Ribosomal and Mitochondrial DNA Variation in Japanese Taro (*Colocasia esculenta* L. SCHOTT)

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The multigene family for 18S-5.8S-26S ribosomal DNA (rDNA) was surveyed in 80 accessions of Japanese cultivated taro (*Colocasia esculenta*). We probed restriction enzyme digests of total DNA with a fragment cloned from the large intergenic spacer region of taro rDNA. Total DNA was probed with a fragment containing mitochondrial genes for ATPase subunits α and 9 from pea. Seven patterns of rDNA and two of mitochondrial DNA(mtDNA) were found. The resulting classification of taros was consistent with previous morphological and biochemical observations. Comparisons with taros from Nepal indicated that some Japanese triploids have received genetic influence from taro in Himalayan region. The actual diploid progenitors of Japanese triploids remain unknown. Comparisons with an Australian example of *C. esculenta* var. *aquaticilis* suggested the Japanese diploids, and some triploids, are at least partly derived from var. *aquaticilis*, which is widespread in the wild in northern Australia and many parts of tropical Asia and the Pacific.

KEY WORDS: *Colocasia esculenta*, classification, ribosomal DNA, ATPase, RFLP.

Introduction

Colocasia esculenta (L.) SCHOTT, a member of the family Araceae, is believed to have a natural origin in Northeast India or mainland Southeast Asia, while its natural distribution range remains enigmatic (COATES *et al.* 1988, MATTHEWS 1991). Taro is a starchy root crop and world production in 1984 was estimated by the FAO as 5,763,000 tons (MORISHITA 1988). Japan produced 397,000 tons in 1988 (ANONYMOUS 1990). Despite its agricultural importance, genetic studies and breeding of this crop are not advanced.

YEN and WHEELER (1968) and COATES *et al.* (1988) surveyed chromosome numbers in wild and cultivated taros and found that triploids ($2n = 3x = 42$) are common in mainland Asia, the Philippines, and Japan, but are generally absent in the Pacific Islands, while diploids ($2n = 2x = 28$) are common in both Asia and the Pacific. Triploids predominate among cultivated taros in Japan (FUKUSHIMA *et al.* 1962, SAKAMOTO *et al.* 1976), Nepal (KAWAHARA 1978), and at high altitudes in Northeast India (KURUVILLA and SINGH 1981).

Japanese taro cultivars were classified into several morphological groups by KUMAZAWA (1956), and again by HIRAI *et al.* (1989) using numerical analysis. The chromosome numbers of many of the groups were reported by FUKUSHIMA *et al.* (1962), KUMAZAWA *et al.* (1956) and HOTTA (1970). HIRAI *et al.* (1989) found that variation in the electrophoretic patterns of corm proteins was congruent with morphological variation. We characterised Japanese culti-

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vars further by rDNA and mtDNA analysis, and investigated their origins by making comparisons with taros from Australia and Nepal.

Nuclear chromosomes in plants contain extensive tandem arrays of rDNA units. Each unit contains genes coding for 18S, 5.8S, and 26S RNAs; and separated by spacer sequences. Insertions, deletions, and point mutations are often found in the large intergenic spacer between the 26S and 18S genes (APPELS and DVORAK 1982, APPELS and HONEYCUTT 1986, DVORAK 1990). Because of this, rDNA analysis has helped in the classification of plant cultivars, and has provided genetic markers suitable for breeding programmes. Phylogenetic analysis of mtDNA variation among species is limited by a high frequency of confounding rearrangements (PALMER 1987, PALMER and HERBON 1988). This frequent mutation increases the chance of detecting different lineages within species.

Materials and Methods

The taro collection at NIVOT in Ano was the immediate source of samples. Accessions from throughout taro growing areas in Japan were tested. The same accession were previously classified by HIRAI *et al.* (1989) according to morphology and the electrophoretic patterns of corm proteins, with the exception of No. 273, which was morphologically identical to the previously described sample of 'Takenokoimo' (No. 47). Nepalese taros maintained at NIVOT and a wild diploid from of *C. esculenta* var. *aquaticus* Hassk, from Jiye Cave in Queensland, Australia (MATTHEWS 1990) were used for comparison.

Chromosome numbers for Japanese morphological groups and varieties were inferred from the classification and chromosome numbers presented by KUMAZAWA *et al.* (1956), or were counted using the method of COATES *et al.* (1988) as follows. Root tips were immersed in 0.2% aqueous colchicine for 2~4 hrs, then fixed in 3:1 ethanol and acetic acid at 4°C, overnight. The material was stained with Feulgen's solution, hydrolysed for 4 min in 1M HCl at 60°C, squashed in a saturated solution of aceto-carmin and 45% acetic acid, on a slide, and examined with a light microscope.

Total DNA was extracted from young rolled leaves as described by APPELS and MORAN (1984). DNA was digested with restriction enzymes and electrophoresed in 0.7% agarose and Tris-borate buffer (MANIATIS *et al.* 1982), at 50V for approximately 1 hr in a Mupid mini-gel apparatus (gel length 6 cm, Cosmo Bio Co. Ltd., Tokyo). For better resolution, some samples were electrophoresed overnight at 20V in 0.8% agarose (gel length 13.5 cm). Each gel was soaked in 0.4M NaOH before transferring the DNA to Hybond N⁺ nylon membrane (Amersham International plc, Amersham). Hybridisations were performed with digoxigenin-labelled DNA probes prepared and detected enzymatically according to the supplier's instructions (Boehringer Mannheim GmbH, Mannheim). Since previous study had demonstrated that six-base cutters have no or only one site, and are not suitable for analysing polymorphism in the spacer region, while Taq I and Hinf I are able to cut out the spacer region, and are useful in this study. Polymorphic Taq I and Hinf I restriction fragments were probed with the 2.8 kbp Taq I spacer fragment contained in pCe 34.11 (Fig. 1). This fragment was subcloned from pCe 34.1, a taro rDNA clone, by MATTHEWS (1990). To map Taq I and Hinf I restriction sites within the spacer region, Eco RI-Pst I fragments from pCe 34.1 were

Fig. 1. Map of the taro ribosomal DNA unit (MATTHEWS 1990), aligned with the clones (pCe 34 series) that were used as probes. Thick lines represent genes, thin lines indicate spacers. Taq I and Hinf I sites outside the large intergenic spacer were not mapped. E=Eco RI, T=Taq I, H=Hinf I, P=Pst I. T* marks the approximate location of the extra Taq I site evident in rDNA patterns III and V.

sub-cloned into pUC 19, giving pCe 34.12 and pCe 34.13. These sub-clones span opposite halves of the spacer region (Fig. 1), and were used as probes for single and double digests of total DNA from taro. Hind III digests of total taro DNA were probed with pMTH 44, which contains the genes for F_1 -ATPase subunit α , and F_0 -ATPase subunit 9, in a 4.4 kbp Hind III fragment of mitochondrial DNA from *Pisum sativum* (NAKAMURA *et al.* 1989, MORIKAMI pers. comm.).

Results

Eighty Japanese accessions displayed a total of seven rDNA patterns, after Taq I or Hinf digestion, and each pattern represented two or more rDNA spacer variants (Fig. 2). Wild taro from Queensland, Australia, displayed a single rDNA spacer variant, characterised by Taq I and Hinf I fragments of 2.8 and 2.9 kbp respectively. This variant, henceforth referred to as the Queensland rDNA variant, was absent from patterns I to III, and present in patterns IV to VII (Fig. 2). The Queensland rDNA variant was also recognized in Australian and Japanese taros in tests with Rsa I and Mbo I and spacer region probes (results not shown). Major triploid cultivars, Ishikawa-wase, Dodare, Hasubaimo and Akame showed 3.4 kbp Taq I fragment and corresponding to 3.2 kbp Hinf I fragment, (pat-

Fig. 2. Ribosomal DNA patterns of Japanese cultivated taros and one wild taro from Queensland, Australia. Total DNA was digested with Taq I or Hinf I and probed with pCe 34.11. For patterns I-VII, the variety names and NIVOT accession no. were (I) Eguimo, 4; (II) Wase-kohasubaimo, 11; (III) Ishikawa-wase maru, 15; (IV) Daikichi, 74; (V) Shogatsuman-amami, 80; (VI) Yatsugashira, 45; and (VII) Okinawa-aokuki, 71. The Queensland (Qld) pattern was from wild *C. esculenta* var. *aquatilis*. The smallest Taq I fragments are not shown (0.9 kbp in II & IV, 0.8 kbp in III & V).

tern II to IV). These fragments were not found in the Japanese diploids (pattern VI to VII) and the Australian wild taro.

Size differences among Taq I and Hinf I fragments were closely correlated except for 3 kbp Hinf I fragments found in patterns II through V (Fig. 2). Small Taq I spacer fragments of approximately 2.0 and 0.9 kbp were found in patterns II and IV, and similar small fragments of approximately 2.1 and 0.8 kbp were found in patterns III and V (Figs. 2 & 3). In each pattern these fragments summed to 2.9 kbp. This size corresponds to the above mentioned 3 kbp Hinf I spacer fragments found in each cultivar. These results suggested that the small Taq I fragments were from spacer variants with an extra Taq I site (Fig. 1). This was confirmed when Taq I and Hinf I sites were mapped by probing single and double digests of total DNA with pCe 34.12 and pCe 34.13 (results not shown). Many Nepalese taros display 2.1 and 0.8 kbp fragments identical to those that represent an extra Taq I site in the Japanese triploid patterns III and V (Fig. 3 and unpublished data).

After Hind III digestion and probing with the mitochondrial DNA clone pMTH 44, Japanese cultivars displayed either a single 8.2 kbp band (pattern I) or a single 6.4 kbp band (pattern II). The wild taro from Queensland and Japanese diploid cultivars displayed mtDNA pattern II, while most of triploid cultivars showed pattern I (Fig. 4, Table 1).

The surveys of rDNA and mtDNA variation in Japanese taros are summarised in Table 1. Results on Nepalese taro are not included in this table. The morphological groups, corm proteins, and chromosome numbers are also shown. Ribosomal and mitochondrial DNA patterns were constant within each of the morphological groups recognised by HIRAI *et al.* (1989).

Fig. 3. Ribosomal DNA patterns of Nepalese and Japanese taros showing an extra Taq I site (smallest fragments shown). Total DNA was digested with Taq I and probed with pCe 34.11. (N) Nepal, accession 149; (V) Shogatsuman-amami, acc. 80; (IV) Daikichi, acc. 74.

Fig. 4. Mitochondrial DNA patterns of Japanese cultivated taros and one wild taro from Australia. Total DNA was digested with Hind III and probed with pMTH 44. Accession numbers and varieties: 2 = Eguimo, 6 = Eguimo 24 = Kohime, 37 = Akame, 43 = Tonoimo, 73 = Yatsugashira. Qld = *C. esculenta* var. *aquatilis*, from Jiye Cave, Queensland.

Discussion

Ribosomal and mitochondrial DNA

rDNA in higher plants is found in high copy number (FLAVELL and SMITH 1974), and is

Table 1. Restriction pattern of ribosomal and mitochondrial DNA of Japanese cultivars of taro (*Colocasia esculenta* Schott)

The corm protein patterns and morphological groups are as recorded by HIRAI *et al.* (1989). Chromosome numbers were inferred to the morphological description by KUMAZAWA *et al.* (1956), and the chromosome count by FUKUSHIMA *et al.* (1962), or counted in this study. The name of each cultivar was listed elsewhere (HIRAI *et al.* 1989). s: separate or un-named group, n.e.: not examined.

Ribosomal DNA			Mito- chondrial DNA pattern	Corm Protein	Morpho- logical group	Chromosome Number (2n=)	Accession Number at NIVOT
Pattern	Extra Taq 1 site	Queens- land variant					
I	—	—	I	E	Eguimo	42	2, 3, 4, 5, 6, 7, 53
					s	n.e.	87 (Eguimo)
					s	n.e.	8 (O-dodare)
II	+	—	I	D	Hasubaimo	42	9, 10, 12, 31, 44, 51, 76, 99, 102
					Dodare	42	11, 13, 24, 25, 26, 27, 28, 29, 32, 40, 54, 57, 58, 82, 97, 101
					s	n.e.	93, 120 (Oonoimo) 98 (Oyazeme)
					Shogaimo	42	55, 86
III	+	—	I	I	Ishikawa-wase	42	14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 30, 50, 88, 94
					s	n.e.	96 (Futagoimo)
					Kurojiku	42	34, 52, 90
IV	+	+	I	A	Akame	42	37, 72, 74, 78, 83, 84
V	+	+	II	A	s	42	80 (Shogatsuman)
VI	—	+	II	T	Tonoimo	28	38, 39, 41, 42, 43, 117, 118
					s	n.e.	89 (Niimo)
					Yatsugashira	28	45, 95, 73
					C	28	273 (Takenokoimo)
					M	28	103 (Migashiki)
VII	—	+	II	B	s	28	104 (Binroshin)
				n.e.	s	28	71 (Okinawa-aokuki)

highly polymorphic (APPELS and DVORAK 1982). This gene is, therefore, extensively used for phylogenetic and evolutionary studies. The insertion and deletion of short subrepeats within the large intergenic spacer region of rDNA is common in higher plants (KNAAK *et al.* 1990, DVORAK 1990, APPELS and HONEYCUTT 1986), so spacer fragment polymorphisms in taro are probably mostly due to such mutations. The size differences among Taq I and Hinf I spacer fragments from taro were generally closely correlated because the restriction sites of both enzymes flank the large intergenic spacer (Fig. 1). The extra Taq I sites in some spacer variants could have been gained or lost by point mutations or small length mutations.

Exchanges of DNA sequences between mitochondrial and other genomes have been reported in a range of plant species (STERN and PALMER 1984). Such exchange is not evident in our results. The single band Hind III patterns from taro (Fig. 4) indicate that there is just one genomic location for the sequences detected by the pea mitochondrial ATPase probe. We presume that patterns I and II represent separate mitochondrial lineages.

Variation in Japanese taros

Almost identical groupings of cultivars are indicated by the rDNA and protein patterns (Table 1). Within the previously recognised morphological groups, the general uniformity with respect to rDNA, mtDNA, and corm proteins, suggests that each group is composed of a single clone. Sexual reproduction by taro under field conditions has not been reported in Japan. We suppose that the triploids are inherently sterile because of their uneven distribution of chromosome during meiosis. Although some taros do flower in Japan, the low temperatures and short days of winter prevent successful maturation and seed production. Climate may be the major limiting factor for sexual reproduction by diploids in Japan. The many diploid and triploid cultivars could have arisen by vegetative mutation among a small number of introduced clones. Alternatively, there could have been many introduction from countries with the same clonal groups.

The associations of un-named morphological groups with named groups, according to rDNA and mtDNA patterns (Table 1), were in all cases consistent with the relationships proposed by HIRAI *et al.* (1989) following the survey of corm protein variation. The morphological groups Kurojiku and Ishikawa-wase displayed identical corm proteins and identical rDNA and mtDNA patterns (Table 1). These observations are consistent with previous suggestions (HIRAI *et al.* 1989) that Ishikawa-wase arose from Kurojiku by a recent bud mutation affecting morphology. The morphological groups Hasubaimo, Dodare, and Shogaimo displayed identical corm proteins and identical rDNA and mtDNA patterns (Table 1). These groups might belong to one clone that has mutated many times, or they might be the sexual offspring of a range of closely related diploids.

Progenitors

The Queensland rDNA variant and mtDNA pattern II were found in the wild Australian example of *C. esculenta* var. *aquatilis*. This diploid variety is widespread in the wild in many tropical areas of Asia and the Pacific (MATTHEWS 1991). Other wild varieties with such a wide range are not known. Var. *aquatilis* may have been a progenitor of Japanese diploid and triploid cultivars with the same rDNA variant or mtDNA pattern. These include all the diploids and the triploids Akame and Shogatsuman (Table 1). In the southern islands of

Japan, *aquaticus* is abundant as a ruderal plant, but is not known to flower (HOTTA 1970, MATTHEWS *et al.* 1992). It seems unlikely that the genotypically diverse cultivar groups arose from var. *aquaticus* within Japan. Except for the above mentioned Akame and Shogatsuman, Japanese triploid cultivars, namely Eguimo, Dodare and Ishikawa-wase showed no Queensland variant, and are suggested to be genetically distant from var. *aquaticus*.

Ribosomal DNA variants with a similar extra Taq I spacer site were found in Nepalese taros and in the Japanese triploids Ishikawa-wase, Futagoimo, Kurojiku, and Shogatsuman (Table 1, Fig. 3). These Japanese varieties may have a genetic influence from taros within or near Himalayan areas such as Nepal and Northeast India, where triploids are common (KAWAHARA 1978, KURUVILLA and SINGH 1981). The apparent absence of tetraploid taros (COATES *et al.* 1988, FUKUSHIMA *et al.* 1962) implies that triploids arose via unreduced gametes produced by diploid parents, rather than by mitotic doubling and subsequent interbreeding between tetraploids and diploids. In either case, triploids must have arisen from breeding diploid populations. These were probably tropical because taro flowering and seed have been recorded in many tropical areas in Asia and the Pacific, and not in temperate areas (MATTHEWS 1990).

The routes of dispersal into Japan.

The present study demonstrated the genetical difference of diploid and triploid taros in Japan. The former have genetic influence from tropical wild taro, and at least a part of triploid showed influence from taros from Himalayan region. This suggests the different dispersal route of taro into Japan. FUKUSHIMA *et al.* (1962) noted that varieties similar in morphology to triploids in Japan are redominant in northern China, and that varieties similar to Japanese diploids are common in southern China. SASAKI (1986) suggested that temperate triploids were introduced to Japan on a northern route from China, along the Yangtze River, and that diploid varieties were introduced from Taiwan via the Ryukyu Islands. Future DNA analyses of taro in the Ryukyu Islands, Taiwan and China may elucidate the proximate routes of taro into Japan.

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日本産サトイモ品種におけるリボソームDNAおよびミトコンドリアDNAの変異

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サトイモリボソーム (rDNA) のスペーサー部分の断片 (Fig. 1) をプローブとして, 日本産サトイモ 80 品種の rDNA を分析した. またエンドウミトコンドリア ATP アーゼのサブユニット α および 9 を含む断片をプローブとして, ミトコンドリア DNA (mtDNA) も分析した. rDNA では 7 種のパターンが得られた. 3 倍体品種の多くは rDNA スペーサー内部に Taq I 切断部位を持っていたが, 2 倍体品種には見られなかった (Fig. 2). mtDNA では 2 種のパターンが認められ, ほとんどの 3 倍体品種はパターン I を, 2 倍体品種はパターン II を示した (Fig. 4). この結果は形態的特徴と塊茎タンパク質電気泳動パターンに基づくサトイモ品種の分類と一致した (Table 1). 日本の 3 倍体品種である '石川早生' は rDNA スペーサー内部にネパール産サトイモの一部と共通な Taq I 切断部位をもっており (Fig. 3), また mtDNA パターンも一致し, この品種がヒマラヤ地方のサトイモの影響を受けたものと示唆された. 一方 '唐芋' 等の 2 倍体品種は 2.8 kb の Taq I 断片を示したが, これはオーストラリア北部に野生するサトイモ変種 *aquaticus* と共通のものであった. また mtDNA パターンも共通であった. この変種は広く熱帯地方に分布するので, 2 倍体品種はこの変種と近縁なものと推定された.