

Gender biasing in *Arisaema* – a unique and rare phenomenon

Preeti Srivastava* and B. K. Banerji

Floriculture Section, National Botanical Research Institute, Rana Pratap Marg, Lucknow 226 001, India

***Arisaema* is flowering plant belongs to monocotyledonous family Araceae (Arum family). The plant is known by many names due to its peculiar flowering habit and the shape of its attractive inflorescence. The plant resembles very much with insectivorous pitcher plant due to its foliar modification like a pitcher of a pitcher plant with attractive colour combination. These colours are mending for attracting the insects for pollination purpose. This unique plant has a long life of 100 years. The plant has alteration behaviour of sex pattern in response to change in ambient environment and or changes in size or age.**

Keywords: *Arisaema triphyllum*, gender biasing, spadix, pulpit, sex switching.

ARISAEMA, commonly known as Jack-in-the-pulpit, belongs to family Araceae. The name 'Jack' has many meanings. One is a nickname for John. Another means 'male', as in jackass. It has also been used for sailor (Jack tar), labourer (steeplejack), a man who does nothing well (Jack of all trades) and for a fellow who went through town carrying a lamp while crying out the time and curfews (Jack-O-Lantern). Jack has also been a common term for the devil. Jack-in-the-pulpit is a little plant with a hiding inflorescence inside. As for sex, the plant is a switch hitter, sometimes Jack, sometimes Jill. Jack-in-the-pulpits are perennials and grow each season from a corm, like an onion. They can live up to 100 years. The shoot will have one or two stems. Each stem usually has three leaves if we are referring to *Arisaema triphyllum*. The pulpit, or spathe, is green, with white, brown or purple stripes. The minister, or spadix, usually has a pale cream spike inside. These plants are either a Jack or a Jill. If you open the flower and look inside, the female has a developing cluster of tiny green berries. The male does not.

About the family

Araceae is a monocotyledonous family (Arum family) of flowering plants in which flowers are borne on a type of inflorescence called a spadix. The spadix is usually

accompanied by, and sometimes partially enclosed in, a spathe or leaf-like bract. The plant is unique due to its resemblance with the pitcher plant and a strange sex pattern in the flowers. This family of 107 genera and over 3700 species is the most diverse in the New World tropics, although it is also distributed in the Old World tropics and north temperate regions. Among the largest inflorescence in the world is that of the Arum *Amorphophallus titanum* (Titan Arum). An interesting peculiarity is that this family includes the largest unbranched inflorescence, that of the Titan Arum, often erroneously called the 'largest flower' and the smallest flowering plant with smallest fruit found in *Wolffia* (duckweed). Some of the important members of the family include *Arisaema*, *Colocasia*, *Zantedesthia*, *Anthurium*, *Xanthosoma*, *Monstera*, etc. There are rare evidences present that elucidate the alteration behaviour of sex pattern in response to change in ambient environment and/or changes in size or age. Many plants have complete flowers that have both male and female parts (hermaphrodite). Some have only male or female parts (dioecious), whereas others have a mix of male and female flowers (monoecious) on the same plant. Some plants even have mixes that include all three types of flowers, where some are only male, some are only female, and some are both male and female (subdioecious). A distinction needs to be made between arrangements of sexual parts and the expression of sexuality in single plants versus the larger plant population.

Distribution

Arisaema comprises about 150 species of forest understorey herbs¹⁻³. About 140 species occur in the Himalayas, southern India, Sri Lanka, China, Korea, Japan and Southeast Asia; one species ranges from Nepal, across Saudi Arabia and Oman to East Africa, five or six species are endemic in East Africa; and three are endemic to North America (Jack-in-the-pulpit, green dragon). *Arisaema* typically occurs in cool temperate environments, including mountain, grassland, with a few species thriving near timberline at 4200–4500 m in the Himalayas and at 3200 m in East Africa (on Mt Ruwenzori). On the basis of geographic distribution range of the genus, most species are deciduous and over winter via underground tubers or rhizomes. Only about 38 species are evergreen.

*For correspondence. (e-mail: prisri.aks1985@gmail.com)



Figure 1. Foliage, inflorescence, fruits and seeds of *Arisaema* species. *a–f*, Foliage and inflorescences of different *Arisaema* species. *g*, Unripe berry (fruit) showing green fruits. *h*, Mature berry (fruit) showing orange fruits. *i*, Bean shape seeds.

Propagation of genus *Arisaema*

Arisaema plants are propagated sexually by bean shaped seeds (Figure 1 *i*) and by vegetative means. The sexually produced diaspores are berries (Figure 1 *g* and *h*) that are spread by birds and asexual propagation occurs via tuber offsets, stolons or rhizomes.

Important *Arisaema* species and their distribution

Morphological description of vegetative and floral characters of five important species (Figure 1 *a–f*) along with their respective distribution is given below.

Arisaema costatum

It is found in high elevations range of 6000–9000 ft in Nepal and neighbouring Tibet. *A. costatum* is a stunning

plant even without a showy inflorescence. The 3 ft tall, reddish petiole is topped with a three-part leaf, similar to *Arisaema speciosum*, which under good conditions, can reach 3 ft wide. In late spring, the peduncle (flower stalk) emerges to nearly 2 ft tall with a large, dark purple and white striped hood which ends in a thin red–purple tail. Inside the hood, the thin black–purple spadix stands out against the ‘pulpit windows’ (hardiness zone 6–8).

Arisaema dahaiense

A. dahaiense is a species, named in 1977, from the Gaoligong (Dahai) Shan region of Western Yunnan, China, that is similar (or identical to) *Arisaema galeatum* (P. Bruggeman, pers. commun.). Although it is similar to many of the hard-to-grow, high Himalayan species, *A. dahaiense* has proven quite growable in our climate. The petiole supports large trifoliate leaves that are similar to

A. speciosum. The hood-like dark purple, yellow-veined spathe and long tongue (spadix) reminds us of *Arisaema griffithii* (hardiness zone 6–7).

Arisaema griffithii (cobra lily)

A. griffithii is commonly known as cobra lily. Although the inflorescence resembles *A. ringens* in shape, it emerges on a short peduncle alongside the tripartite leaf, whereas *A. ringens* sports its inflorescence atop a leafed pseudostem. The long, thin, black tongue of *A. griffithii* hangs from the bizarre, purple and yellow striped, cobra head-like spathe, all held atop a short, 3.6" peduncle in mid-spring. *A. griffithii* occurs in open forests upto 12,000 ft elevation, and for this reason resents summer heat and poor drainage (hardiness zone 5–7). Cobra lily inflorescence (flower heads) consists of many parts, but the two most prominent are the spathe (pulpit) and spadix (Jack). The spathe is the pitcher and/or hood, whereas the spadix is the 'stalk' inside the inflorescence that holds the sex organs. In some species the spathe develops into a long thread-like tail, whereas in other species it is the spadix which copies this habit. Cobra lily plants are composed of an underground tuber, rhizome, or pseudo-rhizome (name for structures on plants like *A. speciosum*, which are intermediate between tubers and rhizomes) that gives rise to either a pseudo stem (carries leaves and inflorescences), or a petiole which only carries the leaf. For species without a pseudo stem, the inflorescence emerges on a short stalk called a peduncle alongside the leaf petiole. For species which have a pseudo stem, the inflorescence emerges either on top of, or at some point along it on a short stem, also called a peduncle. Cobra lily tubers/rhizomes occur primarily as one of two shapes: either discoid like a flying saucer (*A. ringens*) or shaped like a cigar (*A. speciosum*).

On the basis of morphological traits, taxonomists have divided cobra lily species into ten groups:

- (i) Section *Arisaema* – large, three-lobed leaves with a long pendulous (spadix) tongue.
- (ii) Section *Attenuata* – long spadices, central leaflet upturned on emergence.
- (iii) Section *Dochafa* – small, yellow inflorescence.
- (iv) Section *Fimbriata* (Fimbriate spathe species).
- (v) Section *Flagellarisaema* – long tongue (spadix) species.
- (vi) Section *Franchetiana* – large tripartite leaves and flying saucer-shaped tuber.
- (vii) Section *Pistillata* (formerly *Pedatisecta*) – pedate leaf species.
- (viii) Section *Sinarisaema* – radial leaf species.
- (ix) Section *Tortuosa* – long tongue (spadix) species.
- (x) *Arisaema* hybrids.

A. speciosum

A. speciosum has large, three-lobed leaves similar to *Arisaema franchetianum*, except that the leaves are much more deeply veined. The tuber is also quite different, looking more like a long cigar than the typical rounded *Arisaema* tuber. *A. speciosum* typically grows to 2 ft height with attractive cinnamon-patterned petioles. The short peduncle (floral stalk) emerges alongside the leaves in early May (hardiness zone 7–8).

A. speciosum 'Himalayan giant'

It is an amazing form of *A. speciosum*, which often goes by the invalid name of *A. speciosum* var. *magnificum*. It is simply a giant race of *A. speciosum* discovered in India. From one end of the unusual cigar-shaped tuber (plant horizontally), the new growth emerges in late spring. The 30 ft tall, cobra-marked petiole is topped with three dark green, heavily textured leaflets, each edged in red. The inflorescence, which arises from the base on a short peduncle in early May (NC), is composed of a wine and white striped hood, holding a whitish-pink spadix that starts out sturdy and thick, becoming a mere crumpled red thread at the end. Well drained, but slightly moist soils during the dormant period are the key to success with *A. speciosum*.

Pollination

Difference between male and female plants

If the plant has one stem and three leaves, it is usually a male; two stems and six leaves represent a female. Generally the male has bigger corms at the end of the season, and the female has bigger corms at the beginning of the season. Also, female plants show green bumps inside the spathe, that will become future red berries.

The plants are mostly cross-pollinated and the pollination is usually by fungus gnats (Mycetophilidae) and sciarid gnats (Sciaridae), but pollination by nectar-seeking small bees may also play a role^{4,5}.

Pitfall-trap system

One of the more conspicuous diversifications found in this genus is a trap system for pollinators. Kugler⁶ defined a trap as the architecture of a flower or an inflorescence that prevents pollinators from escaping immediately by capturing them briefly until pollination is completed. The trap system in aroids is a modification of the whole inflorescence⁷. A well-known trap system in aroids is the pitfall trap in the genus *Arisaema*^{5,8}. In this system, species always form a spathe tube, and usually form a spadix

appendage, that has been believed to attract pollinators^{2,5}. In *Arisaema*, individual plants produce male or female inflorescences depending on the size of the plant⁹⁻¹⁹. There is a distinguishing difference between the sexes: the male has a small hole at the bottom of the spathe tube, and the female does not^{5,20}.

Sex switching

Some plants undergo the phenomenon called as sex switching, like *A. triphyllum* which expresses sexual differences at different stages of growth. In some Arums smaller plants produce all or mostly male flowers and as plants grow larger over the years, the male flowers are replaced by more female flowers on the same plant. *A. triphyllum* thus covers a multitude of sexual conditions in its lifetime; from nonsexual juvenile plants to young plants that are all male, and as plants grow larger they have a mix of both male and female flowers, to larger plants that have mostly female flowers²¹. Another species of *Arisaema* found in America, commonly called green dragon (*Arisaema dracontium*; Araceae) is a perennial woodland herb capable of switching gender from year to year. Small flowering plants produce only male flowers, but when larger they produce male and female flowers, simultaneously. Distinct male and monoecious phenotypes (referred to hereafter as plants) share a single underlying cosexual genotype²². Other populations have plants that produce more male flowers early in the year and as plants bloom later in the growing season they produce more female flowers. In plants like *Thalictrum dioicum*, all the plants in the species are either male or female. Species that switch gender between seasons make alternative experimental tools for understanding the ecological systems and ecological factors favouring the reproductive allocation of male or female function because there are no gender-based genetic differences. Gender changing behaviour in plants is not restricted to switches from male to female and (vice versa) between seasons. In a number of species plants are male when small and stressed and monoecious when larger, e.g. *Pinus* and *Apodanthera*.

Sex-changing behaviour in *Arisaema*

Arisaema is notorious for its interannual 'sex change' and is the only Araceae, and one of very few angiosperms, that has labile sex determination. Environmental, or labile, sex determination, is a life-history strategy in which sex is determined by the environment and may change during an individual's lifetime^{23,24}. It has evolved an unknown number of times in animals and plants, with *Arisaema* being one of the best-documented cases in plants²⁵. Sex expression in *Arisaema* is dependent on nutrient status, with several reversals possible during a plant's life. Large plants produce staminate and pistillate

flowers or only pistillate flowers, and function as hermaphrodites or females. Small plants produce only staminate flowers. As demonstrated experimentally, and well-known to *Arisaema* growers, size (thus sex) is influenced by resources accumulated in the root-storage organs, with effects carried over for several years and species apparently very long-lived (20 years or more)^{13,14}. All *Arisaema* are sex changers, although literature before 1990 sometimes cited *A. flavum* as consistently producing male and female flowers simultaneously. However, Murata²⁶ discovered sex-changing populations of *A. flavum*, described as subspecies *tibeticum*, leaving the remaining two subspecies of *A. flavum* as the only known non-sex-changing entities in *Arisaema*. Remarkably, subspecies *tibeticum* is diploid, and the two non-sex-changing subspecies are tetraploid and set viable seeds after selfing (automatic selfing is prevented in sex-changing species of *Arisaema*). This suggests a return from environmental sex determination to simultaneous bisexuality concomitant with polyploidy and regular selfing. Because of its unusual male flowers (with a single stamen versus the usual 3-5) and the absence of sex change in two of its three subspecies, *A. flavum* has been seen as 'phenetically most primitive'²⁷, while others have seen it seen as derived^{5,28}. The monophyly and phylogenetic position of this species and the possibility of a secondary loss of environmental sex determination are among the questions studied here. Except for its unusual sexual strategy, *Arisaema* shares its reproductive and vegetative characters with *Pinellia*, a genus of six species in temperate East Asia, and *Typhonium*, a heterogeneous assemblage of about 50 species from tropical Asia, southeast Australia, and tropical Africa (*T. venosum*)²⁹⁻³¹. Species numbers are moot since *Typhonium* is paraphyletic. At least ten species have been transferred between these genera; for example, *A. hirsutum* S. Y. Hu [*Typhonium hirsutum* (S. Y. Hu) J. Murata et Mayo], *A. submonoicum* Gagnep. [*T. horsfieldii* (Miq.) Steenis], and *A. tripartitum* Engl. [*Pinellia tripartita* (Blume) Schott], illustrating the indistinct boundaries of the genera.

Reasons for sex change

According to many authors, sex of an individual of a dioecious plant species is fixed throughout life and determined solely by the genetic composition of an individual and is not responsive to environmental responses. According to Freeman *et al.*²⁴, there are over 25 families and 50 species, including unisexual individuals that have functioned as male at one time and female at another, or have produced hermaphroditic offspring.

Some others think that environmental factors are responsible for alterations in sexual characters. The ratio of male-to-female flowers on individuals of selected monoecious and of male-to-female organs in flowers of perfect flowered taxa has likewise proven to be manipu-

late through alterations of the plant environment as reported in *Catasetum* sp., *Kalanchoe diagraphontium*, *Cucumis sativa* L., etc. through high light intensity; in *Xanthium strumarium* and *Cannabis sativa* through alteration in photoperiod, manipulation of manure as in *A. triphyllum* and *Humulus japonica*. Natural selection is predicted to select for male-biased populations when male fitness is less dependent upon environmental conditions than female fitness, and when the population is in a poor environment^{32–34}. Under better environmental conditions, the sex ratio is expected to become more female-biased, because females will be relatively more fit compared to males³². The sex ratio presumably reflects the relative cost of male reproduction compared to female³⁵.

While working on stony corals³⁶, illustrated that bidirectional sex change has mainly evolved to increase the overall fitness, reinforcing the important role of reproductive plasticity in scleractinian corals in determining their evolutionary success.

Conclusion

Jack-in-the-pulpit (*Arisaema*) plants are beautiful in the woodland garden, with attractive leaves and an unusual flower; some of them being the most compelling garden specimens. They are easy to grow when planted in the proper site. *Arisaema* spp. mainly *triphyllum* is a true dioecious plant as male bisexual plants produce only pollen and female bisexual plants only fruits, or each plant only reproduces through either the male or female function.

- Murata, J., An attempt at an infrageneric classification of the genus *Arisaema* (Araceae). *J. Fac. Sci., Univ. Tokyo, Sect. 3*, 1984, **13**, 434–482.
- Gusman, G. and Gusman, L., In *The Genus Arisaema. A Monograph for Botanists and Nature Lovers*, Ganter Verlag, Ruggell, Liechtenstein, 2002.
- Li, H., Zhu, G. and Murata, J., *Arisaema*. In *Flora of China* (eds Wu, C. Y. and Raven, P.), Science Press, Beijing, China and Missouri Botanical Garden, St Louis, Missouri, USA (in press).
- Murata, J., Ren, C., Murata, H. and Ogawa, S., *Arisaema flavum*, a honey producing Araceae, In 15th International Botanical Congress, Yokohama, Japan, Abstr. 1203, 1993.
- Vogel, S. and Martens, J., A survey of the function of the lethal little traps of *Arisaema* (Araceae), with records of pollinating fungus gnats from Nepal. *Bot. J. Linn. Soc.*, 2000, **133**, 61–100.
- Kugler, H., Einführung in die Blütenökologie, Fischer, Stuttgart, Germany, 1995.
- Richards, A. J., *Plant Breeding Systems*, Chapman & Hall, London, 2nd edn, 1997.
- Van Der Pijl, L., On the flower biology of some plants from Java with general remarks on fly-traps. *Ann. Bogor.*, 1953, **1**, 77–99.
- Schaffner, J. H., Control of the sexual state in *Arisaema triphyllum* and *A. dracontium*. *Am. J. Bot.*, 1922, **9**, 72–78.
- Maekawa, T., On the phenomena of sex transition in *Arisaema japonica*. *J. Coll. Agric., Hokkaido Imperial Univ.*, 1924, **13**, 217–305.
- Policansky, D., Sex choice and the size advantage model in Jack-in-the-pulpit (*Arisaema triphyllum*). *Proc. Natl. Acad. Sci. USA*, 1981, **78**, 1306–1308.
- Bierzuchudek, P., The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecol. Monogr.*, 1982, **52**, 335–351.
- Bierzuchudek, P., Assessing 'optimal' life-histories in a fluctuating environment: the evolution of sex-changing by jack-in-the-pulpit. *Am. Nat.*, 1984, **123**, 829–840.
- Bierzuchudek, P., Determinants of gender in jack-in-the-pulpit: the influence of plant size and reproductive history. *Oecologia*, 1984, **65**, 14–18.
- Lovett-Doust, J. and Cavers, P. B., Sex and gender dynamics in Jack-in-the-pulpit. *Arisaema triphyllum* (Araceae). *Ecology*, 1982, **63**, 797–808.
- Lovett-Doust, J. and Cavers, P. B., Resource allocation and gender in Green Dragon *Arisaema dracontium* (Araceae). *Am. Midl. Nat.*, 1982, **108**, 144–148.
- Kinoshita, E., Size–sex relationship and sexual dimorphism in Japanese *Arisaema* (Araceae). *Ecol. Res.*, 1986, **1**, 157–171.
- Kinoshita, E., Sex change and population dynamics in *Arisaema* (Araceae) I. *Arisaema serratum* (Thunb.) Schott. *Plant Spec. Biol.*, 1987, **2**, 15–28.
- Takashu, H., Life history studies on *Arisaema* (Araceae) I. Growth and reproductive biology of *Arisaema urashima* Hara. *Plant Spec. Biol.*, 1987, **2**, 29–56.
- Barnes, E., Some observations on the genus *Arisaema* on the Nilghiri hills, South India. *J. Bombay Nat. Hist. Soc.*, 1935, **37**, 630–639.
- Ewing, J. W. and Klein, R. M., Sex expression in Jack-in-the-pulpit. *Bull. Torrey Bot. Club*, 1982, **109**(1), 47–50.
- Clay, K., Size-dependent gender change in Green Dragon (*Arisaema dracontium*; Araceae). *Am. J. Bot.*, 1993, **80**, 769–777.
- Charnov, E. L. and Bull, J., When is sex environmentally determined? *Nature*, 1977, **266**, 828–830.
- Freeman, D. C., Harper, K. T. and Charnov, E. L., Sex change in plants: old and new observations and new hypotheses. *Oecologia*, 1980, **47**, 222–232.
- Schlessman, M. A., Gender diphasy ('sex choice'). In *Plant Reproductive Ecology: Patterns and Strategies* (eds Lovett Doust, J. and Lovett Doust, L.), Oxford University Press, New York, 1988, pp. 139–153.
- Murata, J., Present status of *Arisaema* systematics. *Bot. Mag. Tokyo*, 1990, **103**, 371–382.
- Grayum, M. H., Evolution and phylogeny of the Araceae. *Ann. Mo. Bot. Gard.*, 1990, **77**, 628–697.
- Li, H., Himalayas–Hengduan mountains – the center of distribution and differentiation of the genus *Arisaema*. In *Geological and Ecological Studies of Qinghai–Xizang Plateau* (ed. Dongsheng, D.), Science Press, Beijing, China, 1981, vol. 2, pp. 1321–1327.
- Sriboonma, D., Murata, J. and Iwatsuki, K., A revision of *Typhonium* (Araceae). *J. Fac. Sci., Univ. Tokyo, Sect. 3*, 1994, **15**, 255–313.
- Hettterscheid, W. L. A. and Boyce, P. C., A reclassification of *Sauromatum* Schott and new species of *Typhonium* Schott (Araceae). *Aroideana*, 2000, **23**, 48–55.
- Hettterscheid, W. L. A., Sookchaloem, D. and Murata, J., *Typhonium* (Araceae) of Thailand: new species and a revised key. *Aroideana*, 2001, **24**, 30–55.
- Bull, J. J., Sex-ratio evolution when fitness varies. *Heredity*, 1981, **46**, 9–26.
- Bulmer, M. G. and Bull, J. J., Models of polygenic sex determination and sex-ratio control. *Evolution*, 1982, **36**, 13–26.
- Bull, J. J. and Charnov, E. L., How fundamental are Fisherian sex ratios? *Oxf. Surv. Ecol. Biol.*, 1988, **5**, 96–135.
- Charnov, E. L., In *The Theory of Sex Allocation* Princeton, Princeton University Press, Princeton, 1982, p. 355.
- Loya and Sakai, Bidirectional sex change in mushroom stony corals. *Proc. R. Soc. London, Ser. B*, 2008, **275**, 2335–2343.

Received 14 June 2011; accepted 23 December 2011