EDIBLE AROIDS – NEW INSIGHTS INTO PHYLOGENY

R. Krishnan and M.L. Magoon*

SUMMARY

The New World *Xanthosoma sagittifolium* (n = 13) and the Old World *Amorphophallus campanulatus* (n = 14) and *Colocasia antiquorum* (n = 14) seem to have a lower base number than previously realized. Evidence for this comes from two heteromorphic bivalent associations recognized at pachytene, intragenomic pairing at metaphase–I and chromosomal counts in pollen of naturally occurring triploid *Colocasia.* Supporting evidence arises from studies of the control of desynapsis in diploids and triploids and from ecogeographical specialization and cytotaxonomic data of related aroid taxa. The value of these findings and the special problems that they create for conventional approaches to phylogenetic study of the aroids are discussed.

RESUME

Xanthosoma sagittifolium (n = 13) du Nouveau Monde et *Amorphophallus campanulatus* (n = 14) du Vieux Monde, de même que *Colocasia antiquorum* (n = 14) ont vraisemblablement un nombre de bases inférieur aux estimations antérieures. Deux associations hérétomorphiques bivalentes reconnues à l'accouplement pachytène et intragénomique à la métaphase–I et le chiffrage des chromosomes dans le pollen de *Colocasia* triploïde naturel en donnent la preuve. Cela se confirme par des études menées pour controler la désynapse dans les diploïdes et les triploïdes et par la spécialisation écogéographique de même que par des données cytotaxonomiques de groupes aroïdes parentés. La valeur de ces décourvertes et les problemes particuliers qu'elles posent aux méthodes conventionnelles d'étude phylogénétique d'aroïdes sont en cours de discussion.

RESUMEN

Xanthosoma sagittifolium, del Nuevo Mundo, (n = 13) y *Amorphophallus campanulatus* (n = 14) y *colocasia antiquorum* (n = 14) del Viejo Mundo parecen tener un número básico de cromosomas menor del que había sido determinado. La evidencia de esto se deriva de dos asociaciones heteromórficas bivalentes reconocidas en fase de paquiteno, apareamiento intragenomico en metafase–I y conteos cromosómicos en polen de triploides naturales de *Colocasia.* La evidencia que soporta tal situación resulta de estudios de control de desinapsis en diploides y triploides y de la especialización ecogeográfica y datos citotaxonómicos de formas aráceas relacionadas. Se discute el valor de estos descubrimientos y los problemas especiales que crean a los enfoques convencionales sobre el estudio filogenético de las aráceas.

INTRODUCTION

Knowledge of the phylogeny of crop plants by throwing light on past evolution may provide a useful insight into the prospects for future genetic transformation and assist the formulation of breeding programmes.

Aroid genera of economic importance such as *Colocasia, Xanthosoma, Alocasia, Amorphophallus* and *Cytosperma* have received little attention from students of evolution. The edible aroids are well adapted to a variety of environments and under proper management conditions can give very high yields[1,12,14].

Because of the antiquity of their cultivation, plurality of uses and multiplicity of habitats of cultivation, a large diversity exists among the cultivated forms of *Colocasia, Xanthosoma* and other edible aroids. Cytotypes have been reported within the species[14].

The poor flowering of these crops, while of no importance to production of the edible crop, hinders study of phylogeny. It would be helpful if ways could be found to improve this. The existing taxonomic treatment of the edible aroids is controversial, and this also hinders phylogenetic studies. Cytological investigations seem particularly useful in attempts to understand phylogeny and we have therefore concentrated our effort in this direction.

KARYOLOGICAL STUDIES IN *Amorphophallus campanulatus* AND *Xanthosoma saggitifolium*

The chromosomes are readily stainable. We have assessed the relative merits of the three commonest stages for chromosome studies, namely pollen metaphase, mitotic metaphase in root tip cells and pachy-

*Indian Grassland and Fodder Research Institute, Jhansi, (U.P.) India.

tene analyses in meiosis. In *A. campanulatus* the haploid set is n = 14 at root and pollen mitosis. The chromosomes could be separated into six types, including two nucleolar chromosomes. However, at pachytene all the 14 chromosomes of the haploid complement could be individually identified on the basis of relative length, nucleolar association, centromere position and total lengths of hetero- and euchromatin segments in the bivalents. Thus we stress the particular value of pachytene analysis.

INTER- AND INTRA- KARYOLOGICAL COMPARISONS IN *Amorphophallus* AND *Xanthosoma*

We have made intra- and inter- karyological comparisons of representatives of two aroid genera, *Amorphophallus Xanthosoma*. The pachytene karyotypes of these exhibited a number of similarities[5,6]. Two nucleolar chromosomes were present in each genus and they showed remarkable similarity in morphology. The nucleolar chromosomes of these aroids have a heteropycnotic short arm in intimate association with the nucleolus. Two other chromosomes with heteropycnotic short arms also occur in the karyotypes of both genera. It is remarkable that genera of the New World and the Old World aroids have such close karyological similarities.

Likewise, intra-karyological comparisons revealed similarity among several chromosomes in their morphology. In *x. sagittifolium* all the 13 bivalents at pachytene could be assigned to 12 types (A to L) with two similar bivalents in type B. The two type B bivalents were metacentric and rather similar to bivalent type C. The two nucleolar chromosomes, K and L were also homomorphic. Two non-nucleolar bivalents had a heteropycnotic short arm and the other bivalents, types A and I were submetacentric. Similarly, in *A. campanulatus* homomorphic bivalents included the two nucleolar chromosomes, and two non-nucleolar chromosomes with heteropycnotic short arms (chromosomes 3 and 10 and 7 and 11). Thus, in *x. sagittifolium* (n = 13) of the twelve chromosomal types distinguished at pachytene, eight of them including the two type B could be regarded as homeologous reducing the basic number to N = 8. Similarly in *A. campanulatus* eight of the bivalents could be regarded as homeologous which would reduce its basic number to n = 10.

COMPARATIVE KARYOLOGICAL AND CYTOLOGICAL STUDIES IN DIPLOID AND TRIPLOID *Colocasia* AND OTHER AROIDS

In the triploid *C. esculenta* (3n = 24) pachytene study, along with data on chromosomal association at metaphase—I and chromosomal counts in pollen provide clues that strongly support some basic numbers[17]. Diploid *C. esculenta* was investigated and found to have two nucleolar-associated bivalents at pachytene, like those of *Amorphophallus* and *Xanthosoma*. The occurrence of two such nucleolar trivalents with morphologically similar partners as well as high frequency of trivalent association at metaphase—I, suggests an autotriploid origin for triploid *Colocasia*. In this triploid intra-genomic pairing occurred involving one or two chromosomes in as many as 21.6% of pollen mother cells at diakinesis and two heteromorphic bivalent types were identified at pachytene. Thus studies on *Colocasia* provide direct evidence for a lower base than gametic number, in comparison with the less direct data for the same conclusion reached in *Xanthosoma* and *Amorphophallus*.

In *Colocasia*, chromosomal counts in the pollen of both triploids and diploids as well as fertility data provide additional proof in support of a lower base number than the gametic number. Although both diploids and triploids produce pollen of similar size, they are dissimilar in the chromosomal status of their pollen cells. The pollen of triploid plants contained a variable chromosome number ranging from 8 to 25: that of diploid plants contained uniformly 14. The number of triploid pollen carrying less than the 8, the base number, was low, accounting for only 3.5 percent of pollen mother cells seen at prophase or metaphase.

A review of the chromosomal status of some other Aracean genera reveals the existence of other taxa with low basic number. Among them those having low haploid numbers of n = 7, 8 and 9 are *Acorus* (n = 9), *Calla* (n = 7 and 9), *Aglaonema* (n = 8), *Dieffenbachia* (n = 8 and *Typhonium* (n = 8 and 9). The genus *Typhonium*[3,4] is interesting because in the three species *Typhonium cuspidatum* (n = 8), *T. trilobatum* (n = 9) and *T. inapinatum* (n = 13), the former two each have one nucleolar chromosome whereas *T. inapinatum* has two such chromosomes in its haploid complement[6]. The number of nucleolar chromosomes in this genus seems to reflect the ploidy status. As a parallel, we have found in each of the genera *Amorphophallus, Colocasia* and *Xanthosoma* two nucleolar chromosomes.

Chromosomal counts reported for various cultivars (clones) of edible aroids have been widely different. In *Colocasia* the numbers reported included 14,22,24,26,28,29,38 and 42[14]. *Amorphophallus* has n = 26 or 28 and *Xanthosoma* 2n = 24, 26 or 39. A systematic and thorough screening of edible aroids may reveal new chromosomal races of value in breeding and further phylogenetic understanding. Ecogeographical specialization, and vegetative propagation over centuries of cultivation have strongly influenced chromosomal evolution favouring preservation of the cytotypes of clones selected for value in cultivation under different ecological conditions.

STUDIES ON DESYNAPSIS IN AROIDS

Among various abnormalities of chromosome behaviour desynapsis has been a subject of great interest and is better understood than are the genetic mechanisms exerting control over processes of meiosis. Information on the genetic control of desynapsis has been obtained from direct and indirect studies in several angiospermic taxa[13]. Desynapsis has been found to be usually due to one or a few pairs of recessive genes.

In the Araceae desynapsis has been reported in some cultures of *Amorphophallus campanulatus*[13] and *Colocasia antiquorum*[7]. Although both these taxa were diploids, the degree of desynapsis in them differed markedly. The former was classed according to the classification of Prakken[15], as 'medium strong' type and the latter as 'complete' desynapsis. Desynapsis of the 'complete' type was also reported in a triploid cultivar of *Colocasia antiquorum*[8] which showed several differences in chromosome behaviour in comparison with the diploids.

On the available evidence, if seems that the origin of these desynaptic cultivars in the family Araceae results from spontaneous gene mutation. Such cultivars may prove useful for genetic studies on the inheritance of the trait. Such studies in turn may throw lignt on the mechanisms underlying chromosomal pairing and chiasma formation in meiotic prophase and hence relate to the possibilities for genetic recombination.

POLYPLOID ORIGIN OF EDIBLE AROIDS

The evidence presented on the polyploid origin of edible aroids, though somewhat indirect, is all mutually supporting. Taking a long term view on the breeding of edible aroids, the impact of these findings of cruptic polyploidy may have considerable significance since appropriate plant breeding procedures for true diploids are different from those for polyploids[9,10,11]. It is possible that further investigations will throw light on the relation of the various cytotypes to potential productivity.

REFERENCES

1. Coursey, D.G. (1968) The edible aroids. *Wld. Crops.* 20, 25–30.

2. Jos, J.S., Vasudevan, K.N. and Magoon, M.L. (1967) In vitro germination of pollen in aroids. *Ind. Jour. Hort.* 24, 166–72.

3. —————— (1968) Structural hybridity in *Typhonium cuspidatum Genet. Iber.* 20, 1–11.

4. Jos, J.S. and Magoon, M.L. (1970) Pollen mitotic studies in some aroids. *Chromosome Inf. Serv. (Japan)* 11, 4–5.

5. Krishnan, R. Magoon, M.L. and Bai, K.V. (1970a) Karyological studies in *Amorphophallus campanulatus Canad. Jour. Genet. and Cytol.* 69, 187–96.

6. —————— (1970b) Cytological studies in *Xanthosoma sagittifolium* (L) Schott. *Nucleus* 13, 141–7.

7. —————— (1970c) Desynapsis in *Colocasia antiquorum* Schott. *Genetica* 41, 170–8.

8. —————— (1970c) Meiosis in a desynaptic triploid *Colocasia antiquorum Schott.* Genetica Agraria (Italy).

9. Magoon, M.L. and Krishnan, R. (1971a) Problems on the elucidation of genomic evolution in some important tuber crops. Proc. Symp. Genomic concept in Bukaryota, Indian Sci. Congr., Calcutta.

10. —————— (1971b) Genetic improvement of tuber crops in India. Proc. 2nd Int. Symp. sub-tropical and tropical Horticulture, Bangalore.

11. —————— (1972) Plan and prospects for the improvement of tuber crops (other than potatoes). Proc. All-India Symp. Advances in Cytogenetics, Srinagar. 1, 1–19.

12. —————— (1967) Role of root and tuber crops in human nutrition. Proc. Int. Symp. sub-tropical and tropical Horticulture, New Delhi. 1, 46–61.

13. Magoon, M.L. and Sadasivaiah, R.S. (1967) Studies of desynapsis in *Amorphophallus campanulatus* Blume. *Genet. Iber.* 19, 1–12.

14. Plucknett, D.L., de la Pena, R.S. and Obrero, F. (1970) Taro (*Colocasia esculenta*). *Field Crop Abstracts.* 23, 413–26.

15. Prakken, R. (1943) Studies of asynapsis in rye, *Hereditas.* 29, 475–95.

16. Sharma, A.K. and Mukhopadhyay, S. (1965) Cytological study on two genera of Araceae and correct assessment of their taxonomic status. *Genet. Agraria.* 18, 603–16.

17. Vijaya Bai, K. Magoon, M.L. and Krishnan, R. (1970) Meiosis and pollen mitosis in diploid and triploid *Colocasia antiquorum* Schott. *Genetica* 42, 187–98.