CHROMOSOME MORPHOLOGY, MICROSPOROGENESIS AND POLLEN FERTILITY IN SOME VARIETIES OF COCONUT

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Critical cytogenetical and breeding investigations on coconut (*Cocos nucifera* L.) have been few. While breeding investigations are handicapped by the long life-cycle of the plant and its highly cross-pollinated nature (Patel, 1938; Menon and Pandalai, 1958), the small size of the chromosomes and technical problems connected with getting dividing cells with well-differentiated cytoplasm and nucleus render cytological studies difficult. Using microtome sections, Santos (1929) studied the development of the microspore and reported the chromosome number n=16 for coconut. This number has been subsequently confirmed by several workers (Janaki Ammal, 1945; Venkatasubban, 1945; Sharma and Sarkar, 1956).

With the evolution of the squash techniques together with the use of several efficient chemical pre-treatments, a detailed study of the morphology of somatic chromosomes has become relatively simple (Sharma and Sarkar, 1955; Nambiar and Upadhya, 1960). Squash techniques also help in getting good preparations of microsporocytes in various stages of meiosis (Nambiar and Swaminathan, 1960). A study of the morphology of somatic chromosomes and meiosis in pollen mother cells was hence undertaken in some varieties of coconut and the results are reported in this paper.

Materials and Methods

Three coconut varieties—Dwarf Red of local origin, Apricot, a semi-tall strain from the Straits Settlements and an ordinary tall variety of Laccadive islands, belonging to the varietal collection maintained at the Central Coconut Research Station, Kasaragod, were used in the present study. Dwarf Red and Apricot had, on an average, 30 per cent of sterile pollen as judged by stainability in acetocarmine. Laccadive ordinary, on the other hand, had practically all normal pollen (about 5 per cent sterility). For the study of meiosis, flower buds from the inflorescences of these trees were collected 50 to 60 days prior to the opening of the spathe and were fixed in Carnoy's solution (6 absolute alcohol:3 chloroform:1 acetic acid) for 3 hours. The optimum time for fixation was found to lie between 11 a.m. and 1 p.m. The buds were transferred from the Carnoy's mixture to propionic alcohol (1 part of propionic acid staturated with ferric acetate mixed with 3 parts of absolute alcohol). After 24 hours, the buds were transferred to 70 per cent alcohol and stored in a refrigerator. The fixations were made at Kasaragod and the material brought to New Delhi for study. The anthers from the fixed buds were rinsed in 45 per cent acetic acid and then placed for 3 to 5 minutes in a mixture of 5 parts of 45 per cent acetic acid, 4 parts of 45 per cent acetic acid saturated with ferric acetate and 1 part of 1 per cent formalin. This mordanting fluid helped in the intensification of staining. The anthers were then squashed in a drop of aceto-carmine or propino-carmine on a clean glass slide. Analysis was carried out in most cases in temporary preparations but some slides were made permanent for record purposes by passing them through grades of butyl alcohol and then mounting them in neutral balsam.

For the study of somatic chromosomes, the 8-hydroxyquinoline pre-treatment method of Tjio and Levan (1950) was found to be the best. Aesculine pre-treatment

recommended by Sharma and Sarkar (1955) did not give as consistent or as good results as the schedule of Tjio and Levan (1950). Treatment for 2-1/2 to 3 hours with 0·002 M 8-hydroxyquinoline followed by fixation and hydrolysis in NHCl and squashing in acetic-orcein gave preparations with well-spread chromosomes of considerable clarity (Nambiar and Upadhya, 1960). The root tips used in the study of somatic chromosomes were collected from the seedlings obtained from Kasaragod and grown at the I.A.R.I., New Delhi. The cells were in active mitosis between 12 noon and 1 p.m. during the months of October and November under Delhi conditions.

Experimental Results

I. *Somatic Chromosomes.*—Chromosome morphology was studied in an ordinary tall variety of Coconut. All cells with well-spread chromosomes were carefully drawn with a Camera-lucida and each chromosome from the drawings of 5 clear cells was measured carefully with the help of dividers. Measurements of chromosomes from each metaphase plate were then converted into relative lengths, i.e. the length of each chromosome expressed as a percentage of the total chromatin length of the complement. The chromosome index (short arm/long arm ratio) was also determined for every chromosome.

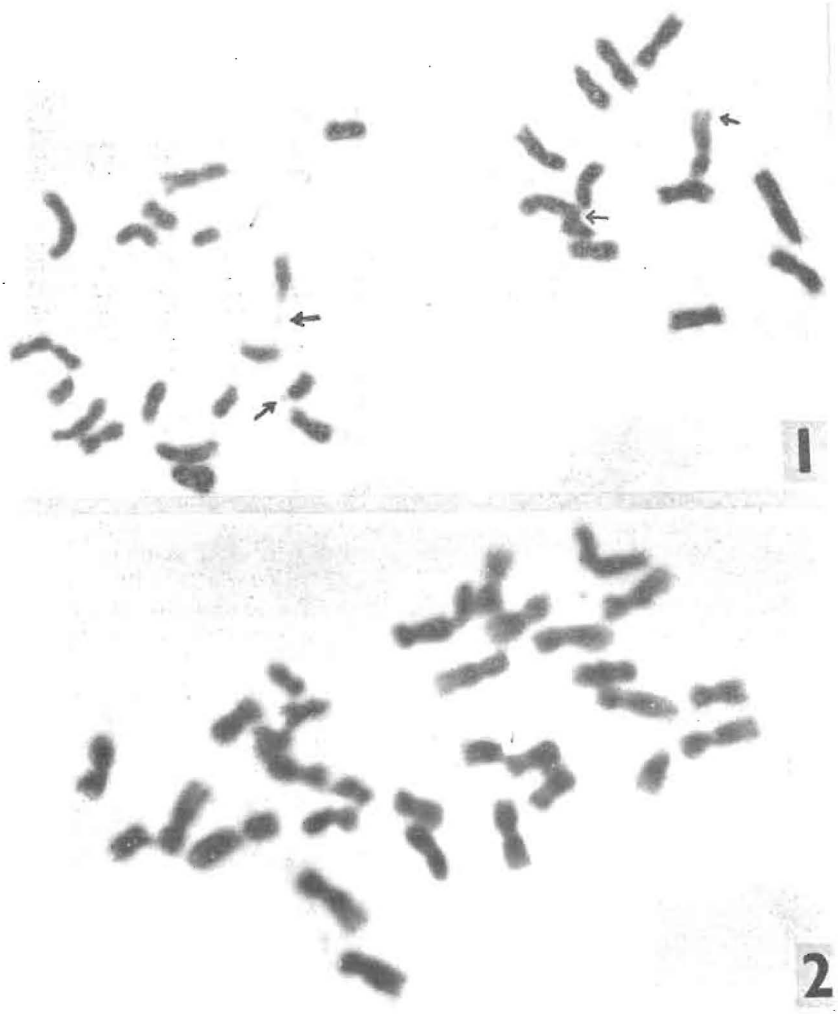
The values obtained from the 5 metaphase plates did not differ from each other appreciably and hence the mean value for each chromosome was used for preparing the idiogram (Text Fig. 1). In the satellite-bearing chromosomes, the length of the satellite/length of the arm bearing the satellite was used to determine the size of the satellite.

In the idiogram, the gap of the primary and secondary constrictions has been kept constant. By using the chromosome index and relative lengths, errors which may arise from possible differential contraction among the same chromosomes in different cells have been avoided. The data relating to the individual chromosomes are given in Table 1. Photomicrographs of two somatic metaphase cells are given in Figures 1 and 2.

Table 1

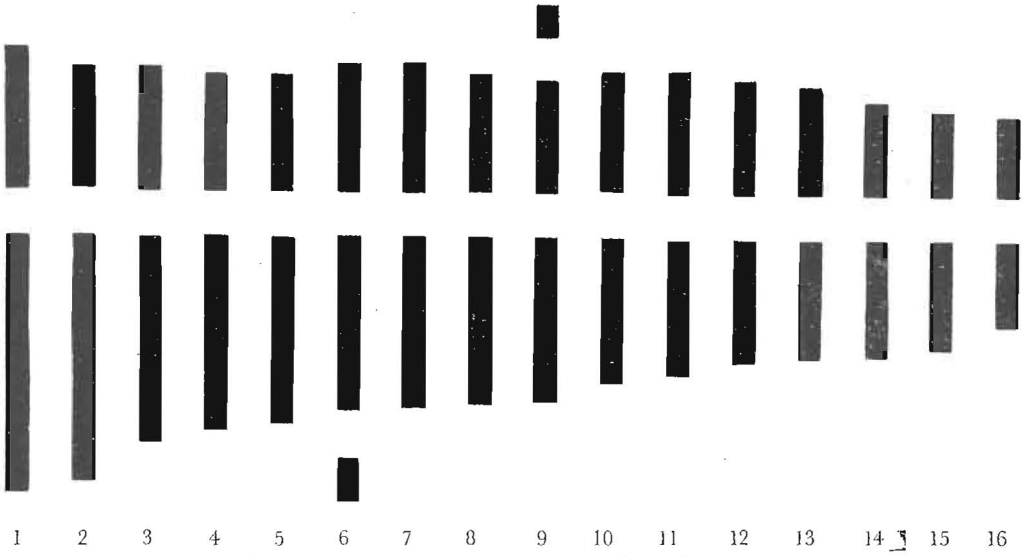
Relative length and index of the chromosomes of a Tall variety of Coconut

Chromosome No.	Relative length (in microns)			S.A./L.A. Index	Satellite	
	Long arm	Short arm	Total		R.L.	Index
1.	5·88	3·23	9·11	0·55		
2.	5·57	2·79	8·36	0·50		
3.	4·65	2·81	7·46	0·59		
4.	4·39	2·65	7·04	0·59		
5.	4·25	2·66	6·91	0·61		
6.	4·02	2·89	6·91	0·71	1·01	0·36
7.	3·87	2·93	6·80	0·74		
8.	3·82	2·67	6·49	0·68		
9.	3·76	2·58	6·34	0·66	0·76	0·27
10.	3·29	2·72	6·01	0·81		
11.	3·12	2·79	5·91	0·88		
12.	2·83	2·57	5·40	0·89		
13.	2·73	2·45	5·18	0·88		
14.	2·67	2·10	4·77	0·77		
15.	2·49	1·83	4·32	0·72		
16.	1·97	1·79	3·76	0·89		



FIGS. 1 & 2. Somatic chromosomes of a tall variety of coconut. The sat-chromosomes are marked with arrows.

A study of the idiogram (Text Fig. 1) an the data in Table 1 would show that (1) two pairs of chromosomes are much longer in comparison with the others; (2) two pairs bear satellites; (3) three pairs are relatively short and (4) all chromosomes have either sub-median or subterminal centromeres. The longer chromosomes were in general more heterobrachial than the shorter ones. The chromosomes bearing satellites occupied the 6th and 9th positions in order of the total chromosome length. The satellite was present on the long arm in chromosome VI, and on the short arm in chromosome IX. Sharma and Sarkar (1956) have also reported the presence of two pairs of sat-chromosomes in the coconut variety studied by them. They found that



TEXT FIG. 1. Idiogram of a tall variety of coconut.

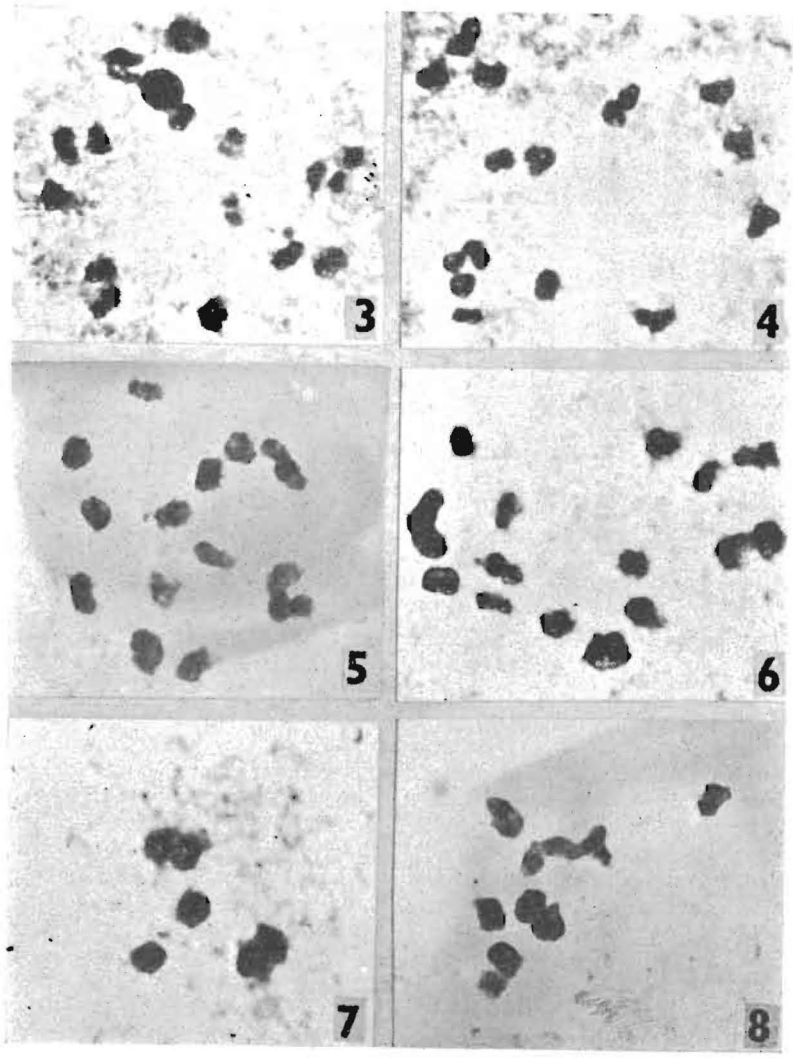
in these two pairs, the primary and secondary constrictions were nearly median and sub-median in position. This, however, was not found to be the case in the variety studied by us.

II. *Meiosis:* (a) *Laccadive ordinary.*—Meiosis was regular in this variety (Table2). There were 16 bivalents at diakinesis and MI (Figs. 3 to 5). Two bivalents were attached to the nucleolus at diakinesis. There were considerable size differences among the bivalents; one bivalent was particularly large and three others were small (Fig. 3). On an average, 77 per cent of the bivalents of a cell had chiasmata in both the arms and 23 per cent were of the rod type with a single chiasma in one of the arms. Among the ring bivalents, 8 per cent had 3 chiasmata each. Anaphase I and subsequent stages were normal. At the sporad stage, a cell with 5 spores was the only abnormality observed (Table 5).

TABLE 2

Chromosome associations at Diakinesis and MI

Variety and Tree No.	No. of P.M.C. studied	Mean frequency per cell		Mean No. of Xta	
		Quadrivalent	Bivalent	per cell	per bivalent
Apricot (X 1/62)	49	0·041	15·918	26·5	1·74
Dwarf Red (XI/75)	54	0·019	15·962	29·03	1·84
Laccadive Ordinary (XI/27)	51	..	16·00	30·57	1·91



FIGS. 3 to 5. Meiosis in Laccadive Ordinary.

FIG. 3. Diakinesis with 2 bivalents attached to the nucleolus. Note the difference in the size of the bivalents.
FIGS. 4 & 5. Metaphase I with 16 bivalents.

FIGS. 6 to 8 Meiosis in Apricot.

FIG. 6. Metaphase I. $1_{IV}+14_{II}$
FIG. 7. A cell with 6 bivalents.
FIG. 8. A cell with 10 bivalents.

(b) *Apricot.*—Besides microsporocytes with regular meiosis, several showing various types of abnormalities were also observed in this variety. In two cells at diakinesis and MI, one quadrivalent and 14 bivalents were observed (Fig. 6). The mean number of chiasmata per bivalent in this variety was lower than that recorded in Laccadive Ordinary (Table 2). The nucleolus, which normally disappears at the end of prophase and reforms at telophase, was found to persist in some cells both during MI and later stages (Figs. 9 and 10). Another interesting abnormality was the occurrence of microsporocytes with varying chromosome numbers in the same anther (Figs. 7 and 8). Such " chromosome mosaic " cells constituted 12·3 per cent of the cells studied at MI (Table 3) and should owe their origin to disjunctional abnormalities during pre-meiotic mitosis.

TABLE 3

Frequency of P.M.Cs with different Chromosome Numbers

Variety	No. of cells with n=					Percentage of Normal cells
	6	8	10	14	16	
Apricot ..	2	1	1	2	43	87.7
Dwarf Red ..					54	100
Laccadive Ordinary ..					51	100

At anaphase I, a dicentric bridge and an acentric fragment were observed in two cells, indicating heterozygosity for an inversion (Fig. 11). Lagging chromosomes were seen at anaphase I and micronuclei occurred at telophase (Table 4; Fig. 12). At the sporad stage, besides normal tetrads, sporads with 1, 5, 6, 7 and 8 spores respectively were also seen (Table 5; Figs. 13 and 14).

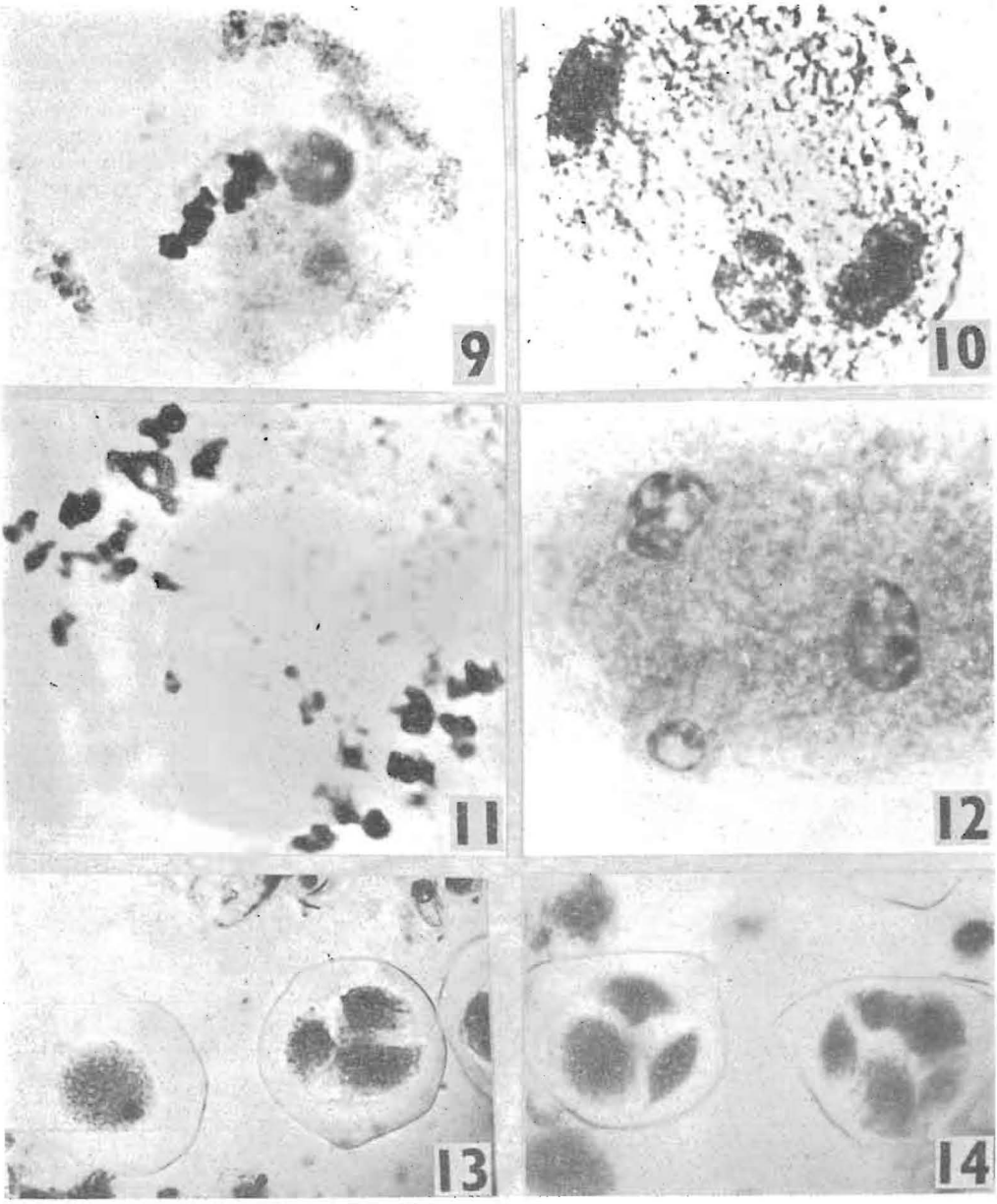
(c) *Dwarf Red.*—In this variety also, several cells with meiotic irregularities were observed. These included the occurrence of (a) one quadrivalent in a cell at MI; (b) inversion bridge at AI, (c) laggards at AI and micronuclei at Telophase I and II and (d) sporads each with 5, 6, 7 and 8 spores respectively (Tables 2, 4 and 5).

Persistent nucleoli and chromosome mosaic cells which were noted in Apricot were, however, not observed in this variety.

TABLE 4

Irregularities at AI and later stages

Variety	Stage	No. of P.M.Cs. studied	Normal P.M.Cs.	No. of cells with		
				Inversion bridge	Laggard	Micro-nuclei
Apricot ..	A-I	46	29	2	15	
	A-II	20	20	..	..	..
	T-I	30	21	..	..	9
	T-II	25	23	..	..	2
Dwarf Red ..	A-I	24	18	1	5	..
	A-II	25	25			
	T-I	25	23	..	..	2
	T-II	25	24	..	..	1



FIGS. 9 to 14. Meiosis in Apricot.

FIG. 9. Metaphase I with a persistent nucleolus.
FIG. 10. Telophase I with a nucleolus persisting in the plasm.
FIG. 11. Anaphase I with a dicentric bridge and an acentric fragment.
FIG. 12. A micronucleus.
FIG. 13. A monad and a tetrad.
FIG. 14. A triad and a pentad.

TABLE 5

Abnormalities at the sporad stage

Variety	No. of sporads studied	Monad	Tetrad	Pentad	Hexad	Heptad	Octad	% of normal sporads
Apricot ..	103	4	74	14	6	2	3	71·8
Dwarf Red Laccadive	214	0	197	8	4	4	1	92·1
Ordinary..	122	0	121	1	0	0	0	99·2

III. *Pollen fertility.*—The frequency of pollen which stain well with acetocarmine was calculated for trees of all the three varieties. Pollen fertility measured in this way was found to vary among the different inflorescences of a spadix and also with the season. However, from data collected over two years, it was clear that certain varieties always tended to possess a higher frequency of sterile pollen than the others. Thus, while Apricot and Dwarf Red had on an average only 70 per cent of well-stained pollen, Laccadive ordinary had over 95 per cent of such pollen. Apricot and Dwarf Red are, therefore, partially pollen sterile.

DISCUSSION

The karyotype of the coconut variety studied by us was characterised by a greater proportion of chromosomes with sub-median centromeres and a considerable difference in size between the largest and the smallest chromosomes of the set. From the meiotic observations as well as from the data of Sharma and Sarkar (1956), it seems likely that most varieties of *Cocos nucifera* may show these features in their karyotypes. The use of karyotype symmetry-asymmetry in the study of species evolution is well-known and in the Ranunculaceae, tribe Helleboreae, Levitsky (1931) showed that the most primitive species tend to have chromosomes possessing median centromeres and of nearly equal size. In order to study the possible connection between increasing asymmetry and other characteristics of the plants concerned, Stebbins (1958) has proposed a new classification of types of symmetry. Similar studies in the Tribe *Cocoineae*, to which *Cocos nucifera* belongs, may yield interesting information.

Varying degrees of pollen sterility have been reported by several workers in varieties of coconut. Patel (1938) found about 25 per cent of sterile pollen grains in six trees while Aldaba (1921) observed 3 to 33 per cent sterility in some varieties in the Philippines. Sharma and Sarkar (1956) have stated, without specifying the percentage of sterility and the name of the variety studied by them, that a high percentage of pollen sterility occurs in coconut. They have further suggested that the " high percentage of pollen sterility stands against the assumption that sexual reproduction becomes effective in the production of fruits, which are abundant in this

species ". Their suggestion that pollination in coconut may provide a stimulus for apomictic reproduction, however, finds no support in the results of the breeding experiments conducted at the coconut research centres in several countries. Aldaba (1921) has estimated that each male flower contains about 272 million pollen grains. Also, the extent of pollen sterility varies among the different flowers of an inflorescence and with the environmental conditions. Hence, for getting an estimate of pollen sterility in a tree it is necessary to carry out detailed quantitative studies over a period of time. In a study lasting for over two years, it was found that the varieties Apricot and Dwarf Red had on an average about 30 per cent pollen sterility while the variety Laccadive Ordinary had only 5 per cent sterility. It is thus clear that coconut trees belonging to different varieties show different degrees of pollen sterility.

A study of microsporogenesis showed that several abnormalities occurred in the varieties Apricot and Dwarf Red. Thus, there were cells with (a) one quadrivalent at diakinesis and metaphase I suggesting heterozygosity for a reciprocal interchange; (b) a dicentric bridge and an acentric fragment at anaphase I indicating heterozygosity for an inversion; (c) nucleoli which persist at metaphase and anaphase; (d) pollen mother cells with varying chromosome numbers; (e) lagging chromosomes at the first and second anaphase; (f) micronuclei at telophase and (g) sporads with varying number of spores. There was also a reduction in chiasma frequency in Apricot and Dwarf Red in comparison with Laccadive Ordinary. Meiosis was regular in Laccadive Ordinary, the only abnormality observed being a pentad at the sporad stage. The data thus suggest that aberrations during meiosis may be responsible for the pollen sterility observed in the varieties Apricot and Dwarf Red. From the occurrence of " chromosome mosaic " cells, it is obvious that abnormalities in cell division also occur during premeiotic stages. The frequency of cells with abnormalities as well as the types of aberrations found were more in Apricot, which is a semi-tall variety, than in Dwarf Red, a pure dwarf strain.

It is of interest that both Apricot and Dwarf Red have dwarf characteristics while Laccadive Ordinary is a tall variety. The dwarf coconut is small in stature and commences flowering as early as the third year after planting and comes to regular bearing in the ninth year. The origin of the dwarf varieties of coconut is not known with any degree of certainty, although several authors have suggested that the dwarfs might have arisen as mutants from the common tall plants (Menon and Pandalai, 1958). While the tall varieties are largely obligatorily cross-pollinated, the dwarfs can undergo self-pollination owing to the overlapping of the female and male phases in the same inflorescence. The various distinctive features of typical dwarf and tall varieties based on data from previous and the present studies are summarised in Table 6.

Because of the several undesirable features they possess, most coconut research workers have advised against the cultivation of dwarf palms on a plantation scale. Some dwarf lines seem to be more vigorous than others and some have good quality of copra but the general experience with dwarf varieties is not encouraging (Tammes, 1955). Crosses between the ordinary coconut and the dwarf varieties occur in nature and have also been made artificially. As a result, all gradations between the two contrasting categories outlined in Table 6 occur. In general, the hybrids have an early bearing habit, nuts of intermediate size and a cross-pollinating nature. Harland (1957) has suggested that the dwarf varieties, by virtue of their being largely self-pollinated and reasonably homogeneous, can be used for identifying the most prepotent males. Haldane (1958) has pointed out that if dwarfness is mainly due to a single gene, the introduction of this gene into the various races of coconut may be desirable since, in some important characters, the hybrids between tall and dwarf strains are superior to the tall parents.

TABLE 6

Contrasting characteristics of Tall and Dwarf coconut

Character	Tall palm	Dwarf palm
Height ..	.. 15 to 18 meters or more	5 to 10 meters
Years needed for first bearing ..	.. 8 to 10	3 to 5
Crowns ..	.. Large	Small
Plant parts ..	.. Large	Small
Vigour ..	.. Healthy	Weak
Pollination ..	.. Largely cross-pollinated	Largely self-pollinated
Average life ..	.. 80 to 90 years	35 to 40 years
Nuts ..	.. Large	Small
Appearance of copra	.. Good	Poor
Percentage of rubbery pieces in copra	.. 0–10	10 to 92
Nuts per picul of copra	.. 200-284	350 to 513
Pollen fertility	.. High	Varying degrees of sterility
Meiotic behaviour	.. Regular	Irregular

From our limited cytological studies, it would be premature to offer suggestions concerning the possible mode of origin of the dwarf palms. It is, however, difficult to refrain from comparing the cytological characteristics of the two semi-dwarf and dwarf varieties studied by us with the results reported in inbred rye by Lamm (1936), Prakken and Müntzing (1942), Müntzing and Akdik (1948) and Rees (1956). All these authors have clearly shown that the behaviour of the chromosomes is less efficient in inbred rye plants than in population plants. The unbalance caused by homozygosity in normally outbred populations may show up at the chromosomal level in different ways in different homozygotes. The occurrence of " chromosome mosaic " cells at meiosis and a poor development of the endosperm in dwarf coconuts suggests that the efficiency of the chromosome mechanism is affected in somatic, gametic and endosperm cells.

If further studies confirm our findings, it would appear that the dwarf and semi-dwarf coconuts occurring in nature are the products of various generations of inbreeding of the normal strains. The following two points appear to support this possibility. First, the tall and dwarf varieties differ in not one but a series of characters (Table 6), all of which seem to be the consequence of different degrees of reduced cell growth and aberrant cell division. Secondly, the F_2 progeny of a dwarf $\times$ tall cross gave a wide range of segregates and it was not possible to interpret the data on any simple genetic basis (Tammes, 1955). Distinct varieties of dwarf coconut occur in Malaya, Philippines, Fiji islands, Ceylon, Viet Nam and India. Also, trees with characters ranging between the two extremes described in Table 6 occur in these countries. It is possible that these dwarfs and semi-talls have arisen through inbreeding among different tall parents. In dwarfs which have attained equilibrium conditions with regard to growth characters inbreeding depression may not occur on selfing. Also, the wide extent of variability found among the dwarfs with regard to yield and quality of nuts would suggest that different varieties of coconut may respond to selfing in different ways.

It is of considerable interest that meiosis was more regular in the pure dwarf variety studied by us than in the semi-tall one. This suggests that meiotic aberrations may be relatively more frequent in early generation inbreds. It is possible that some of the stable and evolved dwarfs might have reached equilibrium conditions with regard to cytological behaviour also. While the results of the present study suggest that the dwarfs now occurring in nature might have evolved over a period of several thousand years through inbreeding among the normal coconut plants, an initial mutation, if any, responsible for their origin might be concerned with the bringing about of an overlapping of the male and female phases of the inflorescences thereby rendering self-pollination both possible and predominant. However, self-pollination can occur in the tall varieties during certain seasons (Patel, 1938; Dwyer, 1938) and a mutation facilitating this process is not a pre-requisite for inbreeding to occur. Alternatively, a situation analogous to that described by Harland (1955) in the maize strains of Trinidad may be responsible for the evolution of stable self-pollinating dwarfs.

Apart from the theoretical interest aroused by the question whether the dwarf palm owes its origin to inbreeding facilitated by the imposition of a self-pollinating device, or due to an one-step mutation, an understanding of the problem is extremely important from the breeding point of view. If the early bearing nature of the dwarf palms is only the consequence of a depressed vegetative vigour, the transference of this character through tall × dwarf crosses can probably be achieved only at the expense of the longevity and prolonged high productivity of the plant. This by itself may not be a serious handicap since by re-planting at more frequent intervals, a high yielding population can be maintained. On the other hand, if the dwarf palms represent homozygous genotypes evolved from tall strains as a result of inbreeding, there may be excellent scope for studying the manifestation of heterosis in crosses among distinct dwarf strains. Unfortunately, most of the breeding work carried out so far relates to only reciprocal crosses between tall and dwarf varieties or among tall strains. The only instance reported in literature of a cross between two distinct dwarfs is the one made by Marechal (1928) between a Malayan dwarf and N'uleka, a dwarf strain from the Fiji islands. The F_1 hybrids of this cross have shown outstanding performance and have been much sought after in Fiji (Parham, 1953). In the light of our studies, it seems desirable that this line of work should be taken up at coconut breeding centres without further loss of time. The technique suggested by Harland (1957) to identify prepotent males can be used to estimate the combining ability of different parents in dwarf × dwarf crosses.

Summary

1. The karyotype of a tall variety of coconut was studied using relative length, and arm ratio and the position and number of secondary constrictions as criteria for classification. A majority of chromosomes had sub-median centromere and there were considerable differences in length. Two pairs were satellited.

2. Microsporogenesis was studied in trees of Laccadive Ordinary, Apricot and Dwarf Red, which are tall, semi-tall and dwarf varieties of coconut respectively. Meiosis was regular in Laccadive Ordinary while irregularities such as heterozygosity for translocations and inversions, reduced chiasma frequency, persistent nucleoli, chromosome mosaic cells, lagging chromosomes at AI and AII, micronuclei at telophase and sporads with varying number of spores were observed in Apricot and Dwarf Red. The frequency of aberrant cells was higher in Apricot.

3. Laccadive Ordinary, Apricot and Dwarf Red had on an average 5, 30 and 30 per cent of sterile pollen respectively in studies carried out over a period of two years.

4. The cytological behaviour of the semi-tall and dwarf varieties resembles that of inbred rye. It is suggested that the dwarf coconut may owe its origin to inbreeding facilitated by the imposition of a self-pollinating device. The dwarf palms may, therefore, offer excellent material for evolving high yielding hybrid trees. The only instance of a cross between two distinct dwarfs reported in the literature supports this view.

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