

Floral trimorphism and monomorphism in continental and island populations of *Eichhornia paniculata* (Spreng.) Solms. (Pontederiaceae)

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Eichhornia paniculata (Spreng.) Solms. (Pontederiaceae) is a short-lived perennial or annual of marshes, seasonal pools and ditches of lowland tropical South America, primarily NE Brazil, and the Caribbean islands of Cuba and Jamaica. Comparisons, made under uniform glasshouse conditions, of populations originating from seed collected in the two regions revealed striking differences in their floral biology and breeding systems. The majority of populations sampled in NE Brazil are tristylous. Floral trimorphism is associated with pollen trimorphism and minor differences in anther size and pollen production among the three stamen levels. Unlike the majority of heterostylous plants the floral morphs of *E. paniculata* are highly self-fertile. Populations sampled on the island of Jamaica are composed exclusively of self-pollinating, semi-homostylous, mid-styled forms. Flowers from these populations are smaller and less showy, with reduced pollen heteromorphism and significantly fewer pollen grains and ovules per flower, in comparison with trimorphic populations from Brazil. Individual genotypes from Jamaican populations display considerable developmental instability in floral expression, particularly with respect to filament elongation of the lower stamen level. It is proposed that self-pollinating populations of *E. paniculata* are evolutionarily derived from tristylous ancestors and that the shift in breeding system is favoured at low density, following population bottlenecks, where pollinator service is unreliable.

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INTRODUCTION

Comparative studies of continental and island populations of plants and animals can provide useful insights into evolutionary processes. Islands offer unique challenges to populations of colonizing species as their isolation from gene flow and differing biota and environments may require radical changes to the genetic structure of populations, leading to adaptive radiation and speciation (Mayr, 1963; MacArthur & Wilson, 1967; Carlquist, 1974; Lack, 1976; Williamson, 1981). Island habitats may be ecologically marginal as well as geographically isolated and accordingly populations may experience stressful conditions, leading to strong directional selection, inbreeding and genetic drift. These influences can result in the disruption of balanced gene complexes, developmental instability and the expression of novel phenotypes (Levin, 1970; Soulé, 1973).

A major question in the study of island populations is whether or not they are less variable than their mainland counterparts for genetic polymorphisms. Founder events, fluctuations in population size and inbreeding in peripheral isolates might all be expected to reduced genetic variation. Some studies confirm this expectation (Dobzhansky, 1957; Clarke & Sheppard, 1963; Selander *et al.*, 1971; Avise *et al.*, 1974) but different types of genetic polymorphism in populations of the same species (e.g. chromosomal versus enzymic in *Drosophila willistoni*) can give conflicting results (Ayala *et al.*, 1971) so we are some way from developing a general theory for the genetic structure of island populations. Furthermore, despite their capacity for long-distance dispersal and island colonization there have been virtually no detailed studies of the ecological genetics of continental and island populations of plants.

Heterostyly is a genetically controlled floral polymorphism in which plant populations contain 2 (distyly) or 3 (tristyly) morphs which differ in style and stamen length, pollen size and incompatibility relationships. The polymorphism is reported from 24 flowering plant families (Ganders, 1979). Since the families are for the most part unrelated it seems likely that heterostyly is polyphyletic in origin and that the similarities in morphological subcharacters of the heterostylous syndrome are the result of convergent evolution. Heterostyly is generally considered to be an outbreeding mechanism which promotes phenotypic disassortative mating between floral morphs (Darwin, 1877; Crowe, 1964; Vuilleumier, 1967; Ganders, 1979). However, a common feature of heterostylous breeding systems is their propensity to break down, giving rise to self-fertilizing homostylous races. While the genetic bases of these changes are reasonably well understood (Ernst, 1955; Dowrick, 1956; Charlesworth & Charlesworth, 1979; Shore & Barrett, unpubl. data) less is known of the selective forces which favour the establishment and spread of homostylous forms (Crosby, 1949; Baker, 1959; Ganders, 1975a; Barrett, 1979).

The genus *Eichhornia* is composed of three primarily trimorphic species (*E. azurea* (Swartz) Kunth, *E. crassipes* (Mart.) Solms., and *E. paniculata* (Spreng.) Solms.) and four monomorphic species (*E. diversifolia* (Vahl) Urb., *E. heterosperma* Alex., *E. natans* (Beauv.) Solms., and *E. paradoxa* (Mart.) Solms.). The presence of residual heteromorphic characters in the monomorphic taxa suggests that they are derived from tristylous ancestors (S. C. H. Barrett, unpubl. data). In the primarily South American *E. azurea* and *E. crassipes*, self-fertilizing

semi-homostylous variants have been documented in Central America (Barrett, 1978, 1979). These patterns suggest that tristylous has broken down on a number of occasions in the genus *Eichhornia* to give rise to self-fertilizing forms.

Little is known about the breeding system of *E. paniculata* and there have been conflicting reports in the literature as to whether the species is trimorphic (Solms-Laubach, 1883) or monomorphic (Johnson, 1924; see review in Ornduff, 1966). The distribution of *E. paniculata* is of interest in connection with geological patterns of breeding system variation since the species exhibits a markedly disjunct distribution. Populations are numerous throughout the states of Ceará, Pernambuco, Sergipe, and Alagoas in NE Brazil and isolated populations have been collected from W Brazil, Paraguay, Argentina and Nicaragua. In addition populations occur on the Caribbean islands of Cuba and Jamaica. This distribution suggested that populations in the centre of the range in NE Brazil may be primarily trimorphic and geographically marginal populations monomorphic and possibly self-fertilizing. In order to evaluate this possibility, field studies in NE Brazil and Jamaica were undertaken and a comparison of the breeding systems and ecological genetics of populations from these regions initiated.

This paper reports on glasshouse studies of populations originating from the two regions and: (1) documents the main features of floral trimorphism in *E. paniculata*; (2) by controlled pollinations determines the compatibility relationships of the floral morphs; (3) demonstrates that population samples from Jamaica are composed exclusively of self-pollinating semi-homostylous forms and (4) compares the reproductive characteristics of trimorphic and monomorphic populations. Following the presentation of results, the evolutionary aspects of breeding system variation and its relationship to island colonization are discussed.

NATURAL HISTORY OF *EICHHORNIA PANICULATA*

With the exception of a report of self-compatibility in the mid-styled morph of *Eichhornia paniculata* (Johnston, 1924), there has been no published experimental work on the species or descriptions of its morphology or natural history. A brief account of the life history and ecology, based on field observations in Brazil and Jamaica, will therefore be given. A detailed examination of the morphology and developmental basis of floral trimorphism in *E. paniculata* has recently been made (Richards & Barrett, 1984).

In contrast to its trimorphic relatives, *E. azurea* and *E. crassipes*, which are long-lived, clonal mat-forming aquatics, *E. paniculata* is a short-lived perennial or annual with an emergent life form. The life history of populations depends largely on available moisture. Where this is available for an extended period plants behave as perennials. In many sites in Brazil and Jamaica, however, moisture levels are uncertain and desiccation results in the complete destruction of living plants. Since individuals exhibit rapid development to reproductive maturity (observed minimum time from germination to flowering = 55 days) populations frequently regenerate from season to season by seed and are annual. The areas of NE Brazil and the southern coastal plain of Jamaica in which *E. paniculata* populations occur are characterized by strongly seasonal climates, and limited, unpredictable rainfall. Populations are found in seasonally

inundated pools, ditches, low-lying pastures and marshes. They can vary from single isolated plants, to colonies of 20–30 individuals or extensive monospecific stands containing several thousand plants. Population size is frequently associated with the certainty of moisture, with permanent marshes containing large populations and seasonal pools smaller populations.

In Jamaica the main flowering period is from December to February following the rainy season. In NE Brazil rainfall patterns are extremely unpredictable and unevenly distributed, resulting in frequent droughts. The region has one of the highest coefficients of variation in total rainfall in the world (Nimer, 1972). As a result flowering can occur at almost any time during the year, although April to June appears to be a major period.

Individual plants of *E. paniculata* display considerable phenotypic plasticity depending on site conditions. Plants can vary in size from 10 cm to 1 m in height. They have a limited capacity for clonal growth by the formation of axillary shoots, but clone size is never extensive and identification of genets is straightforward under field conditions. Inflorescences usually contain between one and 300 showy blue-purple flowers which last for one day and are pollinated primarily by bees.

Following pollination and fertilization, the tiny seeds mature in 14–21 days and are then shed from capsules into the surrounding mud or water. Given the habitat and small seed size it seems likely that birds may be responsible for local as well as long-distance dispersal between aquatic habitats. Germination usually occurs in open, bright situations in warm, shallow water. Considerable mortality occurs during the seed germination and seedling establishment phase as a result of receding water levels.

METHODS

Field collections

The locality, habitat and floral morph representation of *Eichhornia paniculata* populations from which seed material used in this study was collected, are presented in Table 1. Brazilian populations were sampled in April 1980 and May–June 1982 and Jamaican populations in December 1978. In each population a random bulk sample from a minimum of 25 seed parents was collected and stored in envelopes at room temperature until plants were required for experimental work.

Glasshouse culture

Seeds of *E. paniculata* exhibit weak innate dormancy and usually germinate readily, 1–2 months after harvest. Seeds collected from field populations were germinated in the glasshouse by flooding surface sown seed to a depth of 1–2 cm in 7.0 cm pots placed in water-filled plastic containers. Germination occurs more rapidly at water temperatures of 30–40°C. One week after germination the water level was gradually lowered to the soil surface to enable seedlings to establish in air. After 2–3 weeks from germination seedlings were transplanted singly into 10.5 cm pots and placed in flooded plastic containers with water 5–15 cm above the soil surface. Plants were grown in a 1 : 1 : 1 (sand, peat, clay-

Table 1. Localities, habitat and population structure of Brazilian and Jamaican populations of *Eichhornia paniculata* used in this study

Locality	Habitat	Population structure*	Collection date
Brazil (B)			
1. São Caitano, Pernambuco	Pond	T	April 1980
2. Bom Conselho, Pernambuco	Marsh	T	April 1980
3. Jupi, Pernambuco	Pond	D	April 1980
4. Lajedo, Pernambuco	Seasonal pool	M	April 1980
5. Recife, Pernambuco	Roadside ditch	T	May 1982
6. Maranguape, Ceará	Pond	T	June 1982
Jamaica (J)			
1. Slipc, St Elizabeth	Wet Meadow	M	Dec. 1978
2. Wallywash Pond, St Elizabeth	Seasonal pool	M	Dec. 1978
3. Meylersfield, Westmoreland	Marsh	M	Dec. 1978
4. Georges Plain 1, Westmoreland	Rice field	M	Dec. 1978
5. Palmers, Clarendon	Seasonal pool	M	Dec. 1978
6. Harris Savanna, Clarendon	Seasonal pool	M	Dec. 1978
7. Church Pen, St Catherine	Seasonal pool	M	Dec. 1978
8. Fellowship Hall, St Catherine	Roadside ditch	M	Dec. 1978
9. Old Pera, St Thomas	Marsh	M	Dec. 1978
10. Georges Plain 2, Westmoreland	Wet meadow	M	Dec. 1978

*T = trimorphic; D = dimorphic; M = monomorphic.

loam) horticultural mix, which was fertilized regularly with a soluble NPK fertilizer. The air temperature in the glasshouse was maintained at 25–35°C throughout the growing period.

Floral measurements

All floral measurements were undertaken on populations grown under glasshouse conditions. Unless otherwise stated measurements were made on 9–10 plants per population. To document the reciprocal position of anthers and stigmas in the floral morphs of *E. paniculata*, the height of these organs above the base of the ovary was measured on 10 flowers per floral morph from each of four trimorphic Brazilian populations. Stigma and anther heights were also measured on 10 flowers from each of the 10 monomorphic Jamaican populations. Anther heights for each stamen level were derived from the mean of the three stamen heights within a flower. The size of anthers at each stamen level were determined for the floral morphs in two trimorphic Brazilian populations by measuring the length and width of anther sacs under a dissecting microscope. In each population three anthers from each stamen level within a flower were measured on nine flowers per morph.

The equatorial axis of 100 dry pollen grains per stamen level within a flower was measured in each of the floral morphs in four trimorphic Brazilian populations with the aid of an ocular micrometer at $\times 40$ power. Similar measurements were made on 50 pollen grains per stamen level in each of eight Jamaican populations. The amount of pollen produced by each stamen level within a flower was estimated for the floral morphs in a Brazilian population and in eight Jamaican populations using the hemacytometer method of Lloyd

(1965). Anthers of a given stamen level were crushed in a known volume of lactophenol-glycerine containing cotton blue and the number of pollen grains scored in six hemacytometer counts for each sample. Ten or 18 flowers per morph were used from the Brazilian populations and six for each Jamaican population. Ovule number per flower was counted in six flowers per morph in two trimorphic Brazilian populations and in each of eight Jamaican populations. From the pollen production and ovule number data, pollen-ovule ratios per flower (P/O) were calculated for each population.

Controlled pollinations

To determine the compatibility relationships of floral morphs a controlled pollination programme was undertaken from September to November 1980, under pollinator-free glasshouse conditions, using nine plants from each of two trimorphic populations from Brazil. Pollinations were performed daily with the aid of fine forceps from 08.00 to 12.00 hours. Any given inflorescence received a single treatment which was either self-pollination or legitimate (between anthers and stigmas at equivalent levels) cross-pollination. All 18 plants in the experiment received both treatments. Self-pollinations used pollen from both anther levels within a flower, cross-pollinations involved a single pollen donor from the same population as the ovule parent. The number of flowers pollinated and capsules and seeds produced from each plant were recorded.

The degree of self-fertility and capacity for autogamous seed production (auto-fertility) were examined in six plants from each of 10 Jamaican populations from October to December, 1979. Flowers were either self-pollinated as above or left undisturbed in a pollinator-free glasshouse and the number of seeds per capsule was recorded for the two treatments. The data were compared with open-pollinated seed set data from the same populations obtained in the field from randomly sampled inflorescences during December 1978.

Inter-population differentiation

To examine the extent of inter-population genetic differentiation for life history and reproductive characters among Jamaican populations, and to compare this variation with a limited sample of populations from Brazil, ten individuals from each of 14 populations were grown under uniform glasshouse conditions during May–September 1980. The populations compared were B1–4 and J1–10 (see Table 1). Seed from each population was sown on 1 May and seedlings were transplanted singly three weeks later into 10.5 cm pots and arranged in a randomized design on a glasshouse bench. During the subsequent 5 month period, a range of quantitative and qualitative characters were recorded for each of the 140 plants in the experiment. The quantitative characters included days to flowering, plant height, number of flowers per inflorescence, total number of flowers per plant and flower diameter. Qualitative characters included nectar guide and flower colour intensity, and degree of autogamy. Analysis of variance was then used to determine whether significant population differentiation existed among the samples for a range of traits. Not all characters measured are considered in detail here.

RESULTS

*Brazilian populations**Floral trimorphism*

Field observations of stamen and style length in Brazilian populations demonstrate that *Eichhornia paniculata* is morphologically tristylous. Of the 30 populations located in NE Brazil, 22 contained the three style morphs, six contained mid- and long-styled morphs and the remaining two populations were monomorphic for the mid-styled morph. In six of the eight non-trimorphic populations, self-pollinating mid-styled forms, with between one and three anthers of short-level stamens in the mid position, predominated. Further details concerning the relative frequency of floral morphs and nature of modifications in floral trimorphism of Brazilian populations will be presented elsewhere.

Measurements of floral organs in glasshouse grown plants originating from four trimorphic populations of *E. paniculata* reveal that a close correspondence occurs in the height between the stigmas of long styles and anthers of long-level stamens, stigmas of mid-length styles and mid-level anthers and stigmas of short styles and short-level anthers (Table 2). Minor variation among populations in stamen and style length occurs but there was no overlap among the three levels in the length of reproductive organs.

Investigation of anther size in the floral morphs from two populations indicated differences in the size of anthers among the three stamen levels (Table

Table 2. Floral trimorphism in Brazilian populations of *Eichhornia paniculata*. Mean height \pm s.d. (mm) of stigmas and anthers in the three floral morphs grown under glasshouse conditions. Each value is based on 10 flowers per morph, italicized values are stigma heights, the remainder are anther heights

Population	Organ level*	Floral morph		
		Long	Mid	Short
B1	l	<i>16.1\pm0.6</i>	17.8 \pm 0.8	17.8 \pm 1.0
	m	11.2 \pm 0.6	<i>10.7\pm0.4</i>	11.2 \pm 0.9
	s	7.2 \pm 0.4	6.9 \pm 0.7	<i>6.3\pm0.7</i>
B2	l	<i>17.4\pm1.3</i>	18.6 \pm 0.5	18.1 \pm 0.7
	m	11.4 \pm 0.8	<i>11.6\pm0.5</i>	10.3 \pm 0.2
	s	6.6 \pm 0.7	6.9 \pm 0.6	<i>5.9\pm0.7</i>
B5	l	<i>14.6\pm0.5</i>	16.6 \pm 0.8	18.2 \pm 0.7
	m	8.9 \pm 0.8	<i>9.6\pm0.5</i>	9.9 \pm 0.5
	s	4.9 \pm 0.7	5.4 \pm 0.7	<i>5.9\pm0.3</i>
B6	l	<i>15.2\pm1.0</i>	15.6 \pm 0.9	15.0 \pm 0.7
	m	9.0 \pm 0.7	<i>9.6\pm0.7</i>	8.0 \pm 0.7
	s	4.2 \pm 1.1	5.2 \pm 1.1	<i>5.1\pm0.3</i>

*l = long; m = mid; s = short.

3). In general long-level stamens exhibited the largest anthers, anthers of mid-level stamens were intermediate and the smallest anthers occurred in short-level stamens. The styles of the floral morphs differ in colour. Long-styles are purple, mid-styles are lilac and short-styles are white. Unlike many other heterostylous species, stigmatic polymorphisms are not well developed in *E. paniculata*. Only minor differences in the length and density of stigmatic papillae were evident among the floral morphs.

Tristylos populations of *E. paniculata* exhibit size trimorphism of pollen. Pollen size is positively correlated with anther height with long-level stamens producing the largest pollen grains, and short-level stamens the smallest (Table 4). The mean pollen sizes of the three anther levels are significantly different but considerable overlap occurs among the pollen size distributions, particularly between pollen originating from long- and mid-level anthers (Fig. 1).

Estimates of pollen production of the three anther levels indicate a trend of decreasing pollen production with increased anther height and pollen size (Table 5). Pollen and ovule production values for the floral morphs from two trimorphic populations are presented in Table 6. Variation among the floral morphs was recorded, but more detailed sampling is required to establish whether or not morph specific differences occur. Where detailed sampling of pollen production was undertaken (Population B5, 30 plants, Table 5) no

Table 3. Mean length \times width \pm s.d. (mm) of anthers in the floral morphs of *Eichhornia paniculata* grown under glasshouse conditions. Each value is based on three anthers from nine flowers per morph ($N = 27$)

Anther level*	Floral morph		
	Long	Mid	Short
Population B1			
l	—	1.66 ^c \pm 0.11 X.80 ^e \pm 0.02	1.54 ^a \pm 0.8 X.80 ^e \pm 0.02
m	1.49 ^a \pm 0.09 X.78 ^d \pm 0.04	—	1.50 ^a \pm 0.09 X.80 ^e \pm 0.04
s	1.41 ^b \pm 0.06 X.76 ^d \pm 0.05	1.39 ^b \pm 0.48 X.77 ^{de} \pm 0.44	—
Population B2			
l	—	1.63 ^c \pm 0.09 X.80 ^e \pm 0.04	1.69 ^c \pm 0.10 X.73 ^f \pm 0.11
m	1.51 ^a \pm 0.08 X.79 ^e \pm 0.03	—	1.65 ^c \pm 0.15 X.76 ^{ef} \pm 0.13
s	1.39 ^b \pm 0.03 X.79 ^e \pm 0.03	1.32 ^d \pm 0.09 X.73 ^{ef} \pm 0.07	—

Within each population means not significantly different if superscripts (*a, b, c, d, e, f*) are the same. Means compared by LSD following ANOVA. B1 length: $F = 36.02$; d.f. = 5156; $P < 0.001$; width: $F = 5.54$; d.f. = 5156; $P < 0.05$. B2 length: $F = 62.94$; d.f. = 5156; $P < 0.001$; width: $F = 3.56$; d.f. = 5156; $P < 0.05$.

*l = long; m = mid; s = short.

Table 4. Mean equatorial axis \pm s.d. (μm) of pollen grains of the floral morphs of *Eichhornia paniculata* from four Brazilian populations. Plants grown under glasshouse conditions. Each value is based on 100 pollen grains per anther level in each morph

Population	Floral morph	l		m		s	
		M	S	L	S	L	M
B1		66.1 \pm 3.4	68.0 \pm 3.1	63.1 \pm 3.4	65.2 \pm 2.8	54.9 \pm 3.4	55.7 \pm 3.8
B2		68.9 \pm 2.9	69.0 \pm 2.5	64.5 \pm 2.9	63.5 \pm 2.6	53.5 \pm 2.8	54.8 \pm 2.3
B5		70.2 \pm 2.2	70.2 \pm 2.7	65.7 \pm 2.2	64.8 \pm 2.5	55.7 \pm 1.9	55.2 \pm 2.8
B6		66.5 \pm 2.9	70.1 \pm 2.4	65.3 \pm 2.3	66.1 \pm 2.0	56.2 \pm 1.8	52.0 \pm 1.8

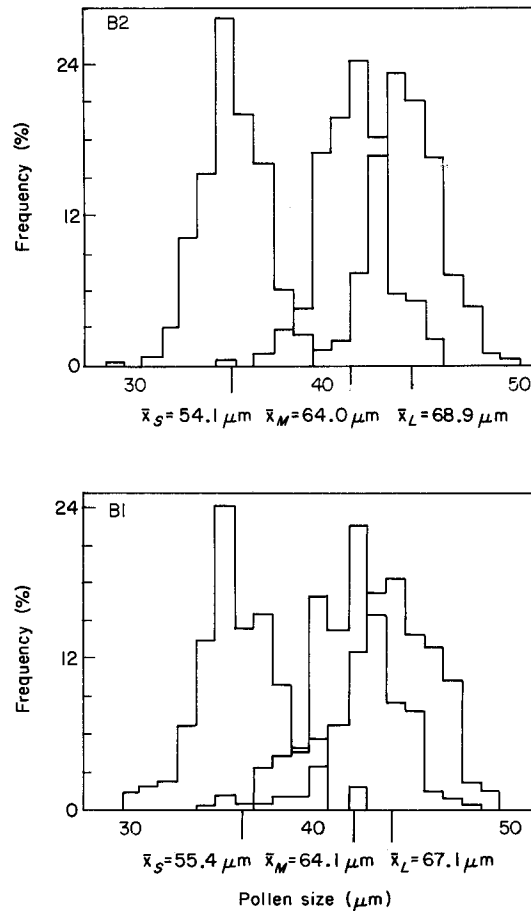


Figure 1. Size trimorphism of pollen in tristylous populations of *Eichhornia paniculata* from Brazil. $N = 200$ pollen grains per anther level in each population. Pollen was obtained from glasshouse grown plants of populations B1 and B2 and measured dry.

Table 5. Pollen production of the three anther levels in the floral morphs of *Eichhornia paniculata*. Each value is the mean \pm s.d. of six replicates from 10 flowers per morph. Plants grown under glasshouse conditions, seed collected from population B5

Anther level	Floral morph		
	Long	Mid	Short
l	—	9620 \pm 852	8842 \pm 1223
m	8324 \pm 948	—	10 000 \pm 1477
s	10 231 \pm 1891	11 055 \pm 2006	—
Total	18 555 \pm 1098	20 675 \pm 2107	18 842 \pm 2237

significant differences in pollen production per flower were obtained. The P/O ratios for populations B1 and B2 were 192.2 and 197.0, respectively.

Compatibility relationships

Controlled pollinations demonstrate that *Eichhornia paniculata* is highly self-compatible. All 18 plants tested produced abundant seed on self-pollination and in all possible combinations of cross-pollinations. Table 7 gives fruit and seed set data for self- and legitimate cross-pollinations. In eight of the 18 plants seed set from cross-pollinations was significantly higher than self-pollinations; six were short-styled individuals and two were long styled. In general the long- and mid-styled plants behaved similarly in the pollination treatments whereas short-styled individuals were markedly less productive of capsules and seed in self-pollinations. This effect may result from residual (weak) self-incompatibility or

Table 6. Pollen production and ovule number per flower of floral morphs in Brazilian populations of *Eichhornia paniculata*. Pollen production values are the mean \pm s.d. of six replicates from 18 flowers per morph within a population. Ovule number is based on 18 flowers per population. All plants grown under uniform glasshouse conditions

Population	Morph	Pollen production	Ovule number	P/O ratio
B1	L	27 127 \pm 5159	98.2 \pm 19.3	276.8
	M	18 520 \pm 6542	113.0 \pm 9.7	163.9
	S	16 021 \pm 8945	118.0 \pm 21.2	135.8
		20 556	109.7	192.2
B2	L	16 302 \pm 5827	87.7 \pm 8.3	185.2
	M	23 246 \pm 3475	93.7 \pm 13.1	194.7
	S	20 489 \pm 1599	97.0 \pm 14.7	211.2
		20 012	92.8	197.0

Table 7. Fruit and seed set following controlled self- and legitimate cross-pollinations of the floral morphs of *Eichhornia paniculata* grown under glasshouse conditions. Nine plants were used per population

Treatment		Flowers pollinated	Percentage fruit set	Total seeds	Means seeds per pollination
Long-styled morph					
B1	self	372	93.0	28 657	77.0
	cross	320	89.7	22 263	69.6
B2	self	188	69.7	8 418	44.8
	cross	211	87.2	14 802	70.2
Mid-styled morph					
B1	self	225	81.3	14 429	64.1
	cross	205	82.9	13 667	66.7
B2	self	141	87.2	7 066	50.1
	cross	165	78.2	6 888	41.7
Short-styled morph					
B1	self	251	49.4	3 759	15.0
	cross	150	76.7	7 458	49.7
B2	self	205	47.8	3 880	18.9
	cross	216	74.1	10 996	50.7

the abortion of developing embryos owing to inbreeding depression. Undisturbed flowers of the three floral morphs set little seed (percentage fruit set and sample size (flowers): L 0.5% (1,179), M 0.3% (795), S 1.7% (645)) indicating that the spatial separation of reproductive organs within flowers is sufficient to prevent autogamy.

Jamaican populations

Floral monomorphism

Field observations of the 10 Jamaican populations surveyed indicated that they were uniformly monomorphic for style length. Individuals in all populations possessed a mid-length style with various numbers of anthers of the short-stamen level adjacent to the stigma. The number of anthers in the mid-length position varied from zero to three. Individual populations were usually characterized by a specific condition. For example individuals in populations J3, J4, and J10 possessed flowers with all three anthers in close proximity to mid-level stigmas. This condition has been referred to as semi-homostyly (Ornduff, 1972; Barrett, 1979). In other populations, e.g. J2 and J5, flowers most commonly exhibited one or two anthers in the mid-length position. Of particular interest was the observation that individual inflorescences in all populations, except those with complete semi-homostyly (J3, J4 and J10), contained flowers with different floral conditions. These included unmodified mid-styled flowers identical in the positioning of reproductive organs to those found in trimorphic populations.

The commonest expression of floral instability involved inflorescences with a mixture of flowers with one or two anthers adjacent to mid-level stigmas. More rarely inflorescences produced a low frequency of unmodified mid-styled

flowers. Of 506 flowers sampled from plants in population J2, 90.0% were modified with one or two anthers adjacent to the mid-style and 10.0% were unmodified mid-styled flowers. The latter floral condition was only observed in populations J2, J5, J6, J7, J8 and J9. Semi-homostylous flowers, with three anthers in the mid-length position, were only observed in populations J3, J4 and J10. Despite the high inter-population and intra-plant variation in the position of short-level stamens, long-level stamens were unmodified.

Associated with developmental instability of floral expression in Jamaican populations of *E. paniculata* were a range of floral abnormalities including flowers with five tepals instead of six, lack of expansion of perianth limbs, twisted asymmetric perianth parts and sterility of pollen produced by long-level stamens. In addition, flowers from all populations were generally smaller (see below) and less showy than the bicoloured flowers of trimorphic populations. Flowers on Jamaican plants were mostly uniform pale lilac or mauve in colour with weakly developed yellow nectar guides which, in some populations, e.g. J3, were barely observable.

Measurements of pollen size from the two anther levels within flowers of Jamaican populations demonstrated a weak pollen size dimorphism. Pollen from long-level stamens is significantly larger than pollen from the lower stamen set (Table 8). However, the degree of dimorphism is less accentuated in comparison with mid-styled plants from trimorphic populations. On average pollen from long-level stamens is 2.8 μm smaller and pollen from short-level stamens is 6.1 μm larger than in unmodified mid-styled plants from Brazil. The greater difference in size of pollen from the lower stamen level is presumably associated with its alteration in position among Jamaican populations. Variation among populations in the size of pollen grains produced by the two stamen levels was also evident (Table 8). The degree of dimorphism varied from 2.1 μm in population J1 to 7.9 μm in population J4.

Estimates of pollen production and ovule number per flower as well as P/O ratios for Jamaican populations are presented in Table 9. In general slightly

Table 8. Floral characteristics of Jamaican populations of *Eichhornia paniculata*. Floral measurements are the mean \pm s.d. of 10 flowers per population, pollen measurements from 50 pollen grains per anther level. All plants grown under uniform glasshouse conditions

Population	Style length	Anther height		Pollen size	
		Lower stamens	Upper stamens	Lower stamens	Upper stamens
J1	11.7 \pm 0.6	10.0 \pm 3.0	15.8 \pm 0.8	57.2 \pm 3.4	59.3 \pm 2.7
J2	11.5 \pm 0.4	9.4 \pm 3.0	15.6 \pm 0.9	59.0 \pm 4.2	63.3 \pm 3.3
J3	11.5 \pm 0.6	11.0 \pm 0.8	15.3 \pm 0.7	58.2 \pm 3.3	62.5 \pm 3.6
J4	11.4 \pm 0.4	10.4 \pm 0.4	13.0 \pm 2.0	55.6 \pm 3.1	63.5 \pm 3.3
J5	10.5 \pm 0.7	8.9 \pm 3.0	14.6 \pm 1.0	—	—
J6	10.8 \pm 0.8	10.0 \pm 2.0	16.0 \pm 1.0	—	—
J7	10.8 \pm 0.4	9.3 \pm 3.0	15.1 \pm 0.6	63.3 \pm 2.8	68.0 \pm 2.5
J8	10.8 \pm 0.4	10.1 \pm 2.0	15.1 \pm 0.9	65.3 \pm 4.0	70.0 \pm 2.2
J9	10.5 \pm 0.3	9.3 \pm 3.0	15.1 \pm 0.6	64.5 \pm 2.9	69.1 \pm 3.1
J10	10.7 \pm 0.8	10.0 \pm 1.4	14.0 \pm 2.0	60.9 \pm 2.0	65.2 \pm 2.0

Table 9. Pollen production and ovule number per flower of Jamaican populations of *Eichhornia paniculata*. Pollen production values are the mean \pm s.d. of six replicates from six flowers per population. Ovule number is based on six flowers per population. All plants grown under uniform glasshouse conditions

Population	Pollen production			Ovule number	P/O ratio
	Lower stamens	Upper stamens	Total		
J1	4168 \pm 1945	1753 \pm 412	5921	60.3 \pm 11.1	98.2
J2	5853 \pm 553	4829 \pm 1285	10 682	63.6 \pm 6.3	168.0
J3	4482 \pm 1697	3431 \pm 2221	7913	77.5 \pm 12.3	102.1
J4	4419 \pm 611	4464 \pm 1160	8883	65.7 \pm 11.2	135.2
J7	3814 \pm 307	2267 \pm 272	6081	59.7 \pm 17.1	101.9
J8	3947 \pm 1247	2295 \pm 883	6242	56.5 \pm 6.5	110.5
J9	8217 \pm 3450	5633 \pm 1095	13 850	85.2 \pm 10.1	162.6
J10	3903 \pm 805	2669 \pm 102	6572	58.3 \pm 5.0	112.7

more pollen is produced by the lower stamens in comparison with the upper stamens, but this difference varies among populations as does the total pollen production per flower. The amount of pollen produced by flowers in Jamaican populations is on average less than half of that produced by the mid-styled morph in trimorphic populations, whereas average ovule number per flower is approximately one third less than the value obtained from Brazilian populations. As a result of this difference the P/O ratios of Jamaican populations are significantly lower than Brazilian populations.

Self-pollination

All Jamaican populations of *E. paniculata* are self-compatible (Table 10). The juxtaposition of anthers and stigmas within flowers gives plants the capacity for autogamous seed set as a result of automatic self-pollination. Accordingly there was little difference in most populations between the seed set per capsule resulting from controlled self-pollinations and in undisturbed flowers. There was no evidence from the seed set data of undisturbed flowers that populations with three anthers adjacent to mid-level stigmas were any more effective at autogamous seed set per capsule in comparison with populations with fewer anthers in the mid-level position.

Fruit and seed set data collected in the field from open-pollinated plants indicate that Jamaican populations are highly fecund. Of the 4138 flowers sampled 89.1% produced fruit. The average number of seeds per capsule was 29.1% higher than obtained in self-pollinations under glasshouse conditions. This difference can probably be attributed to more favourable environmental conditions for pollination and seed maturation in the field.

Inter-population differentiation

Visual observation of the 14 populations from Brazil and Jamaica grown under uniform glasshouse conditions indicated striking differences among populations in growth patterns, flowering capacity and plant size. Statistical

Table 10. Seed fertility of Jamaican populations of *Eichhornia paniculata*. Open-pollinated data collected from field populations in December 1979. Selfed and undisturbed treatments undertaken on plants grown under uniform glasshouse conditions

Population	Open pollinated			Self		Undisturbed	
	$N(\text{flowers})$	Percentage fruit set	seeds/capsule	$N(\text{flowers})$	seeds/capsule	$N(\text{flowers})$	seeds/capsule
J1	966	87.1	70.4 ± 35.2	30	41.1 ± 8.5	6	31.7 ± 9.1
J2	739	90.3	86.5 ± 13.0	47	52.0 ± 14.6	28	46.8 ± 15.9
J3	64	82.8	65.6 ± 22.8	59	49.1 ± 15.1	51	43.2 ± 14.0
J4	724	88.9	68.8 ± 24.9	19	55.1 ± 14.3	—	—
J5	334	85.3	74.6 ± 20.0	61	50.7 ± 10.5	65	49.6 ± 12.9
J6	390	96.4	64.8 ± 16.7	95	56.1 ± 14.0	60	49.4 ± 14.0
J7	229	96.5	46.4 ± 22.4	77	54.4 ± 13.1	42	42.8 ± 12.5
J8	519	86.9	51.8 ± 20.1	45	58.2 ± 15.7	39	58.6 ± 11.4
J9	173	85.0	84.0 ± 27.6	41	40.9 ± 8.8	31	41.5 ± 14.7
J10	—	—	—	17	26.8 ± 9.5	21	52.0 ± 17.1

Table 11. Inter-population genetic differentiation for five quantitative characters among 14 populations of *Eichhornia paniculata* from Brazil and Jamaica. Each value is the mean of 10 plants. Vertical bars indicate statistically homogeneous subsets following Duncan's Multiple Range Test. Plants grown under uniform glasshouse conditions during summer 1980

Days to flowering		Total flowers/plant		Flowers/infl.		Flower diameter (mm)		Plant height at 150 days (cm)	
Pop.	\bar{x}	Pop.	\bar{x}	Pop.	\bar{x}	Pop.	\bar{x}	Pop.	\bar{x}
B2	75.2	J1	31.0	J1	10.9	J10	16.0	J1	33.7
J7	76.7	J10	37.1	J2	11.2	J8	17.4	J2	35.1
B3	76.8	J2	39.0	J10	14.4	J4	17.6	J7	42.0
J5	77.5	J4	46.6	J3	16.2	J9	17.7	J8	45.7
B1	77.5	B4	46.9	J4	17.0	J7	17.9	J5	46.1
J6	78.7	J3	59.1	J8	17.7	J5	18.3	J9	46.1
J8	83.6	B1	83.7	J7	17.9	J1	18.8	J6	49.5
J2	84.6	J6	86.2	B4	19.6	J6	19.5	J10	51.0
J1	85.9	J8	89.0	J5	20.1	J3	20.0	J3	51.4
J9	87.6	J9	90.8	J9	20.2	J2	20.0	J4	52.6
B4	88.1	J7	91.1	J6	20.3	B4	20.0	B4	53.0
J3	88.9	J5	96.1	B1	27.1	B3	22.9	B3	57.8
J4	97.0	B3	115.1	B2	28.7	B1	23.2	B2	58.4
J10	97.2	B2	122.1	B3	29.9	B2	24.3	B1	64.2
<i>F</i> (13 139)	15.86		12.24		18.16		6.01		27.87
<i>P</i>	<0.001		<0.001		<0.001		<0.001		<0.001

analysis of a range of characters measured over a 5 month period supported these visual impressions. There were significant differences among populations following ANOVA for all characters. Population means for five quantitative characters are presented in Table 11, significant inter-population genetic differentiation for each character occurs within the Jamaican and Brazilian samples. The trimorphic (B1, B2) and dimorphic (B3) populations tend to be markedly differentiated from the remaining populations with respect to flowering characters and plant height. The monomorphic Brazilian population (B4) groups with the Jamaican populations for several of these characters. This is of some interest because individuals within this population, in common with those from Jamaica, exhibit modifications of short-level stamens which promote self-pollination. Polymorphic populations from Brazil produce large inflorescences with large flowers and plants are taller than in Jamaican populations. The monomorphic Brazilian population has smaller and fewer flowers per inflorescence and plants are significantly shorter in height than in the remaining Brazilian populations. Although the monomorphic Brazilian population tends to group with the Jamaican populations it should be noted that in height and flower size it is intermediate between the two groups.

There were no clear regional differences between the samples in time to flowering. The three polymorphic Brazilian populations, however, were in the earliest flowering group (Table 11). The monomorphic Brazilian population flowered on average 11 days after the last polymorphic population had commenced flowering. There were striking differences among the Jamaican populations in time to flowering. Two populations from Georges Plain (J4, J10)

flowered together 8 days after all remaining populations and 22 days after the first Jamaican population.

Several months after the experiment was completed almost all individuals in populations J5 and J6 senesced and died despite the availability of nutrients and water. The remaining populations continued to grow and flower. This observation suggests that the plants in these 2 populations may behave as obligate annuals, whereas the remaining populations exhibit a perennial life history. Individuals from populations J5 and J6 were among the most rapid in time to flowering and flowering capacity.

DISCUSSION

A recurrent pattern which has emerged from studies of mating systems in the flowering plants is the shift from cross-fertilization to self-fertilization. Stebbins (1957, 1974) has argued that the evolutionary pathway from obligate outbreeding, based on self-incompatibility, to predominant self-fertilization has probably been followed by more different lines of evolution in the flowering plants than has any other. Certainly numerous authors have inferred such a change based on comparative studies of closely related taxa (examples reviewed in Stebbins, 1974). Despite the importance of this change there is still active debate on the relative importance of the various selective forces thought to be responsible for the shift to self-fertilization (Jain, 1976; Lloyd, 1980). Furthermore, the genetic basis of alterations in mating system parameters is largely unknown.

A major difficulty in the investigation of the evolution of selfing is that when outbreeding is replaced by selfing the change is often rapid and is frequently associated with the development of reproductive isolation by chromosomal rearrangements, polyploidy, or major alterations in floral structure (Baker, 1961; Moore & Lewis, 1965; Gottlieb, 1976). As a result, investigators are often faced with the difficulty of making phylogenetic inferences on the polarity of character state changes among related taxa and are unable to examine directly the genetical mechanisms involved with shifts in breeding system. Despite these problems some workers have identified species in which populations exhibit different mating systems (Lloyd, 1965; Moore & Lewis, 1965; Ganders, 1975 a,b; Rick *et al.*, 1977; Thomas & Murray, 1981; Schoen, 1982) and examination of the distribution, ecology and genetics of populations in these groups has provided greater insight into the processes responsible for the evolution of self-fertilization.

A frequent pattern in species groups in which self-fertilizing populations have established, is the tendency for the selfers to occur at the geographical margins of the range of their outcrossing progenitors or in ecologically marginal sites within the species range. This distribution is in accord with the view that self-fertilizing individuals are at a selective advantage at low density or in establishment after long-distance dispersal (Baker, 1955, 1967) and has led to the suggestion that they are favoured in pioneer habitats or under conditions associated with population bottlenecks in ecologically marginal sites (Stebbins, 1957; Moore & Lewis, 1965; Arroyo, 1974). Such effects are likely to be particularly important in animal pollinated species with specialized pollinators. Outside the range of their normal pollinators and in small, newly founded

populations, highly self-pollinating variants would be favoured via fecundity selection. The high frequency of autogamous plants on the insect impoverished Galapagos (Rick, 1966) and Faeroes Islands (Hagerup, 1951) would appear to be evidence for the importance of selfing as a means of survival under these conditions. In addition, the debilitating effects of inbreeding depression, which would normally retard the 'automatic selection' of selfing genes (see Lloyd, 1980), may be less severe at low density with relaxed biotic selection. The observed patterns of breeding system variation in the genus *Eichhornia* (Barrett, 1978, 1979), as well as several other heterostylous groups in which homostylous forms occur in geographically or ecologically marginal areas (Baker, 1959; Ornduff, 1972; Ganders, 1975a) are in accord with this general model of the evolution of selfing.

Observations of insect visitors to flowers of *E. paniculata* in Jamaica were made during a single month (December, 1978); relatively few pollinators were recorded. All insects were generalists (e.g. *Apis mellifera*) and no long-tongued solitary bees were observed. In contrast, large numbers of specialized solitary bees (e.g. *Florilegus festivus* Smith and *Ancyloscelis* spp.) were observed visiting populations in NE Brazil, particularly those of large size. While these observations are limited and non-quantitative, they are consistent with the view that islands have reduced numbers of specialized bee groups in comparison with continental faunas. Absence of specialized visitors, as well as fluctuations in insect numbers, would likely have a disruptive effect on the functioning of tristylous populations, particularly in a self-compatible species, and may lead to the establishment of self-pollinating variants (Barrett, 1979; Charlesworth, 1979). Among the 30 populations located during field studies in NE Brazil, six contained self-pollinating variants. This indicates that the processes responsible for the breakdown of tristylous populations can be initiated under ecological conditions prevailing within the centre of the range of the species. The six populations were all small and four were south of the main concentration of trimorphic populations in Ceará and Pernambuco (S. C. H. Barrett, unpubl. data). Studies are in progress to examine the ecological and genetic processes responsible for the breakdown of floral trimorphism in Brazilian populations.

Unlike the majority of heterostylous species *E. paniculata* is highly self-fertile. This is likely to mean that its mating system will be especially sensitive to ecological factors such as pollinator type and abundance, plant density and environmental conditions during flowering. It might be predicted that in large populations, with reliable pollinator service, floral trimorphism would promote legitimate pollinations among the floral morphs resulting in outcrossing. In smaller populations, however, increased levels of self-fertilization would be anticipated. The close juxtaposition of anthers and stigmas in semi-homostylous flowers is likely to result in predominant selfing, particularly on Jamaica, where pollinator service may be unreliable.

Comparison of the floral biology of Brazilian (trimorphic) and Jamaican populations of *E. paniculata* revealed several consistent differences involving the size and showiness of floral parts, pollen production and ovule number per flower. These differences frequently distinguish outbreeding and inbreeding taxa (Darwin, 1876; Rollins, 1963; Lloyd, 1965; Ornduff, 1969; Cruden, 1977). After self-fertilization has established in populations with low pollinator service, it would be expected that selection pressures to maintain showy flowers and large

floral displays would be truncated and flower size and attractiveness would diminish accordingly. The reduction in corolla size, uniform colouration of tepals, and loss of nectar guides in Jamaican populations, is paralleled by similar, but less dramatic, alterations in floral display among self-pollinating Brazilian populations. In comparison with most Jamaican populations, self-pollinating individuals in Brazilian populations tended to have larger flowers with more of them per inflorescence. This suggests that these variants may have originated more recently from tristylous forms and selection has not adjusted the floral characters and reproductive economy of populations to the extent that is evident among Jamaican populations.

Considerable developmental instability for a range of floral traits, particularly the lower stamen level, was observed among Jamaican populations. Intra-plant variation in filament length of short-level stamens was also evident among selfing variants from Brazil. In contrast the expression of floral traits in individuals from tristylous populations was relatively uniform. The genetic basis of developmental instability is still poorly understood but can result from insufficient heterozygosity within polygenic systems, wide hybridization or specific gene loci (Rick & Smith, 1953; Lerner, 1954; Jinks & Mather, 1955; Rendel, 1959; Waddington, 1960). It seems likely that inbreeding, leading to a loss in the precision of canalization and a reduced ability to buffer against environmental stimuli, may be the cause of floral instability in *E. paniculata*. Ongoing studies indicate that the variability in expression of filament length in low level stamens is controlled by recessive genes (S. C. H. Barrett, unpubl. data). These are more likely to be fixed in small, inbreeding populations. Mather (1950) demonstrated greater intraplant variance in stamen and style length of inbred lines in horticultural material of *Primula sinensis* in comparison with their F₁ generations. However, these observations in *E. paniculata* seem to be the first report of the widespread occurrence of floral instability in natural populations of a heterostylous plant. The occurrence of other floral abnormalities, such as deformed tepals and the loss of perianth parts, suggests that these traits may be selectively neutral under Jamaican conditions, where pollinators may exert relatively little influence on floral form.

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