacific Sugar Mills Ltd.
Lautoka
Fiji

B. D. H. Latter
Division of Plant Industry
CSIRO
Canberra
Australia