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CYTOGENETICS OF ARECA CATECHU L., A. TRIANDRA ROXB. AND THEIR F_1 HYBRIDS (PALMAE)

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Meiotic observations on two cultivars of *A. catechu*, three ecotypes of *A. triandra* and their hybrids are presented. Intracultivar variation for meiotic behaviour was very high in *A. catechu*. In spite of the high degree of multivalent associations observed in *A. catechu*, pollen fertility was high. The possibility of the frequency of multivalent formation being under genotypic control and being subjected to selection has been indicated.

Chromosome pairing in *A. triandra* and *A. catechu-A. triandra* hybrids revealed that partial desynapsis occurs to varying degrees in both. The higher number of univalents in the hybrids is inferred to be the result of non-homology of certain of the parental chromosomes. The increase in pairing at metaphase I in *A. triandra* and *A. catechu* × *A. triandra* has been attributed to 'distributive pairing'.

The pollen sterility in *A. triandra* is believed to be caused by meiotic abnormalities at various stages. The higher percentage of meiotic abnormalities of one of the parental species, the disharmonious interaction between the genotype of one and the cytoplasm of the other and unbalanced gene combinations appeared to be the possible cause of the high sterility in the hybrids.

It is concluded that there is considerable homology between the chromosomes of *A. catechu* and *A. triandra*. The possibilities of transferring mite resistance and larger number of female flowers from *A. triandra* to *A. catechu* through interspecific hybridisation and back-crossing have been indicated.

Introduction

The genus *Areca* is a habitant of the tropical belt and is widely distributed from the Solomon Is. in the east to the Malagasy Republic in the west (Furtado, 1933; Corner, 1966). Among the species known in the genus, *A. catechu*, the only cultivated species has received some attention of the botanists and cytologists, while other species have not so far been investigated to any appreciable extent. Cytological work in the genus till now, has been confined to the reporting of chromosome numbers, their morphology, and meiotic analysis of a few cultivars of *A. catechu* (Venkatasubban, 1945; Sarkar, 1956; Sharma & Sarkar, 1956; Raghavan, 1957, Bavappa & Raman, 1965) and another species *A. triandra* (Sharma & Sarkar, 1956; Bavappa & Raman, 1965). The present paper deals with the meiosis of two cultivars of *A. catechu*, three ecotypes of *A. triandra* and their hybrids.

Material and methods

Microsporogenesis in two cultivars of *A. catechu* (Local and China), three ecotypes of *A. triandra* (Ceylon, Mauritius and Indonesia), four *A. catechu* × *A. triandra* (Local × Ceylon and Local × Mauritius) and one spontaneous hybrid involving *A. catechu* China as the mother palm was investigated. The palms studied in the two species included the actual parents of the hybrids.

For the study of meiosis, the infrafoliar inflorescence was split open about 90 days prior to leaf fall, to expose the enclosed male flowers. The flower buds were fixed in Carnoy's fluid (6 parts ethyl alcohol, 3 parts chloroform, 1 part acetic acid) for 24 hours and squashed in acetocarmine. Samples of flower buds were fixed from various positions of the inflorescence in individual palms at one hour interval and

Table 1

Chromosome association at diakinesis and metaphase I in *A. catechu*, *A. triandra* and their hybrids

Palm	Diakinesis						Metaphase I						
	No. of PMCs observed	Above quadrivalent Mean	IV Range (Mean)	III Range (Mean)	II Range (Mean)	I Range (Mean)	No. of PMCs observed	Above hexavalent Mean	VI Range (Mean)	IV Range (Mean)	III Range (Mean)	II Range (Mean)	I Range (Mean)
A. catechu													
Local (471)	82		0-2 (0.67)		12-16 (14.66)		53	0.02X + 0.08VIII	0-2 (0.17)	0-5 (0.60)	0-2 (0.16)	4-16 (13.59)	0-2 (0.08)
Local (717)	100				11-16 (15.64)	0-10 (0.72)	87					15-16 (15.96)	0-2 (0.08)
China (111)	82	0.01VI	0-2 (0.15)		12-16 (15.55)	0- 4 (0.24)	63		0-1 (0.02)	0-2 (0.16)		9-16 (15.62)	
China (173)	80		0-2 (0.24)	0-1 (0.01)	12-16 (15.45)	0- 2 (0.11)	43		0-1 (0.02)	0-2 (0.21)		13-15 (15.52)	
A. triandra													
Ceylon-3 (55)	55				8-16 (12.68)	0-14 (6.64)	84				0-1 (0.01)	14-16 (15.73)	0-2 (0.51)
Ceylon-3 (70)	80				6-16 (13.74)	0-20 (4.52)	76					13-16 (15.71)	0-6 (0.58)
Ceylon-3 (87)	96		0-1 (0.03)		7-16 (12.85)	0-18 (6.18)	66					8-16 (14.65)	0-16 (2.70)
Mauritius (109)	49			0-1 (0.06)	5-16 (12.12)	0-22 (7.58)	71				0-2 (0.10)	4-16 (13.46)	0-24 (4.78)
Indonesia-2 (154)	38				4-15 (11.05)	1-24 (9.90)	36			0-1 (0.03)	0-1 (0.03)	8-16 (14.59)	0-16 (2.41)
A. catechu × *A. triandra*													
Palm No. 248	107	0.01VIII + 0.01VI + 0.01IV	0-2 (0.10)	0-3 (0.40)	2-14 (8.92)	0-28 (12.37)	61		0-1 (0.02)	0-1 (0.02)	0-2 (0.12)	5-16 (14.07)	0-10 (3.30)
Palm No. 287	90			0-1 (0.08)	0-16 (11.24)	0-32 (9.28)	114				0-1 (0.06)	10-16 (14.83)	0- 9 (2.16)
Palm No. 288	82		0-1 (0.13)	0-1 (0.05)	8-16 (14.34)	0-14 (2.65)	81			0-1 (0.09)	0-1 (0.06)	11-16 (15.33)	0- 6 (0.90)
Palm No. 307	65				1-16 (10.34)	0-30 (11.32)	97				0-1 (0.01)	13-16 (15.73)	0- 6 (0.51)
Spontaneous hybrid	57		0-1 (0.04)	0-1 (0.09)	4-16 (9.90)	5-24 (11.77)	39				0-1 (0.05)	11-16 (14.33)	0-10 (3.19)

observations from each anther was kept separately to find out within palm variations in microsporogenesis. Maximum dividing PMC's were obtained in the flower buds fixed between 10.30 AM and 11.30 AM.

For assessing pollen fertility, flowers from the middle of the rachilla were collected and anthers which were about to dehisce, squeezed in 1 per cent acetocarmine glycerine (1 : 1). Unstained and shrivelled pollen grains were considered as sterile.

Results

A. catechu

Variation in chromosome pairing was observed not only between the two cultivars Local and China of *A. catechu*, but also between the palms No. 471 and No. 717 belonging to the same cultivar (Local) (Tab. 1). Within-individual variation was also studied but found to be significantly smaller than between-individual variation. While a maximum association of 1 X + 1 IV + 9 II (Fig. 1) was observed in palm No. 471, palm No. 717 had a maximum association of bivalents only (Fig. 2). A maximum of five quadrivalents were observed in the former in about 2 per cent of the PMCs. Abnormalities like bridges, laggards and disorientation of chromosomes were observed in 9.1% and 10.7% of the cells at the anaphase I and anaphase II respectively in this palm. The pollen stainability was 95.4%.

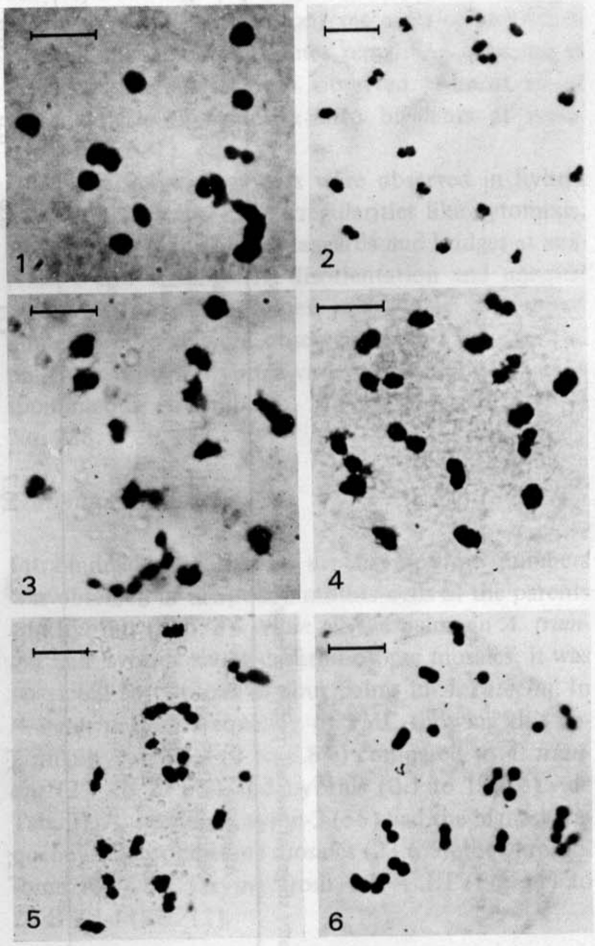
Though the later stages of meiosis were also comparatively normal in palm No. 717, the pollen stainability was only 82.7 per cent (Tab. 2).

Chromosome pairing in the two palms belonging to the cultivar China was almost similar (Tab. 1). Configurations of hexavalents and quadrivalents were observed in both (Fig. 3). Anaphase separation was normal in palm No. 111. But laggards and disorientation of chromosomes were noticed in 6.3 per cent and 4.8 per cent of the cells at anaphase I and anaphase II respectively in palm No. 175 (Tab. 2). The abnormalities observed at tetrad stage and pollen stainability are given in Table 2.

A. triandra

Meiotic observations in three palms belonging to *A. triandra* Ceylon-3 showed that maximum association of only bivalent occurs in palm No. 70 (Fig. 4) and trivalents and quadrivalents in palm No. 55 and 87 (Fig. 5) respectively.

Partial desynapsis of chromosomes was observed in all the palms at diakinesis, the maximum being 20 chromosomes unpaired in palm No. 70 (Tab. 1). Desynapsis observed at diakinesis was followed by an increase in pairing at metaphase-I as reflected by the frequency of bivalents (Tab. 1). At metaphase-I stickiness of chromosomes and cytomixis were observed in all the palms. The details of laggards at anaphase-I and -II, unequal separation of chromosomes,



Figs. 1-6. Microsporogenesis in *A. catechu* (1-3) and *A. triandra* (4-6): (1) Diakinesis (471), 1 X + 1 IV + 9 II; – (2) Early M I (717), 16 II; – (3) Diakinesis (111), 1 VI + 13 II; – (4) Diakinesis (70), 16 II; – (5) Diakinesis (87), 1 IV + 13 II + 2 I; – (6) M I (109), 1 III + 13 II + 3 I. Bars represent 10 μm.

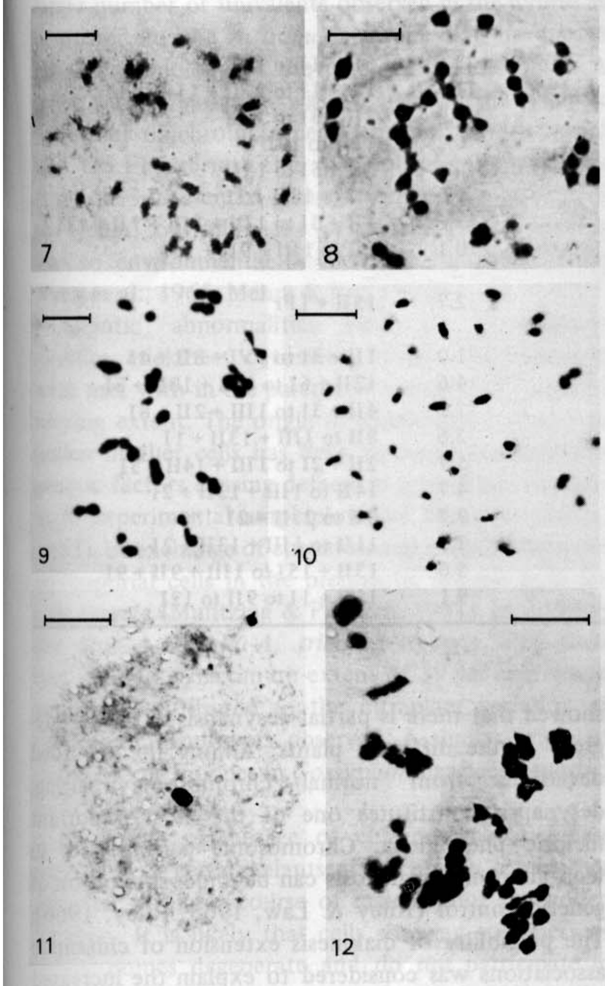
Table 2

Abnormalities at later stages of meiosis, pollen fertility, and nut set in *A. catechu, A. triandra* and their hybrids

Species or hybrid	Anaphase I		Anaphase II		Tetrads						Pollen fertility	Nut set
	Number of cells observed	Cells with bridges, laggards and disorientation (%)	Number of cells observed	Cells with bridges, laggards and disorientation (%)	Number of cells observed	Micronuclei (%)	Monads (%)	Diads (%)	Triads (%)	Super numerary spores (%)	(%)	(%)
A. catechu												
Local (471)	121	9.1	84	10.7	171	0.0	0.0	0.0	12.3	0.0	95.4	26.4
Local (717)	123	11.4	67	1.5	144	0.8	0.0	1.4	2.0	0.0	82.7	36.9
China (111)	163	0.6	70	0.0	67	0.0	0.0	0.0	3.0	0.0	98.2	42.2
China (175)	95	6.3	63	4.8	106	0.0	0.0	2.8	10.4	0.0	95.7	12.0
A. triandra												
Ceylon-3 (55)	148	26.4	81	11.1	178	1.7	0.5	1.7	2.8	0.0	75.5	36.4
Ceylon-3 (70)	110	8.2	67	1.5	140	0.0	0.0	0.7	12.9	0.7	65.4	42.1
Ceylon-3 (87)	106	17.9	77	15.6	147	4.1	0.0	0.7	13.6	2.7	63.3	28.1
Mauritius (109)	44	29.5	41	26.8	175	14.9	1.7	4.6	6.8	0.0	33.1	33.8
Indonesia-2 (154)	80	18.8	57	24.6	164	1.8	1.2	0.0	4.3	0.0	45.2	41.3
A. catechu × *A. triandra*												
Palm No. 248	89	69.7	44	52.3	137	22.6	0.0	2.2	16.1	2.9	3.7	0.5
Palm No. 287	109	14.7	117	16.2	148	4.7	0.0	0.7	8.8	0.0	0.5	0.3
Palm No. 288	87	29.9	93	26.9	185	4.6	0.0	3.2	11.8	4.8	8.3	0.0
Palm No. 307	46	71.7	80	37.5	133	10.9	0.7	0.4	2.3	0.4	6.1	0.0
Spontaneous hybrid	71	46.5	66	31.8	143	12.6	6.3	9.8	15.4	0.0	0.1	0.0

micronuclei at tetrad stage and supernumerary spores observed are given in Table 2.

The chromosome pairing in two other *A. triandra* ecotypes, Mauritius (109) and Indonesia-2 (154), also showed a similar pattern as described above, with a maximum association of trivalents in the former (Fig. 6) and quadrivalents in the latter. Compared to Ceylon-3, the degree of desynapsis was higher with a maximum of 24 chromosomes remaining unpaired at diakinesis in both (Tab. 1; Fig. 7). Increased pairing at metaphase I, as reflected by a decrease in univalent numbers were observed in these ecotypes also (Tab. 1). Details of abnormalities at later stages of meiosis are given in Table 2. The pollen fertility in *A. triandra* ecotypes varied from 33.1% in Mauritius (109) to 75.5% in Ceylon-3 (55).



Figs. 7-12. Microsporogenesis in *A. triandra* (7, 11, 12) and *A. catechu* × *A. triandra* (8-10): (7) Diakinesis (109), 4 II + 24 I; – (8) Diakinesis (248) 1 VIII + 1 V + 1 III + 5 II + 6 I; – (9) M I (Spontaneous hybrid), 1 IV + 11 II + 16 I; – (10) Diakinesis (287), 1 II + 30 I; – (11) PMC (55), 1 II + 1 I; – (12) PMC (55), 27 II + 1 I. Bars represent 10 μm.

A. catechu × *A. triandra*

The chromosome pairing showed a maximum association of one octovalent in hybrid No. 248 (Fig. 8), quadrivalents in hybrid No. 288 and the spontaneous hybrid (Fig. 9) and trivalents in No. 287 and 307. Desynapsis was observed in all the hybrids as in the case of *A. triandra* parent palms, but to an increased extent (Tab. 1; Fig. 10). Extreme cases of desynapsis with all the 32 chromosomes remaining unpaired at diakinesis have also been observed. Almost all of these univalents associate into bivalents at metaphase I (Tab. 1).

Chromosome fragments were observed in hybrid Nos. 248, 287 and 307. Irregularities like cytomixis, stickiness at metaphase I, laggards and bridges at anaphase I and anaphase II, disorientation and unequal separation of chromosomes, micronuclei and supernumerary spores were observed in all (Tab. 2). The pollen fertility in hybrids varied from 0.1 per cent in spontaneous hybrid to 8.3 per cent in hybrid No. 288.

Chromosome mosaics

Intra-individual variation in chromosome numbers was observed in the pollen mother cells of the parents and hybrids (Tab. 3). While all the palms in *A. triandra* and hybrids showed chromosome mosaics, it was restricted to two out of four palms in *A. catechu*. In *A. catechu*, the frequency of PMC showing this abnormality was less (0 to 6.8%) compared to *A. triandra* (2.7 to 23.6%) and hybrids (0.1 to 13.0%) vide Tab. 3). *A. triandra* Ceylon-3 (55) had the highest frequency of chromosome mosaics (23.6%), the chromosome numbers varying from 1 II + 1 I (Fig. 11) to 27 II + 1 I (Fig. 12).

Discussion

Study of meiosis in two cultivars of *A. catechu* showed that there was considerable intracultivar

Table 3

Intra-individual variation in chromosome number ar meiosis in *A. catechu*, *A. triandra* and their interspecific hybrids

Species or Hybrid	Meiotic stage	Number of PMCs observed	Number of PMCs with chromosome mosaic	Percentage	Range of chromosome association
A. catechu					
Local (471)	Diak.	82	–	–	–
	M I	53	–	–	–
Local (717)	Diak.	102	2	2.0	15 II
	M I	87	–	–	–
China (111)	Diak.	88	6	6.8	6 II to 1 IV + 13 II
	M I	66	3	4.5	6 II to 15 II
China (175)	Diak.	80	–	–	–
	M I	43	–	–	–
A. triandra					
Ceylon-3 (55)	Diak.	72	17	23.6	5 II + 1 I to 17 II
	M I	98	14	14.3	1 II + 1 I to 27 II + 1 I
Ceylon-3 (70)	Diak.	87	7	8.0	8 II + 3 I to 15 II
	M I	81	5	6.2	12 II to 19 II
Ceylon-3 (87)	Diak.	103	7	6.8	5 II + 5 I to 15 II
	M I	73	7	9.6	2 II to 18 II + 1 Fr
Mauritius (109)	Diak.	56	7	12.5	4 II + 3 I to 1 IV + 1 III + 7 II + 13 I
	M I	79	8	10.1	7 II to 1 III + 9 II + 13 I
Indonesia-2 (154)	Diak.	38	–	–	–
	M I	37	1	2.7	15 II + 1 Fr
A. catechu × *A. triandra*					
Palm No. 248	Diak.	119	12	1.0	1 II + 3 I to 1 VI + 8 II + 4 I
	M I	64	3	4.6	12 II + 6 I to 1 III + 10 II + 3 I
Palm No. 287	Diak.	97	7	7.2	4 II + 3 I to 1 III + 2 II + 8 I
	M I	117	3	2.6	8 II to 1 III + 13 II + 1 I
Palm No. 288	Diak.	87	5	5.7	2 II + 2 I to 1 III + 14 II + 31
	M I	85	4	4.7	14 II to 1 III + 13 II + 2 I
Palm No. 307	Diak.	72	7	9.7	6 II to 27 II + 2 I
	M I	105	8	7.6	11 II to 1 III + 13 II + 2 I
Spontaneous hybrid	Diak.	60	3	5.0	13 II + 15 I to 1 III + 9 II + 9 I
	M I	44	4	9.1	15 II + 1 I to 9 II to 12 I

variation in meiotic behaviour. While meiosis was normal in palm 717, chromosome associations as high as 1 X + 1 IV + 9 II were observed in the other palm (471) of the same cultivar.

In spite of the relatively high variability in the multivalent association (0-14.8%) observed in *A. catechu*, pollen fertility in all the palms was high. Lack of specific relation between meiotic aberrations and sterility has also been observed in rice (Engle, Chang & Ramirez, 1969). Moreover, fertility is influenced not only by the presence or absence of multivalents but also by other kinds of genetic control (Muntzing, 1956; Gottschalk, 1968; Gottschalk & Kaul, 1974).

The chromosome pairing observed in *A. triandra* showed that there is partial desynapsis of varying degrees in the different plants. Among the recorded deviations from normal chromosome pairing, desynapsis constitutes one of the most important meiotic phenomena. Chromosome pairing and, in fact, all events of meiosis can be under some form of genetic control (Riley & Law, 1965; Riley, 1966). The possibility of diakinesis extension of chiasmate associations was considered to explain the increased pairing at metaphase I compared to diakinesis, but this was insufficient to explain the observations. The increased pairing and consequent regularisation of meiosis from metaphase I onwards in *A. triandra* and its F_1 hybrids might be attributed to distributive pairing (Grell, 1964, 1967; Bavappa & Nair, 1978). A between homologues 'touch-and-go' mechanism normally results in regular anaphase segregation and in balanced spores. But distributive pairing, being in principle homology independent (Grell, 1967), may result in systematic anaphase segregation only and not in balanced spores.

As *A. triandra* is apomictic (Bavappa & Nair, 1975a), this character can be expected to be maintained in the population. The extent of desynapsis is higher in the F_1 hybrids of *A. catechu* and *A. triandra* as compared to *A. triandra*, suggesting that the gene controlling this character may be dominant. The larger number of univalents observed in the hybrid as compared to the *A. triandra* parent may be due to reduced homology of the parental chromosomes. A great deal of variation was observed in the synaptic behaviour of chromosomes of the *A. triandra* parent and the F_1 hybrids. This variation presumably arises from the differential expressivity or segregation of the genes controlling the process (Jauher, 1969) or due to environmental factors (Li, Pao & Li, 1945; Wang et al., 1965; Mehra & Rai, 1972).

Meiotic abnormalities such as chromosome mosaics, stickiness, cytomixis, bridges and fragments were met with in the parents as well as the hybrids to varying extent. The origin of chromosome mosaic in pollen mother cells has been variously attributed to genetic factors causing defects in spindle mechanisms as in experimental amphiploids of *Triticinae* (Sachs, 1952), or exchange of chromosomal material between archesporial cells in the premeiotic mitosis as in *Secale cereale* (Muntzing & Prakken, 1941). In *A. triandra* and *A. catechu-A. triandra* hybrids, cytomixis met with to a maximum extent of 39 per cent seems to have contributed to the intraplant variation of chromosome numbers observed. A similar origin of chromosome mosaics in *Gossypium* has been reported by Sarvella (1958).

The high percentage of chromosome stickiness met with in certain plants of *A. catechu* has neither affected the later course of meiosis, nor the pollen fertility. It is likely that cells showing stickiness of chromosomes degenerate and do not participate in the formation of microspores. Beadle (1932) in *Zea mays* and more recently Martini & Bozzini (1965) in *Triticum* sp. reported stickiness of chromosomes due to a single recessive gene. Mehra & Rai (1970) have shown that in *Collinsia tinctoria* excessive chromosome stickiness during various stages of meiosis is attributable to a recessive gene. The stickiness observed in *A. triandra* and the hybrids suggests that this abnormality is genetically controlled.

In the absence of inversion bridges, the chromosome fragments observed probably had their origin either in chromosome breakages in the early stages of meiosis or in the unequal division of univalents at anaphase. This view is supported by the presence of fragments at metaphase I, and anaphase I and II.

Observations on pollen and female fertility show that in *A. catechu* which has a high pollen fertility, the nut set is less than 50 per cent (Tab. 2). The average fruit set in this species has been reported to be 37.6 per cent (Murthy & Bavappa, 1960). Various events that prevent pollination and fertilization have been listed by Raghavan & Baruah (1956) as possible causes contributing to female sterility in this species. The present observations on fruit set in two cultivars of *A. catechu* confirms the earlier reports on lower female fertility in this species.

In the *A. catechu – A. triandra* hybrids, the nut set was less than one per cent in most of the cases (Tab. 2). It therefore appears that the factors which have been responsible for pollen sterility are also in operation on the female side.

Sharma & Sarkar (1956) reported only 16 bivalents in the first metaphase for *A. catechu* and *A. triandra*. Bavappa & Raman (1965) observed mostly bivalents with a rare quadrivalent in *A. catechu*, and only bivalents in *A. triandra*, and suggested a secondary allotetraploid origin for *A. catechu*. In the present investigation, multivalent pairing was frequently observed in the two species and their F_1 hybrids. While 16 bivalents were of the highest frequency in most of the palms, the maximum configuration observed was decavalent in *A. catechu*, quadrivalent in *A. triandra* and octovalent in *A. catechu-A. triandra* hybrids. The chromosome associations indicate the probability of autopolyploid origin of the two species with restricted multivalent pairing. While autosyndesis may explain the observed chromosomal association in the hybrid to a certain extent, it does not account for the maximum association. It therefore appears that there is considerable homology between the chromosomes of the two species.

The *A. catechu-A. triandra* hybrids studied showed high sterility and hybrid vigour for different characters as can be expected in an interspecific cross involving genetically divergent parents (Bavappa, 1974). Since it has been possible to backcross the hybrids to *A. catechu*, the possibilities of transferring mite resistance and larger number of female flowers reported in *A. triandra* (Bavappa, 1966a,b) to *A. catechu* are bright. As the sterility observed in the hybrids appear to be due to the meiotic abnormalities in *A. triandra*, disharmonious interaction between the genotype and cytoplasm of the parents (Bavappa, 1974) and unbalanced gene combinations, restoration of fertility through repeated backcrosses with *A. catechu* may be feasible.

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