CLASSIC PAPERS ON SUGARCANE

T.S. RAGHAVAN

HUNDRED YEARS OF EXCELLENCE IN SUGARCANE RESEARCH
SBI 100 YEARS
1912 - 2012

Sugarcane Breeding Institute
Coimbatore
2012

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Prof. T. S. RAGHAVAN

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Prof. T. S. RAGHAVAN – Biography

Prof. T. S. Raghavan, M.A., Ph.D., F.R.M.S., FLS, a botanist, cytogenetist and evolutionary biologist par excellence was graduated with Masters in Botany from Madras Presidency College in the year 1926 under the renowned botanist Prof. M. O. P. Iyengar. After graduation he served as demonstrator at the same college. In 1927 he moved to S. B. College, Chenganacherry, Kerala and founded and served as Head, Department of Botany. During the five years tenure he developed the department which became the most admired department in the college. In 1931 he joined Annamalai University and served till 1947. He was deputed for higher studies at Kings College, London during 1935-37. He came back after obtaining doctorate under the guidance of the famous cytogenetists Dr. Ruggles Gates and Dr. Wolfe. His distinguished career at Annamalai University can be appreciated by the following excerpts from The Hindu supplement dated Feb 9 1955 on the occasion of Silver Jubilee of the University –Dr. T. S. Raghavan, Professor and Head of the Department of Botany from 1931-47 was mainly responsible for initiating and organizing teaching and research in botany. A good deal of research work has been carried out in the cytology and cytogenetics of flowering plants. The botanical laboratory has been fully equipped for cytological research. He made in-depth study in cytomorphological studies on several economically important species including *Portulaca tuberose, Nicotiana glutinosa, Spermacoce hispida Linn., Guettarda speciosa Linn., Sesamum orientale,* *Sesamum prostatum, Tridax procumben*s. The data and results of the research work were published in reputed foreign journals including Cytologia, The International Journal of Cytology (Japan), Annals of Botany (England), Planta (Germany), *etc.* The research work besides being in the main fundamental in character, has also kept in its purview the utilitarian aspect. In 1947, he went to Ceylon to serve as the Chief Botanist in the internationally famous Coconut Research Scheme at Lunuwila.

After that assignment he came back to India in 1950 to join the renowned Sugarcane Breeding Institute where world famous scientists like Dr. Barber and Sir T.S. Venkatraman worked earlier. At this institute Dr. Raghavan developed new varieties of cane which the farmers and sugar factories alike found extremely useful. He made several challenging inter generic viz., *S officinarum x Bamboo, Scerostachya x Narenga, Saccharum officinarum x Naranga* etc., He was successful in introgressing Burma *Saccharum spontaneum* into the sugarcane cultivars for broadening the cytoplasmic diversity. His work on diploid parthenogenesis in varietal development, post meiotic endoduplication responsible 2n gamete transmission, phylogenetic studies on the origin of *S. officinarum*, *S. robustum* and *S. edule* were well acclaimed.

He was nominated as fellow of the Linnaen Society and has also served as council member in the Indian Academy of Sciences, when Sir C.V. Raman was President. He was also nominated for the prestigious award as standing collaborator, one among five all over the world, at the International

Cytogenetic Conference at Tokyoin the 1950's After retirement Prof Raghavan returned to teaching, his first love, as UGC professor once again at SB College and later on at Vallabh Vidyapeeth, Anand. Recognizing his contribution to botany during his centenary year 'Prof. T. S. Raghavan Centenary Memorial Scholarship Fund' was created at S.B. College, Chenganacherry, Kerala.

Prof. T.S. Raghavan immensely contributed to the knowledge of Cytogenetics and Phylogenetics study in sugarcane. His research work formed the basis for initiating scientific works on evolution of several crop plants.

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THE SUGARCANES OF INDIA

Some Cyto-genetic Considerations

T. S. RAGHAVAN*
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THE sugarcanes grown in India fall into two distinct types; the thin canes and the thick or the 'Noble' canes. The thin canes are sub-tropical in their distribution and were widely cultivated in North India prior to the introduction of the so-called "Co. canes;" developed at the Coimbatore station. The 'Noble' canes are cultivated to a large extent in the tropical belt of India. Nearly 80 percent of the total four-million acres of sugarcane area of the Indian subcontinent is in North India. It is no wonder, therefore, that these thin sub-tropical canes were called the indigenous canes and by "Indian Canes" these alone were meant. The 'Noble' canes were considered to be a later introduction. Botanically these two types of canes fall into three distinct species of *Saccharum*. Barber[1] in his classical work on the thin canes (indigenous canes) recognized five groups: (1) Mungo, (2) Saretha, (3) Sunnabile, (4) Nargori, and (5) Pansahi; of these, the first four were placed by Jeswiet [14] under *S. Barberi* and the fifth was put in the species *S. sinense*. The 'Noble' canes belong to *S. officinarum*.

The exact origin of the cultivated forms is not fully understood. So far as the cultivated forms in India are concerned, the general belief is that the sub-tropical North Indian thin canes are the indigenous ones, and that the tropical canes were later introductions by one Captain Dick about the year 1827. Cyto-genetical studies at this Station have, however, indicated the possibility of the origin of the so-called indigenous canes from a promiscuous hybridization between *S. officinarum* and *S. spontaneum*.[16] On this basis *S. officinarum* must have been under cultivation in peninsular India from early times. They might have gone out of cultivation due to the attack of some disease to which they are susceptible; and their importation by Captain Dick in 1827 was very likely a reintroduction. In arriving at this conclusion several interesting cyto-genetical features have been taken into account.

Polyploidy in Sugarcanes

Cytologically all the known species of sugarcanes are polyploids having several sets of the basic number of 10 chromosomes. *S. officinarum* is an octoploid having $2n = 80$ chromosomes. The simple diploid forms with 20 somatic chromosomes are yet unknown. The lowest number known is in the form Tanangge, $2n = 60$, whose exact constitution is still a matter of controversy. On account of the high polyploidy and heterozygosity there is a wide range of variation even in selfed progeny. Also most of the seedlings of the selfed progeny do not survive, presumably due to the presence of a large reserve of lethal recessive genes in the genetic constitution of *S. officinarum* which, but for vegetative propagation, might have been the cause of the total extinction of the cultivated forms. For the same reason the exact nature and segregation of the hereditary factors cannot be worked out. The few attempts at inbreeding made at this Station proved—as the above discussion might suggest—the futility of adopting this as a means of improving sugar cane. For instance, seedlings on a large scale were raised from the selfed arrows of *S. Barberi*.[22] None of these represented a real improvement over the parents.

The results from inbreeding proving so limited that interspecific and intergeneric hybridization have been resorted to for breeding improved canes. It is now widely known how the Coimbatore Station was able to get a commercial seedling, Co. 205, by deliberately using *S. spontaneum* as the male parent. The use of these hybrids in a further breeding program mainly consisted of backcrossing these with *S. officinarum* (Nobilization) in

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*I have great pleasure in expressing my grateful thanks to Prof. R. Ruggles Gates, F.R.S., for kindly reading through the manuscript and making valuable suggestions.

OLD AND NEW SUGARCANES

Figure 16

At left is shown a planting of the improved variety CO 419, compared with the noble cane (*S. officinarum*) now grown to a large extent in the tropical zone of India.

order to lessen the undesirable characters like impurities in the juice which were imparted by the *S. spontaneum* parent along with such desirable characters as vigor and disease resistance.

The ease with which interspecific and even intergeneric hybridization is rendered possible in sugarcane is due, in no small measure to its high polyploidy. By itself it is a condition favorable for wide crossability by making autosyndesis almost the rule: namely, the internal pairing of the chromosomes derived from either parent, among themselves. This is because sugarcane is an allopolyploid. Consequently, even though the parental forms are not closely related, sterility does not always occur. While this phenomenon is useful in this respect, it is at the same time the despair of the breeder inasmuch as in a cross, synapsis seldom takes place between the two parental sets of chromosomes. The genetical outcome of this is obvious. Variations giving the parental combinations and their Mendelian segregation are almost impossible. No prediction can be made as to what will result from any particular cross. The high polyploidy, heterozygosity and autosyndesis all combine to make the chances of the reappearance of a particular synthesised variety almost impossible. It may be likened to a card game in which the number of cards dealt each player runs into hundreds. After a particular deal each person gets a large number of cards in a particular combination. An association of all these combinations produces a particular 'effect.' The chances that we can repeat this effect by getting the same combination a second time are almost nil.

Search for the Basic Genome

There are further complications. In a particular cross hundreds of genes in the parental forms have entered into a particular type of association *among* themselves (on account of autosyndesis) and *not between* themselves due to lack of synapsis between the parental chromosomes. It is almost impossible to get the same pattern of association involving all the hundreds of genes distributed over so large a number of chromosomes. Thus in 1916, forty plants of the F_1 generation of *S. officinarum* × *S. spontaneum* yielded in Co. 205, a cane of commercial value, that was immediately released for cultivation.[1] This identical cross was repeated for a number of years and though many thousands of F_1 seedlings were raised, not even a single repetition of Co. 205 or an improved form thereof was recovered.[22] This high allopolyploidy and the consequent autosyndesis being such a great handicap to the plant breeder, an effort was made at this Station by Parthasarathy,[18] to reduce the chromosome number to its basic complement. This was based on his suggestion[16] that generally the genetic or family relationship is close when reduced gametes function, but when the relationship is distant the compatibility of the cross is due to the functioning of unreduced gametes. The procedure adopted was to successively backcross *S. officinarum*, var. Vellai ($2n = 80$) to a closely related genus *Sclerostachya*, ($2n = 30$). It was found that in the first cross with *Sclerostachya*, reduced egg gametes functioned on the *officinarum* side implying a possible close relationship between *S. officinarum* and *Sclerostachya*.

Why, in the first backcross unreduced eggs functioned is not known. But in the second and third backcrosses reduced gametes functioned and in the latter where the chromosome number had been reduced to 40, the meiotic configuration consisted of 20 bodies made up of five trivalents, ten bivalents and five univalents. Of these $2n = 40$ chromosomes, 10 belong to *S. officinarum* and 30 to *Sclerostachya*. That means that the number of *S. officinarum* chromosomes has been reduced to its basic complement, $x = 10$. These ten chromosomes, if they had no homology with *Sclerostachya* should have remained as ten univalents, and the 30 *Sclerostachya* should have been organized into 15 bivalents. Instead, it was found that five of the ten *S. officinarum* chromosomes had paired with five *Sclerostachya* bivalents forming five trivalents. The other five *S. officinarum* chromosomes remained as univalents. The rest of the *Sclerostachya* chromosomes formed ten bivalents. This grouping indicates that the basic complement of ten *officinarum* chromosomes contains five chromosomes homologous to *Sclerostachya*.

In an effort to determine the homology of the remaining five chromosomes, the backcrossed progeny ($2n = 50$) was crossed this year with another closely related genus *Narenga* ($2n = 30$). The seedlings are now in the First Ground Nursery, and a few of them are in the short blade stage. An examination of the pollen mother cells in acetocarmine smears has revealed the presence of 18 to 20 bodies, four or five of which are much bigger than the rest. The backcrossed progeny contains $2n = 50$ chromosomes of which 20 are *S. officinarum* and 30 are *Sclerostachya* chromosomes. In meiosis it forms 25 bivalents; ten bivalents of *S. officinarum* plus 15 bivalents of *Sclerostachya*. This has been crossed with *Narenga* ($2n = 30$). If the ten *S. officinarum* chromosomes held no homology with *Narenga* chromosomes, the meiotic configuration in the cross should show 25 bodies, namely ten univalents of *S. officinarum* and 15 bivalents made up of *Sclerostachya* and *Narenga* chromosomes. This is on the assumption that *Narenga* and *Sclerostachya* chromosomes are near enough to pair with one another. There is justification for this assumption inasmuch as in a cross between *Narenga* and *Sclerostachya*[17] the F_1 hybrid showed $2n = 30$, indicating that reduced gametes had operated. This could not have happened, but for their compatibility. The other alternative is that all of the 40 chromosomes (ten *officinarum* plus 15 *Sclerostachya* plus 15 *Narenga* = 40) should remain as univalents, resulting in complete sterility. However, the unmistakable presence of what appears to be trivalents and the total number of bodies being 18 to 20, indicates the possibility that five of the basic chromosomes of *S. officinarum,* which were established to be components of *Sclerostachya,* also showed homology with *Narenga* chromosomes.

The fact that *Sclerostachya* and *Narenga* cross easily, with complete pairing of chromosomes, need not automatically lead to the expectation that in a cross with the backcrossed progeny, the basic chromosomes of *S. officinarum* which were shown to be a component of *Sclerostachya* would also show the same relationship with reference to *Narenga.* It is quite conceivable that both the two sets of five basic chromosomes of *S. officinarum* may be components of *Narenga,* in which case the meiotic configuration in the cross may be expected to be ten trivalents (O.-S.-N.) plus five bivalents (S.N.). On that hypothesis the three genera involved must have originated from a common putative ancestor, five of whose chromosomes are common to all three, the other five being common only to *Narenga* and *Saccharum,* but not to *Sclerostachya.* But as the configuration obtained is, (as has already been explained) a total of about 20 bodies, all that can be said pending further investigation is that all three genera, *Saccharum, Sclerostachya* and *Narenga* may have had a common origin in respect to these five chromosomes.

Other Generic Crosses

In addition to employing *officinarum* × *Sclerostachya,* backcrossed progeny (in whose gametic cells, the *officinarum* chromosomes are reduced to their basic number) for crossing with *Narenga* and *Erianthus* (*ravennae*), a series of *officinarum* × *Narenga* and *officinarum* × *Erianthus* backcrosses are being made, for the purpose of determining the homology of the other five chromosomes in the basic complement of ten *officinarum* chromosomes. It is worth remembering in this connection that the proximity between *officinarum* and *Narenga* can also be inferred from the fact that in the cross *S. officinarum* var. Vellai ($2n = 80$) × *Narenga* ($2n = 30$) made by Barber[1] it was found that the reduced egg gamete has functioned on the *officinarum* side.[10]

There is another recently-discovered important character through which relationship between *S. officinarum, Sclerostachya* and *Narenga* would appear to be indicated. Investigations at this Station[6] have shown that the presence or absence of starch in the internodal cells of the different species of *Saccharum* and related genera, is not a haphazard phenomenon, but one of taxonomic importance. *S. officinarum* has no starch; nor do *Sclerostachya* and *Narenga.* This feature shared by these three would appear to lend support to the view that they are closely related genetically. At the same time it has to be remembered that *S. officinarum* when crossed with other genera like *Sorghum, Zea Mays* and *Erianthus,* behaves in the same manner as it does with *Narenga,* that is, the reduced egg gametes are functional.[20, 10, 11] To elucidate this point, *Sorghum Durra,* Stapf, *Sorghum halepense,* and *Zea Mays* were crossed with the 50-chromosome *S. officinarum* × *Sclerostachya* backcrossed progeny, in the same manner in which *Narenga* was crossed. It was found, however, that in all these cases only 25 bodies were formed during Metaphase I, that is, ten *S. officinarum* bivalents plus 15 *Sclerostachya* bivalents. Obviously the pollen has not functioned in the cross; whether they are selfed progeny or parthenogenetic derivatives could be determined only by a study of the megasporogenesis. Thus an interesting situation has arisen in that, while in a cross with these genera, *Sorghum Durra, Sorghum halepense* and *Zea Mays* a reduced egg gamete on *S. officinarum* side has functioned, it is found that when *S. officinarum* chromosomes are reduced to their basic number they show no pairing affinity.

On the basis of the suggestion of Parthasarathy[16] already referred to, *Sorghum, Zea* and even *Bambusa* (in which cross also reduced gametes are known to function[12]), should be regarded as being genetically related to *S. officinarum. Prima facie* this may look a bit unnatural especially when it is remembered that on this interpretation, a species which may be regarded as closely related, namely, *S. spontaneum,* would have to be relegated to a distant position, inasmuch as in a *S. spontaneum* cross it is always the diploid egg that functions on the *officinarum* side. Either the suggestion is wrong or we should not be unduly perturbed at such seemingly glaring unlikelihoods which emerge out of this interpretation. For instance, has not *Sclerostachya* been established to have an affinity with *officinarum,* which it has not been possible for *spontaneum* to exhibit? Even so, it may well be that these seemingly distant genera do show some amount of relationship, although not ancestral, in the sense that they may not have had a common origin as revealed by their chromosomes showing no homology to the *officinarum* chromosomes when the latter are reduced to their basic number.

In this short review the several crossing results gathered at the Station are presented and sought to be interpreted mainly on the basis of the above mentioned suggestion. Difficulties encountered in establishing interrelationships on this criterion are also presented and in some cases suggestions have been offered to explain them

SUBTROPICAL VARIETIES

Figure 17

Plantings of an "indiginous" northern Indian thin cane compared with the improved variety CO 213, which replaced it.

Experiments at the Coimbatore Station

Of the several interesting cytogenetic features, the most important is, as has already been mentioned, the capacity of sugarcane to produce the reduced and unreduced type of egg gametes. The contribution of the diploid number by the pistillate parent was first noticed by Bremer in 1923, in natural hybrids between *S. officinarum* var. Zwart Cheribon ($n = 40$) and *S. spontaneum* var., Glagah ($n = 56$). The same feature was observed at the Coimbatore Station in crosses between *S. officinarum*, var., Vellai ($n = 40$) and *S. spontaneum*, Coimbatore, ($n = 32$) by Dutt and Subba Rao.[5] Triploids have also been found to occur among selfed progenies and intra-specific hybrids of *S. spontaneum.*[9]

It was Narayanaswamy who actually found out the mechanism by which the doubling of the chromosomes took place in the pistillate parent.[15] Bremer[3] considered this doubling to be a phenomenon associated with interspecific hybridization in *Saccharum*, the doubling having occurred in the egg cell during fertilization. Narayanaswamy, working on the megasporogenesis of *S. officinarum* and *S. spontaneum*, found a fusion of the two inner megaspore nuclei to give rise to diploid megaspores, this phenomenon being more frequent in *S. officinarum* than in *S. spontaneum*. Unlike other cases of diploid egg formation through such means as absence of pairing, double division of univalents and suppression of first division, the method found in sugarcane seems to be unique. Being a post-meiotic phenomenon its genetic consequence is also important in the extreme. For instance, parthenogenetic derivatives from diploid eggs of such origin show a wide range of variation which would not be possible if the egg had attained its diploid condition by the ordinary means. At this Station such parthenogenetic seedlings were obtained by Janaki Ammal.[13] The seedlings showed variation in sucrose content, fertility, etc.

Besides the formation of diploid gametes some varieties have the capacity to give rise to gametes with chromosome number quite different from its own haploid or diploid number. Such a behavior was observed by Bremer[4] in the variety POJ.100, which when crossed with Kassoer gave rise to seedlings having $2n = 152, 157$, and 148 chromosomes. He attributed this to the unbalanced nature of the hybrid POJ.100. Subramaniam[21] studied the megasporogenesis and has furnished the cytological basis for obtaining seedlings with such unexpected chromosome numbers. Co. 421, a pollen sterile cane, when selfed as well as when crossed with *Coix* or *Bambusa* gave rise to two kinds of seedlings; one looking like the mother parent and having the same chromosome number, $n = 59$, — obviously these are parthenogenetic derivatives—and the other thin and having only $n = 43$ chromosomes. During first division the 59 bivalents arrange themselves into two groups at metaphase. The group on the equatorial region consists of 43 bivalents and the other lying above towards one of the poles had 16 bivalents. An egg cell having 43 chromosomes is formed; but this egg cell is found to be divided before fertilization. Absence of cell wall formation after chromosomal division would result in the doubling of chromosomes. Thus seedlings having $2n = 86$ are formed from such eggs. The resemblance of these thin seedlings to North Indian canes[16] suggested the probable origin of the North Indian canes. Co. 421 itself is a complex *S. officinarum* × *S. spontaneum* hybrid (POJ.2878 × Co.285). POJ.2878 has got the genes of both *S. officinarum*, var., Zw. Cheribon and *S. spontaneum* Glagah. Co.285 is a cross between *S. officinarum* var. Green sport and *S. spontaneum*, Coimbatore. Since a seedling resembling a North Indian cane was derived parthenogenetically from a form in whose constitution *S. officinarum* and *S. spontaneum* had entered, it is believed probable that the thin North Indian canes *S. Barberi* may have arisen by a promiscuous hybridization between *S. officinarum* and *S. spontaneum*.

A series of crosses are being made at this Station in order to gather more data likely to throw light on this question. Firstly, *Barberi* (Saretha $2n = 92$) has been crossed with *S. spontaneum* var. Coimbatore ($2n = 64$). This hybrid has to be successively backcrossed to *S. spontaneum*, which may be expected to reduce the *S. officinarum* chromosomes therein to their basic number. Similarly *S. Barberi*, var. Saretha ($2n = 92$) has been crossed with *S. officinarum* with a view to successive backcrossing with *S. officinarum*. This may be regarded as complementary to the previous series of backcrosses, in that it may be expected to reduce the *S. spontaneum* chromosomes to their basic number. These two series of backcrosses may throw some light on the constitution of *S. Barberi*.

In the meantime the chromosome numbers determined so far in interspecific crosses involving *S. officinarum*, *S. Barberi*, *S. robustum* and *S. spontaneum* would appear to give one an idea of the complexity of determining interrelationships among them. In the cross *S. Barberi* × *S. spontaneum* (Saretha $2n = 92$ and *spontaneum* $2n = 64$) the hybrid P.3146 has shown $2n = 78$ to 80 chromosomes.[19] Obviously reduced gametes have entered into the cross. Investigations at this Station have shown that this non-reduction[15] on the egg side results from the fusion of two haploid nuclei of the spore tetrad. Whether this is universal among all species of *Saccharum* remains yet to be determined. Narayanaswamy's findings were that this was more common in *S. officinarum* than in *S. spontaneum*. Nothing is known so far of the same phenomenon in *S. Barberi* and *S. robustum*; nor is it very clear whether the functioning of the diploid gametes is confined only to the egg side of *S. officinarum*. In the cross *S. officinarum*, var. Vellai, ($2n = 80$) × *S. spontaneum* ($2n = 64$) the hybrid Co.205 showed $2n = 112$, indicating the functioning of the diploid egg on the *S. officinarum* side. In the reciprocal cross *S. spontaneum* ($2n = 64$) × Zwart Cheribon (*S. officinarum* $2n = 80$) the chromosome number was also found to be $2n = 112$ in the hybrid,[19] implying functioning of diploid male gametes on the *S. officinarum* side. The numbers in the reciprocal crosses involving local varieties of *S. officinarum* like Chittan, Kaludai Boothan etc., are being determined. But it seems likely that the unreduced condition need not be restricted to the egg gamete of *S. officinarum*, but that its pollen gamete also may function as a diploid when *S. officinarum* is used as a pollinating parent.

In the cross *S. Barberi*, var. (Saretha $2n = 92$) × *S. spontaneum*, Coimbatore ($2n = 64$), since reduced gametes have functioned it may be taken as an indication of the close relationship between the two. But in the cross made at this Station between *S. officinarum*, var. K. Boothan ($2n = 80$) and *S. Barberi*, var. Saretha ($2n = 92$) the hybrid S.G.377/I, shows $2n = 122$ to 126 chromosomes[19] confirming the observation of Brandes,[2] that in such a cross between *S. officinarum* and *S. Barberi* or *S. sinense*, the monoploid chromosome number of the noble parent is doubled. If, as it is surmised,[16] *S. Barberi* contains both *S. spontaneum* and *S. officinarum* chromosomes, then *Barberi* with *spontaneum* or with *officinarum* should behave in the same manner, namely the monoploid gametes should enter into the cross. The possible reason for this seemingly contradictory behavior would appear to be that in *Barberi* there are more *S. spontaneum* chromosomes than *S. officinarum* chromosomes. Hence the probable proximity of *S. Barberi* to *S. spontaneum.* It is quite likely that if the number of *S. spontaneum* chromosomes increases beyond a certain limit, *S. officinarum* is disturbed and so begins to function as a diploid on its gametic side. That *S. officinarum* and *S. spontaneum* are genetically distant can be inferred from the fact that whenever *S. spontaneum* is used with *S. officinarum,* the latter always contributes unreduced egg gametes to the cross. So if in *Barberi* there are more *S. spontaneum* chromosomes than *S. officinarum* would relish, presumably it at once functions as a diploid. But if the number of *S. spontaneum* chromosomes is considerably reduced *S. officinarum* is not presumably disturbed by their presence and would function with its monoploid egg gametes.

This behavior of *S. officinarum* is easily seen in the successive series of Nobilization. In the Java series of Nobilization the *S. spontoneum* chromosomes go on decreasing from 112 in Glagah to 14 in POJ.2725 in the third Nobilization stage. In the first two stages of Nobilization where 56 and 28 *spontaneum* chromosomes, respectively, are present (in Kassoer and POJ.2364) it is found that the diploid egg functions on the side of *S. officinarum.* But in the third stage of Nobilization where only 14 of the *S. spontaneum* chromosomes are functioning, the reduced gamete on the *S. officinarum* side is seen to function. Thus it would appear that when the proportion of *S. spontaneum* chromosomes to the total falls to about 15 to 20 percent, they cease to affect the *S. officinarum* complement, which consequently begins to function normally by contributing the haploid gamete.

At this Station we have also carried the Nobilization up to the second stage.* The third Nobilization is being carried on. The fact that *S. Barberi* and *S. spontaneum* behave alike in a cross with *S. officinarum* i.e. the functioning of the diploid gamete on the *S. officinarum* side may also be taken as an additional indication of the relationship between *S. Barberi* and *S. spontaneum.* It would appear that support for this interpretation could be had from the starch-content character exhibited by these species of *Saccharum,* to which reference has already been made.[6] There is no starch in *S. officinarum*: but there is starch in *S. spontaneum* and *S. Barberi.* If, as is believed likely, *S. Barberi* arose as a result of promiscuous hybridization between *S. officinarum* and *S. spontaneum,* then the presence of starch in *S. Barberi* would imply more of *S. spontaneum* blood than *S. officinarum* as the presence of Starch in a *spontaneum* character. And this is what has been revealed in a *S. Barberi* × *S. spontaneum* cross. On account of more *S. spontaneum* chromosomes being present in *S. Barberi,* reduced gametes have entered into the cross.

In a cross effected at this Station[19] between *S. officinarum* var. Vellai ($2n = 80$) × *S. robustum* ($2n = 72$) the F_1 hybrid (G.1680) has shown $2n = 76$. The *S. robustum* that we have at this Station came from New Guinea and shows a diploid chromosome number of 72 as against $2n = 84$ reported by Brandes.[2] Presumably there are different karyotypes in this species of *Saccharum.* Obviously in this cross the reduced gametes have functioned, implying a close relationship between *S. officinarum* and *S. robustum.* This is as it should be, for according to Grassl[8] *S. officinarum* arose from *S. robustum* in the New Guinea area. Also in the matter of starch content, both *S. officinarum* and *S. robustum* share the same feature of the absence of starch.[6]

It is also worth mentioning that according to Brandes[2], when a noble cane is crossed with *S. robustum* "there is an increase of chromosomes above the number which corresponds to the sum of the monoploid numbers of the parents, but it is considerably less than the sum of the diploid number of *S. officinarum* and monoploid number of *S. robustum.*" Whether this is a case of functioning of egg gametes with unexpected chromosome numbers such as those derived from a cross between Co.421 and *S. officinarum* variety Poovan is not known.[21] But in the cross made here, reduced gametes have functioned. Brandes himself says "from a morphological point of view it (*robustum*) is much nearer to the Noble varieties than are the forms of *S. spontaneum.*" This cross has confirmed Brandes' view.

In the cross *S. Barberi* (Saretha $2n = 92$) × *S. robustum* ($2n = 72$) the F_1 hybrid (P. 3134) showed $2n = 82$ $(46 + 36)$ chromosomes,[19] which corresponds to the sum of the monoploid number of the parents. If *S. robustum* and *S. officinarum* are very close together then the behavior of *S. robustum* with *S. Barberi* should not be the same as that of *S. officinarum* with *S. Barberi.* In the latter cross an unreduced egg gamete on the *S. officinarum* side has functioned and this was interpreted as possibly being due to more *S. spontaneum* chromosomes being present in *S. Barberi* than *S. officinarum* chromosomes. But in the *S. Barberi* × *S. robustum* cross, only haploid gametes have functioned.

Two interpretations of this are possible. Firstly, it may be that *S. robustum* contains some chromosomes homologous to *S. spontaneum. S. Barberi* is suspected of containing more *S. spontaneum* chromosomes than *S. offi-*

***S. officinarum* var. K. Boothan ($2n = 80$) × *S. spontaneum,* Coimbatore, ($2n = 64$) = Hybrid A 10. This hybrid, $2n = 112$ $(80 + 32)$, represents the 1st Nobilization. Chittan, $2n = 80$ × A 10 ($2n = 112$) = hybrid seedling ($2n = 136$) (2nd Nobilization).[19]

cinarum chromosomes for the reason that in *S. officinarum* × *S. Barberi* haploid gametes have functioned on the *S. officinarum* side, and in the cross *S. Barberi* × *S. spontaneum* reduced gametes have entered into the cross. On the basis of a homology between *S. robustum* and *S. Barberi* the origin of *S. officinarum* from *S. robustum* would not be tenable and so this is not likely to be the cause for the functioning of haploid gametes in the cross *S. Barberi* × *S. robustum.*

The other possibility is that this formation of two kinds of gametes, haploid and diploid, is confined mainly to *S. officinarum* and to a lesser extent to *S. spontaneum* and that *S. robustum* and *S. Barberi* may not show this phenomenon. In that case where only *S. officinarum* has figured in a particular cross can one make use of this criterion for purposes of establishing family relationships. Investigations are in progress at this Station to study in detail the megasporogenesis in all the species of *Saccharum* to find out in which of the species this phenomenon is present and in what proportion these diploid gametes are formed.

It would thus appear that the determination of the phylogenetic relationships between different species of *Saccharum* is fraught with considerable complexity. The various crosses and backcrosses that are being effected and the data that are being gathered in regard to the organization of the gametic cells may in time clear up problems of descent and interrelationship.

Summary

A short review has been given of the cytogenetical work that has been done at the Coimbatore Station, with an indication of the lines along which work is in progress and is being continued.

The work pertains to the constitution of *S. officinarum* and the determination of interrelationship among the various species of *Saccharum* and allied genera. An attempt has been made to interpret interspecific and intergeneric affinities on the basis of several interesting cytogenetical features.

The complexity of the problem of speciation in *Saccharum* has been pointed out with reference to some cytogenetical discrepancies which have been presented in the course of the review.

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A PALM FRUIT FROM KAPURDI (JODHPUR, RAJASTHAN DESERT) *COCOS SAHNII* Sp. Nov.

DURING my survey work of Western Rajasthan, I investigated a collection of fossil impressions on Fuller's Earth taken out from the mines at Kapurdi, known for its early tertiary (Eocene) remains. One of the impressions came out to be *Cocos* species (see Photograph). The full description will be given elsewhere. I have named it after the late Prof. B. Sahni. It is worthy of note that the fossil stem *Palmoxylon Sundaram* Sahni from Sagaur (C.P.), was identified by me in 1938 as a *Cocos* stem and was accepted by Prof. Sahni as such. This discovery of fruit confirms my view that *Cocos* was known in India in early tertiaries.

FIG. 1. Remains of the endocarp of *Cocos sahnii* showing the two eye like depressions at one end. × 1.

Herbarium, K. N. KAUL.
The National Botanical Garden,
Lucknow,
March 6, 1951.

CYTOPLASMIC INHERITANCE IN *SACCHARUM*

THE theory of the "plastogene"[1] recognises the existence of determinants outside the nucleus attached to the plastids having all the properties of nuclear genes including permanence. The existence of another set of extra nuclear determinants "plasmagene"[2] is vouched for by non-mendelian inheritance of which reciprocal differences are the simplest evidence. Breeding results in reciprocal hybrids in *Linum*,[3,4] *Nicotiana*[5] and *Zea*[6] have indicated that certain characters, especially male sterility, are determined at least in part by some condition of the cytoplasm.

Interspecific hybrids in Saccharum are not usually identical reciprocally. The species involved are *S. officinarum*, *S. spontaneum*, *S. barberi* and *S. robustum*. The gross appearance especially in respect of habit and thickness of stem, of reciprocal crosses, in some cases is so glaringly maternal that it sets one thinking if it could not be a case of cytoplasmic inheritance, at least in part in the sense that it could be a case of interaction between genes and cytoplasm. The problem is rendered more interesting in view of the fact that interspecific hybridization in Saccharum does not always involve the union of the haploid parental genomes. If inheritance was purely genic one would expect the hybrid to resemble that parent which had contributed the larger number of chromosomes. In some instances even though the male parent contributed the $2n$ number, the resemblance of the hybrid is more to the maternal parent which contributed the usual haploid number. In some crosses the egg is known to contribute neither its haploid nor its diploid number. The various crosses and reciprocal crosses with their relevant chromosome numbers are given in brief in Table I. The general configuration of the hybrid appears to be influenced greatly by the cytoplasm of the egg parent. However, it is not suggested that this phenomenon is universal among all the varieties of Saccharum species. For instance, while it is marked when the varieties like Chittan and striped Mauritius are used, it is not so pronounced when others like Kaludai Boothan or Black Cheribon are involved. It may well be that this phenomenon of cytoplasmic inheritance is confined only to some varieties.

Support to the view of the existence of cytoplasmic inheritance is to be found in the manifestation of maternal inheritance with regard to the phenomenon of male sterility. Dutt and Krishnaswami[7] and Dutt and Rao[8] have recorded this phenomenon in some spontaneum hybrids. An analysis of the available hybrids suggested that this phenomenon revealed itself only when *S. spontaneum* was involved in the

TABLE I

No.		Parents and their haploid chromosome number				Hybrids	
		Female		Male		Chromosome No. and how derived	Gross appearance (Habit and thickness of stem)
1	A.	*S. officinarum* (K. Boothan)	40	*S. spontaneum* (Coimbatore)	32	112 $(2n+n)$	Like *officinarum*
	B.	*S. spontaneum*	32	*S. officinarum* (K. Boothan)	40	112 $(n+2n)$	Like *officinarum*
	C.	*S. officinarum* (Chittan)	40	*S. spontaneum*	32	$2n=112$ $(2n+n)$	Like *officinarum*
	D.	*S. spontaneum*	32	*S. officinarum* (Chittan)	40	$2n=112$ $(n+2n)$	Like *spontaneum*
2	A.	*S. officinarum*	40	*S. robustum*	36	$2n=76$ $(n+n)$	Intermediate
	B.	*S. robustum*.	36	*S. officinarum*	40	$2n=76$ $(n+n)$	Intermediate
3	A.	*S. robustum*	36	*S. barberi*	46	$2n=82$ $(n+n)$	Like *S. robustum*
	B.	*S. barberi*	46	*S. robustum*	36	$2n=82$ $(n+n)$	Like *barberi*
4	A.	*S. barberi*	46	*S. spontaneum*	32	$2n=78$ $(n+n)$	Like *barberi*
	B.	*S. spontaneum*	32	*S. barberi*	46	$2n=78$ $(n+n)$	Like *S. spontaneum*
5	A.	*S. barberi*	46	*S. officinarum*	40	$2n=86$ $n+n)$	Like *S. barberi*
	B.	*S. officinarum*	40	*S. barberi*	46	$2n=126$ $(2n+n)$	Like *S. officinarum*

cross as the pistil parent. To clarify this point a number of crosses, reciprocal crosses and back crosses were studied, the results of which are briefly indicated in Table II, especially with reference to this particular character of male sterility.

TABLE II

Parents		Hybrid Diploid number and how derived	Male Sterility + present − absent
Female	Male		
officinarum	*spontaneum*	112 $(2n+n)$	−
spontaneum	*officinarum*	112 $(n+2n)$	+
barberi	*spontaneum*	78 $(n+n)$	−
spontaneum	*barberi*	78 $(n+n)$	+
**spontaneum*	*sclerostachya*	79 $(2n+n)$	+
**spontaneum*	*narenga*	79 $(2n+n)$	+
**spontaneum*	*erianthus*	84 $(2n+n)$	+
**spontaneum*	*sorghum durra*	74 $(2n+n)$	+

* Reciprocal crosses of these have just been made and in such of those as in which seedlings result, the expectation is that there will be no male sterility. But the presence of this feature in all these crosses involving *Spontaneum* as the mother is worth noting. The possibility of male sterility being due to the intergeneric nature of the cross must not also be overlooked. But in one known intergeneric cross not involving *Spontaneum* as the pistil parent, the phenomenon has not been seen, *i.e.*, *Officinarum* × *Sclero stachya* $(2n+n)$.

The crossing results obtained so far lead one to the following tentative conclusions:—The difference in inheritance is due to a dissimilarity in the cytoplasm of *Spontaneum* on the one hand and the other forms involved on the other, like *Officinarum*, *Barberi*, etc. Individuals of the F_1 and later generations, both F_2 and back-crosses, resulting from the cros between *Spontaneum* as the female and the others as the male parents, would have cytoplasm contributed by *Spontaneum* whereas the progeny of the reciprocal crosses would have the cytoplasm of the other respective parents. A particular gene or group of genes or even a whole chromosome for bisexuality from *Spontaneum* and *Officinarum* would appear to react normally in their respective cytoplasm. A certain combination of factors seems to produce different phenotypic effects depending upon the derivation of the cytoplasm. When the genes are in a heterozygous condition in *Spontaneum* cytoplasm male sterility is the consequence. If present in that condition, say in *Officinarum* cytoplasm as when *Officinarum* is used as the pistil parent, there is no male sterility. Nor is there an expression of this feature when the genes are in a homozygous condition in *Spontaneum* cytoplasm as in the selfed diploid derivatives of *Spontaneum* or as when *Officinarum* genes come to be implanted in *Spontaneum* cytoplasm by successive back-crossing of *Spontaneum* by *Officinarum*. In other words, the nuclear genes of *Officinarum* and *Spontaneum* are reacting with the plasmagenes of the latter resulting in this defect. A study of the available selfed and back-crossed progeny of the F_1's seems to support the view presented above. In two seedlings of the back-crossed progeny *Spontaneum* × *Sclerostachya* × *Sclerostachya*, the phenomenon is present in one and absent in the other, which is according to expectation. Because if it were purely cytoplasmic as in Wettstein's Funaria, all the back-crossed progeny would show this feature. Since however, it is believed to be a result of the reaction between nuclear genes and cytoplasm, only in those in which the former are in a heterozygous condition in *Spontaneum* cytoplasm, does the phenomenon of male sterility manifest itself. Hence the expectation in the back-crossed progeny is 1 : 1. However, since these are selected seedlings, we have no idea of the large number that would have been rejected in the nursery. That in any case it is cytoplasmic, can be inferred in a negative way by the complete non-occurrence of male sterility in *Officinarum* × *Spontaneum* × *Officinarum* as also in *Officinarum* × *Spontaneum* selfs, because in both cases the concerned nuclear genes though heterozygous (in half the progenies) are in *Officinarum* cytoplasm whereas in the F_2 of what in essence are reciprocal crosses in the sense that *Spontaneum* is the female (*e.g.*, *Spontaneum* × *Sclerostachya* and *Spontaneum* × *Narenga*; though pollen sterile, a few grains are sometimes available in the F_1's to take them to F_2's) the phenomenon is present in the few selected seedlings that are available, since it is in *Spontaneum* cytoplasm that the genes are associated in a heterozygous condition. However, if the entire F_2 population is examined the expectation is that half the number would show this feature, the other half being bisexual. It thus appears that nuclear genes and plasmagenes fit one another in heredity in certain ancestral combinations, but fail to do so in certain recombinations produced by crossing. The most common expression of this failure is male sterility. We cannot, however, count upon either absolute constancy or absolute matrilinear descent, as sorting out of the plasmagenes and contamination by pollen cannot be ruled out altogether.

If the cytoplasm of *Spontaneum* is so distinct from that of the other forms as to change the phenotypic expression of the genes for bisexuality, it may be expected to have at least some effect on the expression of all the other genes. This seems to be the case at least in some cases as for instance in *Spontaneum* × *Barberi*; *Spontaneum* × *Officinarum*, where there are reciprocal differences as regards habit, stature and thickness of stem, in addition to male sterility. However, only where *Spontaneum* is involved is there the expression of male sterility. In some crosses not involving *Spontaneum*, the reciprocal differences are confined to other characters than male sterility, *e.g.*, *Barberi* × *Officinarum*. This would be comparable to the case of tomato[9] where the difference is one of size and expressing itself in F_1 and in the segregating F_2. It is also conceivable that male sterility alone is the outward expression of this interaction, unassociated with other differences of size and habit, in reciprocal crosses. It may then be that the action of all the genes is affected only in respect of that character while in regard to other characters their action is presumably unchanged.

Further experimental work is in progress. The evidence available at present cannot by any means be said to be conclusive. Further studies that are in progress may or may not substantiate the interpretation herein presented tentatively.

T. S. Raghavan.

Sugarcane Breeding Station,
Coimbatore,
December, 1950.

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1851 EXHIBITION SCHOLARSHIP

THE Royal Commissioners for the Exhibition of 1851, London, have awarded the Science Research Scholarship for the year 1951 to Shri. Kamla Kant Pandey, Research Scholar at the Indian Agricultural Research Institute, New Delhi.

CYTO-GENETICS OF SUGARCANE

By T. S. RAGHAVAN, Sugarcane Breeding Institute, Coimbatore

(Received for publication on 27 March, 1951)

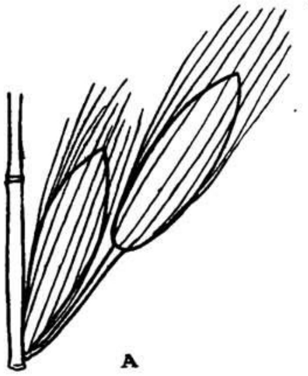
(With Plates V—XI)

THE sugarcanes in cultivation in India are broadly divisible into two groups, the thin canes of the sub-tropical North and the 'Noble' canes of tropical India. Botanically the former are included under the species *Saccharum barberi* and the latter under *S. officinarum*. Though both these species are popularly called sugarcanes, they differ from each other in certain features which may be reagrded as fundamental. Generally even the same species when grown in different environmental conditions may show marked differences. But these affect only the vegetative parts of the plant. The reproductive portions, namely, the floral regions, do not show any change in their configuration or plan of construction. The bean flower for instance will present the same appearance wherever it is grown; it will have the same parts in the same order of arrangement and show the same plan of symmetry. Its stem and leaves, however, may show variation to such a degree as even to make it difficult to be recognized. Hence it is the floral region that is of the utmost importance in establishing the identity of a species and its relationship.

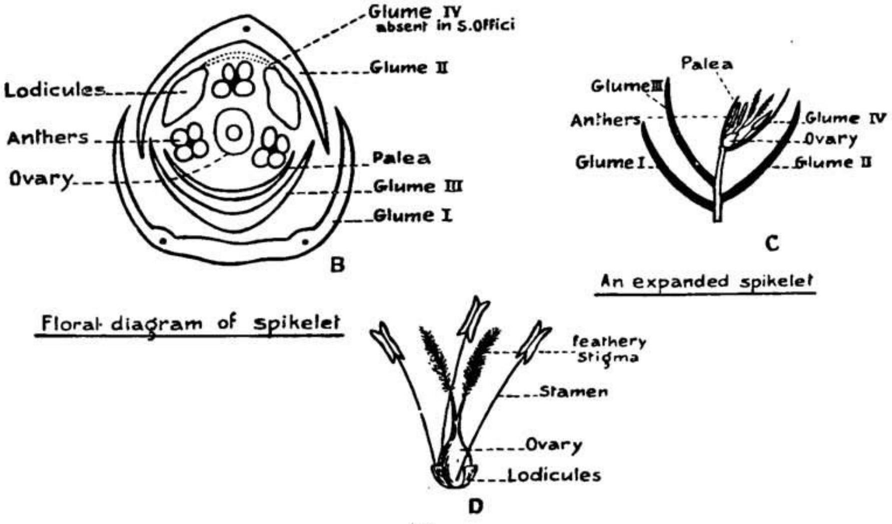
I. *Sugarcanes: Some external features and their morphological significance*

In the sugarcanes, the flowers occur in their thousands, to form the arrow (Plate VI, fig. 2 A) (inflorescence). As in other grasses the unit is a spikelet, two of which occur together at each node, one of them having a stalk and the other none (Plate V, fig. 1 A). Each spikelet consists of a definite number of glumes in the axil of the innermost of which the flower is situated (Plate V, figs 1, B and C). Though this is the general plan of construction, the two species of cultivated canes show differences in some important details. Of the two spikelets, the one without the stalk (sessile) is older in the 'Noble' cane, while it is the stalked spikelet that is older in the North Indian canes. In the matter of the number of glumes in each spikelet, *S. barberi* has four, whereas in *S. officinarum* usually the fourth glume is absent.

The flower itself is highly reduced, the usual showy parts, the sepals and petals, being conspicuous by their absence. It consists of those parts which are directly concerned in reproduction and for which the flower is intended. There are three stamens and an ovary with a single ovule in it, which after fertilization becomes the seed (Plate V, fig. 1, D and Plate VI, fig. 2 B). There are two structures, the lodicules which may be regarded as representing the highly reduced petals and sepals. These and other differences in the floral region coupled with some in the vegetative parts, are full of significance, to the morphologist who seeks to study inter-relationships. Such a study would reveal some interesting things. For instance, while the North Indian and tropical canes of South India differ from one another in these details, the wild cane, namely *S. spontaneum*, shares these characters with the North Indian



Pedicelled and sessile spikelets



An expanded spikelet

Floral diagram of spikelet

Flower

Fig. 1. Floral parts of sugarcane.

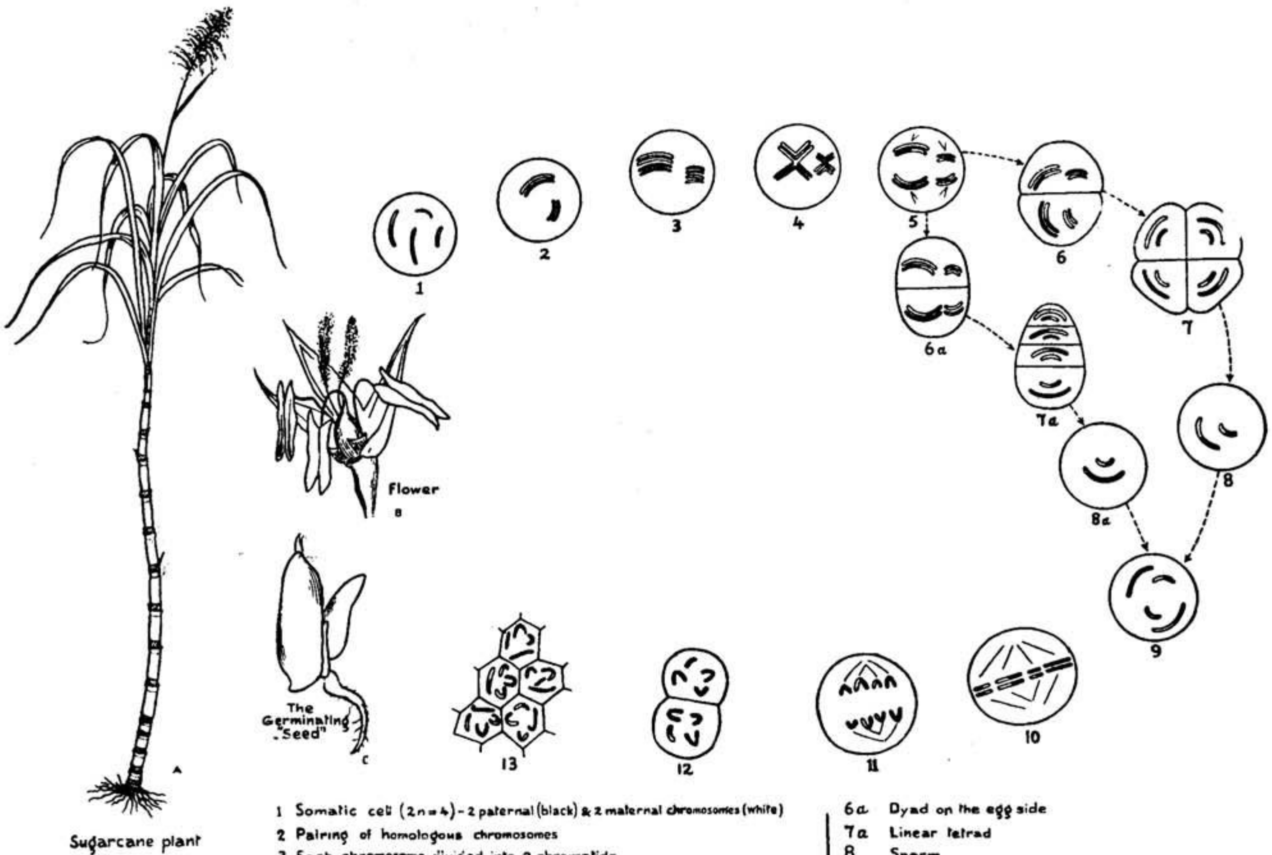
canes. The other likely wild relatives of the sugarcane are Sclerostachya, Narenga and Erianthus. Obviously for establishing relationships, many things, in addition to these morphological details, will have to be studied and taken into consideration.

II. *Breeding in relation to cytogenetics*

Any breeding work to be carried out on scientific lines must involve a knowledge of genetics and cytology. The science of genetics seeks to discover why for instance a bean seed, when sown gives rise to a bean plant and not anything else and how it also happens that one bean plant is not exactly like another. This is intimately related to cytology which is a study of the minute living units, the cells, of which plants and animals are constructed. The cells contain a dense spherical body the nucleus, lying in a viscid fluid, the cytoplasm. It has the character of heredity in itself in that it determines what the offspring is to be like. This is capable of direct demonstration in some lower plants and animals. For instance it is possible to remove the nucleus from the egg of Sea Urchin and fertilize it with sperm of another species. The resulting larva is an exact smaller edition of the male parent from which it had derived the nucleus and shows no influence of its female parent from which it had derived its cytoplasm. Similar transplantation experiments in lower organisms between parts containing nuclei and those not having them show definitely that it is the nucleus that is responsible for the transmitting of characters. The nucleus is composed of a definite number of threads, the chromosomes, on which are located the genes which are the particles concerned in the transmission of hereditary characters. The physical basis for the laws of heredity is to be found in these chromosomes and their behaviour.

III. *The nucleus in vegetative multiplication*

In vegetative reproduction or clonal propagation, such as is almost the rule in sugarcane, the whole of each clone is derived from a piece of one individual and so there is complete uniformity among all the clones. The cytological basis for this is that the cells of which the bud is composed, go on dividing repeatedly accompanied by differentiation to form the daughter cane. This division that takes place repeatedly is mitotic. The chromosomes in the cells composing the body of the plant (somatic chromosomes) are constant for any particular species of plant. In the 'Noble' cane, *S. officinarum*, the somatic number is 80. During the division of the nucleus which precedes cell division, each one of these chromosomes separates into two exact longitudinal halves, the chromatids, one half going to one pole and the other to the opposite, and never will the divided two halves of a chromosome go to the same pole (Plate VI, fig. 2, 9-13). The two daughter nuclei that result, consequently contain the same number of chromosomes. Whatever may be the number of divisions undergone, so long as this mitotic method of division is resorted to, the same number of chromosomes would be kept up, and since the daughter cells of a division are an exact replica of the mother cell, all the genes contained in the latter are present in the daughter in the same number and arrangement and hence the uniformity of individuals resulting from clonal propagation. The number of chromosomes in the mitoses of one individual and of the whole species is constant.



1	Somatic cell (2n=4) - 2 paternal (black) & 2 maternal chromosomes (white)
2	Pairing of homologous chromosomes
3	Each chromosome divided into 2 chromatids
4	Crossing over between two non-sister chromatids
5	I Division (Reductional) separation of the chromosomes
6	Dyad on the pollen side each cell having 2 chromosomes
7	II Division (Mitotic) Tetrad of pollen grains each having 2 chromosomes (Note the change in the quality of chromosomes due to crossing over)
6a	Dyad on the egg side
7a	Linear tetrad
8	Sperm
8a	Egg
9	Fertilised egg having four chromosomes
10	Mitosis - each chromosome divides longitudinally into 2 chromatids
11	Separation of the chromatids
12 & 13	Multiplication of cells by mitotic division of the nucleus

FIG. 2. Chromosome cycle in the life history of Sugarcane (only four Chromosome shown).

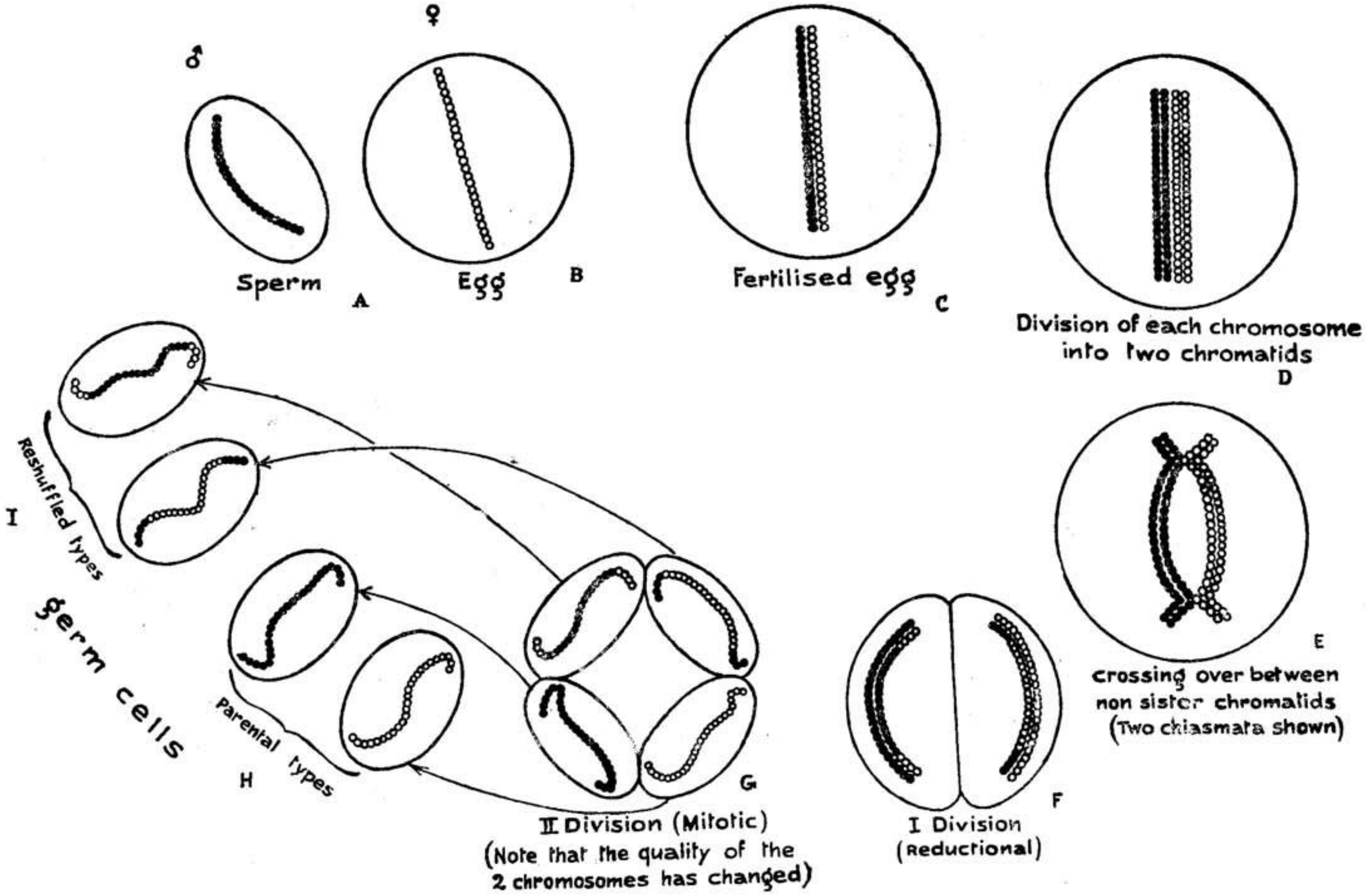


Fig. 3. Fertilization and meiosis : origin of qualitative changes in chromosomes.

IV. *The nucleus in sexual reproduction*

In sexual reproduction a sperm nucleus from a pollen grain (Plate VII, fig. 3 A) enters an egg cell (Plate VII, fig. 3 B) which is many times larger and fuses with the female nucleus. The nucleus of the fertilized egg is thus of mixed origin (Plate VII, fig. 3 C). The new organism developes from this and shows the characters father and mother. Thus the somatic cells of the resulting individual contain two similar sets of chromosomes, one from the egg and the other contributed by the sperm (Plate VI, 1 and 2). In the 'Noble' sugarcanes, 40 chromosomes from the egg nucleus combine with 40 corresponding ones from the pollen nucleus, to give 80 in the embryo, which developes into the sugarcane plant.

In the formation of these germ cells by the parent there must have taken place a process of reduction or a halving of the chromosome number to compensate for the doubling that takes place during fertilization. This reduction division of meiosis, is inevitable in the cell history, wherever there is sexual reproduction, as otherwise the chromosome number would go on duplicating *ad infinitum* from generation to generation. This takes place in the sugarcane, as in all higher plants, during the formation of the reproductive cells, pollen grain and embryo sac. Meiosis consists of two divisions of the nucleus, with only one division of the chromosomes (Plate VII, fig. 3). First, the chromosomes make contact and begin to pair (Plate VII, fig. 3 C); of each pair one is from the sperm and the other is from the egg, which had fused in fertilization to give the plant, from which the germ cells are now being organized. Thus instead of the diploid or 2 n number of chromosomes of mitosis there is a halved or haploid n number of bivalents (Plate VI, 2). And instead of the paired sister halves or chromatids of mitosis produced by reproduction of a single chromosome, there are paired homologous chromosomes brought together by attraction. Suddenly this attraction is followed by repulsion. All the pairs separate. At the same time each chromosome has divided into a pair of chromatids (Plate VI, 3; Plate VII, fig. 3 D). The chromosomes remain in contact at certain points at which the chromatids exchange partners. Under the strain of coiling the partner chromatids break at corresponding points. They uncoil and rejoin in new combinations (Plate VI, 4 and 5; Plate VII, fig. E). The two chromosomes of each bivalent are separated and each nucleus has the haploid or reduced number of chromosomes. On account of the exchange of partners that took place prior to separation, the two chromatids of each chromosome are not throughout sister chromatids. Some portions of the chromosomes are made up of sister chromatids, the others are composed of chromatids from partner chromosome (Plate VII, fig. 3 F). The two daughter nuclei at once divide again, by mitosis (Plate VII, fig. 3, F and G). The chromosomes are already double and the two chromatids of each chromosome separate. Thus four daughter nuclei having the halved number of chromosomes are derived from the mother cell which contained the diploid number of chromosomes (Plate VII, fig. 3, H and I). Meiosis is the same whether it is on the pollen side or on the egg side. The only difference is that whereas in the former all the four pollen grains resulting from the reduction division of the pollen mother cell are functional (Plate VI, fig. 2, 6-8), on the side of the egg three usually degenerate, and only one survives, and that is the embryo sac within which the egg is organised (Plate VI, fig. 2, 6a-8a).

V. Chromosomal basis of heredity

For the plant breeder it is meiosis that is of the utmost importance. The pairing chromosomes are of similar size and shape and are derived from opposite parents in which they have corresponding structures and functions. The four germ cells produced by meiosis are alike only in having the reduced or halved chromosome number (Plate VII, fig. 3, H and I). But in all other respects their nuclei are different. The arrangement of the paired chromosomes (bivalents) has been at random, so that paternal and maternal chromosomes would have been assorted at random also. Their parts have also been reassorted and exchanged by crossing over. It means that the minute hereditary particles, the genes, which are arranged linearly on the chromosomes have been exchanged between paternal and maternal chromosomes, leading to a recombination of hereditary differences. Each mother cell will have given rise to four germ cells, different from one another and different from those produced by any of the mother cells. Thus in sexual reproduction the occurrence of differences between individuals is inevitable. These variations are not only maintained from generation to generation, but also rearranged and redistributed so as to make every varying individual unique. In self fertilized plants, where the male and female germ cells (which ultimately fuse) come from the same or different flowers of one parent plant, the differences among individuals in the progeny are very slight. And if this self fertilization is a regular feature, generation after generation, then we get a pure line or true breeding line. But in cross pollinated plants the variations are more accentuated and wide spread. These variations are the principal working tool of the plant breeder. But before these differences are made use of, it has to be ensured that they are due to hereditary causes and not due to environment. The importance of cytogenetics lies in being able to correlate observed breeding results with chromosomal behaviour. In other words instead of breeding being a hit or miss affair, it is sought to be put on a scientific plane.

VI. *Some cyto-genetical features of sugarcane*

a. Clonal propagation. Sugarcane exhibits several cyto-genetical features, which are at once the hope and despair of the breeder. Of these the most useful is its being asexually propagated. Any good form that we may get by accident (gene mutation) or by hybridisation can at once be fixed, inasmuch as it can be propagated asexually. For instance, among the hybrids between *S. officinarum and S. spontaneum* there was found a seedling (Co. 205) which possessed most of the desired economic characters of the two parents. It was at once multiplied vegetatively and distributed for cultivation. Similarly from the 'Noble' cane variety, striped Mauritius, there arose a red sport (Gillman sport) through gene mutation, which exhibited certain superior economic characters over the parent from which it sprang. It was clonally propagated and distributed for cultivation.

b. Highly heterozygous polyploid: Variations in selfed progeny. A marked feature in sugarcane breeding is that even in selfed progeny there is a very wide range of variation. The reason for this is that sugarcanes are polyploid hybrids, that is, two or perhaps more fundamental forms have entered into hybridization in nature accompanied by chromosome duplication. The various crosses and back crosses that took place during their evolution have made them highly heterozygous for several pairs of genes, that is, several different genes or their associations have entered into their formation. If we consider the behaviour of even simple hybrids which are heterozygous for one or two pairs of genes, then we can realize the complicated behaviour of a form like sugarcane, which is not only heterozygous for several gene pairs, but is also a high polyploid having several sets of such heterozygous chromosomes. If we cross a true breeding tall plant (TT) with a true breeding short plant (tt) we get a hybrid (Tt) which is heterozygous for one pair of genes, the gene T (gene for tallness) contributed by the homozygous tall parent, and the gene t (gene for shortness) contributed by the homozygous short parent. This hybrid Tt would look like that parent whose gene is dominant, say T, or would be intermediate in case there is no dominance. When the hybrid Tt forms sexual cells or gametes, T and t are separated during reduction division and if these two kinds of gametes come into contact at random during self fertilization, four kinds of individuals are formed, (TT), (Tt), (tT) and (tt). Of these the first three will be tall and the fourth will be short, in case of complete dominance. If the hybrid was heterozygous for two pairs of genes, that is, arose from parents differing from one another in respect of two pairs of characters, namely, stature and nature of seed, (TT SS, tall plant with smooth seeds, and tt ss, short plant with wrinkled seeds) the sexual cells formed by such a hybrid will fall into four classes, (TS), (Ts), (tS) and (ts). A random union of these four kinds of gametes in self fertilization would give rise to four kinds of visibly different individuals in the F_2 or second filial generation made up of parental forms TT SS and tt ss as well as those exhibiting now combinations of parental characters, like tall wrinkled (TT ss) and short plants with smooth seeds (tt SS). If a hybrid is heterozygous for several pairs of genes instead of only two, the number of kinds of sexual cells or gametes formed will be proportionately high, namely, 2 to the power of n ($2n^2$), where n represents the number of gene pairs involved and consequently the progeny of the hybrid will fall into as many different visible kinds and hence the wide range of variation. So in sugarcane, which is not only heterozygous to a high degree, but is also a high polyploid, the selfed progeny shows a very wide range of variation. The photograph (Plate VIII, fig. 4 A) shows the selfed progeny of *S. spontaneum* exhibiting variations among themselves. Among the 'Noble' canes, however, only a few forms are self fertile. Even in such forms there is not only variation in selfed progeny but also there is a very large percentage of mortality, only a few seedlings surviving. This is due to the presence of many lethal genes. These are recessive and are kept under suppression by dominant genes. So long as the plant is vegetatively propagated the lethal effect is not manifested. But during sexual reproduction the dominant and recessive genes are separated at meiosis, and among the various recombinations that take place during fertilization, such of the progeny in which the recessive genes, come together without having the protection of the dominant genes, die early. Since the percentage of mortality is very high, it is probable that there is a large accumulation of these recessive lethal genes.

c. Variations in hybrid population and impossibility of repeating combinations. If we cross the sugarcane with another form which is also highly heterozygous, the offspring that result will be a heterogeneous population, no two of which can be alike. The parental characters are found distributed amongst the progeny. If they were merely hybrids from two true breeding parents, all of them should be alike, either resembling one parent completely or the other, according to which of the parental genes are dominant, or they should be intermediate. But here, there is a medley of F_1 population in some of which the earliness of one parent may show itself out and in others the thickness of the other parent may manifest itself. Yet in a few the high sucrose of one of the parents may be incorporated and it may also happen that in a few a combination of some of the desirable characters of the two parents may be found to occur. If in such a heterogeneous population we are able to get a form answering our needs it is obvious that it is impossible to resynthesise such a form by repeating the cross. To this extent the getting of a desirable seedling in the first hybrid generation has necessarily to be a hit or miss method. That is why in our breeding operation many thousands of seedlings are raised by controlled crosses between parents possessing characters whose combination to the largest possible measure is the main objective. The expectation is, the larger the population the greater the chances of securing such an individual. The photographs in Plate VIII, fig. 4B and 4C give an idea of the variations in the progeny of interspecific and intergeneric crosses respectively.

These variations are by themselves of great use to the sugarcane breeder, especially, because the maintenance of the desirable type got out of a matting of highly heterozygous parents is possible through clonal propagation. Otherwise it would not be possible to recover a pure breeding form through sexual means, because the new variety also will be heterozygous since the parents differed by many genes. The offspring which it would produce from seed would show great variation. Only a few of these would be sufficiently like the parents. These plants too would fail to breed true for they also would be heterozygous for a number of genes. After many generations it may be possible to establish a true breeding strain. The time, labour and cost involved are so great as to make this venture not worth while.

d. Fertility of and absence of segregation in sugarcane hybrids. The fact of all the known sugarcane, wild and cultivated being highly heterozygous polyploids reveals in a peculiar manner in species and even generic hybrids. Firstly, there is practically no segregation of parental characters, due to absence of pairing between parental chromosomes. In the hypothetical cross mentioned previously, we have assumed that the chromosomes containing gene pairs Tt and Ss were perfectly homologous and that they pair normally. Segregation was also normal in the sense that the parental forms could be recovered as also recombination of parental characters obtained. But if the two parents were widely different from one another, but near enough for the chromosomes of the two parents to exist side by side in the hybrid, the parental chromosomes would not pair. For instance in a cross between the radish and the cabbage, the hybrid had 18 chromosomes, being the sum of the gametic number of the two parents, namely, 9 from the egg of the radish and 9 from the sperm of cabbage. This intergeneric hybrid set no seeds though flowers were

A

S. Spontaneum (Local)

Selfed progeny

1 Tall plant, Thin yellow green stem, narrow leaves.
2 Tall plant, Thick green stem, wide leaves.
3 Medium sized plant, Thin yellow green stem, Narrow leaves.
4 Tall plant, Thick purple stem, wide leaves.
5 Dwarf plant, very thin yellow green stem, Narrow leaves.

B

Inter-specific cross

S. officinarum Var: Chittan
×
S. Barberi Var: Saretha

1 Tall plant, Medium thick purple stem.
2 Dwarf plant, Thin greenish yellow stem.
3 Tall vigorous plant, Thick greenish yellow stem
4 Dwarf plant, Medium thick stem.
5 Tall plant, very thick greenish yellow stem.

C

Inter-generic cross

S. Spontaneum Local
×
Sclerostachya fusca

1 Tall plant, erect, medium thick, greenish yellow stem.
2 Medium plant, erect, Medium thin yellowish green stem,
3 Tall vigorous plant, Thick purple stem
4 Short plant, Thin yellowish green stem. Spreading habit.
5 Tall plant, Thick yellowish green stem leaves wide

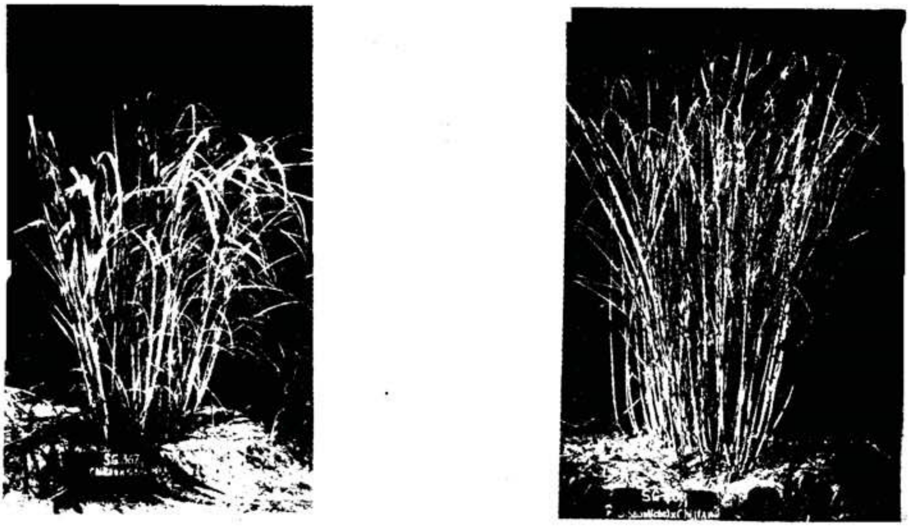
FIG. 4
VARIATIONS IN THE PROGENY OF SACCHARUM AND ITS HYBRIDS

formed. It was sterile. It was found that pairing and exchange of partners that should normally take place between the maternal and the corresponding paternal chromosomes during the formation of the germ cells, egg or sperm, did not happen. This was because, the chromosomes of the two parents did not possess anything in common between them. Hence they remained unpaired as univalents instead of forming bivalents. It may be mentioned in passing that even in closely related species crosses, changes in the genic structure of one or more chromosomes may reduce pairing. The sexual cells that are formed from such partially pairing or non-pairing individuals receive unbalanced assortments of chromosomes in varying numbers and sterility results. But the sterility of a hybrid like that of radish and cabbage hybrid, need not be final. In a few of the sexual cells, eggs and sperms, the nuclei fail to separate during the first division. No partition wall is formed and a single nucleus with all the 18 chromosomes, 9 from cabbage and 9 from radish is formed. The 2nd division which is mitotic, separates this single nucleus into two daughter nuclei each having 18 chromosomes. In this way are formed a few eggs and sperms having the diploid number of chromosomes, instead of the haploid number as normal germ cells should, had they resulted from regular reduction division. If a diploid sperm fertilises a diploid egg, the plant that developes from it is a tetraploid having 36 chromosomes in which four sets of chromosomes are present, two sets from radish and two sets from cabbage. Such an allo-tetraploid derived from hybridization and chromosome duplication is fertile and true breeding. The cytological basis for this is that since two sets of radish chromosomes are present they pair among themselves (autosyndesis) to form 9 bivalents. Similarly the cabbage chromosomes. The difficulty of non-homology between radish and cabbage chromosomes has been thus overcome.

The sugarcane has also had a similar origin through more complex hybridization, backcrossing, etc., accompanied by chromosome duplication. It is thus an allo-polyploid having several sets of the basic 10 chromosomes. If it were merely an allo-tetraploid having been formed by hybridization between two related species or genera accompanied by chromosome duplication, it must also breed true. But the large variation that we find even in selfed progeny show that it is highly heterozygous, derived from the union of germ cells dissimilar in respect of the quantity, quality and arrangement of their genes. Many of these are lethal in *S. officinarum* leading to high mortality of their seedlings. The genetical consequence of this internal pairability of chromosomes is that in most cases the sugarcane hybrids are fertile. Apart from species hybrids as between *S. officinarum* and *S. spontaneum* which are fertile, even intergeneric hybrids show fertility or partial fertility in several cases. For example, *S. spontaneum* with Sclerostachya gave fertile hybrids, which showed variations among themselves. Again the Sorghum cross with sugarcane which was made to introduce a shorter life cycle characteristic of Sorghum, showed among the hybrid progeny several forms which were fertile, They also showed variations in which parental characters were found distributed. The fertility of this cross, for instance, is due to the pairing among themselves of the 40 sugarcane chromosomes and the 20 Sorghum chromosomes, forming 30 bivalents. The variations exhibited by the selfed progeny of such hybrids are not very pronounced and such variations as we find in this F_2 generation are due to exchanges of genes that have taken place among the sugarcane chromosomes on the one hand and among the Sorghum chromosomes on the other, and not between them. In other words in the formation of this F_2 population, no segregation of parental characters was involved according to Mendelian heredity. Consequently, neither the parental forms, that is, pure sugarcane or Sorghum, nor a recombination of distinct parental characters are recoverable.

e. Functioning of diploid gametes : Reciprocal crosses not identical : unpredictability of chromosome numbers in sugarcane hybrids. Another peculiarity which is almost unique in sugarcane hybridization is that no prediction can be made as to what the chromosome number in a particular cross would be like. Normally when two plants are crossed, the gametes, each with its haploid number of chromosomes enter into fertilization and the diploid chromosome number of the hybrid, irrespective of whether it is fertile or sterile, should be the sum of these gametic numbers. For instance, if *S. officinarum* ($n=40$) is crossed with *S. spontaneum* ($n=32$) one should expect the hybrid to show a diploid number of $2n=72$. But we find the hybrid showing $2n=112$. It means that the female parent *S. officinarum* has contributed the diploid number of chromosomes through its egg, which normally should contain only the haploid number of chromosomes, having been derived from a reduction division of the mother cell. On this basis, the resemblance of the hybrid progeny to the female parent is understandable, in that the number of maternal chromosomes far exceed that of the paternal chromosomes. How about the reciprocal cross? In any cross, say, between a tall and a dwarf plant, it should not matter whether it is the tall plant that is used as the female parent, or *vice versa*. But in some *Sacchalrum* hybrids we find a difference in the hybrid progeny in reciprocal crosses. For instance in a cross between *S. officinarum* × *S. spontaneum* (the first parent is the female) the progeny though differing from one another, resemble more the *S. officinarum* parent for which there is cytological justification, as has been indicated above (Plate IX, fig. 5 A). But in the reciprocal cross, having *S. spontaneum* as the mother the progeny resembles more the *S. spontaneum* parent even though it is the *officinarum* that has contributed the diploid number through its sperm (Plate IX, fig. 5B).

This is not all. Some crosses show a number which is neither the sum of the haploid numbers of the parents, nor the sum of the diploid number of one and the haploid number of another. For instance, Co. 453 is a cross between *S. officinarum* variety Black cheribon ($n=40$) and Co. 285 ($n=56$). It should show either $40+56=96$ or $80+56=136$. But it actually has 124. It means that the female parent has contributed, through its egg, a number which is neither its haploid number (59) nor its unreduced number (80), but some unexpected number (68). What the significance of this non-reduction and partial reduction in the formation of the egg is likely to be is not yet known. It also appears likely as disclosed by the *S. spontaneum* × *S. officinarum* crosses that this non-reduction need not be confined to the egg, but that the sperm may also contribute the diploid number. How far this phenomenon is common in all the species of *Saccharum* and to what extent, and if it occurs in related genera also, remains yet to be investigated.



S. officinarum Var: Chittan
×
S. Spontaneum (Local)
(Hybrid - more like S. off)
$2n = 112.$
($2n.80 + n.32$)
♀ ♂

S. Spontaneum (Local)
×
S. officinarum Var: Chittan
(Hybrid - more like S. Spont.)
$2n = 112.$
($n.32 + 2n\ 80$)
♀ ♂

FIG. 5
NON-IDENTITY OF RECIPROCAL CROSS

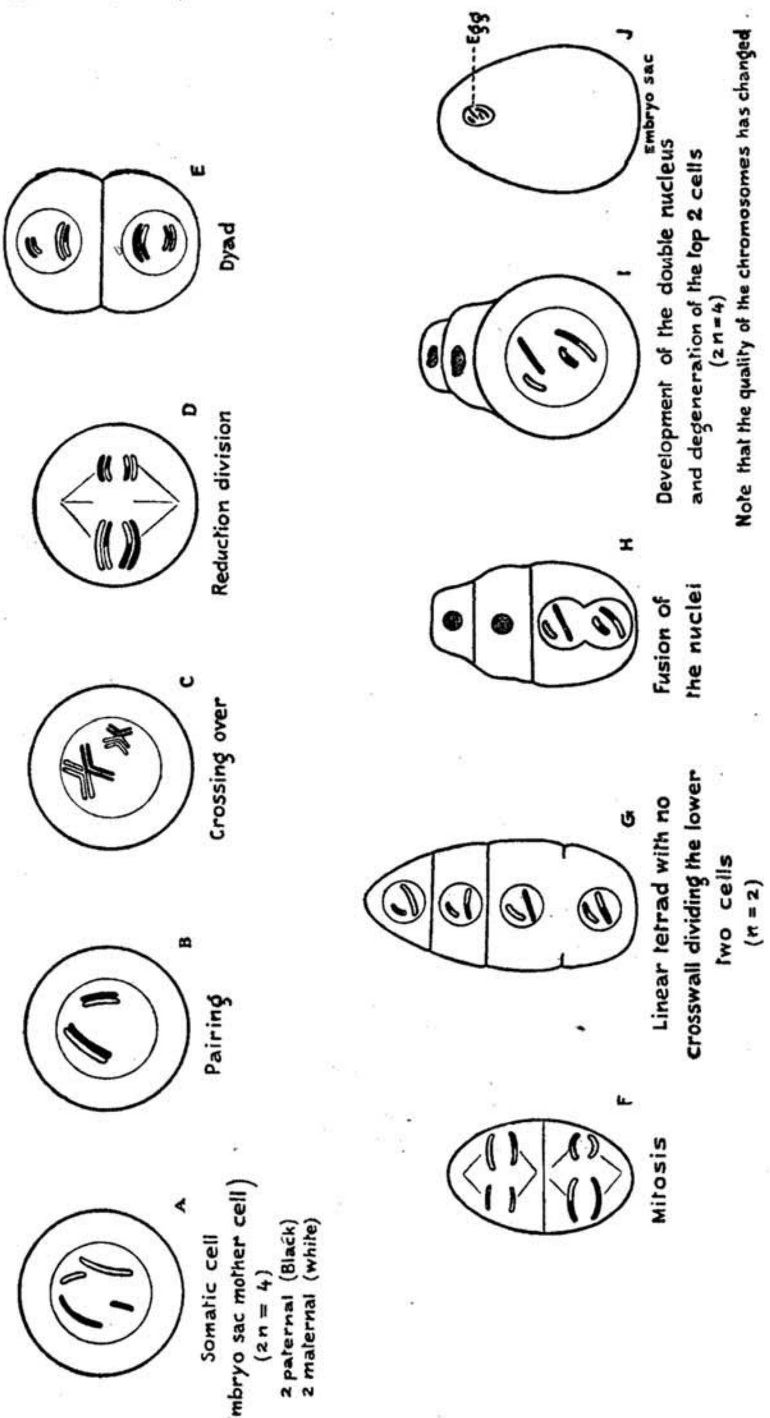


FIG. 6. Formation of diploid egg.

1 Co. 421 2n = 118

2 Thick (Like mother) 2n = 118

3 Thin 2n = 86

FIG. 7

PARTHENOGENETIC DERIVATIVES FROM Co. 421

f. Mechanism of non-reduction in egg parthenogenesis. But the mechanism of this non-reduction of the egg in *S. officinarum* is known. It is also unique. Functioning of diploid eggs in other plants is by no means uncommon. But usually such diploid eggs are formed through suppression of the mitotic division. The diploid chromosomes in the mother cell may not pair at all. No meiosis takes place and the egg comes to possess the somatic number of chromosomes. It is just like any other somatic cell and if by any chance such a diploid egg were to grow into a daughter plant straight away without being fertilized by a sperm, the latter will be just like the mother plant in all respects, because the daughter is actually an outgrowth, from a somatic cell derived by a repeated mitotic division of it. It is for all practical purposes clonally reproduced. Since it is not derived from a vegetative bud as usually clones are, but from an unfertilized egg cell, it is a case of parthenogenesis. The essential feature of such a parthenogenetic derivative is that it is just like the mother, having been asexually formed by repeated mitotic divisions of an unfertilized egg, which for all practical purposes is a somatic cell.

In sugarcane, however, such is not the case. Even parthenogenetic derivatives show variation among themselves. This is traceable to the mechanism by which the diploid egg comes to be organized. Here it is not due to suppression of meiotic division. But reduction division does take place as usual (Plate X, fig. 6, A to F), which means that the homologous chromosomes have paired, exchanged partners and separated, bringing with it a reshuffling of the parental genes. After reduction division four haploid germ cells are formed, two of which fuse to form a single diploid cell (Plate X, fig. 6, G and H) from which the diploid egg is organised (Plate X, fig. 6, I and J). Since such an egg has come into being after reduction division, reshuffling of characters has already taken place during its formation. No two eggs of such origin can be expected to be identical, in respect of the assortment of the parental genes. The consequence is that the plants derived from such eggs, even though without fertilization, show a wide range of variation, in respect of vigour, fertility and even sucrose contents. Sevearl Co. canes like 461, 462, 463, 656, 779 derived from Co. 421 as the mother and different father show only the maternal number of chromosomes obviously they are all a result of parthenogenesis. But they differ from one another in every way. Coupled to this, where the forms so derived have the same chromosome number as the mother, is the phenomenon in which only some of the chromosomes after meiosis, take part in the production of the daughter plant, by parthenogenesis. For instance Co. 421 which is a pollen sterile form, when selfed gives rise to progeny which must obviously have arisen parthenogenetically, because no fertilization could have taken place. Some forms are like the mother and contain the same chromosome number (2n=118). So these are derived from the unfertilized egg cell of the mother, in which the diploid number of chromosomes had come into being, in the manner described above. The others are much thinner. They contain a diploid chromosome number of 86. These have been formed from unfertilised egg in which there were only 86 chromosomes, the remainning not taking part in egg formation. Photographs in Plate XI, fig. 7 show the mother and the two parthenogenetic derivatives. This only makes the range of variation among the parthenogenetic derivatives more marked. It may so happen that among these are found a few with desirable characters, which of course can at once be fixed by vegetative propagation such have the Co. canes mentioned above been derived.

The work of sugarcane breeder is thus interesting in the extreme as he is faced with an element of uncertainty and surprise at every stage. But his problem is to bring it within the operation of Mendelian laws of heredity. One possible way of achieving this is to break down the polyploidy of the species and if this were done, we can make the chromosomes behave in the same way as a normal diploid plant in respect of hybridization. Incidentally we can know something about the origin of the cultivated forms and if this is known it is possible to apply the method for the creation of the desired varieties. From this point of view, the work of the sugarcane breeder is almost the reverse of the breeder of most other plants. The latter usually builds up new forms by chromosome duplication induced artificially by crossing and by treatment with alkaloids like colchicine. But the breeder of sugarcane has to work his way in the other direction by breaking down the polyploidy and reducing the chromosomes to their basic number. In devising suitable methods for this purpose, the several interesting, though unpredictable and in some cases unexplainable crossing results will be of the utmost help, by showing him the possible way by which to proceed among the maze of seeming contradictions, in which sugarcane cyto-genetics abounds.

fungus on any other grass or cereal in India. It is strange that if *E. frumentacea,* is a variety of *E. crus-galli* or *E. colona* any of these grasses has escaped infection by the smut. It could not have gone unnoticed because of the marked deformities it causes on the plant. This present record brings out the affinities of the fungus and the host plants it infects.

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Dept. of Agriculture, M. H. DELVI.
Bangalore,
September 17, 1951.

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1. Mundkur, B. B., *Indian Jour. Agr. Sc.*, 1943, **13**, 631-33.

MULTIPLE BUDS IN SUGARCANE

WHILE one bud is the usual condition in sugarcane, the occurrence of buds more than one was noticed in a few hybrid seedlings. These multiple buds 2 to 4 in number are juxtaposed along the root band almost touching one another. All the buds at a node are of similar size and form. However, not all the nodes in a seedling showed this condition. A few had single buds, some had two buds, and a majority three buds and very few, four buds. The occurrence of multiple buds could be of practical importance especially in sugarcane provided they are viable and give rise to as many daughter culms as there are buds in each node.

The occurrence of multiple buds has been noticed in the following varieties.

(1) Co. 781—(P. 3247 × Co. 440).
(2) P. 7281—(Co. 603 × Co. 449).
(3) P. 335/1—M. 2811 (Vellai × Narenga × [(*S. spontaneum* Glagh × *E. Munja* Spiny) selfed].

Neither of the parental forms in each cross showed this character and if this character expresses itself in the hybrid, the indication is that it is a case of two non-allelic genes acting together to produce a phenotype (so far as this character is concerned) different from that produced by either alone. This is on the assumption that the character in question is genic. If so, this feature must be exhibited by the clonal progeny resulting from these culms.

To test this, setts having one, two, three and four buds from each seedling were planted separately in pots having the ordinary soil mixture of tank silt, sand and farmyard manure. In every case only one bud germinated to form shoots. These were allowed to grow up to maturity and the canes were examined for the presence of multiple buds. There were no more than a single bud at each node. Also the shoots that came out of setts having one, two, three and four buds, were all identical. None of them possessed multiple buds. These were again planted and taken through the next generation. These also showed no trace of this character.

The occurrence of multiple buds is obviously not a genetically inherited character. Presumably it is due to some physiological cause, involving hormones or effect of minor elements on the varieties concerned.

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Coimbatore,
September 26, 1951.

CONTROL OF TERMITES IN SUGARCANE

GUPTA[1] has made certain recommendations towards the control of termites during the period of germination in hot weather. The author has also made attempts to control their attack by the use of tar emulsion, crude oil emulsion and tar emulsion with 'gammexane', the treatments being given with irrigation water. Some measure of success was achieved particularly with the last mentioned treament, but the effect was only temporary and the treatment had to be repeated with each irrigation till the plant got established.

With a view to obtaining effective permanent control over termite attack, an experiment was conducted using two varieties, *viz.*, Co. 419 and Co. 453. The following treatments were given to the setts prior to planting: (1) plugging the cut ends with coal tar, (2) treating the setts for 24 hours in a 2·5% solution of 'gammexane' P. 520, (3) treating the setts for 24 hours in a 5% solution of 'gammexane' P. 520, (4) treating the setts for 24 hours in a 2·5% solution of DDT Geigy's Guesarol 550, (5) treating the setts for 24 hours in a 5% solution of DDT Geigy's Guesarol 550, (6) treating the setts for 24 hours in a 4% solution of the disinfectant 'IZAL'. In addition to these, in a separate experiment the furrows were treated with 5% gammexane dust D. 025 at the rate of 20 lb. per acre at the time of planting (without the other treatments).

Maximum germination was recorded in the treatments with 'gammexane', those with DDT coming next in order. Germination was considerably affected in the treatment with 'IZAL' solution.

The termite attack was maximum in the 'control' and in the treatment with plugged cut ends. The mode of entry was, however, different in the two. In the former the entry was through

This rapid and direct technique requires neither expensive apparatus nor lengthy culture methods. It counts all soil algæ without selection.

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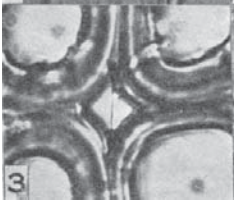
May 29.

Formation of New Cell Walls in Cell Division

IN a recent communication in *Nature*, further evidence was presented by Dr. E. Elliot[1] relating to the concept of Giltay[2], and supported afterwards by Priestley and Scott[3], that at cell division each daughter protoplast secretes a continuous wall around itself. The suggestion was also made that this method of cell-wall formation may prove to be general in the higher plants. Recent work in this laboratory on cell division in the cambium of angiosperms and gymnosperms further supports this suggestion.

Parts of an enveloping parent wall, apparently persisting after division in the ray initials, were observed connecting adjacent cells of a radial file of ray parenchyma cells isolated by simple maceration (Fig. 1). An example, which may perhaps be more important, was observed in the course of a study of the sequence of cell division of the cambium during the development of compression wood in conifer stems. Thin, feebly birefringent membranes, considered to be the remains of the parent cambial cell wall, were detected traversing the well-developed intercellular spaces characteristic of this tissue (Figs. 2 and 3). In normal wood the presence of similar membranes was demonstrated by careful delignification of thin cross-sections by alternate treatments with chlorine water and alcoholic monoethanolamine, with dilute alcoholic acetic acid washes (Fig. 4). Using techniques of simple maceration, demonstration of the parent wall was extremely difficult, as in the mature tissue this wall is not continuous around a radial file of cells and any slight agitation was sufficient to cause the cells to separate. That only fragments of the parent wall can be demonstrated is consistent with the great radial expansion of the cambium daughter cells which occurs during differentiation, following periclinal divisions.



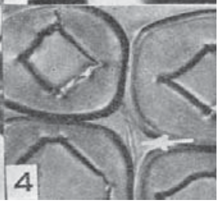


Fig. 1. *Grevillea robusta*. Part of two ray parenchyma cells, isolated by maceration with hydrogen peroxide and acetic acid, showing part of parent wall of the ray initial. Unstained. × 980

Fig. 2. *Pinus pinaster*. Transverse section of compression wood between crossed nicols. Only part of the parent wall traversing the intercellular space is in a position of brightness. × 2,000

Fig. 3. *Pinus pinaster*. An example similar to Fig. 2, photographed with ordinary illumination after staining with safranin. × 980

Fig. 4. *Pinus pinaster*. Transverse section of normal wood after delignification showing parts of the parent wall (marked by arrow). Unstained. × 430

A further point of interest is that the parent wall could not be demonstrated at the tips of cells by either of the techniques referred to above. This may be an indication of tip growth rather than of symplastic readjustment of the cells following cell division in the cambium.

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Sugarcane × Bamboo Hybrids

SUGARCANE × bamboo hybrids were first reported from this Institute by Venkatraman in 1937[1]. In spite of the absence of easily recognizable bamboo characters in the seedlings, Kutty Amma and Ekambaram[2] proved by a critical study of the anatomy and morphology of the seedlings that they were genuine hybrids. This corroborated Janaki Ammal's[3] conclusion arrived at earlier, on the basis of somatic chromosome counts. In these bamboo crosses the pistillate parents employed were the two male sterile Java canes, *POJ*.213 and *POJ*.2725. These were themselves complicated bispecies hybrids —*POJ*.213, involving *S. officinarum* and *S. barberi*; *POJ*.2725, a much more complicated hybrid between a number of *officinarum* and Java *spontaneum* (Glagah). It was felt desirable to repeat the cross, using a simple *officinarum* as the female parent. All the varieties of *officinarum* so far examined show $2n = 80$. For this purpose, *S. officinarum* var. *Vellai* (a local form) was employed and two seedlings were obtained. Examining the mother and the two seedlings derived therefrom through pollination with bamboo, one of the seedlings is very thick, much thicker than the mother, more vigorous and taller. The other is much thinner. Examination of the root-tips revealed a somatic chromosome number of 116 in the thick seedling and 86 in the thin. It is believed that the thick seedling has come into being through the fusion of an unreduced egg of *S. officinarum* (that is, $2n = 80$) with a normal sperm of *Bambusa arundanacea* ($n = 36$). The thin seedling has presumably been formed by the union of an *officinarum* egg having neither the haploid nor the diploid number, with the sperm of bamboo. Functioning of diploid eggs in interspecific and intergeneric crosses, involving *Saccharum*, especially the species *officinarum* as one of the parents, is not an infrequent phenomenon. Almost all interspecific hybrids between *S. officinarum* × *S. spontaneum* have come into being through the operation of the unreduced egg of *officinarum*. Some cases of intergeneric hybrids are known where both the haploid and diploid eggs have functioned in the same cross. The latest known case is that of *S. officinarum* var. *Vellai* × *Narenga* ($2n = 30$), where hybrids showing $2n = 95$ and $2n = 55$ have been obtained (Raghavan unpublished). Functioning of egg with unexpected chromosome number in the formation of sugarcane hybrids is less common. While one such case is known involving a bicomplex hybrid as the pistillate parent, recent investigations have shown that this feature is shared by simple *officinarum* also. For *Co.*453, which is a cross between *S. officinarum* var. *Zw. cheribon* ($2n = 80$) and *Co.*285 ($2n = 112$), showed a chromosome number of 124, indicating that *Zw. cheribon* has contributed through its egg neither the haploid number (40) nor its unreduced number (80) but an unexpected number, that is, 68 [4]. This report is of interest in three particulars. First, instead of complicated bi-species or tri-species, derivatives such as *POJ.* or *Co.* canes, a simple *officinarum* has been employed as the pistil parent. Secondly, viable embryos are obtained from fertilization of not only haploid gametes, as reported by Janaki Ammal[3], but they are also formed from fertilization of unreduced eggs by normal sperms. This brings these bamboo hybrids into a line with *Saccharum* × *Sorghum* hybrids, in the formation of which also both reduced and unreduced eggs have been known to function[5]. Thirdly, the operation of an egg with unexpected chromosome number in the cross has also been vouched for.

Though the gross resemblance of the seedlings is to the mother, namely, sugarcane, the presence of such characters as arched root eyes above nodal buds of peculiar shape and disposition, extra-vaginal nature of the bud piercing the leaf-sheath, the mode of underground branching—these and other features, taken together with the chromosome number, leave very little doubt as to the genuineness of the cross. Perhaps this preponderance of maternal characters may be explicable on the basis of cytoplasmic inheritance, the existence of which was reported by Raghavan[4] in a number of interspecific hybrids in *Saccharum*.

A study of the intergeneric hybrids of *Saccharum*, which is now in progress, makes one believe that the seemingly conflicting phenotypic configurations obtained in several crosses are a result of the interaction of the plasmon with the genes. They seem to support the theory of the plasmon-sensitive genes in that it offers a reasonable foundation for the interaction of plasmon and genes ; the result is that the same genes act differently in different plasmons. It would seem that in sugarcane hybridization more importance should be paid to the mother than to the father in the evolution of economically important seedlings. Also, the absence of fruitful results in the raising of economic seedlings through a particular cross need not be final ; for it is just as likely that hybridization in the opposite direction, wherever such is possible, may result, through this interaction of the plasmon and the genes, in the expression of a phenotype answering to our needs.

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Sex Mechanism in *Coccinia indica* Wight and Arn.

SOME of the diœcious species of Cucurbitaceæ have been cytologically investigated by several previous workers to ascertain whether the morphological differences in flowers between the sexes could be correlated with any observable chromosomal differences of their gametes. So far, only two species among members of this family, namely, *Trichosanthes japonica*[1-3] and *Coccinia indica*[4-6] have been found to possess well-defined sex-chromosomes. In *T. japonica*, the male is reported to be the heterogametic sex, whereas in *C. indica* contrary evidences have been furnished by Kumar and Deodikar[6] and Bhaduri and Bose[4]. The present note is based on the results of a critical cytological investigation of different sex types, such as the diploid male and female, the gynodiœcious form and a triploid male of *C. indica*.

A careful examination of the somatic complement in diploid male (Fig. 1,*a*) and female (Fig. 1,*b*) and of meiotic complement in pollen mother cells has definitely established that male of *C. indica* is the heterogametic sex with XY type of sex-chromosomes. Of this, Y is bigger than X while the latter is morphologically similar to the autosomes. During meiosis this unequal pair exhibits heteropycnosis, non-congression, precocious segregation, etc., which behaviours are characteristic of sex-chromosomes. The chromosome constitution of the male and the female of *C. indica* should, therefore, be represented as $22\,A + XY$ and $22\,A + XX$ respectively. The present investigation has definitely established that Kumar and Deodikar's statement[6] that the male of *C. indica* is homomorphic and the female heteromorphic is no longer tenable.

It has been observed that the chromosome constitution of the gynodiœcious form is similar to that of the normal diploid female ($22\,A + XX$) but, unlike it, is highly sterile. In this the anthers are developed but pollen grain formation is impeded, resulting in sterility of the plant. This provides an example to show that the male organs of a plant can develop

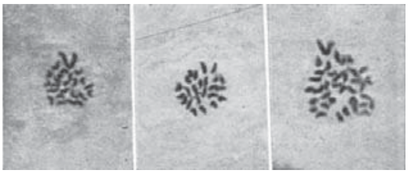
(*a*) (*b*) (*c*)

Fig. 1 (*a*), (*b*), (*c*). Somatic complement of diploid male and female and triploid male respectively. (× 1,100)

THE GENETICAL BEHAVIOUR OF *SCLEROSTACHYA* × *NARENGA* HYBRIDS AND THEIR BACK-CROSSES

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SCLEROSTACHYA AND NARENGA have been found to play a part in the chromosomal constitution of *Saccharum officinarum*. Parthasarathy[1] found that the basic complement of $n = 10$ chromosomes of *officinarum*, is composed of 2 different chromosome complements $n = 5$ each and one of these is similar to 5 chromosomal complement of *Sclerostachya*. Raghavan[2] found that these five chromosomes bore homology to 5 chromosomes of *Narenga* also. The homology of the second set of 5 chromosomes has yet to be ascertained. Thus *Sclerostachya* and *Narenga* appear to be very closely related genetically. The hybrids between these two genera show complete allo-syndesis;[3] nor is there any reciprocal non-identity suggestive of cytoplasmic inheritance. A few characters were chosen for study in these hybrids and back-crosses with their parents. These reveal a few interesting features which are presented in this short paper. The presence of circlet of hairs at the nodes of the flowering culms (*Narenga* character) is dominant over its absence. The occurrence of pedicelled and sessile spikelets (*Narenga* character) is also dominant over its absence (*Sclerostachya*). The absence of hairs on the upper surface of the leaves (*Sclerostachya* character) is dominant over its presence (*Narenga* character). In the matter of the presence of nodal buds in the flowering culms (*Narenga* character), its absence (*Sclerostachya*) is dominant. Table I gives the number of plants examined in regard to these characters and the observations made. It will be seen that except in the character of hairs on the upper surface of leaves, the deviation from expectation is not significant in respect of the other characters. Also the selfed progenies show no appreciable segregation and as such it may be assumed that these are fairly homozygous for most of the characters.

TABLE I

Characters	*Narenga*	*Sclerostachya*	*Narenga* × *Sclerostachya*	*Sclerostachya* × *Narenga*
Circlet of hairs ..	+	−	+142 − 5	+105 − 3
Hairs on upper surface of leaves	+	−	+24 −84	+ 37 −110
Spikelets Pedicelled & Sessile (PS); Both Pedicelled (PP)	PS	PP	PS = 47 PP = 1	PS = 44 PP = 1
Nodal buds	+	−	− 9	− 9

When back-crossed to the respective parents, the following observations were made: In characters like the circlet of hairs, occurrence of pedicelled and sessile spikelets whose presence in *Narenga* is dominant, the back-crossed progeny with the parents would appear to show the

TABLE II

Parents: Female	Parents: Male	Circlet of hairs*	Spikelets †	Hairs on upper surface‡	Nodal buds§
P′ 567/3 (*Naaenga* × *Sclerostachya*)	*Narenga*	+26 − 1	PS = 27 PP = 0	+27 − 0	+26 − 1
P′ 567/3	*Sclerostachya*	+ 4 − 4	PS = 4 PP = 4	− 8 + 0	− 8 + 0
P′ 567/3 (Self)		No survivals			
P′ 568/1 (*Sclerostachya* × *Narenga*)	*Narenga*	+ 8 − 0	PS = 8 PP = 0	+ 8 − 0	+ 8 − 0
P′ 568/1	*Sclerostachya*	+ 2 − 2	PS = 2 PP = 2	− 4 + 0	− 4 + 0
P′ 568/1 (Self)		No survivals			
Ikra	..	+24 − 0	PS = 24 PP = 0	+ 2 −22	+ 2 −22
Ikra	*Narenga*	+14 − 0	PS = 14 PP = 0	+12 − 2	+12 − 2
Ikra	*Sclerostachya*	+ 5 − 4	PS = 5 PP = 4	+ 2 − 7	− 8 + 1
Ikra (Self)		+13 − 5	PS = 12 PP = 6	+ 7 −11	+13 − 5

* + Present (*Narenga* dominant); − Absent (*Sclerostachya* recessive). † PS = Pedicelled & sessile (*Narenga* dominant); PP = Both pedicelled (*Sclerostachya* recessive). ‡ + Present (*Narenga* recessive); − Absent (*Sclerostachya* dominant). § + Present (*Narenga* recessive); − Absent (*Sclerostachya* dominatn).

expected ratio, *i.e.*, with the recessive parent, namely, *Sclerostachya*, we get the 1 : 1 roughly, while with the dominant parent, namely, *Narenga*, all the forms show the character in question. However, in characters like nodal buds in the flowering culms and hairs on the upper surface of leaf whose presence (*Narenga*) is recessive to their absence (*Sclerostachya*), the back-crossed progeny show this interesting feature. When back-crossed to dominant parent (*Sclerostachya*) all show absence of these characters which is as it should be. But when back-crossed to the recessive parent (*Narenga*), instead of the expected 1 : 1, all show the recessive character. It must, however, be admitted that the number of progeny available in these back-crosses is very limited and as such are not capable of statistical analysis. Even so it seems that in back-crosses with *Narenga* the deviation from expectation is highly significant only in respect of characters which are recessive in *Narenga*. Also it was noticed that survivals in these back-crosses are not very high and so far as selfed progeny of F_1's are concerned, there has been practically no survivals. Hence it has not been possible to study the behaviour of these characters in the F_2 population. Even so, it looks as if *Narenga* as the male parent exercises some influence in this matter, even though the character in question is recessive. It remains to be seen what the behaviour will be if *Narenga* and *Sclerostachya* are used as females and the F_1 hybrids as male. It may also be mentioned that the pollen fertility of the F_1's in either direction is well over 90 per cent. Why there are no survivals in the selfed progeny of these F_1's is not yet clear.

The expression of the characters mentioned above was studied in *Ikra* also. It was found that the genetical behaviour of *Ikra* is such as to confirm the belief that it is a natural hybrid between *Narenga* and *Sclerostachya*.[3] In other words, circlet of hairs was found to be present in the nodes of the flowering culm. Nodal buds were found to be absent in the nodes of the flowering culm. They were found to possess pedicelled and sessile spikelets, obviously the expression of dominance of *Narenga* character. In back-crosses with *Sclerostachya* and *Narenga*, the behaviour was also found to be the same, as if *Ikra* was the F_1 hybrid between the two genera, and the interesting feature is that in back-crosses to *Narenga* in which the presence of some *Narenga* characters like nodal buds and hairs on upper surface, is recessive to their absence, all showed the recessive character instead of the expected 1 : 1. This uniform behaviour of these back-crosses involving *Narenga* as the male parent both in *Ikra* as well as artificial hybrids of *Sclerostachya* and *Narenga* is something which is worthy of note.

Table II gives in an analytical manner the expression of the characters in *Ikra* and in the back-crossed progeny available for observation.

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INTERNATIONAL COMPUTATION CENTRE

THE Convention for the setting up of an International Computation Centre was signed at Paris on 6th December, 1951, by Belgium, Egypt, Iraq, Israel, Italy, Japan, Mexico and Turkey.

The Centre is to be in Rome, where the Italian Government has offered a wing of its National Research Council Building. It also has agreed to lend the Centre $ 75,000 without interest for ten years. All the library and documentation facilities of the National Research Council will be at the disposal of the Centre.

The Centre's annual budget is expected to amount to about $ 100,000, which will be made up from the contributions of its member states. For the first year, UNESCO will give the Centre a $ 15,000 grant and a loan of $ 60,000.

I.S.S.C.T. PROCEEDINGS 8TH CONGRESS 1953

SOME CYTOGENETICAL FEATURES AND BREEDING BEHAVIOUR OF A *SACCHARUM SPONTANEUM* DERIVATIVE

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INTRODUCTION

With the discovery that sugarcanes set viable seed, made in the 80's of the last century almost simultaneously but independently in Java and Barbados, interspecific and rarely intergeneric hybridisation has played a prominent part in sugarcane breeding. The emphasis, however, has varied in regard to the appropriate species of *Saccharum* to be used in hybridisation from one country to another to suit their respective needs. For instance in Java the local form of *S. spontaneum* Glagah and to a lesser extent Chunnee, an Indian form of *S. Barberi*, have been used. In U.S.A. the New Guinea forms of *S. robustum* which Brandes collected during his exploration have been extensively employed in breeding work. In India Barber used the Coimbatore form of *S. spontaneum* early in the century. The production of the epoch-making seedling Co. 205, a direct cross between *S. officinarum* and *S. spontaneum* by Barber opened up great possibilities in the establishment of a sound Sugar Industry in North India, and paved the way for stopping the imports of sugar into India (VENKATRAMAN, T. S. 1920). While *spontaneum* imparts desirable characters like disease-resistance and vigour, it also introduces impurities in the juice. And this has been tackled by the process of nobilization and also by the use of *S. Barberi* as one of the parents. In this manner is being built up year after year, a large number of bispecies and trispecies hybrids, some of which have been released for cultivation on a commercial scale. A large majority of these, however, are employed as parents, possessing as they do certain desirable individual characteristics and therefore capable of being exploited through judicious hybridisation between selected parental forms so as to bring about an optimum combination of the desirable characters.

THE ROLE OF S. SPONTANEUM IN BREEDING

In the production of all these hybrids, both those which have become commercial canes and those which have and are becoming good parents, *S. spontaneum* has always been employed as the pollen parent. Seldom, if ever, has it been used as the mother. Presumably the reason for this is that being a profuse producer of pollen which in many forms is known to be self-fertile, the chances of procuring crosses using such a form as a pistillate parent are indeed remote. Emasculation of individual flowers (in the spikelets)

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is almost an impossibility, and cannot obviously be employed for large scale production of hybrid seedlings. The few protogynous forms (DUTT, N. L. and KRISHNASWAMI, M. K., 1943) which could be employed as pistillate parents without the fear of self pollination, have not so far been utilised in this manner for one reason or another.

To these disadvantages may be added the recently-found phenomenon of cytoplasmic inheritance in some interspecific hybrids of Saccharum (RAGHAVAN, T. S., 1951a). It was found that reciprocal crosses were not identical. For instance if *S. officinarum* is used as the female and *S. spontaneum* as the male, the hybrid shows a gross resemblance to the mother. With *S. spontaneum* as the female the hybrid is much thinner and the resemblance is more to the mother. While the universality of this non-identity of reciprocal hybrids is not suggested, definite existence, especially when some varieties of the species are employed, appears to be beyond doubt. When such is the case, there is no point in using the thin wild form, *S. spontaneum*, as the mother, for the offspring from such a mating would all be thin due to maternal inheritance.

While speaking of *S. spontaneum* in breeding work, it would be well to remember a few facts about this remarkable species. It has a wide geographical distribution ranging from the slopes of the Himalayas to the Indonesian tropics. The multiplicity of geographical forms offer a wide range of material for introducing such specific desirable characters as resistance to diseases, cold, drought, salinity, etc. Recognising the importance of *S. spontaneum* in sugarcane breeding, an intensive programme for the collection of the eco-types from all parts of India has been at work for some time now and the breeding value of these forms is being assessed. But so far at this Institute, only the Coimbatore form of *S. spontaneum* has been employed in the evolving of economic crosses and that too only as the pollen parent. The Coimbatore form of *spontaneum* is thin and has a diploid chromosome number of 64. When used as female, after taking ample precaution to exclude self pollination, principally by the adoption of a simple device evolved at this Institute, known as the bamboo tube technique, the hybrid shows the general configuration of *spontaneum*. The bamboo tube technique consists of delaying the emergence and dehiscence of the anthers, so as to prevent self pollination. Into a bamboo tube, 2′–3′ long, closed at both ends, is inserted the unopened arrow. Due to spatial limitations and physiological conditions like high humidity and temperature, the elongation of the filaments is checked which prevents the anthers from becoming pendulous. The dehiscence is thereby delayed. As soon as the bamboo tube is drawn out, the emergent stigmas are dusted with the desired pollen. Such of those anthers (which are still undehisced) as have emerged through the elongation of the filaments are removed by passing the hand over the arrow with a gentle pressure. The tube is re-inserted. This operation is repeated every morning for 6–7 days, which is the time usually required for the completion of the anthesis of the entire arrow. This resemblance to the mother is all the more remarkable since in all such crosses, done recently (RAGHAVAN, T. S., 1951b, c), the hybrids show a diploid chromosome number of 112, that is, *spontaneum* as mother has contributed the normal haploid number through its egg, while *officinarum* as the staminate parent has contributed the unreduced number. The normal expectation under such circumstances, would be for the hybrid to resemble more closely that parent which has contributed the larger number of chromosomes. That such however, is not the case has been suggested to be due to the influence of the maternal cytoplasm. If at all a *spontaneum* is to be employed as a mother, it should be one which is fairly thick – thicker than the local form and showing very desirable growth habit such as tallness, erectness.

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profuse tillering and non-susceptibility to lodging. If in such a form more sucrose could be introduced with a diminution of fibre, the expectation is that such a form would suit the vast cane tracts of North India, very well. It may be stated in parenthesis that nearly 80% of the total 4 million acres of cane area of the Indian sub-continent are in the sub-tropical North India where, because of the limitations due to climate, the canes that grow are thin – more akin to the once flourishing *S. Barberi* than to the thick canes of tropical South which resemble the "noble" canes *(S. officinarum)* that were in cultivation prior to the introduction of the Co. canes. Such a form was to be found in Co. 745 which is a derivative form of Burma *spontaneum*.

ORIGIN OF MATERIAL

S. spontaneum Burma was collected near Mandalay in 1929 and since then is being propagated at the Coimbatore Sugarcane Breeding Institute. This form is outstanding in that it grows to a height of over twelve feet, tillers profusely by means of underground stems and possesses a splendid erect habit. The internode is long as compared to other *spontaneums*. It also varies from the other Indian forms in habit, ligule shape, lamina, sheath, culms, and width of the leaf. While the Indian forms of *S. spontaneum* are characterised by a deltoid ligule, with the laminae narrowed at the base, and have a tufted or prostrate habit, the Burma form, in common with other East Indian forms, possesses a crescent-shaped ligule, with laminae not narrowed at the base, and has an erect habit. The Burma form shows important differences even from some of the East Indian forms. So much does this differ from others that a relegation to a separate sub group in the main group, viz., *Aegyptiacum* has been suggested (PANJE, 1933). During all these years this form has flowered but once. However it flowers very often in Karnal (N. India) where perhaps the climatic conditions are favourable for its flowering and it flowers during November.

There is another similar case of *S. spontaneum* (Lahore) which does not flower at Coimbatore but flowers at Karnal. HUSSAINY (1951) thinks that temperature, humidity and sunlight must have played important role in inducing the variety to flower at Karnal. It was found that the mean temperature of above 85° F. and humidity of below 60% are ideal for the vegetative growth of this *S. spontaneum* (Lahore). But this temperature and humidity which influence good growth at Karnal are not reached at Coimbatore. Hence the plant is dwarfed at Coimbatore and is fairly vigorous at Karnal. At the time of the change in the plant from the vegetative to the reproductive phase, there is a sudden fall in temperature and a quick shooting up of humidity at Karnal, whereas at Coimbatore during that period of transformation the temperature remains almost the same and humidity instead of shooting up comes down. Under such conditions at Coimbatore it would not flower.

Being a native of Burma where humidity is very high, the same causes are perhaps responsible for the flowering of this variety at Karnal where conditions are more akin to those in Mandalay than to those at Coimbatore. A single arrow was produced in 1933 which was left unbagged; it yielded a number of seedlings which showed marked differences in their morphological characters. One among this progeny was particularly selected for its vigour and erect habit and given a Co. number, viz., Co. 745.

Co. 745 is a tall, medium, and vigorous cane with a good erect habit. The culm has a yellow green colour. The internodes are long and sometimes more than a foot in length.

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The nodes are slightly swollen. The leaves are straight and show a slight bend at the tip. The ligule is crescentiform. The arrow is short (and compressed) in contrast to other Co. canes, and looks grey with a slight purplish tinge. In these characteristics, it resembles more or less its mother, *S. spontaneum* Burma. But the culms of Co. 745 are more robust than those of its mother. With all these characteristics its sucrose is very poor and an analysis of the juice has given only 5.5 % sucrose (10 months crop) and its brix (with hand refractometer) varies from a minimum of 4 % to a maximum of 9 %.

BREEDING BEHAVIOUR

Co. 745 flowers frequently and forms profuse pollen and so is a good male parent. It has been used on many Co. canes for breeding economical types and as expected imparted good vigour to the progeny; but the seedlings did not have much sugar. Hence there are not many Co. canes with the parentage of Co. 745. This low sucrose is almost characteristic of the first generation hybrids involving the Java forms of *S. spontaneum* as the staminate parents in contrast to the Coimbatore forms which as pollen parents have yielded F_1 seedlings with a comparatively high sucrose capable of being released to the cultivator, e.g., Co. 205. Perhaps being a derivative from a form which is a member of the sub group *Aegyptiacum*, it shares this character with the Java form, which is also a member of the same sub group. It may be that other members of the *Aegyptiacum* sub group may also reveal the same feature.

For the first time Co. 745 was used as a female parent and controlled as well as open crosses were effected by using Co. 285 as a male parent. Co. 745 is an early flowerer. It flowers about the second week of September, a time when the rich *officinarums* and the majority of the Co. canes are not yet in bloom. Consequently only the earliest among the early flowering varieties of the Co. canes could be used as pollen parent. Co. 285 (*S. officinarum* var. Green Sport × *S. spontaneum* Coimbatore) is one such form. Even here the last stages of flowering of Co. 745 and the initial stages of the flowering of Co. 285 synchronised. Two crosses, a controlled bagged cross and an open cross with Co. 285 as the male parent were effected. Co. 527, another early flowerer was also employed as pollen parent. But the hybrids were not vigorous. Selfing was also done as a control. *S. spontaneum* Coimbatore and *S. spontaneum* Java (Glagah) were also employed as pollen parents. Reciprocal crosses with Co. 285 as female were also made. A number of seedlings were raised and Table I gives the germination data of the crosses.

TABLE I

Sl. No.	*Cross*	*Germinations.* (*30 days counting*)	*No. of seedlings transplanted in 1st Ground nursery*	*No. of seedlings taken to 2nd Ground nursery*
1.	Co. 745 Self	2	2	2
2.	Co. 745 × Co. 285 (bagged cross)	1385	108	90
2a.	Co. 745 × Co. 285 (open cross)	495	120	100
3.	Co. 745 × *S. spontaneum* Coimbatore	750	272	100
4.	Co. 745 × *S. spontaneum* Glagah	813	192	100
5.	Co. 285 × Co. 745 (bagged cross)	604	200	100

References p. 485.

It will be seen that the self of Co. 745 does not give many seedlings (only two seedlings were got) and hence it may be regarded as almost self-sterile. The pollen grains, however, are uniform and viable as could be judged by the iodine test. It may, therefore, be presumed that the majority of the seedlings obtained are true crosses. There were no other canes in flower at the time the crosses were effected, except those which were used as pollen parents. Reciprocal crosses were also made using Co. 745 as the male. As expected seedlings with Co. 285 as female parent were short as the mother, unlike the cross with Co. 745 as mother where the seedlings showed the tall erect habit of Co. 745.

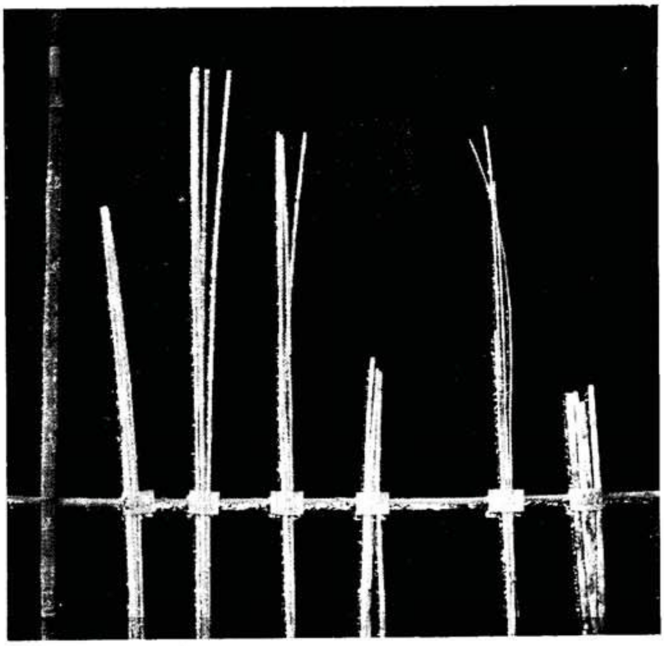

Plate I. 1. Co. 745 (Pistillate parent); 2. Co. 745 × Co. 285 (Hybrid seedling); 3. Co. 745 × Co. 285 (Hybrid seedling); 4. Co. 285 (staminate parent); 5. Co. 745 × Co. 527 (Hybrid seedling); 6. Co. 527 (staminate parent).

Chromosome counts also confirmed their hybrid character. In the photograph (Plate I) are shown millable canes of the parents and two seedlings. Co. 745 shows a height of about 7′; Co. 285 is 5′ and the two seedlings are over 8′ in height. The other parent Co. 527 and the seedling derived therefrom are also in the photograph to bring out maternal inheritance.

The progenies of the two crosses (1) Co. 745 × Co. 285 (open cross) and (2) Co. 745 × Co. 285 (controlled cross) were taken up for detailed study. About 100 seedlings in each of the crosses were carried on to the 2nd Ground Nursery. Tiller counts were recorded for all the individual seedlings in the 2nd Ground Nursery. Brix of all the seedlings as also of the parents was determined through the hand refractometer. The first reading was recorded during December 1951 when the crop was about seven months old and the range of variation of brix reading was from 8 % to 19 %. The second reading was made during

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January 1952 when the crop was eight months old and the range of variation of brix was found to fall between 9 % and 22 %. The hand refractometer reading of the parents, viz., Co. 745 and Co. 285 also were taken at the same age. Co. 745 showed 4 % and 9 % and Co. 285 showed 13 % and 19 %. It will be seen that the brix of all the seedlings recorded were well above that of Co. 745 and hence it may be said that we have succeeded to some extent in introducing more sugar in Co. 745. However, the fibre percentage is comparatively high. A complete juice analyses of eleven promising samples were made. The data are given in Table II.

A number of promising seedlings were carried over for further trial through sett propagation. The average number of tillers per sett were recorded at 6 months and 7 months. Data pertaining to the number of tillers given by seedlings and those produced by respective sett plantings became available with reference to a large number of forms. A comparison between seedling-tillers and sett-tillers showed, as was expected, a diminution of number in the latter. The proportion of reduction in the several cases recorded showed variability. However, since the seedlings-tillers were recorded at 10 months and compared with sett-tillers at 7 months, a further considerable increase in the latter may be expected in the next three months. Even so the number of sett-tillers may not equal corresponding seedling-tillers. Incidentally, the number of tillers at 6 months and 7 months has been recorded to give an idea of the approximate increase in the number of tillers during an interval of a month. Brix through hand refractometer was recorded in a number of cases and compared to brix readings of respective seedlings of about the same age. The hybrids flower earlier than Co. 745, having inherited the early flowering habit from Co. 285. So when brix readings were taken, those from the flowering and non-flowering culms were recorded separately and as expected, the flowering culms recorded higher readings than the unflowered ones. These data are presented in Table III. It will be seen from the table that the sucrose in the hybrids is decidedly more than in the female parent, viz., Co. 745 and in a few cases even more than that of Co. 285. One of the seedlings in the bagged cross seedling No. 60, shows a comparatively low fibre percentage, only as much as in Co. 285. Its height at 10 months (millable cane) is 7′ compared to 8′ of Co. 745 and 5′ of Co. 285. The weight per cane is 1.00 lb. compared to 1.00 lb. of Co. 745 and 1.12 lb. of Co. 285. The average number of tillers per planted stool in the hybrid at 7 months is 8 compared to 10.5 of Co. 745 and 5.2 of Co. 285. Since it attains maturity at 10th month, it may be expected that the number of tillers would increase further. Even if it gives a slightly lesser tonnage per acre than Co. 745, the sugar per acre will be decidedly more than from Co. 745, because of the pronouncedly higher sucrose in the hybrid. Compared to Co. 285, the sucrose per acre will be markedly higher also because even though the sucrose percent juice may be approximately the same as in Co. 285, the increase in tonnage is considerable. Encouraging as these figures are, further crossing of the seedling with other forms is likely to lessen the fibre percentage which will enhance its commercial value.

CYTO-GENETICAL

There is polyploidy and to some extent aneuploidy within the species, *S. spontaneum*, associated with taxonomic differences. A chromosome survey of about 30 forms of *S. spontaneum* has indicated that forms with smaller numbers are found in North North West India and the geographical trend of distribution is from North West to South East

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TABLE II

Sl. No.	*Cross.*	*Seedling Number*	*Average weight per cane lb*	*Height of millable cane at 10th month ft*	*Brix (Hand Refractometer) readings*		*Juice Analyses – 10th month*				
					7th month	*8th month*	***Brix***	***Sucrose***	***Purity***	***Reducing sugars***	***Fibre***
1.	C. 745	—	1.00	8	4.0	9.0	9.46	5.56	58 8	0.99	28.68
2.	Co. 285	—	1.12	5	13.0	19.0	16.54	13.73	83.0	1.04	19.00
3.	Co. 745 × Co. 285. (open cross)	10	1.00	6½	10.0	14.0	17.15	14.19	82.7	0.55	22.86
4.	Do.	40	1.10	7	10.0	16.0	19.17	14.38	75.01	1.65	28.68
5.	Do.	51	0.70	5½	19.0	20.0	18.55	15.89	85.7	0.30	22.11
6.	Do.	59	1.00	8	18.0	19.0	19.98	16.09	80.5	1.19	25.00
7.	Do.	93	1.00	6	15.0	18.0	16.27	13.50	83.0	1.17	22.27
8.	Co. 745 × Co. 285 (bagged cross)	20	0.91	8	13.0	17.0	18.10	15.19	83.9	0.79	27.89
9.	Do.	40	0.92	7	10.0	14.0	16.79	13.05	77.69	0.78	21.92
10.	Do.	51	1.10	8	10.0	15.0	18.40	15.07	81.91	0.79	26.4
11.	Do.	60	1.00	7	15.0	18.0	17.05	14.26	83.7	0.97	18.73
12.	Do.	61	0.86	5	14.0	20.0	18.35	15.70	85.5	0.85	28.95
13.	Do.	70	0.71	6½	12.0	16.0	15.74	12.55	79.7	0.69	25.05

in respect of higher polyploid forms (PARTHASARATHY, N. and UBBA RAO, K. S.).

The Burma *spontaneum* shows a somatic chromosome number of 96. It has been suggested (JANAKI AMMAL and SINGH, 1936) that this form may be a triploid with a basic number of X = 32 and that it might have arisen through a natural cross between an Indian form with $n = 32$ and a tetraploid form like "Gigas" form of Sumatra with $n = 64$. The single arrow produced in 1933 by the Burma *spontaneum* and left unbagged yielded a number of seedlings whose somatic numbers ranged from 96 to 124. As the arrow was unbagged and since there is possibility of cross pollination, much value cannot be placed on the different chromosome numbers got in the above progeny. However, the chromosome numbers fall within the expected chromosomal frequency exhibited by the progeny of a triploid with $2n = 96$. Co. 745 is one of such derivatives showing a chromosome number of $2n \doteq 108$ (RAGHAVAN, T. S., unpublished).

Co. 285 has $2n = 112$, having arisen through the union of unreduced egg of *S. officinarum* var. Green Sport ($2n = 80$) and the normal sperm of *S. spontaneum* Coimbatore ($2n = 64$).

On account of the fact that sugarcanes are highly heterozygous polyploid complexes, it will be futile to expect uniformity in the phenotypic expression of the F_1 hybrids of the cross between Co. 745 and Co. 285. Even so, on account of the suspected influence of the plasmon, there is a fair degree of uniformity among the first generation hybrids, which show a predominantly maternal type of inheritance. The parental characters and their expression in a few hybrids, chosen from open as well as bagged crosses are shown in Table IV. The differences that do exist among the seedlings are presumably due to the interaction of the plasmon with the genes. However, were the inheritance purely genic, one would expect a much wider range of variation and not so much of approximation to the pistillate parent in the majority of the characters involved.

In our studies on cytoplasmic inheritance, it was found that whenever *S. spontaneum* Coimbatore was used as the female parent there was expression of male sterility as a maternally inherited character. In crosses not involving *spontaneum* the reciprocal differences are confined to characters other than male sterility. Nor was this phenomenon exhibited when *spontaneum* was used as the pollen parent. The *spontaneum* used in these crosses was the Coimbatore form. In conformity with these findings, it is found that Co. 745 also behaves in a similar manner; when used as the mother, male sterility is exhibited by the offspring and that is what we find in the cross Co. 745 × Co. 285.

Co. 285 × Co. 745 shows a haploid chromosome number of $n = 55$. The reciprocal cross, viz. Co. 745 × Co. 285 showed also the same number indicating that reduced gametes have entered into the cross. However, on account of extensive male sterility in the cross, Co. 745 × Co. 285, meiotic counts of pollen mother cells could be made only in the few pollen mother cells available in the lower portion of the anther, the upper portion having undergone extensive transformation. The meiotic counts were confirmed by somatic counts in root tips, showing that the seedlings are a result of the union of haploid gametes. Co. 745 is a seedling from open cross of Burma *spontaneum*. There is nothing to prevent pollen from any other Co. cane having entered into its formation. But its behaviour in regard to the expression of the phenomenon of male sterility as a maternally inherited character indicates that in common with the Coimbatore form of *spontaneum*, this also shows the character. Its chromosome number also falls within the expected range in the progeny of its triploid mother. All the morphological characters seen in it are those usually associated with *spontaneum*: shape of ligule, ligular process, pres-

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TABLE III

Sl. No.	Cross	Seedling Number	Tillers from seedlings at 10 month)	Tillers from setts per 10 ft. row			Average No. of tillers per stool at 7 months	Percentage seedling/setts tillers	Height of millable cane from sett at 7 months	Brix of canes from setts at 7 months	
				No. of clumps per row	at 6 months	at 7 months				Flowered culms	Nonflowered culms
1.	Co. 745		—	7	57	74	10.5		5′ 2″	6.0	4.0
2.	Co. 285		—	9	29	47	5.2		1′ 8″	16.0	13.0
3.	Co. 745 × Co 285 (bagged)	1	14	8	51	56	7.5	50	4′ 10″	14.0	13.0
4.	Do.	20	22	9	46	67	7.5	27.7	4′ 0″	13.0	11.0
5.	Do.	40	25	10	58	74	7.4	30	3′ 11″	12.0	8.0
6.	Do.	51	25	12	68	90	7.5	30	4′ 3″	15.0	10.0
7.	Do.	60	33	11	66	87	8.0	24	4′ 0″	—	14.0
8.	Do.	61	12	7	28	37	5.3	44	3′ 0″	13.0	10.0
9.	Do.	70	32	10	63	95	9.5	30	3′ 5″	15.0	12.0
10.	Co. 745 × Co. 285 (open)	10	26	10	53	67	6.7	26	4′ 2″	15.0	10.0
11.	Do.	40	25	9	50	61	6.8	26	3′ 6″	14.0	12.0
12.	Do.	51	23	10	60	87	8.7	38	4′ 2″	15.0	14.0
13.	Do.	59	23	11	65	88	8.0	35	3′ 11″	14.0	12.0
14.	Do.	93	20	11	60	71	6.5	32.5	4′ 4″	15.0	12.0
15.	Do.	31	17	11	56	74	6.7	40	5′ 4″	14.0	12.0

TABLE IV

List of characters	Co. 745 (Female parent)	Hybrids of Co. 745 × Co. 285				Co. 285 (male parent)
		Seedling No. 1 (bagged)	Seedling No. 51 (bagged)	Seedling No. 60 (bagged)	Seedling No. 60 (open)	
Habit	Erect	Erect	Erect	Erect	Erect	Fairly erect.
Stem thickness at 7 months	0.8″	0.9″	0.8″	0.7″	0.8″	0.9″
Stem height (upto the last transverse mark)	7′ 0″	6′ 9″	6′ 2″	6′ 6″	7′ 10″	3″ ′5
Lenght of internode	6.0″	5.6″	7.7″	5.5″	6.6″	3.8″
Leaf-sheath	Spiny	Spiny	Spiny	Glabrous	Glabrous	Glabrous
Leaf: erect or drooping	Erect; drooping near the tip	Erect; drooping near the tip	Erect; drooping near the tip	Erect; drooping near the tip	Erect; drooping near the tip	Erect; drooping well below the tip
Ligule	Crescentiform	Crescentiform	Crescentiform	Crescentiform	Crescentiform	Deltoid
Ligular process	Absent	Indicated	Indicated	Indicated	Indicated	Present
Spikelets	Pedicelled older	Pedicelled older	Pedicelled older	Pedicelled older	Pedicelled older	Sessile older
Pistillody	Absent	Present (initial stages only)	Present		Present	Absent

ence of glume IV, root eyes etc. Its sucrose content also is as poor as in other *spontaneums* in spite of the fact that it is much thicker than the Coimbatore form. This would not be the case if any Co. or P.O.J. cane had entered into its composition. Also at the time the Burma *spontaneum* flowered here, there was practically no Co. cane or any officinarum in bloom.

The cross Co.745 × S. spontaneum Coimbatore ($2n = 64$) showed a haploid chromosome number of 43. The hybrid seedling of Co.745 × S. spontaneum Java (Glagah, $2n = 112$) showed $n = 54$-55. It means that in these crosses, presumably haploid gametes have functioned. This phenomenon may also be taken to indicate that Co.745 is a *spontaneum* derivative, for if it had in its chromosomal make up any large proportion of *officinarum* chromosomes due to open pollination, the expectation is that diploid egg would have functioned on the part of Co.745. For all these reasons, it is safe to conclude that Co.745 is a *spontaneum*, having arisen through the selfing of its mother, the Burma *spontaneum*.

The cross Co.285 × Co.745 or vice versa can, therefore, be regarded as the first stage in "spontanisation" in that Co.745—a *spontaneum* derivative—has been crossed to an *officinarum* × *spontaneum* hybrid such as Co.285. It has been found that into this cross reduced gametes have entered. The same is the case if we use *S.spontaneum* Coimbatore instead of Co.745, e.g., Co.285 × *spontaneum* Coimbatore or vice versa gives $n = 44$ (RAGHAVAN, T. S., unpublished). In the corresponding "nobilisation" cross, viz., *S.officinarum* × *(S.officinarum* × *S.spontaneum)*, the unreduced egg of *S.officinarum* has functioned, e.g.,

S.officinarum var. Chittan × Co.205 = $2n = 136$.
($2n=80$) ($2n=112$)

In the second stage of "nobilisation" viz., [(*S.officinarum* × (*S.officinarum* × *S.sponta neum*)) × *S.officinarum*], the reduced egg is known to operate, e.g.,

[(*S.officinarum* var. Chittan × (*S.officinarum* var. K. Boothan × *S.spontaneum* Coimbatore)]
$2n=80$ $2n=112$
× *S.officinarum* var. Chittan = $n = 54$
($2n=80$) $2n=136$

In the corresponding second stage of "spontanisation" ((*S.officinarum* × *S.spontaneum*) × *S.spontaneum*) × *S.spontaneum*, reduced egg and sperm enter into the cross, e.g.,

(Co.205 × *S.spontaneum*) × *S.spontaneum* Coimbatore = $2n=76$
$2n=112$ $2n=64$ $2n=64$

(RAGHAVAN, T. S., unpublished). The suggestion made elsewhere (RAGHAVAN, T. S., 1951b) that this had something to do with the proportion of *spontaneum* chromosomes in the total chromosome complement of the hybrid appears to stand supported; for while in "nobilisation" a reduction in the proportion of the *spontaneum* chromosomes restores compatibility, in "spontanisation" an increase in the proportion of the *spontaneum* chromosomes appears to bring about the same result.

SUMMARY

A general account has been given of *S. spontaneum* in respect of its geographical distribution, its role in breeding and cytogenetic behaviour. The origin of Co. 745 – derivative from a Burma form of *spontaneum* has been described. For the first time a *spontaneum* derivative, such as this, has been employed as a pistillate parent for the evolution of an economic cane. The part that cytoplasmic inheritance plays in regard to this has been indicated in the light of previous findings.

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There is self sterility in Co. 745. Most of the seedlings of the cross with Co. 285, an early flowering cane, are hybrids. This has been confirmed cytologically. These show a preponderantly maternal type of inheritance, with more sucrose introduced by the male parent. One of the seedlings has a comparatively low fibre percentage and has the potential to become a suitable cane for the North Indian belt. Further crossing of this and other seedlings with rich, low-fibre-containing Co. canes, which is in progress, is expected to bring about a lessening of fibre and an increase in sucrose.

Some cyto-genetical features of this form and its crosses have been described in detail, and the conclusion has been reached that, though it is a product of open pollination, it is a selfed derivative of the Burma *spontaneum*.

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DISCUSSION

Mr. Stevenson said that in his experience F. *officinarum-spontaneum* hybrids did not tend to resemble the *officinarum* female particularly, but were intermediate between the parents, and showed some variability in type.

Mr. Grassl said he was interested in the possibility of cytoplasmic inheritance as it might be important in relation to the inheritance of such characteristics as mosaic resistance.

Mr. Stevenson pointed out the complex nature of the inheritance of mosaic resistance. He had had no indication of cytoplasmic inheritance in crosses in which P.O.J. 2878 had been used as either male or female; resistant or immune individuals had been bred from both types of cross.

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SOME ASPECTS OF SUGARCANE BREEDING IN RELATION TO ITS CYTO-GENETICAL PECULIARITIES

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The methods followed in sugarcane breeding are necessarily a consequence of its cyto-genetical features. Inbreeding and pure-line selection are almost impossible. The presence of a large accumulation of recessive lethal genes, results in there being practically no survivals in the selfed progeny. Compared to the basic chromosome number 10 for the tribe to which sugarcane belongs, the different species of *Saccharum* are high multiples thereof. *S. officinarum* of which we have a collection of more than 150 varieties are octoploids except Kajla which shows $2n = 68$. In *S. barberi* within which there are four well-defined groups the chromosome numbers vary from 82 to 140. In *S. robustum* the range of chromosome numbers is from 60 to 144. In *S. sinense*, 118 to 122. In *S. spontaneum* it is 54 to 128. Thus the simplest material available shows a high degree of genetical impurity. Orthodox methods of breeding in such highly heterozygous polyploid complexes can be of no avail. While autosyndesis makes segregation along Mendelian expectation almost impossible, it also confers the advantage of wide crossability provided the parental chromosomes are compatible enough to co-exist alongside of one another in the hybrid complement. Such wide crosses with bamboo, *Sorghum*, maize, *Sclerostachya* and *Narenga* are traceable to this phenomenon. The ultimate effect of all this and other features to be mentioned later down, is that there is bound to be a large element of chance in sugarcane breeding which cannot by any means be eliminated altogether.

While these are to be expected in forms of the genetical make-up of sugarcanes, there are certain features which may be regarded as unique some of which are of direct importance in sugarcane breeding. Of these the most recently noticed is the phenomenon of cytoplasmic inheritance (Raghavan, 1951 *a*). Neither a wholly maternal inheritance nor its universality is suggested. There does however, appear to be an interaction between the genes and the plasmon resulting in a configuration leaning more towards the mother than to the father, not easily explicable on the basis of purely genic inheritance. This would appear to explain why in several hybrids there is very little expression of the male characters irrespective of the number of chromosomes contributed by either parent. For instance recently two seedlings were derived from a cross between sugarcane and bamboo (Raghavan, 1952). This cross was different from those made previously (Venkatraman, 1937), in that for the first time, a pure *officinarum* (var. Vellai) was used as the mother instead of complicated bispecies and trispecies hybrids like Co. or POJ. canes. The gross resemblance of both was to the sugarcane. One was thick and the other thin. The former came into being by the union of a diploid egg with the sperm of bamboo. In the latter it is presumed that an egg with an unexpected number of chromosomes has functioned. Apart from chromosome numbers there are a few characters of the male parent which point to the seedlings being genuine hybrids, like the arched root eyes, the bud piercing through the sheath, underground branching of stem, etc. Even so the hybrids are cane-like. Nor can it be generalised as a rule that the thinness of the second hybrid is due to its having received lesser number of chromosomes from the mother. For cases are known where in the same cross hybrids have come into being having chromosomes $2n$ from the egg and $2n$ from the sperm, and $2n$ from the egg and n from sperm. And yet the general configuration of all the hybrids is more or less similar showing that the dosage effect of certain of the parental chromosomes is very limited. The latest known such case is *S. spontaneum* × Sweet *Sorghum* ($2n = 74$ and $2n = 84$); in *S. officinarum* var. Chittan × *Sclerostachya* and *Saccharum robustum* × *Sclerostachya* both $n + n$ and $n + 2n$ hybrids have been got but with no phenotypic differences (Raghavan, unpublished). On the other hand, there are crosses, where seedlings of a cross, though having the same chromosome number, show different phenotypic expressions, *e.g.*, *S. officinarum* var. Zw. Cheribon × *S. spontaneum* ($2n = 112$). If, however, a detailed study of the characters and their inheritance is made, it is possible to classify them into three—those which are affected by dosage of genes, those showing complete dominance and those showing no definite pattern of inheritance. Of these the last named is preponderant. These discrepancies can only be explained on the basis of an inheritance which is neither purely gene-controlled nor purely maternal, but a result of an interaction between the genes and the maternal cytoplasm. From this point of view, it is reasonable to bestow more care to the mother than to the father in sugarcane breeding.

Another phenomenon which is likely to play an increasingly important part in sugarcane breeding is parthenogenesis. It is known that when self-sterile or pollen-sterile forms of Co. or POJ canes or selfed are dusted with pollen from distant genera, the latter acts as a stimulus and induces diploid parthenogenesis. In pure *officinarum* the flowering is so rare and erratic that it has not been studied properly so far. Also the presence of a large number of recessive lethal genes makes survivals few. The exact method of coming into being of an unreduced egg is not known definitely. It is likely to be through endomitosis in the basal spore of the linear tetrad, such as Bremer (1948) has indicated. Narayanaswamy (1940) has said that there takes place a fusion of the two basal spores of the linear tetrad. It has not yet been possible to confirm this finding. In either case, the most important point is that the diploid spore and from it the diploid egg, comes into being not through suppression of meiosis, but is the result of a post-meiotic process, and as such tantamount to fertilisation. So all the vagaries that one can expect in seedlings arising out of fertilisation in a polyploid complex like sugarcane, can be expected in parthenogenetic derivatives as well. And that is what we find. A number of Co. canes having well-known pollen-sterile forms as mother—and generally only such forms are used provided they are otherwise desirable—were examined cytologically and they showed the maternal somatic number indicating their parthenogenetic origin. For example, Co. 462, Co. 463, Co. 656, Co. 779, have all arisen from Co. 421, a pollen sterile form and show only the maternal diploid number 118, even though the staminate parent used in each case has been different. So also Co. 678, Co. 797, Co. 798 and Co. 811 which have presumably arisen parthenogenetically from Co. 603. The very fact of their being different Co. cane numbers is itself proof of the fact that they are widely different from one another. All these variations are a consequence of parthenogenesis being almost a substitute for fertilisation in sugarcane. There are so many chromosomes in the polyploid complex and the pairing autosyndetic, that the resulting phenotypic configurations are many and unpredictable, even though they are all derived parthenogenetically. In addition to diploid parthenogenetic derivatives a few cases are known where daughter seedlings have come into being containing neither the diploid number nor the haploid number. Usually they contain a number less than the diploid number and more than the haploid. The latest known case is that of Co. 602 ($2n = 118$). In selfs of this, we get two types of seedlings, one having the diploid number and the other having $2n = 96$. Obviously 11 bivalents have been eliminated and the remaining 48 bivalents have undergone doubling through endomitosis. The case of *S. officinarum* D. 74 ($2n = 80$) $\times$ *S. spontaneum* ($2n=64$) giving seedlings with 112 and one with $2n = 60$ may also be interpreted on the basis that the former are crosses ($2n + n$), but that the latter are a product of parthenogenesis from an egg with 60 chromosomes. The same is the case with Co. 421 ($2n = 118$) from which in addition to diploid plants, a few having $2n = 86$ were got (Parthasarathy, 1946; Subramaniam, 1946). It means that not only has chromosome elimination taken place *en bloc* but also side by side, a process of doubling of the functioning group of chromosomes through endomitosis (Parthasarathy, 1951). These two opposing processes of deletion and doubling bring into existence new chromosome races exhibiting a wide range of variability. This is bound to play a very important part in sugarcane breeding. That the sugarcanes are able to withstand such elimination *en bloc* is due to their high polyploidy.

Very recently there was observed a case where two parthenogenetic derivatives from *S. officinarum* var. Striped Vellai, showed a number higher than the diploid number (Raghavan, unpublished). How exactly the egg came to possess this number is not known. But this only makes the problem more interesting and it looks as though that in sugarcane breeding parthenogenesis has played and is playing a more important part than has hitherto been surmised.

There is also evidence of such eggs brought into being through these opposing forces of numerical diminution and multiplication of chromosomes and therefore having neither the haploid nor the diploid number, taking part in fertilisation. Co. 453 a thickish cane, now becoming popular in North India (some parts of Uttar Pradesh and Bihar) is one such (Raghavan, 1951 *b*).

In applying the laws of genetics to sugarcane breeding, one is confronted with the difficulties that one may expect in dealing with a plant of its genetical constitution, *e.g.*, the simplest material available is highly polyploid with an equally high degree of genetical impurity and as such there is generally an absence of Mendelian segregation on expected lines due to autosyndesis. The important genes in sugarcane are those controlling the physiological rather than morphological reaction—sucrose content, disease resistance, etc., and these are characters which cannot be easily identified.

In addition to these inherent difficulties, the special cytogenetical features characteristic of sugarcane of which some idea has been given only tend to make breeding more complicated and unpredictable.

The discovery of an increasingly larger element of chance seems inevitable in sugarcane breeding as more details come to light of its cyto-genetics.

The main problem therefore is to bring sugarcane breeding within the operation of laws of Mendelian Heredity. This can be achieved by reformation of the original but unknown diploid progenitor. With such simplification a high degree of genetical purity may be expected to be restored. One step towards such a simplification is haploid parthenogenesis of which no sign exists so far. Chromosome elimination *en bloc* such as has been described may perhaps be made use of in some manner. Another way is by continued back-crossing with forms which are likely to have played a part in the origin of sugarcane. This is being done. But the problem is to bring about an elimination of all chromosomes other than those of sugarcane. Studies of the meiotic configuration in such back-crossed progeny have indicated the possibility of *Sclerostachya*, *Narenga*, *Sorghum* and perhaps *Erinathus* having entered into the constitution of the progenitors of *S. officinarum* (Raghavan, 1951 *c*).

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GENERAL

G. 1—THE PROBLEM OF "DETERIORATION" OF SUGARCANE VARIETIES

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INTRODUCTION

Except in breeding work seedlings are seldom used in sugarcane cultivation. Propagation is vegetative and the so called varieties are really clones in each of which the genotype is fixed and as such the daughter individual is an exact replica of the mother from whose bud it has come into being. The cytological basis for this is too well known to need a detailed recounting. The daughter plant arises by repeated divisions of the meristematic cells of the bud or the 'eye' of the sett. Millions of cells are thus brought into existence by repeated divisions accompanied by tissue differentiation. The divisions being mitotic, there is no change in respect of the quality, quantity or the arrangement of the genes with which the chromosomal threads are linearly studded. These being the vehicles for the transmission of characters, the cells brought into being through such an equational division are all identical so far as the qualitative and quantitative distribution of the genes is concerned. Whatever the number of divisions, the same number and arrangement of the genes are kept up, and the inevitable consequence of this repetition of the genotype is the complete identity of the daughter to the mother. In sexual reproduction there is not only a numerical halving of the genes during formation of the gametes but there is also a qualitative change inasmuchas there is an exchange of genes between the parental chromosomes through chiasma formation. A re-shuffling of parental characters cannot, therefore, be avoided at fertilisation. Hence variations in a sexually produced progeny are a marked feature. If for instance a hundred seeds of sugarcane are planted the seedlings show great dissimilarity ; some have many tillers, while others have but a few ; some have long and others short internodes ; some may grow vigorously while others have little energy and produce little sugar. These are only a few of the innumerable variations that exist among seedlings produced from seed of the same stool of sugarcane. And if seeds from any one of these 100 cane seedlings are again planted, the next generation of seedlings will again all be different among themselves and from the seedlings of the first generation. A plant that shows such diversity in its heredity is said to be heterozygous. Sugarcane is not only a hyterozygote in the sense that it has been derived from the union of sexual cells of possibly more than two parental forms and therefore dissimilar in respect of its quantity, quality and arrangement of the genes, but it is also a high polyploid, the chromosomes having undergone duplication at different levels of its evolution. The genetical consequence of sugarcane being such a highly heterozygous polyploid complex, as also its bearing on breeding have been dealt with elsewhere in the several papers (Raghavan 1951 a, b, c, 1952, 1953 a, b, c).

All the same, the fact remains that good varieties of cane have deteriorated after a number of years of cultivation. The way in which some of our older Co. canes have gone out of cultivation in this country is a direct consequence of this "running out". Elsewhere also older ones are reported to have given poorer results after long periods of cultivation (Stevenson, 1943, 1947). Indeed such a deterioration after a number of years in large scale cultivation is considered to be characteristic of sugarcane varieties everywhere (Stevenson, 1951). It means that either the variety has changed or the environment has changed or both. The unchangeableness of a plant propagated vegetatively tends to accentuate the problem. However the "fixity of the genotype" in a clone need not be absolute. In assessing the possible causes for deterioration one has to contend with the fact of the changeableness of the genotype, however rare it may be in a vegetatively propagated plant like sugarcane as also of the disturbance of what may be termed the edaphic equilibrium.

CHANGEABLENESS OF THE VARIETY

This can happen even in a plant of fixed genotype through causes involving either a numerical alteration of chromosomes or not. Of these, the latter is more common. Sugarcane is well known to be susceptible to mutation. Many of the older varieties have thrown out colour variants as sports. Gillman sport, Striped Vellai, Striped Cheribon, Striped Mauritius, Panchrangi are well known examples. Recently a useful purple striped sport has been isolated from one of the seedlings of a cross between Co. 603 × Co. 449 (Raghavan 1953 b). In most of the cases cited above, chromosome numbers have been determined and they are known to correspond to the mother which gave rise to the sport in question. So it is a change that has been undergone by the variety unaccompanied by any numerical alteration of the chromosomes. This may come about either through a different gene assortment[2] or through gene mutation Direct visual observation of such aberrations as deletion, translocation. inversion etc. which usually bring about an alteration of gene arrangement is impossible in a plant like sugarcane where the size and the number of chromosomes preclude it. Evidence of such changes of gene arrangement, in the shape of bridge and fragments, chromosome rings, formation of micro nuclei etc. in meiosis, are not available either. In the mutants examined so far, meiosis is found to be regular. However the problem is rendered complicated by the existence of autosyndesis. Gene mutation seems to be the more probable cause for the origin of these sports. It is known that such striped sports as Panchrangi, Striped Mauritius, Striped Cheribon etc. revert back to their original unstriped condition ; it means that due to instability, the mutated genes have reverted back to their original condition. Officinarum varieties like "Namam", "Pattapatti" etc. which have long been under commercial cultivation, are presumably products of gene-mutation. The forms from which they arose are not on record. But it is obvious that due to their proved superiority they have been favoured in preference to the original varieties which consequently have gone out of the picture altogether.

It has been possible to isolate these sports, because the characters concerned in mutation are easily recognisable by the eye. However the most important economic characters in a variety, such as quality of juice, yield, resistance to drought, waterlogging, pests and diseases are quantitative ones and as such cannot easily be recognised in the field. It is conceivable that mutations involving these polygenes may throw out forms which though unrecognisable in the field, are nonetheless mutants perhaps inferior to the original type. If such forms of poorer fundamental yielding ability are unwittingly grown and cultivated over a number of years, the resultant adulterated stock shows poorer commercial results. To obtain experimental evidence of varietal deterioration through such a cause, would be very difficult.

Differences in characters other than yield, juice quality, etc. may also be involved in mutation. McIntosh (1944) has recorded that the variety B. 725 changed in two important respects within a comparatively short time. It began to produce arrows profusely where it had previously arrowed but sparingly. It also lost the objectionable habit of back rooting from the nodes of recumbent canes. These changes may be interpreted as having been brought about by mutation resulting in a changed genotype. They were certainly real changes and not due to change of climate or attributable to other external conditions. It is difficult to explain them on any other basis.

In addition to these genotypic changes in which no numerical alteration of the chromosomes has been involved, there appears to be a possibility of genotypic equilibrium being disturbed as a result of changes in chromosome number also.

Elimination of chromosomes during mitosis in the somatic tissue has been observed recently (Raghavan 1953 b). In the seedling P'878/1 (Zw. Cheribon × Co.285), elimination of chromosomes *en aloc* was observed associated with the formation of an accessory spindle. If such a cell develops into a bud it will be of a different cytological constitution from the original plant. Somatic elimination such as this opens out a new possiblity for the coming into being of new chromosome races. A preliminary examination of the collection of *S. robustum* varieties shows that their origin is to be sought in this phenomenon. It is conceivable, however rare an occurrence it may be, that some cases of running out may be the result of new chromosome variants having been brought into existence through such an elimination of somatic chromosomes *en bloc*. From this point of view, it would be worth-while determining the chromosome number of the visibly deteriorated material and comparing it with the original.

Elimination of chromosomes *en bolc* during meiosis is now known to be a common feature in sugarcane. The only case recorded previously was that on Co. 421, which was later interpreted by Parthasarathy (1951) on this basis. Since then this phenomenon has been observed in quite a few forms. For the first time this phenomenon has been recently observed in *S. robustum* Co. 602 as also in Kassoer (Raghavan 1953 a, b). The coming into being of an egg with an unexpected chromosome number is thus accounted for. Its subsequent parthenogenetic development after chromosome duplication presumably through endomitosis as suggested by Bremer (1948) ushers into being seedlings having neither the haploid number nor the diploid number of the mother. Such is the origin of parthenogenetic derivatives of *S. robustum* having $2n=84$ and $2n=62$, of Co. 602, $2n=118$ and $2n=96$ and of Kassoer $2n=136$; $2n=112$ (Raghavan 1953 a, b). Since meiotic elimination appears to be not uncommon, somatic elimination is also not unlikely though perhaps more infrequent than the former. And in probing into the probable causes of deterioration, this possibility, however remote its likelihood may be, cannot be excluded.

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CHANGEABLENESS OF SOIL

According to Arceneaux (1949), there is no basis to assume that the variety itself changes. If that were so, the expression 'deterioration of a variety' would be misleading and out of place. But enough has been said to indicate that the changeableness of the variety, even though propagated vegetatively, is a possibility which we may not ignore altogether. It may well be that it is the changes of the environment that matter more than anything else in the falling off in yields after a period of time, so far as a particular variety is concerned. Even so, genotypic changes involving either an alteration of chromosome number or otherwise, are also a factor that must be taken into account in this connection.

In the absence of genotypic changes of a variety, such as have been given an idea of, varietal deterioration is traceable to decrease in soil fertility or poorer soil tilth. The fundamental basis of good cultivation is the maintenance of soil fertility. While the breeder can evolve varieties of fundamental higher yielding capacity, by itself it would be of little avail if there were no proper husbandry. A higher yielding variety naturally impoverishes the soil more than one of poorer capacity and so it is obvious that more manure should be replaced to maintain the balance. The inherent difference in yield between varieties is dependent primarily upon the capacity to utilize available soil nitrogen. Normally therefore, other factors not operating, increase in yield from a variety of inherent high yielding capacity, can be obtained or at least the high yield maintained by increased fertilization to make good the depletion. However, Van Dillewijn has shown that fertilisation beyond a particular level (above 200 lbs. of Nitrogen per acre) is not only uneconomical but also injurious. The other alternative is to substitute a variety with a lower Nitrogen index (Stevenson 1947).

It must, however, be kept in mind that the introduction of a new variety in the place of an older deteriorating one is not meant to be an expedience to encourage neglect of good husbandry. Hardy (1944) warns "where a planter can obtain largely increased yields from lands of diminishing fertility by the simple procedure of replacing an old variety by a newer more vigorous strain, without necessarily having to maintain a high standard of cultivation, he tends naturally more and more to overlook the need for soil maintenance. The down grade changes are insidious. Like a bad habit they go on unexpected, until suddenly it is realised, perhaps too late, that soil exhaustion has arrived and that even the most vigorous new variety will no longer yield an increase".

Baver (1949) admits the possibility that new variety introduction merely serves to mask a gradual soil deterioration. While these fears may have a basis, it goes without saying that side by side with variety replacement good cultivation and maintenance of good soil tilth must be kept up at the usual efficient level.

The importance of maintaining soil fertility and good tilth is well illustrated by the history of sugarcane growing in British Guiana (Stevenson, 1947). There has been a gradual shift of sugarcane estates from the coast to the interior due to loss of soil fertility and tilth, leading to conditions under which sugarcane cannot be grown economically. Areas towards the coast have been successively abandoned and a shift made inland. There is also the fact that good results were obtained by growing the varieties which showed decline in yield on virgin land. Hence shifting went on.

In spite of proper manuring and good husbandry, it has been found that a variety may give progressively poorer results after long periods of cultivation. Such "runout" varieties would doubtless give good yield in virgin land, i.e. land in which sugarcane has not been grown before. Or even if grown on land in which another variety has been growing, the results are likely to be better so far as the deteriorated variety's perforformance is concerned. It is not, therefore, as if, good cultivation and manuring will automatically arrest deterioration and help maintain the original varietal yield. For a period of time, the duration depending on the variety and the environment, proper fertilisation helps the variety to keep up its yielding capacity, but after long period of cultivation, there is a falling off in productivity. Changes in variety are indicated and definitely helpful. It is, therefore, not merely a question of what may be called the macro-elements of the soil principally nitrogen but is also possibly associated with micro-elements. To these must be added micro-organisms also. In other words, it is a problem associated with soil micro-environment.

The fundamental yielding capacity of a variety is dependant upon its ability to use soil Nitrogen, the proper replenishment of which is a *sine qua non* to keep up the soil equilibrium so far as this principal element is concerned. A disturbance creates a lessening of yield. Just as the nitrogen requirement by varieties is differential, even so, it may well be that the same is the case in regard to micro-elements also. If the soil is exhausted of certain micro-elements beyond a certain level, the equilibrium is disturbed and deterioration sets in. We know little about the role of trace elements and while we replenish Nitrogen, we take no notice of these micro-elements. The equilibrium remains in a disturbed condition even though Nitrogen is being replaced. Another variety whose requirements of these micro-elements are different may thrive well under these altered conditions and hence it is that varietal changes seem necessary from time to time.

While speaking of micro-environment, the most important constituent of it namely, the soil pathogens, must be given their proper consideration. Specific strains of (of fungi like) red rot and of mosaic virus capable of attacking a particular variety may be very rare at first and so the variety is considered resistant; but as the variety is kept up for a long time in cultivation, different strains come into being perhaps through mutation of the pathogens which may become capable of attacking the variety involved. What was once resistant becomes susceptible. This is also one of the main factors contributing to the falling off in yield. A quick change of variety not allowing time for the soil pathogens to bring themselves either through mutation or through persistence to attack a hitherto resistant variety may help ward off deterioration of that variety through this cause. For instance distinct biological forms of red rot fungus differing in growth characters as determined by artificial culture media, were found to be associated with different cane varieties and these showed differential parasitism. Similarly mosaic virus is known to exist in a range of types which differ in their degree of virulence. It is essentially a question of a proper balance between the plant and its environment. This includes, both macro and micro, the former made of elements like N and perhaps P, and the latter constituted by micro elements and micro-organisms. And the balance is indeed delicate.

In this connection it is also worth remembering that the discovery of a symptomless virus disease on the variety Q. 28, makes the problem more complicated (Mungomery, 1949). This disease evidently of a virus nature has no distinguishing symptoms except a decrease in yield, especially in ratoons. This serves to emphasise the part played by diseases in varietal deterioration.

HETEROSIS OR HYBRID VIGOUR

There is another angle from which the problem of deterioration may be looked at (Willcox, 1952). The superior qualities shown by some of the seedlings may be regarded as a consequence of hybrid vigour. Strictly speaking this is an expression that can be applied only to crosses between two homozygous races. For example, in the corn two well established pure-breeding strains are selected and crossed. The hybrid corn shows 20--30% greater yield than either parent. This is sold to farmers. But if seeds produced by these hybrids are planted, the yield is even less than what would be given by either grand parent. The hybrid vigour is already lost in this second generation. In cyto-genetical parlance this property of the F_1 hybrid falling outside the range of the parental characters termed heterosis, is due to a special combination of dominant and recessive genes which become segregated in later generations. So every year the hybrid seeds have to be produced by the mating of homozygous strains. The same may be true of sugarcane also.

The deterioration of varieties is in large part due to the gradual obliteration of hybrid vigour over a longer or shorter period of time even though they, are vegetatively propagated.

So from this point of view also quick changes of varieties are indicated to offset loss of hybrid vigour by a particular variety.

However the anology between corn and sugarcane is not quite sound. Firstly there can be no question homozygosity so far as sugarcane is concerned. Secondly the running out of corn in the second generation is due to the segregation of the dominant and recessive genes through whose special combination vigour manifested itself in the F_1 generation. In sugarcane, there is no F_2 generation, for the hybrids are all propagated vegetatively. There is, however, marked vigour shown by the seedling, if particular parents are used in hybridisation. It is generally true to say that chromosomes of *S. spontaneum* (Coimbatore) through the male exert a vigorating influence. It has also been found out that while a mere multiplication of officinarum characters beyond its octoploid level, is associated with loss of vigour and ultimate lethality, in association with spontaneum chromosomes, the deleterious effect brought about by the increased officinarum characters is offset (Raghavan 1953 b).

SUMMARY AND SUGGESTIONS

A variety may deteriorate through its own change of the environment. Genotypic change is mainly through gene mutation. Changes involving numerical alteration in chromosomes are also to be considered a possibility in the light of recent findings in the shape of elimination of chromosomes *en bloc* from somatic tissues. A determination of chromosome counts in visibly deteriorated material may show whether or not there has been any alteration of chromosome number. It is suggested that just as mutant arise with new easily-recongnisable qualitative characters like stripes, colour variations, etc. mutation may also affect quantitative characters like yield and juice quality unaccompanied by any other recognisable variation.

So far as these genotypic changes of the varieties are concerned, as being at least partly responsible for a falling off in yield, no control is conceivable. Neither mutation nor soil can individually and severally explain the phenomenon of deterioration. It is principally a question of the equilibrium of the variety with the environment for which it was bred. A gradual change in soil conditions and the building up of specialsed races of soil pathogens under conditions of single variety cultivation, must be held responsible for deterioration. Deterioration is more marked under these conditions in ratoons than in plant crop. The importance of good culture and tilth cannot be over emphasised. But this will help only upto the stage upto which the variety is in equilibrium with its micro-environment. Until such time as we are in a position to control, quicker change of varieties seems to be the possible remedy. The economic life of the present day seedling should be shorter than it used to be. The breeding material we now have is so varied and profuse that it should be possible to introduce new seedlings more quickly. We have reached a stage in sugarcane breeding where spectacular results in yield cannot be expected as in the early days for the simple reason that we are near the pinnacle. The differences between those holding the field and those that are bred, the best among them of course can only be slight, so that not much will be lost by a quicker ringing out of varietal changes. It is here that the anology with corn may be beneficial. In corn, the cultivators are supplied with hybrid seed produced-anew every year. Since breeders of canes are also producing seedlings every year in their hundreds, can we not make use of these for replacing deteriorated material ? A method should be evolved, for shortening not only the process of selection of seedlings, but also of their testing. So far as the former is concerned, it is not known how far a chemical analysis of the seedlings for nitrogen can be useful in shifting the potential high yielders from poor yielders, with consequent saving of time. According to the inverse yield-nitorgen laws, the smaller the percentage of nitrogen in a seedling, the greater is its potential yielding capacity. A quicker method of testing at the different stations, coupled with the enlistment of the cooperation of well known factory farms in this regard, should make it possible to have a number of seedlings ready for each region, which may be employed for replacement as soon as deterioration of an older variety is noticed. It is said (McIntosh 1934) that the differential responses shown by varieties to different environmental conditions can be predicted by detailed growth and periodicity studies of seedlings. If its utility in this regard is established, then the time of testing new varieties will be greatly reduced, and as such a number of seedlings must be available at any time suitable for different enviromental conditions which can be drawn upon for replacement of vartieties that show signs of deterioration. It may be that the newer varieties may not show the superiority of the older variety in its heyday. Even so it is worthwhile trying these for a few years and then if necessary bring back the original if in the meantime a better cane has not been bred.

For obvious reasons, deterioration is generally more marked in the ratoons than in plant crop. This only emphasises the fact that the soil micro-environment plays a more important part than changes of genotype of the concerned variety. A case of this kind was noticed recently in the Pugalur area in South India, which is almost entirely under Co. 419. The lands are fertile, being mostly wetlands, irrigated by channels from the Cauvery. Manuring is at about 250 lbs. level of N and a variable number of ratoons are taken. Not long ago, the crushing period in the only factory situated in that area extended almost throughout the year. But there has been a marked fall in the productivity. A high incidence of smut was apparent. It seems to me that this is a case of deterioration, being a result of a combination of circumstances associated with soil micro-environment. I, therefore, suggested (Raghavan 1953 c) that at least a portion of the cane area should be planted with some cane other than Co. 419 as a temporary measure. Varietal trials in the Liaison Farm of that area have proved that Co. 471 is superior in performance to Co. 527 and so can be employed as an early cane and Co. 449 as a mid-late cane instead of Co. 419. Such an experiment if carried out over an appreciable area, may be useful in eliciting the information whether or not a change of variety would be useful at all as has been suggested under these conditions. Also instead of the entire area being under one cane, Co. 419, which is a mid-late season cane, it would be useful to have at least 30% of the area under an early cane like Co. 471 so as to bring about a better balance of cane sequence. It may be also useful after a few years to interchange them, *Viz.* the area under Co. 471 to be replaced by Co. 449 and that of the latter by Co. 471. This is also likely to help keep up the equilibrium between the varieties and the environment. However not all cases of apparent falling off in yield can be put down to deterioration of the variety concerned. In most cases it is a question of the soil not being in a position to keep pace with the nutritional requirements of the crop and this can be set right by a proper manurial application. An apparently deteriorated material of Co. 419 as reported in Padegaon was grown here under normal conditions of tilth and soil husbandry and it was found that the yield was in no way significantly inferior to the normal crop of Co. 419. Cases are also known where the almost complete absence of other major elements such as Nitrogen in the soil have been responsible for poor growth. Turner (1947) has recorded such a case in Antigua. B. H. 10/12, grown in Antigua, looked almost scrub like. It gave the appearance of being seriously deteriorated. By means of field experiments, it was found that sugarcane in Antigua needed applied Phosphate as well as Nitrogen. When phosphate and Nitrogen were applied in the right amount at the right time, the variety took on its normal appearance. In this case the deterioration was apparent only and due to phosphate starvation. Similarly, Chardon (1947) has found that varietal deterioration in Porto Rico was due to disease. The effect of mosaic was cumulative. Successive ratoons were more and more affected and it was first thought to be deterioration. Tops of these plants when grown elsewhere did just as well as originally. This, therefore, led them to believe that there really was no deterioration. In this case poor soil management had a lot to do with performance of varieties. Hence the problem of deterioration, its detection, as well as its cure bristles with difficulties. If after eliminating possible causes of lowering in yields like disease, soil management and fertilisation, there is still no recovery to normal expected level of yield, then it is obviously a case of deterioration the cause for which may have to be sought elsewhere. A change of variety under those circumstances is difinitely called for.

When talking of new varieties, it is inevitable with the old concept of a general-performance variety must recede to the back-ground. Each seedling may be expected to give of its best under a particular set of environmental conditions. These environmental conditions suitable for a particular variety would also become increasingly circumscribed as more and more hybrid seedlings continue to arrive year after year through breeding operations. The inevitable consequence of this trend will be that new varieties will have to be bred for narrower and narrower tracts. A variety which today may be serving a comparatively large area will have to yield place to a number of newer varieties adapted to a limited set of environmental conditions within that original tract. If such seedlings are kept ready, replacement would be possible as and when deterioration is detected.

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Cyto-genetics in Relation to Sugarcane Breeding[1]

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It is known that sugarcane was grown in India and China before the beginning of recorded history and was introduced to the western tropics at the end of the 15th century. Sugarcane breeding commenced towards the close of the last century with the discovery made synchronously though independently in Java and Barbados of the capacity of the sugarcane flowers to set viable seed. It is remarkable that within the short period of about sixty years, a complete change over to seedling canes has come about. The original sugarcane varieties are only grown here and there; their cultivation is declining so rapidly that soon they will be of historic interest only. Their place is being taken by hybrid canes produced at breeding stations of different cane growing regions.

It is equally remarkable that even after about sixty years of practice, sugarcane breeding still remains to a large extent a hit or miss affair "in which the main pointer is the determination through study of the offspring of those varieties which most readily pass on disirable characters" (Leake, 1953). By the use of such selected seedlings as parents, the chance of securing valuable varieties is increased. Paradoxical as it may sound, the more cyto-genetical features of sugarcane are unearthed, the greater appear the uncertainties connected with its breeding behaviour. The origin of these uncertainties is traceable to polyploidy, heterozygosity, cytoplasmic inheritance and chromosome eliminations *en bloc* (Raghavan, 1951 a, b, c, 1952 a, b, 1953 a, b).

Arising out of these basic causes, there is a manifestation of several cytogenetic features, some of which may even be regarded as almost unique to sugarcanes.

While polyploidy entails considerable disadvantages, it confers one advantage, viz., autosyndesis and the consequent viability of the seedlings provided the parental chromosomes are compatible enough to co-exist to make up the hybrid complement. Thus interspecific and even intergeneric crosses are possible to obtain more commonly than in any other plant. But this facility useful in itself, can be of little avail to the breeder whose object is to have a directed programme. Synapsis seldom takes place between parental sets of chromosomes. It is almost always between the chromosomes of either parent between themselves. Coupled with this, the heterozygosity

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[1] Based on the material presented at the Symposium on "Genetics in relation to crop production" at the 41st Session of the Indian Science Congress.

of the chromosomal material from both the parents—and most parental material is at least interspecific—renders infinite the odds against securing any desired combination. Repetition of well known crosses, which are being made as a definite part of our breeding programme, have so far failed 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 now. Though several thousands of seedlings were raised, selected and carried on further, there is not yet found an exact replica of either Co. 419 or Co. 421. A few show a phenotypic configuration almost identical with the original, but their brix, sucrose and habit preclude their being assigned to that class.

The most economically important characters in sugarcane like yield, juice quality, disease resistance, height and thickness, appear to be quantitative and in the absence of other complications, one may expect a polygenic pattern of inheritance, within the frame work of Mendelian heredity. In most crop plants, the yield, in common with the rest of the quantitative characters, is polygenic. On the basis that a large number of growth genes are operating, some favourable and some unfavourable, the wide variations in populations from heterozygous stock are understandable. Since the number of such genes is likely to be more than the number of chromosomes, one has to contend with the phenomenon of linkage also. When the unfavourable growth genes are masked by the presence of favourable dominant genes—and it is known that in cultivated plants the favourable genes often show dominance in the inheritance of polygenic characters—they are hard to detect; their elimination by selection becomes difficult. If the number of chromosomes is small as for example in Maize, the location of growth genes becomes possible, and as such only a few generations of selfing are enough to fix the growth genes. Such inbred lines are particularly favourable for genetical analysis. When inbred material such as these are crossed, F_1 hybrid shows increased vigour. This heterosis is obviously due to special combination of dominant genes. The case of hybrid corns is worth remembering in this connection. In sugarcane, however, the location of growth genes is almost impossible, since there appears to be a very large accumulation of recessive lethal genes, as could be judged from there being practically no survivals in the selfed progeny. In this connection the work at Barbados (Stevenson, 1943, 1950) where cyto-genetical research is being carried on in a programme which includes an analysis of the breeding material and the production of inbreds for use in synthesising hybrids of known constitution, is bound to be watched with interest. Apart from the problem of lethality, there is the complication of parthenogenesis also. Most of the noble canes are self-sterile. In a few as in *Vellai*, the anthers do not dehisce at all. In those in which there is pollen, there are practically no survivals in the selfed population. The few that do, are either products of diploid parthenogenesis or of other cytological aberrations. Seldom does normal fertilisation occur. For instance recently 4 seedlings resulted from the selfing of an *officinarum* (Raghavan, 1953 b). One of them showed the "triploid number" ($2n=120$). Presumably the seedling arose out of a triploid egg, parthenogenetically. There can be no question of pollination, for there was no anther dehiscence at all.

But the presence of heterosis is vouched for, by the seedlings involving *S. spontaneum* (Coimbatore) as the male parent, showing increased vigour. The (unsatisfactory nature of the) juice quality in such seedlings is sought to be improved by nobilization. As nobilization proceeds, the vigour is often said to decline and from this point of view, it may be said that vigour behaviour is a polygenic character in that it is correlated with number of *spontaneum* chromosomes present. This is also said to be associated with resistance to Sereh and Mosaic (Stevenson, 1943). According to him the genes responsible for immunity are carried by the chromosomes of *S. spontaneum* (presumably "Glagah"). As nobilization (in the Java series) is taken upwards, the number of *spontaneum* chromosomes decreases step by step and the cause of increased susceptibility and decreased vigour is attributed to this diminution of *spontaneum* chromosomes. The same phenomenon was noticed in the nobilization of "64-chromosomed Indian *spontaneums*" by Uba Marot in Mauritius. In this series resistance testing showed that immunity to gumming disease was associated with *spontaneum* chromosomes (Stevenson, 1940). In our studies on nobilization, however, of which two examples are given specifying the number of *officinarum* and *spontaneum* chromosomes composing the seedling at the different levels, no decrease in vigour was found, as progress in nobilizaton advanced.

Nobilization

Series I

1.	Green Sport $2n=80$	× *S. spontaneum* (Coimbatore) $2n=64$	Co. 285 ($2n+n$) $2n=112$	(*officin.* + *spont.*) 80 + 32
2.	Chittan $2n=80$	× Co. 285 $2n=112$	P′ 451/1 ($2n+n$) $2n=136$	(*officin.* + *spont.*) 120 + 16
3.	P′ 451/1 $2n=136$	× Chittan $2n=80$	P′ 749/1-3 ($n+n$) $2n=108$	(*officin.* + *spont.*) 100 + 8

Series II

1.	Green Sport $2n=80$	× *S. spontaneum* (Coimbatore) $2n=64$	Co. 285 ($2n+n$) $2n=112$	(*officin.* + *spont.*) 80 + 32
2.	Zw. Cheribon $2n=80$	× Co. 285 $2n=112$	Co. 453 ($68+n$) $2n=124$	(*officin.* + *spont.*) 68+40 16
3.	Co. 453 $2n=124$	× Chittan $2n=80$	P′ 899/3 ($n+n$) $2n=102$ 62+40	(*officin.* + *spont.*) 94 + 8
3a.	Kaludai Boothan $2n=80$	× Co. 453 $2n=124$	P′ 886/1 ($2n+n$) $2n=142$ 80+62	(*officin.* + *spont.*) 134 8

In fact some of the seedlings of third nobilization e.g., Co. 453 ×

S. officinarum var. Chittan, *S. officinarum* var. Kaludai Boothan × Co. 453 etc. have been selected for their vigour, sucrose and habit. It may also be mentioned that these are on a par with POJ. 2878 and POJ. 2725 so far as their position in the ladder of nobilization is concerned, and as such they could not have been the "wonder canes" that they were, had they not shown vigour.

In these crosses, one may see the expected dosage effect of the genes, in the sense that as the number of *officinarum* chromosomes increases there is greater approximation to the noble canes both in regard to qualitative and quantitative characters.

From our observations it seems that the presence of even such a small number as 8 *spontaneum* chromosomes is enough to sustain the vigour of the seedlings.

However not all crosses are explicable on this basis of the dosage effect of genes. In several hybrids, there is very little expression of the male characters irrespective of the number of chromosomes contributed by either parent. The case of sugarcane × bamboo hybrids (Raghavan, 1952 b; 1953 a) can be cited as one of the latest observed examples in this regard. Cases are known where in the same cross, hybrids have been formed from the union of diploid sperms with diploid eggs ($2n+2n$), a normal sperm with a diploid egg ($2n+n$), a normal sperm with a haploid egg ($n+n$) or a diploid sperm with a normal egg ($n+2n$). Yet in all these cases the phenotypic expression exhibited by the different seedlings of a particular cross, is almost the same, whatever the cytological mechanism by which they have come into being. As examples the following recently-observed cases may be cited: *S. spontaneum* ($2n=64$) × Sweet *Sorghum* ($2n=20$) gave two seedlings, one a result of $2n+n$ and the other $2n+2n$. Both showed phenotypic identity. In crosses between *S. officinarum* var. Chittan and var. Zw. Cheribon and *Sclerostachya*, two types of seedlings, $n+n$ and $n+2n$, were indistinguishable. In *S. officinarum* var. Vellai × *Sclerostachya* (Govindaswamy, 1948), four types of seedlings were got, all resembling one another, viz., $n+n$, $2n+n$, $n+2n$ and the fourth in which the egg contributed neither the diploid nor its haploid number, but a number lower than the former and higher than the latter. Presumably this arose through elimination of chromosomes. This shows how little effect there is on the configuration of the seedlings through the dosage of the genes involved. On the other hand, there are cases where seedlings of a cross though having the same chromosome number, showed different phenotypic expressions (Raghavan, 1953 a). These discrepancies are explicable only on the basis of an inheritance which is neither purely gene-controlled nor purely maternal, but is the consequence of an interaction between the genes and the maternal cytoplasm. If this is conceded, it follows that more care should be bestowed on the mother than the father in sugarcane breeding.

This appears to be so on account of another cause also and that is parthenogenesis. Many of the Co. canes are now known to be parthenogenetic derivatives. The latest investigated cases are those of Co. 678, Co. 797, Co. 798 and Co. 811 which are presumed to have been derived parthenogenetically from Co. 603. All have the same diploid number as the mother. It is known that the formation of the diploid egg is not through a suppression of meiosis but is a post-meiotic phenomenon and as such equivalent to fertilisation. Hence even though they are all parthenogenetically derived, they show the wide variations that are characteristic of seedlings arising out of hybridisation of polyploid complexes like sugarcane. The number of chromosomes is so large and the pairing autosyndetic that the resulting phenotypic expression is varied and unpredictable, even though they have all originated parthenogenetically.

In addition to diploid parthenogenetic derivatives a few cases are known where daughter seedlings have come into being containing neither the diploid number nor the haploid number. Usually they contain a number less than the diploid number and more than the haploid. The latest known case is that of Co. 602 ($2n=118$). In selfs of this, we get two types of seedlings, one having the diploid number and the other having $2n=96$. Presumably 11 bivalents have been eliminated and the remaining 48 bivalents have undergone doubling through endomitosis as has been suggested by Bremer (1948).

Of such elimination of chromosomes *en bloc* we have recently seen an indication in *S. robustum*. Figure 1 is a photomicrograph of meiotic metaphase in pollen mother cell showing two groups of bivalents. The accessory spindle is not clear in the microphotograph. A similar process of elimination in the embryo sac mother cell accompanied by a doubling of chromosomes through endomitosis of the surviving group would result in the functioning of an egg, having a chromosome number which is neither the haploid nor the diploid number. If such an egg develops parthenogenetically we get a seedling having that unexpected number. Figure 2 shows photographs of *S. robustum* ($2n=84$) and parthenogenetic derivatives therefrom as a result of crossing it with distant genera viz, Teosinte, Coix and *Sorghum durra*. The thicker seedlings show the maternal number $2n=84$ while thinner ones show $2n=62$, being post-elimination products. However, complete identity between the 84 chromosomed mother and its parthenogenetic derivatives even though showing

Fig. 1. *S. robustum*. Meiotic metaphase in pollen mother cell showing chromosome elimination *en bloc*.

the same number is lacking, because of the fact of the bringing into existence of the diploid egg through a post-meiotic endomitosis and not through a suppression of meiosis. The case of Co. 421 earlier recorded by Subramanian, (1946) was later interpreted on this basis (Parthasarathy, 1951 a).

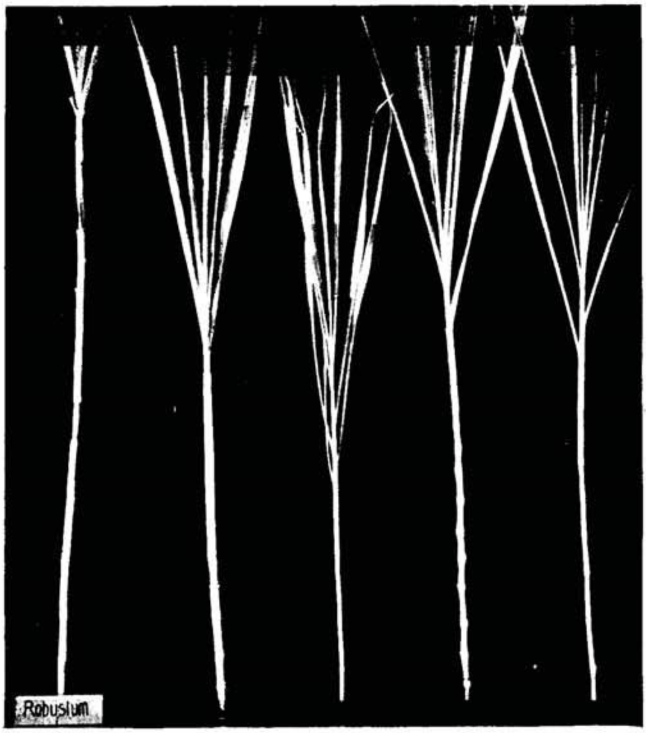

Fig. 2. Photograph of parthenogenetic derivatives from *S. robustum*. *L to R*: *S. robustum* ($2n=84$); *S. robustum* × Teosinte ($2n=84$): *S. robustum* × Coix ($2n=62$); *S. robustum* × *Sorghum durra* ($2n=84$); *S. robustum* × *Sorghum durra* ($2n=62$).

In Figure 3 are shown photographs of such parthenogenetic derivatives from Co. 602. The diploid chromosome number of Co. 602 is 118. The previous report quoted by Parthasarathy (1946) was 126. In selfs and in crosses with distant genera like Maize and Coix, we get two kinds of seedlings, one having the maternal number and the other having 96. The latter are thinner than the former. This is brought out in the photographs. Two facts seems worthy of note. Firstly, in all these cases of parthenogenetic seedlings, the pollen from the staminate parent merely stimulates the development of the egg. Secondly, in each case, Co. 602 and *S. robustum*, the number of chromosomes eliminated seems to be definite. In Co. 602 all the parthenogenetic seedlings got through either selfing or through crossing with distant genera, fall only into two groups, one having the maternal number and the other having 96. We do not get any number other than these two. Similarly in *S. robustum* we get the maternal number 84 and 62. Why there should be an elimination of such a definite number and not a haphazard elimination, is not known. It may be a coincidence that in both Co. 602 and in *S. robustum* the number of chromosomes eliminated is the same namely 22.

These two opposing processes of deletion and doubling bring into existence new chromosome races exhibiting a wide range of variability. Among the *robustums* kindly sent to us by Brandes, is a form which has $2n=62$. This is almost identical with the 62 chromosomed seedling derived parthenogenetically after elimination of 11 bivalents from an 84-chromosomed mother *robustum*. This phenomenon is bound to play a very important part in sugarcane breeding. That the sugarcanes are able to withstand eliminations of such large numbers of chromosomes is due to their high polyploidy.

There is also evidence of such eggs brought into being through these opposing forces of numerical diminution and multiplication of chromosomes and therefore having neither the haploid nor the diploid number, taking part in fertilization.

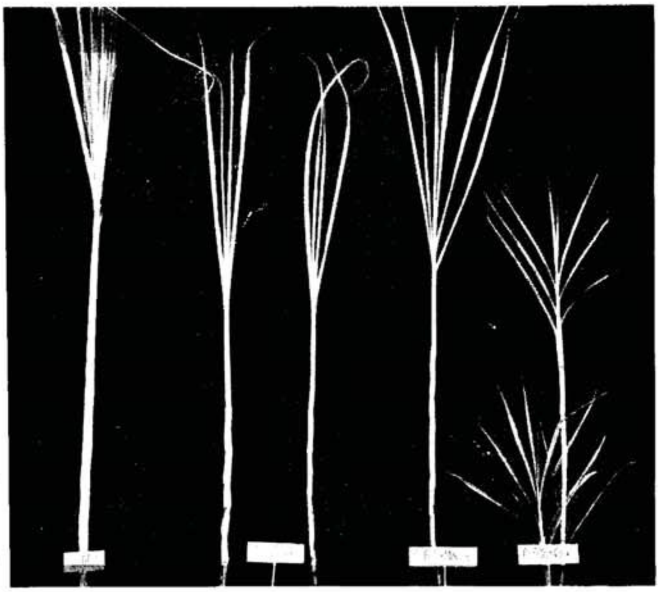

Fig. 3. Photograph of parthenogenetic seedlings of Co. 602. *L* to *S*; Co. 602 ($2n=118$); Self ($2n=118$); Self ($2n=96$); Co. 602 × Maize ($2n=96$); Co. 602 × Coix ($2n=96$).

In addition to Co. 453, a thickish cane, now becoming popular in North India (some parts of Utta Pradesh and Bihar) (Raghavan, 1951 b) the following cases have been recently recorded in this connection (Raghavan, unpublished): *S. robustum* ($2n=84$) × *Sclerostachya* ($2n=30$) gave seedlings having $2n=57$, 53 and 55 chromosomes (Fig. 4). This means that in these seedlings, eggs having 42, 38 and 40 chromosomes have respectively functioned. That these are crosses and not parthenogenetic derivatives is known by the occurrence of definite *Sclerostachya* characters in the hybrids. Also *Sclerostachya* is not a distant genus in the sense Coix, Teosinte or Maize are with reference to *S. robustum*, which usually do not take part in fertilization but merely stimulate parthenogenetic development of the egg. It is known that *Sclerostachya* crosses easily with *Saccharum* species especially *S. officinarum* and *S. robustum*. Indeed it has been found out that it has played an important part in the origin of *S. officinarum*. *S. officinarum* and *S. robustum* are closely related as could be inferred from their easy crossability and the functioning of haploid eggs and sperms in the crosses. Very probably the former have come from the latter. As such, *Sclerostachya* may be expected to show and does show, wide crossability and compatibility with *S. officinarum* and *S. robustum*. Hence all these are real crosses with *Sclerostachya*. Photograph in Figure 4 shows the different seedlings of the cross. The case of *S. officinarum* var. Vellai ($2n=80$) × *Sclerostachya* ($2n=30$) mentioned earlier showing $2n=60$ is also an example of this where an egg having an unexpected chromosome number–45–has functioned in a cross with *Sclerostachya* giving a seedling having $2n=60$ which is neither $n+n$ nor $2n+n$ nor even $n+$ 2n.

Fig. 4. Photograph of seedlings of cross between *S. robustum* ×*Sclerostachya*: functioning of different chromosomed-eggs in the same cross *L* to *R*: *S. robustum*$=2n=84$: P'801/43$=2n=53$ $(38+15)$; P'801/1$=2n=55$ $(40+15)$; P'801/57$=2n=57$ $(42+15)$; *Sclerostachya*$=2n=30$.

The difficulties of handling sugarcane as a genetical material would be apparent from what has been said so far. Indeed Parthasarathy (1951 b) is of the opinion that sugarcane is not a suitable material for genetical studies. That is the inevitable consequence of its being a complex polyploid hybrid. The problem of bringing sugarcane breeding within the operation of the laws of Mendelian heredity, bristles with difficulties. The only way of restoring a high degree of genetical purity appears to be to reform or rediscover the original but unknown diploid progenitor. Backcrossing with forms which are likely to have played a role in the origin of sugarcane, while bringing about the desired result, introduces at the same time the very complicated problem of eliminating chromosomes other than those of sugarcane. So far as one can see, only haploid parthenogenesis of which no sign exists, offers a possible solution. It is also likely that eliminations such as have been recorded and described may be useful as being a step towards haploidy. In this connection, the indication of such elimination *en bloc* such as has been recorded for the first time in a "pure" *Saccharum* species namely *S. robustum* as opposed to the previous record in a bispecies hybrid like a Co. cane, is full of promise; it is likely that eliminations exist in other species of *Saccharum* also. Efforts are also being made to induce haploidy especially by the application of cold at the time the linear tetrad is being organised, in a selfed-arrow. For it is at that period that the diploid basal spore comes to be formed presumably through endomitosis. If that were prevented by some extraneous means, the expectation is that a normal spore would form a normal reduced egg from which a haploid seedling may develop.

So far as the evolution of economically better varieties of sugarcane is concerned, it is bound to involve a very large element of chance, which cannot by any means be eliminated altogether, the genetical constitution of sugarcane being what it is. In the production of improved varieties, the methods of selection and testing are as important as hybridzation. "It includes a study of the fundamental causes of variability in seedling populations, the differential response shown by varieties under distinct environments, and the way in which adaptation to particular localities may be understood from a knowledge of individual growth types" (Stevenson, 1943). The importance of growth and periodicity studies in distinguishing particular varietal growth types was first recognised by McIntosh (1934) while searching for the reasons responsible for the differential responses shown by varieties in different localities. From a study of such features as the time and extent of tiller formation, cane growth rate, and arrowing, it may be possible to forecast the type of conditions to which a seedling will be most suitable. As new seedling varieties come into cultivation in increasing numbers, the old concept of a general-purpose variety is receding to the back-ground. Each seedling may be expected to give of its best under a particular set of environmental conditions. Maximisation of production can be achieved only by breeding new varieties for different tracts, each adapted for a comparatively narrow range of environmental conditions. Hence the importance of testing each new promising variety in different types of environment cannot be over emphasised. How far this knowledge of seedling growth types is likely to be of practical utility in selecting seedling for different conditions of soil environment such as drought, waterlogging, salinity, etc. is not clear. If its utility in this regard is established, it will obviate the laborious process of testing each new promising variety in different environments. From this point of view the term "sugarcane breeding" need not be restricted to the narrow sense of hybridisation alone, but it comprehends individual varietal response to differential environments. As hybrid seedlings continue to grow in number with the passage of time, due to availability of increasing parental varietal stock, the environmental conditions suitable for a particular variety become more and more circumscribed. The inevitable consequence of this trend will be that new varieties will have to be bred for increasingly narrow tracts. A variety which today may be serving a comparatively large area, will have to yield place to a number of newer varieties, each being adapted to a limited set of environmental conditions within that original tract. Whether this selection is made by actually growing these seedlings in the different environments—necessarily a laborious and time-consuming process—or through the short cut of assessing suitability (of a variety to a specific environment) by a knowledge of individual seedling growth types—its practical usefulness in this regard does not appear to have been yet established—the outstanding fact that emerges out of these circumstances is that testing and selection are as important as hybridization and as such sugarcane breeding means in essence, breeding for a set of environmental conditions, whose scope may be expected to become increasingly circumscribed, as progress in breeding advances.

Summary

A brief reference to the cyto-genetical peculiarities of sugarcane is made as affecting the methods adopted in its breeding. Diploid parthenogenesis, with and without chromosome elimination, has been observed in *S. robustum* and Co. 602. This is likely to play an important part in the origin and establishment of new chromosomal races, as well as in breeding. Some of the Co. canes derived from crossing are now suspected to be parthenogenetic derivatives. This along with cytoplasmic inheritance that is now known to be present in some of the sugarcanes, makes it necessary to bestow more care to the mother than to the staminate parent in sugarcane breeding.

The formation of diploid eggs is believed to be due to post-meiotic endomitosis of the spore tetrad. Hence the variations in the parthenogenetic seedlings. Eggs with unexpected chromosome number presumably owe their origin to chromosome elimination associated with duplication of the functioning group. Such eggs are also shown to take part in fertilisation besides giving rise to parthenogenetic seedlings. The presence of a large element of chance in sugarcane breeding seems inevitable and cannot be eliminated.

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SUGARCANE AS A MATERIAL FOR GENETICAL STUDIES

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INTRODUCTION.

Sugarcane breeding commenced towards the close of the last century with the discovery made independently in Java and Barbados of the capacity of the sugarcane flowers to set viable seeds. Then onwards within a short period of about sixty years, the hybrid canes had a sway over the indigenous canes grown in the diverse parts of this country and the other sugarcane growing countries of the world. It can well be added that the original sugarcane varieties are only grown here and there, their cultivation declining so rapidly that it is feared that soon they may become extinct.

One remarkable feature about sugarcane breeding is that even today after nearly about 60 years of practice, it still remains to a large extent a hit or miss affair. Hence the methods followed in sugarcane breeding are based on its cytogenetical features. It is nonetheless true that the more the cytogenetical features of sugarcane are unearthed the greater appear the uncertainties connected with its breeding behaviour. The origin of these uncertainties is traceable to many factors — polyploidy, heterozygosity, cytoplasmic inheritance and parthenogenesis preceded by chromosome elimination *en bloc* or not, differential functioning of the gametes in fertilisation, absence of and sometimes carpricious expression of the dosage effect of genes -- these have been dealt with in a series of published papers (Raghavan, 1951 a, b, c ; 1952 a, b and 1954 ; Parthasarathy, 1946, 1948 and 1951).

GENETICAL CONSTITUTION AND CYTOGENETICAL FEATURES.

The fundamental fact about sugarcane is that as a breeding material, it is different from other crop plants. This of course is due to its genetical constitution which in its turn is dependent upon its evolution. The noble cane for example is a highly heterozygous polyploid with $2n=80$ chromosomes with a basic number of $x=10$. It could be described as an allo-octoploid. Because of this feature, there is a wide range of variations among the selfed progeny in such of those species as in which there are survivals. This is due to its high polyploid nature ; two or more fundamental forms have presumably entered into hybridisation in nature accompanied by chromosome duplication at different levels of its evolution. The various crosses and back-crosses that took place during their evolution have made them highly heterozygous for several pairs of genes. The prolonged vegetative propagation and somatic mutations might have increased the heterozygosity. Further there is a large reserve of lethal genes as in *officinarum* which operates against the survival of the selfed progeny.

While polyploidy entails considerable disadvantages, it confers one advantage viz., autozyndesis and the consequent viability of the seedlings of even distant crosses, provided the parental chromosomes are compatible enough to co-exist to make up the hybrid complement. Thus interspecific and intergeneric crosses are possible more commonly than in any other plant. Synopsis seldom takes place between the chromosomes of the opposite parents. It is almost always among the chromosomes of either parent only i.e., autosyndetic. Coupled with this the heterozygosity of the chromosomal material from both the parents renders infinite odds against anticipating any desired combinations. Repetition of well known crosses have so far failed to give a variety identical with the original. For instance parental crosses for Co. 419 (POJ. 2878 x Co. 290) and Co. 421 (POJ. 2878 x Co. 285) have been repeatedly made for about four years. Though several thousand seedlings were raised and studied, there is not yet found an exact replica of either Co. 419 or Co. 421.

Another peculiarity which is almost unique in sugarcane hybridisation is that no prediction can be made as to what the chromosome number in a particular cross would be like. Normally when two plants are crossed the offspring which results will have the '2n" number which will be the sum of the haploid numbers of the parents concerned. *Saccharum* differs from other crops in this respect that it contributes on the egg side n, 2n and unexpected number of chromosomes, for instance, if an *officinarum* ($n=40$) is crossed with a *spontaneum* ($n=32$), the hybrid that results would show $2n=112$ being the product of $2n+n$. In some intergeneric crosses, as for example with *Narenga* or *Sclerostachya*, *Saccharum* has been found to contribute 68 chromosomes which is neither its haploid nor its diploid number. Zw. Cheribon with Co. 285, has contributed 68 chromosomes instead of either 40 (n) or 80 (2n) to form Co. 453 (Raghavan 1951 a, 1952 a, b).

Reciprocal differences have indicated the presence of cytoplasmic inheritance in many forms which fact has been corroborated by the recorded occurrence of male sterility as a maternally inherited character in crosses involving *S. spontaneum* as the pistil parent (Raghavan, 1951 c).

Apart from the problem of heterozygosity and lethality, there is the complication of parthenogenesis also. Many of the noble canes are self sterile, and in some the anthers do not dehisce at all. Even these in which there is pollen shedding there are practically no survivals in the selfed population. The few that do survive are products of diploid parthenogenesis. It is now known that many of the economic crosses are parthenogenetically derived (Raghavan 1954 a) and 1954 b) and as such this phenomenon appears to play a very important role in sugarcane breeding. The formation of the diploid egg is not through a suppression of meiosis, but is a post-meiotic phenomenon and as such equivalent to fertilization. Hence seedlings derived from such parthenogenesis show wide variations that are characteristic of seedlings arising out of hybridisation of polyploid complexes like sugarcane. Nor is it all : Instead of diploid eggs, egg gametes with unexpected chromosome numbers also develop into parthenogenetic seedlings showing unexpected chromosome numbers. Due to these complications, there is very little that could be done for purification of sugarcane. Thus inbreeding and pure line selections are of little avail in sugarcane breeding.

In some crosses an apparent dosage effect of the genes is seen. This is especially so in the nobilization and spontanisation back-crosses. In some instances, the dosage effect of the chromosomes is to some extent masked by the interaction of the maternal cytoplasm with the genes. This is well seen in the first generation hybrids between *S. officinarum* x. *S. spontaneum* and their reciprocal crosses. There are yet a few instances in which the dosage effect of *officinarum* genes does not appear to affect phenotypic expression. For instance P′ 899/3 is a product of 2nd nobilization involving Co. 453 as the mother having come into being through n+n. The number of *officinarum* chromosomes in this is 94 in a total complement of 102. In its reciprocal cross (which is comparable to POJ. 2725) the chromosome constitution is quite different being a product of 2n+n. As such the number of *S. officinarum* chromosomes in this seedling (P′ 890/1) is very high *i.e.*, 134 in a total complement of 142. In spite of this, however, the seedlings of the crosses are almost identical reciprocally in their gross external features indicating an apparent ineffectiveness of the increased dosage of officinarum genes.

Another peculiar phenomenon recently observed in the hybrids of *Saccharum* is the elimination of chromosomes during mitosis in the somatic tissue. In a seedling P′ 878/1 (Zw. Cheribon × Co. 285) during mitotic division in the root tip cells, elimination of a small number of chromosomes as a group after the formation of an accessory spindle has been noted. Such elimination of chromosomes in group or groups can give rise to plants having widely deviating chromosome numbers. This, in a way, can be considered as a process quite the reversal of polyploidy and it is rather paradoxical that on one side there is the formation and functioning of unreduced gametes and on the other, there is the reduction of chromosomes through elimination of chromosomes *en bloc*.

These are some of the difficulties confronting the sugarcane breeder ; the vagaries of sugarcane which are the necessary consequences of its genetical constitution and evolution, render it a difficult material for genetical studies. Some data gathered in representative intra-specific, inter-specific and inter-generic crosses are presented and wherever possible statistically analysed.

CROSSES STUDIED

A. Intra-specific :

S. officinarum x. *S. officinarum*:—(a) Creole x Purple Mauritius, (b) Purple Mauritius x Creole, and (c) their F_2 as well as their back-crosses.

B. Inter-specific :

S. officinarum x *S. Barberi* :—(a) K. Boothan x Saretha, (b) Saretha x K. Boothan, (c) K. Boothan x Katha, and (d) Katha x K. Boothan.

C. Inter-generic :

S. spontaneum x *Sclerostachya* and its F_2 and back-crosses

D. Miscellaneous crosses :

Co. 605 x P. 8331 and its reciprocal cross.

Co. 678 x P. 8331 and its reciprocal cross.

Characters like rind colour, shape of the bud, ivory markings on the rind, tillering, ligule, ligular process, leaf sheath, leaf length and width (lamina), height and thickness of the culms were studied.

A. Intra-specific cross.

S. officinarum var. Creole x *S. officinarum* var. Purple Mauritius :

Creole is a medium thick cane (about 2.6 cms. diameter) having green stem with a very light yellow tinge. It is erect in habit and grows to a height of approximately 4 ft. The leaves which are not as broad as those of Purple Mauritius, stand out erect without drooping. The drying leaves clasp the stem loosely but do not self strip as in the case of Purple Mauritius. Purple Mauritius is a thick cane (3.8 cms. in diameter) having a deep purple rind colour (and hence the name). It is erect in habit and grows upto approximately 5 ft. in height. Its foliage is erect but the tip of the leaves droop. It is practically self stripping.

Stem colour : To study the inheritance of rind colour, Creole as pistillate parent, was crossed with Purple Mauritius and six F_1 seedlings were obtained. Four of the seedlings were deep purple, one light purple and one green. The reciprocal cross yielded nine seedlings of which seven are deep purple, one light purple and one green. The purple rinded seedling No. 2 of Purple Mauritius x Creole, was selfed and thirty F_2 seedlings were obtained. The rind colour of these seedlings are as follows —7 purple, 11 light purple, 3 green with purple tinge and 9 green. The same seedling was back-crossed with purple Mauritius and it yielded 78 seedlings of which 31 were purple 27 light purple, 1 light purple with green tinge, 2 green with purple tinge, 1 green with traces of purple and 16 green. Table 1 and Table 2 summarize the results obtained in these crosses. The majority of the F_1 seedlings have either dark purple or light purple rind but there is one individual in the cross eitherway that had green rind colour like Creole. It is also worthy to note that no colour which can be regarded as intermediate was observed.

TABLE 1.

INHERITANCE OF RIND COLOUR IN CREOLE (GREEN) × PURPLE MAURITIUS (PURPLE) AND ITS RECIPROCAL CROSS

	Purple	Light purple	Light purple with green tinge	Green with purple tinge	Green with trace of purple	Green
F_1	4	1	—	—	—	1
Reciprocal cross	7	1,	—	—	—	1
F_2	7	11	—	3	—	9
Back-crosses	31	27	1	2	1	16

TABLE 2.

GOODNESS OF FIT OF RATIOS IN F_2 AND BACK-CROSS PROGENIES.

Values	F_2 progeny					Back-cross progeny			
	3 : 1 ratio		1 : 2 : 1 ratio			1 : 0 ratio		1 : 1 ratio	
	Purple	Green	Purple	Intermediate	Green	Purple	Green	Purple	Green
Observed	21	9	7	14	9	62	16	62	16
Expected	22·5	7·5	7·5	15	7·5	78	0	39	39
x^2	0·130		0·4			—		13·5	
Probability	0.70—0.80		0.80—0.90			0.0		·001	

In the F_2 progeny, the ratios 3:1 and 1:2:1 are good fits, the latter being slightly better as indicated by the probability values. However, these inheritance ratios are not in keeping with the phenotypic expression of the F_1 plants, since a 3:1 ratio would require purple colour and 1:2:1 ratio an intermediate colour in all the F_1 seedlings.

For the back cross progeny, the observed values do not fit into either of the expected ratios.

Hence the inheritance of rind colour does not appear to follow normal Mendelian segregation.

B. Inter-specific crosses.

2. *S. officinarum* x *S. Barberi* :—

K. Boothan x Saretha and its reciprocal.

K. Boothan x Katha and its reciprocal.

In these crosses only the F_1 seedlings were available eitherway and these were analysed to see the reciprocal differences if any' as regards particular traits.

In the first cross *S. officinarum* var. K. Boothan has been used as the pistil parent and var. Saretha as the staminate parent. Seventy five seedlings were obtained as the F_1 of the direct cross and in its reciprocal only 25. Characters such as the number of tillers bud shape, ligule, ligular process, leaf sheath, ivory markings on the culm, height, thickness, leaf length and leaf width have been studied. The analyses of the results are presented in Tables 3 to 7. It will be seen from the summary of these that the reciprocal differences are significant in most of the cases.

Inheritance of characters in reciprocal matings of

S. officinarum x *S. Barberi*

TABLE 3.

I. TILLERS.

K. BOOTHAN × SARETHA

	Tiller numbers						
	3-6	7-10	11-14	15-18	19 & above	Total	Mean
K. Boothan X. Saretha	16	36	17	4	2	75	7.4
Saretha X. K. Boothan	—	4	5	4	12	25	17.3
Total	16	40	22	8	14	100	

X^2 = 32.82 Highly significant.

	Below 4	4-7	8-11	12 & above.	Total	Mean
K. Boothan X Katha	3	10	6	2	21	6.8
Katha X K. Boothan	6	8	1	3	18	5·7
Total	9	18	7	5	39	

$X^2 = 2{\cdot}69$ not significant.

TABLE 4.

II. HEIGHT.

	4′	5′	6′	7′	8′	9′	10′	Total	Mean
K. Boothan X Saretha	2	3	8	26	17	13	6	75	7′-9″
Saretha X K. Boothan	5	5	12	3	—	—	—	25	5′-7″
Total	7	8	20	29	17	13	6	100	

Mean height for the two populations is significantly different.

	Below 4′	4′	5′	6′	7′	8′	Total	Mean
K. Boothan X Katha	2	—	3	3	4	8	20	7·1
Katha × K. Boothan	15	2	—	1	—	—	18	3·8
Total	17	2	3	4	4	8		

Mean height for the two populations is significantly different.

TABLE 5.

III. THICKNESS.

	.25"- ·45"	.46"- ·65"	.66"- ·85"	·86"- 1·05"	1·06"- 1·25"	1·26"- 1·45"	1·46"- 1·65"	Mean
K. Boothan × Saretha	—	2	13	25	24	10	1	1·03
Saretha × K. Boothan	14	11	—	—	—	—	—	0·44
Total	14	13	13	25	24	10	1	

The crosses differ significantly in their mean thickness.

	Below 0·4"	0·4"	0·6"	0·8"	1·0"	1·2"	Total	Mean
K. Boothan × Katha	—	1	4	11	4	1	21	0·35"
Katha × K. Boothan	2	8	6	1	—	1	18	0·58"
Total	2	9	10	12	4	2	39	

The crosses differ significantly in their mean thickness.

TABLE VI

IV. LEAF LENGTH.

	23.5" 29.5"	29.6" 35.5"	35.6" 41.5"	41.6" 47.5"	47.6" 53.5"	53.6" 59.5"	59.6" 65.5"	Mean	Standard deviation
K. Boothan × Saretha	1	5	13	18	22	13	3	46.1"	7.72"
Saretha × K. Boothan	7	7	6	4	1	—	—	34.4"	6.40"
Total	8	12	19	22	23	13	3		

	20"	25"	30"	35"	40"	45"	50"	55"	Mean
K. Boothan × Katha	—	1	—	3	3	4	7	2	47-3"
Katha × K. Boothan	8	8	2	—	—	—	—	—	24.8"
Total	8	9	2	3	3	4	7	2	

The crosses differ significantly in their mean leaf length.

TABLE VII

V. LEAF WIDTH

	0.3"	0.6"	0.9"	1.2"	1.5"	1.8"	2.1"	2.4"	Total	Mean
K. Boothan × Saretha	—	—	1	12	30	22	9	1	75	1.73"
Saretha × K. Boothan	17	6	2	—	—	—	—	—	25	0·54"
Total	17	6	3	12	30	22	9	1	100	

The crosses differ significantly in their mean leaf width.

	Below 0·6"	0.6"	0.8"	1.0"	1.2"	1.4"	1.6" & above	Total	Mean
K. Boothan × Katha	—	—	—	3	1	9	8	21	1.5
Katha × K Boothan	9	6	3	—	—	—	—	18	0.57
Total	9	6	3	3	1	9	8	39	

The crosses differ significantly in their mean leaf width.

C. Inter-generic cross.

S. spontaneum x *Sclerostachya* and its F_2 and back-crosses.

A large population of seedlings consisting of the F_1, F_2 and back-crosses were available, in an intergeneric cross bwetween *S. spontaneum* Coimbatore x *Sclerostachya*. The *S. spontaneum* used as the pistil parent in this cross is a local form with 2n=64 chromosomes. It is a perennial wild grass, often forming well defined tufts, varying in height from 5-7 feet with thin round or oval stem, putting forth lanceolate panicles with profuse fertile pollen. This is mostly used for infusing vigour in the progeny.

The male parent used is a wild 'Terai' grass having 2n=30 chromosomes. The culms are vigorous, tall, reedlike, attaining a height of 6′, stem round, fistular, underground runners present, with root eyes absent. The inflorescence is short, linear, oblong panicle, copper-coloured and having profuse fertile pollen. This is increasingly used now for vigour, early flowering and disease resistance.

Summary of the Results.

Character	*S. officinarum* x Saretha Reciprocal	*S. officinarum* x Katha and Reciprocal
1. Tillers	Highly Significant	Not Significant.
2. Height	Significantly different	Significantly different.
3. Thickness	Differ significantly	Differ significantly

4.	Leaf length	Significantly different.	Differ significantly.
5.	Leaf width	Differ significantly	Differ significantly.
6.	Bud shape	Significant	Not significant.
7.	Ligule	Not significant	Significantly different.
8.	Ligular process	Highly significant	No significant difference.
9.	Ivory markings	Not significant	Not significant.

TABLE VIII

DISCRIMINATING CHARACTERS OF S. *Spontaneum* COIMBATORE AND *Sclerostachya*

No.	Character	S. Spontaneum Coimbatore ♀	Sclerostachya
1.	Tillering	13	50
2.	Height of the stalk	79"	60"
3.	Leaf length	38"	33"
4.	Leaf width	0.3 cm.	1.0 cm.
5.	Brix in juice	8.0%	3.0%

Twenty one hybrids were obtained. The chromosome number of the hybrids (2n=79) revealed the functioning of diploid egg. The tables 9 to 13 show the inheritance as regards tillers, height, leaf length and width and brix.

So far as tillers are concerned, the means of the parent types differ by 37 tillers. The maximum of tillers in the hybrid is only 24, and this was exhibited by only one seedling. The mean for F_2 is 14.9 which is close to that of F_1. The coefficient of variation of the F_2 is as much as 50.8. Some plants are found in this generation with tillers as many as the mean of *Sclerostachya*, and some with tillers as few as that of *S. spontaneum*, with others ranging in between. But the number of individuals having few number of tillers (as that of the pistil parent *S. spontaneum*) is more than the ones, resembling the opposite parent. These facts may best be interpreted by assuming that these two probably differ by a series of factors for tillering, that these lack dominance and that their segregation in F_2 is responsible for the increased variability which this generation shows. This assumption will hold good only in cases where the chromosomes are known to pair allosyndetically. The autosyndetic pairing of the chromosomes in *Saccharum* and allied genera precludes this possibility. The seeming behaviour of the trait, in accordance with theory of multiple factor

TABLE IX

FREQUENCY DISTRIBUTION OF THE NUMBER OF TILLERS WITH THE MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION.

	0-4	4-8	8-12	12-16	16-20	20-24	24-28	28-32	32-36	36-40	40-44	44-48	Total	Mean	Standard deviation	Coefficient of variation
P_1 (S. SPONTANEUM)														13		
P_2 (SCLEROSTACHYA)														50		
F_1	—	0.5	2.5	6	7.5	3.5	1	—	—	—	—	—	21	16.7±.9	4.2	25.1
F_2	—	10.5	37.5	26.5	16.5	7	5	3.5	5	1	5	1.5	119	14.9±.72	7.57	50.8
Back-cross with SCLEROSTACHYA	0.5	1·5	7.5	8	5.5	3	2	1	—	—	—	—	29	15.2±1.1	5.9	30.8

Note : For those seedlings where the number of tillers come on the border line, half of them are put in each class.

Remarks : The variances of F_2 and back-cross are significantly different from those of F_1 ($F_2 > F_1$). This is the only character in which the result seems to conform with the theory of polygenic inheritance (but the distribution is not symmetrical).

$$n \text{ (The number of independent effective factors)} = \frac{D^2}{8(V_{F_2} - V_{F_1})}$$

By this formula "*n*" works out to be between 4 and 5.

If with these values of *n*, we try to find out the expected frequencies, the fit will be extremely poor, as the majority of the values are nearer the parent having smaller number of tillerings. Also quite an appreciable number of observations are below the parental value.

TABLE X

FREQUENCY DISTRIBUTION OF THE HEIGHT OF CANE WITH MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION

	31.5-37.5	37.5-43.5	43.5-49.5	49.5-55.5	55.5-61.5	61.5-67.5	67·5-73·5	73.5-79.5	79.5-85.5	85.5-91.5	91.5-97.5	Total	Mean	Standard deviation	Coefficient of variation
P_1 (S. SPONTANEUM)									1				79		
P_2 (SCLEROSTACHYA)						1							60		
F_1					1	3	1	8	1	4	3	21	79 ±2.4	10.8	13.6
F_2	3	6	19	32	31	18	6	1	—	—	—	116	55.2± .76	8.16	14.7
Back-cross (F_1 × SCLEROSTACHYA	2	2	1	2	9	10	2	—	—	1	—	29	58.6±2.08	11.2	19.1

REMARKS

$$\frac{\text{Variance } F_1}{\text{Variance } F_2} = 1.7 \text{ significant } (F_2 < F_1)$$

Variance of back-cross is not significantly different from variance of F_1

The observation is in contradiction to the Multiple factor hypothesis theory

TABLE XI

FREQUENCY DISTRIBUTION OF LEAF WIDTH (IN INCHES) WITH MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION

	.3 or below	.4	.5	.6	.7	.8	.9	1.0	1.1	1.2	1.3	1.4	Total	Mean	Standard deviation	Coefficient of variation
P_1(S. SPONTANEUM)	1													0.3		
P_2(SCLEROSTACHYA)								1						1.0		
F_1	2	—	1	2	2	3	2	4	1	3	—	1	21	0.85±.068	.313	36.8
F_2	5	12	25	45	14	9	3	—	1	1	—	1	116	.59±.016	.17	28.8
Back-cross with SCLEROSTACHYA	2	3	8	8	5	3	—	—	—	—	—	—	29	.57±.025	.17	29.9

Remarks :

$$F\ (20.115) = \frac{\text{Variance of } F_1}{\text{Variance of } F_2} = 3{\cdot}35 \text{ highly significant.}$$

F_1 is more inclined towards the parent with smaller leaf width.

The inheritance is not in accordance with the Mendelian Law. The approximate formula for finding the effective number of genes $n = \frac{D^2}{8(V_{F_2} - V_{F_1})}$ gives negative values of n.

TABLE XII

FR QUENCY DISTRIBUTION OF BRIX IN JUICE OF CANES WITH MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION

	4.5-6.5	6.5-8.5	8.5-10.5	10.5-12.5	12.5-14.5	14.5-16.5	16.5-18.5	18.5-20.5	20.5-22.5	Total	Mean	Standard deviation	Coefficient of variation
P_1 (S. SPONTANEUM)											8.0		
P_2 (SCLEROSTACHYA)											3.0		
F_1	6	4	5	4	2	—	—	—	—	21	8.6±.6	2.8	32.5
F_2	1	9	18	20	21	18	13	11	5	116	13.6±0.34	3.66	26.9
Back-cross with SCLEROSTACHYA	—	3	4	15	3	—	2	1	—	28	11.8±.51	2.7	22.8

Remarks : The variance of F_1 is not significantly different from that of F_2 and back-cross. This is again in contradiction with the theory.

TABLE XIII

FREQUENCY DISTRIBUTION OF THE LEAF LENGTH (IN INCHES) WITH MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION.

	26·5-30.5	30.5-34.5	34.5-38.5	38.5-42.4	42.5-46.5	46.5-50.5	50.5-54.5	54.5-58.5	58.5-62.5	62.5-66.5	66.5-70.5	70.5-74.5	Total	Mean	Standard deviation	Coeffi-cient of variation
P_1 (S. SPONTANEUM)			1											38		
P_2 (SCLEROSTACHYA)		1												33		
F_1	—	—	1	—	—	1	7	3	4	2	2	1	21	57.2±1.7	7.9	15.4
F_2	1	7	25	35	25	18	5	—	—	—	—	—	116	41.8± .47	5.04	12.0
Back-cross with SCLEROSTACHYA	3	—	11	4	8	3	—	—	—	—	—	—	29	39.6±1.05	5.6	14.1

Remarks : Variance of F_1 is significantly greater than the variance of F_2.
Variance of F_2 does not differ significantly from the variance of back-cross.
Variance of F_1 is significantly greater than the variance of back-cross.
According to the multiple factor hypothesis the variance of F_1 should be less than both F_2 and back-cross.
The observed result is in contradiction with the theory.

TABLE XIV
DATA ON HIGH YIELD AND HIGH SUCROSE COMBINATIONS
(In reciprocal crosses)

Serial No.	Cross	Number of seedlings		Brix %								Weight per Cane in lbs.							
		Total	Examined	Maximum	Minimum	15—16	17—18	19—20	21—22	23—24	Remarks (Statistical)	Maximum	Minimum	Below 1 lb	1.01—2.00	2.01—3.00	3.01—4.00	4.01—4.50	Remarks (Statistical)
I.	Co.605 x P.8331	280	181	24.0	15.0	8	86	72	14	1	x^2 54.80 $x^2_{(3)}$ 11.345 0.01 *Highly significant* There are more number of seedings with greater brix in the cross P.8331 x Co. 605 than in its reciprocal.	3.25	0.54	34	125	21	1	—	x^2 14.47 $x^2_{(2)}$ 9.21 .01 *Highly significant* There are more number of seedlings with higher weight per cane in the cross Co. 605 x P. 8331 than in its reciprocal.
	P.8331 x Co. 605	280	198	24.0	15.0	5	38	84	53	17		3.50	0.50	69	113	11	2	—	
II.	Co.678 x P.8331	150	120	23.0	13.0	36	53	27	3	1	x^2 12.090 $x^2_{(3)}$ 11.345 0.01 *Significant* There are more number of seedings with higher Brix in the cross P·8331 x Co. 678 than in its reciprocal.	3.00	0·75	11	83	26	—	—	x^2 19.843 $x^2_{(2)}$ 9.21 .01 *Significant* There are more number of seedlings with higher weight per cane in the cross Co. 678 x P. 8331 than in its reciprocal.
	P.8331 x Co.678	210	170	22.0	14.0	32	50	64	24			2.60	0.50	41	115	14	—	—	
	Co.605					15.0												4.50	
	Co.678								21.0							2.40			
	P.8331								22.0						1.82				

hypothesis, may be purely a chance, or it may be that some of the chromosomes have paired allosyndetically to give this segregation. Seedling No. 3 of the F_1 was back-crossed with *Sclerostachya*, and 29 seedlings were obtained. One interesting feature about the behaviour of these back-crosses, is that inspite of the back-crossing with the parent (*Sclerostachya*) seedlings having more traits of *Sclerostachya* were not recovered.

As regards height, even though the behaviour is similar to that of tillers, the variants of F_1/F_2 is significant and the variance of the back-cross is not significantly different from the variance of F_1, which is contrary to the multiple factor hypothesis. The same is the case with the leaf length and width, and brix also. One peculiar feature observed in the case of brix is that though the parents concerned have 8 (*S. spontaneum*) and 3 (*Sclerostachya*) some of the F_1 hybrids have brix to the extent of 12-14, and still more 20-22 in some of the F_2 population. This may be due to either cumulative effect of genes, or due to some peculiar combination of genes unknown. The variance of F_1 as regards brix is not significantly different from that of F_2 and back-crosses. This is again in contradiction with the multiple factor hypothesis.

D. Miscellaneous crosses.

Co. 605 x P. 8331.

P. 8331, a complicated hybrid, is now increasingly used as one of the parents for introducing riches to juice. Likewise Co. 605 gives seedlings with high yield. Combinations of these two parents and their reciprocal crosses are expected to give a number of seedlings combining the richness of P. 8331 and the high yielding capacity of Co. 605.

A total of nearly 379 seedlings in the crosses either way were studied. P. 8331 as mother in the above cross has yielded a large number of seedlings with high brix ; as many as 80% of the total population appear to have inherited the maternal richness. Likewise Co. 605 as mother has yielded seedlings having high yield. This seems to support the existence of cytoplasmic inheritance.

CONCLUSIONS

The difficulties of handling sugarcane as a genetical material would be apparent from what has been said so far. Indeed Parthasarathy (1951 b) is of the opinion that sugarcane is not a suitable plant for genetical studies. That of course is the inevitable consequence of its being a complex polyploid hybrid. The vagaries exhibited in the crosses studied such as the clear-cut absence of dominance or recessive characters, the absence of uniform intermediate nature of the F_1 hybrids, and absence of segregation and failure to recover the parental types in the F_2 go to prove the statement made above. The only way of restoring a high degree of genetical purity appears to be to get at some lower diploid forms which may be the progenitors of sugarcane. Back-crossing with forms which are likely to have played a role in the origin of sugarcane while bringing about the desired result, introduces at the same time a very complicated problem of how to eliminate the chromosomes other than those of sugarcane.

So far as the evolution of economically better varieties of sugarcane is concerned, it is bound to involve a very large element of chance which cannot be eliminated altogether. Hybridisation, selection and testing are the most important features in the evolution of economic types. As Stevenson (1943) points out "it includes a study of the fundamental causes of variability in seedling populations, the differential response shown by varieties under distinct environments, and the way in which adaptation to particular localities may be understood from a knowledge of individual growth types". From a study of such features, as the time and extent of tiller formation, cane growth rate and the arrowing, it may be possible to forecast the type of conditions to which a seedling will be most suitable. Each seedling may be expected to give of its best under a particular set of environmental conditions. It looks as if maximisation of production can be achieved only by breeding newer varieties for different tracts each adapted to a comparatively narrow range of environmental conditions. Hence the importance of testing each new promising variety in different types of environments cannot be overemphasised. From this point of view the term 'sugarcane breeding' need not be restricted to the narrow sense of hybridisation alone but it comprehends individual varietal response to differential environments.

SUMMARY

The inter-relationship between genetics and plant breeding has been emphasised. From the realm of art, plant breeding has passed on to the realm of an exact science with the re-discovery of laws of Mendelian heredity at the turn of the century. In the earlier investigations into the field of heredity, data were gathered by methods considered purely genetical. With the discovery of the presence of the genes, the hereditary units, genetics has come to assume a new complexion. Correlation of data obtained by genetical procedure with observations made by cytological technique, has become the rule in present day practice. This dual approach - 'cyto - genetics'— involves a sound knowledge of statistical methods.

The methods followed in sugarcane breeding are of necessity a consequence of its cyto-genetical features. The fundamental fact to remember about sugarcane in this connection is that as a breeding material, it is different from the other crop plants. This, of course, is due to its genetical constitution which in its turn is dependent upon its evolution. It is a highly heterozygous polyploid complex with a large reserve of lethal genes which especially in the *officinarums* are responsible for there being practically no survivals in the selfed progeny. It is the clonal propagation that has made it survive the competition. The presence of diploid parthenogenesis in most of the pollen sterile forms adds to the complexity. There is therefore very little that could be done for "purifying" sugarcane. Thus inbreeding and pure-

line selection are of little avail in sugarcane breeding. The vagaries exhibited by sugarcane as a breeding material and their cytological basis have been briefly described. Phenomena such as elimination of chromosomes *en bloc*, semblance of dosage effect of genes in some crosses and its absence in others, irregular phenotypic expression not easily explicable by established cytological causes, the presence of some sort of cytoplasmic inheritance in some crosses, non-segregation of parental characters due to autosyndetic pairing of the chromosomes—these have been indicated. For genetical studies sugarcane is not a favourable material.

The data that have been gathered are presented in a statistically analysed form. In some crosses, the reciprocal differences with reference to particular characters, have been found to be statistically significant indicating the presence of an inheritance which is based upon an inter-action of the genes with the maternal cytoplasm. This has been found to apply even in cases where economic characters like yield and sucrose have been taken into consideration.

Some of the characters like tiller number, height, leaf length and width, appear *prima facie* polymeric in their inheritance. But on subjecting the collected data to statistical analysis, it was found that they did not conform to the expectation.

Similarly when single qualitative characters are taken for genetical analysis, it was found that they did not conform to either monogenic or digenic inheritance. This is according to highly impure material, and the chances of establishing homozygosity are practically nil, owing to inherent cyto-genetical complications.

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excellent impression of the industries. The author is to be congratulated, and Dr. Hallam L. Movius, jun., who edited it, and the American Philosophical Society are to be thanked for the production of a very important publication which fills a gap in our knowledge of early Palæolithic cultures in the Leipzig region.

A Barking Crayfish

An unusual example of a 'barking' crayfish has been reported from Newcastle, Australia (*Austral. Mus. Mag.*, 12, No. 2). Only one other example of the species (*Linuparus trigonus*) had previously been recognized around the Australian coastline; that specimen was also collected in seas adjoining the temperate eastern quarter of the continent and as recently as 1949. Both occurrences are surprise distributions of a crayfish which belongs to the Japanese seas. The strange noise made by the species has probably passed unnoticed until it was heard by Athol D'Ombrain as a harsh, grating noise. Its source was not located until some time after the death of the Newcastle specimen. Finally it was traced to the inner angles of the heavy basal joints of the stubby antennæ, immediately in front of the eyes. Here there are two smooth-lined cavities which enclose and bear upon a pair of highly polished bosses when the antennæ assemblage is thrown backwards over the head. Even after death a semblance of this friction-produced sound could readily be achieved by hand manipulation. The purpose of the 'barking' is not clear.

Zoological Nomenclature

The International Commission on Zoological Nomenclature gives notice that as from December 26, 1956, it will start voting on the following cases involving the possible use of its plenary powers for the purposes specified against each entry. Full details are given in the *Bulletin of Zoological Nomenclature* (12, Pt. 3): (1) *Lepidurus* Leach, 1819, validation; *Triops* Schrank, 1803, determination of gender and designation of type species for (Cl. Crustacea, Order Decapoda); (2) Apodinae Hartert, 1897, (Cl. Aves), validation; (3) *volvulus* (emend. of *volvulas*) (*Filaria*), validation of, as from Leuckart, [1892] (Cl. Nematoda); (4) *Asaphus* Brongniart, 1822, validation of and designation of type species for; *cornigerus* Schlotheim, 1820 (*Trilobites*), suppression (Cl. Trilobita). Comments should be sent as soon as possible to Francis Hemming, Secretary to the Commission, 28 Park Village East, Regent's Park, London, N.W.1.

Cytogenetics and Breeding of Sugar-Cane

The improvement of sugar-cane (*Saccharum officinarum*) by breeding and selection is of comparatively recent origin. Much work, however, is now going on in different tropical regions. T. S. Raghavan (*Proc. Indian Acad. Sci.*, **43**, B, 2, 100; 1956) has pointed out that although the main aim in breeding work is to obtain high-yielding commercial cane, breeding for resistance to diseases is of great importance in some regions. Hybridization of different species of *Saccharum*, and sometimes of different related genera, has been necessary to obtain strains well suited to the needs of different regions. Where cane develops under favourable conditions, the noble (*S. officinarum*) and highly nobilized varieties have given good results as parents, while in less favourable areas *S. spontaneum* and *S. barberi* have given more satisfaction. At Coimbatore, *S. spontaneum*, and in Florida *S. robustum*, have proved of value in breeding programmes. Important intergeneric crosses are those with bamboo and *Sorghum*. Sugar-cane 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 responsible for there being practically no survivals in the selfed progeny. It is only 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. The occurrence of parthenogenesis and of chromosome elimination has raised new issues which are now recognized in the cytogenetic approach to practical problems. Lists of crosses and of parental and hybrid chromosome numbers are given.

Use of Silage in British Agriculture

Fermented green fodder has now come to be recognized as a valuable supplement to the traditional roots and hay for winter feeding of cattle. It also fits in admirably with the present-day intensification in Britain of grassland management based on increased use of fertilizer. It is therefore important that the facts concerning silage making and use should be brought thoroughly up to date and presented in a clear practical manner together with just enough of the theory to make the rules comprehensible. This task has been admirably carried out by a group of officers of the National Agricultural Advisory Service and published as a revision (the seventh) of Bulletin No. 37, "Silage", of the Ministry of Agriculture (pp. 58+4 plates. London: H.M.S.O., 1956. 3*s*. net). Silage, properly made, has a feeding value about twice that of roots and rather more than that of hay, reckoned on a starch-equivalent basis. It is readily eaten by cattle, and fortunately many of the operations of growing, cutting, carting and making lend themselves to mechanization, an aspect of the subject which rightly occupies an important place in the treatment. Grass is not the only crop suitable for silage making, though it is the most important; the use of arable crops, including by-products such as sugar-beet tops, is dealt with. The addition of extra carbohydrate as molasses to high-protein crops in order to secure a favourable fermentation is also explained. On the national level, any farming practice which can reduce the expensive imports of concentrated feeding stuffs into Britain deserves official encouragement. To put the facts before farmers is clearly a step in the right direction.

A Survey of Atomic Energy

The spring issue of *Studies*, the Irish quarterly review, contains an interesting article entitled "Atomic Structure and Atomic Energy", by Prof. T. S. Wheeler, professor of chemistry in University College, Dublin, in which he gives an excellent summary of our present knowledge of the structure of the atom and the production of atomic energy. The component parts of the atom, isotopes, the relationship between matter and energy, nuclear fission, the uranium and plutonium bombs, nuclear reactors, and the British programme of nuclear

C. B. 16

INTERNATIONAL SOCIETY OF SUGAR CANE TECHNOLOGISTS
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THE PHYLOGENY OF SACCHARUM AND RELATED GENERA

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INTRODUCTION

The study of the origin of cultivated canes, is of immense value to the plant breeder, in the task of evolving new varieties suited to the varied environmental conditions. While many agronomical characters as those connected with yield and quality, are seen in cultivated plants, those constituting hardiness, resistance to diseases, drought and pests, are often met with in wild relatives. The importance of this aspect of breeding was first realised by Vavilov who explored regions that constituted the centres of origin of the more important crop plants and made a remarkable collection of the related wild forms. As a result of such a collection, potato breeding has been revolutionised making it possible to tackle the most important problems of synthesising fungus and virus resistant varieties. Muntzing (1951) successfully introduced the desirable genes of *Secale* into *Triticum* with the result that the "*Triticales*" are capable of growing in sandy soils where no wheat can grow and yet yield as high as 90% of the best wheats; in addition, they have good baking quality, high protein content, early maturity and winter hardiness.

Being the bearers of heredity characters the chromosomes have a direct bearing on evolutionary processes, and as such are invaluable guides, in tracing out phylogeny. The number and morphology of chromosomes and other karyological features (Babcock, Stebbins and Jenkins, 1942), the number of nucleoli and satellites (Gates, 1937), together with the pairing behaviour (Sax, 1935), and secondary association (Lawrence, 1931; Gatschecide, 1937; Nandi, 1936; Raghavan et. al., 1939, 1947) have been useful pointers to interspecific and intergeneric relationship. In the evaluation of taxonomic relationship, the degree of chromosomal pairing is often an unmistakable measure of the degree of affinity between the concerned species. In species with the same chromosome number, the greater the number of bivalents, the greater the fertility, and the closer the relationship, as has been found for example by Clausen (1931) in Viola, e.g., *V. tricolor* $(n=13) \times$ *V. alpestris* $(n=13)=13_{ii}$. The pairing behaviour in plants with different chromosome numbers has been classified by Tackholm (1922) into three main types. They are firstly Drosera Scheme of pairing, where the affinity between the chromosomes of the two parents is greatest, and where the chromosomes of the parent with the lesser number pair with their homologues in the other parent, the rest remaining in an unpaired condition, e.g., *Triticum* (Sax, 1928), *Nicotiana tabacum* ($n=24$) x *N. sylvestris* ($n=12$)$=12_{ii}+12_i$ (Goodspeed and Clausen, 1927), *Brassica Juncea* ($n=18$) x *B. campestris* ($n=10$) $=10_{ii}+8_i$ (Ramanujam and Sreenivasachar, 1943). Secondly in the *Hieracium-Boreale* type, there is only weak affinity, e.g., *Nicotiana tabacum* ($n=24$) x *N. glutinosa* ($n=12$) (0 to 8_{ii}, Raghavan and Srinivasan, 1941). Finally in the *Pygrarea* type there is little or no affinity e.g., *Nicotiana* (Goodspeed, 1934), *Crepis* (Collins and Mann, 1923).

Cytogenetical studies and the pairing behaviour between the genomes of the parents concerned have now established the origin of many cultivated plants through hybridisation and chromosome duplication. The wheats may be taken as an example. Species of wheat fall into three groups, diploid *einkorn* wheats ($2n=14$), tetraploid *emmer* or hard wheats ($2n=28$) and hexaploid *vulgare* or soft wheats ($2n=42$). The work of Sax, Kihara and others showed that the chromosome complement of emmer wheats contains a set of 7 chromosomes similar to those of *einkorn* wheat and a set of 7 other chromosomes derived from another plant. Vulgare wheats contain 14 pairs of chromosomes similar to the *emmers* and 7 pairs similar to those found in the genus *Aegilops*. Thus the *emmer* wheats must have arisen as allotetraploid hybrids. The *vulgare* wheats are allohexaploid hybrids derived from *emmer* like and *Aegilops* like ancestors. It is now known that the *emmers* are allo-tetraploid having 7 pairs of chromosomes from *T. monococcum* (AA) and 7 pairs from *Agropyron triticeum* (BB). The bread wheats (*T. aestivum*) belonging to the *vulgare* group, are allohexaploids (AABBDD) with three groups of 7 pairs each, of which AA and BB are contributed by the *emmer* wheat (*T. monococcum* and *Agropyron triticeum*) and DD from *Aegilops squarrosa*.

The American cottons *Gossypium barbadense* and *G. hirsutum* having 26 pairs of chromosomes ($2n=52$) are now known to be amphidiploid derivatives from crosses between two species having $2n=26$. A group of diploid species ($2n=26$) occurs in a wild state in Central America and another group also having the same chromosome number occurs in the old world, tropical Asia, Africa etc. The New world tetraploid cottons contain 13 pairs similar to those found in American diploids and 13 pairs similar to those found in Asian diploids. The tetraploid species presumably arose through hybridisation between the American and Asiatic diploids and doubling of the chromosome complements. Similarly the cultivated *Brassica juncea* ($2n=36$) is an amphidiploid, having the genomes of *Brassica campestris* ($n=10$) and *B. nigra* ($n=8$) (Ramanujam and Srinivasachar, 1943). Goodspeed (1934) after a study of *Nicotiana* says "that there is no justification for a disbelief in the significance of pairing as indication of relationship". Ramanujam (1937) is of the view that "while conjugation of chromosomes indicates a kind of homology between them, non-conjugation does not necessarily always mean non-homology" and as such counsels caution before arriving at any conclusion,

TAXONOMY AND DISTRIBUTION OF SACCHARUM AND RELATED GENERA

The genus *Saccharum* has a wide range of distribution, a proper understanding of which is essential before the various inter-relationships are studied. This genus ranges from the colder regions of the subtropics down to the tropical areas of Java, Sumatra, etc. *S. officinarum* flourishes well in the tropical belts of South India, Java and New Guinea. *S. Barberi* is confined to the subtropical belt of India, while *S. sinense* is a native of China. *S. robustum* is limited to the polynesian islands of New Guinea, New England and New Hebrides. *S. edule* is endemic to New Guinea and does not occur on the islands east of Hebrides. Only *S. spontaneum* is seen in all these areas, with its diversified habit, adapted to the different ecological conditions of the tropical and temperate regions, including the colder Himalayan slopes. Of the related genera, special mention may be made of *Sclerostachya, Narenga* and *Erianthus* whose taxonomic position is controversial. Till very recently these were included in the genus *Saccharum-Sclerostachya* under *Eu-Saccharum, Narenga* as *S. narenga* - while most of the species of Erianthus were regarded as species of *Saccharum*.

CHROMOSOME NUMBERS IN SACCHARUM AND RELATED GENERA

Compared to the basic number of 10, to which this tribe belongs, these species are all allo-polyploids of a high order. *S. officinarum*, excepting variety Kajla (2n = 68, Parthasarathy 1946), is an octoploid (Bremer 1925; Dutt and Subba Rao 1933; and Raghavan, unpublished). *S. spontaneum* has the widest range from 2n=40 to 2n=128 (Parthasarathy and Subha Rao 1946; Moriya 1950; Janaki Ammal 1936; Starret 1948). *S. Barberi* has four well defined chromosomal groups ranging from 2n=82 to 124, while *S. sinense* shows 2n=118-122 (Bremer 1925; Subramaniam 1946). *S. robustum* has chromosome numbers from 2n=60 to 120 (Starret quoted from Artschwager 1948 ; Grassl 1946), while *S. edule* has 2n=70 to 120 (Grassl 1946). A study of the few *robustum* clones available at this Institute reveals numbers different from those reported by Starret with 2n=64, 72, 80, 84 and 96 (Sundararaghavan 1954). The genus *Erianthus* can be divided into 3 sub-groups, and the various species under them have the diploid numbers from 20 to 60 (Subba Rao and Raghavan, 1951). *E. maximus* is reported to have 2n=60-100 (Grassl, 1946). The diploid number of *Sclerostachya* (Venkatraman and Parthasarathy, 1942) and *Narenga* (Bremer, 1925) is 30.

INTER-RELATIONSHIP BETWEEN SACCHARUM AND ITS RELATED SPECIES AND GENERA

The several cyto-genetic features exhibited by sugarcane have been published in a series of recent papers (Raghavan 1951 a, b, c, 1952, 1953, 1954 a, b). Leake (1953) summarising the above papers, points out that the origin of uncertainties associated with *Saccharum* in hybridization is threefold, and can be traced to high polyploidy, heterozygosity and autosyndesis. To these may be added the recently discovered cytoplasmic inheritance which makes the progeny resemble the mother more than the staminate parent (Raghavan 1951 b) making it desirable to bestow more attention on the mother than on the father in sugarcane breeding. Even in the simplest material available, a high amount of genetical impurity is evident and as such orthodox methods of breeding in such a highly heterozygous population are of no avail. Diploid parthenogenesis, absence of haploidy, and the inability to inbreed owing to the operation of lethal factors, and autosyndesis make segregation along Menedelian lines difficult and as such it is almost impossible to break down the high polyploidy. Handicapped by these disadvantages Parthasarathy (1951) attempted to reduce *S. officinarum* to its basic complement (x = 10) by successfully backcrossing it with the related genus *Sclerostachya*.

(i) *S. officinarum* and *Sclerostachya*.

S. officinarum var. Vellai (2n = 80) was crossed with *Sclerostachya* (2n = 30) and the hybrids were repeatedly backcrossed with *Sclerostachya*. Excepting for the first backcross, reduced gametes functioned on both sides in the other backcrosses. In the third backcross, a plant was obtained with 2n = 40 chromosomes made up of 10(0) + 30 (S) (0 = *officinarum*; S = *Sclerostachya*). In the absence of homology between *S. officinarum* and *Sclerostachya* chromosomes, the normal expectation would be $\underset{0}{10_i}+\underset{SS}{15_{ii}}$. However, the meiotic configuration of 20 bodies made up of i.e., $\underset{SSO}{5_{iii}}+\underset{SS}{10_{ii}}+\underset{0}{5_i}$ gave the clue that out of the 10 chromosomes of *S. officinarum*, 5 paired with the bivalents of *Sclerostachya* forming 5_{iii}, while the other 5 *officinarum* chromosomes remained as univalents, leaving 20 chromosomes of *Sclerostachya* to pair autosyndetically forming 10_{ii}. It means that out of the basic complement of x = 10, 5 chromosomes of *S. officinarum* have homology with 5 chromosomes of *Sclerostachya* (Govindaswamy, 1948).

(ii) *Saccharum officinarum* and *Narenga*.

Raghavan (1951 a, c) crossed the 2nd backcrossed progeny of *S. officinarum* x *Sclerostachya* hybrid $(2n=\underset{0}{20}+\underset{S}{30}=50)$ with Narenga. The meiotic configuration in the mother was as a rule regular forming 25_{ii} indicating autosyndetic pairing $\underset{00}{10_{ii}}+\underset{SS}{15_{ii}}$. The hybrids with *Narenga* showed 20 bodies at meiosis $(\underset{OSN}{5_{iii}}+\underset{O}{5_i}+\underset{SN}{10_{ii}})$. Had the *S. officinarum* chromosomes failed to exhibit any homology with *Sclerostachya* or *Narenga* chromosomes, the normal expectation would be either $^{*}\underset{N}{15_i}+\underset{S}{15_i}+\underset{O}{10_i}$ or $\underset{O}{10_i}+\underset{SN}{15_{ii}}$. The latter configuration $(\underset{O}{10_i}+\underset{SN}{15_{ii}})$ would indicate an allosyndetic pairing between *Narenga* and *Sclerostachya* chromosomes, which may be a justifiable premise in view of the fact that the F_1 hybrids of *Narenga* x *Sclerostachya* formed 15_{ii} regularly (Parthasarathy, 1947). Instead of the above two expected configurations, the occurrence of 5_{iii} and 5_i seems to point out the homology

* S = Sclerostachya. N = Narenga. O = S. officinarum.

between 5 chromosomes of *Narenga* and *officinarum*. In other words the three genera *S. officinarum*, *Narenga* and *Sclerostachya* have had a common origin from a putative ancestor, 5 of whose chromosomes are common to all the three (Raghavan 1951 a, c).

(iii) *Saccharum officinarum* and *Sorghum*.

Cytological analyses of certain intergeneric hybrids i.e., *S. officinarum* x *Sorghum halepense* (Govindaswamy, 1948) have indicated the homology of 2 chromosomes of *Sorghum* with 2 of *S. officinarum* suggesting thereby that these 2 genera have a minimum of two chromosomes in common between them.

(iv) *Saccharum officinarum* and *Saccharum spontaneum*.

In order to study the inter-relationship between *S. officinarum* and *S. spontaneum*, the backcross method of breaking up the polyploidy and bringing the chromosomes to the basic level was adopted. The high fertility and the easy crossability contributed greatly to the success of these backcrossings (Raghavan, unpublished).

In the formation of F_1 of *S. officinarum* ($2n=80$) x *S. spontaneum* (Coimbatore) ($2n=64$), unreduced egg functioned on the part of the noble parent, resulting in hybrids with $2n=112\ (\underset{0}{80}+\underset{Sp.}{32})$ (O = *officinarum*; Sp. = *spontaneum*). This feature is now found to be the rule, whatever *officinarum* may be used as mother. The F_1 was nobilised by using *S. officinarum* as mother. Again unreduced gametes functioned on the *officinarum* side, the resultant hybrids showing 136 chromosomes $(\underset{2n+n}{80+56}=\underset{0}{120}+\underset{Sp.}{16})$. This seedling was crossed with *S. officinarum*, a further stage in nobilization with this difference however, that *S. officinarum* was used as the staminate parent. The offspring showed $2n=108$ chromosomes which is the result of normal fertilization, i.e., $n+n=68+40=\left[(\underset{0}{60}+\underset{Sp.}{8})+\underset{0}{40}\right]$. It may be seen that in the series of crosses, the number of *spontaneum* chromosomes has been successively reduced from 32 to 16 and from 16 to 8 resulting in 100 *officinarum* chromosomes and 8 *spontaneum* chromosomes in the final progeny.

The meiotic behaviour of these hybrids in which the *spontaneum* chromosomes have been reduced to eight, throws light on the basic number as well as homology. In MI 53 bodies were seen made up of $45_{ii}+5_{iii}+3_{i}$. If the 8 *spontaneum* chromosomes had enough homo-
00 00Sp. Sp.
logy between themselves, i. e., if the basic number had been 4, instead of 8, they would have formed 4_{ii}, leaving the *officinarum* chromosomes to pair autosyndetically, with the result 54_{ii} would have been observed. It would, however, have meant that the basic complement of 8 is itself made up of two sets of 4 chromosomes. On the other hand, complete lack of homology between *S. spontaneum* and *S. officinarum* chromo-

somes would have resulted in 58 bodies, i.e., $\underset{00}{50_{ii}}+\underset{Sp.}{8_i}$, in which case all the 8 chromosomes of *S. spontaneum* remain as univalents. The occurrence of 5_{iii} seems to indicate that 5 chromosomes of *S. spontaneum* have paired with 5_{ii} of *S. officinarum* forming 5_{iii} and the rest of the 3 *spontaneum* chromosomes remain as univalents; the 45_{ii} observed are the result of 90 *officinarum* chromosomes pairing autosyndetically.

The chromosomal constitution of the hybrids at successive levels of nobilization is given below. As expected *officinarum* chromosomes assume greater preponderance as nobilization advances.

Variety	Parentage	Chromosome number 2n	Constitution	Thickness of stem	Brix in juice
Green sport		80	0 80	3.5 cms.	17.4
Chittan		80	0 80	3.6 cms.	17.9
S. spontaneum (Coimbatore) (CBE)		64	sp. 64	0.76 cms.	8.0
Co. 285	G. sport x S. spont. (CBE)	112	0 sp. 80 32	1.93 cms.	14.5
P' 451/1	Chittan x Co. 285	136	0 sp. 120 16	2.14 cms.	14.5
P' 749/1	P' 451/1 x Chittan	108	0 sp. 100 8	2.25 cms.	14.7

(v) *S. officinarum*, *S. robustum*, *Sclerostachya* and *Narenga*.

Brandes and Sartoris (1936) record that "when a noble cane is crossed with *S. robustum*, there is an increase of chromosomes above the number which corresponds to the sum of the monoploid numbers of the parents, but it is considerably less than the diploid number of *S. officinarum* and the monoploid number of *S. robustum*". According to them, 32 chromosomes of *S. robustum* pair allosyndetically with 32 chromosomes of *S. officinarum* and the remaining chromosomes of both the parents get doubled. The hybrids thus, instead of having n+n $(40+42)=82$, have $2n=100$ which may be represented as follows : $\underset{0}{32}+\underset{R}{32}+\underset{00}{(8\times 2)}+\underset{RR}{(10\times 2)}=100$ (0=officinarum; R.=*S. robustum*). Accordingly this would seem to indicate that auto as well as allosyndesis take place in these hybrids. Grassl (1946) summarising the results, points out the following main reasons for considering *S. robustum* as being closely related to *S. officinarum*.

(i) The occurrence of chromosome number in multiples of 10 in both these groups.

(ii) The increase of about 18-20 chromosomes in *S. officinarum* and *S. robustum* hybrids "which is only about one-half as great as when *S. spontaneum* is used as the male parent" (against *S. officinarum*) and consequently it is surmised that *S. robustum* and *S. officinarum* possibly have as many as 20 chromosomes in common.

(iii) The absence of IV glume in both *S. robustum* and *S. officinarum*.

(iv) Some of the 'noble' canes from Micronesia and Polynesia, resemble very much the artificial hybrids between *S. officinarum* and *S. robustum*.

The morphological characters of the hybrids between *S. officinarum* and *S. robustum* produced at this Station reveal the characters of both the parents even though they are more disposed towards the mother presumably because of the influence of the maternal cytoplasm (Raghavan, 1952; Sundararaghavan, 1954). There seems to be little doubt about the hybrid nature of these seedlings. The male parent (*S. robustum*) has a fertility of 90 to 96 per cent while the mother Vellai is male-sterile. The hybrids, however, have a fertility of 60 to 70 per cent. The hybrids produced here have come into being through the functioning of haploid gametes $(40_{O}+42_{R})$ (O=S. officinarum; R=S. robustum), a fact which is corroborated by the findings of Li and Shang (1951). It has been suggested by Parthasarathy (1946) that "reduced gametes function, when genetic relationship is close, but unreduced gametes function when the two species are distantly related". In this connection it may be pointed out that whenever either *S. Barberi* or *S. spontaneum* is used as male on *S. officinarum*, only diploid gametes are contributed by the mother (Raghavan, a, c). In other words, the functioning of n or 2n eggs on the part of *S. officinarum* has a direct bearing on the staminate parent. Even though the functioning of reduced or unreduced egg cannot be taken as an unfailing indication of genetic relationship, yet the behaviour of *S. officinarum* can be utilised to some extent to determine genetic relationship. The functioning of normal haploid gametes in the cross *S. officinarum* x *S. robustum* almost as a rule and vice versa, may be taken as a fair indication of their affinity.

Additional evidence seems to be forthcoming through a study of *S. robustum* x *Sclerostachya* and *S. robustum* x *Narenga* hybrids. In the hybrids between *S. officinarum* (2n=80) and *Sclerostachya* (2n=30), the F_1 shows 2n=55 (being the product of normal fertilization). The meiotic configuration is $25_{ii}+5_{i}$ (Govindaswamy, 1948). The 5 univalents because of their larger size, could be identified as belonging to *Sclerostachya* indicating that the chromosomes of *S. officinarum* pair by means of autosyndesis forming 20_{ii}, while the haploid complement of *Sclerostachya* forms $5_{ii}+5_{i}$. In the three sets o 5 chromosomes each making up the haploid complement of *Sclerostachya* only 2 sets are homologous enough to form bivalents autosyndetically while the third set remains unpaired as univalents. The absence of any other association than those of bivalents indicates that the 3rd set of 5 chromosomes, is non-homologous with either of the other sets.

In the hybrids of *S. robustum* x *Sclerostachya* and *S. robustum* x *Narenga*, the most common meiotic configuration is $26_{ii}+5_{i}$, while chromosomes of *S. robustum* pair autosyndetically forming 21 bivalents, the Sclerostachya complement forms $5_{ii}+5_{i}$. However, the occurrence of 28 bivalents and 1 univalent in some cases seems to indicate that the 3rd set of 5 chromosomes of *Sclerostachya* pairs allosyndetically with S. robustum. The occurrence of $28_{ii}+1_{i}$ may be due to either of the two following configurations :—

$$^{*}\underset{RR}{18_{ii}}+\underset{SS}{5_{ii}}+\underset{RS}{5_{ii}}+\underset{R}{1_{i}} \quad \text{or} \quad \underset{RR}{19_{ii}}+\underset{SS}{5_{ii}}+\underset{RS}{4_{ii}}+\underset{S}{1_{i}}$$

*(R=*S. robustum* ; S=*Sclerostachya*)

Either way, it indicates partial allosyndesis between 4-5 chromosomes of *Sclerostachya* and *S. robustum*. The same conclusion is reached from the study of *S. robustum* x *Narenga* hybrids. It may be pointed out that Janaki Ammal (1942) while studying *S. officinarum* x *Narenga* hybrids, has observed a maximum of 2_{iv} and 2_{iii} thereby suggesting allosyndesis between *S. officinarum* and *Narenga* chromosomes. Also in the hybrids of *S. robustum* x *S. officinarum*, *S. robustum* x *Sclerostachya* and *S. robustum* x *Narenga* trivalents and quadrivalents are seen which may be due to the allosyndetic pairing of *S. robustum* chromosomes with the chromosomes of the other parents.

In the light of the above observation *S. robustum*, *S. officinarum*, *Sclerostachya* and *Narenga*, seem to have 4-5 chromosomes common between them. Since it has been established that *Sclerostachya* and *S. officinarum* are closely related, it is not surprising that *S. robustum* should show affinity to *Sclerostachya*. After all, *Sclerostachya* is not a distant genus in the same sense as Coix, Maize or Teosinte are and as such it is likely to have played an important role in the origin of *S. officinarum*. In fact the affinities between *S. robustum* and *Sclerostachya* seem to confirm indirectly the close relationship between *S. robustum* and *S. officinarum*. Both *S. officinarum* and *S. robustum* have many important characters common between them, such as size, easy shedability of the leaves, the absence of the 4th glume and the absence of the internodal starch (Dutt and Narasimhan, 1950). There are, however, some differences between the two in morphological features. For eg., the spikelets of *S. robustum* are smaller than those of *S. officinarum*; there are minor differences between the two species in the venation of the glumes also. It might be that both *S. robustum* and *S. officinarum* may have had a parallel evolution. While hybrids with *Sclerostachya* as mother and *officinarum* as staminate parent are impossible to get, the readiness with which *S* *robustum* has crossed with *Sclerostachya* as the pistillate parent seems to indicate that *S. robustum* is the more primitive of the two.

(vi) *Saccharum robustum* and *Saccharum spontaneum.*

S. robustum differs from *S. spontaneum* in the absence of the 4th glume, the sparser and shorter nature of the hairs on the main axis of the inflorescence, the broader and larger nature of the inflorescence, and the smaller size of the spikelets. However, the polyploid nature of these species in multiples of 8 or 10, the aneuploid nature of certain clones, and lower sugar content seem to suggest probable affinities between the two.

It is worthy of note that in spite of repeating the cross for 3 years, only 2 seedlings were derived between *S. robustum* × *S. spontaneum*, while the reciprocal cross failed to yield any seedlings at all. Significant also is the fact that while *S. robustum* crosses readily with *Sclerostachya* or *Narenga*, few or no hybrids are got with *S. spontaneum*, in spite of the high degree of fertility in both these species. The two hybrids of *S. robustum* ($n=42$) × *S. spontaneum* ($n=32$) have been derived through the functioning of $n+n$ gametes [($2n=42+32$)$=74$].

Apart from the genera dealt above the genus *Erianthus* also seems to have played a part in the evolution of the noble cane. Grassl (1946) is of the opinion that *E. maximus*, might have been the ancestor of cultivated *Saccharum*. According to him, "the noble canes are more closely related to *S. robustum* and *Erianthus maximus*. There may have been separate origins of sweet forms in both these groups but it seems more likely that the main origins were from *S. robustum*". The main support for the above view (i.e., from *E. maximus*) is the presence of an awned 4th glume in some of the *S. officinarums*. It may be, however, added that besides the Mungo group of *S. Barberi*, *Saccharum officinarum* × *Sorghum* hybrids as also some of the *Sclerostachya* × *Narenga* hybrids possess awned 4th glumes—probably a case of reversion. As such the presence of awn cannot be taken as a sure indication of close relationship. Similarly the resemblance between *E. arundinaceus* and the cultivated noble canes in some morphological characters has been advanced as proof of inter-relationship between the two. The non-flowering nature of *E. arundinaceus* has so far stood in the way of effecting crosses and obtaining cyto-genetic evidence in this regards.

ORIGIN OF SACCHARUM BARBERI

Chromosomal studies in the genus *Saccharum* have pointed out the capacity of *S. officinarum* and *S. spontaneum* to produce haploid as well as diploid eggs, the functioning of 2n eggs being a postmeiotic phenomenon. Narayanaswamy (1940) is of the view that the fusion of 2 megaspores in a linear tetrad, leads to diploid egg formation, while Bremer (1949) thinks endomitosis in the chalazal megaspore of the linear tetrad as being responsible for this. In either case, it is post meiotic and as such even parthenogenetic derivatives from such diploid eggs, show neither uniformity among themselves nor identity with the mother. Besides this *S. officinarum* is capable of contributting egg gametes having neither the diploid nor the haploid number (through accessory spindle formation and consequent elimination of chromosomes *en bloc*) (Subramaniam 1946; Parthasarathy 1946, 1951; Raghavan 1954 a, b).

Co. 421 (2n=118) was observed to give rise to two kinds of eggs, viz., 86 and 118 respectively, each capable of developing parthenogenetically. The seedlings derived from the former resembled the North Indian canes in morphological features. Struck by the close resemblance between these and the *S. officinarum* x *S. spontaneum* hybrids such as Co. 205, Co. 206, Co. 285 and Co. 291, to the North Indian canes, Parthasarathy (1946) suggested the origin of *S. Barberi* from *S. officinarum* through natural hybridisation with *S. spontaneum*. In morphological characters such as stem thickness, nature of leaves, root system and mode of tillering North Indian canes are intermediate between the two. In the floral characters, there is a mingling of characters of both the parents, with a preponderance of *spontaneum* characters. In features, such as sucrose content, fibre-content and resistance to diseases, *S. Barberi* occupies an intermediate position. The mode of underground branching clearly indicates their hybrid origin (Barber, 1916). The presence of ligular process is a character inherited from *S. officinarum*. In fact throughout the memoirs of Barber, there is a vague suggestion about the hybrid origin of the thin canes; he did not express it because he believed that *S. officinarum* was not indigenous to India. Substantial support to this view is lent by the discovery by Mukerjee (1949) of natural hybrids between *S. officinarum* and *S. spontaneum* in a wild state in the north east regions of India where it is most likely, this impact has taken place.

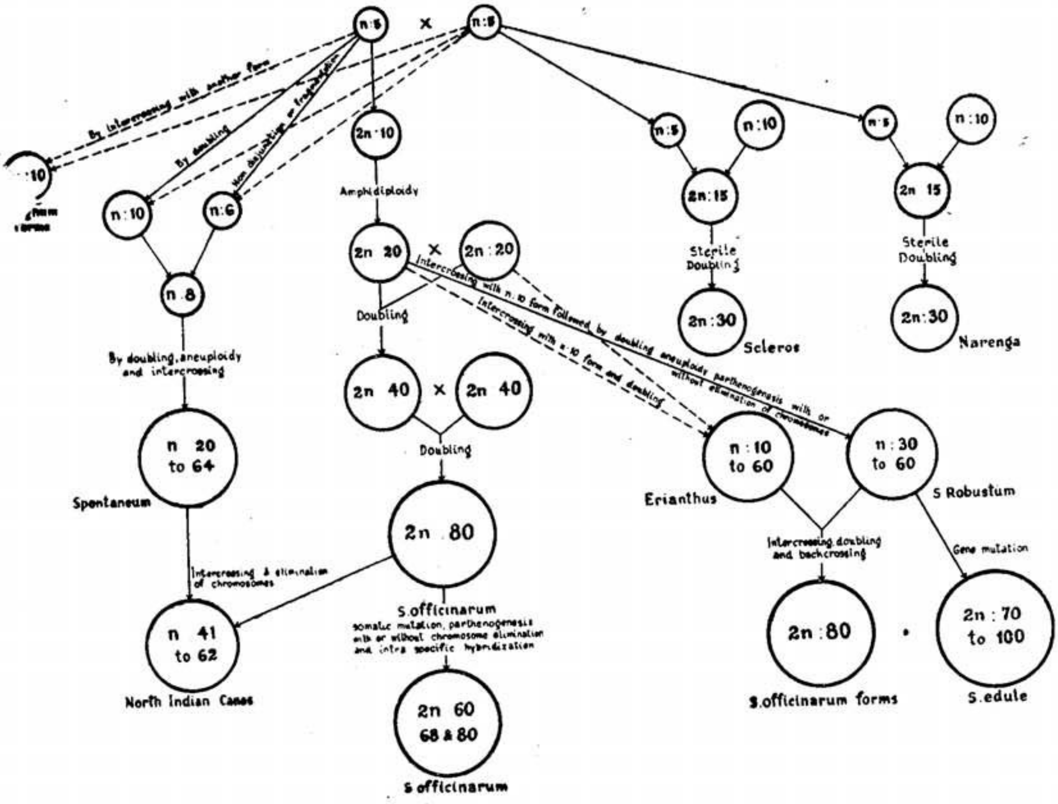
The high fertility of the hybrids and the parents, as well as the functioning of diploid eggs and eggs with varying numbers, would have permitted free intercrossing and back-crossing, resulting in hybrid swarms. Geographical isolation, would account for the diversified sub-groups each with specific chromosome numbers. Accepting the above view would mean that *S. officinarum* is not foreign to India, but was actually present earlier than *S. Barberi*, having been responsible for its origin.

SUMMARY AND CONCLUSION

In the light of evidence available so far, the probable phylogeny of *Saccharum* and related genera has been represented diagrammatically.

It may be considered that *Saccharum* and its related forms have originated from a common ancestor with a basic complement of 5 chromosomes ($x=n=5$). This putative ancestral form might have crossed with another 5-chromosomed-form resulting in sterile hybrids presumably because of differences in structure though not in number; escape from sterility was effected through amphidiploidy. Intercrossing and backcrossing to the parents presumably led to different lines, each stabilizing itself at particular chromosomal levels. A study of the chart reveals how *Saccharum*, *Sclerostachya* and *Narenga* have had a common origin in respect of 5 chromosomes.

HYPOTHETICAL PHYLOGENY OF SACCHARUM AND ALLIED GENERA



From the n=5 type, two forms might have come into existence one with n=10 and another with n=6, the former by a process of doubling and the latter, either by nondisjunction or fragmentation resulting in a secondarily balanced number. These two by further intercrossing would give rise to x=8 forms, which by intraspecific hybridisation polyploidy and aneuploidy might have resulted in diversified groups showing intergrading numbers. Such a method as postulated above, seems to be the basis for the origin of the various *spontaneums*.

Two views can be advanced for the origin of the *officinarums:* either both *Saccharum officinarum* and *Saccharum robustum* have had a common origin or the latter gave rise to the former :—

(i) According to the first suggestion, it would mean that *S. officinarum* and *S. robustum* should have diverged at the 2n=20 level. The 2n=20 forms would have crossed with forms with an identical chromosome number but a structurally different genomed type to give rise to sterile hybrids. Amphidiploidy and further intercrossing followed by doubling will result in octoploids. On the other hand, *S. robustum* taking a different line from that of *S. officinarum* at the 2n=20 level would by a similar process have given rise to higher polyploids which by means of diploid parthenogenesis preceded by elimination of chromosomes or not resulted in aneuploids and lesser polyploids. The different chromosomal races of S. robustum found are presumably a result of these cytological phenomena. (ii) If we regard *S. robustum* as having given rise to *S. officinarum* then the origin of the noble canes has to be explained differently. From the 2n=20 ancestor evolution proceeded along two different lines, one culminating in *S. robustum* and the other in *Erianthus*. Sweeter forms presumably arose from *S. robustum* and these through natural hybridisation with species of *Erianthus* such as *Erianthus maximus* and further backcrossing with *S. robustum* probably resulted in the noble canes, improvement of which was mainly by further selection.

Once the different lines of evolution of *S. officinarum*, *S. spontaneum* and *S. robustum* are established, it is easy to postulate the origin of *S. Barberi* and *S. edule*. Gene mutations in *S. robustum* presumably resulted in *S. edule*, which because of its pulpy and abortive inflorescence passed off for a new species of *Saccharum* (Lennox 1938). The above assumption is based on the fact that *S. edule*, except for minor variations such as the presence of a velvety leaf blade, and absence of so hairy a sheath, differs very little from *S. robustum*.

In sub-tropical India, in the regions of Bihar, Bengal and Orissa, natural hybridisation between *S. officinarum* and *S. spontaneum* probably laid the foundation for the origin of *S. Barberi*. The presence of naturally occurring hybrids between *officinarum* and *S. spontaneum* recently discovered by Mukherjee (1949) lends substantial support to this theory of the probable origin of *S. Barberi*. The origin of the various chromosomal sub-groups of *S. Barberi* is traceable to the capacity of *S. officinarum* to contribute besides haploid and diploid eggs, gametes with unexpected chromosome numbers also through elimination of chromsomes *en bloc*. Apparently these two opposing processes of chromosome eliminations on the one hand and chromosome multiplication on the other hand, through endomitosis, both acting side by side paved the way for the origin of new chromosomal races with a high range of variability suited to the various geographical areas. The evolution of North Indian canes with unrelated chromsome numbers can be explained on the basis of the above phenomenon. The new races possibly stabilised themselves in the different tracts and were geographically isolated from one another. Where the geographical isolation broke down, intercrossing between the various sub-groups presumably took place resulting in newer hybrids. In some of the groups, isolation favoured the accumulation of genic differences to such an extent as to render these groups distinct from one another; this evidenced by the wide range of fertility (from highly fertile Saretha group, to completely sterile Mungo group) in these various forms.

With the data on hand, it would appear that in the phylogeny of *Saccharum*, polyploidy, interspecific and inter-generic hybridization and apomixis appear to have played a more important role than gene mutation and structural changes. The above picture is only tentative subject to revision in the light of further knowledge that future findings may throw.

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

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CONTENTS

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

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; yet 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* × *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* × *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 parthenogenetic 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* ($2n = 80$) × *Sorghum* ($2n = 20$) crosses the hybrids showed $2n = 50$ ($n + n$) and 90 ($2n + n$) (Janaki Ammal; 1941; Raghavan, 1953 *a*) while *S. officinarum* × 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 × *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 × *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 $2n = 118$ and 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. × 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 × 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.

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 ($2n = 118$) × *S. officinarum* var. Striped Mauritius ($2n = 80$)	Co. 463 ($2n = 118$)
2	Co. 421 × *S. officinarum* var. Poovan ($2n=80$)	Co. 602 ($2n = 118$)
3	Co. 421 × Co. 453 ($2n = 124$)	Co. 656 ($2n = 118$)
4	Co. 602 ($2n = 118$) × Coix, *Sorghum*, Teosinte etc. (all $2n = 20$)	$2n = 118$
5	Co. 603 ($2n = 118$) × E.K. 28 ($2n = 80$)	Co. 817 ($2n = 118$)
6	Co. 603 × P′ 63/32 ($2n = 120–24$)	Co. 909, Co. 910, Co. 811 (all $2n = 118$)
7	POJ. 2725 ($2n = 106–08$) × *Sorghum durra* ($2n = 118$)	Co. 356 ($2n = 106–108$)
8	POJ. 2725 × B. 3412 ($2n = 80$)	Co. 407 ($2n = 106–108$)
9	POJ. 2725 × *S. spontaneum* Coimbatore ($2n = 64$)	Co. 455 ($2n = 106–108$)

TABLE II

Parthenogenesis Preceded by Elimination of Chromosomes en bloc

Sl. No.	Cross	Hybrid
1	Co. 421 ($2n = 118$) self	P'212/8 ($2n = 86$)
2	Co. 602 ($2n = 118$) × Coix ($2n = 20$)	Seedling No. 18 ($2n = 96$)
3	Co. 602 × Maize ($2n = 20$)	Seedling No. 20 ($2n = 96$)
4	Co. 603 ($2n = 118$) × P'63/32 ($2n = 120–24$)	Co. 803 ($2n = 108$)
5	Co. 603 ($2n = 118$) × P' 63/32 ($2n = 120–24$)	Co. 804 ($2n = 108$)
6	Co. 603 × Co. 449 ($2n = 118$)	P. 8388 ($2n = 104$)
7	Co. 603 × Co. 449 ($2n = 118$)	P. 8415 ($2n = 84–86$)
8	Co. 603 self	P' 1010/1 ($2n = 104$)
9	*S. robustum* self ($2n = 84$)	P' 868/1 ($2n = 80$)
10	*S. robustum* ($2n = 84$) × Coix ($2n = 20$)	P'875/1 ($2n = 62$)
11	*S. robustum* × *Sorghum* ($2n = 20$)	P'873/2 ($2n = 62$)
12	Kassoer ($2n = 136$) Self	P' ($2n = 112$)

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B-11 BREEDING BEHAVIOUR OF CO. 421 IN RELATION TO ITS CYTO-GENETICS

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INTRODUCTION

CYTO-GENETICAL studies in sugarcane are intended to rationalise breeding by correlating breeding results with observed cytological phenomena. On account of the presence of large accumulation of recessive lethal genes, high polyploidy and hetrozygosity, in breeding and pure line selection are almost ruled out in sugarcane breeding. There are however certain other genetical features which are of direct importance to breeding. The high polyploidy and consequent easier compatibility, the phenomenon of cytoplasmic inheritance, the functioning of eggs with haploid, diploid and a number of chromosomes different from either the haploid or the deploid, deploid parthenogenesis and parthenogenesis preceded by elimination of chromosomes enbloc are some of the important cytological features that play an important part in sugarcane breeding. These have been dealt with in a series of papers (Raghavan 1951a, 1951b, 1951c, 1953, 1954, 1956; Raghavan and Govindaswamy 1956a, 1956b; Parthasarathy 1946, 1951; Bremer 1923, 1929; Brandes and Sartoris 1936; Janaki Ammal 1939, 1951; Subba Rao and Raghavan 1951; and Sundararaghavan, 1954).

BREEDING BEHAVIOUR of Co. 421 ($2N=118$)

Though meiosis in Co. 421 is regular, only about 8 to 10 per cent of the pollen is fertile. Even that pollen is not shed as the anthers do no dehisce and hence it may be considered as completely male sterile. But in spite of its male sterility when the arrows are bagged, a few seedlings are obtained most of which are thin and a few are thick. The thick types showed $2n=118$ chromosomes, the same number as that of the mother Co. 421 while the thin types always shown $2n=86$ chromosomes. The former are obviously diploid parthenogenetic derivatives and the latter being parthenogenetic ones through elimination of 16 bivalents at meiotic metaphase and then doubling through endomitosis (Bremer 1949) or fusion of the two lower-most cells of the linear tetrad (Narayanaswamy 1940). Why there should be this elimination of the same number of chromosomes is not clearly known.

When dusted with pollen of distant genera such as Coix, Maize and bamboo, the same types of seedlings, thick and thin were obtained parthenogenetically which when examined showed $2n=118$ and $2n=86$ chromosomes respectively. Some of the Co. canes like Co. 462, Co. 463, Co. 656 and Co. 779 in which Co. 421 was used as the female parent with other male parents having the chromosome number different from Co. 421, were found to be diploid parthenogenetic derivatives. Hence it is evident that Co. 421 does not seem to cross freely with other male parents.

In only one case namely in the cross between Co. 421 and *S. officinarum* variety Poovan it was reported that egg gamete has contributed 86 chromosomes in the development of the hybrid seedling (Subramaniam, 1946 and Parthasarathy, 1951). But a re-examination of Co. 602 (Co. 421 x *S. officinarum* var. Poovan) showed as $2n=118$ indicating that it is not a cross but a parthenogenetic derivative. Thus it seems that up till now not a single seedling has been isolated which can be considered a true hybrid with Co. 421 as female parent.

It is in this context that the crosses now being reported for the first time with Co. 421 as pistillate parent have to be viewed. Their bearing on its usefulness as a breeding material can be assessed against this background. *Saccharum spontaneum* Coimbatore ($2n=64$) and *S. spontaneum* Glagah ($2n=112$) were used as staminate parents and the F_1 progeny was fairly large, i.e., 2,265 and 1,533 seedlings respectively. The seedlings of the crosses presented a fairly uniform phenotypic expression (Table I).

TABLE I

Table showing the morphological characters of the F_1

Sl. No.	Variety	Parentage	Thickness Cm.	Height feet	Leaf sheath	Leaf width ins.	Ligule	Brix	Chromosome no. 2n.
1.	P' 589/1	Co. 421 × S. Spont. CBE	1·50	7½	glabrous	0·8	Deltoid	18·0	75
2.	P' 589/2	,, ,,	1·50	7½	,,	0·7	,,	18·0	75
3.	P' 589/3	,, ,,	1·40	6	,,	0·6	,,	14·0	75
4.	P' 589/4	,, ,,	1·55	7	,,	0·7	,,	14·0	75
5.	P' 589/5	,, ,,	1·50	8	,,	0·8	,,	17·0	75
6.	P' 590/1	Co. 421 × S. spont. Glagah	1·45	8	spiny	0·9	cresentiform	12·0	99
7.	P' 590/2	,, ,,	1·42	8½	,,	1·0	,,	14·0	99
8.	P' 590/3	,, ,,	1·33	8½	,,	0·9	,,	12·0	99
9.	P' 590/4	,, ,,	1·65	9	,,	0·9	,,	11·0	99

The somatic chromosome numbers of the seedlings were determined to be $2n=75$ and $2n=99$ in the cross Co. 421 x spontaneum Coimbatore and Co. 421 x spontaneum Glagah respectively. As Co. 421 is known to give rise only to two types of seedlings parthenogenetically, the thick type with $2n=118$ and the thin type with $2n=86$ chromosomes, the above seedlings with $2n=75$ and $2n=99$ chromosomes are therefore genuine hybrids, the 43 chromosomed egg having functioned in fertilisation. Though a large number of seedlings were cytologically examined at random, no cases were found indicating the functioning of normal eggs ($n=59$) or unreduced eggs ($2n=118$). The functioning of 86 chromosomed egg has also not been vouched for. It appears therefore, that this cross is of interest for more than one reason. Firstly, this is the first time in which Co. 421 as female has given rise to genuine hybrids. Secondly this is one of the rare instances in which a hybrid has come into being through the operation of an egg whose chromosome number is less even than its haploid number.

Besides the chromosome numbers, the morphological data (Table I and II) also show clearly the true hybrid nature of these seedlings. Because of the functioning of the

TABLE II

Inheritance of characters of Co. 421, spontaneum Coimbatore, *Spontaneum Glagah* and the F_1 hybrids.

Co. 421 × S. Spontaneum Coimbatore.

Sl. No.	Characters	Co. 421 ♀ 2n=118	F_1 2n=75 (n=43+n=32)	Spontaneum Coimabtore 2n=65 ♂
1	Thickness	2·75 cm.	Intermediate	0·8 cm.
2.	Rows of root eyes	3	Intermediate	1·2
3.	Leaf sheath	Spiny	..	Glaborous
4.	Ligule	Deltoid	Deltoid	Deltoid
5.	Leaf width	Broad	..	Narrow
6.	Height	9 ft.	Intermediate	6 ft.
7.	Brix	21·0	Intermediate	8·0

Co. 421 × S. Spontaneum Glagah

Sl. No.	Characters	Co. 421 ♀ 2n=118	F_1 2n=99 (n=43+n=56)	spontaneum Glagah 2n=112=♂
1.	Thickness	2·75 cm.	Intermediate	0·95 cm.
2.	Rows of root eyes	3	Intermediate	2
3.	Leaf Sheath	Spiny	Spiny	Spiny
4.	Ligule	Deltoid	..	Cresentiform
5.	Leaf width	Broad	..	Narrow
6.	Height	9 ft.	..	7 ft.
7.	Brix	21·0	Intermediate	6·0

43 chromosomed egg with the two different spontaneums namely *S. spontaneum* Coimbatore and *S. spontaneum* Glagah as the male parents, all the seedlings are thin, ranging from 1·3 to 1·65 cms. in thickness as compared to 2·75 cms. in Co. 421. The brix is also greatly reduced 14·18 per cent and 11·14 per cent in the hybrids Co. 421 x *S. spontaneum* Coimbatore and Co. 421 Spontaneum Glagah respectively from 21·9 per cent of Co. 421.

Even between the two progenies of Co. 421 x spontaneum Coimbatore and Co. 421 x spontaneum Glagah, there is a marked difference as regards leaf sheath, ligule, leaf width, height and brix due to the influence of the different male parents. The hybrids of Co. 421 x spontaneum Coimbatore have glabrous leaf sheath while it is spiny in the hybrids of Co. 421 x spontaneum Glagah. The ligule is deltoid in the former case whereas it is cresentiform in the latter. The leaves are comparatively narrower, the height is shorter and the brix is higher in the hybrids Co. 421 x spontaneum Coimbatore than those of Co. 421 x spontaneum Glagah.

It seems from the observations made that Co. 421 gives rise to mostly thin types of seedlings either parthenogenetically or in the cross as seen above with spontaneums. In the year 1954-55 four crosses were effected using Co. 421 as mother and Co. 419, Co. 929, Co. 954 and P. 8331 as male parents. Most of the seedlings were thin (Table III) and showed 2n=86 chromosomes while the thick ones showed 2n=118, indicating their parthenogenetic origin.

TABLE III

Table showing per cent of thin seedlings.

Sl. No.	Year	Cross	No. of seedlings raised	Thick seedlings	Thin seedlings	Per cent of thin seedlings
1.	1954–55	Co. 421 × Co. 419	300	68	232	77%
2.	1954–55	Co. 421 × Co. 929	100	12	88	88%
3.	1954–55	Co. 421 × Co. 954	100	9	91	91%
4.	1954–55	Co. 421 × P. 8331	105	33	72	69%

DISCUSSION

For many years Co. 421 was crossed as a female parent using other Co. canes as staminate parents for evolving economical canes and the few selections from them were later on proved to be parthenogenetic ones and not a true cross. For example Co. 447, Co. 467, Co. 462, Co. 463, Co. 467, Co. 602, Co. 656 and Co. 779 are some of the Co. canes derived from Co. 421 and show 118 chromosomes in the somatic cells, the diploid chromosome number of Co. 421, thus revealing their non-hybrid nature. Hence it is evident that the cross-ability of Co. 421 as a female parent is very low the only known real hybrids are those that have been described in this paper.

Co. 421 gives rise to seedlings when dusted with pollen from other Co. canes or members of other genera such as Coix, Maize, Teosinte and bamboo. Seedlings are also got when Co. 421 is selfed. This shows clearly that parthenogenesis is almost the rule in Co. 421 as the seedlings obtained from the above cases are all non-hybrids as the cytological observations have shown. Several varieties of sugarcane that are pollen sterile are known to have given rise to parthenogenetic seedlings of such origin when selfed or dusted with pollen of distant genera (Janaki Ammal, 1941; Raghavan, 1953).

Even in parthenogenesis, the phenomenon of functioning of the female gamete with a number which is neither the haploid nor the diploid number of chromosomes is traceable to the peculiar feature of elimination of chromosomes en-bloc and subsequent endomitosis or fusion of the two lowermost cells of the megaspore mother cells. This sort of double process in parthenogenesis seems to be more common in Co. 421 and accounts for the thinness of most of the seedlings in the progeny.

As the majority of the mother cells seems to have the nucleus with chromosomes less than the diploid (86) or even the haploid number (43), it is natural to expect the egg with a lower number of chromosomes entering in fertilisation of a cross. Hybrids with 86 chromosomed egg are not met with so far but parthenogenetic derivatives having 2n=86 chromosomes are numerous. The hybrids between Co. 421 and spontaneum Coimbatore, Co. 421 and spontaneum Glagah dealt with in the present paper are genuineones resulting from the egg with 43 chromosomes, less than the haploid number of chromosoems.

of Co. 421, and the normal sperms of spontaneums in fertilisation. It is because of the functioning of the egg with 43 chromosomes, 16 chromosomes less than the normal haploid number 59, the resulting hybrids are all thin.

That parthenogenesis plays in sugarcane breeding a more important role than has hitherto been surmised, has already been indicated (Raghavan, 1956). The behaviour of Co. 421 in this regard seems to reinforce that view. All the seedlings so far got out of Co. 421 are known to be parthenogenetically derived. Even here it gives rise to comparably a few thick seedlings and a large proportion of thin seedlings, the latter being parthenogenetic derivatives preceded by chromosome elimination. Obviously, the few thick seedlings that got selected and allowed the status of Co. canes were diploid derivatives. Its low crossability in that it mostly functions parthenogenetically and the fact that even in parthenogenesis it is preceded by 'en-bloc' elimination of chromosomes resulting in thin seedlings, are the two facts that have to be kept in mind in using Co. 421 as a material for breeding economic types.

It is conceivable that among the few thick diploid derivatives, there may be some useful forms. The way in which the diploid egg is formed being a post-meiotic process, even though parthenogenetically formed, the seedlings show a reshuffling of chromosomes. Even so, it appears that Co. 421's usefulness as a breeding material appears to be circumscribed owing to these phenomena described in the paper.

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