THE EVOLUTIONARY SIGNIFICANCE OF SUGAR ACCUMULATION IN *SACCHARUM*

By T. A. Bull* and K. T. Glasziou†

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Summary

Sugar levels in the various species of the *Saccharum* complex suggest an evolutionary increase in sugar content. Under suitable ecological conditions, survival through sucker growth may be dependent on rapid mobilization of stored carbohydrate. Selection pressure for sucrose storage would then occur if sucrose was more readily remobilized than other storage carbohydrates. It is suggested that this ecological situation occurred in New Guinea, and that natural and not human selection lead to the evolution of *S. officinarum*.

The relationships between total sugars, moisture content, and fibre content indicate that there is an apparent physiological limit to sugar accumulation in the genus *Saccharum* at about 27% of the fresh weight.

I. Introduction

Throughout the world the development of higher yielding sugar-cane varieties from current breeding stocks is proving increasingly difficult. One possibility for further advance may be through the use of wide crosses involving selected ancestral types to introduce new sources of variability, and the success of this approach is dependent on knowledge of species relationships and phylogeny in *Saccharum* and related genera.

Systematic identification of species within *Saccharum* is difficult, due largely to vegetative propagation of many hybrid and polyploid types of low seed fertility. The overlapping of virtually all of the diagnostic characters is illustrated by Brandes' (1958) modification of Jeswiet's key for species identification, and by Bor (1960) who included in *Saccharum* many species generally placed in *Erianthus*. Brandes accepted the species *S. sinense* Jesw. and *S. barberi* Jesw. and regarded them as cultivated plants, even though Parthsarathy (1947) considered that these forms originated in Northern India through natural hybridization between local forms of *S. spontaneum* L. and cultivated *S. officinarum* L. The morphological similarity and cross-fertility of *Saccharum* species substantiate Stebbins' (1956) view that they are members of an evolving polyploid complex, and suggests that they developed from a common gene pool.

Speciation in the genus is associated by Brandes (1958) with the inundation of the Malaysian land mass in the late Cretaceous. *S. spontaneum* is considered to be the original widespread type, and *S. robustum* to have evolved under isolation in New Guinea in response to local environmental conditions. Brandes postulates that *S. officinarum* was produced through selection by New Guinea natives of sweet, succulent

* Botany Department, University of Queensland, St. Lucia, Brisbane.

† David North Plant Research Centre, The Colonial Sugar Refining Co. Ltd., Toowong, Brisbane.

forms of *S. robustum*. Some of the variability in *S. officinarum* may be due to occasional flowering and seed setting in native gardens, although Brandes doubts whether the natives have practised any breeding from their selection.

The genus *Saccharum* is closely related to at least four other genera, *Erianthus*, *Miscanthus*, *Sclerostachya*, and *Narenga*, which are included in the "*Saccharum* complex" by Mukherjee (1957). Celarier (1956) suggested that *Saccharum* evolved from *Erianthus* and that *Miscanthus* is possibly an ancestral form for the complex.

A survey of sugar and fibre contents has been made in *Saccharum* and related genera to determine the range of variability and to obtain information on factors which may limit sucrose production in sugar-cane.

TABLE 1

MEAN VALUES FOR SUCROSE, REDUCING SUGARS, AND FIBRE LEVELS FOR MEMBERS OF THE SACCHARUM COMPLEX

Genus and Species	No. of Clones	Mean Sucrose Content (% fresh wt.) ±S.E. of Mean	Mean Reducing Sugars (% fresh wt.) ±S.E. of Mean	Mean Fibre Content (% fresh wt.) ±S.E. of Mean
Erianthus				
maximus	3	2·24±0·44	0·73±0·23	26·4±0·9
arundinaceus	2	0·62±0·16	0·61±0·17	30·3±0·3
Miscanthus				
*floridulus**	5	3·03±0·56	0·79±0·24	51·0±2·0
Saccharum				
spontaneum	10	3·96±0·46	0·44±0·20	33·9±2·1
*spontaneum**	30	5·35±0·38	1·66±0·06	31·8±0·9
robustum	10	7·73±0·83	0·27±0·02	24·8±1·6
sinense	2	13·45±0·02	0·38±0·08	12·8±2·0
officinarum	25	17·48±0·35	0·32±0·02	9·8±0·4

* Samples received from Lautoka, Fiji.

II. METHODS AND MATERIALS

Clones of *S. spontaneum*, *S. robustum*, *S. officinarum*, *S. sinense*, *Erianthus arundinaceus*, *E. maximus*, and several hybrid and commercial varieties were sampled in early summer and analysed for sugar content. The clones were part of a 12-months-old, irrigated cane collection at the David North Plant Research Centre, Brisbane.

Samples from the three basal internodes of five stalks were bulked for each variety, subsampled, and extracted with hot 70% ethanol. Total and reducing sugars were determined on the ethanolic extracts by the method of Hoffman (1937). Other subsamples were dried to constant weight at 70°C, and fibre was assessed as dry weight minus total sugars. No sugars other than sucrose, glucose, and fructose were detected on paper chromatograms.

Some results have been included for *S. spontaneum* and *Miscanthus floridulus* (Labill.) Warb. samples received from Lautoka, Fiji.

III. Results

The mean values of sucrose, reducing sugars, and fibre expressed as percentage of fresh weight for eight species of the *Saccharum* complex have been summarized in Table 1. In Figure 1 the total sugar content as percentage of fresh weight is plotted against the fibre content (percentage fresh weight) for all clones sampled. Similar plots for moisture content against fibre content and for moisture content against total sugars are presented in Figures 2 and 3. Least squares regression lines are fitted to each set of data.

An estimate of environmental variance from the regression line has been included in Figure 1, and is represented at the 99% confidence level.

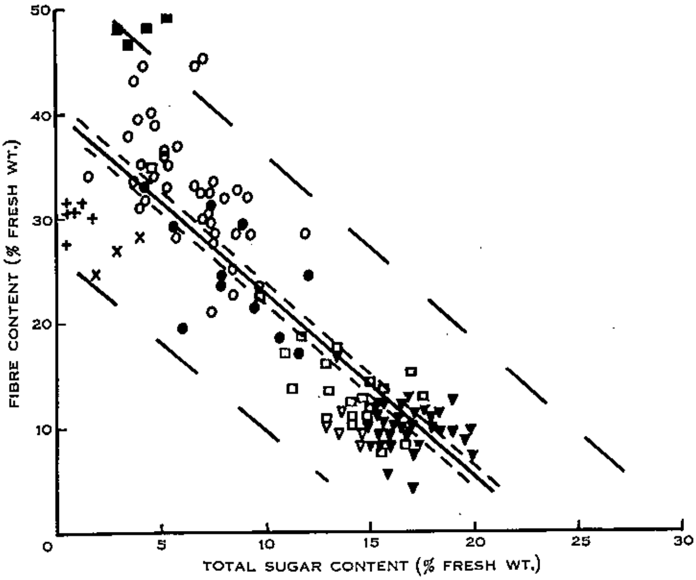

Fig. 1.—Correlation between total sugar and fibre contents within the *Saccharum* complex, with 99% confidence limits (— — — —) and an estimate of environmental variance (- - - -). $r = -0 \cdot 92$, significant at $0 \cdot 1\%$.

○ *S. spontaneum* ● *S. robustum* ▼ *S. officinarum* ▽ *S. sinense* □ *Saccharum* hybrids and commercial canes × *Erianthus maximus* + *E. arundinaceus* ■ *Miscanthus floridulus*

IV. Discussion

The positions of the species on the regression line in Figure 1 conform with their proposed evolutionary positions. The lowest sugar levels occur in *Miscanthus* and *Erianthus*, and the highest in *S. officinarum* and its derivatives. The wild species *S. spontaneum* and *S. robustum* occupy intermediate positions, and exhibit considerable variability, although the sugar levels in the former are lower than the latter (Table 1). This relationship supports the phylogenetic theory and suggests that natural selection for higher sugar levels has been involved in the evolution of the *Saccharum* complex, culminating in the genotypes classed as *S. officinarum*. Mather and Harrison (1949) have shown that intensive selection for a single character is commonly accompanied by correlated detrimental changes in other characters. *S. officinarum* typically exhibits sparse flowering and low fertility, but these characters can be restored, with a subsequent loss in sugar content (Fig. 1) by hybridization with *S. spontaneum*, thus further suggesting that selection in *Saccharum* has been largely for higher sugar content.

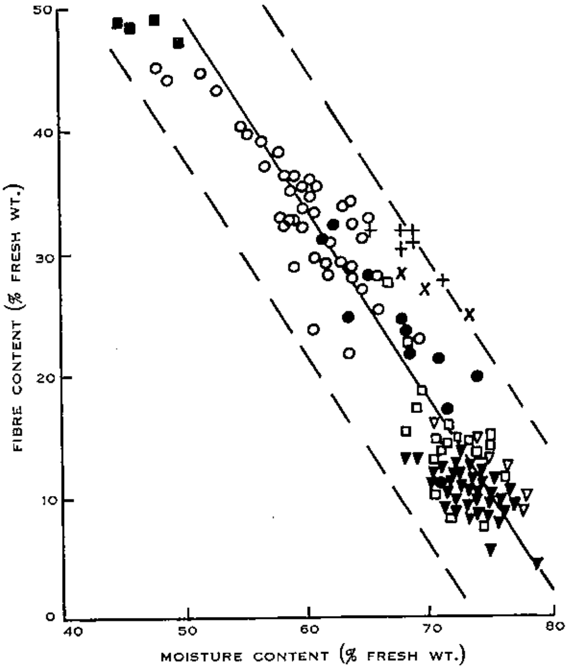

Fig. 2.—Correlation between fibre and moisture levels for members of the *Saccharum* complex, with 99% confidence limits. $r = -0\cdot94$, significant at $0\cdot1\%$.

○ *S. spontaneum* □ *Saccharum* hybrids and commercial canes
● *S. robustum* × *Erianthus maximus*
▼ *S. officinarum* + *E. arundinaceus*
▽ *S. sinense* ■ *Miscanthus floridulus*

On the assumption that 5% fibre content is a minimum for the structural requirements of a cane stalk, it is possible, from the 99% confidence limits of Figure 1, to estimate the maximum possible sugar content in *Saccharum* at about 27% of the fresh weight with a minimum moisture content of 70% (Fig. 2). From the clones available it appears that these values represent the limits of sugar and moisture balance imposed by the genetic constitution of the complex. Although the correlation between total sugar and moisture content is significant (Fig. 3), moisture is more closely correlated with fibre (Fig. 2), indicating that osmotic effects of high sugar concentrations do not limit accumulation.

While Brandes (1958) suggests that *S. officinarum* has been derived solely by human selection, it may be argued that this species has evolved naturally as the present climax of sugar accumulation in the genus, as shown by the general trend in Figure 1. In certain natural habitats in New Guinea competitive superiority in *Saccharum* has probably depended at least partly on the ability of the mature stalks to accumulate large amounts of sugar which can be rapidly mobilized to support sucker growth. During the dry, non-growing season photosynthesis is channelled into sugar accumulation in mature stalks. These then sustain a burst of sucker growth

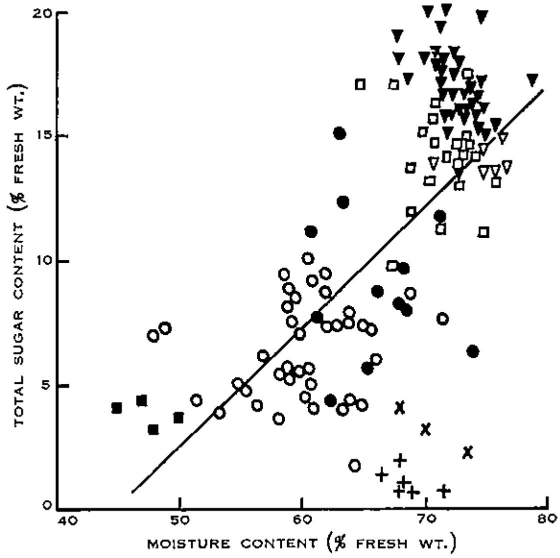

Fig. 3.—Correlation between total sugar and moisture contents for members of the *Saccharum* complex. $r = 0 \cdot 61$, significant at $1 \cdot 0\%$.

○ *S. spontaneum*	□ *Saccharum* hybrids and commercial canes
● *S. robustum*	× *Erianthus maximus*
▼ *S. officinarum*	+ *E. arundinaceus*
▽ *S. sinense*	■ *Miscanthus floridulus*

in the monsoonal season, as suckers initially obtain their sugar from mature stalks until such time as they reach sunlight. If sucrose is more readily mobilized than other storage carbohydrate, selection would favour high sugar levels to maintain sucker growth for 12 weeks or more until the stems can penetrate a canopy 6–8 ft above ground level. The high mobility of sucrose in the sugar-cane stalk in response to environmental changes has been shown by Glasziou *et al.* (unpublished data).

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