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SEXUAL REPRODUCTION IN *EICHHORNIA CRASSIPES* (WATER HYACINTH)

I. FERTILITY OF CLONES FROM DIVERSE REGIONS

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SUMMARY

(1) Comparative glasshouse studies with nine clones of *Eichhornia crassipes* from diverse regions were conducted to determine whether sterility factors are responsible for the low levels of sexual reproduction reported for the species.

(2) Eight of the nine clones flowered regularly throughout the study period. A single clone from Guyana did not flower. All flowering clones were mid-styled and possessed dimorphic pollen of high viability.

(3) Pollination success was markedly affected by temperatures below 20 °C. Seed production was significantly lower following pollinations conducted 24 h after flower opening compared with those made 2 h after flower opening.

(4) In a controlled pollination programme, all clones exhibited a high level of seed fertility. Of 2546 flowers pollinated, 94·7% produced capsules with an average of 143·3 seeds per capsule. There were no significant differences in seed set between self- and cross-pollinations of clones from Louisiana, Florida, Mexico and southern Brazil. Seed set was significantly higher in cross-pollinations than self-pollinations in clones from California, Sudan, Zaire and Calcutta.

(5) Comparisons of the growth and reproductive performance of families obtained from self- and cross-pollinations failed to detect any significant expression of inbreeding depression.

(6) Although clonal propagation is the most widespread mode of reproduction in *E. crassipes*, the genetic potential for sexual reproduction is probably still present in the majority of populations.

INTRODUCTION

Sexual reproduction in *Eichhornia crassipes* (Mart.) Solms (water hyacinth) was first reported almost a century ago (Müller 1883). However, the factors controlling flowering, seed formation and seed germination are still poorly understood. Reports from throughout the adventive range of *E. crassipes* comment on the absence or rarity of seeds and seedlings under field conditions (Smith 1898; Bruhl & Sen 1927; Agharkar & Banerji 1930; Backer 1951; Bock 1966; Tag el Seed & Obeid 1975) and recent workers have minimized the importance of sexual reproduction in *E. crassipes* (Baker 1965; Sarukhan 1974; Mulcahy 1975). Nevertheless, sexual reproduction has been reported in both the native and adventive range of *E. crassipes* (Ridley 1930; Haigh 1936, 1940; Wild 1961; Pettet 1964). Furthermore, in seasonal environments, where vegetative parts are periodically destroyed by desiccation, seeds can be important in maintaining populations from year to year (Barrett 1977b, 1979).

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Since *E. crassipes* occurs in both tropical and temperate regions, the factors responsible for limiting sexual reproduction probably vary from one area to another. Smith (1898) suggested that the absence of seed formation in North America is due to abnormalities in pollen development related to continuous vegetative reproduction. *Eichhornia crassipes* possesses the outbreeding mechanism known as heterostyly (Müller 1883; Barrett 1977b). In the majority of heterostylous species, floral heteromorphism is associated with a physiological self-incompatibility system (Vuilleumier 1967). This fact has led to the suggestion that seed formation is prevented in populations monomorphic for style form because of the inferred presence of self-incompatibility (Anon 1957; François 1964; Baker 1965; Ranwell 1967). In Malaysia, where only the mid-styled form of *E. crassipes* has been reported, fruits are unknown (Backer 1951). Sculthorpe (1967 p. 281) suggested that the mid-styled form in this region is self-incompatible and that the heterostylous condition is 'disadvantageous to the species'. Penfound & Earle (1948) believed that because the mid-styled form predominates in Louisiana, pollination by insects rarely occurs. Sterility of clones was reported by Faegri & Van der Pijl (1971) although the cause of sterility is not known. Bock (1966) and Bahadur (1968, 1977) were unable to germinate seeds of *E. crassipes* from California and India respectively. Bahadur (1968) suggested that the apparent inviability of seeds may be associated with the 'loss of sexual selection in the species'.

Most studies of *E. crassipes* have been undertaken in a single geographical region and, with the exception of Müller's early work (1883) they have all been in different parts of the adventive range of the species. Due to clonal propagation and the apparently low levels of sexual reproduction in the species, it has been suggested that a limited number of genotypes, perhaps in some cases only one, may be represented in parts of the adventive range (Mulcahy 1975). This presents difficulties in assessing the levels of sterility and potential for sexual reproduction in the species. In wide ranging species such as *E. crassipes* the reproductive biology can only be accurately described from studies of genetic material and field studies from throughout the distribution of the species.

In the present investigation, clonal material from populations throughout the range of *E. crassipes* was utilized. The aim of this study is to determine to what extent genetic factors such as sterility and physiological self-incompatibility are responsible for the low levels of sexual reproduction reported in *E. crassipes*. The pollen and seed fertility of clones from diverse regions are described and the growth and reproductive performance of progeny obtained from self- and cross-pollinations compared to detect the presence of inbreeding depression phenomena. In addition, results of earlier pollination studies of *E. crassipes* are reviewed and compared with those of the present study.

MATERIALS AND METHODS

Nine clones of *Eichhornia crassipes* were obtained from populations in different geographical regions. Clones from Calcutta, Zaire (Congo River), the Nile (Khartoum, Sudan), Guyana (Mon Repos Agricultural Research Station) and southern Brazil (Porto Alegre) were obtained from C. Parker, Weed Research Organization, Oxford, and those from Louisiana (Orleans Parish) and Florida (Hosfoud, Calhoun County) were collected by J. Neff, University of California, Santa Cruz. Clonal material from Mexico (Xochimilco), California (Stockton, San Joaquin County) and Costa Rica (Palo Verde Marsh, Guanacaste Province) was obtained by the author. Voucher specimens of all collections are deposited in the Herbarium of the University of California, Berkeley. Clonal material

from each region was grown from a single ramet in plastic tubs (30 litre capacity) in a heated glasshouse at Berkeley, California during 1975–1976.

Controlled pollination programme

Three preliminary experiments were undertaken to determine the most suitable conditions for pollination studies of *E. crassipes*. Clonal material from California was utilized in each experiment. Flowers were artificially self-pollinated with forceps using pollen from the long anther level. The number of flowers producing capsules and the number of seeds per capsule were recorded.

Effect of temperature on seed production

Plants due to flower within 72 h were placed in a light regime of 16 h light, 8 h dark, under five temperature regimes (5, 10, 15, 20 and 25 °C) in separate growth chambers. All pollinations were undertaken 1–3 h after anthesis, which generally occurred on the first day. Some inflorescences, especially those at 5 and 10 °C, flowered on the second day. All pollinations were completed within 48 h. Over 100 flowers were pollinated at each temperature regime. To observe pollen tube growth, five styles from each treatment were fixed in alcohol and stained with cotton blue in lactophenol.

Effect of time of pollination on seed production

Flowers of *E. crassipes* can remain open for 1–2 days, depending on the temperature during flowering. Pollinations were undertaken 2 and 24 h after flowers had opened and the effects on seed production were compared.

Effects of submergence and non-submergence of floral axis on seed production

In floating populations of *E. crassipes*, bending and in many cases submergence of the floral axis occurs 12–48 h after anthesis. Agharkar & Banerji (1930) suggested that under conditions of low humidity, submergence of the floral axis is necessary for normal seed production. However, submergence of the infructescence presents difficulties during the harvesting period in a large scale pollination programme. In order to assess the effects of submergence and non-submergence on seed production, all flowers on thirty-one inflorescences were pollinated on the same day. Fifteen infructescences were allowed to develop under water and the remainder, by placing the floral axes on the outside of the tub, were forced to develop in air. Seed production was compared in the two treatments.

Using information obtained from these experiments a large scale pollination programme was undertaken during the summer of 1976. Flowering clones were artificially pollinated with the aid of fine forceps, in a pollinator-free glasshouse. The temperature of the glasshouse ranged between 25–35 °C during the pollination programme and all flowers were pollinated 2–4 h after opening. Separate self-pollinations with pollen from both anther levels of a flower were undertaken. Each clone was also outcrossed to a long-styled clone grown from seed obtained in Costa Rica. Both legitimate (between stigmas and anthers at equivalent heights) and illegitimate (between stigmas and anthers at different heights) pollinations were made. Infructescences developed in an aerial environment and after 18–21 days capsules were harvested. Capsule and seed production from self- and cross-pollinations were compared by analysis of variance.

Performance of selfed and outcrossed families

Selfed and outcrossed families of twenty genotypes obtained from the artificial self- and cross-pollinations of eight clones of *E. crassipes* were grown in a heated glasshouse at

the University of Toronto in a randomized design from April–December 1978. The seed used was 2 years old and had been stored dry in envelopes at room temperature. Each genotype was grown in a 10 cm diameter pot in a 1:1:1 sand, peat, loam soil mix which was kept saturated throughout the experiment. The following growth and reproductive characters were recorded for each genotype except where indicated: seedling biomass at 65 days; total ramet production; total ramet biomass; number of genotypes flowering in family; time to flowering; numbers of flowers produced; numbers of capsules produced after artificial self-pollination; numbers of seeds set per flower after self-pollination. The performances of selfed and outcrossed families were compared within each clone by one way analysis of variance or a Mann-Whitney U test following F tests for homogeneity of variance.

RESULTS

Floral characters

With the exception of the Guyana clone, all clones flowered under glasshouse conditions during 1976. All flowering clones were mid-styled (Table 1). Pollen grains from the long anther level were significantly larger than grains from the short anther level in each clone. Pollen stainability was in excess of 90% in all clones except those from southern Brazil (83·5%) and Florida (77·7%).

TABLE 1. Floral and pollen characters in clones of *Eichhornia crassipes*

Origin	Style form	Fls. per inflorescence $\bar{x}$, (n) ± S.D.	Pollen size (μm)* long stamen / short stamen $\bar{x}$ ± S.D.	Pollen stainability(%) long stamen / short stamen
California	Mid	8.3 (68) ± 1·5	88·6 ± 3·8	97·2
			77·1 ± 3·6	97·2
Louisiana	Mid	5·2 (25) ± 1·0	85·6 ± 3.7	98·5
			76·0 ± 3·7	94·5
Florida	Mid	5·9 (40) ± 1·3	86·7 ± 4.8	82·3
			78·4 ± 4·3	73·0
Mexico	Mid	5·7 (62) ± 1·4	87·7 ± 4·3	90·5
			79·2 ± 4·0	90·3
S. Brazil	Mid	6·2 (61) ± 1·4	90·9 ± 3·5	84·5
			79·7 ± 4·3	82·5
Sudan	Mid	7·3 (47) ± 1·8	89·3 ± 3·7	95·3
			78·4 ± 2·9	97·3
Zaire	Mid	6·9 (51) ± 1·9	84·3 ± 2·9	99·5
			73·6 ± 3·2	99·3
Calcutta	Mid	7·2 (37) ± 1·6	85·6 ± 3·5	98·0
			72·8 ± 2·7	98·3

* Differences between pollen sizes of the 2 anther whorls (n = 400 for each whorl) within each clone are all significant ($P < 0.001$).

Controlled pollination programme

Preliminary experiments

Capsule and seed production resulting from pollinations conducted at different temperature regimes varied greatly. At 5 and 10 °C almost no seeds were produced (Fig. 1). At 15 °C, 18·2% of flowers pollinated produced capsules with an average seed set per capsule of 19·4. At 20 and 25 °C, almost all pollinated flowers produced seed and seed set per capsule was seven times greater than at 15 °C. The difference in seed set per capsule between flowers pollinated at 20 and 25 °C was not statistically significant. In flowers

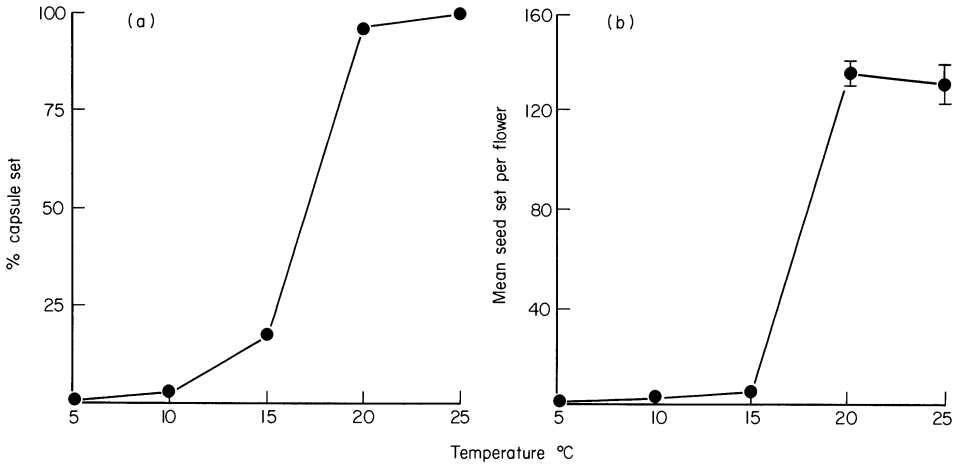

FIG. 1. The effect of temperature on (a) capsule production (b) seed production in *Eichhornia crassipes*. The limits given are ± s.e.m.

pollinated at 20 and 25 °C a large proportion of pollen grains had germinated after 8 h and some pollen tubes had reached ovules. In the 5 and 10 °C treatments, pollen germination had occurred after 32 h but there was no penetration of stylar tissue by pollen tubes. The average seed set per flower in flowers pollinated 24 h after opening was significantly lower than in flowers pollinated 2 h after opening (Table 2). There was no statistical difference in capsule or seed production in submerged v. aerial treatments of pollinated flowers.

TABLE 2. The effect of pollination time and submergence of the floral axis on seed production in *Eichhornia crassipes*

	No. flowers pollinated	% fruit set	Mean no. seeds per pollination	S.E.	Significant difference
1. Time of pollination					
2 h	187	96·3	171·8	10·2	$F = 22{\cdot}74$ ($P < 0{\cdot}001$)
24 h	124	91·9	107·3	8·8	
2. Submergence of floral axis					
Submerged	135	97·8	171·9	9·7	$F = 2{\cdot}93$ (N.S.)
Aerial	146	99·3	194·3	8·7	

Self-pollination

Artificial self-pollinations of flowers in all clones resulted in high levels of capsule and seed set. Of 1465 flowers self-pollinated, 92·6% produced capsules with an average of 133·6 seeds per capsule. Within clones there were no significant differences in seed set between self-pollinations with pollen from either of the two anther levels. The overall seed production resulting from self-pollinations varied significantly among clones ($F = 14{\cdot}90$, $P < 0{\cdot}001$). Clones from California and Zaire set most seeds per flower and the Calcutta clone least.

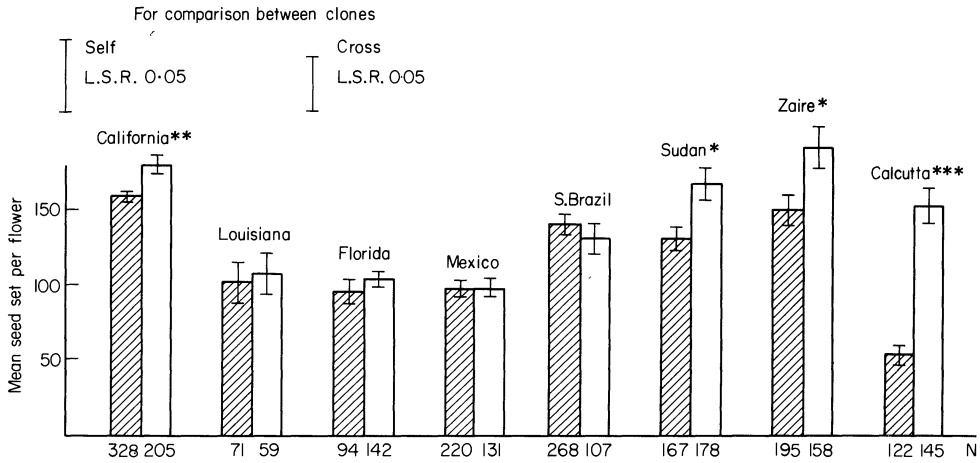

FIG. 2. Seed production following artificial self- and cross-pollinations of clones of *Eichhornia crassipes*. ▨ self pollinations; □ cross pollinations; $*P < 0{\cdot}025$, $**P < 0{\cdot}01$, $***P < 0{\cdot}001$. The limits given on the histograms are ± s.e.m. N = number of pollinations made.

Cross pollination

Percentage capsule set from artificial cross-pollinations of all clones was near maximal. Of the 1081 flowers cross-pollinated, 97·4% produced capsules with an average of 155·7 seeds per capsule. There were significant differences between clones in seed production following cross-pollinations with the long-styled clone ($F = 11{\cdot}99$, $P < 0{\cdot}001$). In clones from Louisiana, Florida, Mexico and Brazil, the average seed set of self- and cross-pollinations did not differ significantly. In the Calcutta, California, Zaire and Sudan clones, seed set was significantly higher following cross-pollination than self-pollination (Fig. 2). This pattern was most strongly developed in the Calcutta clone where seed set after cross-pollination was three times as great as that from self-pollination. With the exception of the Calcutta clone, the overall differences in seed fertility among clones were generally similar for self- and cross-pollinations.

Performance of selfed and outcrossed families

In clones from California, Mexico and the Sudan, there were no significant differences in any of the comparisons made between the performances of selfed and outcrossed families (Tables 3, 4, 5). In pre-reproductive comparisons of seedling vigour and clonal growth, the performances of families from Louisiana, Florida and Calcutta were significantly different. In each clone outcrossed families produced a greater yield of ramets than selfed families (Table 3). In two comparisons, the selfed families gave significantly greater yields than the outcrossed families. These differences were in seedling and ramet biomass in clones from Zaire and Brazil respectively. For these two clones, differences between the remaining seven characters in selfed and outcrossed families were not significant.

Families obtained from the Louisiana and Calcutta clones exhibited differences in flowering behaviour with selfed families taking significantly longer to flower than did outcrossed families. Genotypes obtained from self-pollinations of the Louisiana clone produced significantly fewer flowers than those obtained from cross-pollinations (Table 4).

Table 3. Growth and ramet production of selfed and outcrossed families of *Eichhornia crassipes* grown under uniform glasshouse conditions

Clone	Family	$\bar{x}$ dry wt. (mg). of 65-day old plant ± S.D.	Significant difference F	$\bar{x}$ no. of ramets produced during 1978 ± S.D.	Significant difference F	$\bar{x}$ dry wt. (g) of ramets produced during 1978 ± S.D.	Significant difference F
California	Self	245·6 ± 57·8	0·63	8·0 ± 1·3	0·50	2·14 ± 0·40	0·01
	Cross	229·6 ± 66·3		8·4 ± 2·1		2·16 ± 0·41	
Louisiana	Self	209·8 ± 36·1	10·31**	8·0 ± 1·3	3·06	1·81 ± 0·37	27·92**
	Cross	252·0 ± 44·5		8·8 ± 1·3		2·45 ± 0·38	
Florida	Self	162·9 ± 39·2	1·38	7·3 ± 1·3	13·22**	1·77 ± 0·32	10·09**
	Cross	145·7 ± 50·2		9·4 ± 2·1		2·16 ± 0·43	
Mexico	Self	188·2 ± 38·8	0·02	8·9 ± 2·5	2·01	2·03 ± 0·45	0·02
	Cross	179·5 ± 13·4		10·2 ± 3·1		2·05 ± 0·44	
S. Brazil	Self	158·6 ± 42·1	1·60	7·4 ± 1·0	U = 210	2·13 ± 0·39	7·01*
	Cross	133·7 ± 74·8		7·8 ± 1·9		1·84 ± 0·27	
Sudan	Self	195·7 ± 64·9	1·35	7·6 ± 1·6	2·45	2·10 ± 0·33	0·26
	Cross	175·2 ± 41·0		8·4 ± 1·3		2·16 ± 0·37	
Zaire	Self	220·3 ± 74·5	12·23**	7·2 ± 1·1	U = 264	2·28 ± 0·40	1·21
	Cross	151·7 ± 41·8		8·1 ± 1·8		2·14 ± 0·34	
Calcutta	Self	169·0 ± 41·4	7·41**	8·0 ± 2·0	5·70*	1·95 ± 0·69	5·62*
	Cross	211·4 ± 53·8		9·6 ± 2·1		2·43 ± 0·55	

All comparisons of selfed and outcrossed families non-significant except where indicated. *P = $<0·05$, **P = $<0·01$.

TABLE 4. Flowering behaviour of selfed and outcrossed families of *Eichhornia crassipes* grown under uniform glasshouse conditions

Clone	Family	No. flowering genotypes (n = 20)	$\bar{x}$ time (days) to flowering ± S.D.	Significant difference F	Total flower prod. of family	$\bar{x}$ no. of fls. per genotype ± S.D.	Significant difference
California	Self	20	163·0 ± 36·8	0·42	306	15·3 ± 6·7	0·12
	Cross	20	155·4 ± 37·5		292	14·6 ± 6·0	
Louisiana	Self	19	152·1 ± 27·4	U = 263*	225	11·3 ± 5·3	10·85**
	Cross	20	137·9 ± 13·9		346	17·3 ± 6·3	
Florida	Self	18	158·7 ± 29·2	0·06	176	8·8 ± 5·4	1·27
	Cross	19	161·2 ± 31·9		214	10·7 ± 5·3	
Mexico	Self	16	180·0 ± 34·9	0·01	145	7·3 ± 6·2	0·11
	Cross	16	180·6 ± 42·0		159	8·0 ± 7·2	
S. Brazil	Self	20	148·2 ± 24·9	0·13	332	16·6 ± 7·2	0·36
	Cross	19	151·0 ± 23·1		304	15·2 ± 7·5	
Sudan	Self	20	140·7 ± 14·3	3·10	363	18·2 ± 6·2	0·69
	Cross	20	149·7 ± 17·7		329	16·5 ± 6·8	
Zaire	Self	19	145·1 ± 24·5	0·43	315	15·8 ± 7·0	0·08
	Cross	20	150·7 ± 28·6		304	15·2 ± 4·7	
Calcutta	Self	15	179·0 ± 45·2	U = 170·5	149	7·5 ± 6·7	2·21
	Cross	15	139·2 ± 16·8		225	11·3 ± 9·3	

All comparisons of selfed and outcrossed families non-significant except where indicated. *P = $<0·05$, **P = $<0·01$.

TABLE 5. Fruit and seed production following controlled self-pollinations of selfed and outcrossed families of *Eichhornia crassipes* grown under uniform glasshouse conditions

Clone	Family	No. of genotypes	Total fls. pollinated	% fruit set	Mean seeds per pollin.	Standard error	Significant difference F
California	Self	10	57	93·0	135·7	14·4	0·42
	Cross	14	87	96·6	150·7	16·6	
Louisiana	Self	14	74	100·0	140·0	12·6	0·23
	Cross	13	79	96·2	130·5	15·5	
Florida	Self	8	39	94·8	120·5	16·8	0·54
	Cross	12	73	93·2	138·1	15·8	
Mexico	Self	11	56	92·9	137·3	21·3	0·10
	Cross	12	64	100·0	144·9	11·7	
S. Brazil	Self	18	99	96·7	171·3	14·7	0·01
	Cross	12	69	100·0	171·7	15·3	
Sudan	Self	15	90	95·6	158·5	19·6	0·04
	Cross	16	106	99·1	154·0	13·5	
Zaire	Self	13	75	96·0	190·7	15·2	0·39
	Cross	11	67	98·5	176·5	16·6	
Calcutta	Self	7	50	92·0	126·8	30·9	0·12
	Cross	8	46	95·7	114·6	18·9	

All comparisons of seed set following self-pollination in selfed and outcrossed families are non-significant.

Comparisons of the numbers of flowering genotypes per family and the levels of fruits and seeds produced following self-pollination were not significantly different between selfed and outcrossed families of all eight clones (Tables 4, 5).

DISCUSSION

The dramatic spread of *Eichhornia crassipes* during the past century has largely been accomplished by the intentional transport of plants by man for ornamental purposes, followed by rapid clonal propagation once the species has entered a suitable aquatic habitat. Clonal propagation is presently the most widespread form of reproduction in *E. crassipes*. Reports from different parts of the range of the species indicate that in many populations sexual reproduction is rare or non-existent. In species in which vegetative reproduction occurs exclusively for long periods of time, the loss of powers of sexual reproduction can result from the accumulation of mutations affecting seed and pollen fertility. Such mutations are normally selected against in sexual populations (Baker 1972, Gibbs 1976). These facts have led to the suggestion that populations of *E. crassipes* are sterile, although the types of sterility involved have not been identified.

In this study, material from a wide geographical range was studied experimentally in order to determine the relative fertility of clones of *E. crassipes*. Eight of the nine clones flowered regularly throughout 1976. Flowering was most prolific between May–October although limited flowering occurred throughout the winter months. The Guyana clone did not flower during the 12-month period although the clone subsequently flowered in April 1977 and again in October 1978 and was mid-styled.

In the artificial pollination programme capsule production was near maximal in all of the flowering clones investigated. Of the 2546 flowers pollinated 94·7% produced capsules, with an average of 143·3 seeds per capsule. All eight clones exhibited a high degree of

self-compatibility, although the level of seed production varied among the clones. Percentage capsule set was significantly higher from total cross-pollinations than from total self-pollinations (SP, 92·6; CP, 97·4; $\chi^2 = 28{\cdot}12$; $P = <0{\cdot}001$). Average seed set per capsule following self-pollinations was 133·6 compared to 155·7 for cross-pollinations. The higher capsule and seed set of cross-pollinations is primarily due to the behaviour of clones from Calcutta, California, Zaire and the Sudan, where cross-pollinations resulted in increased seed set over self-pollinations. Clones from Louisiana, Florida, Mexico and southern Brazil exhibited little to no difference in seed set between self- and cross-pollinations.

Differences in seed production between artificial self- and cross-pollinations of flowering plants are usually attributed to the operation of a self-incompatibility system which reduces the number of ovules that is fertilized following self-pollination (Lloyd 1968). If this interpretation is true in *E. crassipes*, self-incompatibility appears to be weak in some clones and absent in others. Elsewhere weak self-incompatibility has been demonstrated in a Costa Rican population of *E. crassipes* (Barrett 1979) and in the related *Eichhornia azurea* (Barrett 1978).

The results of pollination studies in *E. crassipes* by other workers have varied greatly. In India Bruhl & Sen (1927), Agharkar & Banerji (1930) and Bahadur (1968) self-pollinated mid-styled plants from Calcutta and Hyderabad respectively. Although seed was obtained in each study, capsule and seed set were uniformly low. They obtained 38·3% ($n = 201$ flowers) and 19·6% ($n = 561$ flowers) capsule set respectively, whereas Bahadur (1968) reported 63·4% capsule set ($n = 101$ flowers) with an average seed set per pollination of 10·9. Bock (1966) obtained 10·0% capsule set ($n = 430$ flowers) from self- and cross-pollinations of mid- and long-styled plants from California and Louisiana. Mulcahy (1975) found near maximal capsule set following cross-pollinations of mid- and long-styled clones from Florida. However, self-pollinations were significantly less productive of capsules and seed. Pollinations performed by Haigh (1936) in Ceylon and by Tag el Seed & Obeid (1975) in the Sudan gave variable but generally low values.

When compared to the present study, the level of capsule and seed set in earlier investigations is generally low. The factors responsible for this disparity are difficult to determine. Since only one style form was utilized by most workers, it is not possible to evaluate whether low seed set was due to self-incompatibility, genetic sterility or an unfavourable pollination environment. In Bock's study, capsule production was equally low in both self- and cross-pollinations indicating that self-incompatibility was probably not responsible for the low numbers of capsules she obtained. Agharkar & Banerji (1930) and Tag el Seed & Obeid (1975) suggested that the low seed set they obtained may be causally related to high temperature and low humidity conditions during flowering.

Some workers have been unsuccessful in attempts at germinating seeds obtained from self-pollinations of *E. crassipes* (Bock 1966; Bahadur 1968, 1977) and Mulcahy (1975) has suggested that inbred progeny of *E. crassipes* might be expected to be less vigorous than their parents. In general, the results of the present study do not appear to support this suggestion. Although seed germination was not compared quantitatively in this study, previous germination tests involving the Californian clone and two additional clones from Brazil (Amazonia) demonstrated no significant differences in the viability of 1-year-old seed obtained from self- and cross-pollinations (Barrett 1977a). Observations of the levels of seed germination in the family comparisons undertaken in this study indicated a uniformly high degree of germination in all families.

The subsequent growth and flowering behaviour of families revealed a complex pattern with no overall trend among the clones. Unlike some previous pollination studies involving artificial self- and cross-pollinations (Darwin 1888; Grant 1954, 1975; Ray & Chisaki 1957;) no marked indications of inbreeding depression (e.g. weak or sub-vital genotypes) were observed. Clones from California, Mexico and the Sudan exhibited no significant differences between the performances of selfed and outcrossed families. Apart from two comparisons in which yields from selfed progeny were greater than those from outcrossed progeny all remaining comparisons between the two families were non significant in clones from southern Brazil and Zaire.

Only in families derived from Louisiana and Calcutta clones were there consistent differences between inbred and outbred families. In four of the eight comparisons which were made, the outbred progeny performed better than the selfed families. These findings indicate that in the flowering clones which were studied, seed produced by inbreeding is viable and potentially capable of producing vigorous and fertile offspring.

Although the major form of reproduction in *E. crassipes* is vegetative propagation, the results of this study indicate that *E. crassipes* still retains the potential for sexual reproduction in many regions of the world. This suggests that the absence or low levels of sexual reproduction in many present day populations is unlikely to be due to strictly genetic factors such as sterility associated with continuous vegetative propagation or strong self-incompatibility. A mixture of style forms is not necessary for the production of viable seed in natural populations as is the case in the majority of heterostylous species. These findings indicate that environmental factors must play a major role in limiting sexual reproduction in populations of *E. crassipes*.

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REFERENCES

Agharkar, S. P. & Banerji, I. (1930). Studies in the pollination and seed formation of water hyacinth (*Eichhornia speciosa* Kunth). *Agricultural Journal of India*, **25**, 286–296.

Anon (1957). Report of the symposium on *Eichhornia crassipes*, *Commission for technical co-operation in Africa south of the Sahara/Scientific council for Africa south of the Sahara, C.C.T.A/C.S.A.* Publs. 27, Pp. 1–31.

Backer, C. A. (1951). Pontederiaceae. *Flora Malesiana Bulletin* Series 1, **4**, 255–261.

Bahadur, B. (1968). Heterostyly in *Eichhornia crassipes* (Mart.) Solms. *Journal of Genetics*, **60,** 14–16.

Bahadur, B. (1977). Heterostyly in *Eichhornia crassipes* (Mart.) Solms. *Journal of Indian Botanical Society*, **56**, 299–306.

Baker, H. G. (1965). Characteristics and modes of origin of weeds. *The Genetics of Colonizing Species* (Ed. by H. G. Baker and G. L. Stebbins), pp. 147–68. Academic Press, London and New York.

Baker, H. G. (1972). Human influences on plant evolution. *Economic Botany*, **26,** 32–43.

Barrett, S. C. H. (1977a). *Breeding systems in* Eichhornia *and* Pontederia, *tristylous genera of the Pontederiaceae.* Ph.D. dissertation, University of California, Berkeley.

Barrett, S. C. H. (1977b). Tristyly in *Eichhornia crassipes* (Mart.) Solms (Water Hyacinth). *Biotropica*, **9,** 230–238.

Barrett, S. C. H. (1978). Floral biology of *Eichhornia azurea* (Swartz) Kunth (Pontederiaceae). *Aquatic Botany*, **5**, 217–228.

Barrett, S. C. H. (1979). The evolutionary breakdown of tristyly in *Eichhornia crassipes* (Mart.) Solms (Water Hyacinth). *Evolution*, **33**, 499–510.

Bock, J. H. (1966). *An ecological study of* Eichhornia crassipes *with special emphasis on its reproductive biology*. Ph.D. dissertation, University of California, Berkeley.

Bruhl, P. & Sen, J. (1927). On the production of ripe seeds by artificial pollination of *Eichhornia speciosa*. *Journal of the Department of Science, Calcutta University*, **8**, 1–8.

Darwin, C. (1888). *The Effects of Cross and Self Fertilization in the Vegetable Kingdom*. John Murray, London.

Faegri, K. & Van der Pijl, L. (1971). *The Principles of Pollination Ecology* (2nd edn) Pergamon, Oxford.

François, J. (1964). Observations sur L'hétérostylie chez *Eichhornia crassipes* (Mart.) Solms. *Acad. R. Sci. Outre-Mer (Brussels) Bull. Séances*, **1964**, 501–519.

Gibbs, P.E. (1976). Studies on the breeding system of *Oxalis tuberosa* Mol. *Flora*, **165**, 129–138.

Grant, V. (1954). Genetic and taxonomic studies in *Gilia* IV. *Gilia achilleaefolia*. *Aliso*, **3**, 1–18.

Grant, V. (1975). *Genetics of Flowering Plants*. Columbia University Press, New York and London.

Haigh, J. C. (1936). Notes on the water hyacinth (*Eichhornia crassipes* Solms.) in Ceylon. *Ceylon Journal of Science*, **12**, 97–108.

Haigh, J. C. (1940). The propagation of water hyacinth (*Eichhornia crassipes* Solms.) by seed. *The Tropical Agriculturalist*, **94**, 296–297.

Lloyd, D. G. (1968). Pollen tube growth and seed set in self-compatible and self-incompatible *Leavenworthia* (Cruciferae) populations. *New Phytologist*, **67**, 179–195.

Mulcahy, D. L. (1975). The reproductive biology of *Eichhornia crassipes* (Pontederiaceae). *Bulletin of the Torrey Botanical Club*, **102**, 18–21.

Müller, F. (1883). *Einige Eigenthümlichkeiten der Eichhornia crassipes*. *Kosmos*, **13**, 297–300.

Penfound, W. T. & Earle, T. T. (1948). The biology of the water hyacinth. *Ecological Monographs*, **18**, 447–472.

Pettet, A. (1964). Seedlings of *Eichhornia crassipes:* a possible complication to control measures in the Sudan. Nature, **201**, 516–517.

Ranwell, D. S. (1967). Introduced aquatic, freshwater and salt marsh plants—case histories and ecological effects. *Towards a New Relationship of Man and Nature in Temperate Lands*, Vol. **3**, pp. 27–37. IUCN publication No. 9. Morges.

Ray, P. M. & Chisaki, H. F. (1957). Studies on *Amsinckia* I. A synopsis of the genus, with a study of heterostyly in it. *American Journal of Botany*, **44**, 529–536.

Ridley, H. N. (1930). *The Dispersal of Plants throughout the World*. L. Reeve and Co., Ashford.

Sarukhan, J. (1974). Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L., and *R. repens* L. II Reproductive strategies and seed population dynamics. *Journal of Ecology*, **62**, 151–177.

Sculthorpe, C. D. (1967). *The Biology of Aquatic Vascular Plants*. Edward Arnold, London.

Smith, R. W. (1898). A contribution to the life history of the Pontederiaceae. *Botanical Gazette*, **25**, 324–337.

Tag el Seed, M. & Obeid, M. (1975). Sexual reproduction of *Eichhornia crassipes* (Mart.) Solms in the Nile. *Weed Research*, **15**, 7–12.

Vuilleumier, B. S. (1967). The origin and evolutionary development of heterostyly in the angiosperms. *Evolution*, **21**, 210–226.

Wild, H. (1961). Harmful aquatic plants in Africa and Madagascar. *Kirkia*, **2**, 1–66.

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