Cytology of Coconut

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Abstract

The chromosome number in coconut is $2n=32$. Karyomorphological studies show slight differences between Tall and Dwarf varieties. Meiosis was generally regular in Tall cultivars and in hybrids between Tall and Dwarf, while several irregularities have been reported in the Dwarf and semi-tall cultivars. Pollen fertility is very high in Talls and hybrids as compared to that in Dwarfs and semi-talls. Meiotic irregularities are commonly met within the 'spicata' palms and these are believed to have originated from Talls.

Free nuclear division has been reported in coconut milk. C-mitosis leading to high ploidy level and several chromosome abnormalities occur in developing endosperm. In Philippines 'makapuno' nuts, the endosperm development is very abnormal. An inverse relationship between ploidy level and oil content has been also observed by some authors.

The two existing views on the origin of Dwarfs from Talls, namely, mutant origin or by continuous inbreeding, are presented. Another possibility that both Talls and Dwarfs might have had a common origin in a single ancestral form has been proposed.

Introduction

Cytological studies on coconut are few, though the palm is of great economic importance and has been used by man from time immemorial. The first report appeared in 1929 when Santos reported the gametic number of a Philippine coconut variety to be 16. Subsequently, reports on chromosome number have been published by several workers (Janaki Ammal, 1945; Venkatasubban, 1945; Sharma and Sarkar, 1956; Ninan, Pillai, and Joseph, 1960; Abraham, Mathew, and Ninan, 1961). Their studies and those that followed have confirmed the somatic number of coconut to be $2n=32$ (Nambiar and Swaminathan, 1960; Swaminathan and Nambiar, 1961; CCRS Annual Report, 1962-63; Raveendranath and Ninan, 1973). Nambiar and Upadhyaya (1961) outlined a pretreatment staining procedure—fixing—for the study of coconut root cells.

The review is divided into three parts, karyomorphology, meiotic

studies, and endosperm cytology, along with a concluding section on cytological evidences on the origin of Dwarf coconuts.

Karyomorphology

Nambiar and Swaminathan (1960) found that the majority of chromosomes in Tall palms had sub-median centromers and that they differed considerably in length. In the West Coast Tall (WCT) variety, two pairs of chromosomes were much longer and three pairs relatively short. They observed two satellited chromosome pairs, the satellites occurring on the long arm of chromosome VI and short arm of chromosome IX. Sharma and Sarkar (1956) also observed two pairs of SAT-chromosomes in the coconut variety studied by them. Raveendranath and Ninan (1963) compared the karyotypes of WCT, spicata, Chowghat Dwarf Green (CDG), and Chowghat Dwarf Orange (CDO) and found that the main distinguishing feature between the karyotypes of Tall and Dwarf forms was the presence of the secondary construction in Talls, on the long arm of chromosome VI, while in Dwarfs, on the long arm of chromosome III. But, this stated difference does not seem to be consistent. In the material studied in our Institute, chromosomes VI and XII were found to be satellited (Ann. Rep. 1962-63; 1973). The total length of the chromosome complement was higher in CDG than in WCT. Table 1 gives the comparative features of the WCT and CDG karyotypes.

TABLE 1. Relative length and index of the chromosomes of WCT and DG varieties*

Chr. no.	WC Tall		Dwarf Green	
	Relative length (in microns)	S.A./L.A. (index)	Relative length (in microns)	S.A./L.A. (index)
I	9.11	0.55	8.92	0.60
II	8.36	0.50	8.38	0.58
III	7.46	0.59	8.06	0.60
IV	7.04	0.59	7.28	0.58
V	6.91	0.61	7.04	0.65
VI	6.91	0.71[1]	6.80	0.72[3]
VII	6.80	0.74	6.58	0.65
VIII	6.49	6.68	6.43	0.71
IX	6.34	0.66[2]	5.80	0.74
X	6.01	0.81	5.80	0.80
XI	5.91	0.88	5.58	0.79
XII	5.40	0.89	5.37	0.75[4]
XIII	5.18	0.88	5.03	0.74
XIV	4.77	0.77	4.53	0.76
XV	4,32	0.72	4.23	0.80
XVI	3.76	0.89	3.97	0.83

*WCT data from Nambiar and Swaminathan (1960); DG data from Thankamma Pillai and Vijayakumar (unpublished).

[1]Satellite on the long arm.

[2]Satellite on the short arm.

[3]Satellite on the short arm.

[4]Satellite on the long arm.

Meiotic Studies

Nambiar and Swaminathan (1960) and Nambiar, Thankamma Pillai, and Vijayakumar (1970) observed significant differences in the meiotic behaviour between different cultivars of Tall and Dwarf forms, and between open pollinated and inbred populations. WCT and Laccadive Ordinary, another Tall cultivar, showed normal meiosis. Nambiar and Swaminathan (1960) observed many meiotic abnormalities in the cultivars Apricot and Dwarf Red.

Pachytene analyses conducted by the two senior authors on CDG showed that it had 7 subterminal, 7 submedian, and 2 median chromosomes. The short arm of chromosome VI and long arm of chromosome XII have nuclear organizer regions (Ann. Rep. CPCRI. 1973). This observation differs from that of Nambiar and Swaminathan (1960) on Talls and Raveendranath and Ninan on Dwarfs (1973). Thankamma Pillai and Vijayakumar (unpublished data) studied the meiosis of nine cultivars and hybrids (Table 2) and found that percentage of abnormalities was highest in Dwarf Green and Dwarf Orange. In D × T and T × D hybrids, chromosome abnormalities and sterility were very slow. The higher chromosome abnormalities and sterility in Dwarfs may be due to the higher degree of inbreeding in them. Nambiar et al. (1970) have also studied the cytology of open pollinated and inbred lines (also Ann. Rep. CPCRI, 1971).

Spicata are Tall palms differing from ordinary Talls in inflorescence character and breeding behaviour. They produce unbranched inflorescences and show a high degree of suppression of male flowers. Their cytology has been studied by Ninan and his coworkers (Ninan et al., 1960; Ninan and Satyabalan, 1963; Ninan and Nambiar, 1974). The meiosis was irregular with inversions, translocations, and many other abnormalities. Like Talls, spicata palms are predominantly outbreeders. They are believed to have arisen from Talls through mutation. However, Child (1974) considered spicata as a distinct variety because of the existence of a Dwarf form also.

In addition to the above studies on karyomorphology and meiosis, there have also been reports on the cytology of an abnormal palm (Thankamma Pillai and Vijayakumar, 1972), on palms affected with root (wilt) disease (Nambiar and Prasannakumari, 1964) and also on a bulbiferous palm (Raveendranath, Nair, and Ninan, 1975), Parthenogenesis was also known to occur (Venkataraman, 1928). The only report on haploidy was by Whitehead and Chapman (1962) who isolated a haploidy seedling from 31 twin seedlings raised by them. Ninan and Raveendranath (1965) has observed a haploid embryo in a WCT palm.

Endosperm Cytology

As early as in 1927 Quisumbing and Juliano studied the development of the ovule and the embryosac in coconut. The development of the endo-

TABLE 2. Meiotic behaviour of some varieties and hybrids

Cultivar/ hybrid	Chiasma frequency		Percentage of irregularities at				Percentage of pollen sterility (non-stainability)
	per cell	per bivalent	Diakinesis and Metaphase	Anaphase I & II	Telophase I & II	Sporad stage	
WC Tall	28.9	1.8	6.4	1.9	0.3	0.7	3.6
Laccadive Ordinary	27.6	1.7	7.6	1.8	1.7	0.9	3.5
Andaman Giant	28.5	1.8	4.9	2.1	2.5	1.0	3.0
CDG	26.8	1.7	26.1	8.5	6.6	9.4	32.2
CDO	27.1	1.7	19.6	7.9	5.1	6.6	21.9
T×D hydrid	28.5	.8	6.8	1.8	1.3	0.8	2.9
D×T hybrid	27.6	1.7	10.3	2.8	2.6	2.5	7.8

sperm has been described in detail by Cutter and coworkers (Cutter, Wilson, and Dube, 1952 a, b; Cutter and Freeman, 1854; Cutter, Wilson, and Freeman, 1955). They made interesting observations on the occurrence of free nuclei in the liquid syncytial endosperm commonly known as coconut milk. Free nuclear divisions in the coconut water have also been reported by Dutt (1953) and Abraham and Thomas (1962). But biochemical analysis of coconut water by Mondal, Mandal, and Biswas (1970a, b) did not support the above view on the presence of free nuclei.

Abraham and coworkers (Abraham and Mathew, 1963; Abraham, Ninan, and Gopinath, 1966) noted that in about 6 month old nuts, the nuclei of the developing endosperm tissue varied considerably in size. They found that the tissue adjacent to the endothelium was normally triploid ($3x=48$), less frequently hexaploid ($6x=96$), and still less frequently dodecaploid ($12x=192$). They proposed that higher ploidy levels arose by c-mitosis. They also recorded an inverse relationship between ploidy levels of endosperm and oil content. In the Tall variety, the outer, middle, and inner parts differed in the oil content, the percentage being 75.7, 54.1 and 41.1, respectively. They analysed Laccadive Tall, S.S. Apricot, CDG, CDO, and Philippine makapuno nuts and found that the last one had the lowest oil content and also the highest ploidy level (Abraham, 1963; Abraham et al., 1965).

The Philippine makapuno coconuts are peculiar in having loose jelly like endosperm filling the entire cavity. They do not germinate and this is ascribed to an incompatibility reaction between a normal embryo and abnormal endosperm (Abraham et al., 1965). These authors reported high ploidy levels ($48x$ and above) in the buttery endosperm which according to them arose through amitosis and nuclear fusion. Cruz and Ramariz (1968) found two types of cells in this endosperm, normal cells and microcells. They thought that the latter originated from normal cells through budding. Chromosome counts ranged from 32 to 96 ($2x$ to $6x$) with 48 as the most frequent number.

Recently, de Guzman and colleagues have succeeded in culturing the embryo from these nuts on artificial medium and have reported a high recovery of makapuno character (de Guzman, 1969; Balaga and de Guzman, 1970; de Guzman and del Rosario, 1974; de Guzman, Rafols, and del Rosario, *this Symposium*).

Cytological Evidence on the Origin of Dwarf Coconuts

Two hypotheses have been advanced to explain the origin of Dwarfs. The first one considers Dwarfs to have evolved by a recessive mutation from Talls (Handover, 1919; Anonymous, 1921; Jack and Sands, 1922; Pancho, 1960). According to the second hypothesis, the Dwarfs and semi-Talls occurring in nature are the products of several generations of inbreeding of Tall palms (Nambiar and Swaminathan, 1960; Swaminathan and Nambiar, 1961).

Comparative studies on the meiosis of Talls and Dwarfs (Sharma and Sarkar, 1956; Nambiar and Swaminathan, 1960; Ninan et al., 1961; Abraham et al., 1961; Ann. Rep. CPCRI, 1972, 1973) reveal that meiosis in the former was more normal. It was therefore assumed that the Talls were the ancestral types, and that the Dwarfs, semi-Talls, and spicata were the derived ones. In support of this, it has been pointed out that the Philippine Dwarf palm Tambulilid is known to be of recent mutant origin (Pancho, 1960).

One criticism that can be levelled against the hypothesis on the origin of Dwarfs from Talls by a process of inbreedin is that in many Pacific Islands, natural inbreeding isolated populations of coconut have been existing for thousands of years. If continued inbreeding leads to Dwarfs, we would expect predeminantly Dwarf populations in these areas. But this is not the case (Whitehead, 1966). There are also no cytological morphological, or genetical evidences to prove such a hypothesis, Moreover, some Dwarfs, such as the Fijian Dwarf, are highly heterogeneous and generally outbreeders. These conditions should not happen if the origin of Dwarfs has been through continuous inbreeding. It is therefore possible that both Talls and Dwarfs had a common origin from a single ancestral form and they underwent a certain degree of divergence during the course of evolution. The Dwarfs have got definite adaptive value in its early seed bearing habit, and greater seed production. In the course of domestication and co-existence much natural crossings might have taken place leading to the establishment of intermediate populations and the present day cultivated Dwarfs. Experimental verification of any of these hypotheses is not easy in a species like coconut, and much more basic studies are required before we can arrive at an acceptable conclusion on the origin of Dwarfs.

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Discussion

B.R. Murthy : What is the comparative cytology of (a) Dwarfs obtained from Tall palms ; (b) Dwarfs obtained by inbreeding; and (c) different Dwarfs varieties and their crosses ?

Ravindran : There are no conclusive data on these. (a) Cytology of the Dwarf segregants of a Tall palm has been reported. They had very high degree of meiotic abnormalities and pollen sterility of 43%. (b) We have not come across any information on this, (c) Cytology of different Dwarfs like those from India and Malaysia have been studied. However, data on the cytology of D×D hybrids are not available.