Genetic variation in continental and island populations of *Eichhornia paniculata* (Pontederiaceae)

D. E. Glover* and
S. C. H. Barrett

Department of Botany, University of Toronto,
Toronto, Ontario, Canada M5S 1A1

Genetic variation was examined at 21 allozyme loci in 11 populations of *Eichhornia paniculata* (Pontederiaceae) from N.E. Brazil and Jamaica. Populations from Jamaica are genetically depauperate with respect to electrophoretically detectable variation, containing a significantly lower number of polymorphic loci, alleles per locus, mean observed heterozygosity and genetic diversity than Brazilian populations. These measures were significantly correlated with the outcrossing rate (t) of populations. The allozyme data were used to examine the patterns of genetic variation within and between populations by estimates of gene correlation and Nei's gene diversity statistics. Populations within both regions are highly differentiated from one another, with those from Jamaica more strongly so. Brazilian populations contain more variation than is distributed among populations, while the reverse pattern occurs among Jamaican populations. The genetic distance between Jamaican populations is less than between Brazilian populations as a result of the low overall variability on the island. It is proposed that the founding of populations on Jamaica by long-distance dispersal, genetic drift and high levels of self-fertilisation all contribute to reducing levels of genetic variation in Jamaican populations.

INTRODUCTION

Floristic and faunistic studies of islands have been frequent, particularly with regard to factors that influence adaptive radiation and speciation, degree of endemism and community organization (Darlington, 1957; MacArthur and Wilson, 1967; Carlquist, 1974; Lack, 1976; Williamson, 1981). Because opportunities for gene flow are often reduced and island habitats may be ecologically as well as geographically marginal, island populations can act as natural experiments of the effects of isolation and directional selection on the genetic structure of populations. Comparison of continental and island populations in several animal groups have provided particularly valuable insights into evolutionary processes (Dobzhansky, 1957; Clarke and Sheppard, 1963; Avise *et al.*, 1974; Ayala *et al.*, 1971). Despite their vagrancy and capacity for long-distance dispersal, there have been few studies of the ecological genetics of continental and island population of plants. With this in mind, the present study was designed to contrast the

levels of genetic variability and degree of genetic differentiation in continental and island populations of the diploid, tristylous, emergent aquatic *Eichhornia paniculata* (Pontederiaceae).

Eichhornia paniculata has a markedly disjunct geographical distribution. Populations are numerous throughout the states of N.E. Brazil, also occur on the Caribbean islands of Cuba and Jamaica and isolated populations are reported from Nicaragua and W. Brazil (Barrett, 1985a; Glover and Barrett, 1986). The founding and establishment of populations in the Caribbean region likely resulted from long-distance dispersal, although the direct source area and time of colonisation is unknown. Nevertheless, because such dispersal events are likely to be infrequent, it may be predicted that populations on the island of Jamaica should display lower levels of genetic variation than populations from N.E. Brazil. Data on the distribution of style morphs in *E. paniculata* is consistent with this suggestion. While populations in N.E. Brazil most commonly contain the three style morphs, on Jamaica the short-styled morph is absent, and self-pollinating semi-homostylous variants of the mid-styled morph predominate

* *Present address*: Department of Botany and Plant Sciences, University of California, Riverside, California 92521, U.S.A.

(Barrett 1985a, b). Absence of the short-styled morph from Jamaica is indicative of a genetic bottleneck associated with island colonisation. Selfing forms would be favoured in establishment on Jamaica following long-distance dispersal.

In this study, allozyme data are used to examine gene diversity and patterns of genetic differentiation between 11 populations from the two regions. Since populations within and between the two regions also vary in floral morphology (Barrett, 1985a) and mating system (Barrett *et al.*, 1987; Glover and Barrett, 1986), an additional objective of the study was to examine whether differences in the mating systems of populations are associated with contrasting genetic structures.

MATERIALS AND METHODS

Sites and sampling

Seed families were collected in May–June 1982 from 6 populations of *Eichhornia paniculata* in

N.E. Brazil (B) and 5 populations from Jamaica (J) during January 1983. Populations sampled in N.E. Brazil were chosen to represent the range of floral morph structures (trimorphic: long-, mid- and short-styled morphs, hereafter L, M, and S, respectively; dimorphic: L, M; and monomorphic: M) observed for the region, whereas in Jamaica all populations encountered during the 1983 season were sampled. The distribution of populations are mapped in figure 1 and information on locality, morph structure and outcrossing rate are presented in table 1. Further details of the habitat, population size and floral biology of populations are given in Glover and Barrett (1986).

Electrophoretic procedures

Horizontal starch gel electrophoresis was used to obtain allozyme data for 11 enzyme systems. An initial screening of plant tissues indicated that enzyme activity was consistently highest in mature buds, and as a result this tissue was used in all
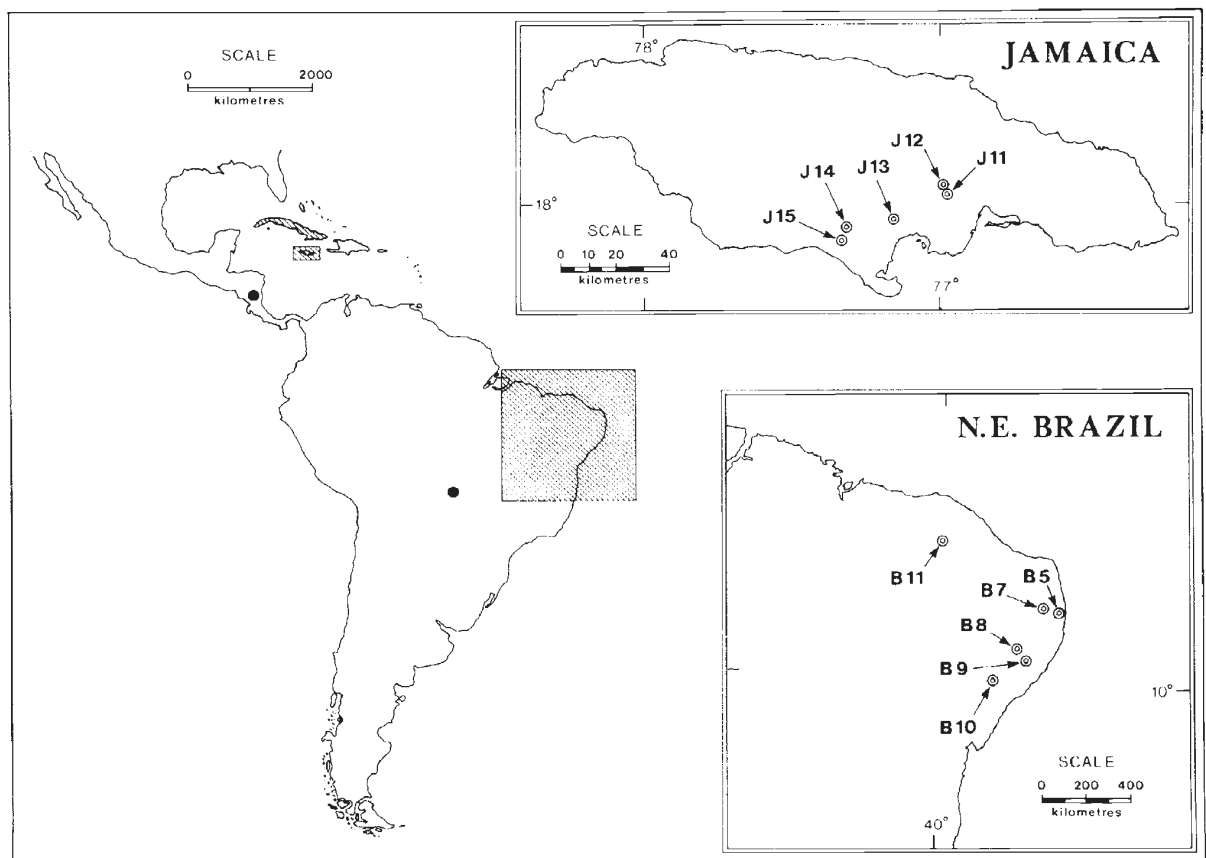

Figure 1 Distribution of *Eichhornia paniculata* and location of populations studied in N.E. Brazil and Jamaica. Isolated populations are reported from Nicaragua and W. Brazil.

Table 1 Location, morph structure and multilocus estimates of outcrossing rate (*t*) in populations of *Eichhornia paniculata* from N.E. Brazil and Jamaica. Data on outcrossing rates and their standard errors are from Glover and Barrett (1986). T = trimorphic, D = dimorphic, M = monomorphic for style morph

Designation	Locality	Morph structure	Outcrossing rate (*t*)	S.E.
B5	Recife, Pernambuco, Brazil	T	0·96	0·025
B7	Vitória de S. Antão, Pernambuco, Brazil	T	0·84	0·086
B11	Quixadá, Ceará, Brazil	T	0·94	0·023
B9	União dos Palmares, Alagoas, Brazil	D	0·49	0·027
B10	Arapiraca, Alagoas, Brazil	D	0·77	0·067
B8	Murici, Alagoas, Brazil	M	0·47	0·140
J15	Pridee, Clarendon, Jamaica	D	0·68	0·087
J14	Rhymsbury, Clarendon, Jamaica	D	0·29	0·070
J12	Angels, St. Catherine, Jamaica	D	0·47	0·090
J11	Angels, St. Catherine, Jamaica	M	—*	—
J13	Rosewell, Clarendon, Jamaica	M	—*	—

* No isozyme variation detected at 21 loci; plants autogamous.

assays. Three buds from an individual plant were placed in a well of a glass grinding tray and homogenised in 3 drops of extraction buffer (0·05 *M* K₂HPO₄ with 1 mg/ml of dithiothreitol) to which a spatula tip of PVPP (polyvinylpolypyr-rolidone) was added. The homogenate was absorbed onto filter paper wicks and loaded with the aid of forceps into a slit cut along the cooled gel.

Gels were prepared with Sigma starch at an 11 per cent w/v concentration and 10 g sucrose. Three buffer systems were used: (A) Continuous Histidine citrate, *p*H 6·5 (Cardy *et al.*, 1981), (B) Discontinuous Li-borate/Tris-citrate, *p*H 8·3 (Cardy *et al.*, 1981), (C) Discontinuous Poulik, *p*H 8·3–8·6/7·9 (modified from Mitton *et al.*, 1977). Electrophoresis was conducted in a glass front refrigerator at 0–4°C. Wicks were removed after 10 minutes. The voltages maintained for the different buffer systems were as follows:

Buffer system	Voltage	mA	Running time	Front migration
A	400–475	50	6 h	9·5 cm
B	180–250	50	5 h	8·0 cm
C	125–175	50	5 h	8·0 cm

A standard 375 ml gel provided 6 slices (each 1·5 mm thick). The top and bottom slices were discarded, and the remaining slices were placed in styrofoam trays for staining. Table 2 lists the enzyme systems stained, the number of loci scored, the buffer systems used and references for staining procedures. Gels were scored immediately following incubation and soaked overnight in a 5:5:1 solution of methanol:water:glacial acetic acid for preservation.

Table 2 Enzymes, number of loci and buffer systems used during study of *Eichhornia paniculata*

Enzyme		No. loci scored	Buffer system	Stain reference
Oxidoreductases:				
Diaphorase	(DIA)	1	B	Vallejos 1983
Glutamate dehydrogenase	(GDH)	1	B	Cardy *et al.* 1980
Isocitric dehydrogenase	(IDH)	2	A	Cardy *et al.* 1980
Malate dehydrogenase	(MDH)	3	A	Cardy *et al.* 1980
Peroxidase	(PER)	1	A	Shaw and Prasad 1970
6-Phosphogluconate dehydrogenase	(PGD)	2	A	Cardy *et al.* 1980
Shikimic dehydrogenase	(SKD)	2	A	Vallejos 1983
Transaminases:				
Glutamate-oxaloacetate transaminase	(GOT)	3	B	Cardy *et al.* 1980
Phosphoglucomutase	(PGM)	2	A	Cardy *et al.* 1980
Hydrolases:				
Acid Phosphatase	(ACP)	1	A	Scandalios 1969
Isomerases:				
Phosphoglucose isomerase	(PGI)	3	C	Cardy *et al.* 1980

For a given enzyme system the locus coding for the most anodally migrating protein was designated 1, the next 2, and so on. Allozymes and their corresponding alleles are identified by a lower case letter. The allele coding for the most anodally migrating allozyme was designated a, the next b, and so on. Inheritance studies that confirm the genetic models that account for the observed isozyme variation are detailed in Glover (1985) and S. C. H. Barrett (unpublished data). In population B11, several patterns that were not easily interpreted were observed at MDH-2. Because segregation analysis of crosses is not completed, this population was left out of all analyses that included MDH-2. For PGI-3 a null allele was detected in populations B5, B9 and B10. Heterozygotes involving the null allele were indistinguishable from homozygotes aa or bb. Without extensive progeny testing of populations in which the null allele occurs, the frequency of alleles a, b, and n cannot be determined. Accordingly, these populations were omitted from analyses that included PGI-3.

Population structure

Three parameters that summarise population structure were introduced by Wright (1951); F_{IT}, F_{ST} and F_{IS}. An analysis of variance estimation approach to these parameters has been advocated by Weir and Cockerham (1984) and is used here. After consideration of bias introduced when unequal and finite sample sizes, multiple alleles and multiple loci are not accounted for, and in the interest of standardising estimators, they present a more robust set of parameters related to F-statistics such that $F \simeq F_{IT}$, $\theta \simeq F_{ST}$, and $f \simeq F_{IS}$ (Cockerham, 1969, 1973). F describes the correlation of genes within individuals and is approximately the fixation index in the total population, θ describes the correlation of genes between individuals within populations and measures the differentiation between populations. The correlation of genes within individuals in a given population is denoted by f, which describes the relationship of the observed heterozygosity to that expected under panmixia (Hardy–Weinberg equilibrium) and is approximately equivalent to Wright's fixation index. The parameters are related by $f = (F - \theta)/(1 - \theta)$. Computational formulas are given in Weir and Cockerham (1984). The variance of the estimators when multiple loci are used can be approximated by the jackknife procedure (Miller, 1974), omitting one locus at a time and calculating the variance among the resulting estimates.

Gene diversity

The degree of gene differentiation when population structure is hierarchical can be analysed using Nei's gene diversity statistics (Nei, 1973). The gene diversity in the total population, H_T, is given by $H_T = H_S + D_{ST}$ where H_S is the gene diversity within subpopulations and D_{ST} the gene diversity between subpopulations. The gene diversity between populations, G_{ST}, relative to that of the total assemblage of populations, is given by $G_{ST} = D_{ST}/H_T$. The inter-populational gene diversity relative to the intra-populational gene diversity is given by R_{ST}, where $R_{ST} = \bar{D}_m/H_S$ and $\bar{D}_m$ is a measure of within subpopulation diversity calculated from D_{ST} by excluding the comparisons of subpopulations with themselves. These statistics can be measured using data from one or more loci. Nei and Roychoudhury (1974) advocate the use of a large number of randomly chosen loci that include both polymorphic and monomorphic loci. Data from all loci were included in this analysis.

RESULTS

Allelic richness and observed heterozygosity

Among the 11 populations of E. paniculata, a total of 21 loci were scored. Of these, 13 were polymorphic in at least one population. Allele frequencies for polymorphic loci are presented in the Appendix. The remaining eight loci (IDH-1, IDH-2, MDH-1, PGD-2, SKD-1, SKD-2, PGM-2, PGI-1) were monomorphic in all populations examined.

In Brazilian populations, 36 alleles were detected among the 21 loci compared to 24 alleles in Jamaican populations. The representation of alleles in Jamaica is moderately differentiated from a simple subset of alleles sampled from Brazil. Of the total array of alleles in all populations, 46·3 per cent were shared by the two regions. Thus 17 (47 per cent) of the Brazilian alleles were found only in that region, while 5 (21 per cent) of the Jamaican alleles were diagnostic for the island. Two of the three polymorphic loci in Jamaica were invariant in all Brazilian populations. Of the 9 loci that were monomorphic in Jamaica but polymorphic in Brazil, 6/9 were fixed for the most common Brazilian allele, 1/9 was fixed for the least common allele, and 2/9 were fixed for alleles only recorded from Jamaica.

The mean number of alleles per locus ($\bar{K}$, where the frequency of the least common allele is $>0·05$), the percentage of loci polymorphic (P, where a locus is polymorphic when the frequency of the

most common allele is <0·95) and the mean observed proportion of loci at which an individual is heterozygous ($\bar{H}_0$, scored by direct count) are presented in table 3 for each population, with the regional mean for each value. Overall, $\bar{K}$ ranged from 1·0 to 1·45, P ranged from 0 to 35, and $\bar{H}_0$ ranged from 0 to 12·0. Brazilian populations are significantly richer in alleles than Jamaican populations as measured by $\bar{K}$ ($t = 2·99$, df = 9, $p < 0·02$) and P ($t = 2·86$, df = 9, $p < 0·05$). In addition, individuals in Brazilian populations are on average more heterozygous than individuals in Jamaican populations ($t = 2·94$, df = 9, $p < 0·05$). Two populations (J11, J13) were invariant at all 21 allozyme loci. At two of the three loci at which variation was detected in Jamaica, the populations were fixed for different alleles.

Table 3 Mean number of alleles per locus ($\bar{K}$), per cent of loci polymorphic (P), and mean observed heterozygosity ($\bar{H}_0$), in populations of *Eichhornia paniculata* from N.E. Brazil and Jamaica

Population	No. of loci	$\bar{K}$ (SD)	PLPP	$\bar{H}_0$ (SD)
Brazil				
B5	20	1·45 (0·67)	35·0	11·3 (18·6)
B7	21	1·24 (0·53)	19·0	7·8 (15·9)
B11	20	1·35 (0·57)	30·0	12·0 (19·9)
B9	20	1·30 (0·46)	30·0	7·0 (11·4)
B10	20	1·25 (0·43)	25·0	7·9 (13·9)
B8	21	1·05 (0·21)	4·7	0·8 (3·2)
Mean		1·27 (0·37)	23·8	7·8 (1·98)
Jamaica				
J15	21	1·14 (0·35)	14·3	5·0 (12·3)
J14	21	1·14 (0·35)	14·3	2·3 (5·9)
J12	21	1·09 (0·29)	9·5	2·5 (8·0)
J11	21	1·00 (0·0)	0·0	0·0 (0·0)
J13	21	1·00 (0·0)	0·0	0·0 (0·0)
Mean		1·07 (0·27)	7·6	2·0 (1·4)

Multilocus estimates of outcrossing rate, using the method of Ritland and Jain (1981), have been calculated for nine of the 11 populations (Glover and Barrett, 1986); the exceptions are the two invariant populations. Outcrossing rate (t) was significantly rank correlated with $\bar{K}$ ($r_s = 0·788$, $n = 9$, $p = 0·012$), P ($r_s = 0·758$, $n = 9$, $p = 0·018$) and $\bar{H}_0$ ($r_s = 0·900$, $n = 9$, $p = 0·001$) (fig. 2).

Population structure

Table 4 presents estimates of gene correlation for *E. paniculata* populations in N.E. Brazil and Jamaica. For N.E. Brazil, the significant, positive $\hat{F}$ value indicates a correlation of genes within
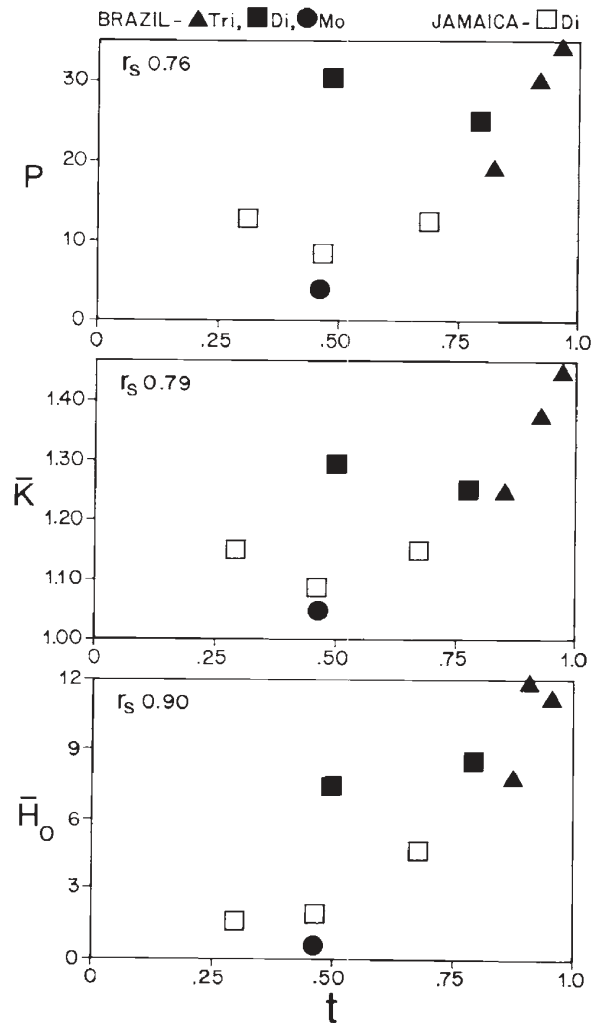

Figure 2 The relationship between outcrossing rate (t) and several population genetic parameters (P = proportion of loci polymorphic, $\bar{K}$ = mean number of alleles per locus, $\bar{H}_0$ = mean observed heterozygosity in populations of *Eichhornia paniculata* from N.E. Brazil and Jamaica.

individuals. Thus there is an overall heterozygote deficiency when Brazilian populations are treated as a panmictic unit. $\hat{F}$ would be equal to $\hat{f}$ if populations were representative of the region as a whole, and differentiation was negligible. However, in Brazil, the magnitude of $\hat{\theta}$ almost entirely explains the overall correlation and indicates that population differentiation is pronounced. The contribution due to the average correlation of genes within individuals (within populations), $\hat{f}$, is minor. Brazilian populations, on average, are slightly less heterozygous than expected under Hardy–Weinberg equilibrium. In

Table 4 Estimates of gene correlation for populations of *Eichhornia paniculata* in N.E. Brazil and Jamaica. The parameters are related to *F*-statistics such that $F \approx F_{IT}$, $\theta \approx F_{ST}$, and $f \approx F_{IS}$

	No. of loci	$\hat{F}$ (S.E.)*	$\hat{\theta}$ (S.E.)*	$\hat{f}$ (S.E.)*
All populations	12	0·574 (0·014)	0·528 (0·014)	0·096 (0·005)
Brazilian populations	10	0·384 (0·009)	0·324 (0·010)	0·088 (0·005)
Jamaican populations	3	0·734 (0·009)	0·633 (0·009)	0·275 (0·041)

* The variance was estimated by jackknifing across loci, following the method of Miller (1974).

contrast, in Jamaica, $\hat{F} = 0.734$, and a significant component is explained by differences among populations ($\hat{\theta} = 0.633$), but a significant within individual (within population) correlation is also evident ($\hat{f} = 0.275$) (table 4). Within Jamaican populations, on average, heterozygotes are deficient.

When the amount of inbreeding is known, the observed fixation index can be compared with F_e, the expectation at inbreeding equilibrium, when the mating system is the only factor causing inbreeding. $F_e = (1 - t)/(1 + t)$ and is the inbreeding coefficient expected at equilibrium with an outcrossing rate t. The difference is ΔF as given in Brown (1979). Positive values of ΔF indicate a heterozygote deficiency while negative values indicate an excess of heterozygotes, in comparison with inbreeding equilibrium expectation ($\Delta F = 0$). For each region, the mean ΔF is close to panmictic expectation. Thus, in Jamaica, the average deficiency of heterozygotes ($\hat{f} = 0.275$) is accounted for by selfing. In fact, on average, a small excess of heterozygotes is observed. However, individual populations in both regions are heterogeneous. Populations B10 and J14 have a deficit of heterozygotes, and populations B9 and J15 have an excess of heterozygotes (table 5). A number of factors can contribute to a deficit of heterozygotes (Brown, 1979); the most likely are (a) population substructuring with regard to allele frequency, and (b) restricted neighbourhood size with near neighbour mating. Excess of heterozygotes may be attributed to selection at the marker locus (or genes linked to it).

Gene diversity

The mean total gene diversity for Brazilian populations is more than twice that of Jamaican populations ($\bar{H}_T = 0.15$ and $\bar{H}_T = 0.06$, respectively; table 6). The within population component H_S, also known as the "expected heterozygosity", or "Nei's gene diversity", is the mean proportion of loci at which a given individual can be expected to be heterozygous. $\bar{H}_S = 0.09$ for Brazilian populations

and $\bar{H}_S = 0.03$ for Jamaican populations (table 6). Genetic diversity is significantly correlated with outcrossing frequency in the nine populations for which t has been estimated ($r_s = 0.85$, $n = 9$, $p = 0.004$).

In addition to differences between Brazil and Jamaica in the total gene diversity, the partitioning of variation into population components differs between the two regions. The amount of diversity among Brazilian populations is smaller ($\bar{G}_{ST} = 0.40$) than for Jamaican populations ($\bar{G}_{ST} = 0.57$) (table 6). In Jamaica, more diversity is spread between populations ($\bar{R}_{ST} = 1.70$), while in Brazil more variation is contained within populations ($\bar{R}_{ST} = 0.81$).

Nei's genetic distance (Nei, 1972) is calculated from allele frequencies across all loci, and all pairs of populations are compared. Values range from 0 to ∞, 0 between populations that share all alleles at the same frequency, and ∞ between populations that have no alleles in common. The average genetic distance between Brazilian populations was $\bar{d} = 0.085$ and $\bar{d} = 0.049$ for Jamaican populations. The data illustrate the effect of including

Table 5 Comparison of $\hat{f}$ with $\hat{F}_e$ in nine populations of *Eichhornia paniculata* from N.E. Brazil and Jamaica

Population	No. of loci	$\hat{f}$	$\hat{F}_e$	ΔF
Brazil				
B5	7	0·038	0·010	0·028
B7	6	0·112	0·087	0·025
B11	6	0·046	0·031	0·015
B9	6	0·234	0·342	−0·108
B10	5	0·267	0·129	0·138
B8	2	0·366	0·361	0·005
			Mean	0·017
Jamaica				
J15	3	0·209	0·550	−0·341
J14	3	0·339	0·190	0·149
J12	2	0·329	0·361	−0·032
			Mean	−0·075

Table 6 Gene diversity in *Eichhornia paniculata* from N.E. Brazil and Jamaica. Except where noted, six populations were included for Brazil and five for Jamaica

Locus	H_T Brazil	H_T Jamaica	H_S Brazil	H_S Jamaica	G_{ST} Brazil	G_{ST} Jamaica	R_{ST} Brazil	R_{ST} Jamaica
DIA-1	0·17	0·00	0·12	0·00	0·25	—	0·40	—
GDH-1	0·30	0·00	0·20	0·00	0·34	—	0·61	—
MDH-2	0·12*	0·00	0·11*	0·00	0·12*	—	0·17*	—
MDH-3	0·17	0·00	0·11	0·00	0·36	—	0·67	—
PER-1	0·47	0·00	0·29	0·00	0·38	—	0·75	—
PGD-1	0·04	0·00	0·04	0·00	0·10	—	0·14	—
GOT-1	0·00	0·36	0·00	0·14	—	0·62	—	2·07
GOT-2	0·00	0·49	0·00	0·21	—	0·58	—	1·70
GOT-3	0·47	0·00	0·30	0·00	0·36	—	0·68	—
PGM-1	0·63	0·49	0·26	0·23	0·56	0·54	1·71	1·47
ACP-2	0·20	0·00	0·15	0·00	0·23	—	0·36	—
PGI-2	0·38	0·00	0·22	0·00	0·43	—	0·89	—
PGI-3	0·49**	0·00	0·16**	0·00	0·68**	—	4·29**	—
Mean	0·15	0·06	0·09	0·03	0·40	0·57	0·81	1·70

* Population B11 was not included because of difficulties of interpretation.
** Populations B5, B9 and B10 contained a null allele at this locus and were therefore not included in the analysis.

monomorphic loci in the genetic distance function. Jamaican populations have a larger proportion of their variation between populations ($R_{ST} = 1·71$; table 6), and a larger among population component of the overall fixation index ($\hat{\theta} = 0·633$; table 4), than Brazilian populations ($R_{ST} = 0·81$; table 6; $\theta = 0·324$; table 4). But because the total amount of diversity is small in Jamaica, the genetic distance between populations is less than that between Brazilian populations. The average genetic distance between Jamaican and Brazilian populations is 0·267. An unweighted pair group method cluster analysis of genetic distance presented as a dendrogram illustrates the distinctness of Brazilian and Jamaican populations (fig. 3).

To determine if an association of geographic and genetic distance between populations within Brazil and Jamaica occurs, a significance test was performed using a non-parametric measure of

Figure 3 UPGMA clustering based on Nei's genetic distance (d) among populations of *Eichhornia paniculata* from N.E. Brazil and Jamaica.

association (Dietz, 1983). The test statistic, K_c, is a measure of association of two matrices (genetic distance and geographic distance) and the significance is determined by generating a probability distribution of K_c, under the null hypothesis of no association, based on all possible permutations of the matrices (Dietz, 1983). No association between genetic and geographic distance was detected in either region; for Brazil, $K_c = -4$ ($p = 0·325$, *ns*), and for Jamaica $K_c = -11$ ($p = 0·186$, *ns*).

DISCUSSION

To interpret the causes responsible for the amount and pattern of genetic variation within and among populations of *E. paniculata*, two overriding factors need to be considered. The first involves the evolutionary history of the species in the Caribbean and the probability that colonisation of Jamaica involved a genetic bottleneck. The second concerns the evolutionary breakdown of tristyly to semi-homostyly in the species and its effect on altering the mating system of populations from outcrossing to selfing. These processes acting in concert or alone can result in changes in the genetic structure of populations; the discussion will therefore consider their relative importance.

When populations are founded by a small number of individuals, and subsequent growth is slow, the genetic consequences are a reduction in average heterozygosity and loss of alleles (Nei *et al.*, 1975). Since genetic bottlenecks may be expected during island colonisation, we may anticipate
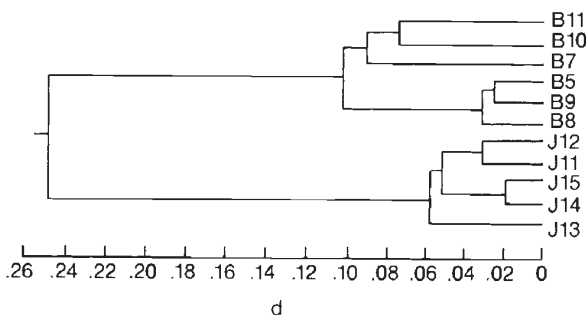
a reduction in the genetic variation of island populations, particularly in plant species such as *Eichhornia paniculata*, which commonly exhibit relatively small population sizes (Barrett, 1985a, b). In this study it was found that on the island of Jamaica, *E. paniculata* is depauperate with respect to allozyme variability, at both regional and poulational levels. Values for $\bar{H}_T$, $\bar{H}_S$ and $\bar{K}$ were significantly lower than those from N.E. Brazil.

Owing to island isolation, a restricted number of dispersal events is probably the most important factor determining the reduction in total allozyme diversity of *E. paniculata* populations in Jamaica. Support for this view comes from comparisons of genetic variation between plant populations that are geographically marginal but not necessarily isolated from populations at the centre of the range. Relative to source populations, peripheral populations can be either less heterozygous (Rick *et al.*, 1977; Yeh and Layton, 1979; Guries and Ledig, 1982), equally heterozygous (Levin, 1977, 1978), or more heterozygous (Harding and Mankinen, 1972; Jain and Martins, 1979; Bosbach and Hurka, 1981) than those that occupy the centre of the range. However, where insular populations have been compared with mainland populations, gene diversity has been found to be reduced or completely absent (Rick and Fobes, 1975; and see Schwaegerle and Schaal, 1979).

The origins and evolutionary history of *E. paniculata* in the Caribbean region are uncertain. The occurrence of all three style morphs in N.E. Brazil and the presence of close tristylous relatives in the region suggest that *E. paniculata* may have originated in lowland tropical South America (Barrett, 1985a). If this is true, it seems reasonable to postulate that the Caribbean concentration of populations is a derived centre. The direct source region for Jamaica and the time of colonisation are, however, unknown. The neighbouring island of Cuba would seem to be the most likely primary source, following early establishment of *E. paniculata* in Central America and the Caribbean from lowland S. America. Studies of the genetic structure of Cuban populations of *E. paniculata* would be useful in evaluating this suggestion. The occurrence of several isozyme alleles in Jamaica that were not detected in the survey of Brazilian populations supports the view that *E. paniculata* has a long history in the Caribbean and, unlike its close relative, the water hyacinth (*E. crassipes*), is not a recent immigrant to the region (Barrett, 1979).

Self-fertilisation is common in colonising plant species (Baker, 1955; Brown and Marshall, 1981; Price and Jain, 1981). As a consequence, it is often difficult to separate the effects of genetic bottlenecks and levels of inbreeding on gene diversity. The expected consequence of self-fertilisation on the genetic structure of populations is to decrease heterozygosity within populations, allowing selection to operate on homozygous lines (Jain, 1976). Loss of alleles and a reduction in polymorphic loci are secondary responses to drift, selection and contraints on gene flow. Empirical evidence relating plant mating systems to genetic variability at the species level are for the most part consistent with these expectations. The surveys conducted by Hamrick *et al.* (1979), Brown (1979), Gottlieb (1981) and Loveless and Hamrick (1984) have all found a general reduction in the number of alleles per locus, the per cent of loci polymorphic and various indices of genetic diversity in primarily selfing as opposed to primarily outcrossing species. In addition, studies of closely related species with contrasting mating systems have also revealed patterns in accord with the survey data (Gottlieb, 1973; Brown and Jain, 1979; Levin, 1978; Layton and Ganders, 1984). Few within-species comparisons have been made that quantify both the mating system and the level and distribution of gene diversity in plant populations. In some studies, a positive correlation has been demonstrated between measures of genetic variation and outcrossing rate (Rick *et al.*, 1977; 1979; Schoen, 1982), whereas in others no association was found (Jain, 1978; Yeh and Layton, 1979; Ganders *et al.*, 1985). In *E. paniculata* the per cent of loci polymorphic, mean number of alleles per locus, mean observed heterozygosity and gene diversity were all significantly correlated with outcrossing rate. However, it should be noted that this association is strongly influenced by differences in the amount of genetic variation between populations in Brazil and Jamaica so that caution is required in interpreting the results. A larger sample of populations from Brazil with contrasting mating systems is required to fully establish the relationship between mating behaviour and genetic variation within populations.

A shift towards self-fertilisation can increase the distribution of genetic variation among populations as a result of drift and local selection. In *E. paniculata*, values for the inter- to intra-population ratio of gene diversity indicate that in Jamaica a greater proportion of the gene diversity is distributed between populations than is contained within them. Although the reverse pattern occurs in Brazil, in absolute terms Brazilian populations are more differentiated than those in Jamaica ($\bar{D}_{ST} = 0\cdot059$ and $\bar{D}_{ST} = 0\cdot033$ for Brazil and Jamaica, respectively). These data are in accord

with the survey of Brown (1979) who found that inbreeders exhibited about five times the diversity of outbreeders relative to their intra-population variation, or about twice the level in terms of absolute ($\bar{D}_{ST}$) values.

The genetic structure of *E. paniculata* populations observed on the island of Jamaica can be ascribed to (a) genetic bottleneck(s), (b) self-fertilisation and (c) drift and/or selection following colonisation. It is not possible to rule out the contribution of any of these mechanisms. However, some evidence suggests that neither genetic bottlenecks nor self-fertilisation alone could produce the levels and patterns of variation observed in *E. paniculata* populations. A genetic bottleneck would not explain the difference between Brazil and Jamaica in the partitioning of genetic diversity among populations. Differentiation within Jamaica is governed by factors subsequent to the founding of populations on the island.

The importance of self-fertilisation can be examined by comparing populations from the two regions that share similar mating systems. Dimorphic populations in Brazil and Jamaica displayed overlapping ranges in estimates of outcrossing frequency; $t = 0.49$, 0.77 in Brazil; $t = 0.29$, 0.47, 0.68 in Jamaica, yet measures of allelic richness, observed heterozygosity and gene diversity were consistently higher in all dimorphic Brazilian populations than dimorphic Jamaican populations. Similarly, monomorphic (containing only M individuals) Jamaican populations were invariant electrophoretically, whereas the single monomorphic Brazilian population was variable at DIA-1 and PGI-3. These data, while limited, suggest that when the effect of mating system is roughly accounted for, Jamaican populations possess substantially less genetic variability at allozyme loci than their Brazilian counterparts. This difference probably reflects the contrasting evolutionary histories of populations in the two regions.

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Appendix Allele frequencies for thirteen polymorphic loci surveyed in eleven populations of *Eichhornia paniculata* from N.E. Brazil (B) and Jamaica (J). Locus "1" represents the most anodally migrating locus for a system. Allele "*a*" represents the most anodally migrating allele at a locus. Sample size (N) is given for each locus and population

Locus	Allele	Population										
		B5	B7	B11	B9	B10	B8	J15	J14	J12	J13	J11
DIA-1	a	0·93	1·00	1·00	0·94	0·59	0·99	0·00	0·00	0·00	0·00	0·00
	b	0·07	0·00	0·00	0·06	0·41	0·01	1·00	1·00	1·00	1·00	1·00
	N	284	200	400	187	67	143	80	80	80	80	80
GDH-1	a	0·00	0·00	0·53	0·11	0·46	0·00	0·00	0·00	0·00	0·00	0·00
	b	1·00	1·00	0·47	0·89	0·54	1·00	1·00	1·00	1·00	1·00	1·00
	N	800	200	405	192	79	150	80	80	80	80	80
MDH-2	a	0·07	0·02	*	0·23	0·00	0·00	0·00	0·00	0·00	0·00	0·00
	b	0·93	0·98	*	0·77	1·00	1·00	1·00	1·00	1·00	1·00	1·00
	N	1356	215		473	70	150	80	80	80	80	80
MDH-3	a	0·91	0·53	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00
	b	0·09	0·47	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00
	N	1356	215	400	473	70	150	80	80	80	80	80
PER-1	a	0·25	0·67	0·28	0·00	0·77	0·00	0·00	0·00	0·00	0·00	0·00
	b	0·61	0·33	0·72	1·00	0·23	1·00	1·00	1·00	1·00	1·00	1·00
	c	0·14	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00
	N	766	217	410	200	80	150	80	80	80	80	80
PGD-1	a	1·00	1·00	0·88	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00
	b	0·00	0·00	0·12	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00
	N	800	200	287	100	65	150	80	80	80	80	80
GOT-1	a	1·00	1·00	1·00	1·00	1·00	1·00	0·66	0·14	1·00	1·00	1·00
	b	0·00	0·00	0·00	0·00	0·00	0·00	0·34	0·86	0·00	0·00	0·00
	N	1409	186	402	462	75	150	80	80	75	80	80
GOT-2	a	0·00	0·00	0·00	0·00	0·00	0·00	0·70	0·87	0·27	1·00	0·00
	b	1·00	1·00	1·00	1·00	1·00	1·00	0·00	0·00	0·00	0·00	0·00
	c	0·00	0·00	0·00	0·00	0·00	0·00	0·30	0·13	0·73	0·00	1·00
	N	1409	186	402	462	75	150	80	80	75	80	80
GOT-3	a	0·56	0·41	0·76	0·60	0·00	0·00	0·00	0·00	0·00	0·00	0·00
	b	0·44	0·59	0·24	0·40	1·00	1·00	0·00	0·00	0·00	0·00	0·00
	c	0·00	0·00	0·00	0·00	0·00	0·00	1·00	1·00	1·00	1·00	1·00
	N	1409	186	402	462	75	150	80	80	75	80	80
PGM-1	a	0·04	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00
	b	0·81	0·00	0·09	0·81	0·02	1·00	0·35	0·16	0·72	1·00	0·00
	c	0·15	1·00	0·59	0·19	0·23	0·00	0·65	0·84	0·28	0·00	1·00
	d	0·01	0·00	0·32	0·00	0·75	0·00	0·00	0·00	0·00	0·00	0·00
	N	1249	215	412	466	64	150	80	73	76	80	80
ACP-2	a	0·13	0·14	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00
	b	0·55	0·80	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00
	c	0·32	0·07	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00	0·00
	N	1415	215	400	500	75	150	80	80	80	80	80
PGI-2	a	0·00	0·01	0·56	0·25	0·70	0·00	0·00	0·00	0·00	0·00	0·00
	b	1·00	0·99	0·44	0·75	0·30	1·00	0·00	0·00	0·00	0·00	0·00
	c	0·00	0·00	0·00	0·00	0·00	0·00	1·00	1·00	1·00	1·00	1·00
	N	1200	201	398	507	77	150	80	80	80	80	80
PGI-3	a	**	0·03	0·00	**	**	0·85	0·00	0·00	0·00	0·00	0·00
	b	**	0·97	1·00	**	**	0·15	1·00	1·00	1·00	1·00	1·00
	N		201	398			140	80	80	80	80	80

* Due to interpretation difficulties, MDH-2 was not scored in this population.

** A null allele was present at this locus in these populations. Heterozygotes could not be distinguished.