テンナンショウ属のアロザイム分化: (2) フデボテンナンショウ節

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journal or publication title	The journal of phytogeography and taxonomy
volume	42
number	1
page range	17-20
year	1994-06-25
URL	http://doi.org/10.24517/00055643

J. Phytogeogr. & Taxon.
42 : 17-20, 1994

Jin Murata* , Takayuki Kawahara** and Dedy Darnaedi*** : Allozyme Differentiation in *Arisaema* (Araceae) (2) Section *Fimbriata*

邑田　仁*・河原孝行**・デディ ダルナエディ***：テンナンショウ属の
アロザイム分化（2）フデボテンナンショウ節

Abstract

To provide genetic background for the systematics of *Arisaema*, allozyme differentiation in *Arisaema* was intended to study. In this study, four representative species of three different subgroups of sect. *Fimbriata* were examined by electrophoresis with 12 enzyme systems. The average genetic distance between the three subgroups of the sect. *Fimbriata* ranged from 0.37 to 0.48, which is far smaller than the values between the species of the sect. *Tortuosa* (0.83-1.37) (Murata and Kawahara 1994). Sect. *Fimbriata* is not so much differentiated genetically as is expected from its morphological diversity, especially in shoot organization.

Key words: allozyme, *Arisaema*, systematics, tropics.

Allozyme differentiation in *Arisaema* section *Fimbriata* was examined. Through a cladistic analysis based on morphology (Murata, 1990), a putative monophyletic group consisting of sections *Fimbriata* and *Decipientia* is separated as the sister group of all other sections, with two synapomorphies, i.e. evergreen leaves and well developed petiolules longer than adjacent inner rachises. Section *Decipientia* consists of two similar species distributed from southwestern China to north eastern India, while sect. *Fimbriata* is a fairly large group with some 20 species and distributed widely in tropical and subtropical SE Asia. In comparison to other sections of *Arisaema*, sect. *Fimbriata* is morphologically quite diversified. In other sections, intrasectional differentiation is recognized in the colour and shape of spathe and spadix appendix and mode of dissection of leaf blade. In sect. *Fimbriata*, differentiation is recognized not only in these characters but also in shoot organization such as phyllotaxis, position of normal leaves on the sympodial unit, position of lateral continuation shoot, and occurrence of accessory buds. Murata (1984) further divided this section into three subgroups, *Fimbriata* 1, 2 and 3. This study aims to examine the extent of genetic differentiation of this morphologically diverse section with reference to four species of three subgroups, i.e., *Arisaema grapsospadix* Hayata (*Fimbriata* 1), *A. laminatum* Blume and *A. inclusum* (N. E. Brown) v. Steenis (*Fimbriata* 2), and *A. filiforme* Blume (*Fimbriata* 3).

Materials and methods

Living plants from seven natural populations (Table 1) were transplanted to the Botanical Gardens, University of Tokyo. Chromosome numbers of the sample populations were previously determined as diploid (2n=24 in *A. laminatum* and *A. inclusum* and 2n=28 in *A. grapsospadix* and *A. filiforme*). Voucher specimens are preserved in the Herbarium, University of Tokyo (TI).

Horizontal starch gel electrophoresis was conducted with 12 different enzyme systems ; alcohol

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Table 1. A list of populations examined

Population name	Sample number	Locality (voucher specimen)
A. filiforme(1)	17	S. Kalimantan, Mt. Batu Besir (Murata, Dec. 18, 1990)
A. filiforme(2)	10	E. Kalimantan, Mt. Batu Harum (Murata, Dec. 18, 1990)
A. filiforme(3)	8	E. Kalimantan, Mt. Babi (Murata, Dec. 20, 1990)
A. filiforme(4)	18	W. Java, Mt. Gede (Murata 25616)
B. inclusum	26	W. Java, Mt. Gede (Murata 17701)
A. laminatum	20	S. Kalimantan (Murata *et al.* 26175)
A. grapsospadix	27	Taiwan, Tengchu (Murata 27028)

Table 2. Allele frequences at 15 loci in the populations examined

Locus	Allele	*A. filiforme* (1)	(2)	(3)	(4)	*A. grapso-spadix*	*A. inclusum*	*A. laminatum*
Gdh	a	1.00	1.00	1.00	0.72	1.00		
	b						0.02	
	c				0.04		0.69	0.95
	d				0.02		0.29	0.05
Mdl-1	a						0.02	
	b	1.00	1.00	1.00	1.00	1.00	0.98	1.00
Mdh-2		1.00	1.00	1.00	1.00	1.00	1.00	1.00
Mdh-3		1.00	1.00	1.00	1.00	1.00	1.00	1.00
Idh	a						1.00	
	b	0.15		0.19	0.19	0.94		0.25
	c	0.85	0.95	0.81	0.81	0.06		0.20
	d		0.05					0.55
Pgm-1	a					0.09		
	b	0.44	0.75			0.59		
	c	0.56	0.25	1.00	1.00	0.31		
	d						0.21	
	e						0.71	1.00
	f						0.04	
Pgi-2	a					0.42		
	b						0.46	
	c				0.53		0.54	0.45
	d			0.06		0.40		
	e	0.18						
	f			0.94	0.39			
	g				0.06	0.08		0.45
	h	0.68	0.90		0.03			
	i							0.10
	j		0.10					
	k	0.15				0.10		
6Pgd	a						0.98	
	b					1.00	0.02	0.45
	c	0.95	1.00	1.00	1.00			0.43
	d	0.06						0.13
Tpi-1	a					0.04		
	b	1.00	1.00	1.00	1.00	0.94	0.98	0.98
	c					0.02	0.02	
	d							0.03
Tpi-2	a					0.04		
	b	1.00	1.00	1.00	1.00	0.94	0.98	
	c					0.04	0.02	1.00
Skd	a							0.15
	b				1.00			
	c	1.00	1.00	1.00				0.85
	d					0.91	1.00	
	e					0.09		
Lap	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Ald	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Adh	a				0.03		0.04	
	b	1.00	1.00	1.00	0.97	1.00	0.96	1.00
Me	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 3. Gene diversity statistics for the populations examined

	P(%)	A	H
A. filiforme(1)	27	1.33	0.092
A. filiforme(2)	20	1.20	0.046
A. filiforme(3)	13	1.13	0.030
A. filiforme(4)	27	1.47	0.104
A. grapsospadix	40	1.53	0.113
A. inclusum	53	1.47	0.109
A. laminatum	40	1.41	0.149

P=Proportion of polymorphic loci; A=number of allels per locus; H=gene diversity.

Table 4. Mean genetic identities (upper triangle) and genetic distances (lower triangle) for populations examined

	1	2	3	4	5	6	7
1. *A. grapsospadix*	×	0.65	0.59	0.67	0.68	0.71	0.69
2. *A. inclusum*	0.42	×	0.75	0.69	0.64	0.66	0.64
3. *A. laminatum*	0.53	0.29	×	0.69	0.75	0.74	0.72
4. *A. filiforme*(4)	0.40	0.38	0.36	×	0.88	0.88	0.84
5. *A. filiforme*(2)	0.38	0.45	0.29	0.12	×	0.94	0.90
6. *A. filiforme*(1)	0.35	0.42	0.30	0.13	0.06	×	0.99
7. *A. filiforme*(3)	0.38	0.44	0.32	0.17	0.10	0.01	×

dehydrogenase (ADH), aldorase (ALD), glutamate dehydrogenase (GDH), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), malate dehydrogenase (MDH), malic enzyme (ME), phospho-glucoisomerase (PGI), phosphoglucomutase (PGM), 6-phospho-gluconate dehydrogenase (6PGD), shikimate dehydrogenase (SKD) and triose phosphate isomerase (TPI). ME was resolved using a tris citrate gel buffer system (0.042M tris, 0.007M citric acid, 0.004M LiOH, 0.025M bolic acid, pH7.6) and an electrode buffer consisting of lithium-borate (0.039M LiOH, 0.263M boric acid) (Soltis *et al.*, 1983). 6PGD and IDH were resolved in a system with a gel buffer of 1:3 dilution of the following electrode buffer and an electrode buffer of 0.065M L-histidine (free base) and 0.007M citric acid (pH6.5) (Cardy *et al.*, 1981). For the analysis of other enzyme systems and statistics, the same procedure as preceding paper (Murata and Kawahara, 1994) was applied.

Results and Discussion

A total of 15 loci, *Adh, Ald, Gdh, Idh, Lap, Mdh-1, Mdh-2, Mdh-3, Me, Pgi-2, Pgm-1, Skd, Tpi-1, Tpi-2,* and *6Pgd,* were used for genetic analysis. Table 2 shows the frequencies of alleles at the 15 loci in the populations examined. *Ald, Me, Mdh-2* and *Mdh-3* are fixed for the same allele in all plants examined. $Tpi\text{-}1^{b}$, Adh^{b} and $Mdh\text{-}1^{b}$ are found to be major in all populations examined. No other alleles are commonly found in all populations. Idh^{a} is specific to *A. inclususm.* Gene diversity statistics (Table 3) was calculated from the values in Table 2. The proportion of polymorphic loci (P) and gene diversity within populations (H) are generally lower in the populations of *A. filiforme.* The values of Nei's (1972) genetic distance (Table 4) between sample populatuions were calculated using allelic frequencies shown in Table 2. A phenogram (Fig. 1) was constructed by the neighbour-joining method (Saitou and Nei, 1987) based on the genetic distances.

The four populations of *A. filiforme* of *Fimbriata* 3 form a single cluster. The genetic distances among the populations of *A. filiforme* are smaller than the values normally found between congeneric species in the flowering plant (Crawford, 1983). The interpopulational genetic distances between Kalimantan and that of Java (D=0.12-0.17) are considerably larger than between the populations within Kalimantan (D=0.01-0.10). Geographical differentiation between the two islands is recognized also in morphology: Kalimantan plants are characteristic with green spathe while Javan plants are characteristic with purple spathe.

Arisaema inclusum and *A. laminatum*, which belong to *Fimbriata* 2, form another cluster. This supports morphological recognition of this subgroup, *Fimbriata* 2 (Murata, 1984). The genetic distance between *A. inclusum* and *A. laminatum* (D=0.287) is relatively low but well exceeds the lowest value normally found between congeneric species (Crawford, 1984).

From Table 4, average genetic distance among the three subgroups, i.e. *Fimbriata* 1 (*A. grapsospadix*), *Fimbriata* 2 (*A. laminatum* and *A. inclusum*) and *Fimbriata* 3 (*A. filiforme*), are calculated to be D=0.48 (between *Fimbriata* 1 and 2), 0.

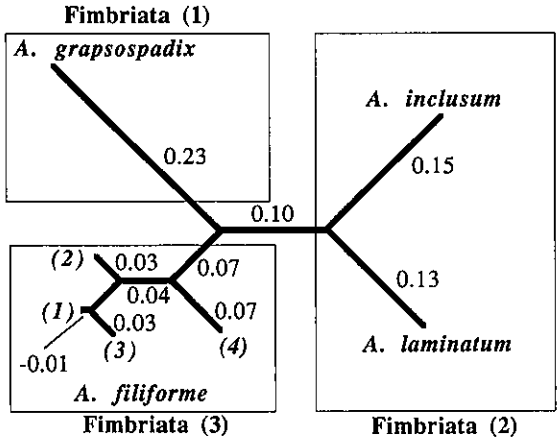

Fig. 1. A genetic distance phenograms of examined populations by neighbour-joining method. Values are standard genetic distances.

37 (between *Fimbriata* 2 and 3) and 0.38 (between *Fimbriata* 1 and 3), respectively. These values are far smaller than the value between the species of sect. *Tortuosa* (0.83-1.37) and comparable to the values between the geographically distant populations of *A. thunbergii* (0.33-0.57), and *A. negishii* and *A. heterocephalum* of sect. *Clavata* (0.35) (Murata and Kawahara, 1994). Consequently, sect. *Fimbriata* is cosidered as genetically not so much diversified as is expected from its morphological diversity. Sect. *Fimbriata* is a single section in tropical regions. Differentiation of shoot organization might progress rapidly as adaptation for tropical habitat.

This study was supported by Grant-in-Aid for Scientific Research No. 02640534 and 05640785 from the Ministry of Education, Science and Culture, Japan to J.M.

References

Cardy, B.J., Stuber, C.W., and Goodman, M.M. 1981. Technics for starch gel electrophoresis of enzyme from maize (*Zea mays*), revised. Instl. Stat. Mimeogr. Ser. **1317**. North Carolina State University.

Crawford, D.J. 1983. Phylogenetic and systematic inferences from electrophoretic studies. *In*: Tanksley, S.O. and T.J. Orton (eds.), Isozyme in plant genetics and breeding, Part A, pp.257-287. Elsvier, Amsterdam.

Murata, J. 1990. Present status of *Arisaema* systematics. Bot. Mag. Tokyo **103**: 371-382.

Murata, J. and Kawahara, T. 1994. Allozyme differentiation in *Arisaema* (Araceae) (1) Sections *Clavata* and *Tortuosa*, with special reference to the systematic position of *A. negishii*. J. Phytogeogr. Taxon. **42**: 11-16.

Nei, M. 1972. Genetic distance between populations. Am. J. Bot. **63**: 2448-1453.

Odrzykoski, I.J., and Gottlieb, L.D. 1984. Duplications of genes coding 6-phosphogluconate dehydrogenase in *Clarkia* (Onagraceae) and their phylogenetic implications. Syst. Bot. **9**: 479-489.

Saitou, N. and Nei, M. 1987. The neighbour-joining method; A new method for reconstructing phylogenetic trees. Mem. Biol. Evol. **24**: 189-204.

Soltis, D.E., Haueler, C.H., Darrow, D.C., and Gastony, G.J. 1983. Starch gel electrophoresis of ferns: a complication of grinding buffers, gel and electrode buffers, and staining schedules. Am. Fern J. **73**: 9-27.

摘　要

熱帯・亜熱帯に広く分布するテンナンショウ属フデボテンナンショウ節におけるアロザイムの分化を調べた。この節は，生殖器官の多様化ばかりでなく，他の節では見られない独特の分化（シュート構成の分化）を節内で生じており，形態的には非常に多様性に富んだ節である。フデボテンナンショウ節はさらに3亜群に分けられるが，本研究ではこの節の遺伝的な分化を調べるため，3亜群の4種7集団について検討した。この結果，フデボテンナンショウ節の3亜群間の遺伝的距離Dは0.37から0.48の間であった。これは，先に報告した結果（Murata & Kawahara, 1994）と比較すると，Tortuosa節の種間で0.83から1.37であったのに比べてはるかに小さく，ウラシマソウ種内の地理的に離れた集団間（0.33から0.57）や*Clavata*節のシマテンナンショウとアマミテンナンショウの種間（0.35）にほぼ匹敵する。このことから，フデボテンナンショウ節は，形態的な多様化は著しいが遺伝的にはあまり分化が進んでいない群であるとみなすことができる。シュート構成が熱帯という環境で急速に適応分化したのかも知れない。

(received December 27, 1993; accepted March 24, 1994)