THE BREEDING SYSTEM OF *PONTEDERIA ROTUNDIFOLIA* L., A TRISTYLOUS SPECIES

BY S. C. H. BARRETT

*Department of Botany, University of California,
Berkeley, California 94720, U.S.A.*

SUMMARY

Populations of *Pontederia rotundifolia* in the Lower Amazon and Costa Rica are tristylous. A strong pollen trimorphism is associated with differences in stamen and style length in the three floral forms. The results of a controlled pollination programme with thirty individual plants of *P. rotundifolia* demonstrate that floral trimorphism is accompanied by a physiological self-incompatibility system typical of many heterostylous plants. Legitimate pollinations are considerably more productive of seed than illegitimate pollinations. Individual plants exhibit differences in the strength of self-incompatibility, but in general, short-styled plants possess the strongest self-incompatibility, long-styled plants are intermediate and mid-styled plants have the weakest self-incompatibility. Large differences in the strength of self-incompatibility are expressed in self-pollinations with pollen from the two anther levels of each style form.

Natural populations of *P. rotundifolia* often contain only a single style form or contain unequal proportions of style forms. Seed set, resulting from moderate self-compatibility, occurred in a Costa Rican population that contained only short-styled plants. Two populations associated with rice cultivation in the Lower Amazon contained equal proportions of the three style forms. The seed set of the three forms within these populations was similar. The floral trimorphism and breeding system of *P. rotundifolia* are compared with those of the related *P. cordata* and *Eichhornia crassipes*.

INTRODUCTION

Pontederia (=Reussia) *rotundifolia* L. (Pontederiaceae) is a lilac-flowered, perennial, emergent aquatic that occurs throughout the Neo-tropics with extensions into southern Brazil and Argentina (Castellanos, 1958; Lowden, 1973). It is particularly common in the Amazon region where it is a colonizer of early stages of hydroseres (Junk, 1970). *Pontederia* is one of two genera in the Pontederiaceae that possess the rare form of floral heteromorphism known as tristyly (Solms-Laubach, 1883). Many conflicting reports concerning the nature of heterostyly have been made for genera in this family (see Ornduff, 1966), but complete tristyly has been reliably recorded in *Pontederia* (Solms-Laubach, 1883; Hazen, 1918; Ornduff, 1966; Lowden, 1973) and *Eichhornia* (Barrett, in prep.).

The Pontederiaceae is one of three angiosperm families in which tristyly is known to occur. Various aspects of tristyly in members of the other two families, the Lythraceae and Oxalidaceae, have received considerable attention (Hildebrand, 1887; Darwin, 1877; Eliot, 1892; Barlow, 1923; Stout, 1925; Fisher and Mather, 1943; Fyfe, 1956; Ornduff,

1964, 1975; Mulcahy, 1964; Dulberger, 1970). In contrast, extensive investigations of floral trimorphism in taxa of the Pontederiaceae have been limited to *Pontederia cordata* L. (Hazen, 1918; Ornduff, 1966) and *Eichhornia crassipes* (Mart.) Solms (François, 1964; Mulcahy, 1975; Barrett, in prep.). The present paper presents the results of an investigation of the floral trimorphism and breeding system of *Pontederia rotundifolia*. In addition a study of the representation and seed set of floral forms in natural populations occurring in the Lower Amazon and in Costa Rica is described.

Tristyly, and the more widespread distyly, are complex floral mechanisms which are believed to promote outcrossing in flowering plants (Darwin, 1877). Tristylous species are characterized by plants of three types, each possessing a distinctive syndrome of floral characters. The floral forms are: (1) flowers with long styles and two anther levels below the stigmas (mid and short); (2) mid-styled flowers with one set of anthers above the stigmas (long) and one set below (short); (3) short-styled flowers with two anther levels above the stigmas (mid and long).

Hildebrand (1866) and Darwin (1877) were largely responsible for describing and interpreting the functional significance of tristyly. In controlled pollinations of tristylous *Oxalis* spp. and *Lythrum salicaria* L. they found that pollinations between anthers and stigmas at equivalent levels produced more seed than pollinations between anthers and stigmas at different levels. Darwin termed these types of pollinations legitimate and illegitimate, respectively, and interpreted the positional relationships of organs as a mechanism for promoting insect-mediated pollinations among forms with anthers and stigmas at equivalent levels. Recent studies of heterostylous plants have attempted to substantiate Darwin's ideas on the adaptive significance of heterostyly (Levin, 1968; Ornduff, 1970, 1971, 1975; Mulcahy and Caporello, 1970; Ganders, 1974). The results of some of these studies are conflicting, but they generally indicate that heterostylous systems are not as 'efficient' at promoting outcrossing as earlier workers had assumed.

Although Hildebrand's original usage of the term heterostyly was morphological, Darwin restricted its meaning to include only cases where there is an association of a physiological incompatibility system with floral heteromorphism. Recent studies have demonstrated that this association is by no means universal (Ray and Chisaki, 1957; Mulcahy, 1964; Martin, 1967) and for this reason the term is used here with its original morphological connotation.

Tristyly in the Pontederiaceae

The presence of tristyly in the Pontederiaceae was first recorded by F. Müller (1871, 1883). While living in southern Brazil, he collected three members of the family that exhibit floral heteromorphism. One of these, an unidentified species of *Pontederia*, possessed all three floral forms. In the other species, *Eichhornia azurea* (Sw.) Kunth and *E. crassipes*, only two floral forms were found. However, H. Müller (1873) and later Darwin (1877) suggested that both *Eichhornia* species were probably trimorphic. After a century of conflicting reports (see François, 1964; Ornduff, 1966), this suggestion has recently proven to be correct (Barrett, in prep.). The identity of Müller's tristylous Pontederia has never been established, although Hazen (1918) suggested that it may have been *Pontederia rotundifolia*. Solms-Laubach (1883) first reported tristyly in *P. rotundifolia* and in a recent monographic study of the genus *Pontederia* Lowden (1973) records tristyly in *P. rotundifolia* L., *P. sagittaria* Presl, *P. subovata* (Seub.) Lowden and *P. cordata* L. His report for the last species confirms earlier reports of tristyly by Legget (1875a, 1875b), Halsted (1889) and Hazen (1918).

MATERIALS AND METHODS

Populations of *Pontederia rotundifolia* were studied in two geographical regions. Plants used for floral and pollen measurements, controlled pollinations and in field studies were obtained from two populations in the Lower Amazon during September–December 1974. The populations occurred in cultivated and abandoned rice fields at Boca de Jari (Jarilandia), Amapa, Brazil. Field studies of two populations at Arenal, Guanacaste Province, Costa Rica were conducted during November 1975.

Measurements of floral parts and pollen grains were made on ten flowers from different individuals of each style form. Stigma and anther heights were measured from the base of the style. The equatorial and polar axes of 100 dry pollen grains were measured for each floral form. A controlled pollination programme was undertaken using thirty individual plants of *P. rotundifolia*. Plants were grown in plastic tubs in insect-free enclosures. Flowers were emasculated and pollen was transferred to stigmas using forceps. Pollinations were made daily between 08.00 and 11.00 hours. The mean number of flowers per plant pollinated in each pollen carpel combination was 43.0 (range 10–162). Fruits were harvested 18–20 days after pollination. Since in *P. rotundifolia* fruits are one-seeded, fruit set is equivalent to seed set.

Four populations were sampled in order to determine the representation of floral forms in each population. Inflorescences were gathered randomly from different individuals in each population and the style form was recorded. In dense populations a minimum distance of 5 m between individuals was used in order to prevent repeated counting of plants. Three populations were sampled in order to compare the seed set of floral forms within each population. One hundred infructescences of each style form represented in the populations were randomly harvested from different individuals. The proportion of flowers producing fruits on each infructescence was recorded.

RESULTS

Floral trimorphism

Measurements of style and stamen heights in *Pontederia rotundifolia* show that three floral forms can be clearly distinguished (Table 1). The mean style and stamen heights are distinct and there is a reciprocal correspondence between the heights of the stigmas and anthers of the three floral forms.

In common with many tristylous species, pollen trimorphism accompanies the differences in stamen and style lengths in *P. rotundifolia* (Table 2). In the floral forms there is a clear correlation between anther level and pollen grain size. Pollen grains from the long set of anthers are largest, those from the mid level anthers are intermediate and the smallest pollen is produced by the short anther level. The mean sizes of pollen grains from the two anther

Table 1.*Mean height and standard deviation (mm) of stigma and anthers
in the three floral forms of* Pontederia rotundifolia.

| Floral form | Stigma height | Anther height | | |
		Long stamen	Mid stamen	Short stamen
Long-styled	12.7 ± 0.6	–	7.4 ± 0.6	1.4 ± 0.7
Mid-styled	7.0 ± 0.2	12.6 ± 0.3	–	1.7 ± 0.5
Short-styled	1.4 ± 0.2	12.9 ± 1.0	7.0 ± 0.5	–

levels of each floral form are significantly different. Size dimorphism of pollen is greatest in mid-styled plants and least in short-styled plants.

Breeding system

Traditionally, most workers studying breeding systems of heterostylous species have presented pooled crossing data for the various pollen carpel combinations. This is presumably because the variability in performance of individual plants was not great. In this study, results for individual plants as well as pooled data are presented for each of the twenty-four pollen carpel combinations. This method has been adopted in order to draw attention to the considerable variability in strength of incompatibility among individual plants.

Table 2. *Measurements of equatorial and polar axes (mean and standard deviation in μm) of pollen grains of* Pontederia rotundifolia.

Floral form	Long-level anther		Mid-level anther		Short-level anther	
	Equatorial axis	Polar axis	Equatorial axis	Polar axis	Equatorial axis	Polar axis
Long-styled	–	–	61.5 ± 4.3	23.7 ± 1.5	39.4 ± 2.8	17.4 ± 1.3
Mid-styled	78.1 ± 3.5	28.2 ± 1.6	–	–	43.1 ± 2.8	16.8 ± 1.6
Short-styled	75.1 ± 4.0	27.9 ± 1.8	58.2 ± 3.0	22.3 ± 1.5	–	–

(a) *Self-pollinations.* The results obtained by self-pollinating each floral form with pollen from either of the two anther levels establish the presence of a physiological incompatibility system in *P. rotundifolia.* Seed set in self-pollinations is generally lower than that obtained from legitimate pollinations (Table 3). However, in self-pollinations, the incompatibility behaviour of pollen from the two anther levels of each form is markedly different in each of the three floral forms. Self-pollinations of long-styled plants using pollen from the mid anther level were moderately productive of seed, whereas pollen from the short anther level produced almost no seed. In long- and short-styled plants, the anther level nearest the stigma produced pollen with the weakest incompatibility reaction in self-pollinations. In mid-styled plants, pollen from the long anther level produced considerably more seed in self-pollinations than pollen from the short anther level.

Interestingly, in the plants tested the strength of self-incompatibility varies with style form. Using the combined results obtained from self-pollinations with both anther levels as an estimate of overall self-incompatibility, mid-styled plants possess the weakest self-incompatibility, long-styled plants are intermediate and short-styled plants have the strongest self-incompatibility. However, large variation in the results of individual plants was obtained (e.g. percentage seed set from Lxm/L: plants L6 = 7.4%, L7 = 97.4%; Mxs/M : plants M1 = 0%, M7 = 58.8%; Sxm/S : plants S1 = 13.4%, S10 = 62.6%).

(b) *Intra-form illegitimate pollinations.* The results of intra-form pollinations confirm that the strength of incompatibility in illegitimate pollinations varies with style form. The same sequence in levels of incompatibility was obtained with intra-form as with self-pollinations. Furthermore, the mean number of seeds set per plant from both types of

pollination were similar. However, the behaviour of individual plants in self- and intra-form pollinations varied considerably. In some plants, incompatibility was relaxed when pollen from different individuals of the same style form was used (L6, S2), whereas in other cases incompatibility was strengthened in intra-form pollinations (M7).

(c) *Inter-form illegitimate pollinations.* There was no significant difference in seed set for corresponding anther levels in inter-form and self-pollinations of mid- and short-styled plants. However, in long-styled plants, an unexpected difference in seed set between self- and inter-form pollinations was obtained with pollen from the mid anther level. Inter-form pollinations produced significantly less seed than self-pollinations ($F = 23.84$ (1,22) $P < 0.001$). The reason for this difference in incompatibility reaction is not known. There was almost no seed produced when pollen from the short anther level of mid-styled plants was applied to stigmas of long-styled plants. This result is similar to that obtained in self-pollinations with pollen from short anther levels.

(d) *Legitimate pollinations.* Legitimate pollinations of the three floral forms produced considerably more seed than illegitimate pollinations. In each floral form there was no difference in seed set using pollen from each of the two possible anther levels. The seed set of long- and mid-styled forms was similar whereas short-styled plants produced less seeds than the other two forms. The difference in fertility between short-styled plants and the combined results of mid- and long-styled plants is statistically significant ($F = 12.54$ (1,40) $P = 0.01$).

Population structure

Four natural populations were sampled to determine the representation of floral forms in each one. In the populations associated with rice cultivation in the Lower Amazon, statistically significant isoplethy occurs (Table 4). This equal representation of floral forms is typical of some tristylous species and has been recorded for *Lythrum salicaria* L. (Darwin, 1877; Halkka and Halkka, 1974) and *Lythrum junceum* (Dulberger, 1970). In *L. salicaria* populations, unequal proportions of style forms has also been reported (Haldane, 1936; Schoch-Bodmer, 1938; Fisher and Mather, 1943). In Costa Rican populations, there was an imbalance of floral forms. The marsh population contained only short-styled plants. The population occurring by the River Arenal was composed of approximately equal proportions of long- and short-styled individuals but there were only four mid-styled plants present. In four populations of *Pontederia rotundifolia* sampled by Lowden (1973) in Central America all contained unequal proportions of floral forms. In two of the populations only one form was represented, and in the remaining two populations two forms were present.

Seed set

In order to estimate the seed set of floral forms within three populations, 700 infructescences bearing a total of 14,617 fruits were harvested. The percentage seed sets of the three populations were significantly different from one another (pop. 1:66, pop. 2:80.8, pop. 3:23.5).

Within the two populations associated with rice cultivation, there were no significant differences in either the number of flowers produced per inflorescence or the numbers of seeds produced per infructescence in the three floral forms. This suggests that although the style forms differ in their degree of self-compatibility, this does not play an important role in determining the relative seed set of the floral forms in isoplethic populations. However, in

Table 3. *Seed set in controlled pollinations of* Pontederia rotundifolia

Long-styled

Cross*	Fls. pollinated	Fls. prod. seed	Percent. seed set	Av. no. of fls. poll. per plant	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	Av. seed set per plant
A. L × s/L	247	2	0.8	49.4	0	–	–	2.4	–	–	0	–	0	0	0.5
L × m/L	506	304	60.1	63.3	71.4	53.3	92.9	89.8	–	7.4	97.4	–	48.7	61.4	65.3
B. L × s/L	135	3	2.2	27.0	0	0	3.7	7.7	–	–	0	–	–	–	2.3
L × m/L	301	203	67.4	43.0	59.4	47.6	–	81.1	–	59.4	95.2	42.9	–	71.4	65.3
C. L × s/M	159	4	2.5	39.8	3.9	–	–	0	–	–	4.0	0	–	–	2.0
L × m/S	583	104	17.8	64.8	23.8	6.4	22.4	14.0	–	16.7	59.4	13.9	15.2	18.0	21.1
Total illegitimate	1931	620	25.1	47.9											25.1
D. L × l/M	301	267	88.7	37.6	95.7	76.3	–	–	100.0	84.9	93.3	82.2	100.0	95.5	91.0
L × l/S	362	341	94.2	45.3	94.3	–	100.0	94.1	100.0	–	95.0	93.6	91.9	90.0	94.9
Total legitimate	663	608	91.7	41.3											93.0

Mid-styled

Cross*	Fls. pollinated	Fls. prod. seed	Percent. seed set	Av. no. of fls. poll. per plant	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	Av. seed set per plant
A. M × s/M	328	91	27.4	46.9	0	0	0	–	0	–	58.8	–	35.1	0	13.7
M × l/M	287	197	68.6	41.0	47.1	38.9	68.0	–	70.6	–	65.5	81.8	75.3	–	63.8
B. M × s/M	164	9	5.5	27.3	–	–	–	–	8.3	0	3.2	17.9	0	8.3	6.3
M × l/M	154	101	65.6	22.0	–	73.7	50.0	–	46.7	55.6	42.9	80.8	93.1	–	63.3
C. M × s/L	119	17	14.3	23.8	13.3	–	8.0	–	0	–	37.5	–	–	–	11.8
M × l/S	279	185	66.3	31.0	38.5	75.4	57.1	65.4	100.0	72.2	19.4	76.9	96.0	–	66.8
Total illegitimate	1331	600	41.3	32.0											37.6
D. M × m/L	271	243	89.7	38.7	88.5	92.1	–	–	76.5	–	100.0	89.1	100.0	95.5	91.7
M × m/S	158	140	88.6	31.6	–	89.6	–	–	100.0	–	90.0	80.0	92.2	–	90.4
Total legitimate	429	383	89.2	35.2											91.1

Short-styled					S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	
A. S × l/S	220	2	0.9	44.0	-	1.1	-	-	-	1.5	-	0	0	0	0.5
S × m/S	561	197	35.1	70.1	13.4	27.6	50.8	-	31.6	39.1	-	26.1	50.0	62.6	37.7
B. S × l/S	238	2	0.8	47.6	1.9	-	-	-	-	0	-	0	0	0	0.4
S × m/S	279	128	45.9	55.8	33.1	61.5	0	40.0	52.6	-	-	-	-	71.8	51.6
C. S × l/M	279	0	0	34.9	0	0	-	-	0	0	-	0	0	0	0
S × m/L	456	128	28.1	65.1	24.7	26.3	-	-	40.0	22.0	-	15.0	61.4	21.0	30.1
Total illegitimate	2033	457	18.5	52.9											20.1
D. S × s/L	264	201	76.1	33.0	63.7	-	96.2	-	92.3	87.1	100.0	65.2	83.3	61.9	81.2
S × s/M	181	137	75.7	30.2	68.2	92.9	-	-	-	-	90.0	80.6	88.9	59.3	80.2
Total legitimate	445	338	76.0	31.6											80.6

* = Style form (♀) x anther level/style form (♂)
A = Self pollinations
B = Intra-form illegitimate pollinations
C = Inter-form illegitimate pollinations
D = Legitimate pollinations

Table 4. *The representation of floral forms in natural populations of* Pontederia rotundifolia

Population and habitat	Long	Mid	Short	Total	X^{2*}
Lower Amazon 1. Abandoned rice field	161	161	134	456	3.1928
2. Cultivated rice field	483	524	527	1534	2.3639
Costa Rica 3. Marsh	0	0	270	270	—
4. Riverbank	27	4	31	62	20.5450

* X^2 for goodness of fit to a 1:1:1 ratio.

Table 5. *Seed set in natural populations of* Pontederia rotundifolia

Population and habitat	Total fls. sampled	Total fls. prod. seed	Percentage seed set	Mean no. fls. per inflorescence	Mean no. seeds per infructescence
Lower Amazon 1. Abandoned rice field					
Long-styled	2701	1915	70.8	27.0	19.2
Mid-styled	2728	1715	62.9	27.3	17.2
Short-styled	2891	1892	65.4	28.9	18.9
2. Cultivated rice field					
Long-styled	3489	2776	79.6	34.9	27.8
Mid-styled	3464	2867	82.8	34.6	28.7
Short-styled	3774	3022	80.1	37.7	30.2
Costa Rica 3. Marsh					
Short-styled	1833	430	23.5	18.3	4.3

anisoplethic populations or those containing only a single style form (e.g., pop. 3), self-compatibility can be important in allowing some seed set to occur.

DISCUSSION

Pontederia rotundifolia is the third member of the Pontederiaceae for which the compatibility relationships of the three floral forms have been studied experimentally. There is a strong resemblance between the breeding system of *P. rotundifolia* and that of its congener *P. cordata* (Ornduff, 1966). In both species floral trimorphism is associated with a physiological self-incompatibility system typical of many tristylous species. Although the overall strength of self-incompatibility appears to be weaker in *P. rotundifolia*, the relationship between the incompatibility reactions of different combinations of pollen and carpels is strikingly similar. In both species, self-incompatibility is strongest in the short-styled form, weaker in the long-styled form and weakest in the mid-styled form. The breeding system of the two *Pontederia* species contrasts with that exhibited by *Eichhornia crassipes*. In this

species floral trimorphism is accompanied by a high degree of self-compatibility (François, 1964). There is little difference in seed set between legitimate and illegitimate pollinations of the three floral forms and differential incompatibility in the two anther levels of each form is absent (Barrett, in prep.). Associated with these differences in breeding behaviour between the two genera are differences in the degree of pollen trimorphism. Both *Pontederia* species possess a strong pollen trimorphism whereas in *Eichhornia crassipes* size trimorphism is weakly developed.

Self-incompatibility was present in the thirty individuals of *Pontederia rotundifolia* tested in this study. However, the strength of self-incompatibility varied greatly among individual plants. In general, self-pollinations using pollen from one set of anthers produced no seed, whereas seed was frequently obtained if pollen from the alternative set of anthers was utilized. This positional relationship is a feature of tristylous species with weak self-incompatibility (see Darwin, 1877). Pollen from the mid anther levels of long- and short-styled plants and from the long anther level of mid-styled plants possessed the weakest incompatibility. This indicates that differential incompatibility between the two anther levels of each style form exists in illegitimate as well as legitimate pollinations in *P. rotundifolia*. Differences in incompatibility behaviour of pollen within a flower are probably due to the effect of different somatic tissues of each anther level on pollen development (Mather, 1948). Recent studies by Heslop-Harrison and co-workers (1973, 1974) have indicated that the tapetal layer may be important in determining the incompatibility reaction of some pollen grains. Individual plants varied one from another in the amount of differential incompatibility exhibited by the two anther levels. This indicates that the expression of self-incompatibility involves quantitative rather than qualitative changes in pollen-stigma relationships and suggests that there had been a gradual weakening of self-incompatibility with allelle changes at a number of loci. Mather (1943) and Pandey (1960) have demonstrated polygenic modification of the strength of self-incompatibility alleles in species with homomorphic incompatibility systems. In heteromorphic incompatibility systems gradual changes in the strength of self-incompatibility are thought to be due to the variable expressions of modifier genes rather than the oligogenes responsible for major changes in morphological sub-characters of heterostyly (Mather and De Winton, 1941; Mather, 1950).

Populations of *P. rotundifolia* commonly contain a single style form or are composed of unequal proportions of style forms (anisoplethy). Inequality of floral forms has been recorded in the Oxalidaceae and Pontederiaceae (Faberge, 1959; Mulcahy, 1964; Ornduff, 1964, 1966, 1974; Barrett, in prep.). Anisoplethy can result from an imbalance of forms in the initial colonizing individuals followed by vegetative reproduction (Ornduff, 1964) and by own-form fertilization in species with a degree of self-compatibility (Crosby, 1949; Mulcahy, 1964). The presence of only short-styled plants in the marsh population in Costa Rica is probably a result of vegetative reproduction of initial short styled coloniser(s). In the small population at River Arenal, both vegetative spread and own-form fertilizations could be responsible for the inequality of forms. In the rice field populations of the Lower Amazon, enough sexually produced generations appear to have been produced for an isoplethic equilibrium to have been reached. In the controlled pollination programme the three style forms were found to differ in their degree of self-compatibility. However this does not appear to influence the representation of floral forms in the isoplethic populations. This could be due to several factors including: (1) rarity of own-form fertilizations due to low illegitimate pollen flow; (2) gametophyte competition favouring legitimate pollen; (3) low viability of seed from own-form pollinations. In view of recent studies of pollen flow (see introduction), all of which have demonstrated that considerable amounts of illegitimate

pollen are deposited on stigmas, it seems unlikely that the first of these factors is important. It is not known if either of the other two factors are operating to maintain an isoplethic equilibrium in the rice field populations.

Seed set in the three populations sampled in this study differed significantly. The low seed set of population 3 was due to its monomorphic structure, which resulted in an absence of legitimate fertilizations. Since these types of fertilizations are more productive of seed than those resulting from own-form pollinations, seed set was well below that of the two mixed populations. The reasons for the difference in seed set between the two mixed populations must be more complex. The difference is attributed to a number of interacting factors including the pattern of style forms in the populations (see Levin, 1974; Ornduff and Weller, 1975) and the effect of inflorescence density on insect visitation. Plants in the abandoned rice field were up to 1 year old and reproduction was predominantly by vegetative means. In the resulting clones, adjacent inflorescences were often of the same style form and the density of inflorescences was relatively low. In the cultivated rice field, due to cultivation techniques, reproduction was mainly by seed. At the commencement of each rice season the field was flooded, resulting in the emergence of large numbers of seedlings of *P. rotundifolia*. Synchronous flowering of plants began after 45-55 days and densities of up to twenty inflorescences per m^2 were commonly recorded. At the end of the season the plants were destroyed during the burning of rice stubble and fallow cultivations. No quantitative estimates of the pattern of style forms within the populations were obtained. However, the subjective impression gained whilst sampling population structure was of a high degree of segregation (see Pielou, 1961) or clumping of style forms in population 1 and a relatively random distribution of the floral forms in population 2. In population 2, the high density of floral forms combined with the synchronous flowering of even-aged individuals is thought to have played a major role in maximizing seed set. Large numbers of insect visitors (mostly *Ancyloscelis* sp. apiformis group, Anthophoridae; *Apis mellifera* L., Apidae and species of Hesperiidae) were observed visiting flowers in this population. Percentage seed set per plant was 91.6% of that obtained in the controlled pollination programme. Increased levels of seed set associated with high flowering density have been reported in *Astragalus canadensis* L. by Platt, Hill and Clark (1974). In population 1, the likelihood of illegitimate pollen flow, and thus reduced seed set, was enhanced by the pattern and density of inflorescences.

The presence of self-compatibility in *Pontederia rotundifolia* enables some seed formation regardless of population structure. In colonizing situations often associated with aquatic habitats, self-compatibility and vegetative reproduction play a major role in the establishment and early growth of populations (Baker, 1955, 1974). In stable habitats where mixed populations occur, tristyly serves to promote outcrossing and the consequent genetical recombination, as well as maximizing seed set. This flexibility in the breeding system, combined with moderate powers of vegetative propagation and water dispersed seeds (Schulz, 1942) gives *P. rotundifolia* considerable colonizing abilities and perhaps accounts for its widespread occurrence in aquatic habitats of the Neotropics.

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