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The Mass Selection Reservoir and Sugarcane Selection

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Summary. A method is proposed which extends the mass reservoir technique to the breeding of clonally propagated crops. The first phase produces a diverse array of clones by sexual recombination. Then the selection phase is conducted in one genotypically heterogeneous population. Such a population is termed a *mass selection reservoir* (MSR). In each generation of agricultural bulk planting, competitive ability is supplemented with a regime of artificial selection among propagules for fixing the rate at which each component genotype is advanced.

A MSR programme has been initiated in sugarcane in Fiji. An analysis of the variation in selection characters demonstrated significant clonal effects at the single stalk (propagule) level. Sugar concentration was particularly repeatable on this basis. After two generations of selection, the MSR's performance at the population level at least equalled that of the best current commercial clone, Ragnar. It is therefore likely to include superior isolates of one or more clones.

Two possible artificial selection methods are compared. These arise from either a linear (L) or multiplicative (M) combination of the two major selection criteria, sugar concentration and stalk weight. Although the M series differs genotypically from the L series, there is little difference to date in their respective population performances.

Introduction

The mass reservoir is a modern approach to the problem of maintenance and exploitation of germplasm variability (Harlan, Martini and Stevens, 1940; Suneson, 1956; Simmonds, 1962) although its origins go back at least to the bulk breeding methods of Nilsson-Ehle (Allard, 1960). In the sexually reproducing crops for which it was devised, two basic processes continually modify the population, namely, *recombination* and *natural selection* (Allard and Hansche, 1964). Recombination can assemble favourable gene complexes from initially ill-adapted introductions. Natural selection improves the population performance, particularly when the breeder includes selection for economically desirable characters. After a number of cycles, either the composite population or various isolates from it can furnish commercial varieties (Allard, 1967).

The extension of this principle to clonally propagated crops such as sugarcane is not readily apparent. The mass reservoir technique relies on a strong relationship between sexual reproductive fitness and the economic value of the product. Secondly, each cycle of selection necessarily requires a cycle of sexual reproduction and therefore genetic recombination. Thus the genotypic array in any particular generation is transient. In clonally propagated crops, sexual reproductive fitness has no obvious relation to economic worth and selection can operate on clones independent of genetic recombination.

We propose that the mass reservoir method can be applied to clonally propagated crops in two distinct phases. In the first phase, dynamic recombination is achieved by the usual breeding methods for intercrossing desirable parents. The second phase is one of clonal selection achieved by differential propagation of clones in a composite population. We will term such a population, a *mass selection reservoir* (MSR).

The MSR is a population of many clones of near commercial type which are asexually propagated as fixed genotypic entities. The clonal composition in successive generations changes in response to the generations of selection. The object is to produce either superior isolates or a mixed population for commercial exploitation. This paper describes the MSR procedure and the population response which has occurred in a sugarcane population. The genotype response has been described elsewhere (Brown, 1971).

Materials and Methods

The base population comprised 534 different sugarcane clones chosen from among 10,191 original seedlings in 1966. Most commercial hybrid seedling populations come from a wide variety of cross types (Brown, Daniels and Latter, 1968). They usually contain a high proportion of obviously inferior genotypes, and so a single stalk was cut from only 5102 of the 10,191 seedlings. The selected stalks were processed by an objective screening method to select the entries for the MSR programme. This included steps which can be typical of a MSR selection procedure.

(1) 838 (16%) of the stalks were discarded because their cross-sectional area was less than 4.0 cm². This thickness was the approximate 5% lower confidence limit estimate of stalk thickness shown by 200 stalks of a standard variety, Homer.

(2) Each stalk was punched to extract a 2–5 ml. juice sample and the total soluble solids (mostly sucrose) concentration estimated as °brix using a hand refractometer. The stalks were separated into unit °brix piles (e.g. 26, 25 . . . 10° brix).

(3) The single stalks were weighed and the heaviest stalks in each class were selected as follows:

Brix Class	*24.5*	*23.5*	*22.5*	*21.5*	*20.5*	*19.5*	*18.5*	*17.5*	Total
No. Stalks	367	902	1100	974	523	256	87	55	4264
No. Selected	282	292	161	78	37	21	2	—	873

(4) The base population of 534 stalks (clones) was chosen from these 873 after assaying the top four vegetative buds (as single-eye setts in four separate pots) for germination ability and the remainder of each stalk for acceptably low fibre % fresh weight. Each clone chosen was allocated a unique number for future identification purposes.

Two months later, one pot of each clone was planted at random in the field, $1^1/_2$ feet apart in rows $4^1/_2$ feet wide. An equal number of pots of the best commercial clone currently available (Ragnar) was also planted to monitor the effect of subsequent selection. The MSR and the commercial clone were compared in a randomized complete block design with 11 replications and 50 plants per plot. All plants received fertilisation at the rate of 350 lbs. sulphate of ammonia and 220 lbs. superphosphate per acre.

The site of this field trial is a steep hillside near Penang, Fiji. The soil is shallow and phosphate deficient and exposed to the wind for many months of the year.

In 1967 the $10^1/_2$ months old crop was harvested and the following variables estimated for each stalk,

x_1 = sugar concentration in the juice (°brix)
x_2 = weight of single stalks (kilograms)
x_3 = cross-sectional area (C.S.A.) of the stalk (square cms.).

The most appropriate measure of the economic value of a single stalk is the weight of sugar it contains ($x_4 = 10\, x_1\, x_2$ grams sugar per stalk). The selection regime may be based on x_4 itself, which is essentially a multiplicative combination of two components x_1 and x_2. In this case the next generation designated M-1, consists of the stalks with the highest x_4 values.

However, the task of measuring both x_1 and x_2 on a large number of stalks is a formidable one. Therefore, the following sequential procedure was tested. Let n_s represent the population size, i.e. the number of stalks which each furnish a single plant or stool for each generation at the time of planting into the field. At harvest, the crop will approximate to $N \simeq 5\, n_s$ stalks. Each stalk is labelled according to its clone origin from a field plan and is processed as follows: — (1) Discard about 20% using a rapid screening for stalk C.S. area. (2) Measure the sugar concentration of each of the remaining stalks, and sort into piles to obtain a one-dimensional distribution for unit °brix. (3) Piles with highest brix stalks are selected irrespective of stalk weight until about $0.2\, n_s$ stalks have been chosen. Piles with less than modal brix values are discarded. (4) Weigh the stalks in the remaining piles and separate into weight classes to obtain a two-dimensional array. (5) Assign an index value (s) to each pile as follows:

$$s = x_1 + \frac{(b - m)}{(w - v)}\, x_2$$

where b = maximum brix value of the weighed piles
v = minimum weight value within the b brix class
m = modal brix value
w = maximum weight value within the modal brix class.

The selection index ascribes the same value to the heaviest stalks of the lowest acceptable sugar as to the lightest stalks of the sweetest weighed sugar pile. (6) Select piles of stalks with highest s values until $1.1\, n_s$ stalks are selected. This allows for germination failures and ensures that a population size of n_s can be planted in the field. This method is essentially a linear combination of two components x_1 and x_2 and hence the first resulting generation is designated L-1.

Using the data collected at the 1967 harvest of the base population, about 250 stalks were selected for each of the L-1 and M-1 populations separately. Two potted plants were established from each of the 143 stalks which were common selections for L-1 and M-1 and one plant for the remainder. When the plants were transferred to the field the L-1 and M-1 populations were regarded as separate treatments along with 250 Ragnar stalks in a randomized block with five "replications". Each replication consisted of 50 plants (stools) allocated at random. In 1968, the selection process was repeated i. e. another round of L selection in L-1, and another round of M selection in M-1. This resulted in generations L-2 and M-2 which were planted along with Ragnar in the same way as for L-1 and M-1. The population size of each remained at about 250 plants.

Results

A. Analysis of variance and covariance of stalks and stool characters

The linear model to be used for the individual measurements is:

$$X_{ijk} = \mu + C_i + S_{j(i)} + \varepsilon_{k(ij)}$$

where X_{ijk} is the value of the variable for the k^{th} stalk belonging to the j^{th} stool of the i^{th} clone. The analysis of variance or covariance follows the form given in Table 1 i.e. a nested or hierarchical design with unequal number of treatments. The constants N, n_s and n_c represent the total number of stalks, stools and clones respectively. The coefficients k_1, k_2 and k_3 of the variance components were estimated using Kempthorne's (1957, p. 242) formulae.

There are three sets of data for consideration; the stalk data obtained in 1967 from the base population (x_1, x_2, x_3 and x_4), the stalk data gathered in 1968 in generation M-1 (x_1, x_2 and x_4), and the stool data from the same generation, in which

y_1 = mean sugar concentration of the stalks in one stool (°brix)

Table 1. *Form of the analysis of variance for measurement characters*

Source	d.f.	M.S.	E. M. S.
Between clones	$n_c - 1$	MS_c	$\sigma^2 + k_2\, \sigma_s^2 + k_3\, \sigma_c^2$
Between stools within clones	$n_s - n_c$	MS_s	$\sigma_e^2 + k_1\, \sigma_s^2$
Between stalks within stools	$N - n_s$	MS_e	σ_e^2
Total	$N - 1$		

Values of constants	Gene-ration	N	n_c	n_s	k_1	k_2	k_3
1967 data	Base	2402	507	507	—	4.74	4.74
1968 stalk data	M-1	1171	137	241	5.06	4.70	8.51
1968 stool data	M-1	241	137	241	1	1	1.76

y_2 = total weight of cane in one stool (kilograms)
y_3 = number of stalks in one stool
y_4 = weight of sugar in one stool = 10 y_1 y_2 (grams brix)
y_5 = length of average stalk (cms.).

Base population results, 1967. Table 2 gives the estimates of the between stalks-within stools (σ_e^2) and the between stools/clones ($\sigma_s^2 + \sigma_e^2$) components of variance. Since each clone is represented by only one stool in this generation, stool effects are confounded with clone (genetic) differences. In testing the null hypothesis that $\sigma_c^2 + \sigma_s^2 = 0$, the F ratios were 13.4, 3.01, 3.15 and 3.70 for x_1 to x_4 respectively. Thus the joint effect of clone and stool differences is highly significant. The relative size of the component measuring this joint effect suggests that sugar concentration (x_1) is the most repeatable (Brown et al., 1968) of the four characters.

Table 2. *Variance component estimates in the 1967 base population for characters measured on single stalks*

Source	d. f.	Sugar Concn. (x_1) σ^2	%	Stalk Weight (x_2) σ^2	%	Weight Sugar Per Stalk (x_4) σ^2	%	Stalk C.S. Area (x_3) σ^2	%
Clones/stools	506	4.41	72	.015	30	650	31	.82	36
Stalks	1895	1.69	28	.036	70	1440	69	1.45	64

The clonal correlations in Table 3 (above the diagonal) indicate the relationship between the characters. They show that there is virtually no correlation between sugar and stalk weight. Of the components of economic yield (x_4), stalk weight (x_2) predominates because it has a larger coefficient of variation. However, sucrose concentration (x_1) cannot be neglected as a selection criterion because it is economically important and cannot fall below a minimum acceptable level.

Table 3. *Matrix of correlation coefficients between pairs of stalk characters in the base population: clonal coefficients above the diagonal and environmental coefficients below the diagonal*

		x_1	x_2	x_4	x_3
Sugar concentration	(x_1)	—	.03	.45	−.34
Stalk weight	(x_2)	.37	—	.90	.52
Weight sugar per stalk	(x_4)	.51	1.00	—	.30
Stalk C.S. area	(x_3)	.21	.72	.70	—

Selection scheme L employs a preliminary screening for stalk thickness. Although this variable is favourably related to yield ($r = .30$), it is negatively related to sucrose concentration ($r = -.34$) in this generation. This points to a possible serious defect in the scheme. To examine this problem further, Table 4 shows the effect of the preliminary screening on the base population means. If the 729 insufficiently thick stalks had not been discarded in the selection of L-1, 313 (43%) of them would have been discarded in the next step (sugar concentration measurement) anyway, because of insufficient extractable juice. Also, discarding the 729 thin stalks had a negligible effect on the mean sugar concentration of the base population, but markedly improved its mean stalk weight.

Table 4. *The effect of discarding the 25% thinnest stalks of the base population on the sugar concentration and stalk weight*

	C.S. Area (cm²)	Stalks without Juice	Stalks with Juice Number	Sugar	Total Stalk Number	Stalk Weight
Total		461	2402	18.8	2863	.45
Discard	0−3.7	313	416	19.0	729	.23
Accept	> 3.8	148	1986	18.7	2134	.53

These points support the utility of screening for stalk thickness in the L selection method. In addition Brown et al. (1969) have shown that thin stalks tend to exceed the commercial level for fibre concentration.

M-1 generation results for single stalks, 1968. In the 1968 M-1 generation, 66 clones were represented by more than one stool and so it was possible to separate clone and stool effects. The patterns observed in this generation (Tables 5 and 6) agree with those of the base population (Tables 2 and 3). About 30% of the total variation between single stalks for sucrose concentration and 65% for stalk weight and weight of sugar per stalk are attributable to variation between the single stalks themselves.

Table 5. *Variance component estimates in the 1968 M-1 generation for stalk characters*

Source	d. f.	Sugar Concn. (x_1) σ^2	%	Stalk Weight (x_2) σ^2	%	Weight Sugar Per Stalk (x_4) σ^2	%
Clones	136	2.48	50	.033	32	1770	33
Stools	104	1.12	23	.005	5	240	4
Stalks	930	1.33	27	.064	63	3460	63

Table 6. *Clonal, stool and stalk correlation coefficients for pairs of stalk characters in the M-1 generation*

Source	d. f.	Pair of Characters: Sugar Concn. Stalk Weight ($x_1 \cdot x_2$)	Sugar Concn. Weight Sugar Per Stalk ($x_1 \cdot x_4$)	Stalk Weight. Weight Sugar Per Stalk ($x_2 \cdot x_4$)
Clones	136	.05	.29	.96
Stools	104	.12	.51	.95
Stalks	930	.28	.38	.98

Table 5 shows that the stool effects were highly significant ($F = 5.27$) for sugar concentration but not for the weight characters. Thus to test for significant clone effects for sugar, the ratio $M\,S_c/M\,S_s$ was used. This is permissible because $k_1 > k_2$. For the weight characters, the ratio $1034\,M\,S_c/(930\,M\,S_e + 104\,MS_s)$ was the test statistic. These F values (3.96, 5.50 and 5.49) indicate highly significant deviation from the null hypothesis $\sigma_c^2 = 0$.

The high stool component of variance for sugar concentration (x_1)does not mean that the stools within a clone are necessarily more "variable" for this character than the weight characters (x_2, x_4). Indeed the within clone coefficients of variation were 7, 38 and 40% respectively, which agrees with expected trends. Significant stool effects in the hierarchical design arise from effects peculiar to different stools (of the same clone) but common to each stalk of any one stool. For example, translocation of sucrose between stalks of the same stool could reduce the variation between the stalks and thereby emphasise differences between stools.

Selection did not show the expected decline in clonal (genetic) variance for weight of sugar per stalk (x_4). A possible reason for this is that the 1967 growing season proved to be much poorer than that in 1968. Lewontin (1966) showed that the variance of the logarithms of measurements gives a measure of intrinsic variability, as it removes any linear dependence on the mean. Thus the variance components were estimated for $\log_e(x_i)$ in the 1967 base and 1968 M-1 data. Table 7 gives these estimates for three stalk variables. In all three cases the estimate of the environment (stalk) variance (σ_e^2) on the log scale declined. This suggests a more uniform environment for the smaller population in the better year. To examine the change in the clonal (genetic) variance, some estimate of σ_c^2 in the base population is needed. This was obtained by assuming that the ratio σ_s^2/σ_e^2 was constant in the base and M-1 populations. Hence σ_c^2 in the base population for x_1 equals $12.8 - ((5.6 \times 2.6)/2.9)$. These approximate estimates are bracketed in Table 7. An alternative method for splitting the between stool/clone component in the base population is to assume that σ_s^2 was constant. In fact, the σ_s^2 estimates obtained by either of these two methods lead to the following conclusions.

First, the genetic variance for weight of sugar per stalk (x_4) has declined after selection by 18%. Second, this decline has *not* been achieved at the expense of a decline in the genetic variance for stalk weight (x_2) but rather in that for the other component, sugar concentration (x_1) by 33%. Thus response to selection for x_4 was achieved primarily by selecting genetically sweeter clones, despite the fact that the other component, stalk weight was more intensely related to yield. The basis of this effect is probably a pronounced genotype × year interaction for stalk weight.

M-1 generation results assessed on a stool basis, 1968. The M-1 stalk data can be considered another way i.e. by defining a set of stool characters (y_i) as described previously. The results of variance and correlation analysis for these characters are shown in Tables 8 and 9. The F values for the test of the hypothesis that clonal (genetic) effects are zero ($\sigma_c^2 = 0$) are 4.0, 1.72, 1.91 and 2.52 respectively, all of which exceed the F value at $\alpha = 0.01$ level. The number of stalks per stool (y_5) is a moderately repeatable character. It shows a weak positive association with sugar concentration (y_1) and a moderate relation to weight of sugar per stool (y_4).

To sum up the results of these analyses: a considerable portion of the variation in the characters measured on single stalks (which form the selective criteria in a MSR) is genotypic. This is especially so for sugar concentration. The pattern of joint variation of these characters would not prevent selective improvement. What then has been the effect of selection on the overall performance of the MSR?

Table 7. *Variance component estimates for the log transformed stalk characters in the 1967 base population and 1968 M-1 generation*

Population	Sugar Concn. (x_1)		Stalk Weight (x_2)		Sugar Per Stalk (x_4)	
	Base	M-1	Base	M-1	Base	M-1
Component						
σ_c^2	(7.8)	5.2	(67)	69	(94)	76
$(\sigma_c^2 + \sigma_s^2)$	12.8		94		136	
σ_s^2	(5.0)	2.6	(27)	21	(42)	28
σ_e^2	5.6	2.9	235	186	306	203
Total	18.4	10.7	329	276	442	397

Approximate estimates of σ_c^2 and σ_s^2 for 1967 shown in brackets. All values have been multiplied by 10^3.

Table 8. *Variance component estimates in the 1968 M-1 generation for characters measured on a whole stool basis*

Source	d. f.	Sugar Concn. (y_1) σ^2	%	Stool Weight (y_2) σ^2	%	Weight Sugar Per Stool (y_4) σ^2	%	No. of Stalks per Stool (y_5) σ^2	%
Clones	136	2.49	64	0.62	29	39000	34	1.74	46
Stools	104	1.42	36	1.51	71	75000	66	2.02	54

Table 9. *Matrix of correlation coefficients between pairs of stool characters in the M-1 generation: clonal coefficients above the diagonal and environmental coefficients below the diagonal*

		y_1	y_2	y_4	y_5
Sugar Concentration	(y_1)	—	.30	.51	.20
Stool Weight	(y_2)	.18	—	.97	.51
Weight Sugar Per Stool	(y_4)	.30	.98	—	.51
No. of Stalks Per Stool	(y_5)	.13	.81	.80	—

B. The Overall Population Performance

The effects of selection can be assessed first by studying the survival patterns of individual genotypes. These results are to be presented elsewhere but the major conclusion is that two generations of selection (in addition to random loss) has profoundly changed the genotypic composition. Also only 29 clones are common to both the L-2 and M-2 generations.

Another means by which the effect of selection can be assessed is the comparison of the performance of the MSR populations with the known superior commercial clone, Ragnar. Table 10 summarises the character means from the available data. The first point to notice is the striking difference in performance between years for both the Ragnar standard and the MSR populations. A severe drought occurred in 1967, whereas 1968 was an average growing season. The standard clone Ragnar proved particularly susceptible to the 1967 drought and the base population was substantially superior in this year. In 1968 after one round of selection, even though the Ragnar performed much better than in 1967, both the L and M populations still significantly exceeded Ragnar, both on sugar per stalk (x_4) and sugar per stool (y_4) basis. However, Ragnar remained superior in tillering (y_3). That this difference did not enable Ragnar to outyield the MSR was due to the superior stalk weight (x_2) of the MSR population.

Table 10. *Character means at harvest of the various "treatments" on a single stalk basis and on a stool basis*

		1967 Ragnar	Base	1968 Ragnar	L-1	M-1
Stalk Characters						
Sugar concentration	(x_1)	17.3	18.7	22.0	23.6	22.5
Stalk weight	(x_2)	.30	.51	.52	.62	.69
Stalk C. S. area	(x_3)	5.0	5.2	—	—	—
Percent "thin stalks"		5	5	5	25	—
Sugar per stalk	(x_4)	51	93	114	144	153
Stool Characters						
Sugar concentration	(y_1)	17.4	18.9	22.0	23.6*	22.4
Stool weight	(y_2)	1.7	2.4	3.13	3.16	3.34
No. of stalks	(y_3)	5.5	4.7	6.0	5.1	4.9
Sugar per stool	(y_4)	296	454	689	746	745
Length of average stalk	(y_5)	—	—	111	139	137

* Assuming $y_1 = x_1$

A comparison of L-1 and M-1 shows that they differ to date in yield components (x_1, x_2, y_1, y_2) but not in their overall sugar per stool (y_4) performance. As the genotypic structure of these populations differs (Brown, 1971), some difference in quantitative attributes would be expected. Population L is superior for sugar concentration, whereas population M is superior for stalk and stool weight.

Stalk C.S. area (x_3) results were recorded at harvest of the base population but not at harvest of L-1. Thus, mean C.S. area cannot be directly compared between the two generations. Instead, the percentage of stalks rejected at each screening can be compared. Rejection at the L-1 harvest was 25% compared with 5% at harvest of the base population (Table 10). The negative clonal correlation observed between stalk sugar concentration and stalk thickness (Table 3) may explain this phenomenon. Selection for high sucrose has reduced stalk thickness relative to Ragnar. This decrease occurred despite the discarding of thin stalks in the L selection scheme. The former effect was more pronounced because the selection intensity for sugar was much greater than that for thickness.

Summarising, the data of Table 10 shows that the MSR populations are already commercially superior to Ragnar for the characters studied. It is obviously necessary to continue the procedure to see whether this superiority is maintained.

Discussion

The mass selection reservoir of clonally propagated material generates data which is pertinent not only to the agronomic problem of developing adapted varieties but also to the general theory of selection. This arises because the MSR is monitored on two levels i.e. that of the component clones (their frequency and quantitative attributes) and that of the whole population (population means compared with a standard clone).

The unit of selection and propagation is the single stalk. This represents a considerable reduction in the size of an experimental unit for estimating metric characters. We (Brown et al., 1968) have previously studied the variation of characters in a field plot, one row × eight feet long and found considerable genetic variance for characters such as sugar concentration, stalk thickness etc. However, this is no guarantee that any genetic gain from selection based on their single stalk equivalent characters would be possible. Environmental variance and experimental error could make such measurements meaningless. Thus the results of Tables 2, 5 and 8 are particularly striking and infer single stalk measurements are meaningful. The analysis of variation has predicted real selection gain. Further, the significant changes in genotypic frequencies compared with the changes expected under random selection (Brown, 1971) strongly supports this interpretation.

It is desirable to link these points with an analysis of the generation means. A direct measure of the selection response R (Falconer, 1960) was not available because an unselected population has not been maintained from one generation to the next. In addition, the 1968 growing season was so much better than that of 1967 that the means of the L-1 and M-1 generations for sugar concentration (x_1) exceeded their values as selected in 1967 (see Table 11). Also the

Table 11. *Statistics of the selected populations at planting and harvesting compared with their value in the base population*

		Base (1967)			*L*-1 (1968)		*M*-1 (1968)	
		Harvest	*L*-1 Selections	*M*-1 Selections	Harvest	*L*-2 Selections	Harvest	*M*-2 Selections
No. of clones		507	105	140	99	54	137	91
No. of stools		507	—	—	206	—	241	—
No. of stalks		2402	250	250	1052	250	1171	249
Sugar concn.	(x_1)	18.7	22.2	20.8	23.6	25.3	22.5	23.3
Stalk weight	(x_2)	.51	.72	.90	.62	.75	.69	1.14
Stalk C.S. area	(x_3)	5.2	5.6	6.6	—	—	—	—
Sugar per stalk	(x_4)	93	159	180	144	190	153	258

results for Ragnar cannot be used to estimate the means of the base population in 1968, because genotype×environment interaction was present. For example, the Ragnar stalk weight (x_2) improved from 0.30 kgs. to 0.52 kgs., whereas in *M*-1, both selection and the improved growing season only raised this variable from 0.51 to 0.69 kgs. These effects cannot be treated additively.

However, we can estimate the base population means for 1968 by combining the results of *L* and *M* differentials and responses. Define *r*, the repeatability, as the regression of propagule mean in generation $t+1$ on its value in generation t, and assume its value to be the same in both the *L* and *M* series. Since *L*-1 and *M*-1 selections were taken from the same base population in 1967, two equations in two unknowns (the regression coefficient *r*, and the estimates of the performance of the base population in 1968, X_u) are formed. For example, for sugar concentration (x_1),

$$23.6 - X_u = r\,(22.2 - 18.7) \qquad (1)$$

and

$$22.5 - X_u = r\,(20.8 - 18.7) \qquad (2)$$

where in equation 1, 23.6 is the mean °brix of *L*-1 in 1968, 22.2 is the mean °brix of stalks selected for *L*-1 in 1967 from the base population (as in Table 11) and 18.7 is the mean of the base population in 1967. The values of r for the three characters x_1, x_2 and x_4 are 0.79, 0.39 and 0.43 which agree reasonably well with the repeatability estimates in Table 2. The values of X_u for the same characters are 20.8, 0.54 and 116.

In 1967, the base population exceeded Ragnar for characters x_1, x_2 and x_4 by appreciable margins (Table 10). However, when we compare the estimated 1968 base population performances (X_u) determined above with the 1968 Ragnar results (Table 10), Ragnar was superior to the base for sucrose concentration (x_1) and equal for the yield characters x_2 and x_4. The loss of superiority of the base population over Ragnar with the improvement in growing conditions in 1968 confirms that there is genotype × environment interaction present. But more importantly, the *L*-1 and *M*-1 populations exceeded the estimated base population performance for x_1, x_2 and x_4, thus confirming again the effectiveness of these single stalk selection methods.

Conclusions

The bulk population concept which has been successfully applied to cereal breeding, can be extended to clonally propagated crops such as sugarcane. The selection phase is achieved in a mass selection reservoir (a genetically heterogeneous population) in which a regime of artificial selection of propagules supplements competitive ability. The genotypic structure changes with the resultant improvement in the yield of the population.

Populations selected in the experiment reported in this paper now yield in excess of the commercial clone Ragnar. Either superior isolates are presently included in their composition or the mixtures of clones is superior to their constituents or both. The two methods of selection (*L* and *M*) compared here do not differ profoundly for economic performance attributes as yet, although they have elicited different genotypic responses. There are almost twice as many clones in *M*-2 as in *L*-2.

The results of Allard and Adams (1969) suggest that the development of superior mixtures is more likely to follow a history of mutual selection in a bulk population, than simply mixing commercial varieties which were selected for pure stand performance. The MSR technique should test the utility of this hypothesis in sugarcane agronomy.

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References

1. Allard, R. W.: Principles of Plant Breeding. New York: John Wiley 1960. — 2. Allard, R. W.: Population structure and performance in crop plants. Ciencia e Cultura **19**, 145–150 (1967). — 3. Allard, R. W., Adams, J.: Population studies in predominantly self-pollinating

species XIII. Intergenotypic competition and population structure in barley and wheat. Amer. Nat. **103**, 621—645 (1969). — 4. Allard, R. W., Hansche, P. E.: Some parameters of population variability and their implications in plant breeding. Adv. in Agron. **16**, 281—325 (1964). — 5. Brown, A. H. D.: The persistence of genotypes in a sugarcane mass selection reservoir (1971, in preparation). — 6. Brown, A. H. D., Daniels, J., Latter, B. D. H.: Quantitative genetics of sugarcane. I. Analysis of variation in a commercial hybrid sugarcane population. Theoret. Applied Genet. **38**, 361—369 (1968). — 7. Brown, A. H. D., Daniels, J., Latter, B. D. H.: Quantitative genetics of ugarcane. II. Correlation analysis of continuous characters in relation to hybrid sugarcane breeding. Theoret. Applied Genet. **39**, 1—10 (1969). — 8. Falconer, D. S.: Introduction to Quantitative Genetics. Edinburgh: Oliver and Boyd 1960. — 9. Harlan, J. R., Martini, M. L., Stevens, H.: A study of methods in barley breeding. U.S.D.A. Tech. Bull. 720 (1940). — 10. Kempthorne, O.: An Introduction to Genetic Statistics. New York: John Wiley 1957. — 11. Lewontin, R.: On the measurement of relative variability. Syst. Zool. **15**, 141—142 (1966). — 12. Simmonds, N. W.: Variability in crop plants, its use and conservation. Biol. Rev. **37**, 422—465 (1962). — 13. Suneson, C.A.: An evolutionary plant breeding method. Agron. J. **48**, 188—190 (1956).

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