# SIZE-DEPENDENT GENDER CHANGE IN GREEN DRAGON (ARISAEMA DRACONTIUM; ARACEAE)<sup>1</sup>

### **KEITH CLAY**

#### Department of biology. Indiana University. Bloomington, Indiana 47405

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 genotype. Four populations in southern Louisiana were sampled to determine frequencies and size distributions of male and monoecious plants, and to determine the relationship of plant size with male and female Rower production in monoecious plants. Male plants were significantly smaller than monoecious plants and made up 34%-78% of Rewiring plants within populations. Flower number (average = 120) was weakly positively correlated with size. Monoecious plants produced an average of 169 flowers (90 female) and had 100% fruit set, with individual berries containing an average of 2.5 ovules and 1.3 filled seeds. Male flower number was negatively correlated, and female flower number positively correlated, with basal stem diameter. Extrapolation of regression slopes suggested that green dragon should become completely female at a size 20% larger than the largest plant observed in this study. A simple model of inflorescence

development is presented to illustrate how the reproductive system of green dragon is related to that of jack-in-the-pulpit (*A. Triphyllum*), which exhibits a more distinct switch between male and female phenotypes.

Individuals of some plant species reproduce as males during part of their lifetimes and as females at other times (Policansky, 1982). The phenomenon of sex changing has been referred to by many terms including sex reversal, phase choice, diphasy, sequential gender, and sequential hermaphroditism (Lloyd, 1979; Schlessman, 1988). Here I use gender change to describe both the qualitative and quantitative changes in the degree of maleness and femaleness between years in green dragon. The size advantage model postulates a selective mechanism for gender changes between seasons (Ghiselin, 1969). If an individual's reproductive success as a male or female is related to size or age, and that relationship differs for each sex, then selection should favor individuals that can change to the most successful gender for its size or age (Charnov, 1982). Thus, a number of plants flower as males when they are small or subject to stressful environmental conditions, and as females when larger or growing under better conditions (Gregg, 1978; Lovett-Doust and Cavers, 1982b; McArthur and Freeman, 1982; Bierzychudek, 1984; Kinoshita, 1986; Condon and Gilben, 1988, Schlessman, 1988). Presumably, reproducing as a female is more demanding than reproducing as a male given the energetic costs of embryo development and fruit maturation (Hibbs and Fischer, 1979; Bierzychudek, 1984). Species that switch genders between seasons make attractive experimental systems for understanding the ecological factors favoring reproductive allocation to male or female function because there are no gender-based genetic differences. Gender changing behavior in plants is not restricted to switches from male to female (and vice versa) between



Fig. 1. Morphology of green dragon plant and inflorescence.

seasons. In a number of species plants are male when small or stressed and monoecious when larger (Smith, 1981; Lovett-Doust and Cavers, 1982a; Floyd, 1983, Whitham and Mopper, 1985). For example, Floyd (1983) found that most small trees of Pinus edulis produced only male cones while large trees were monoecious; similarly, smaller plants of Apodanthera undulata (Cucurbitaceae) flowered as males while larger plants were monoecious (Delesalle, 1989). Probably even more common are monoecious species that exhibit quantitative, as opposed to qualitative, shifts in male or female flower number as a function of size, age, environmental quality, or genetic factors (Abul-Fatih, Bazzaz, and Hunt, 1979; Smith, 1981; Lechowicz, 1984; McKone and Tonkyn, 1986; Solomon, 1989). The direction of gender change with size or growing conditions is not consistent across taxa (Freeman et al., 1981; Ackerly and Jasienski, 1990), and floral sex ratios are highly plastic within populations (Willson and Ruppel, 1984; Burd and Alien, 1988). A wide variety of gender changing behaviors can be found in the genus Arisaema (Araceae) (Schaffner. 1922; Hotta, 1971; Kinoshita. 1986). This study focuses on green dragon (Arisaema dracontium [L.] Scholt.), a woodland, herbaceous perennial found throughout much of eastern North America (Gleason and Cronquist, 1963). It overwinters as a corm and produces a single shoot early in the spring bearing a single compound leaf with spirally arranged leaflets (Fig. 1). A flowering shoot produces a single inflorescence consisting of a spathe surrounding an elongate spadix which bears the flowers (Fig. 1) (Schaffner, 1922; Lovett-Doust and Cavers, 1982a). A given inflorescence bears solely male (staminate) flowers or a mixture of male and female (pistillate) flowers. Therefore, reproductive plants are phenotypically either male or monoecious. In monoecious plants (=phenotypes), male flowers are produced above female flowers on the spadix (Fig. 1). Schaffner (1922) indicated that the species changes genders such that one genotype may switch among nonflowering, male, or monoecious phenotypes during different seasons. In general, nonflowering plants are smaller than males, which in turn are smaller than monoecious plants (Schaffner, 1922; Lovett-Doust and Cavers, 1982a). In the congener jack-in-the-pulpit (A. triphyllum [L.] Schott.) large plants are generally female rather than monoecious (Policansky, 1981; Lovett-Doust and Cavers, 1982b; Bierzychudek, 1984). However, 10%-20% of flowering plants in some A. triphyllum populations are monoecious and they are intermediate in size to male and female plants (Schaffner, 1922; Ewing and Klein, 1982; Lovett-Doust and Cavers, 1982b). The strategy of gender changing exhibited by green dragon may represent a transitional or alternative expression of the more distinct strategy exhibited by jack-in-the-pulpit and other Arisaema species (Hotta, 1971; Kinoshita, 1986). The purpose of this study was to extend the earlier work of Schaffner (1922) and Lovett-Doust and Cavers (1982a) to test the predictions of the size advantage model in relation to a species where reproductive phenotypes are either male or monoecious. Specifically, monoecious plants should allocate proportionally more energy toward female reproduction with increasing size. An increase in female gender can be achieved in four ways as illustrated in Fig. 2. In addition, the hypothesis that size-dependent switching between male and monoecious phenotypes represents an evolutionary pathway to male/female switching was tested by examining size-related changes in male and female flower numbers in monoecious plants. Only the patterns shown in Fig. 2C and 2D will produce completely female plants, and pattern 2C seems unlikely since flower production decreases with increasing plant size. Species of Arisaema are ideal subjects for investigations of gender changes because individuals produce only a single inflorescence per year with a fixed number of male and female flowers that is determined the previous season.

### MATERIALS AND METHODS

Four populations of green dragon were examined in this study. All were located in similar bottomland hardwood forests in East Baton Rouge Parish, Louisiana. Two of the populations (1 and 2) were sampled in 1985 and 1986 while population 3 was sampled in 1985 only and population 4 in 1986 only. Approximately 50 flowering individuals each were sampled in populations 1, 2, and 3 in the spring of 1985 by cutting off the stem (technically a pseudostem) at ground level and returning the above-ground portion of the plant to the laboratory for further analyses. Four measures of plant size were recorded: basal stem diameter, height, leaf area (measured with a LiCorr 3000 leaf area meter), and dry weight. For the latter measure all aboveground plant parts except the spadix were dried for 48 hr at 80 C before they were weighed. The portion of the spadix bearing flowers was labeled and placed in formaldehyde-acetic acid-alcohol (FAA) for later examination when the numbers of male and female flowers were counted. Each flower is borne on a small mound arising from the cylindrical spadix. Male flowers produced two anthers (a small percentage of flowers had one or three anthers) while female flowers produced a single stigma arising from the ovary. Later in the summer the same populations were revisited and fruits were collected from ten monoecious plants per population. The infructescence of green dragon ripens 2 to 3 months after flowering and consists of a cluster of red berries containing one to several seeds each. The red berries are highly visible and presumably are dispersed by mammals and birds. In the laboratory the percentage of female flowers setting fruit was quantified and the number of seeds per berry counted for ten randomly selected berries per individual. Seeds were plump and filled or small and shriveled. Either all ovules were not fertilized or some fertilized ovules were aborted before maturation. The two seed types were recorded separately. The following spring, 1986, populations 1 and 2 were sampled again and population 4 was sampled for the first time (population 3 was not sampled because of the difficulty in finding 50 plants in 1985). Inflorescences were collected from approximately 50 plants in each population and stored in FAA as before. In two of the populations, most flowering plants were male so additional time was spent searching for monoecious plants for better representation in the sample. Thus, after sampling 50 plants at random in each population, an additional 12, four, and nine monoecious plants were sampled in populations 1, 2, and 4,



## **Plant Size**

### Fig. 2. Four possible mechanisms by which monoecious plants become increasingly female with increasing size

respectively. Basal stem diameter was measured in the field, and the vegetative part of the plant was left in place. Basal stem diameter discriminated between male and monoecious plants in the 1985 samples better than height, weight, or leaflet number (see Results). Kinoshita (1986) also utilized basal stem diameter (pseudostem diameter) as the best measure of plant size in six Japanese species of *Arisaema*. The length of the appendix, a bright orange extension of the spadix functioning as a pollinator attractant, was measured to determine whether it was related to gender or total flower production. Flower types and numbers were quantified for each collected inflorescence as in the 1985 sample. Fruits were not collected in 1986.

One-way ANOVAs were conducted to determine whether male and monoecious plants differed in basal stem diameter and how relative sizes varied among populations. The relationship between plant size and the total numbers and types of flowers produced by each individual were explored by regressing male flower number on stem diameter for male plants and male, female, and total flower number on stem diameter for monoecious plants. The relationship between plant size and the percentage of female flowers in monoecious plants was also explored by regression analysis. Lloyd's (1979) G, the measure of a plant's "femaleness," was calculated from the equation G = g/(g + aE) where g is the number of female flowers on a plant, a is the number of male flowers, and  $E = \sum g/\sum a$  for the whole population. Pure female plants have a value of 1 while pure male plants have a value of 0. The G value for intermediates depends not only on the phenotype of the plant but also on the population sex ratio. All statistical analyses were conducted with SAS statistical programs (Helwig and Council, 1979).

1900													
	All plants population							Male plant population					
	1		2	3		1-3	1		2	3		1-3	
HTa	0.24		0.13	b		0.06							
DI	0.38		0.37	0.12		0.27							
LA	0.30		0.35	0.07		0.13	0.39		0.09			0.06	
WT	0.42		0.24	0.12		0.17	0.33						
		Monoecious plants											
		Ma a	le flowers			Femal pop	e flowers ulation			All flo ugog	owers lation		
	1	2	3	1-3	1	2	3	1-3	1	2	3	1-3	
HT	0.18	0.54		0.15	0.21	0.58		0.12		0.40			
DI	0.28	0.76	0.26	0.28	0.42	0.85	0.11	0.34	0.18	0.62		0.06	

Table 1. Significant correlations of plant size measures with flower numbers in all plants, male plants, and monoecious plants measured in



<sup>a</sup> HT = plant height, DI = basal stem diameter, LA = leaf area, WT = dry weight

<sup>b</sup> Nonsignificant correlation (P > 0.05)

Fig. 3. Size distributions of male and monoecious plants in six populations x year combinations.

#### RESULTS

In the 1985 samples, flower number was significantly correlated with measures of plant size in most samples (Table 1). Considering male and monoecious plants combined, basal stem diameter exhibited the greatest correlation with total flower number in two of three populations and all three populations combined. Dry weight provided a slightly higher correlation with flower number in population 1. Considering only male plants, leaf area provided the best correlation with flower number although most correlations were weak and nonsignificant (Table 1). In monoecious plants, the largest correlations with both male and female flower number were with basal stem diameter in each population and all populations combined (Table 1).

Table 2. Basal stem diameter (in mm) and frequencies of male monocious green dragon plants

				Monoecious plants	S
	Male	plants			
Population -	N	Mean basal	N	Mean basal	% of
1 — 1985	17	$6.0 \pm 0.4^{*}$	32	$9.6^{*^{b}} \pm 0.5$	65
1 – 1986	17	$6.0 \pm 0.3$	45	10.7* ± 0.4	66
2 – 1985	38	5.6 ± 0.2	15	8.7* ± 0.7	30
2 – 1986	39	$6.4 \pm 0.3$	15	10.1* ± 0.7	22
3 – 1985	25	$6.0 \pm 0.3$	36	9.7* ± 0.4	59

4 – 1986	35	7.4 ± 0.3	24	11.0* ± 0.3	29
Total	171	6.3 ± 0.1	167	10.1* ± 0.2	46

<sup>a</sup>  $\pm 1$  standard deviation

<sup>b</sup> Denotes that basal stem diameter wassignificantly larger than c gender in the same population and over all populations.

<sup>c</sup> Grand mean of all plants sampled.

All measures of plant size were significantly correlated with each other. Given these relationships, subsequent analyses were conducted with basal stem diameter as the independent variable. Only basal stem diameter, a nondestructive measure of plant size, was measured in 1986 samples.

The percentage of flowering plants producing only male flowers ranged from 35% in population 1 up to 70% in population 2 in the 1985 sample (Table 2). In 1986 an excess of monoecious plants was sampled beyond the random sample of 50 flowering plants from each population. The percentage of male plants in the initial sample of 50 ranged from 34% in population 1 to 78% in population 2 (Table ~). There was no statistical difference in the percentage of male plants in 1985 and 1986 in populations 1 and 2. Population 1 remained male dominated while population 2 remained monoecious dominated..

For each population/year combination there was a significant difference (P < 0.0001) in basal stem diameter between male and monoecious plants (Table 2). Overall, male plants averaged 6.3 mm while monoecious plants averaged 10.1 mm. There were significant differences (P < 0.05) in stem diameter of male plants, and monoecious plants, among the six population/year combinations. Population 4 had the biggest male plants and the biggest monoeceous plants, while population 2 (in 1985) had smallest males and the smallest monoecious plants average. Male plants in population 4 were only 1.3 mm smaller on average than monoecious plants in population 2. Over all populations, male plants ranged from 3 mm to 12 mm in size while monoecious plants ranged from 5 mm to 21 mm in size (Fig. 3). There was some overlap in stem diameter between male and monoecious plants in all populations with the larger male plants being bigger than the smaller monoecious plants (Fig. 3). The critical transitional size appeared to be 8-10 mm with few male plants larger than 10 mm and few monoiecious plants smaller than 8 mm.

Male plants produced an average of 120 flowers (Table 3). In contrast, monoecious plants produced an average of 168 flowers (79 male and 84 female). Thus, on average, monoecious plants produced 52% female flowers and only about two-thirds of the number of male flowers as male plants. In every population/year combination, the number of male flowers produced by monoecious plants was significantly less (P < 0.0001) than the number of male flowers produced by male plants but total flower number was significantly greater for monoecious plants (P < 0.0001). Male flower number on both male and monoecious plants differed significantly among populations (P < 0.05), but female flowers per population (E) ranged from 0.21 up to 0.63 (Table 3). Male flowers were in the majority in all population/year combinations.

	Male plants	М	lonoecious plan	its		
Population -	# Male	# Male	# Female	% Female	G <sup>a</sup>	E <sup>a</sup>
1 — 1985	128.4 ± 7.1	86.8 ± 5.1	88.5 ± 7.7	49%	0.64	0.57
1 — 1986	132.4 ± 5.5	84.4 ± 5.1	96.3 ± 6.4	53%	0.64	0.63
2 – 1985	120.1 ± 3.7	68.7 ± 6.1	83.3 ± 10.2	53%	0.84	0.22
2 – 1986	117.3 ± 3.4	59.8 ± 4.2	99.5 ± 4.5	62%	0.89	0.21
3 – 1985	104.6 ± 7.1	73.4 ± 4.8	76.0 ± 5.3	51%	0.67	0.52
4 — 1986	122.7 ± 3.7	83.2 ± 6.1	93.8 ± 7.7	52%	0.81	0.25
Total <sup>b</sup>	120.1 ± 3.7	78.8 ± 2.3	89.2 ± 3.0	52%	0.74	0.40

Table 3. Mean numbers and types of flowers produced by male and monoecious plants of green dragon

<sup>a</sup> Defined in text following Lloyd (1979).

<sup>b</sup> Grand mean of all plants sampled.

Most monoecious plants produced between 45% and 70% female flowers, but there were a number of monoecious plants that produced extremely male or female biased flower ratios (Fig. 4). The percent female flowers in a monoecious inflorescence corresponds to Delesalle's (1989) coefficient M, the morphological femaleness. Several plants produced largely male inflorescences with less than 5% female flowers while other plants produced predominantly female inflorescences (> 80% female flowers) with 20 or fewer male flowers. Monoecious plants with less than 5% female flowers averaged 7.1 mm basal stem diameter while plants with greater than 80% female flowers averaged 13.2 mm. One all-female plant was found in population 3. It produced 77 flowers and was 12 mm in basal stem diameter. Lloyd's measure of quantitative gender G varied from 1.0 in the single pure female plant to 0.01 in one monoecious plant in population 1 (in 1985) that produced one female flower and 156 male flowers. Averages within populations ranged from 0.89 to 0.64, largely reflecting differences in the proportions of male and monoecious plants among populations (Table 3).

The relationship between flower number and plant size was explored with regression analysis. Considering only male plants, the regression of male flower number on basal stem diameter gave a positive slope for five of six population/year combinations, but in only two cases was the slope significantly different from 0 (Table 4, population 4 and population 2 in 1986). When all populations were considered together, there was a significant positive slope for male flower number on basal stem diameter (P < 0.0001).

Considering monoecious plants, there was a significant negative slope of male flower number on stem diameter in four of six population/year combinations and when all populations were considered together (P < 0.0001) (Table 4). Thus, male flower number declines with increasing size of monoecious plants. In contrast, the slope of female flower number on basal stem diameter was positive and significantly different from 0 in all six population/year combinations and when all populations were considered together (P < 0.0001)(Table 4). The regression analyses suggest that Fig. 2D most closely represents the situation in green dragon.

Denulatia		Male plants	6	Monoecious plants							
Populatio n - vear	Ν	/lale flower	S	Ν	Aale flower	S	Female flowers				
n year	Slope	SE <sup>a</sup>	P<	Slope	SE	P<	Slope	SE	P<		
1 – 1985	+5.9	3.9	NS <sup>b</sup>	-5.9	1.7	0.0018	+14.3	1.8	0.0001		
1 – 1986	+4.3	4.1	NS	-4.7	1.7	0.008	+13.9	1.3	0.0001		
2 – 1985	+4.1	2.9	NS	-7.1	1.4	0.0003	+15.3	1.5	0.0001		
2 – 1986	+5.8	1.7	0.0019	-1.6	1.6	NS	+11.0	1.9	0.0001		
3 – 1985	-2.5	5.1	NS	-6.9	2.0	0.0017	+11.7	1.6	0.0001		
4 – 1986	+7.9	2.0	0.0003	-6.1	3.6	NS	+14.4	2.1	0.0001		

Table 4. Regressions of basal stem diameter on flower numbers for male and monoecious plants.

<sup>a</sup> ±1 standard error.

<sup>D</sup> P > 0.05, nonsignificant.

When the percentage of female flowers was regressed against basal stem diameter in monoecious plants, there was a significant positive slope for five of the six population/year combinations (Fig. 5). Only population 2 in 1986 was divergent, with a weaker and nonsignificant positive slope. Considering all six samples together, there was a significant positive slope that, when extrapolated, suggests that plants with a stem

diameter of approximately 25 mm should be completely female (Fig. 5). The largest plant observed in this study had a stem diameter of 21 mm (Fig. 3).

 Table 5. Ovule and seed number per berry of green dragon<sup>a</sup>



Populatio	n	Number of berries with X numbers							
		0	1	2	3	4	5	6	seed
1	Ovules	1	20	13	36	24	5	1	
	Seeds	1	71	22	4	2	0	0	55%
2	Ovules	0	15	35	26	23	1	0	
	Seeds	1	68	28	2	1	0	0	58%
	Ovules	0	21	53	24	2	0	0	
1						PERCENT FEMALE FLOWERS	2-a 10 BASAL STEW	20 DIAMETER	2-86 30 (mm)
	Seeds	7	82	11	0	0	0	0	

<sup>4</sup> Ten berries per inflorescence were sampled in 1995 from each of ten monoecious individuals per population.

Fruits were sampled from ten plants in each of the three populations sampled in 1985. Of berries sampled, 291 of 300 (98%) produced at least one seed (Table 5). The few female flowers that did not produce a berry were located at the transition zone on the spadix where male flowers stopped and female flowers began. Ripe berries typically contained a mixture of plump, ripe seeds and shriveled, undeveloped seeds. On average, each berry contained 2.5 ovules and 1.2 seeds (Table 5). Thus, approximately one-half of the ovules did not develop into seeds. While many berries contained three or more ovules, only 2% of the berries contained three or more ripe seeds. There were significant differences among populations and among individuals within populations for both ovule and seed number per berry (P < 0.0002). The percentage seed set differed among individuals within populations (P < 0.0001), but not among populations.

The appendix was measured on flowering plants sampled in 1986. There were no differences between male and monoecious plants in appendix length in any population; on average, the length of the appendix was 11.4 cm in male plants and 12.2 cm in monoecious plants.

### DISCUSSION

Green dragon plants exhibit a qualitative change in gender with increasing plant size when formerly smaller male plants reach a size sufficient to begin producing female flowers. The critical size appeared to be about 8 mm basal stem diameter. In a study of Asian *Arisaaema*, the frequency of male plants declined rapidly above 10 mm basal stem diameter in all six species examined (Kinoshita, I986). Other studies of *Arisaaema* species have also revealed threshold sizes for gender although differences in measures of plant size prevent direct comparison (Policansky, 1981, Bierzychudek, 1984; Takasu, 1987). Size/gender relationships documented in other plant families (e.g., Araliaceae, Cucurbitaceae) also suggest such thresholds for gender change (Schlessman, 1987; Delesalle, 1989). The fact that there is variation in size thresholds both within and among populations points to the importance of environmental variability and possible genetic differences among plants (see Table 2).

Green dragon also exhibits a quantitative change in gender with increasing plant size. Monoecious plants produce more female flowers and fewer male flowers with increasing size, leading to increasingly female plants. Extrapolation of regression slopes suggests that pure female plants would be common in size classes greater than 25 mm stem diameter. The single female plant found indicates the potential for green dragon individuals to exhibit pure female phenotypes. An

anecdotal observation also supports the hypothesi s that very large green dragon plants will become female. In June 1989, a stand of green dragon plants located in the Blomquist Gardens on the Duke University campus, Durham, North Carolina was observed where the majority of

Fig.5 Regression slopes of percent female plants on basal stem diameterfor each population x year combination. Slopes for 2-86 and 4-86 are not significantly different from 0. The dotted line is the slope for all populations and years combined. plants had pure female phenotypes. Many of the plants were 1-1.5 m tall with basal stem diameters up to 40 mm. However, the possibility of genetic differences among green dragon populations in their gender expression cannot be discounted.

The relationship between plant size and gender found in this study is in general agreement with two previous studies. Schaffner (1922) examined populations of green dragon around Columbus, Ohio and found that male plants formed the large majority of flowering plants in all populations and that they were generally smaller than female plants. Observations of plants transplanted to the greenhouse showed that individuals often changed from monoecious to male or from male to monoecious in consecutive years. More recently, Lovett-Doust and Cavers (1982a) examined populations of green dragon near London, Ontario, Canada. They found that monoecious plants were larger and produced more flowers than male plants, which predominated in all sites examined, unlike this study. Male plants produced an average of 133 flowers (compared to 120 here) while monoecious plants produced an average of 110 female and 80 male flowers (90 and 79, respectively, here). Neither Schaffner (1922) nor Lovett-Doust and Cavers (1982a) reported pure female plants of green dragon.

No previous studies of *Arisaema* have demonstrated the qualitative change in gender of monoecious plants shown here that could lead to pure female plants. In a study of a gender-changing cucurbit, Delesalle (1989) found no relationship between gender and plant size in monoecious plants. Other monoecious plants, that do not exhibit the qualitative sex-changing behavior of *A. dracontium*, often do exhibit a quantitative shift in gender with plant size. For example, both ragweed and teosinte are wind-pollinated herbaceous species that become increasingly male with plant size (Abul-Fatih, Bazzaz, and Hunt, 1979; Burd and Allen, 1988). In contrast, wild rice becomes increasingly female with size (Willson and Ruppel, 1984). A positive association between plant size and female flower number has been documented in several *Arisaema* species where monoecious plants are rare or lacking (Bierzychudek, 1982; Kinoshita, 1986; Takasu, 1987).

The question arises as to why green dragon plants from wild populations rarely exceed 20 mm in stem diameter where pure female plants are most likely to be found. Size is a function of age in many plants, and survival schedules may result in few plants that survive long enough to reach large sizes. However, In *Arisaema* and many other perennial herbacious plants, plant size can be labile with plants getting smaller or larger between years (Schaffner, 1922; Meagher and Antonovics, 1982; Schlessman, 1987). Therefore, plant size may be only weakly correlated with age beyond a certain point in green dragon. Reductions in plant size and reversions in phenotypic gender have been induced in several species of *Arisaema* by removing leaf area, reducing the size of the corm, and increasing fruit production (Schaffner, 1922, 1925; Maekawa, 1927, Sierzychudek, 1984; Kinoshita, 1986). Schlessman(1987) has also reported gender reversions from hermaphrodite to male in dwarf ginseng plants shrinking from one year to the next.

Fruit production probably represents an important source of year-to-year size changes in green dragon although damage to above and below-ground parts may also occur frequently. In this study essentially all female flowers produced ripe berries containing an average of 1.2 ??lled seeds. This result contrasts strongly with results from the congeneric jack-in-the-pulpit where Bierzychudek (1982) found that fruit set was pollinator limited. Lovett- Doust, Lovett-Doust, and Turi (1984) reported that the rate of fruit and seed set varied widely in *A. triphyllum*, and Bierzychudek (1984) demonstrated that high levels of fruit set reduced plant size the following year. While the effect of fruit set on subsequent plant size has not been examined, it seems unlikely that *A. dracontium* would differ substantially from *A. triphyllum*. High levels of fruit set in green dragon may reduce the size of monoecious plants, preventing them from exceeding the critical minimum size to become all female. Self-pollination could increase Fruit set and more strongly affect size changes between seasons, than if individual plants were unisexual. Compatibility in green dragon or other monoecious *Arisaema* has not been investigated (Meeuse, 1985), but Treiber (1983) reported that jack-in-the-pulpit was self-incompati ble.

The genus Arisaema exhibits a range of reproductive systems in Asia where species diversity is far higher than in North America (Meeuse, 1985). Hotta (1971) surveyed gender expression in several species of *Arisaema* and found three basic categories. One group of species produced male inflorescences on smaller plants and monoecious inflorescences on larger plants similar to green dragon. A second category included species where small plants bore male inflorescences, intermediate-sized plants bore monoecious inflorescences, and the largest plants produced completely female inflorescences. The final group of species produced only male inflorescences (on small plants) or female inflorescences (on larger plants) with only a minority of plants producing monoecious inflorescences. This is similar to what many have reported for North American jack-in-the-pulpit. Six Japanese species of *Arisaema* all showed the latter pattern, although a few monoecious plants were found in some species (Kinoshita, 1986).

Gender expression in all Arisaema species may have a similar underlying mechanism. Although jack-in-the-pulpit is

widely cited as an example of gender switching from male to female phenotypes, its breeding system may more closely resemble the second group of Asian *Arisaema* reported by Hotta (1971), which have an intermediate monoecious stage, than the third group that change only between male and female plants. Monoecious jack-in-the-pulpit plants are reported by Schaffner (1922), Camp (1932), Rust (1980), Treiber (1980), Ewing and Klein (1982), and Lovett-Doust and Cavers (1982b). Of 22 flowering jack-in-the-pulpit plants examined near Indiana University, two were monoecious (Clay, unpublished data). Thus, jack-in-the-pulpit often exhibits a sequence of male-monoecious-female plants with increasing size, although monoecious phenotypes are a minority of flowering plants. Similarly, green dragon may exhibit a sequence of male-monoecious-female plants with increasing size, although female plants are very large compared to the average plant size.

A simple model of floral development is sufficient to explain gender expression in Arisamma (Fig. 6). Male, monoecious, and female inflorescences are produced with male inflorescences being produced by the smaller flowering plants and female inflorescences being produced by the larger flowering plants. The difference between green dragon and jack-in-the-pulpit is the range of plant sizes where monoecious inflorescences are produced. In green dragon, the range is quite broad (Fig. 6A) while in jack-in-the-pulpit the range is very small (Fig. 6B). Long-term demographic experiments where individuals with manipulated resource levels and fruit set are compared over time with control plants would elucidate the critical transition sizes illustrated in Fig. 6. Environmental heterogeneity and genetic differences among populations would result in variation in the critical sizes where gender expression changes. The model presented in Fig. 6 assumes that the plant is able to "assess" the size of its stored food reserves in the corm during inflorescence development. The determinate inflorescence that emerges in spring develops at the end of the previous growing season. In monoecious plants, female flowers are produced at the base of the spadix while male flowers are produced at the top of the spadix. Plants with a high proportion of female flowers produce male flowers only along a short length of the spadix at the top of the inflorescence while monoecious plants with mostly male flowers produce only a few female flowers at the base of the spadix. During inflorescence development the length of time the meristem differentiates male flowers and the point at which it switches to female flowers, if it does, are critical determinants of gender in green dragon. The mechanism by which plant size and floral development are linked represents an important area for future research.

The decline in male flower number with plant size in monoecious plants may resect the greater energetic costs of female flowers and fruits although it does not directly explain the inverse correlation between male and female flower number. An inverse correlation could occur as a result of developmental constraints limiting the total number of flowers in an inflorescence; an increase in female flower number would directly reduce the number of male flowers. However, in this study there was a significant positive regression of flower number with stem diameter in monoecious plants, indicating that inflorescence size increases with plant size.

Monoecious species with indeterminate inflorescences are less likely to exhibit the clear relationships between plant size and gender found in where monoecy is expressed.

exhibit the clear relationships between plant size and gender found in where monoecy is expressed. this study. In species likegreen dragon, the determinate inflorescence develops over a relatively short period of time when the physical environment and the plant's resource status remain relatively constant. *Arisaema* species make only a single

developmental decision about floral development per season. In contrast, species that flower indeterminately through the growing seasons repeatedly develop male vs. female flowers over a wide and unpredictable range of environmental and plant resource conditions, making plant size/gender relationships more difficult to assess.

The adaptive differences in floral development between green dragon and jack-in-the-pulpit are of interest given that both species commonly grow intermixed in many areas. Further, their phenology is very similar, suggesting both species are subjected to similar environmental conditions during inflorescence development and maturation. Limited observations suggest that the same pollinators visit both species (Clay, personal observation) and hybridization between the species has recently been reported (Sanders and Burk, 1992). Selection for "niche differentiation" of the reproductive systems of the species may operate where they co-occur, as has been shown for flower color in sympatric



Phlox (Levin, 1985). Monoecy in green dragon could reduce interspecific pollen flow with jack-in-the-pulpit.

#### LITERATURE CITED

- ABUL-FATIH, H. A., F. A. BAZZAZ, and R. HUNT. 1979. The bi??? of *Ambrosia trifida*. III. Growth and biomass allocation. *New tologist* 83: 829-838.
- ACKERLY. D. D., AND M. JASIENSKI. 1990. Size-dependent varia??? of gender in high density stands of the monoecious annual, *Ambr???* artemisiifolia. Oecologia 82: 474--477.
- BIERZYCHUDEK, P 1982. The demography of jack-in-the-pulpit, a ??? est perennial that changes sex. *Ecological Monographs* 52: 3?? 351.
- ------. 1984. Assessing "optimal" life histories in a fluctuating environment: the evolution of sex-changing by jack-in-the-pulpit, *American Naturalist* 123: 829-840.
- BURD, M., and T. F. H. ALLEN. 1988. Sexual allocation strategies of wind-pollinated plants. Evolution 42:403-407.
- CAMP, W.H. 1932. Sex in Arisaema triphyllum. Ohio Journal of Science 32: 147-151.
- CHARNOV, E. L. 1982. The theory of sex allocation. Princeton University Press, Princeton, NJ.
- CONDON, M. A., AND L. E. GILBERT. 1988. Sex expression of *Gura*?? and *Psiguria* (Cucurbitaceae): neotropical vines that change sex. *American Journal of Botany* 75: 875-884.
- DELASALLE. V..A. 1989. Year-to-year changes in phenotypic gender of a monoecious cucurbit, *Apodanthera undulata*. *American Journal of Botany* 76: 30-39.
- EWING, J. W., and R. M. KLEIN. 1982. Sex expression in jack-in-the-pulpit. Bulletin of the Torrey Botanical Club 109: 47-50.
- FLOYD, M.E. 1983. Dioecy in five *Pinus edulis* populations in the Southwestern United States. American Midland Naturalist 110: 405-511.
- FREEMAN, D. C., E. D. MCARTHUR, K. T. HARPER, and A. C. BLAUER. 1961. Influence of environment on the floral sex ratio of monoecious plants. *Evolution* 35: 194-197.
- GHISELIN, M. T. 1969. The evolution of hermaphroditism among animals. Quarterly Review of Biology 44: 189-208.
- GLEASON, H. A. and A. CRONQUIST. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. Van Nostrand, New York. NY.
- GREGG, K. B. 1978. The interaction of light intensity, plant size, and nutrition in sex expression in *Cycnoches* (Orchidaceae). *Selbyana* 2: 212-223.
- HEDWIG, J. T., and K. A. COUNCIL. 1979. SAS user's guide: statistics, version 5. SAS Institute Inc., Cary, NC.
- HIBBS, D. E., and B. C. FISCHER. 1979. Sexual and vegetative reproduction of striped maple (*Acer pensylvanicum*). Bulletin of the Torrey Botanical Club 106: 222-226.
- HOTTA, M. 1971. Study of the family Araceae, general remarks. Japanese Journal of Botany 20: 269-310.
- KINOSHITA, E. 1986. Size-sex relationship and sexual dimorphism in Japanese Arisaema (Araceae). Ecological Research 1: 157-171.
- LECHOWICZ, M. J. 1984. The effects of individual variation in physiological and morphological traits on the reproductive capacity of the common cocklebur, *Xanthium strumarium* L. *Evolution* 38: 833-844.
- LEVIN, D. A. 1985. Reproductive character displacement in Phlox. Evolution 39: 1275-1281.
- LLOYD, D. G. 1979. Parental strategies of angiosperms. New Zealand Journal of Botany 17: 595-606.
- LOVETT-DOUST, J., and P. B. CAVERS. 1982a. Resource allocation and gender in the green dragon, *Arisaema dracontium* (Araceae). *American Midland Naturalist* 108: 144--148.
- -------. 1982b. Sex and gender dynamics in jack-in-the-pulpit, Arisaema triphyllum (Araceae). Ecology 63: 797-808.
- LOVETT-DOUST, L., J/; PVETT-DOUST, and K. TURI. 1986. Fecundity and size relationships in jack-in-the-pulpit, Arisaema triphyllum (Araceae). American Journal of Botany 73: 489-494.
- MAFKAWA, T. 1927. On intersexualism in Arisaema japonica. Japanese Journal of Botany 3: 205-216.
- MCARTHUR, E. D., AND D. C. FREEMAN. 1982. Sex expression in *Atriplex canescens*: genetics and environment. *Botanical Gazette* 143: 476-482.
- MCKONE. M. J.. AND D. W. TONKYN. 1986. Intrapopulation gender variation in common ragweed (Asteraceae: Ambrosia artimisiifolia L.), a monoecious. annual herb. Oecologia 70: 63-67
- MEAGHER. T., AND J. ANTONOVICS. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: life history studies. *Ecology* 63: 1690-1700.
- MEEUSE. B. J. D. 1985. Arisaema. In A. Haley [ed.] Handbook of flowering, vol, 1, 511-516. CRC Press, Boca Raton, FL.
- POLICANSKY, D. 1981. Sex choice and the size advantage model in jack-in-the-pulpit. *Proceedings of the National Academy of Sciences*. USA 78: 1306-1308.
- ----- 1982. Sex change in plants and animals. Annual Review of Ecology and Systematics 13: 471-495.
- RUST, R. W. 1980. Pollen movement and reproduction in *Arisaema triphyllum*. *Bulletinof the Torrey Botanical Club* 107: 539-542. SANDERS, L. L., and C. J. BURK. 1992. A naturally occurring population of putative *Arisaema triphyllum* subsp. *Stewardsonii*
- x A. dracontium hybrids in Massachusetts. Rhodora 94: 340-347.
- SCHAFFNER, J. H. 1922. Control of the sexual state in *Arisaema triphyllum* and *Arisaema dracontium*. *American Journal of Botany* 9: 72-78.
- ----- 1925. Experiments with various plants to produce change of sex in the individual. *Bulletin of the Torrey Botanical Club* 52: 35-47.
- SCHLESSMUN, M. A. 1987. Gender modification in North American ginsengs. Bioscience 37: 469-475.
- -----. 1988. Gender diphasy ("sex choice"). *In* J. Lovett-Doust and L. Lovett-Doust [eds.], Plant reproductive ecology: patterns and strategies, 139-153. Oxford University Press, New York, NY.
- SMITH, C. C. 1981. The facultative adjustment of sex ratio in lodgepole pine. American Naturalist 18: 297-305.
- SOLOMON. B. P. 1989. Size-dependent sex ratios in the monoecious wind-pollinated annual, *Xanthium strumarium*. *American Midland Naturalist* 121: 209-218.
- TAKASU. H. 1987. Life history studies on Arisaema (Araceae) I. Growth and reproductive biology of Arisaema urashima Hara.

Plant Species Biology 2: 29-56.

TREIBER, M, 1980. Biostematics of the Arisaema triphyllum complex. PhD. dissertation. University of North Carolina. Chapel Hill, NC.

- WHITHAM, T. G., and S. MOPPER. 1985. Chronic herbivory: impacts on architecture and sex expression of pinyon pine. *Science* 228: 1089-1091.
- WILLSON, M. f., and K. P. RUPPEL. 1984. Resource allocation and floral sex ratios in *Zizania aquatica*. *Canadian Journal of Botany* 62: 799-805.

<sup>1</sup> Received for publication 28 December 1992. revision accepted 5 March 1993. The author thanks M. Surd, V. Delesalle, and L. Delph for helpful comments on the manuscript, Mary Stovall and David Guaicara for help with the field and laboratory work, and Jenny Sullivan for kindly providing the drawing of green dragon. This research was supported in part by NSF grant BSR-8400163.