Asynapsis in Cassava¹

J. S. Jos, K. Vijaya Bai and R. B. Nair

Central Tuber Crops Research Institute, Trivandrum 695017, India

Received May 6, 1982

Cassava (*Manihot esculenta* Crantz) is an important root crop which forms a major staple food in a number of tropical countries. While screening the germplasm, different types of male sterile and partially sterile clones have been already identified (Jos *et al.* 1966, Magoon *et al.* 1968, Jos and Nair 1979 and Jos and Bai 1981). Recently a completely male sterile clone has been found among the exotic genetic stocks and detailed meiotic studies revealed it to be asynaptic. The present communication reports the cytological behaviour of this asynaptic clone.

Materials and methods

The clone Ce-258 is maintained vegetatively through stem cuttings. The buds were fixed in a mixture of 3 parts of alcohol to one part of propionic acid. The anthers were smeared with propionocarmine and detailed analyses of the different stages of meiosis were made from temporary preparations. A few slides were made permanent for record purposes. All plants belonging to Ce-258 were found to be asynaptic. To facilitate comparison, the meiosis of a normal pollen fertile clone was also studied.

Results and discussion

Male fertile cassava

The chromosome number was $2n=36$. At pachytene, pairing was complete and 18 bivalents were noticed (Fig. 1). At MI also 18 bivalents were observed which aligned regularly as a plate (Fig. 2). The mean chiasma frequency was found to be 1.5 per bivalent. Anaphase I separation was normal with 18 chromosomes at each pole. The second meiotic division was also regular resulting in 98% pollen fertility (Fig. 3).

Asynaptic cassava (Ce-258)

At pachytene all the chromosomes remained as univalents without any semblance to pairing (Fig. 4). In detailed analysis the respective homologue chromosomes, differentiated on the basis of karyomorphology (Magoon *et al.* 1969) were observed remaining as separate univalents. There was an absence of even loose pairing at pachytene.

At MI, 150 PMCs were screened for chromosome association. More than 97

¹ Publication No. 337. Central Tuber Crops Research Institute.

% of cells showed 36 univalents (Fig. 5). However, 4 PMCs showed bivalent like association of which 3 PMCs had one each (Fig. 6) and one PMC showed 2 bivalent like configuration (Fig. 7). The mean number of bivalent was only 0.03 per cell. The bivalents failed to exhibit any visible chiasmata and the association was invariably only at the ends. In cassava, mean chiasma frequency has been already reported to be 27.8 per cell at MI (Bai *et al.* 1972) and the present fertile clone studied also showed a mean frequency of 1.5 per bivalent. It has been reported that negative relationship exists between chiasma frequency and univalent frequency but the competition to form chiasmata between chromosomes enhances the number of chiasmata in the available bivalents (Sjodine 1970, Omara and Hayward 1978) suggesting that the chiasma frequency in the asynaptic clone of cassava should be more than 1.5 per available bivalent if they are true bivalents. But there was a complete absence of chiasmata in Ce-258.

The bivalent-like association was as low as 0.03 per cell and the loose association was also only at the end and the lack of well defined chiasma and the absence of any pairing at pachytene suggest that the bivalents were not true bivalents but they were only univalents lying closely together due to factors other than true pairing.

Frequently all the chromosomes were found scattered. In about 10% of PMCs, some univalents were found oriented along the equatorial plane (Fig. 8). Apparently no spindle apparatus was organised at this stage as could be adduced by the occurrence of randomly distributed univalents all over the cytoplasm. For the same reason the onset of AI separation could not be demarcated in majority of PMCs. In about 15% of PMCs, the onset of AI was marked by the precocious movement of 3 to 13 chromosomes to either poles and by the division of univalents (Figs. 9, 10). However, frequently all the 72 chromosomes were found scattered showing that the chromosomes had undergone equatorial division also even though the later stages were not well defined. The failure in the movement of chromosomes and non-organization of poles resulted in irregular groupings of chromosomes (Fig. 11), leading to the formation of cells with more than 4 nuclei (Fig. 12) and later in the development of polyads with micronuclei (Fig. 13). The pollen were 100% sterile and of various sizes and micropollen were also present (Fig. 14).

The phenomena of asynapsis and desynapsis are closely similar and can be delineated only on the basis of pairing at zygotene or pachytene. A complete or partial failure of chromosomes of the complement to pair at zygotene or pachytene resulting in univalents is described as asynapsis (Randolph 1928, Beadle 1931) whereas premature separation is ascribed to desynapsis (Sharp 1934). Due to difficulties in making good preparations at pachytene, there are only few reports of true asynapsis and others are of doubtful nature or only desynapsis (Gottschalk and

Figs. 1-14. 1-3: Meiosis in pollen fertile clone. 1, normal pachytene showing 18 II's. $\times 800$. 2, MI with 18 II's. $\times 800$. 3, fertile pollen. $\times 70$. 4-14: Meiosis in asynaptic clone Ce-258. 4, pachytene showing univalents. $\times 800$. 5, MI with 36 I's. $\times 800$. 6, MI showing 34 I+I II like association. $\times 100$. 7, MI showing 32 I+2 II like association. $\times 800$. 8, AI with a few univalents in the equatorial plane. $\times 800$. 9, AI showing the division of 5 I's. $\times 800$. 10, AI showing the division of 11 I's. $\times 320$. 11, AII showing scattering and irregular groupings of chromosomes. $\times 400$. 12, T II with 10 nuclei. $\times 250$. 13, polyad with micronuclei. $\times 250$. 14, completely sterile pollen. $\times 70$.

Kaul 1980). The lack of pairing at pachytene in the material under present study clearly establishes it is asynaptic. The occurrence of asynapsis in cassava and in the genus *Manihot* is being reported for the first time.

Asynapsis has been classified into four categories on the basis of the extent of pairing and the number of bivalents (Miller 1963). Since the presence of as low as 0.03 bivalent like association has been already concluded to be not true bivalents and the type of asynapsis noticed in Ce-258 is 'complete'.

Asynapsis has been attributed to a variety of causes such as abnormal external conditions (Prakken 1943, Wang *et al.* 1965), loss of chromosome or deficiency (Baker and Morgan 1969), by a single recessive gene (Stephens and Schartz 1963, Miller 1963) or occasionally by a highly polygenic system (Gottschalk and Klein 1976). It has been also reported that asynapsis in the mutants was due to the absence of proline in the anthers (Katayama 1962). The presence of pollen sterility in all the plants of the clone Ce-258 throughout the season rules out environmental factor and suggests it is of genic nature.

The material studied presently, showed a complete absence of fruit set and the female flowers abscised very early indicating the extent of asynapsis is 'complete' in megasporogenesis also manifesting total female sterility. The presence of complete male and female sterility makes it difficult to study the genetics of asynapsis in this clone.

Summary

A completely male sterile clone was identified in the germplasm and detailed meiosis showed it to be asynaptic. At pachytene all the chromosomes remained as univalents without any semblance to pairing. MI also showed 36 univalents in 97% of pollen mother cells. The bivalent like association in MI was as low as 0.03 per cell but the absence of pairing at pachytene and the lack of well defined x'mata suggested that they were only univalents lying closely together due to factors other than true pairing. The later stages were not well defined and univalents were noticed to divide. The scattering of chromosomes and irregular groupings resulted in polyads consequently all the pollen were sterile. The type of asynapsis noticed was 'complete'. The presence of pollen sterility in all the plants of Ce-258 throughout the season ruled out environmental factors and suggested it was of genic nature.

Acknowledgement

We are indebted to Shri P. K. Thomas, Director for providing facilities and encouragements for completing this study.

References

- Bai, K. V., Jos, J. S. and Nair, R. G. 1972. Amphidiploidy in the genus *Manihot*. Chromo. Infor. Service 13: 23-35.
- Baker, R. L. and Morgan, D. T. 1969. Control of pairing in maize and meiotic interchromosomal effects of deficiencies in chromosomes. Genetics 61: 91-106.

- Beadle, G. W. 1931. A gene in maize for supernumerary cell divisions following meiosis. *Cornell Agric. Exper. Sta. Mem.* **135**: 1-12.
- Gottschalk, W. and Kaul, M. L. H. 1980. Asynapsis and desynapsis in flowering plants, 1. Asynapsis. *The Nucleus* **23**: 1-15.
- and Klein, H. D. 1976. The influence of mutated genes on sporogenesis. A survey on the genetic control of meiosis in *Pisum sativum*. *Theor. Appl. Genet.* **48**: 23-24.
- Jos, J. S., Magoon, M. L., Sadasivaiah, R. S. and Appan, S. G. 1966. Studies on sterility in cassava. *Ind. J. Hort.* **23**: 177-184.
- and Nair, S. G. 1979. Pachytene pairing in relation to pollen fertility in five cultivars of cassava. *Cytologia* **44**: 813-820.
- and Bai, K. V. 1981. Functional male sterility in cassava. *Curr. Sci.* **50**: 1035-1036.
- Katayama, T. 1962. Morphological and cytogenetical studies on the progenies of the asynaptic wild senna, *Cassia tora* Linne. *Sci. Bull. Fac. Agri. Kyushu Univ.* **19**: 257-261.
- Magoon, M. L., Jos, J. S. and Vasudevan, K. N. 1968. Male sterile cassava. *The Nucleus* **11**: 1-6.
- , Krishnan, R. and Bai, K. V. 1969. Morphology of the pachytene chromosomes and meiosis in *Manihot esculenta* Crantz. *Cytologia* **34**: 612-626.
- Miller, O. L. 1963. Cytological studies in asynaptic maize. *Genetics* **48**: 1445-1466.
- Omara, M. K. and Hayward, M. D. 1978. Asynapsis in *Lolium perenne*. *Chromosoma* **67**: 87-96.
- Prakken, R. 1943. Studies of asynapsis in rye. *Hereditas* **29**: 475-495.
- Randolph, L. F. 1928. Chromosome numbers in *Zea mays* L. *Cornell Agri. Expt. Sta. Mem.* **117**: 1-12.
- Sharp, L. W. 1934. *Introduction to Cytology*. McGraw Hill, New York.
- Sjodine, J. 1970. Induced asynaptic mutants in *Vicia faba* L. *Hereditas* **66**: 215-232.
- Stephens, J. C. and Scharf, K. F. 1965. Asynapsis and its inheritance in *Sorghum vulgare* Pers. *Crop Sci.* **5**: 337-339.
- Wang, S., Yeh, P., Lee, S. S. Y. and Li, H. W. 1965. Effect of low temperature on desynapsis in rice. *Botan. Bull. Acad. Science* **6**: 197-207.
-