Theoretical and Applied Genetics 39, 79–87 (1969)

Quantitative Genetics of Sugarcane

III. Potential for Sucrose Selection in *Saccharum spontaneum*

A. H. D. BROWN, J. DANIELS, B. D. H. LATTER and M. KRISHNAMURTHI

Summary. 1. A project has been initiated to explore the possibilities of selection for higher levels of sucrose storage in the wild species *S. spontaneum*, using a representative sample of parental clones under conditions of natural crossing.

2. The aim of the programme is the development of superior clones to represent the wild species in conventional breeding programmes, which involve repeated backcrossing to *S. officinarum*.

3. An analysis of the first generation following the intercrossing of 21 parental types without emasculation, has demonstrated extensive genetic variability within and between progeny groups for fibre, sucrose, reducing sugars and yield grade.

4. Fibre and sucrose percent fresh weight are characters of high repeatability (0.4–0.6), and show little evidence of non-additive genetic effects. Individual plant performance for these characters can therefore be taken as a satisfactory basis for selection in this material.

5. The average degree of self-fertilization occurring under conditions of natural crossing has been estimated to be $0.69 \pm .13$, based on analyses of the quantitative genetic data for fibre and sucrose percent fresh weight.

6. The within-family genetic variance observed is of the order of five times that expected if the parental clones were homozygous. Much of the genetic variability induced within-families is therefore due to self-fertilization of heterozygous parental material, though the exact proportion cannot be deduced from the present data.

7. The initial response to selection for increased sucrose percent fresh weight is predicted to be of the order of 50% of the population mean. Comparable responses in subsequent cycles of the programme appear to be possible, provided an adequate degree of outcrossing can be achieved by controlled pollination techniques.

8. The genetic correlations between sucrose and other characters of importance are favourable to the objectives of the breeder, or else of a low order. There is no general relationship between the somatic chromosome number of the parental clones and the mean sucrose level of their progeny.

1. Introduction

Modern commercial hybrid sugarcanes are derived from relatively few original crosses between clones of the wild species *S. spontaneum* and the "noble" canes (*S. officinarum*). Some of the crosses occurred naturally, and others were made by plant breeders when clones of the two species happened to flower at the same time, because of abnormal environmental conditions. Subsequent backcrossing to the noble canes (nobilization) has incorporated extensive genetic variation from *S. officinarum* into commercial breeding populations, but no further sampling of gametes from *S. spontaneum* is normally involved in this process.

The use of interspecific hybridization in sugarcane breeding has enabled the vigour and disease resistance of the wild species to be combined successfully with the capacity for sucrose storage evolved in the noble canes. It nevertheless appears unlikely that anything like the full potential of the method has so far been utilized, either in respect of the sample of wild clones involved, or of the breeding procedures normally used in the "nobilization" process. A possible extension of present breeding methods involves the selection and intercrossing of high sucrose forms of *S. spontaneum*, so that superior parental clones could be deliberately produced to represent the wild parent in nobilization programmes. The possible advantages of this method are twofold: — (1) a wide array of potential *S. spontaneum* genotypes may readily be surveyed and combined before interspecific hybridization is attempted; and (2) the number of generations of backcrossing to *S. officinarum* required for the production of commercial types may be appreciably reduced.

In 1961, sugarcane breeders in Fiji and Australia initiated a project to explore the possibilities of selection for higher levels of sucrose storage in *S. spontaneum*, using a representative sample of parental clones under conditions of natural crossing. In this paper, an analysis is given of the performance of the progeny in the first generation in terms of sucrose content, reducing sugars, fibre and yield grade. An estimate of the average degree of self-fertilization is derived, and the design of future testing and breeding procedures is discussed.

2. The Nature of the Species

Saccharum spontaneum is the most primitive surviving form of the genus *Saccharum*. It includes a wide range of forms with somatic chromosome numbers varying from 40–128 (PANJE and BABU, 1960), though BULL (1965) has presented evidence suggesting that some clones of *S. spontaneum* with high chromosome numbers may be natural hybrids between *S. spontaneum* and *S. officinarum*. The species is endemic in the tropics of Africa, Asia, the East Indies and Micronesia, and extends into the subtropics in the Middle East, Turkmenistan, India and Japan. *S. spontaneum* has a wide range of adaptability, being found in lush tropical jungle, open savannah, sandy river beds, desert, swamps, saline swamps, at altitudes up to 8,000 feet, and at tem-

peratures falling as low as −20 °F. (BRANDES *et al.* 1938; MUKERJEE, 1949; BRANDES, 1950; WARNER and GRASSL, 1958).

The forms of *S. spontaneum* range from 0.5 to 6.5 metres in height, with thin stalks ranging from 0.4 to 2.0 cm in diameter (ARTSCHWAGER, 1942). The stalks are numerous, typically forming dense cane breaks in the wild, and are extremely tough with fibre varying from 25 to 45% of the fresh weight (BULL, 1965). The sugar content of the stalks varies from 1 to 10% of the fresh weight (MUKERJEE, 1949).

The natural breeding system of the species is not known. However, *S. spontaneum* selfs readily, and the self-progeny are vigorous (PANJE and ETHIRAJAN, 1960). Hybrid swarms have also been recorded with *S. robustum* in New Guinea (WARNER and GRASSL, 1958), so that there is some evidence for a combination of inbreeding and outcrossing in the species as a whole.

There are many indications that the noble cultivated canes (*S. officinarum*) evolved from the wild species *S. robustum* in New Guinea, either by the selective agency of primitive man or by natural selection in rain forest (ARTSCHWAGER and BRANDES, 1958; BULL and GLASZIOU, 1963). *S. robustum* is either a specialized form of *S. spontaneum* (JANSEN, 1953; REEDER, 1948) or has evolved from it (GRASSL, 1964). In view of (i) the emergence of *S. officinarum* in an isolated area of the total range of *S. spontaneum* via *S. robustum*, and (ii) recent drastic selection by primitive man for the "noble" type of cane, it would be remarkable if all the genetic potential for sucrose accumulation and yield were represented in present collections of *S. officinarum*. There must exist many useful genes which have not survived this evolutionary progression, and there is an obvious need for a systematic study of the breeding potential of primitive forms (DANIELS, 1965).

3. Materials and Methods

The collection of 41 clones of *S. spontaneum* available at the commencement of this project has a wide range of flowering time in Fiji (January to May), and only 21 of the forms flowered sufficiently close together to be included in polycrosses. These clones are listed in Table 1, together with their country of origin and somatic chromosome numbers.

The parental clones were growing in portable drums, and as soon as four clones were flowering simultaneously, a polycross was set up by moving these particular drums together and intermingling the flowers as much as possible. As other clones flowered they were included in the polycross, but at no stage were there more than 8 clones flowering at the same time. No attempt was made to induce male sterility in the flowers from which seed was to be harvested.

The seed was collected in mosquito net bags, and when mature was sown in flats of sterile soil in the greenhouse. When approximately 6 cm in height the seedlings were transplanted to 5 cm diameter metal pots, and at the same time single eye setts of the female parent clones were planted in pots. Two parents, viz. Mbeya and Tukuyu 2, were missing at this stage having succumbed to downy mildew disease (*Sclerospora sacchari*). The material was transplanted to the field in November 1963, when the seedlings were approximately 45 cm in height.

Table 1. *Origin and chromosome numbers of clones included in polycrosses*

Clone	Country of Origin	Chromosome Number (2 n)	Reference*
Burma	Burma	96	(5)
Kloet	Java	112	(2)
Krakatau	Java	126	(1)
Mandalay	Burma	96	(6)
Mbeya	Tanganyika	128	(5)
Mol 488	Java	112	(5)
Mol 4009	Java	112–113	(5)
Mol 5903	New Guinea	ca. 80	(4)
Mol 5904	New Guinea	80	(4)
28 NG 101	New Guinea	80	(4)
51 NG 2	New Guinea	80	(4)
51 NG 26	New Guinea	82	(4)
SES 205A	West Bengal	64	(3)
SES 356	Nepal	60	(3)
Sumatra 1	Sumatra	112	(8)
Sumatra 2	Sumatra	105–107	(8)
Tabongo	Celebes	80	(1)
Tukuyu 2	Tanganyika	120–124	(8)
USDA 1286	Java	112	(8)
US 56-4-1	Thailand	96	(7)
US 56-13-7	Thailand	ca. 80	(7)

* *References:* (1) BREMER (1932); (2) BREMER (1961); (3) PANJE and BABU (1960); (4) PRICE (1957a); (5) PRICE (1957b); (6) PRICE (1957c); (7) PRICE (1959); (8) PRICE (pers. comm.).

The field design consisted of 25 blocks, each of 21 sub-blocks, the 21 progeny groups being allocated at random to the sub-blocks separately within each block. Within each sub-block, 10 seedlings and a single stool of the corresponding female parent were planted at a spacing of 4′6″, the position of the parent clone being chosen at random. At harvest in August 1964, there were 4,976 surviving seedling progeny, and 432 parent stools.

Each plant was given a visual grade for yield (total weight of stalks) at harvest, and the offspring were subjectively classified into two groups, viz. those judged by comparison with the female parent to be the result of self-fertilization, and those apparently produced by outcrossing. Determinations were then made of fibre, total sugars and reducing sugars as a percentage of the fresh weight of the stalks, for each plant in the experiment (BROWN et al., 1968).

4. Statistical Analysis

The basic analysis of variance of measures of *progeny* performance is set out in Table 2, together with the expectations of the mean squares in terms

Table 2. *The analysis of variance of progeny performance*

Source of variation	d. f.	Expectation of mean square*
Blocks	24	$\sigma_e^2 + k\sigma_i^2 + 21\,k\sigma_b^2$
Families	20	$\sigma_e^2 + k\sigma_i^2 + 25\,k\sigma_f^2$
Blocks × families	480	$\sigma_e^2 + k\sigma_i^2$
Within sub-blocks	4,451	σ_e^2

* $k = 9.5$ denotes the harmonic mean number of progeny per sub-block.

of four components of variance: (i) σ_b^2, measuring the extent of environmental variation among blocks; (ii) σ_f^2, measuring the genetic variation among "true" family means for the character concerned; (iii) σ_i^2, a component which includes both family x blocks interaction effects and environmental variation among sub-blocks within blocks; and (iv) σ_e^2, measuring the extent of variation within sub-blocks, due to both genetic and environmental variation within progeny groups. Because of the unequal numbers of surviving progeny per sub-block, the analysis is based on sub-block means, combined with a direct estimate of the variance within sub-blocks.

A number of stools of the parental clones were also missing at harvest, and analyses of *parental* performance were therefore carried out without regard to the block structure of the experiment. The following components of variance were then derived: (i) σ_g^2, measuring the extent of genetic variation among the parental clones, and (ii) σ_w^2, the residual variance among stools of the same clone, *including* environmental variation among blocks. It will be necessary to pay particular attention to the composition of this latter component in comparisons made with statistics derived from other analyses.

The covariance between parent and progeny mean performance has been estimated (i) from the mean values for both parents and progeny averaged over all blocks (Table 3), and (ii) from the individual values for parental performance, together with the corresponding sub-block progeny mean values, i.e. a pooled within-blocks covariance, including both genetic and environmental effects. An unbiased estimate of the *genetic* covariance between parent and progeny mean has then been derived from these two measures.

5. Results

In Table 3 are set out the mean values for each of the characters observed, for both parent clones and the derived progeny groups. The approximate standard error of estimation of an individual mean value is given at the foot of the Table, together with the overall means of each population, excluding Mbeya and Tukuyu 2. Finally, the mean difference between

Table 3. *Mean performance of parent and progeny clones*

Parent clone	Fibre % fresh weight		Sucrose % fresh weight		Reducing sugars % fresh weight		Yield grade	
	Parent	Progeny	Parent	Progeny	Parent	Progeny	Parent	Progeny
Burma	36.5	33.6	3.56	3.37	0.70	0.98	5.8	6.6
Kloet	31.5	32.7	2.90	3.51	0.68	0.80	5.5	6.1
Krakatau	30.1	31.6	3.59	4.06	0.91	0.89	4.1	5.9
Mandalay	34.3	33.3	2.58	2.63	1.10	1.48	5.5	4.5
Mbeya	†	36.0	†	2.28	†	1.66	†	5.0
Mol 488	32.0	33.3	2.37	3.12	0.93	1.00	4.9	6.4
Mol 4009	30.5	32.5	3.68	3.79	0.56	0.76	4.2	5.9
Mol 5903	34.4	34.0	2.47	2.82	0.51	0.60	5.2	5.6
Mol 5904	34.6	35.5	3.29	3.81	0.77	0.75	5.2	6.1
28 NG 101	35.4	33.8	3.43	3.66	0.81	0.80	5.8	6.7
51 NG 2	33.4	33.3	2.51	2.65	0.69	0.71	3.6	5.3
51 NG 26	32.6	32.5	3.22	3.51	0.93	1.09	2.6	5.7
SES 205A	31.6	32.3	3.79	3.81	0.84	0.88	5.3	5.2
SES 356	38.8	37.8	2.72	2.93	0.78	0.82	2.0	3.4
Sumatra 1	28.7	28.8	5.58	5.57	0.85	1.22	4.4	5.0
Sumatra 2	35.4	34.2	4.13	3.97	0.62	0.84	4.5	6.6
Tabongo	33.7	33.1	3.78	3.96	1.02	1.01	5.2	6.8
Tukuyu 2	†	31.4	†	3.39	†	1.47	†	6.2
USDA 1286	31.8	33.4	3.48	3.81	0.74	0.73	5.6	6.4
US 56-4-1	35.4	33.4	4.35	4.35	0.61	0.71	6.3	6.4
US 56-13-7	32.0	32.4	4.78	4.45	0.71	1.14	4.5	3.8
Approx. S.E.	0.55	0.36	0.15	0.10	0.05	0.05	0.4	0.2
Overall Means*	33.3	33.2	3.48	3.67	0.78	0.91	4.8	5.7
Progeny-Parent Mean Difference	−0.1 ± .14		+.19 ± .03		+.13 ± .02		+0.9 ± 0.1	

† Parental clones not included in experiment.
* Values for Mbeya and Tukuyu 2 are not included in the overall progeny means.

Table 4. *Components of variance derived from analysis of parental and progeny generations*

Component		Fibre % fresh weight	Sucrose % fresh weight	Reducing sugars % fresh weight	Yield grade
Parental clones					
Parents	(σ_g^2)	5.7 ± 1.9	0.67 ± .22	.019 ± .006	1.07 ± .38
Residual*	(σ_w^2)	7.8 ± 0.5	0.54 ± .04	.118 ± .008	2.98 ± .21
	Total	13.5 ± 1.9	1.21 ± .22	.136 ± .011	4.05 ± .42
Progeny groups					
Blocks	(σ_b^2)	1.8 ± 0.6	0.08 ± .02	.063 ± .018	0.09 ± .04
Families	(σ_f^2)	2.9 ± 0.9	0.52 ± .16	.075 ± .024	0.80 ± .25
Interaction	(σ_i^2)	2.5 ± 0.2	0.19 ± .02	.065 ± .005	0.64 ± .06
Residual	(σ_e^2)	7.6 ± 0.2	0.55 ± .01	.090 ± .002	3.00 ± .06
	Total	14.8 ± 1.1	1.34 ± .16	.293 ± .029	4.53 ± .26
P-O Covariance					
Genetic	(cov_g)	3.5 ± 1.2	0.55 ± .18	.022 ± .009	0.58 ± .27
Environmental†	(cov_e)	2.1 ± 0.2	0.26 ± .02	.052 ± .005	0.18 ± .08
	Total	5.6 ± 1.2	0.81 ± .18	.075 ± .010	0.76 ± .28

* Includes environmental variation among blocks.
† Environmental covariance between sub-blocks within blocks.

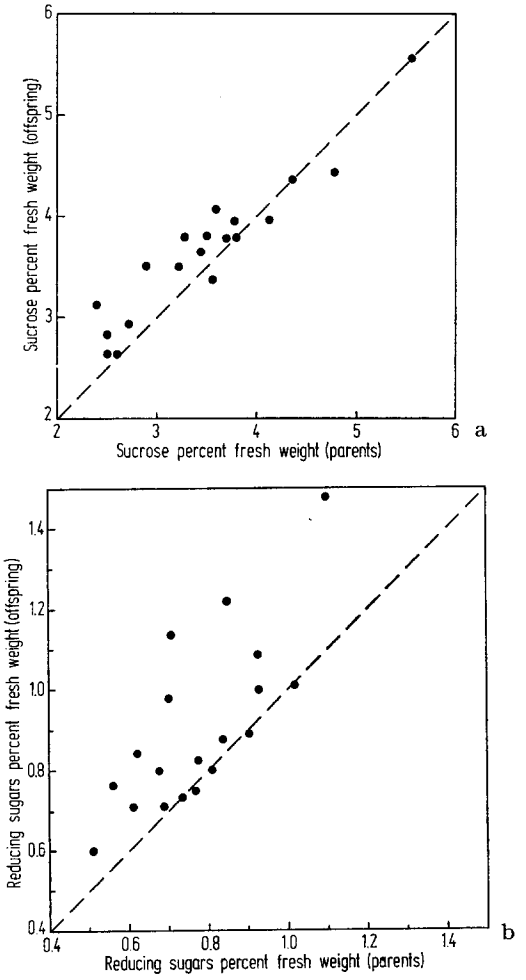

Fig. 1. The relationship between polycross progeny mean and female parent performance in *S. spontaneum*: (a) sucrose percent fresh weight; (b) reducing sugars percent fresh weight (Table 3)

the progeny and parent populations is given for each character, with the corresponding standard error.

The design of the experiment was such that comparisons of parent and progeny mean performance can be made with considerable accuracy. For fibre and sucrose percent fresh weight, the overall means of progeny and parents are in close agreement (Table 3), though the difference in the case of sucrose is statistically significant. By comparison, reducing sugars shows pronounced non-additive behaviour, with an overall progeny mean which exceeds that of the parents by 17%, and a range of variation among progeny means which is conspicuously greater than that among parental clones (Figure 1). The mean yield grade of the progeny seedlings is also appreciably greater than that of the parental setts, and it seems likely that subjective assessment of yield has been influenced by the difference between the two types of experimental material.

The components of variance derived from the analyses of parental values, and the analyses of progeny performance, are given in Table 4 for each of the four characters, together with the components of covariance describing the relationship between parental value and progeny mean. Significant genetic variation among parental clones and among progeny group means is shown by all characters, and the genetic covariance between parental and progeny mean performance is also significant in each case. Note also that the environmental covariances between parent and offspring are all significant, because of the physical association of parent stools and progeny seedlings in each sub-block of the experiment.

In Table 5 are presented estimates of the important genetic and clonal parameters which can be derived from the components in Table 4; viz. measures of

Table 5. *Derived estimates of genetic and clonal parameters*

Parameter	Fibre % fresh weight	Sucrose % fresh weight	Reducing sugars % fresh weight	Yield grade
Repeatability (r_c)				
Parents	0.42 ± .09	0.55 ± .08	0.14 ± .05	0.26 ± .07
Progeny*	0.47 ± .05	0.60 ± .06	0.60 ± .07	0.34 ± .05
Within-family**	0.34 ± .05	0.34 ± .05	0.46 ± .04	0.20 ± .06
P-O Regression (b_{op})	0.26 ± .06	0.45 ± .10	0.16 ± .06	0.14 ± .06
Intra-family correlation†	0.20 ± .05	0.39 ± .08	0.26 ± .06	0.18 ± .05

† The ratio of the between-family component to the total phenotypic variance.
* $1 - \sigma_w^2/(\sigma_b^2 + \sigma_f^2 + \sigma_i^2 + \sigma_e^2)$ ** $1 - \sigma_w^2/(\sigma_b^2 + \sigma_i^2 + \sigma_e^2)$.

clonal repeatability (BROWN *et al.*, 1968) for the parents, for the progeny population as a whole, and for individuals within progeny groups; the *genetic* regression of offspring on parent value; and the intraclass correlation for the progeny population. Estimates of repeatability for the progeny generation have been derived by assuming the environmental variation to be equal to σ_w^2, the measure of variability within parent clones.

It should be emphasized that the individual plant is the unit of observation in this study (cf. BROWN *et al.*, 1968). The repeatability of a single measurement on a parental individual is then the ratio of the component of variance among parental clones (σ_g^2) to the total phenotypic variance among stools ($\sigma_g^2 + \sigma_w^2$), including environmental variation among blocks. For sucrose and fibre the parental repeatability values are high, as are the corresponding measures for the progeny generation, indicating that individual plant performance is a satisfactory basis for selection in this material (LATTER, 1964).

Within-family repeatability provides a direct measure of the genetic variation induced within progeny groups by the polycross procedure. The observed values for fibre, sucrose and reducing sugars clearly indicate that selection among genotypes within families is likely to be an effective procedure. In a later section we will discuss selection schemes designed to capitalize particularly on within-family genetic variability for sucrose percent fresh weight. However, at this point it is appropriate to discuss in some detail the genetic composition of families produced by polycrossing without emasculation in *S. spontaneum*.

The degree of self-fertilization

An estimate of the average degree of self-fertilization under polycrossing can be derived from a comparison of the component of variance among progeny group means (σ_f^2) and the genetic parent-offspring covariance (cov_g), for characters showing additive genetic variation (LATTER, 1965a, b). Fibre and sucrose percent fresh weight are acceptable traits for this purpose in the present study, but it would be inappropriate to attempt similar calculations with reducing sugars or yield grade in view of their pronounced non-additive behaviour.

It is necessary to assume: (i) that genetic effects are additive for the trait under examination; (ii) that the polycross procedure gives rise to a proportion 1-S of offspring produced by outcrossing without restriction of male parentage, and a proportion S produced by self-fertilization; and (iii) that S is the same for all parental clones. It can then readily be shown (LATTER, 1965a) that the ratio σ_f^2/cov_g has expectation $^1/_2 (1 + S)$. The derivation of estimates of this ratio for fibre and sucrose percent fresh weight is given in detail in Table 6, leading to a combined estimate of the degree of selfing of $\hat{S} = 0.69 \pm 0.13$.

Assumptions (ii) and (iii) are unlikely to be strictly true in this particular study. It is readily shown that an estimate of $\hat{S}$ derived in the manner indicated will provide an *overestimate* of the average degree of self-fertilization, if either of these two assumptions is invalid. However, in each case the bias is likely to be of a minor order.

Table 6. *Estimation of the degree of self-fertilization*

Character	σ_f^2 †	cov_g	σ_f^2/cov_g	$\hat{S}$
Fibre % fresh weight	2.83 ± .91	3.54 ± 1.22	0.80 ± .12	0.69 ± .13
Sucrose % fresh weight	0.49 ± .15	0.55 ± .18	0.89 ± .07	

† Component of variance among progeny groups excluding those derived from Mbeya and Tukuyu 2.

On the basis of a subjective classification of the offspring by visual comparison with the corresponding parental clone, it has been estimated that the average degree of self-fertilization was of the order of 90 to 94%. No great reliance can be placed on the absolute magnitude of this figure, for in a comparable trial involving clonal replication, a given genotype has often been classified both as a self- and a crossprogeny in

Table 7. *Correlation coefficients derived from the analysis of the progeny generation. Above diagonal: genetic correlations. Below diagonal: phenotypic correlations*

	Fibre	Sucrose	Reducing sugars	Yield grade
Fibre		− .65* ± .14	− .18 ± .22	− .15 ± .22
Sucrose	− .20* ± .02		− .15 ± .21	+ .14 ± .22
Reducing sugars	− .05* ± .02	− .15* ± .02		− .33 ± .20
Yield grade	+ .07* ± .02	+ .12* ± .02	− .05* ± .02	

* Significantly different from zero in absolute value.

different blocks of the experiment. However, the observations do provide corroborative evidence of a high incidence of self-fertilization in this material under conditions of natural crossing.

Genetic and Phenotypic Correlations

In Table 7 are given the genetic correlation coefficients, based on components of variance and covariance between progeny groups, and the corresponding phenotypic correlation derived from the total mean squares and products of the analyses of progeny performance. It can be seen that the only relationship of any consequence is that between fibre and sucrose. The environmental correlation between these two variables, estimated from within-clone variability in the parental population, is nonsignificant (−.05 ± .05). If this estimate is taken to be appropriate to the progeny population, the clonal correlation between fibre and sucrose can be calculated to be −.34 ± .07.

This last figure is of the same order as that given by BROWN *et al.* (1969) for the corresponding clonal correlation in a commercial hybrid breeding population, viz. −.46 ± .08. Note, however, that both the genetic and phenotypic relationships between sucrose and reducing sugars are of a particularly low order in the present unselected population of *S. spontaneum*. This contrasts with the close negative associations found by BROWN *et al.* (1969) in a selected hybrid population of high mean sucrose level.

6. Discussion

Heterozygosity of the Parental Clones

For all four characters measured, extensive genetic variation has been detected *within* progeny groups produced by polycrossing without emasculation. From the data of Table 4, the estimated ratios of between-family genetic variance to total genetic variance in the progeny population are 0.41, 0.65, 0.43 and 0.52 for fibre, sucrose, reducing sugars and yield grade respectively, with a mean figure of 0.50. It has in addition been deduced that the average degree of self-fertilization in this material is of the order of 70%, and it can be shown that these two observations imply an appreciable average degree of heterozygosity in the parental genotypes.

If all the parental clones were *homozygous*, the variance component among families would be expected to be $^1/_4 (1 + S)^2 \sigma_g^2$, for an additive genetic character (LATTER, 1965 a), where S denotes the degree of self-fertilization. The total genetic variance in the progeny population would be equal to $^1/_2 (1+S) \times \sigma_g^2$, and the ratio of between-family to total genetic variance is therefore expected to be $^1/_2 (1+S)$. With $S = 0.69$ the ratio is 0.84, compared with the observed figure of 0.50. The within-family genetic variance observed is therefore of the order of 5 times that anticipated on the basis of the hypothesis of homozygosity, and there can be no doubt that much of the genetic variance induced within families is due to self-fertilization of heterozygous parental material.

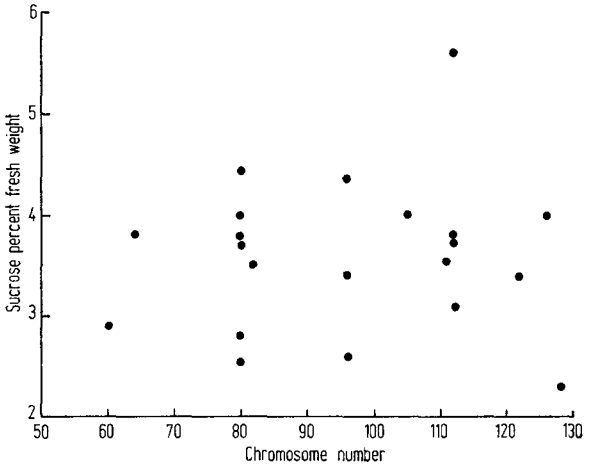

Fig. 2. The relationship between the somatic chromosome number of parental clones, and the mean sucrose level of their polycross progeny

The Potential for Sucrose Selection

In this synthetic population of *S. spontaneum*, the ultimate objective is the breeding of superior genotypes to represent the species in nobilization programmes. In particular, it is the aim of the project to produce clones with higher levels of sucrose storage than are to be found in naturally occurring forms, by recurrent cycles of interbreeding and selection. From Figure 2 it can be seen that there is no overall relationship between the somatic chromosome number of the parental clones and the mean sucrose level of their progeny. No general tendency towards an increase in chromosome number is therefore anticipated as the result of selection. However, in this first generation, any concentration on progeny of the high-sucrose parent Sumatra 1 in the choice of breeding material will obviously cause some increase in mean chromosome number.

The overall distribution of sucrose percent fresh weight in the progeny population is shown in Figure 3,

together with the parental clone means. Of the total observed variance, 60% has been shown to be genetic in origin. It can therefore be predicted that truncation selection of 100 elite clones on the basis of sucrose level (a selection intensity of 2%, with a selection differential equal to 3.2 units) should change the mean of the population from its initial value of 3.6% to 5.5%. This must be judged a very substantial rate of gain, and with an adequate degree of outcrossing in subsequent cycles of the programme, there is no obvious reason why comparable responses should not be realized in each generation.

Under truncation selection of this intensity (100/4976), approximately 56% of the chosen clones are

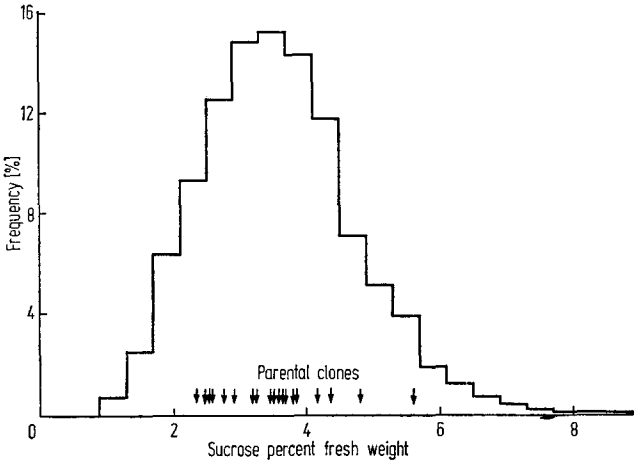

Fig. 3. The frequency distribution of individual measurements of sucrose percent fresh weight in the progeny generation, together with the parental clone means. Approximately 60% of the total progeny variance has been estimated to be genetic in origin

derived from Sumatra 1 as female parent, and 7 of the 21 original clones are not represented as female parents. Though these latter clones may have made some contribution as pollen parents to the genetic constitution of the selected clones, it appears that elimination of potential parents on the basis of their own performance would be a desirable modification of the initial screening procedure. The observed correlation of parental mean and progeny mean value for sucrose in this experiment was $0.95 \pm .02$ (Figure 1 a). It must be emphasized, however, that the parental means in this study are derived from a randomized field trial involving 25 replications, and a comparable degree of precision would be necessary if a collection of clones of *S. spontaneum* were to be screened for sucrose without progeny testing. The possibility also exists that important specific combining ability effects could remain undetected.

If a breeding population were to be based on a very small sample of the available collection of forms of *S. spontaneum*, a disproportionate contribution from some individual parents in the first generation of selection would clearly be undesirable. Prior screening of the collection would largely eliminate this problem, but a combination of between- and within-family selection, giving equal representation to each selected polycross family, would achieve the same objective. The sacrifice in terms of selection response in the first generation, for a range of between-family selection intensities from 0.50 to 0.10, can be gauged from Table 8. The comparable response predicted for truncation selection based on individual performance is 1.92 units. Within-family selection alone is expected to give a response of 0.75 units, based on the deduction that 34% of the within-family variance is genetic in origin.

Table 8. *Predictions of initial rate of response in percent sucrose under alternative screening procedures*†

Selection intensity*		Predicted response to selection		
Between families	Within families	Between families	Within families	Total response
0.50	0.04	0.57	0.66	1.23
0.25	0.08	0.89	0.57	1.46
0.20	0.10	1.08	0.54	1.62
0.10	0.20	1.42	0.43	1.85

* The total selection intensity in each case is 0.02.
† Predictions are based on estimates of clonal repeatability, and therefore apply strictly to selection without recombination.

A further problem arising in this study concerns the status of the high-sucrose parent Sumatra 1. If this clone were a natural hybrid between *S. spontaneum* and *S. officinarum*, it could be undesirable to include its progeny in further cycles of the programme. The only satisfactory definition of a "true" *S. spontaneum* clone in this particular context appears to be a purely operational one, viz. that the observed fibre and sucrose levels of the clone be outside the range of first nobilization crosses. On this basis, Sumatra 1 must be judged a legitimate member of the present population.

The possibility remains that a backcross derivative may be included in the breeding population by the use of the above criterion, so that *S. officinarum* chromosomes would be present at low frequency in the population. If the frequency of pairing between *S. officinarum* and *S. spontaneum* chromosomes is higher under these circumstances than is the case in a conventional nobilization programme, useful genetic recombinants may occur and be selected on the basis of yielding ability and capacity for sucrose storage. However, if there is a complete absence of pairing between chromosomes of the two species, it may not be possible fully to realize the objectives of the project as far as sucrose level is concerned.

The results of this study emphasize the need for more extensive outcrossing in the early cycles of the programme. ALLARD and HANSCHE (1964) have in

fact recommended the use of interstrain hybrids in the synthesis of mass reservoirs with low levels of natural outcrossing, to expedite the formation of an effective recombinational system. Techniques have recently been developed by which pollen shedding can be controlled, and self-fertilization largely prevented in *S. spontaneum* (Krishnamurthi, 1967), and the experimental control of flowering in the species is now much better understood. Many of the operational difficulties in the project may very likely be overcome in the immediate future by the use of these procedures.

Acknowledgments

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

7. Zusammenfassung

1. Es wird über ein begonnenes Programm zur Erforschung der Möglichkeiten einer Selektion auf höheren Sucrosegehalt bei der Wildspecies *Saccharum spontaneum* unter Verwendung eines repräsentativen Satzes von Elternklonen unter natürlichen Kreuzungsbedingungen berichtet.

2. Das Ziel ist die Entwicklung von besseren Klonen, um die Wildspecies in konventionelle Zuchtprogramme einzuführen unter Einschluß von wiederholter Rückkreuzung mit *S. officinarum*.

3. Eine Analyse der nach Kreuzung von 21 Elterntypen ohne Emaskulation folgenden 1. Generation hat eine beträchtliche genetische Variabilität innerhalb und zwischen den Nachkommenschaftsgruppen bezüglich des Faseranteils, Sucrosegehalts, Gehalts an reduzierenden Zuckern und Ertrags ergeben.

4. Der Faser- und Sucroseprozentsatz im Frischgewicht sind Merkmale mit hoher Wiederholbarkeit, sie zeigen nur geringe nichtadditive genetische Effekte. Für diese Merkmale kann daher der Ertrag der Einzelpflanze als befriedigende Basis für eine Selektion in diesem Material angesehen werden.

5. Der durchschnittliche Grad der Selbstbefruchtung bei natürlicher Kreuzung wurde auf der Grundlage von Analysen quantitativer genetischer Daten für Faser- und Sucrosegehalt im Frischgewicht auf $0.69 \pm .13$ geschätzt.

6. Es wurde festgestellt, daß die genetische Varianz innerhalb der Familie $5\times$ so groß wie die ist, die erwartet wurde, wenn die Elternklone homozygot waren. Ein großer Teil der genetischen Variabilität innerhalb der Familien ist daher auf Selbstbefruchtung von heterozygotem Elternmaterial zurückzuführen, der genaue Anteil kann allerdings aus den vorliegenden Daten nicht geschlossen werden.

7. Die Anfangsergebnisse der Selektion auf gesteigerten Sucrosegehalt im Frischgewicht werden auf 50% des Populationsdurchschnitts geschätzt. Vergleichbare Daten im weiteren Programm scheinen möglich, vorausgesetzt, daß ein entsprechender Grad der Fremdbefruchtung durch kontrollierte Bestäubung möglich ist.

8. Die genetischen Korrelationen zwischen dem Sucrosegehalt und anderen wichtigen Merkmalen sind günstig für die Erreichung der Zuchtziele. Es besteht keine generelle Beziehung zwischen der somatischen Chromosomenzahl der Elternklone und dem durchschnittlichen Sucrosegehalt ihrer Nachkommenschaft.

References

1. Allard, R. W., and P. E. Hansche: Some parameters of population variability and their implications in plant breeding. Adv. Agron. **16**, 281–325 (1964). — 2. Artschwager, E.: A comparative analysis of the vegetative characteristics of some variants of *Saccharum spontaneum*. U. S. Dept. Agric. Tech. Bull. No. 811 (1942). — 3. Artschwager, E., and E. W. Brandes: Sugarcane (*Saccharum officinarum* L.). Origin, classification, characteristics and descriptions of representative clones. U. S. Dept. Agric. Agriculture Handbook No. 122 (1958). — 4. Brandes, E. W.: Changes in seasonal growth gradients in geographically displaced sugarcane. Proc. int. Soc. Sug. Cane Technol. **7**, 1–32 (1950). — 5. Brandes, E. W., G. B. Sartoris, and C. O. Grassl: Assembling and evaluating wild forms of sugarcane and closely related plants. Proc. int. Soc. Sug. Cane Technol. **6**, 128–153 (1938). — 6. Bremer, G.: On the somatic chromosome numbers of sugarcane forms and the chromosome number of indigenous Indian canes. Proc. int. Soc. Sug. Cane Technol. Bull. No. 20 (1932). — 7. Bremer, G.: Problems in breeding and cytology of sugarcane. I. A short history of sugarcane breeding. The original forms of *Saccharum*. Euphytica **10**, 59–78 (1961). — 8. 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**, 361–368 (1968). — 9. Brown, A. H. D., J. Daniels, and B. D. H. Latter: Quantitative genetics of sugarcane. II. Correlation analyses of continuous characters in relation to hybrid sugarcane breeding. Theoret. Applied. Genet. **39**, 1–10 (1969). — 10. Bull, T. A.: The taxonomic significance of quantitative morphological characters and physiological studies in *Saccharum*. Proc. int. Soc. Sug. Cane Technol. **12** (1965, in press). — 11. Bull, T. A., and K. T. Glasziou: The evolutionary significance of sugar accumulation in *Saccharum*. Aust. J. biol. Sci. **16**, 737 to 742 (1963). — 12. Daniels, J.: Improving sugarcane breeding methods to increase yields. Proc. int. Soc. Sug. Cane Technol. **12**, (1965, in press). — 13. Grassl, C. O.: Problems relating to the origin and evolution of wild and cultivated *Saccharum*. Indian J. Sugarcane Res. & Devlpmt. **8**, 106–116 (1964). — 14. Jansen, P.: Notes on Malaysian grasses. I. Reinwardtia **2**, 225–350 (1953). — 15. Krishnamurthi, M.: Personal communication (1967). — 16. Latter, B. D. H.: Selection methods in the breeding of cross-fertilized pasture species. In: Grasses and Grasslands (C. Barnard, ed.), chapter 10, pp. 168–181. London: MacMillan 1964. — 17. Latter, B. D. H.: Quantitative genetic analysis in *Phalaris tuberosa*. I. The statistical theory of open-pollinated progenies. Genet. Res. **6**, 360–370 (1965a). — 18. Latter, B. D. H.: Quantitative genetic analysis in *Phalaris tuberosa*. II. Assortative mating and maternal effects in the inheritance of date of ear emergence, seed weight and seedling growth rate. Genet. Res. **6**, 371–386 (1965b). — 19. Mukerjee, S. K.: Studies in *Saccharum spontaneum* and allied grasses. I. Preliminary report on collection. Indian J. Genet. Plant Br. **9**, 47–58 (1949). — 20. Panje, R. R., and C. N. Babu: Studies in *Saccharum spontaneum*. Distribution and geographical association of chromosome numbers. Cytologia **25**, 152–172 (1960). — 21. Panje, R. R., and A. S. Ethirajan: Studies in *Saccharum spontaneum*. Preliminary studies in inbreeding. Proc. int. Soc. Sug.

Cane Technol. **10**, 751—754 (1960). — 22. PRICE, S.: Cytological studies in *Saccharum* and allied genera. II. Geographical distribution and chromosome numbers in *S. robustum*. Cytologia **22**, 40—52 (1957a). — 23. PRICE, S.: Cytological studies in *Saccharum* and allied genera. III. Chromosome numbers in interspecific hybrids. Bot. Gaz. **118**, 146—159 (1957b). — 24. PRICE, S.: Cytological studies in *Saccharum* and allied genera. IV. Hybrids from *S. officinarum* (2n = 80) × *S. spontaneum* (2n = 96). J. Hered. **48**, 141—145 (1957c). — 25. PRICE, S.: Cytological studies in *Saccharum* and allied genera. V. Chromosome numbers in *Saccharum*, *Erianthus*, *Narenga* and *Sclerostachya* from Thailand and Vietnam. Cytologia **24**, 342 to 347 (1959). — 26. REEDER, J. R.: The *Gramineae-Panicoideae* of New Guinea. J. Arnold Arb. **24**, 257—392 (1948). — 27. WARNER, J. N., and C. O. GRASSL: The 1957 sugarcane expedition to Melanesia. Hawaiian Planters' Rec. **55**, 209—236 (1958).

A. H. D. BROWN, J. DANIELS,
M. KRISHNAMURTHI
Agricultural Experiment Station
South Pacific Sugar Mills Ltd.,
Lautoka (Fiji)

B. D. H. LATTER
Division of Plant Industry,
CSIRO, Canberra (Australia)