



Cyto-palynological Studies in Taro (*Colocasia esculenta* (L.) Schott.)-An Overview

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Abstract

Taro (*Colocasia esculenta* (L.) Schott.) is an important tuber crop that can adapt well to different agro-climatic conditions. It is a vegetatively propagated crop with many morphotypes. The interrelationships between cytological and palynological features of individual plants have been used in solving several taxonomic problems. While number, size and morphology are the main chromosomal features of karyomorphology, the shape and symmetry of pollen grains, the architecture of its wall, exine stratification, exine sculpture and structure, number, position and size and shape of aperture are some of the palynological features of taxonomic importance. Even though there were attempts in the cytological studies of taro, information available on the pollen morphology of taro is meagre and fragmentary. At the same time, there is considerable paucity of detailed cytotaxonomic work based on karyotype analysis at the sub specific level in taro. Sixty accessions of taro procured from three South Indian states and an exhaustive collection of a large number of accessions from all over India studied at the Central Tuber Crop Research Institute, Kerala, India, forms the basis of the present review. An attempt has been made in this review to document the major cytopalynological studies carried out so far in taro.

Key words: *Colocasia esculenta*, karyomorphology, cytotype, palynology, inaperturate, exine ornamentation, echinate excrescence, spine morphism

Introduction

Taro (*Colocasia esculenta* (L.) Schott.) is an important tuber crop belonging to the monocot family Araceae. The family is highly heterogenous and consists of about 110 genera with over 2500 species. The rapidity and efficacy of its vegetative propagation have brought about its establishment and worldwide distribution, especially in the humid tropical and subtropical regions. The plant is mainly grown as a tuber crop for its edible corms and cormels or as a leafy vegetable. The crop is also commercially important as it is being used in the starch industry and for the production of animal feed. Taro is characterized by having stout underground rhizomes bearing stolons. Leaves are peltate with hanging blades. Inflorescences are appendaged.

Cytological information has been a major tool widely used in the discussions of systematic relationships, phylogeny and evolution of related plant groups. Data of intra-specific variation in chromosome morphology is important for determining the interrelationships of accessions *vis-a-vis* for clustering them. Karyomorphological information scored in terms of a variety of pertinent parameters provides dependable clues for tracing the direction of karyotype variation that leads to speciation and evolution. A host of workers have studied the chromosomes of taro, but reports of detailed karyomorphological study of the crop are sparse. Pollen morphology has been recognized as a potential supplementary tool in dealing with taxonomic problems and for elucidation of systematic relationships of angiosperms. Electron microscopy has made it possible

to describe exine architecture with precision, and has been used to detect even subtle variations of pollen wall features. The information available on the pollen morphology of taro is meagre and fragmentary. Hence, an attempt has been made in this paper to document the available information on intraspecific pollen morphology and karyomorphology of taro, which will further help in the genetic improvement of the crop.

Taxonomy

Because of a long history of vegetative propagation, some confusion and discord prevails concerning the taxonomy of taro. The plant originally described as *Anum esculentum* and now referred to as *Colocasia esculenta* (L.) Schott. is known by different popular names such as taro, dasheen, eddoe, curcas, old cocoyam etc. Systematization of Purseglove (1979) included one species with two botanical varieties: *C. esculenta* (L.) Schott. variety *esculenta* (syn var. *typica* A.F. Hill), named as dasheen and *C. esculenta* (L.) Schott. variety *antiquorum* (Schott.) (syn. var. *globulifera* Engl and Krause) named as eddoe. The main difference between the typical *esculenta* and *antiquorum* is in the shape and size of the main corm and cormels. A larger central or main edible corm and smaller "side" cormels or suckers characterize *Colocasia esculenta* var. *esculenta* genotypes. *Colocasia esculenta* var. *antiquorum* genotypes usually have a relatively smaller central corm, which often may be inedible and well-developed edible side cormels (Plucknet, 1983). Another difference is in the length of the sterile tip (appendix) of the spadix. The sterile tip of the spadix of eddoe is usually much longer in comparison with that of dasheen. However, the differences in this character are not always obvious because of wide variations within each group.

Innumerable cultivars and wild forms exist in the taxon which exhibit a wide range of variability in all the plant parts, both vegetative and floral. The profound intraspecific variability in the species complex may be the result of somatic mutations (O' Hair and Asokan, 1986), genetic recombinations resulting from open pollination and seed setting in flowering varieties (Lebot, 1999), chromosome aberrations, both numerical and structural (Sreekumari, 1992). There also exists intergrades in many characters. Moreover, the genetic base of the species has been shrinking over the years owing to gene erosion by depletion of many cultivated forms during the long history of continuous vegetative

propagation. All these have virtually imposed great problems for taxonomic study of the species complex.

Origin and distribution

Taro is believed to have originated in South Central Asia, probably in India or Malay Peninsula (Rivers, 1926; Onwueme, 1999). From its center of origin, taro spread eastward to the rest of South East Asia and to China, Japan and Pacific Islands. From Asia, taro spread westward to Arabia, Egypt and the Mediterranean region. Later, voyagers took it, first across the continent to West Africa and later on slave ships to the Caribbean and the Americas (Yen and Wheeler, 1968). Keleny (1962) is of the opinion that Malaysia is the actual centre of origin, where wild forms are still found. However, due to its wide tropical and subtropical distribution with greater concentration of wild and cultivated forms along with the other few taxonomically related species such as *C. fallax* and *C. affinis* in Nepal, Sub Himalayan tract and North Eastern India, *C. manii* from upper Assam, *C. gracilis* in Sumatra and *C. virosa* in West Bengal etc. points to the Indo-Malayan origin of the crop (Plucknet et al. 1970; Plucknet, 1976). However, further cytological and electrophoretic investigations on taro from different parts of India made Kuruvilla and Singh (1981) to confirm its North East Indian origin. According to Ivancic and Lebot (2000), *C. esculenta* originated probably between Myanmar and Bangladesh, although there is not enough evidence to prove it.

Taro is mostly cultivated in Asia, Africa and the Pacific as well as the Caribbean Islands. In the Pacific Islands it is an important economic crop, besides being a staple in countries like Fiji, Papua New Guinea, Western Samoa, Vanuatu etc. in the South Pacific region. However, the largest area of cultivation is in West Africa, which therefore accounts for the greatest quantity of production (Onwueme, 1999). In India, taro is cultivated in almost all states right from the foot hills of the Himalayas to the coastal areas in the South. Studies on geographical distribution of diploids and triploids showed that triploids predominate in hilly regions whereas diploids are mostly confined to the plains (Kuruvilla and Singh, 1981; Zhang and Zhang, 1990; Sreekumari and Mathew, 1992). Majority of the cultivated and wild genotypes are diploids. Triploids were documented in India, Nepal, Australia, Japan, New Caledonia, New Zealand, the Philippines and Timor (Coates et al., 1988). Kuruvilla and Singh

(1981) reported that clones collected from North Eastern hills of Meghalaya were diploids and triploids and those from the plains of South India were diploids.

Cytology

Cytological studies in taro indicated that the species existed in two ploidy levels, diploids with $2n = 2x = 28$ and triploids with $2n = 3x = 42$ chromosomes (Yen and Wheeler, 1968; Vijaya Bai et al., 1971; Kawahara, 1978; Ramachandran, 1978; Kuruvilla and Singh, 1981; Coates et al., 1988; Sreekumari and Mathew, 1989; 1991a; 1992 and Lebot et al., 2004). However, there are some reports of chromosome counts which are different from $2n = 28$ or $2n = 42$ such as $2n = 22, 26$, and 38 (Sharma and Sarkar, 1963), and $2n = 32, 44$ and 46 (Subramanian, 1979). Some of these could be aneuploid variants of 28 and 42. Mookerjea (1955) reported a stray number as low as $2n = 14$.

Because of the shy flowering habit of taro, especially the cultivated ones, meiotic studies have been sparse in this species (Vijaya Bai et al., 1971; Ramachandran, 1978; Sreekumari and Mathew, 1993). Vijaya Bai et al. (1971) and Sreekumari and Mathew (1993) studied meiosis in diploid and triploid taro and suggested that meiosis in diploids was normal with regular pairing, bivalent formation and normal anaphase separation. This resulted in high degree of pollen fertility in diploids. While, in triploids, on the other hand, meiosis was irregular due to formation of uni, bi and trivalents leading to unbalanced anaphase separation resulting in pollen sterility.

Basic chromosome number

Cytological literature on taro, especially on materials from India indicates some confusion regarding the basic chromosome number within the species complex. Darlington and Wylie (1955) suggested two basic chromosome numbers for the species, viz., $x = 12$ and $x = 14$. Meiotic and karyomorphological data according to Krishnan and Magoon (1977) favored the contention of $x = 7$ as the basic chromosome number. However, subsequent studies on Indian material and exotic material such as those from the Pacific region, Australia, New Zealand and Papua New Guinea confirmed $x = 14$ as the basic chromosome number, occurring either as diploid with $2n = 2x = 28$ or triploids with $2n = 3x = 42$ (Vijaya Bai et al., 1971; Ramachandran, 1978; Kuruvilla and

Singh, 1981; Coates et al., 1988; Sreekumari and Mathew, 1992). Recent investigations using fluorescent *in situ* hybridization with ribosomal DNA probe (Kokubugato and Konishi, 1999) also showed strong evidence for the basic chromosome number $x = 14$.

Karyomorphology and cytotypes

There is considerable paucity of detailed cytotaxonomic work based on karyotype analysis at the sub specific level in taro. Karyomorphological study in Indian taro at the Central Tuber Crops Research Institute, Thiruvananthapuram, Kerala, India, revealed that the chromosomes were medium sized ranging from 1.33 to $4.55 \mu m$ and no absolutely metacentric (m-type) chromosomes were evident in any of the taxa studied. The karyotypes were of the graded type with no sharp intrakaryotypic size difference of chromosomes. Chromosomes were of four size classes viz., A, B, C and D category and majority of them belonged to the C-group. They were of medium asymmetry, mostly belonging to 2A and 2B and rarely to the 3A and 3B categories. (Sreekumari and Mathew, 1989; 1991a; 1991b; Nusaifa Beevi, 2009; Nusaifa Beevi et al., 2009). A cytological study on three species of *Colocasia* from Yunnan revealed that there were differences among species in the number of m- and sm- type chromosomes (Zhiyum et al., 2003). They observed that in *C. gongii* the karyotype consisted of 22 m- and 6 sm- type of chromosomes, while in two other species viz., *C. gaoligongensis* and *C. gigantea* the karyotype was with 20 m- and 8 sm- type of chromosomes.

It is well known that detailed karyomorphological study in species complexes, as has been executed in a variety of angiosperm families, can yield substantial evidence of intraspecific karyotype variability as a sequel to operation of various cytological phenomena which cause chromosome structural alterations. As far as the species *C. esculenta* is concerned, few such studies have been known previously, of which those of Coates et al. (1988), Sreekumari and Mathew (1995) and Nusaifa Beevi et al. (2009) are the most notable.

Coates et al. (1988), while making chromosome study in a number of clonal samples of taro from Australia, New Zealand, the Philippines and parts of North East Asia recognized five karyotypically distinct cytotypes, two in diploid and three in triploid taro. The distinction

centered on the morphology of three of the relatively large chromosomes, 3, 7, and 9. Their diploid cytotype I represented majority of plants in which the somatic complements were characterized by m-type homologous pairs in respect of the three marker chromosomes (mm mm mm). The somatic complement of the other cytotype (I-I) differed from cytotype-I in respect of chromosome No.7 which was heteromorphic for a pericentric rearrangement, one of the homologues being acrocentric (t-type) and the other m-type (mm tm mm). One of the triploid cytotypes designated as I-3 was an autotriploid which was postulated to be a derivative of the diploid cytotype-1 (mmm mmm mmm). The second triploid cytotype (I-I-3) differed from the triploid cytotype I-3 in respect of chromosome No.7 which was heteromorphic with two acrocentrics and their homologue m-type (mmm ttm mmm). This cytotype had been postulated as a derivative of the diploid cytotype I-I. The third triploid cytotype detected from clonal samples from New Zealand, Nepal and Japan was very distinct from the rest in that all three markers were homomorphic acrocentrics (ttt ttt ttt). Based on the data, they projected a hypothesis of two separate lineages of the plant within the contemporary taro populations of the region.

Subsequently, based on the results of a detailed karyomorphological study of a large collection of Indian taro from a wide range of geographical regions of India, Sreekumari and Mathew (1995) detected 12 distinct cytotypes centered on a few markers (1, 3, 7, 9), of which six were diploids and the other six triploids. In one each of the diploid and triploid cytotype, all the four markers were homomorphic m-types, and in the others, both diploid and triploid cytotypes, the markers showed changed morphology, which they pointed out to have arisen by varying degrees and magnitudes of chromosome structural repatterning, mostly by pericentric inversions.

Based on the karyomorphological differences centered on the same marker chromosomes 1, 3, 7, 9, Nusaifa Beevi et al. (2009) detected a few karyotypically distinct cytotypes among sixty taro accessions of South Indian states. Among the diploid accessions, all the four marker chromosomes were consistently m-types in great bulk (29 accessions) and the cytotype of this category of accessions was referred to as '2a' type (mm mm mm mm). In another set of 22 accessions, chromosome

number 7 was homomorphic st-type and this was referred to as '2b' cytotype (mm mm stst mm). In a third group of four accessions, all the four marker chromosomes were of st-type and this was referred to as '2c' cytotype (stst stst stst stst).

Among the triploids, the cytotype '3a' constituted the bulk and in them all the four marker chromosomes, 1, 3, 7 and 9 were metacentric or rarely homozygous submetacentric (mmm mmm mmm mmm). In another group of triploids the marker chromosome 7 was homomorphic st-type and the marker 9 homomorphic sm-type. This cytotype was referred to as '3b' (mmm mmm ststst smsmsm). In another triploid accession, chromosome number 1 was homomorphic m-type, and the other three markers (3, 7 and 9) were of homomorphic st-type. This cytotype was referred to as '3c' type (mmm ststst ststst ststst).

Out of the six cytotypes recognized by Nusaifa Beevi et al. (2009), four of them (two diploids and two triploids) fitted very well with the cytotypes recognized by Sreekumari and Mathew (1995) and one diploid and one triploid were new ones. One of the new diploid cytotypes (stst stst stst stst) was found to be the fore runner of the hypothetical diploid (tt tt tt) predicted by Coates et al. (1988). Based on the features of the cytotypes recognized by Sreekumari and Mathew (1995) and Nusaifa Beevi et al. (2009), a tentative scheme of phylogeny and evolution of Indian taro forms had been projected (Sreekumari et al., 2010). According to the scheme proposed, out of the 14 karyotypically distinct cytotypes recognized among the Indian taro forms so far, Line-I included six cytotypes, of which three were diploids and three triploids and Line-II comprised eight cytotypes, of which four were diploids and four triploids. The cytotype, in which four marker chromosomes were homomorphic m-type, was postulated to be the earliest evolved cytotype from which the others in the same line as well as those in Line-II were considered to have evolved by operation of at least three processes such as (1) chromosome structural re-patterning, (2) auto triploidy and (3) hybridization between diploid cytotypes followed by allotriploidy. The tentative scheme also proposed two possibilities of origin and evolution of the present day taro forms: (1) the two lines of cytotypes referred to earlier originated and evolved from a common $2n = 14$ ancestral prototype or (2) Line-1 as the earlier evolved

condition from the ancestral type from which Line-II evolved into an apparently separate line during the early periods of diversification of the species complex. The overall similarity in gross karyomorphology between accessions of the two lines and overlapping of many plant morphological characters between the two may outweigh in favour of the second possibility.

Palynology

Palynological evidences are reckoned as dependable tools for solving taxonomic problems and for elucidation of systematic relationships and phylogeny of higher plants (Saad, 1972; Nair, 1974). Pollen characters which have high taxonomic importance have been grouped into five categories, of which those relating to the germinal aperture are considered to be of primary importance, exine surface ornamentation secondary and the others such as exine strata, pollen size and shape, tertiary. It was already reported that the pollen grains of Araceae were spherical or globose, inaperturate and echinate with spinose excrescence system (Sharma, 1967; Walker and Doyle, 1975; Jayalekshmi, 1992; Xue et al., 2003). The 1-2-colpate as well as inaperturate conditions occurred in the family (Sharma, 1967). According to Hesse (2002), Araceae is characterized not only by a stunning variability in exine ornamentation, but also by a rich diversity of exine stratification and aperture character. He explained that the monosulcate and inaperturate conditions dominated in the family and opined that inaperturate pollen, mainly found in the Aroideae, may be correlated with the kettle trap mechanism of pollination. The ultrastructure of pollen walls was characterized by the absence of a stable sporopollenin exine layer in the sub family Aroideae. Nusaifa Beevi and Sreekumari (2009) studied pollen morphology in a number of flowering accessions and detailed palynological description was made using LM and/or SEM observations at the Central Tuber Crops Research Institute, Kerala, India. Light Microscopic studies revealed that pollen grains in taro occurred as monads, which were inaperturate, globular or spherical, small to medium sized with spinous excrescence system.

Pollen wall architecture

The nature of pollen wall provides a multitude of phylogenetically important characters including pollen wall morphology, its structural components such as

stratification and external structural elements leading to exine structural sculpturing. The study of the acetolysed pollen wall usually refers to the study of exine, since in acetolysed pollen grains intine is lacking. *Colocasia* was found to be less resistant to acetolysis (Nusaifa Beevi, 2009). It has been reported that in Araceae the exine (strata) consists of a perforated tectum, an interstitium formed generally by granular columellae, and a robust foot layer together making the ektexine, and a thin endexine (Grayum, 1992; Hesse, 2002; 2006).

Exine sculpturing

Nusaifa Beevi and Sreekumari (2009) made a detailed study on the basic excrescence system in taro which revealed that the exine sculpturing pattern of *Colocasia* is echinate and the excrescence shape was spinate. The excrescence system had a complex structure and consisted of an external spine and a basal hold. The basal hold consisted of an upper socket, into which the spine incorporated and a basal plate from which the socket arose. These basal plates were arranged together to form the surface topology. In between adjacent basal plates, there were interplate groove which were deep or shallow. Based on the size, shape and arrangement of basal plates and nature of basal plates, five basic types of exine ornamentation pattern were recognized in taro. Simple tilate condition was characterized by cultivars, while, composite tilate condition existed in majority of wild ones. Triploid cultivars exhibited an entirely different ornamentation pattern with warts or tubercles in the interspinal area (Nusaifa Beevi and Sreekumari, 2011). Nusaifa Beevi and Sreekumari (2009) reported spine morphism in taro and observed that along with monomorphic spines, the accessions showed dimorphism and trimorphism. Dimorphic and trimorphic spines were observed in wild accessions. According to Nair (1961), spinate echinate system was the least evolved one as far as evolutionary progression was considered. Occurrence of spine morphism in taro led to the conclusion that this species complex might be in the initial stages of evolution with regard to the excrescence system.

Pollen size polymorphism

Pollen size was considered to be an unstable character as it was often affected by the method of preparation (Walker and Doyle, 1975). Nusaifa Beevi and Sreekumari (2009) reported that taro accessions studied from South

Indian states exhibited pollen size polymorphism, but the difference was not striking and varied between 15-25 μm in diploids and 22-28 μm in triploids. Pollen size polymorphisms had been attributed to the internal and external environmental conditions that prevailed during pollen development, changes in ploidy, and genetic variations (Darlington, 1965; Ong and Rao, 1973).

Conclusion

Detailed karyomorphology of taro throws light into the origin and evolution of the species complex. The constancy of chromosome number observed in the species here and those cited in the literature by several scientists indicated that aneuploid changes have not played a major role in the evolution of the species. The marker chromosome pairs in all the diploid and triploid cytotypes identified here were appreciably same in size irrespective of the difference in position of their centromere. The shift in centromeric position that occurred in them could be the result of pericentric inversion rather than deletion. It may also be rationalized that the transformation in the marker chromosomes from the metacentric state to submetacentric or subtelocentric condition might have occurred initially in the diploid group, and from them carried over to the triploids during their formation by autopolyploidy. Thus, the triploid cytotypes presently identified might be direct derivatives from the corresponding diploid cytotypes. In the tentative scheme of phylogeny and evolution of Indian taro forms, it is proposed that, of the two lines of cytotypes referred to, the Line-I is postulated to have evolved from an ancestral $2n=14$ prototype. The present day $2n=28$ plant is considered to be a diploidized tetraploid from the $x=7$ ancestor. As far as palynological study is concerned, it was suggested that fundamental spinate system commonly occurs in taro and this species complex might be in the initial stages of evolution with regard to the excrescence system. Along with spines, spinules and warts appearing in certain accessions, resulted in spine morphism. The variations observed in the size, shape, arrangement and pattern of basal plates, as well as the occurrence of spine morphism were correlated with the ploidy status and habitat to a certain extent.

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