THE BEARING OF CERTAIN RECENT CYTO-GENETICAL FINDINGS ON SUGARCANE BREEDING

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I. INTRODUCTION

As compared with other economic plants the improvement of sugarcane by breeding is of relatively recent origin. The discovery of the fertility of sugarcane seed was made by Soltwedel in Java in 1888 and independently by Harrison and Bovell in Barbados in 1889. Since then the work on sugarcane breeding has been vigorously pursued in Barbados, Java, Coimbatore and Hawaii, among the older Experiment Stations and at Canal Point, Florida and others among the later-established Stations.

While the main aim at the Sugarcane Breeding Stations is the evolving of high-yielding commercial canes with high sucrose content, many Experiment Stations have had to grapple with the necessity of breeding varieties resistant to one or the other of sugarcane diseases. The emphasis has also varied with regard to the utilisation of appropriate species of Saccharum and in certain cases, of different genera, in hybridisation to suit the needs of various cane-growing regions. Where cane develops under favourable conditions the noble (S. officinarum) and highly nobilised varieties have given good results as parents, while in less favourable areas 100

S. spontaneum and S. barberi have given more satisfaction. The sereh disease in Java led to the nobilisation of Chunnee and Glagah. The Coimbatore Station, for instance, has paid increasing attention to the utilisation of the wild S. spontaneum while the Station at Canal Point, Florida, has utilised S. robustum.

Much advance was registered in the breeding of sugarcane varieties by the utilisation of wide and distant genera in the breeding programme with a view to the enrichment of genetic material available to the breeder. Notable inter-generic crosses are those of sugarcane with *Sorghum* (Venkatraman and Thomas, 1932), (Raghavan, 1953 a) and Bamboo (Venkataraman, 1937). For the first time a "pure" officinarum, viz., Vellai, has been successfully crossed with Bamboo, one of them showing promise (Raghavan, 1952 a).

Sugarcane as a breeding material is fundamentally different from other commercial crops. It is a highly heterozygous polyploid complex with a large reserve of lethal genes, which especially in S. officinarum are resposible for there being practically no survivals in the selfed progeny. It is only the clonal propagation that has made it survive.

Arising mainly out of its genetical impurity and high allopolyploidy no prediction can be made as to the nature of the progeny to be expected in a cross. The high heterozygosity of the chromosomal material of both the parents renders odds against anticipating any desired combination. Consequently, repetition of well-known crosses has failed so far to give a variety identical with the original. For instance parental crosses for Co. 419 (POJ. 2878 × Co. 290) and Co. 421 (POJ. 2878 × Co. 285) have been repeatedly made for about 4 years. Though thousands of seedlings have been raised and studied there is not yet found an exact replica of either Co. 421 or Co. 419 (Raghavan, 1951 a, 1953).

Success in sugarcane breeding, therefore, depends to a large extent on the raising of a large population of seedlings. Thousands of seedlings are raised in bulk as well as semi-bulk scale crosses in the hope of getting some at least, with the desired combination of characters, and selections are made on the basis of suitability to different sets of environmental conditions. At Coimbatore the time interval from crossing upto the selection of Co. canes from the final test plots is about 4 years and the number of seedlings gets filtered down to about 25 from the lakhs of seedlings raised by hybridisation. These Co. canes are sent to the various State Stations for further extensive trials and only those canes are released that are found suitable for a particular set of environmental conditions.

II. UNPREDICTABILITY—INEVITABLE IN SUGARCANE BREEDING

Most of the interesting breeding peculiarities exhibited by sugarcane are traceable mainly to their being polyploid hybrid complexes (Parthasarathy, 1946, 1951 b, Raghavan, 1951 a, b, c, d). The selfed progeny shows a wide range of variation, which in the case of S. officinarum shows a very high rate of mortality owing to the presence of a large accumulation of recessive lethal genes in its genetical constitution. In addition, all sugarcanes are highly heterozygous and so all individuals resulting from selfing, varietal or species crosses are heterozygous also. The parental characters are found distributed among the progeny in an unpredictable manner. In some, the earliness of one parent may manifest itself; in others, the vigour of the parent; vet in a few, the high sucrose of one of the parents may be incorporated and it may also happen that in a very few a combination of most of the desirable characters of the two parents may be exhibited. It is obvious that such a seedling got out of mating of two highly heterozygous individuals cannot be re-synthesised. Fortunately for the sugarcane breeder such a form can be maintained through vegetative propagation.

For the reason that sugarcane is a polyploid complex, interspecific and even inter-generic hybrids are frequently fertile due to auto-syndesis, provided the two parental sets of chromosomes are compatible enough to exist side by side in the hybrid. Apart from species hybrids like S. officinarum $\times S$. spontaneum, which are fertile, even inter-generic hybrids have shown fertility or partial fertility. The progeny from such fertile hybrids, though resembling one another, shows variation due to exchange of genes among the chromosomes of the respective parents, and not between them and the overall effect of the rearranged parental sets of chromosomes on the general configuration of the individual.

In sugarcane hybridisation no prediction can be made of what the chromosome number in a cross would be. In interspecific hybrids, S. officinarum $\times S.$ spontaneum, S. officinarum as the egg parent is known to contribute the diploid number. In reciprocal crosses S. officinarum contributes the unreduced number through its sperm (Raghavan, 1951 a, d). Nor is there gross identity between reciprocal crosses indicative of cytoplasmic inheritance (Raghavan, 1951 b, 1953 b, 1954). There is reason to suspect the presence of cytoplasmic inheritance as being an interaction between the genes and maternal cytoplasm. Non-reduction in the egg is due in some cases to fusion of the two lowermost megaspores in the linear tetrad (Narayanaswami, 1940) and in some other cases endomitosis of the lowermost tetrad (Bremer, 1949). Being a post-meiotic phenomenon, diploid partheno-

genetic derivatives exhibit wide variations, which would not be the case had the diploid egg come into being through suppression of meiosis. The way in which the male contributes the diploid number is variable. Many S. officinarum varieties as Zw. Cheribon, Chittan and Striped Mauritius, exhibit dispermy, while in the other species such as S. spontaneum or S. robustum diploid and polyploid pollen grains are common (Sundraraghavan, 1954).

In the evolution of some economic seedlings the egg is known to contribute a chromosome number which is neither its haploid nor its unreduced number. Sometimes, in the same cross, S. officinarum is capable of contributing haploid and diploid eggs, as well as eggs with an unexpected chromosome number through elimination of chromosomes. In S. officinarum $(2n = 80) \times Sorghum (2n = 20)$ crosses the hybrids showed 2n = 50 (n + n)and 90 (2n + n) (Janaki Ammal; 1941; Raghavan, 1953 a) while S. offici $narum \times Bamboo (2n = 72)$ hybrids showed 2n = 116 (n + n) and 2n = 86(unexpected egg + n, Raghavan, 1952 a). The contribution of eggs with 68 chromosomes on the part of the noble cane has been recorded in a few crosses, S. officinarum var. Lakhapur \times Sclerostachya (2n = 83, Raghavan, 1952 b); S. officinarum var. Zw. Cheribon × Co. 285 (2n = 112) [Co. 453 (68 + 56) = 124, (Raghavan, 1951 a, c)]. In S. officinarum × Sclerostachya crosses all the four types, namely n + n (2n = 55), n + 2n (2n = 70), 2n + n (2n = 95) and unexpected egg + n (2n = 60) have been recorded (Govindaswami, 1948). The lowest number contributed by S. officinarum egg is 28, which is surprisingly enough, lower than the haploid number of S. officinarum (D. $74 \times S$. spontaneum Coimbatore = (2n = 60) (Parthasarathy, 1946, 1951 a).

III. PARTHENOGENESIS AND CHROMOSOME ELIMINATION, MAJOR FACTORS IN SUGARCANE BREEDING

In some of the pollen-sterile forms, parthenogenesis is common. So far no case of haploid parthenogenesis has been seen. The few cases that are known are diploid derivatives from unreduced eggs of pollen-sterile forms. Diploid parthenogenesis, being post-meiotic, the progeny shows wide variations due to recombination of genes as if the diploid egg has come into being through fertilisation. As such this phenomenon is of the utmost usefulness in sugarcane breeding. Many of the Co. canes are now known to be parthenogenetically derived. Table I gives the list of some Co. canes with their respective parents. Care has been taken to include in the list only such cases as show different chromosome numbers among the parents. In all these cases cited, the hybrid Co. canes show only the maternal number irrespective of the chromosome number of the paternal parent. Obviously

there is a very large number of other cases of parthenogenesis where there is numerical identity between the pistillate and the staminate parents.

Apart from diploid parthenogenesis, parthenogenesis preceded by elimination of chromosomes en bloc has been found to be of frequent occurrence. Important pollen-sterile canes, like Co. 421, Co. 602 and Co. 603, have shown this phenomenon. Co. 421 gives two types of seedlings parthenogenetically, one thick type with normal diploid number of 2n = 118and the other, thin type with 2n = 86 chromosomes (Parthasarathy, 1946, 1951 b; Subramanian, 1946). In the same way Co. 602 gives rise to seedlings having 2n = 118 and 2n = 96 chromosomes, the former being diploid parthenogenetic derivative and the latter being a parthenogenetic derivative after chromosome elimination (Raghavan, 1954). As shown in Table II, Co. 803, Co. 804, P. 8388, P. 8415 and P' 1010/1 are all parthenogenetically derived preceded by chromosome elimination from Co. 603, the chromosome numbers being 2n = 108, 108, 104, 86 and 104 respectively, while the chromosome number of Co. 603 itself is 2n = 118 (Raghavan, 1953 a). For the first time this phenomenon has been observed in a "pure" species of Saccharum, viz., S. robustum. When S. robustum with 2n = 84 is selfed or crossed with distant genera, it is capable of giving rise to seedlings with 2n = 84, 80 and also 2n = 62 chromosomes (Sundraraghavan, 1954; Raghavan, 1954). So also Kassoer with 2n = 136 when selfed gave a seedling with 2n = 112 chromosomes (Raghavan, 1953 b).

Thus it seems abundantly clear that the phenomena of parthenogenesis and chromosome elimination play a more important role, than has been realised so far, in sugarcane breeding. It also appears that because of cytoplasmic inheritance and parthenogenesis the mother is bound to play a more important role than the staminate parent in sugarcane breeding.

IV. CYTOPLASMIC INHERITANCE—ITS ROLE IN SUGARCANE BREEDING

Since the finding of the existence of cytoplasmic inheritance in Saccharum (Raghavan, 1951 b, 1954), it has been made possible to anticipate to some extent the gross general appearance among the progeny of a cross, in the sense that there is a greater approximation to the mother than to the staminate parent. The non-expression of paternal characters in well-known inter-generic crosses with Bamboo, Sorghum and maize as male parent is now explicable on the basis of cytoplasmic inheritance. While the phenomenon has been more or less quite apparent as regards easily recognizable qualitative characters, it has been found that this holds good even in respect of quantitative characters like yield, purity, etc.

Further evidence in support of the above generalization is indicated by the findings of Liu and Li (1953). In tracing out the degree of mosaic resistance in noble canes, according to them, the hybrids maintain a good amount of tolerance to mosaic even though *S. spontaneum* chromosomes get reduced by slow degrees during successive stages of nobilisation. They point out that the presence of a few chromosomes of *S. spontaneum* (7–8) is sufficient for imparting resistance to mosaic.

In the early days of sugarcane breeding, S. spontaneum was extensively used because of the vigour and hardiness that it imparted to its progeny. Among such bispecies hybrids (having the genes of two forms in their constitution), mention may be made of Co. 205, Co. 285, Co. 421, Co. 432, Co. 453, Co. 605, etc., of which Co. 421 is doing well in certain parts of the tropics and the rest are sub-tropical. S. Barberi canes are also comparatively hardy and their juice quality is far superior to that of S. spontaneum, almost equalling that of the tropical canes. Hence it was thought desirable to build up tri-species hybrids (having the genes of three species in their constitution) using Barberi also as one of the parents. Such hybrids which have made a mark in North India are Co. 312, Co. 313, Co. 331, etc. In the tropics Co. 419, Co. 449, Co. 467, Co. 475 and Co. 527 are among those that have proved useful.

Among bispecies hybrids, which have not become commercial canes, but which could be employed as parents in breeding work, mention may be made of such forms as P. 3247 and P. 4626. By themselves they do not give high yields and therefore cannot be of commercial importance, but possess certain desirable individual characters which could be exploited through hybridisation. For instance P. 4626 is a derivative from the rich 'noble' cane Fiji B, whose soft-rindedness and good juice quality it has inherited. It is generally employed as a parent for evolving chewing canes as also rich canes of satisfactory yield. Among the recently released Co. canes, a number of them Co. 819 to Co. 831, have the 'blood' (= genes) of P. 4626 in them. Co. 475 and Co. 603 are promising canes having the genes of P. 3247 in their constitution.

From the tri-species hybrids also a number of parents have been isolated. One of the most outstanding is P. 2607, which though lacking in sucrose, imparts high tonnage and vigour to the seedlings. Co. 777 which was raised to Co. status recently is a derivative from this parent.

In addition to these three species of *Saccharum*, other genera have also been employed for building up good parents and economic types. The closely related genera *Narenga* and *Sclerostachya* were employed to impart resistance to water-logging, drought (hardiness) and diseases (Parthasarathy

and Venkatraman, 1942). A derivative from Narenga (P'201/1) having S. officinarum, S. spontaneum and Narenga in its constitution is proving useful as a parent. The recently released Co. canes, Co. 827 to Co. 831 (Fiji B, G. $C.\times P'$ 201/1) have been derived from using this as a parent.

Another good parent is P' 63/32 (Janaki Ammal, 1941) which has in its composition not only genes from the two species of Saccharum, viz., S. officinarum and S. spontaneum, but also those of the genus Imperata. This usually imparts high juice quality, as also earliness to its seedlings. Co. 644 is one such derivative. Recently a number of seedlings having this as one of the parents have been raised to the status of Co. canes. The cross Co. $603 \times P'63/32$ has given a number of forms, viz., Co. 803 to Co. 814, with different useful characters distributed among them.

SUMMARY

In sugarcane breeding the appropriate species of Saccharum and in certain cases of different genera, have been utilised to suit the needs of the various cane-growing regions. The Coimbatore Station for instance has paid increasing attention to the utilisation of S. spontaneum while the Station at Canal Point, Florida, has utilised S. robustum. The Spontaneum Expedition Scheme is in furtherance of this objective.

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io ie rt iy The cyto-genetical basis for the (seemingly capricious) breeding behaviour of sugarcane, has been briefly indicated. Parthenogenesis and chromosome elimination coupled with cytoplasmic inheritance, seems to indicate the greater importance which has to be bestowed upon the pistillate parent in sugarcane breeding. The constitution of some of the important economic seedlings, has been explained from this point of view.

TABLE I

Diploid Parthenogenesis

Sl. No.	Cross	Hybrid
1 .	Co. 421 $(2n = 118) \times S$. officinarum var. Striped Mauritius $(2n = 80)$	Co. 463 $(2n = 118)$
2	Co. $421 \times S$. officinarum var. Poovan $(2n=80)$	Co. $602 (2n = 118)$
3	Co. $421 \times$ Co. $453 (2n = 124)$	Co. $656 (2n = 118)$
4	Co. $602 (2n = 118) \times \text{Coix}$, <i>Sorghum</i> , Teosinte etc. (all $2n = 20$)	2n = 118
5	Co. $603 (2n = 118) \times E.K. 28 (2n = 80)$	Co. $817 (2n = 118)$
6	Co. $603 \times P' 63/32 (2n = 120-24)$	Co. 909, Co. 910, Co. 81 (all $2n = 118$)
7	POJ. 2725 $(2n = 106-08) \times Sorghum durra$ (2n = 118)	Co. 356 $(2n = 106-108)$
8		Co. $407 (2n = 106-108)$ Co. $455 (2n = 106-108)$
	(2n = 64)	Co. 155 (2n — 100 100)

TABLE II

Parthenogenesis Preceded by Elimination of Chromosomes en bloc

Sl. No.	Cross Hybrid				
2 Co. $602 (2n = 118)$ 3 Co. $602 \times$ Maize (2i) 4 Co. $603 (2n = 118)$ 5 Co. $603 (2n = 118)$ 6 Co. $603 \times$ Co. $449 (2n + 10)$ 7 Co. $603 \times$ Co. $449 (2n + 10)$ 8 Co. $603 \times$ Co. $449 (2n + 10)$ 9 S. robustum self (2n + 10) 10 S. robustum (2n = 10)	\times P'63/32 (2n = 120-24) Co. 803 (2n = 108) \times P' 63/32 (2n = 120-24) Co. 804 (2n = 108) 2n = 118) P. 8388 (2n = 104) 2n = 118) P. 8415 (2n = 84-86) P' 1010/1 (2n = 104) x = 84 P' 868/1 (2n = 80) x = 84 P'875/1 (2n = 62) x = 84 P'873/2 (2n = 62)				
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