A comparison of size and sexual expression in populations of *Arisaema macrospathum* Benth. and *A. dracontium* (L.) Schott (Araceae)

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ABSTRACT

The sexual expression or breeding system for tropical populations of *Arisaema macrospathum* was compared with that of its temperate counterpart, *A. dracontium*. Although *A. macrospathum* populations are morphologically very similar to *A. dracontium*, they differ markedly in sexual expression. Temperate populations of *A. dracontium* are andromonoecious, while those of *A. macrospathum* occurring in cloud forest were found to bear only unisexual flowers, staminate or pistillate with monoecious individuals completely lacking. Male plants produced a mean of 42.7 flowers/spadix while females produced a mean of 60.9. For males, number of flowers/spadix showed a significant, positive relationship with plant size as measured by basal stem diameter, but no relationship was detected for females. Non-flowering and male plants did not differ in size, but were significantly smaller than female plants as is typical for the congeneric *A. triphyllum* and probably switch gender under similar circumstances also. Considering the entire geographic range, *A. dracontium* exhibits a gradual decline in plant size, number of flowers/spadix for males, and an increase in the expression of female plants along a north-south gradient. This gradual decline in size would appear to extend into populations of *A. macrospathum* and suggests a close evolutionary relationship. Differences in sexual expression between the two species may be related to geographical isolation and the presence or absence of competing congeneric species.

KEY WORDS

Arisaema macrospathum, Araceae, sexual expression, cloud forest, Mexico.

INTRODUCTION

Arisaema macrospathum Benth., *A. dracontium* (L.) Schott and *A. triphyllum* (L.) Schott are the three *Arisaema* species found in North America (Correll & Johnston, 1979; Gleason & Cronquist, 1991; McVaugh, 1993). These perennial species are distributed mostly in temperate regions from southern Canada (Ontario and Quebec; Yang *et al.*, 1999) through the eastern United States and south into Mexico, particularly along the montane east coast (Johnston *et al.*, 1989: McVaugh, 1993). *Arisaema dracontium* and *A. triphyllum* have been the subject of a number of ecological and evolutionary studies (Bierzychudek, 1982, Lovett-Doust & Cavers, 1982, Clay, 1993, Yang *et al.*, 1999) and both have long been known to change sex between seasons (Schaffner, 1922; Bierzychudek, 1984). Sexual expression of individual plants is usually related to plant size and environmental factors affecting plant size such as nutrition, leaf area, and corm size.

Typically, populations of *A. dracontium* are composed of male plants bearing only staminate flowers or monoecious plants bearing staminate and pistillate flowers (Schaffner, 1922; Lovett-Doust & Cavers, 1982; Clay, 1993; Boles, 1996); the breeding system is thus said to be andromonoecious. On rare occasions, strictly female plants bearing only pistillate flowers have been noted. In studies by Schaffner (1922)

involving 872 plants, and Lovett-Doust & Cavers (1982) involving 964 plants, no female individuals were ever observed. However, in a study by Clay (1993) involving 338 individuals a single female individual was recorded. It may be noted that this last study was conducted around Baton Rouge, Louisiana which is in the southern portion of the species' distribution. Populations in Mexico are considered a distinct species, *A. macrospathum* (Correll & Johnston, 1979; Johnston *et al.*, 1989; McVaugh, 1993). McVaugh has described *A. macrospathum* as being dioecious since all individuals produce only one flower type, staminate or pistillate. Over the past few years, we have been studying the pollination ecology and floral thermogenicity of *Magnolia tamaulipana* found in cloud forest of the Biosphere Reserve El Cielo, Tamaulipas, Mexico (Dieringer *et al.*, 1999). It was here that we began a preliminary study on reproductive biology of *A. marcrospathum* in cloud forest. Data collection included population size, population density, number of flower and non-flowering individuals, number and sex of flowers produced per individual, and plant size.

MATERIALS AND METHODS

The El Cielo Reserve lies just south of the Tropic of Cancer within the Sierra Madre Oriental along the eastern coast of northern Mexico (23°12′–23°03′N and 99°18′–99°07′W; for a detailed description of the area, see Puig *et al.*, 1987). Cloud forest (bosque mesófilo de montaña; Rzedowski, 1978) is a moist, montane vegetation type and in eastern Mexico typically contains both temperate (e.g. *Quercus, Carpinus, Liquidambar, Platanus, Pinus*) and tropical (e.g. *Engelhardtia, Clethra, Dendropanax, Podocarpus*) elements. At El Cielo, cloud forest vegetation typically occurs between 800–1,600 m. The study population was located along side the road running between the ejidos San José and La Gloria at approximately 1,600 m elevation. On May 20, 1998, plants in the study area were past-flowering; all spathes and spadices were present although spathes were dry and papery. The population size and density were estimated by marking off the area containing plants with a meter tape and counting all individuals. In addition whether plants had flowered or not and sexuality of flowering plants was recorded. All plants within the population plus additional plants encountered nearby were used to record data on number of flowers produced for each plant and basal stem diameter as a measure of plant size (Clay, 1993). A total of 47 past-flowering plants were sampled, 33 from the study population and 14 from the surrounding area. Spadices of all 47 plants were fixed in alcohol and returned to the lab to count the number of flowers under a dissecting scope. Basal stem diameter was measured using a vernier caliper accurate to 0.01 mm.

RESULTS

The population area measured 50 × 25 meters and contained 147 plants for a density of 0.12 plants/m^2. Of the 147 plants, 33 (22.4%) were flowering and of these 33, 24 (16.3%) were males and 9 (16.1%) were females. Only plants with unisexual flowers, staminate or pistillate, were observed. No monoecious individuals were ever noted while non-flowering and male plants did not differ in size, female plants were significantly larger than either non-flowering or male plants (Table 1). Non-flowering plants ranged in size from 2.8–7.8 mm in basal stem diameter, male plants ranged from 2.4–7.3 mm, and female plants ranged from 5.0–15.0 mm.

Male plants produced a mean of 42.7 flowers/spadix (SE = 1.9, range 30–75) and female plants a mean of 60.9 flowers/spadix (SE = 3.0, range 34–82; Table 2). The relationship between plant size and flower production was examined using correlation. Number of flowers/spadix showed no significant relationship with plant size or basal stem diameter for females ($r = -0.09$, $N = 20$, $P = 0.72$; Pearson correlation) (Fig. 1) while male plants showed a significant, positive relationship

Table 1. One-way ANOVA comparison of mean basal stem diameter (mm) between non-flowering, male, and female sexual morphs of *Arisaema macrospathum* at the Biosphere Reserve El Cielo in 1998.

Sexual morph	N_{plants}	Mean basal stem diameter	Range	SE	F	P
Non-flowering	25	4.43[a]	2.8–7.8	0.24		
Males	27	5.09[a]	2.4–7.1	0.23	20.74	0.0001
Females	20	7.41[b]	5.0–15.0	0.52		

Means sharing the same letter are not significantly different ($P > 0.05$, Scheffe's multiple comparison test).

($r = 0.39$, $N = 26$, $P < 0.05$; Pearson correlation) (Fig. 1).

DISCUSSION

The study population, as well as all plants of *Arisaema macrospathum* observed at the Biosphere El Cielo, produced only unisexual flowers. No monoecious individuals were observed. This is exactly as described for *A. macrospathum* by McVaugh (1993) although he categorized the species as dioecious.

Previous studies by Schaffner (1922) have demonstrated that both *A. dracontium* and *A. triphyllum* are capable of changing sex. We presume that populations of *A. macrospathum* are also capable of changing sex. Our above observations would then suggest they represent a situation similar to *A. triphyllum* where most individuals produce only unisexual flowers, but are capable of switching gender and that populations of *A. macrospathum* should not be categorized as dioecious.

Studies by Clay (1993) indicate that some American populations of *A. dracontium* also have the potential to produce female plants. In Clay's study of 339 plants, one female plant was observed measuring 12 mm in diameter and producing 77 flowers, values similar to those at El Cielo. In addition, Clay reported that plants growing in a botanical garden in North Carolina may eventually produce

Table 2. A comparison of mean number of flowers per plant for male, monoecious, and female sexual morphs in populations of *Arisaema dracontium* and *A. macrospathum* along a north-to-south latitudinal gradient. Parentheses contain sample size.

	Male plants	Monoecious plants		Female plants	
Population	#♂	#♂	#♀	#♀	Reference
Arisaema dracontium					
Ontario, Canada	133 (35)	80 (35)	110	—	Lovett-Doust & Cavers, 1982
Louisiana, USA	120.2 (171)	78.8 (167)	89.2	77 (1)	Clay, 1993
Arisaema macrospathum					
Tamaulipas, Mexico	42.7 (27)	—	—	60.9 (20)	this study

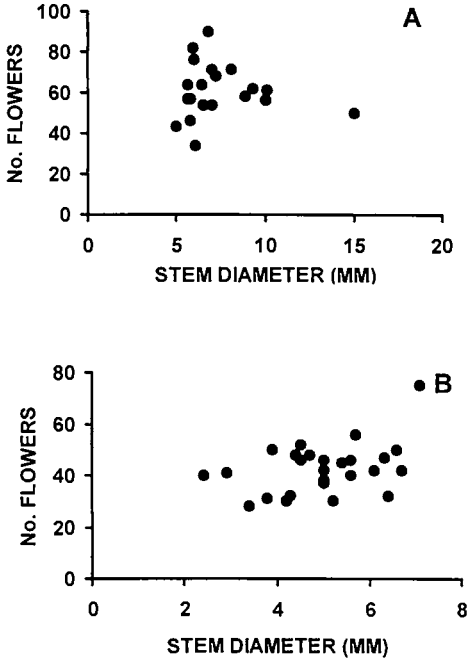

Fig. 1. Scatter-plot of flower number per plant versus basal stem diameter (mm) for sexual morphs of *Arisaema macrospathum* at the Biosphere Reserve El Cielo, Tamaulipas, Mexico in 1998. A. Female plants. B. Male plants.

only pistillate flowers. These data clearly indicate that populations of *A. dracontium,* although andromonoecious in the field, possess the capability of producing only female individuals given the right environmental conditions.

Compared to previous studies on *A. dracontium,* male plants of *A. macrospathum* produced fewer flowers/spadix but were similar in size (Tables 1, 2 and 3). Considering both species, a north-to-south latitudinal gradient can be discerned for size of plants, flower number of males and expression of individuals bearing only pistillate flowers. In southern populations, plants are smaller in stem diameter, males produce fewer flowers/spadix, and the number of pure pistillate flowered individuals increases.

The relationship between number of flowers/spadix and plant size do not fit any models for the evolution of female plants from an originally andromonoecious population (Clay, 1993). Clay has suggested that, in temperate areas, co-occurrence of *A. dracontium* with *A. triphyllum* and pollinator sharing between the two species may select for andromonoecy to reduce competition for pollinators. To our knowledge, *Arisaema triphyllum* does not occur in Mexico. From this perspective, unisexual plants may be selectively favored over andromonoecious plants in the absence of pollinator competition, andromonoecy never having existed in the Mexican populations of *A. macrospathum.*

The north-to-south gradient in flower number, plant size, and expression of female individuals observed for *A. dracontium* extends directly into populations of *A. macrospathum* in northern Mexico and suggests these two species are derived from a common ancestral population. *Ar-*

Table 3. Mean basal stem diameter (mm) for male, monoecious, and female sexual morphs in populations of *Arisaema dracontium* along a north-to-south latitudinal gradient. Parentheses contain standard errors.

Population	Male plants	Monoecious plants	Female plants	Reference
Ontario-1	8.9 (0.1)	15.0 (0.4)	—	Boles, 1996
Ohio-1	9.0 (0.1)	14.1 (0.2)	—	Boles, 1996
Indiana-4	8.1 (0.7)	12.4 (0.4)	—	Boles, 1996
Florida-1	—	9.8 (0.4)	—	Boles, 1996
Louisiana, USA	6.3 (0.1)	10.1 (0.2)	12.0	Clay, 1993
Louisiana-1	—	8.9 (0.5)	—	Boles, 1996

isaema dracontium and *A. macrospathum* would therefore be sister species. We speculate that the most likely mechanism for the splitting of the original population into two species to be geographic isolation across the arid Rio Grande valley and into the mountains of Mexico and consequent reproductive isolation. The lack of competing congeneric species in Mexico selected for plants bearing unisexual flowers and therefore added to the genetic divergence between the two groups.

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