Theoretical and Applied Genetics 38, 361—369 (1968)

Quantitative Genetics of Sugarcane

I. Analysis of Variation in a Commercial Hybrid Sugarcane Population

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. The statistical techniques of quantitative genetic analysis have been applied to the study of variation in a sugarcane breeding population of interspecific hybrid origin.

2. A comparison has been made of estimates of heritability based on sire or dam components of variance alone. The overall equality of these two statistics has been taken as evidence that pollen contamination, self-fertilization and parthenogenetic reproduction are unimportant sources of disturbance in the genetic analysis of the population.

3. From an analysis of plot means it has been concluded that all twenty-four primary characters show significant clonal variation, the overall mean value for clonal repeatability being 0.48. For sixteen of the variables, the estimate of heritability based on the component of variance among full-sib family groups was also significant, the mean value of this parameter being 0.29.

4. For ten of the primary characters, the estimate of clonal repeatability differed significantly from the estimate of heritability. In every case the repeatability value was the greater of the two. It cannot be concluded that non-additive genetic variance is the major factor responsible, since the use of selected clones as parental material, and disassortative mating for some easily observed characters, appear to provide a sufficient explanation of the disparity.

5. The irregular transmission of unpaired chromosomes derived from *S. spontaneum*, *S. robustum* and *S. sinense* may possibly contribute to the observed difference between heritability and repeatability. No other serious departure was observed from expectations based on diploid inheritance.

6. The analyses show fibre percent fresh weight and sucrose percent dry matter to be particularly strong clonal characters. The measure of sucrose per plot, which includes variability for yield of cane, has a heritability of 0.24, a repeatability of 0.43, and a high coefficient of variation (46%).

7. Comparisons of the breeding population with two commercial standards have indicated that selection among genotypes within the present population could lead to significant improvement in any one of the commercially important characters. Further gains with subsequent cycles of hybridization and selection are also strongly indicated. No information has as yet been obtained on the magnitude of genotype × years interaction effects.

1. Introduction

The importance of reliable estimates of population parameters in the design of systematic plant breeding programmes is now generally recognized for both cross- and self-fertilized species (ROBINSON et al., 1949; JOHNSON et al., 1955). Statistical analyses of the variation shown by quantitative characters in a given breeding population can in many instances be interpreted genetically, enabling predictions to be made of rates of response to artificial selection, and of correlated responses to be expected in unselected characters.

However, sugarcane breeders have been unwilling to apply the techniques of quantitative genetics to their material (DANIELS, 1965), partly because of the interspecific hybrid origin of commercial sugarcane populations. The usual breeding procedure involves the 'nobilization' of wild species, the most important being *Saccharum spontaneum* (2 n = 40—128), by successive backcrossing to the *cultivated* sugarcanes *S. officinarum* (2 n = 80). The objective has been to incorporate the disease resistance and vegetative vigour of the wild parent into the 'noble' canes, and *commercial* breeding populations are made up largely of advance backcross lines and their derivatives.

It is well known that *S. officinarum* usually transmits its somatic chromosome number when used as the female parent in interspecific crosses with *S. spontaneum*, despite the fact that normal gametes are generally involved in crosses with other noble varieties. In the first backcross (BC 1), using the interspecific hybrid as pollen parent, 2 n transmission on the maternal side is also common (PRICE, 1963). In later backcrosses and in intercrosses involving the resulting clones, n + n inheritance is usual and meiosis is essentially regular, due presumably to a high frequency of autosyndetic pairing. Multivalent associations are rare, but univalents are common in all stages of backcrossing (BREMER, 1961; PRICE, 1963). Commercial sugarcane varieties derived by nobilization have a somatic chromosome number of approximately 100—120 or more. A further complication is suggested by reports that parthenogenetic reproduction may be possible in *Saccharum* (PRICE, 1959; BULL, 1966).

In the present study, conducted in Fiji, the statistical techniques of quantitative genetics have been applied to a typical commercial hybrid sugarcane population, assuming complete outcrossing and normal diploid inheritance. The objectives of the experiment were: (1) to study the applicability of these techniques to cytologically complicated breeding populations; (2) to examine the pattern of variation shown by the full range of quantitative characters of economic interest; and (3) to characterize the relationships among the variables studied. This paper describes the experiment in full, and reports on the first two objectives.

2. Terminology

The procedures available for estimating 'heritability' in quantitative genetics depend either on the partition of phenotypic variation between and within family groups, or on the correlation of parent and

offspring performance. The genetic interpretation of these estimates depends on the nature of the families concerned, and on the procedure of estimation. In species which may be clonally propagated, there is the additional possibility of measuring the 'repeatability' of performance of individuals of the same genotype (Hansche and Brooks, 1965).

In this series of papers the term *heritability* will be reserved for parameters estimated from the resemblance between related but distinct genotypes, and *clonal repeatability* will be used for parameters based on resemblance between propagules of the same genotype replicated in time and/or space. When describing the relationship between two different quantitative characters measured on the same individuals, the terms *genetic correlation* and *clonal correlation* respectively will be used to indicate the same distinction. These terms have an operational justification in that they are used to make two different kinds of prediction in sugarcane breeding, and in work with other asexually propagated species. A measure of clonal repeatability indicates the reliability of selection, and the potential response within a given population of clones; clonal correlations indicate the correlated responses to be expected following selective elimination of clones from the population. The terms heritability and genetic correlation predict advances and correlated responses expected in the succeeding generation, following the intercrossing of a selected group of clones.

A number of authors have estimated repeatability in replicated clonal material, interpreting the measure as 'heritability in the broad sense' (Burton and DeVane, 1953; Scossiroli et al., 1963). Kneebone (1958) has compared estimates obtained from clonal propagules of sand bluestem with those derived from a study of open-pollinated progeny groups, without detecting large differences. However, Kehr and Gardner (1960) estimated that the additive genetic variance for yield in alfalfa accounted for only one-third of the between clone variance, and ascribed the difference to non-additive genetic effects. Comstock et al. (1958) also concluded that a major fraction of the genetic variance observed in a study of strawberry progenies could be interpreted as due to epistatic effects.

The use of clonal repeatability to estimate the total genetic variance present in a population, i.e. heritability in the broad sense, or degree of genetic determination (Falconer, 1960), ignores the possibility that non-heritable effects may be transmitted during vegetative reproduction (Libby and Jund, 1962), thereby contributing to the observed between-clone variation. On the other hand, although estimates of half-sib and full-sib correlations can be combined to give a measure of the total genetic variance, provided epistatic interactions between loci can be ignored, a very extensive experiment is required if such a measure is to have any degree of accuracy (Mode and Robinson, 1959). An estimate of clonal repeatability may therefore be extremely valuable in many instances, in that it provides an upper limit to the degree of genetic determination.

Table 1. *Ancestry of parental clones*

Group	Number of parents		Description
	Males	Females	
A	1	6	*S. officinarum* (noble canes)
B	1	—	*S. spontaneum* (Tabongo)
C	—	1	*S. officinarum* × *S. spontaneum* BC 1 (2nd nobilization)
D	11	14	*S. officinarum* × *S. spontaneum* BC 2+ (3rd and later nobilizations)
E	11	18	Complex hybrids involving *S. officinarum*, *S. spontaneum* and *S. sinense*
F	—	4	Complex hybrids involving *S. officinarum*, *S. spontaneum* and *S. robustum*
G	2	4	Complex hybrids involving *S. officinarum*, and more than one clone of *S. spontaneum*
H	1	—	*S. officinarum* and *S. sinense* derivative

3. Material and Methods

From among crosses made in the course of the normal sugarcane breeding work in Fiji, a set of 47 were chosen to provide the material for this study. The crosses involved 27 male-fertile clones which were used only as male parents, and 47 clones which were used only as females. Seed was collected from the female parent in each cross. One male was used in six crosses, one in four crosses, four in three crosses, four in two crosses, and 17 were involved in only one cross each.

The origin of the parental clones is summarized in Table 1, and the general pattern of the mating scheme is set out in Table 2. A wide range of genotypes typical of sugarcane breeding populations is represented in the parental set, nine of the clones being commercial varieties. From Table 2 it can be seen that crosses have been made essentially at random with respect to the major categories, though there is a first nobilization included, and a tendency to intercross the complex hybrid groups F, G and H. Omission of these minor groups of parents does not appreciably reduce the total genetic variance for any character studied, and the parental material has therefore been treated as representative of an interbreeding population.

Techniques for the reliable control of flowering in sugarcane are only now being developed (Daniels, 1965), and it was for this reason that material from the regular breeding programme was used. The popu-

Table 2. *The crossing scheme in terms of groups in Table 1*

	Males						Totals
	A	B	D	E	G	H	
Females							
A	1	1	3	1			6
C			1				1
D			9	5			14
E			11	7			18
F			2	1	1		4
G			1	1	1	1	4
Totals	1	1	27	15	2	1	47

lation structure therefore differs to some extent from that envisaged in the theory of quantitative genetic analysis, and these deficiencies must be kept in mind when interpreting the statistics presented in this paper. The following points in particular should be emphasized: (1) The pedigrees of sugarcane clones are sometimes doubtful, as femaleness is really a reflection of the degree of anther dehiscence, and many clones are self-fertile. (2) Sugarcane pollen is highly mobile, and even with the usual precautions there can be small amounts of contamination in regular field crosses (SKINNER, 1959). (3) Disassortative mating is normally practised for some of the main characters, especially components of yield.

Three full-sib progeny were chosen at random from each biparental family at stage-2 of the normal variety testing programme. At this stage each genotype is represented by an 8-foot row, and the clones planted are derived by mild selection for agronomic type in stage-1 which involves original seedlings. The chosen progeny were planted in plots consisting of a single 8-foot row, using a replicated design with a total of 12 randomized sub-blocks. Each sub-block contained 49 plots to accommodate 47 test clones, one from each biparental family, and two standard commercial varieties. A group of four such sub-blocks, originally chosen at random, constitutes a "block" in which each family is represented by a single progeny clone.

The trial was planted in May, 1964, with spray irrigation to assist germination. At eight weeks, plots showing poor germination were supplied with additional setts, or young stools were transplanted.* Soil tests indicated a deficiency of phosphorus, and a dressing of 450 lb/acre of superphosphate was therefore applied together with 110 lb/acre of ammonium sulphate to assist early growth. When the material was 8 months old and vigorously growing, it was flattened by a hurricane. The lodged cane was harvested, but no measurements were possible. Most of the characters in this study have therefore been assessed in the first ratoon crop†, which was harvested in September, 1965, when 9 months old.

4. Characters Observed

The characters measured are distinguished in this section by an identification number which is also to be used in later papers. This facilitates discussion of the results, and also enables the formulae for calculation of derived variables to be readily set out.

Plant Crop

A germination count of the number of shoots per plot (x_1) was made two weeks after planting. A similar count (x_2) was made after four weeks. At 20 weeks each plot was given a visual yield grade for early growth (x_3), and a count of number of stalks per plot (x_4) was made when the crop was 30 weeks old. In visual grading of plots for yield, estimates are expressed relative to the commercial standard, which is given a rating of 10.

Ratoon Crop

A count was taken of the number of leafhoppers (*Perkinsiella vitiensis*) per plot (x_5) at 10—13 weeks. Diurnal fluctuation in numbers necessitates counting during a fixed two-hour period over a number of days. *Perkinsiella* is a vector of the virus responsible for Fiji disease of sugarcane. The number of stalks per plot (x_6) was also counted at the same time.

When the crop was 11—12 weeks old, 20 leaf blades were taken from the top visible dewlap leaves (T.V.D.) in each plot, and the following five characters measured: leaf weight (x_7) in grams/leaf, leaf moisture content expressed as percent fresh weight (x_8), and leaf nitrogen (x_9), phosphate (x_{10}) and potassium (x_{11}), each measured as percent dry weight. At 16 weeks, a visual yield grade was given to each plot for early growth (x_{12}).

Harvest Variables

The following eight field characters were measured at harvest: mean leaf width (x_{13}) and leaf length (x_{14}), each measured in centimetres and based on a sample of ten T.V.D. leaves; a visual yield grade (x_{15}), the actual plot yield of clean cane in pounds (x_{16}), and the number of stalks per plot (x_{17}); and from a within-plot sample of five stalks, the number of nodes (i.e. leaves) per stalk (x_{18}), mean stalk length (x_{19}) in cm, and mean stalk cross-sectional area in sq. cm (x_{20}) were estimated.

A 12-stalk sample was also taken from each plot for measurements of the following four biochemical characters: starch content (x_{21}) expressed as p.p.m. of soluble solids, total sugars (x_{22}) and reducing sugars (x_{23}) in an alcohol 3:1 extract of fibrated cane, both expressed as percent of the extract (CILLEKENS, 1965), and finally a measure of fibre, i.e. water-insoluble matter (x_{24}), expressed as percent fresh weight.

Derived Variables

In addition to these twenty-four primary characters, the derived variables listed in Table 3 were

Table 3. *Variables derived from the primary characters listed in the text*

Number	Character	Derivation
x_{25}	Total sugars % fresh wt.	$x_{22}\,(400 - x_{24})/100$
x_{26}	Reducing sugars % fresh wt.	$(x_{23}/x_{22})\,x_{25}$
x_{27}	Sucrose % fresh wt.	$x_{25} - x_{26}$
x_{28}	Sucrose % juice	$(100\,x_{27})/(100 - x_{24})$
x_{29}	Sucrose % dry wt.	$(100\,x_{27})/(x_{24} + x_{25})$
x_{30}	Sucrose % total sugars	$(100\,x_{27})/x_{25}$
x_{31}	Dry matter % fresh wt.	$x_{24} + x_{25}$
x_{32}	Sucrose per plot (lb)	$(x_{16}\,x_{27})/100$
x_{33}	Dry matter per plot (lb)	$(x_{16}\,x_{31})/100$
x_{34}	Juice per plot (lb)	$x_{16}\,(100 - x_{24})/100$
x_{35}	Volume of cane per plot (litres)	$(x_{17}\,x_{19}\,x_{20})/10^3$
x_{36}	Specific gravity (gm/cc)	$0.454\,(x_{16}/x_{35})$
x_{37}	Mean weight per stalk (lb)	x_{16}/x_{17}
x_{38}	Mean node volume (ccs)	$(x_{20}/x_{18})\,x_{19}$
x_{39}	Mean node length (cm)	x_{19}/x_{18}
x_{40}	Mean leaf area (sq. cm)	$x_{13}\,x_{14}$
x_{41}	Total leaf area per plot (sq. m)	$(x_{40}\,x_{17}\,x_{18})/10^4$
x_{42}	Total leaf weight per plot (Kg)	$(x_7\,x_{17}\,x_{18})/10^3$

* Vegetative propagation is by use of short stem cuttings known as setts. A process of tillering gives rise to a number of stalks collectively termed a stool.

† The crop produced by renewed growth from the remaining underground portions.

calculated. In the computer programme written for this study, the formula for the estimation of total sugars (x_{25}) involved an adjustment factor in the denominator of $1 + 0.003\,703\ x_{22}$, but the effect of this correction is negligible over the range of values concerned.

Within-Plot Variances

Five stalks were sampled from each plot to provide estimates of x_{18}, x_{19} and x_{20}, and it was therefore possible to calculate within-plot variances for these three variables and also for x_{38} and x_{39}. In the discussion to follow, the measure of within-plot variance corresponding to variable x_i will be denoted by s_i^2, and will be considered as a new variable in its own right. The logarithmic transformation has been used in all analyses of variance and covariance of the observed s_i^2 values.

5. Statistical Analyses

The basic analysis of variance for this study is set out in Table 4. The coefficient of 20.5 in the expectation of the between-sires mean square (S) allows for variation in the numbers of dams per sire (Kempthorne, 1957, p. 421). The expectation of the between-families mean square (F) has been derived in such a way that σ_f^2 is almost exactly equal to the component of variance among *unrelated* full-sib families.

Table 4. *The analysis of variance table*

Source of variation	d.f.	Mean square	Expectation
Sub-blocks	11		
Families	46	F	$\sigma_e^2 + 4\,\sigma_i^2 + 11.8\,\sigma_f^2$
Sires	26	S	$\sigma_e^2 + 4\,\sigma_i^2 + 12\,\sigma_d^2 + 20.5\,\sigma_s^2$
Dams within sires	20	D	$\sigma_e^2 + 4\,\sigma_i^2 + 12\,\sigma_d^2$
Blocks × families	92	I	$\sigma_e^2 + 4\,\sigma_i^2$
Residual	414	E	σ_e^2

If the parental material had been randomly chosen from the previous generation, and if the additional requirements of random mating and normal diploid inheritance were satisfied, the components of variance in Table 4 would have the following expectations in the absence of epistatic interactions between loci: (i) $\sigma_s^2 = \frac{1}{4}\,V_A$, where V_A denotes the additive genetic variance present in the breeding population; (ii) $\sigma_d^2 = \frac{1}{4}\,V_A + \frac{1}{4}\,V_D$, where V_D denotes the dominance variance; (iii) $\sigma_i^2 = \frac{1}{2}\,V_A + \frac{3}{4}\,V_D + V_C$ where V_C denotes the variance due to non-heritable effects transmitted during clonal reproduction; and (iv) $\sigma_e^2 = V_E$, the environmental variance among plots. In the context of the present study, the component σ_f^2 can be taken to be equal to the sum of the expectations of σ_s^2 and σ_d^2.

If the total phenotypic variance among plots within sub-blocks is denoted by $\sigma_p^2 = \sigma_f^2 + \sigma_i^2 + \sigma_e^2$, and the variance among 'true' clone means is $\sigma_c^2 = \sigma_f^2 + \sigma_i^2$, each character can be described by the following four population parameters: (i) $h_s^2 = 4\,\sigma_s^2/\sigma_p^2$, a measure of heritability in the narrow sense, i.e. of the additive genetic variance as a fraction of the phenotypic variance displayed: (ii) $h_d^2 = 4\,\sigma_d^2/\sigma_p^2$, a measure of the degree of genetic determination of the character in the absence of epistasis; (iii) $h_f^2 = 2\,\sigma_f^2/\sigma_p^2$, a measure of heritability based on the between-families component, which includes all the additive genetic variance and roughly one-half the dominance variance; and (iv) $r_c = \sigma_c^2/\sigma_p^2$ which measures clonal repeatability.

Standard errors of estimates of these four parameters, and of differences among them, were derived by means of large sample formulae given by Mode and Robinson (1959). In determining the standard error of an estimate of h_s^2, no account was taken of variation in the size of sire groups. Estimates of h_s^2 and h_d^2 from this experiment have very large standard errors, and h_f^2 and r_c provide the most useful genetic information for individual quantitative characters. Nevertheless, estimates of heritability based on sire or dam components alone, averaged over all characters, are of particular value in defining the nature of the breeding population under observation.

6. Results and Discussion

Scale Transformations

In the choice of a suitable scale for the analysis of each quantitative variable, attention was paid initi-

Table 5. *The effects of changes of scale on estimates of genetic parameters*

Variable	C.V.	Scale	Symmetry*	Heritability (h_f^2)	Repeatability (r_c)
Sucrose % dry wt. (x_{29})	12	x	38	.55 ± .16	.75 ± .03
		$-\log(70 - x)$	45	.51 ± .16	.72 ± .03
Mean leaf area (x_{40})	20	x	62	.26 ± .15	.73 ± .03
		$\log x$	57	.25 ± .15	.72 ± .03
Yield grade (x_{15})	34	x	43	.20 ± .09	.26 ± .05
		$-\log(14.5 - x)$	45	.23 ± .09	.25 ± .05
Stalks per plot (x_{17})	47	x	62	.25 ± .14	.64 ± .04
		$\log x$	53	.20 ± .12	.53 ± .04
Reducing sugars (x_{26})	54	x	66	.31 ± .13	.57 ± .04
		$\log x$	55	.26 ± .12	.52 ± .04
Starch content (x_{21})	79	x	57	.38 ± .13	.55 ± .04
		$\log x$	51	.53 ± .14	.58 ± .04
Leafhopper count (x_5)	87	x	57	.18 ± .08	.21 ± .05
		$\log(1.6 + x)$	49	.38 ± .11	.34 ± .05

* The percentage of family means which are less than the overall population mean. A symmetry value appreciably greater than 50% indicates a long tail in the positive direction, i.e. a positively skewed distribution.

ally to the relationship between mean and variance, and to the symmetry of the overall distribution. Where more than one transformation was tested, the symmetry of the distribution of family means was taken as a guide to the suitability of the scale used.

It is clear from the estimates of heritability and repeatability presented in Table 5 that only in extreme cases are the population parameters conspicuously altered by changes of scale. Important changes were observed with transformation in the case of starch content and leafhopper count, and both these characters show particularly high coefficients of variation (i.e. $100\,\sigma_p/\bar{x}$) on the untransformed scale. For each of these two characters, the effect of the appropriate scale transformation was to increase appreciably the estimate of heritability.

Nature of the Breeding Population

Estimates of the essential population parameters are given in Table 6 for each of the twenty-four primary variables. The scale transformations used in the estimation of heritability and repeatability are indicated where necessary in the Table, but the mean and coefficient of variation refer throughout to the untransformed scale of measurement. Table 7 sets out the corresponding estimates for the derived variables. The standard errors of each measure of heritability and repeatability are given in both Tables.

All twenty-four primary variables showed significant clonal variation, as measured by r_c (Table 6), and sixteen of the estimates of heritability based on the between family component (h^2_f) were significantly

Table 6. *Estimates of population parameters for the primary variables. Means and coefficients of variation refer to the untransformed scale of measurement*

Number	Character	Mean	C.V.	Heritability (h^2_f)	Repeatability (r_c)
x_1	Shoots per plot at 2 weeks	3.6	99	.37 ± .13	.57 ± .04
x_2	Shoots per plot at 4 weeks	8.6	48	.28 ± .12	.46 ± .05
x_3	Early yield grade	7.8	28	.18 ± .11	.40 ± .05
x_4	Stalks per plot: [log x]	31	36	.20 ± .11	.42 ± .05
x_5	Leafhoppers: [log (1.6 + x)]	17	87	.38 ± .11	.34 ± .05
x_6	Stalks per plot: [log x]	53	39	.00 ± .08	.31 ± .05
x_7	T.V.D. leaf weight (gm)	5.0	25	.37 ± .11	.38 ± .05
x_8	T.V.D. leaf moisture (%)	77.4	2.2	.13 ± .12	.54 ± .04
x_9	Leaf nitrogen % dry wt.	1.92	8.3	−.02 ± .06	.15 ± .04
x_{10}	Leaf phosphate % dry wt.	.228	15	.30 ± .10	.29 ± .05
x_{11}	Leaf potassium % dry wt.	1.64	9.0	.32 ± .11	.41 ± .05
x_{12}	Early yield grade	8.5	24	.37 ± .11	.38 ± .05
x_{13}	T.V.D. leaf width (cm)	5.35	16	.42 ± .15	.71 ± .03
x_{14}	T.V.D. leaf length (cm)	163	10	.02 ± .14	.72 ± .03
x_{15}	Yield grade: [− log (14.5 − x)]	8.0	34	.23 ± .09	.25 ± .05
x_{16}	Yield per plot (lb)	66	44	.30 ± .12	.48 ± .05
x_{17}	Stalks per plot: [log x]	36	47	.20 ± .12	.53 ± .04
x_{18}	Nodes per stalk	15.7	14	.55 ± .14	.63 ± .04
x_{19}	Stalk length (cm)	174	16	.47 ± .13	.54 ± .05
x_{20}	Stalk cross-sectional area (sq. cm)	4.0	26	.26 ± .15	.70 ± .03
x_{21}	Starch: [log x] (p.p.m.)	192	79	.53 ± .14	.58 ± .04
x_{22}	Total sugars % extract	3.49	12	.42 ± .13	.52 ± .05
x_{23}	Reducing sugars % extract	0.19	54	.31 ± .13	.57 ± .04
x_{24}	Fibre % fresh wt.	13.7	15	.34 ± .15	.72 ± .03

Table 7. *Estimates of population parameters for derived variables. Means and coefficients of variation refer to the untransformed scale of measurement*

Number	Character	Mean	C.V.	Heritability (h^2_f)	Repeatability (r_c)
x_{25}	Total sugars % fresh wt.	13.3	12	.43 ± .13	.53 ± .05
x_{26}	Reducing sugars % fresh wt. [log x]	0.71	54	.26 ± .12	.52 ± .04
x_{27}	Sucrose % fresh wt.	12.6	15	.43 ± .13	.55 ± .04
x_{28}	Sucrose % juice	14.6	14	.37 ± .13	.50 ± .05
x_{29}	Sucrose % dry wt.: [− log (70 − x)]	46.7	12	.51 ± .16	.73 ± .03
x_{30}	Sucrose % total sugars: [− log (100 − x)]	94.4	3.7	.31 ± .13	.54 ± .04
x_{31}	Dry matter % fresh wt.	27.0	8.3	.10 ± .11	.45 ± .05
x_{32}	Sucrose per plot (lb)	8.3	46	.24 ± .11	.43 ± .05
x_{33}	Dry matter per plot (lb)	18.0	46	.27 ± .12	.49 ± .05
x_{34}	Juice per plot (lb)	57	43	.29 ± .12	.47 ± .05
x_{35}	Volume of cane per plot (litres)	24	46	.24 ± .11	.37 ± .05
x_{36}	Specific gravity (gm/cc)	1.29	20	−.01 ± .05	.07 ± .04
x_{37}	Mean weight per stalk (lb)	1.91	28	.31 ± .14	.60 ± .04
x_{38}	Mean node volume (cc)	44	28	.17 ± .13	.62 ± .04
x_{39}	Mean node length (cm)	11.2	16	.67 ± .14	.63 ± .04
x_{40}	Mean leaf area: [log x] (sq. cm)	875	20	.25 ± .15	.72 ± .03
x_{41}	Leaf area per plot: [log x] (sq. m)	49	48	.15 ± .12	.49 ± .04
x_{42}	Leaf weight per plot (Kg)	5.8	56	.31 ± .12	.48 ± .05

Table 8. *Mean values for heritability based on sire components (h_s^2), dam components (h_d^2) and family components (h_f^2), and for repeatability (r_c), averaging over the primary variables (x_1-x_{24})*

Class of Variable	h_s^2	h_d^2	h_f^2	r_c
Preharvest (x_1-x_{12})	.30 ± .07	.18 ± .07	.24 ± .03	.39 ± .02
Harvest ($x_{13}-x_{24}$)	.29 ± .09	.38 ± .10	.34 ± .04	.58 ± .02
Means	.29 ± .06	.28 ± .06	.29 ± .03	.48 ± .02

greater than zero. Of the derived characters (Table 7), all except specific gravity showed significant r_c values, and 13 of the 18 estimates of heritability were significant.

The individual estimates of heritability based on sire or dam components alone, i.e. h_s^2 and h_d^2, are of little interest because of their large standard errors. However, the values of these parameters averaged over the full range of primary variables give useful indications of the nature of the breeding material under study. The mean values are given in Table 8 for comparison with the corresponding means of h_f^2 and r_c. Those variables measured prior to harvest (x_1-x_{12}) have been considered as a separate group from those measured at harvest ($x_{13}-x_{24}$).

The equality of the average estimates of h_s^2 and h_d^2 demonstrate the reality of the contribution of the male parent to progeny performance, and there can be no doubt that parthenogenetic reproduction is the exception rather than the rule in this breeding population. Self-fertilization must also be rare in the crosses involved in this study. It can be inferred that differences in general combining ability among the parental clones are largely responsible for the observed variation among progeny group means, taking an overall view of the range of characters measured.

The mean values of repeatability (r_c) are appreciably greater than those of heritability (h_f^2 or h_d^2) for both preharvest variables and those measured at harvest (Table 8), and it can be seen from Figure 1 that almost all primary variables contribute to the difference between the two types of measure. Possible factors responsible for an overall difference between r_c and h_f^2 are: (1) pollen contamination of the field crosses; (2) non-additive genetic variance due to epistatic gene effects; (3) restriction of genetic variation among the parental set due to prior testing and selection; (4) disassortative mating for some of the components of yield; (5) departures from diploid inheritance, and (6) non-heritable clonal or "seed" effects.

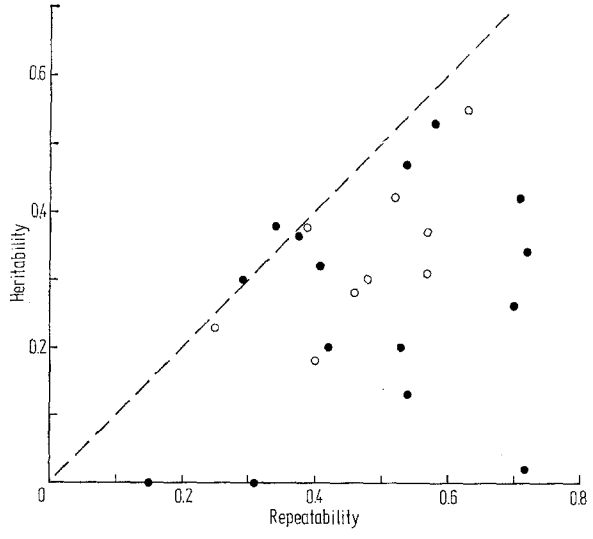

Fig. 1. The relationship between heritability (h_f^2) and repeatability (r_c) for the primary variables x_1-x_{24}. Open circles indicate characters for which the population mean is appreciably different from the commercial standards

Pollen contamination can be discounted as an important factor in this study, because of the evidence for an approximately equal contribution from male and female parents to the mean performance of full-sib progeny groups (Table 8).

It is not possible to conclude that epistatic variance is the prime factor responsible for the disparity between repeatability and heritability, as have Comstock et al. (1958) in a comparable study with strawberries. These authors have pointed out that epistatic effects are expected to be most pronounced for traits showing a marked depression in mean progeny performance, following random intercrossing of elite clones. It can be seen from Figure 1 that there is no obvious distinction in the present study between characters for which the population mean is markedly different from the commercial standards, and those for which the mean is roughly equal to that of the standards. There is, moreover, no difficulty in accounting for the observations in terms of the remaining factors listed above.

For characters of moderate heritability showing additive genetic variation alone, the use of selected clones as parental material is known to reduce appreciably the genetic variance among progeny group means (Robertson, 1961). For a trait of heritability 0.50, for example, with parental clones selected on the basis of their own performance with intensity $P = 0.01$, it is to be expected that heritability estimated from the between-family component would be roughly $h_f^2 = 0.27$, i.e. 54% of the true value. Disassortative mating for visual characters such as leaf width, leaf length, stalk thickness and stalk number will also tend to reduce the magnitude of between-family genetic variance for these and correlated traits.

It must also be remembered that in the production of commercial hybrid sugarcane clones, the breeding procedures of 'nobilization' and of planned outcrossing lead to the occurrence of isolated chromosomes derived from *S. spontaneum*, *S. robustum* and *S. sinense*, which remain unpaired during meiosis (Price, 1963). If the probability of transmission of such 'wild' chromosomes in crosses is sufficiently low, it can be shown algebraically that their contribution to within-family variability is proportionately greater than that expected from normal diploid segregation. It is therefore possible that the discrepancy between estimates of h_f^2 and r_c may in part be due to this phenomenon, particularly for traits such as leaf length, leaf area, stalk thickness, stalk number, reducing sugars and fibre, which are conspicuously different in wild and noble canes.

Non-heritable clonal effects may be important for individual characters such as the germination scores, but the greater difference between r_c and h_f^2 for harvest *vs.* pre-harvest variables (Table 8) makes it unlikely that such effects are the prime explanation of this phenomenon.

Individual Characters

The numerical data presented in Tables 6 and 7 can most readily be discussed by considering related groups of characters in turn.

(i) *Germination counts.* The earlier count (x_1) showed a skewed distribution, but a scale transformation changed the genetic parameters only slightly. The differences between repeatability and heritability for x_1 and x_2 are both non-significant, but the estimates suggest that non-heritable clonal effects may be important. The heritability of germination count is sufficiently high to justify selection for this character, which is of obvious importance in establishment.

(ii) *Yield grades.* The estimates of repeatability for the visual yield grades (x_3, x_{12}, x_{15}) lie in the range 0.25—0.40, which is below the average of the measured variables, but the heritability estimates nevertheless average 0.26. The distribution of yield grade at harvest (x_{15}) is negatively skewed, while yield itself (x_{16}) is symmetrically distributed, suggesting a reluctance on the part of the observer to give high grade scores. This tendency was not apparent in the visual assessments made at 16—20 weeks.

(iii) *Stalk counts.* The distribution of stalk number per plot in this breeding population was positively skewed, with a few clones having very high counts. For stalk number at harvest (x_{17}), the range of clone means was 12—119 on the untransformed scale, with an overall mean of 36. The means for the two commercial standards, Pindar and Homer, were 40 and 43 respectively. Estimates of repeatability of the stalk counts (x_4, x_6, x_{17}) were in the range 0.31—0.53, but the mean heritability is only 0.13. It appears that the count taken from the plots following harvest (x_{17}) is more accurate than the earlier counts made on the standing crop.

(iv) *Leafhopper count.* There is certainly good evidence from this study for a habitat or feeding preference on the part of the insect (x_5), which is dependent on a varietal character of moderately high repeatability and heritability. The relationship between leafhopper count and the other variables observed in this study will be considered in a later paper in this series. Here we are concerned to demonstrate a genetic component in the pattern of incidence of leafhoppers among plots in the trial.

(v) *Leaf characters.* The index of total leaf area per plot (x_{41}) shows average repeatability (0.49), but the estimate of heritability is not significantly different from zero. Mean leaf area itself (x_{40}) shows high repeatability (0.72), but non-significant heritability, due to the apparently low heritability of leaf length (x_{14}). On the other hand, the index of total leaf weight per plot (x_{42}) had moderately high heritability (0.31) and repeatability (0.48), the estimates being very similar to those for mean leaf weight itself (x_7).

The chemical analyses have shown genetic variation to be appreciable for both phosphate (x_{10}) and potassium (x_{11}) levels in the population, but genetic variation in nitrogen percent dry matter (x_9) was of a low order, due possibly to a high overall level of nitrogen nutrition. These analyses are of particular interest in that they are used as a basis for fertilizer recommendations.

(vi) *Physical characters at harvest.* Total yield per plot (x_{16}) has a high coefficient of variation (44%), with moderate heritability (0.30) and average repeatability (0.48). The overall mean corresponds to 36 tons of cane per acre, with a range of clone means from 8—77 tons per acre; Pindar and Homer, the commercial standards, yielded 56 and 43 tons respectively. It must be emphasized, however, that yielding ability in this trial is not necessarily a reflection of yield in pure stands, since competitive ability is an important component of yield in small plots (SKINNER, 1961).

Variation in both node length (x_{39}) and stalk length (x_{19}) is highly heritable in this population. Stalk thickness (x_{20}) has a high repeatability value (0.70), but only modest heritability (0.26). The genetic parameters for total sucrose, dry matter and juice per plot (x_{32}, x_{33}, x_{34}) are all very similar to those for yield itself (x_{16}), which is the component with the largest coefficient of variation.

Despite the average to above average repeatability of all components used in the derivation of specific gravity (x_{36}), there appears to be no genetic variation for this character in the population. The two components with the highest coefficients of variation are yield (x_{16}) and stalk number (x_{17}), which will be shown in a subsequent paper to be positively correlated. However, the ratio of these two components alone, i.e. mean stalk weight (x_{37}), is highly repeatable and heritable. The procedure of estimation of specific gravity cannot then be held responsible for the low values of the observed genetic parameters for this character.

(vii) *Biochemical characters.* The formulae for estimation of total sugars percent fresh weight (x_{25}) and reducing sugars percent fresh weight (x_{26}) are presented in Table 3. A comparison of the genetic parameters for these characters (Table 7) with those of the primary variables expressed as percent solvent extract (x_{22}, x_{23}), shows them to be little influenced by the variation in percent fibre (x_{24}) in this population. Because of the high mean level of sucrose percent total sugars (94.4%), genetic variation in sucrose percent fresh weight (x_{27}) is reflected in the measure of total sugars percent alcohol extract (x_{22}), and the genetic parameters for these two variables are almost identical. Nevertheless, appreciable heritable variation is shown by sucrose percent total sugars (x_{30}), with a heritability of 0.31 and a repeatability of 0.54.

The clone means for sucrose percent fresh weight ranged from 8.2—16.2 with a mean of 12.6, compared with the values of 14.2 and 14.8 for the commercial standards Pindar and Homer. For sucrose percent total sugars the clone means ranged from 84—98 with a mean of 94.4, compared with 97% for each of the standards.

Fibre content expressed as percent fresh weight (x_{24}) shows high repeatability (0.72) and a moderately

high heritability (0.34), which is somewhat lower than that obtained in an earlier study (Brown, 1965). The overall mean of 13.7 compares favourably with levels of 13.5 and 12.2 in the commercial standards, and the range of clone means was 10.6—18.4. Starch content (x_{21}) is highly heritable, with a range of clone means from 40—910 and an overall mean of 192. Pindar and Homer averaged 200 and 330 p.p.m. respectively.

Of the derived characters, sucrose percent dry weight (x_{29}) is perhaps the most interesting, in that it shows the highest heritability, and a distribution which is very markedly skewed in the negative direction. Such a distribution suggests the population is approaching a well-defined upper limit. Pindar and Homer averaged 50.3 and 54.0%, whilst the clone means ranged from 30.3—59.1 with an overall population mean of 46.8%.

Table 9. *Estimates of population parameters for the measures of within-plot variability*

Basic Character	Variable analysed	Heritability* (h_l^2)	Repeatability* (r_c)
Nodes per stalk (x_{18})	$\log s_{18}^2$	.27 ± .10	.31 ± .05
Stalk length (x_{19})	$\log s_{19}^2$	.11 ± .07	.12 ± .04
Stalk c.s. area (x_{20})	$\log s_{20}^2$	.38 ± .14	.65 ± .04
Node volume (x_{38})	$\log s_{38}^2$	.26 ± .14	.60 ± .04
Node length (x_{39})	$\log s_{39}^2$	.09 ± .09	.33 ± .05

* Heritability and repeatability here refer to the nature of variation in individual plot estimates of $\log s_i^2$, the known sampling variance of an estimate based on 4 degrees of freedom, having been subtracted from the total observed variation.

(viii) *Within-plot variability.* The results of analyses of variance of the measures of within-plot variability ($\log s_i^2$) are presented in Table 9. In the calculation of the estimates of heritability and repeatability, cognizance has been taken of the theoretical sampling variance ($2/n$) of an estimate of $\log s_i^2$ based on n degrees of freedom when the basic variable is normally distributed. The genetic parameters then refer to the nature of variation in plot values of $\log s_i^2$ each based on a very large sample of stalks.

All five variability measures show significant repeatability, and three are significantly heritable. However, in a succeeding paper in this series it will be shown that in each case the measure of within-plot variance is highly correlated with the plot mean for the basic character concerned. In the case of cross-sectional area (x_{20}) this leads to a detectable positive skewness in the overall distribution of plot means.

Acknowledgments. We are particularly grateful to Dr. D. S. Falconer for his suggestions regarding terminology, and to the Colonial Sugar Refining Company Limited for permission to publish the data.

Zusammenfassung

1. An einer aus interspezifischen Kreuzungen stammenden Zuckerrohr-Zuchtpopulation wurde zur Untersuchung der Variabilität die statistische Technik der quantitativen Analyse angewandt.

2. Ein Vergleich der Heritabilitätsschätzungen wurde sowohl auf der Grundlage der Varianzkomponenten der männlichen als auch der weiblichen Eltern angestellt. Die Übereinstimmung dieser beiden Statistiken wird als Hinweis betrachtet, daß Pollenverunreinigungen, Selbstbefruchtung und Parthenogenese nur eine unwesentliche Störungsquelle bei der genetischen Analyse der Population bilden.

3. Aus der Untersuchung der Parzellenmittelwerte ging hervor, daß alle 24 Hauptmerkmale eine signifikante klonale Variation zeigen; der Durchschnittswert für die klonale Wiederholbarkeit war 0,48. Bei 16 der Variablen war die Heritabilitätsschätzung auf Grund der Varianzkomponenten bei den Gruppen von Vollgeschwistern ebenfalls signifikant, der Durchschnitt dieses Parameters betrug 0,29.

4. Die Schätzung der klonalen Wiederholbarkeit wich bei 10 Hauptmerkmalen signifikant von der Heritabilitätsschätzung ab. In jedem Fall war der Wiederholbarkeitswert größer. Es kann nicht angenommen werden, daß die nichtadditive genetische Varianz der verantwortliche Hauptfaktor ist, da die Verwendung selektierter Klone als elterliches Material und die zufällige Kombination bei einigen leicht erkennbaren Merkmalen eine ausreichende Erklärung dieser Ungleichheit zu liefern scheint.

5. Die irreguläre Übertragung ungepaarter Chromosomen von *S. spontaneum*, *S. robustum* und *S. sinense* kann vielleicht zu der beobachteten Differenz zwischen Heritabilität und Wiederholbarkeit beitragen. Für Schätzungen auf der Grundlage diploider Vererbung wurden keine weiteren bedeutenden Abweichungen beobachtet.

6. Die Untersuchungen ergeben, daß der Faseranteil, das Frischgewicht und der Sucrosegehalt der Trockensubstanz besonders ausgeprägte klonale Eigenschaften sind. Die Messung des Sucrosegehaltes je Parzelle, die die Variabilität des Ertrags des Zuckerrohrs mit umfaßt, hat eine Heritabilität von 0,24, eine Wiederholbarkeit von 0,43 und einen hohen Variationskoeffizienten (46%).

7. Vergleiche der Zuchtpopulation mit zwei Handelssorten haben ergeben, daß eine Auslese unter den Genotypen der Population zu einer signifikanten Verbesserung bei jedem der wirtschaftlich wertvollen Merkmale führen könnte. Weitere Erfolge dürften bei Bastardierungs- und Selektionszyklen zu erwarten sein. Über die Größe der Interaktionseffekte Genotyp × Jahre konnte bisher keine Information erlangt werden.

References

1. Bremer, G.: Problems in breeding and cytology of sugar cane. II. The sugar cane breeding from a cytological view-point. Euphytica **10**, 121—133 (1961). — 2. Brown, A. H. D.: Correlation between brix in juice and fibre in commercial hybrid sugar cane populations. Proc. int. Soc. Sug. Cane Technol. **12**, in press (1965). — 3. Bull, T. A.: Transmission of somatic chromosome numbers in *Saccharum* L. Aust. J. Sci. **28**, 466—467 (1966). — 4. Burton, G. W., and E. H. DeVane: Estimating heritability in tall fescue (*Festuca arundinacea*) from replicated clonal material. Agron. J. **45**, 478—481 (1953). — 5. Cillekens, A. A. J.: Automation of sugar analysis for physiological research and breeding with sugarcane. Proc. int. Soc. Sug. Cane Technol. **12**, in press (1965). — 6. Comstock, R. E., T. Kelleher and E. B. Morrow: Genetic variation in an asexual species, the garden strawberry. Genetics **43**, 634—646 (1958). — 7. Daniels, J.:

Improving sugarcane breeding methods to increase yields. Proc. int. Soc. Sug. Cane Technol. **12**, in press (1965). — 8. FALCONER, D. S.: Introduction to Quantitative Genetics. Edinburgh: Oliver and Boyd 1960. — 9. HANSCHE, P. E., and R. M. BROOKS: Temporal and spacial repeatabilities of a series of quantitative characters in sweet cherry (*Prunus avium* L.). Proc. Amer. Soc. Hort. Sci. **86**, 120—128 (1965). — 10. JOHNSON, H. W., H. F. ROBINSON and R. E. COMSTOCK: Estimates of genetic and environmental variability in soybeans. Agron. J. **47**, 314—318 (1955). — 11. KEHR, W. R., and C. O. GARDNER: Genetic variability in Ranger alfalfa. Agron. J. **52**, 41—44 (1960). — 12. KEMPTHORNE, O.: An Introduction to Genetic Statistics. New York: Wiley & Sons 1957. — 13. KNEEBONE, W. R.: Heritabilities in Sand Bluestem (*Andropogon halii* Hack) as estimated from parental clones and their open-pollinated progenies. Agron. J. **50**, 459—461 (1958). — 14. LIBBY, W. J., and E. JUND: Variance associated with cloning. Heredity **17**, 533—540 (1962). — 15. MODE, C. J., and H. F. ROBINSON: Pleiotropism and the genetic variance and covariance. Biometrics **15**, 518—537 (1959). — 16. PRICE, S.: Critique on apomixis in sugarcane. Econ. Bot. **13**, 67—74 (1959). — 17. PRICE, S.: Cytogenetics of modern sugarcanes. Econ. Bot. **17**, 97—106 (1963). — 18. ROBERTSON, A.: Inbreeding in artificial selection programmes. Genet. Res. **2**, 189—194 (1961). — 19. ROBINSON, H. F., R. E. COMSTOCK and P. H. HARVEY: Estimates of heritability and the degree of dominance in corn. Agron. J. **41**, 353—359 (1949). — 20. SCOSSIROLI, R. E., A. FERRARI and G. HAUSSMAN: Genetic variability for quantitative characters in alfalfa. In: Statistical Genetics and Plant Breeding, ed. by W. D. HANSON and H. F. ROBINSON. National Academy of Sciences — National Research Council Pub. **982**, 597—607 (1963). — 21. SKINNER, J. C.: Controlled pollination of sugarcane. Bur. Sug. Exp. Stas. Q., Tech. Comm. 1959, No. 1, 1—20 (1959). — 22. SKINNER, J. C.: Sugarcane selection experiments. 2. Competition between varieties. Bur. Sug. Exp. Stas. Q., Tech. Comm. 1961, No. 1, 1—26 (1961).