

Tristyly in *Eichhornia crassipes* (Mart.) Solms (Water Hyacinth)

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ABSTRACT

Recent workers have considered *Eichhornia crassipes* (Mart.) Solms to be distylous since the short-styled form had not been reliably recorded. This "missing" form was recently found in the Lower Amazon, and the species should now be considered tristylous. Populations of *E. crassipes* in the native and adventive range are characterized by the predominance of a single style form, a condition atypical for heterostylous species. In most of the adventive range of *E. crassipes* the mid-styled form predominates, with long-styled forms occurring less frequently. The short-styled form is apparently restricted to tropical South America. Associated with floral trimorphism in *E. crassipes* is a weak pollen trimorphism. The three floral forms of *E. crassipes* are highly self-compatible. Within style forms there is little difference in seed production between self and legitimate pollinations. During a study of populations in the Lower Amazon, the major insect visitor to flowers of *E. crassipes* was the bee *Ancyloscelis gigas*. Of 1208 flowers sampled from four monomorphic populations, 67.5 percent produced seed. In the majority of populations of *E. crassipes* tristily does not function as an outcrossing mechanism due to population structure.

THE WATER HYACINTH *Eichhornia crassipes* (Mart.) Solms is a heterostylous, free-floating aquatic member of the monocotyledonous family Pontederiaceae. During the past century it has spread from its native range in the New World tropics to achieve a world-wide distribution (Little 1965, Sculthorpe 1967). Man has played a major role in facilitating this spread, both deliberately (Backer 1951, Vietmeyer 1975) and unintentionally. Today *E. crassipes* is considered one of the most dangerous aquatic weeds, and considerable annual expenditure results from attempts at eradicating its extensive mats from reservoirs, canals, and rivers.

Due to the economic importance of *E. crassipes* a large body of literature, concerned with various phases of its life history, has accumulated in recent years (see Penfound and Earle 1948, and Bock 1966 for reviews). Despite this attention, little is known about seed reproduction in *Eichhornia*, and, in particular, the type and manner of functioning of its breeding system. In 1957, speakers at a symposium on the problem of the weed in Africa deplored the shortage of information on seed reproduction (Anon. 1957). Due to its extensive vegetative growth (see Penfound and Earle 1948) workers have tended to minimize the importance of sexual reproduction in *E. crassipes* (Baker 1965, Mulcahy 1975). Sexual reproduction has not been reported in certain parts of the adventive range, such as California (Baker 1965, Bock 1966). However, in tropical regions seed reproduction can occur and is important in aiding the spread of *E. crassipes* (Ridley 1930, Haigh 1936, Pettet 1964).

Most workers have studied *E. crassipes* in its adventive range, and very little is known of the reproductive biology of populations in the native range (Sculthorpe 1967). The purpose of this paper is to describe the floral trimorphism and breeding system of *E. crassipes* and to report the findings of a study of populations in the Lower Amazon Basin where *E. crassipes* is considered to be native (Schwartz 1927).

TRISTYLY IN *Eichhornia crassipes*

The Pontederiaceae is one of three flowering plant families which possess the form of floral heteromorphism known as tristily. Tristylous species are characterized by plants of three types differing in floral morphology. 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 the stigmas (short); (3) short-styled flowers with anthers at two levels above the stigmas (mid and long). Tristyly and the more widespread distily are floral mechanisms which promote outcrossing between floral forms (Darwin 1877). Ever since Fritz Müller (1871, 1883) reported mid- and long-styled forms of *E. crassipes* in southern Brazil, there has been disagreement and confusion as to whether *E. crassipes* is distylous or tristylous. The first report of tristily was made in the English edition (1883) of "Die Befruchtung der Blumen durch Insekten" by Herman Müller (1873). However, this report of tristily is the result of an apparent mistranslation by D'Arcy W. Thompson of the original German edition, where no mention is made of the short-styled

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form. Although H. Müller and later Darwin (1877) stated that *E. crassipes* was probably trimorphic, these statements were based on the assumption that the missing short-styled form would be found (Bock 1966). Since then there have been erroneous (Bir Bahadur 1968) and unsubstantiated (Hauman-Merck 1913) reports of the short-styled form, statements that *E. crassipes* is tristylous (Agharkar and Banerji 1930, Täckholm and Drar 1950, Willis 1951), as well as an incorrect report by Wild (1961) that the styles of this species are "sometimes of three different lengths in the same plant." In reviewing heterostyly in *E. crassipes*, both François (1964) and Ornduff (1966, 1974) considered that there was insufficient evidence for the existence of the short-styled form, and recent workers have considered the species to be presently distylous (Bock 1966, Faegri and van der Pijl 1971, Mulcahy 1975).

STYLE FORM DISTRIBUTION AND POPULATION STRUCTURE.—The predominance of a single style form of *E. crassipes* in a particular geographical area has been noted by previous workers (Müller 1883, Haigh 1936, Penfound and Earle 1948, Backer 1951, Haldane 1960, Bock 1966, Sculthorpe 1967, Mulcahy 1975, Tag el Seed and Obeid 1975). In most of the adventive range of the species, mid-styled plants are most commonly encountered, with long-styled plants occurring occasionally or not at all (fig. 1). There

are no documented reports of short-styled plants of *E. crassipes* in the adventive range nor of populations containing equal proportions of style forms, even though this is a typical condition in many heterostylous plants.

In 1974, I found populations of the short-styled form of *E. crassipes* in the Lower Amazon Basin of Brazil (Barrett 814, UC). The discovery of these plants demonstrates that *E. crassipes* is tristylous (fig. 2A and B). The populations occurred in an extensive area of campos de varzea (marshland) associated with the River Jari. The nearest settlement to the population was Boca de Jari (Jarilandia), 15 km from the confluence of the Jari and Amazon rivers.

The short-styled form predominated in the populations sampled. Of the nine populations studied, four contained only short-styled plants, one consisted solely of long-styled plants, and four populations were mixed with short-styled plants predominating. Several thousand flowering short-styled individuals but no more than 50 long-styled plants were found in all populations. Despite a thorough search no mid-styled plants were located. Populations of *E. crassipes* growing in the Middle Amazon were sampled in 1975 by W. Junk (pers. comm.). In the seven lakes he surveyed, over 90 percent of the flowers examined were from short-styled plants. A few long- and mid-styled plants were found, but in each case they were in populations where short-styled plants predominate.

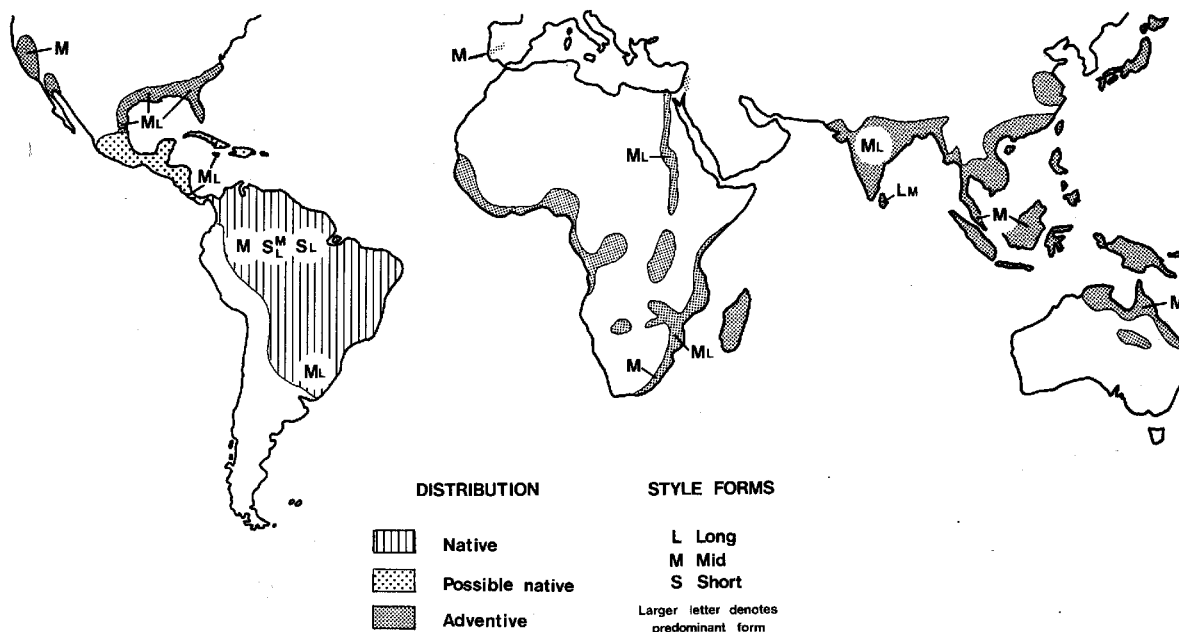


FIGURE 1. The geographical distribution of style forms in *Eichhornia crassipes*. Data on style form distribution derived from personal observation and literature reports. Distribution map of *E. crassipes* modified from Sculthorpe (1967).



FIGURE 2. Floral trimorphism in *Eichhornia crassipes*; (A) from left to right, inflorescences of long-, mid-, and short-styled forms of *E. crassipes*; (B) from top to bottom, longitudinal sections of flowers of long-, mid-, and short-styled forms; (C) short-styled flowers, showing nectar guide and concealed short style; (D) free-floating habit and vegetative reproduction by stolons.

ated. Two additional localities for short-styled plants were located by surveying herbarium sheets from Amazonian herbaria (Black 48-3001, Ilha São Sebastião e Nazaré, Pará IAN; and Cavalcante 485, Belém, Pará MG).

FLORAL TRIMORPHISM.—Measurements of the lengths of floral parts were made on 10 flowers from different individuals of each style form of *E. crassipes*. Measurements of style and stamen lengths show that three floral forms can be clearly distinguished (table 1). The mean style and stamen lengths are distinct, and there is a reciprocal correspondence between the position of the stigmas and anthers of the three

TABLE 1. Mean height and standard deviation (mm) of stigma and anthers in the three floral forms of *Eichhornia crassipes*.

Floral form	Stigma height	Anther height		
		Long stamen	Mid stamen	Short stamen
Long-styled	35.4±0.7	—	24.9±0.9	15.8±0.9
Mid-styled	24.6±0.8	31.5±1.1	—	14.2±1.0
Short-styled	15.0±1.0	30.0±0.6	22.5±0.6	—

floral forms. Accompanying the differences in style and stamen lengths are differences in style coloration and length of stigmatic papillae. The short styles are completely white; the mid and long styles are white, apart from the top 8 mm of mid styles which are lavender and the top 11 mm of long styles which are purple.

In some parts of the range of *E. crassipes* there are differences in the perianth color of the three floral forms. Long-styled plants in the Lower Amazon could be distinguished at a distance from short-styled plants because of their pale lilac to almost white petals. Short-styled plants possessed violet to rose petals. Müller (1883) found (in southern Brazil) that petals of long-styled plants were lighter in color than those of mid-styled plants, whereas Haigh (1936) found in Ceylon, that mid-styled flowers

were paler in color than long-styled flowers. Color differences of this type are not always associated with style form in other parts of the range of *E. crassipes* (Bock 1966, Barrett pers. observ.).

In many tristylous species pollen grains from the long set of anthers are largest, those from the mid level anthers are intermediate in size, and the smallest pollen grains are produced by the short anther level (Darwin 1877). In the Pontederiaceae, strong pollen trimorphism is present in *Pontederia cordata* L. (Hazen 1918) and *Pontederia rotundifolia* L. (Barrett 1977a), but there have been conflicting reports for mid- and long-styled forms of *E. crassipes*. Bock (1966) reports pollen monomorphism whereas Darwin (1877), Bir Bahadur (1968), and Mulcahy (1975) report pollen heteromorphism.

In plants of *E. crassipes* from the Amazon and California, the mean size of pollen grains from the two anther levels of each floral form differ significantly (table 2). However, size trimorphism is weak in *E. crassipes*, with a considerable overlap in the range of pollen sizes from different anther levels. In contrast to many tristylous species exhibiting pollen trimorphism, there is no correspondence between the mean size of pollen from the same anther levels of different style forms. In some cases, correspondence occurs between different anther levels, e.g., the size of pollen grains from the long and mid anther levels of short-styled plants do not differ significantly from those of the mid and short anther levels of long-styled plants respectively.

BREEDING SYSTEM.—A controlled pollination program was undertaken using 50 short- and 50 mid-styled plants and 20 long-styled plants. Short- and long-styled plants were obtained from four populations in the Lower Amazon. Mid-styled plants were collected from a population near Stockton, California. Plants were grown in plastic tubs in insect-free enclosures. Pollinations of short- and long-styled plants were conducted in the Lower Amazon between October and December 1974. Pollinations of mid-styled

TABLE 2. Measurements of sizes of pollen grains (mean and standard deviation in μ) in the three floral forms of *Eichhornia crassipes*.

Floral form	Long-level anther		Mid-level anther		Short-level anther		t^a
	Equatorial axis	Polar axis	Equatorial axis	Polar axis	Equatorial axis	Polar axis	
Long-styled	—	—	83.5±4.5	28.7±2.3	75.6±3.7	27.5±1.7	13.6
Mid-styled	88.6±3.8	30.3±2.1	—	—	77.1±3.6	26.3±1.4	22.0
Short-styled	82.1±4.3	30.2±3.3	76.9±4.7	27.7±1.9	—	—	8.2

^aDifferences between mean pollen size of two anther levels of each floral form are all significant ($P < .001$). $N = 100$ for each anther level of a style form.

plants were made at Berkeley, California, during the summer of 1975.

In plants on which no artificial pollinations were undertaken, a small amount of autogamous seed set occurred (table 3). Autogamy occurred more frequently in mid-styled flowers than in short- and long-styled forms. Percentage fruit set was near maximal in all artificial pollinations. In all forms, legitimate pollinations (between anthers and stigmas at

large tristylous flowers, conspicuous yellow nectar guides, and nectar rewards and would therefore seem to be adapted to insect pollination. However, there have been few reports of insect visitation to *E. crassipes*. Brühl and Sen (1927), Penfound and Earle (1948), and Tag el Seed and Obeid (1975) commented on the absence or paucity of insect visitors in India, southeast U.S.A., and the Sudan, respectively. To my knowledge, there are no published reports of insect visitors to *E. crassipes* in its native range.

In the Lower Amazon, four groups of bees were observed visiting flowers of *E. crassipes*. *Ancyloscelis gigas* Fr. (Anthophoridae) and a species of Megachilidae collected pollen and nectar and species of *Trigona* (Meliponidae) and Halictidae collected pollen only. All four bee groups started to forage on flowers when they opened between 0800 and 0830 hrs. Foraging activity was usually completed by late morning, with pollen-collecting bees finishing between 0930 and 1000 hrs and nectar-collecting bees leaving flowers between 1100 and 1200 hrs.

During the period of study (September-December 1974), the long-tongued bee *Ancyloscelis gigas* was the most frequent visitor to flowers of *E. crassipes*. *Ancyloscelis gigas* is known only from the Amazon region (C. Michener, pers. comm.), and other species of the genus *Ancyloscelis* have been observed visiting flowers of *E. crassipes* (C. Michener, pers. comm.) and *Pontederia rotundifolia* (Barrett 1977a). *Ancyloscelis gigas* was only observed visiting flowers of *E. crassipes* whereas the pollen-collecting bees were observed on flowers of other species.

Records of the foraging activities of *A. gigas* were made on three consecutive mornings (5-7 December) between 0830 and 1130 hrs at a population growing in a canal. In this population, *E. crassipes* produced an average of 18.2 flowers per inflorescence. Inflorescences flowered for 1-2 days with the majority of flowers opening on the first day. Flowers opened for one day only (cf. Penfound and Earle 1948, Bock 1966, Vietmeyer 1975). Individual bee movements to 1085 inflorescences and 3050 flowers were recorded over a three-day period (table 4). Forty-one percent of the visits to an inflorescence were to a single flower, and 20.2 percent were to two flowers. Twelve percent of the visits made were to more than five flowers per inflorescence.

SEED PRODUCTION.—Estimates of capsule and seed set for four monomorphic populations of *E. crassipes* are presented in table 5. Of 1208 flowers sampled from all populations, 67.5 percent produced seed. This finding indicates that self-compatibility allows seed formation in populations composed of a single style form. Nevertheless, the number of seeds pro-

TABLE 3. *Controlled pollinations of the three floral forms of Eichhornia crassipes.*

AUTOGAMOUS SEED SET.				
Style form	No. flowers undisturbed	No. flowers producing capsules	Percentage capsule set	Av. seed set per flower
Long-styled	65	0	0	0
Mid-styled	152	15	9.9	4.5
Short-styled	121	1	0.8	0.1
ARTIFICIAL POLLINATIONS.				
Style form and cross ^a	No. flowers pollinated	No. flowers producing capsules	Percentage capsule set	Av. seed set per pollination
Long-styled				
L x m/L	115	102	88.7	117.4
L x s/L	85	79	92.9	136.4
L x l/S	113	107	94.7	151.8
Mid-styled				
M x l/M	173	170	98.3	155.2
M x s/M	155	155	100.0	160.0
M x m/S	35	35	100.0	177.2
Short-styled				
S x l/S	550	544	98.9	217.4
S x m/S	545	541	99.2	233.9
S x s/L	213	212	99.5	260.3

^aStyle-form (♀) x anther level/style-form (♂).

equivalent levels) were slightly more productive of seed than self-pollinations, but these differences were not statistically significant. There was no significant difference in seed set using either anther level in self-pollinations. A significant finding was the marked difference in seed set per flower obtained from pollinations of the three style forms. In legitimate pollinations, short-styled plants produced an average of 260.3 seeds per flower whereas mid- and long-styled plants produced 177.2 and 151.8 seeds per flower, respectively. In illegitimate pollinations, short-styled plants were also substantially more fecund than mid- and long-styled forms. The basis for these differences in fecundity between the three style forms in *E. crassipes* is not known.

POLLINATION SYSTEM.—*Eichhornia crassipes* has

duced per capsule was considerably lower than obtained using the same plants in the controlled pollination program. Seed set in the most productive population (pop. 2) was 16 percent of that resulting from artificial self-pollinations of short-styled plants.

TABLE 4. Foraging activity of *Ancyloscelis gigas* on flowers of *Eichhornia crassipes* in the Lower Amazon.

No. of flowers visited per inflorescence	No. of inflorescence visits	Percentage inflorescence visits
1	448	41.3
2	219	20.2
3	118	10.9
4	105	9.7
5	65	6.0
6	42	3.9
7	27	2.5
8	19	1.8
9	12	1.1
10	10	0.9
>10	20	1.8
Total	1085	100

TABLE 5. Capsule and seed set in natural populations of *Eichhornia crassipes* in the Lower Amazon.

Population and habitat	Style form	No. of flowers sampled	Av. no. flowers per inflorescence	No. flowers producing capsules	Percentage capsule set	Av. seed set per flower
1. Stream	Short	328	17.2	123	37.5	6.7
2. Canal	Short	346	18.2	295	85.3	36.4
3. Marsh	Short	297	22.9	263	88.6	23.5
4. Pool	Long	237	15.8	134	56.5	17.8

Plants from the two populations exhibiting the most disparate values for capsule and seed set were equally fertile in the artificial pollination program. This discovery suggests that the difference obtained in seed productivity ($F = 19.5818$ (1,37) $p < 0.001$) probably resulted from different ecological factors at the two sites. Observations made daily from September to December 1974 revealed that flowers in the two populations were visited by different groups of insects. The stream population (pop. 1) was visited solely by small pollen-collecting bees. The bees confined their activities to collecting pollen from long and mid anther levels, and thus the opportunity for pollen transfer to the deep-seated, short styles was restricted. The only insect visitors to flowers at the canal population (pop. 2) were long-tongued bees. Bees transferred pollen to short stigmas with their heads while feeding on nectar.

DISCUSSION

Tristyly is one of the rarest and most complex outcrossing mechanisms found in flowering plants. It occurs in only three angiosperm families and consists of an integrated syndrome of morphological and physiological characters. Such a system could only have evolved as a result of strong selection pressures exerted over a considerable period of time (Ornduff 1972).

The presence of tristyly in *E. crassipes* presents some interesting evolutionary problems. Due to the high dispersability of the free-floating life form of *E. crassipes* and rapid methods of clonal propagation (fig. 2D), the majority of populations are monomorphic or contain a predominance of one style form. Populations with equal proportions of the three style forms, a situation typical of some tristylous species (Dulberger 1970, Halkka and Halkka 1974, Barrett 1977a), have never been reported in *E. crassipes*. Thus, due to population structure, the normal functioning of tristyly as an outcrossing mechanism is prevented in most populations. In populations containing more than one style form, self-compatibility further disrupts outcrossing by allowing the possibility of self and illegitimate fertilizations to occur. Tristyly in *E. crassipes* can therefore be viewed as a relatively primitive reproductive system, and in most present-day populations of *E. crassipes* it is non-functional.

In addition to preventing the normal functioning of tristyly, the free-floating habit limits sexual reproduction by enabling *E. crassipes* to colonize many habitats unfavorable for seed germination and seedling establishment. The germination requirements for seeds of *E. crassipes* are complex, but, generally, under field conditions, water temperatures of 28-36°C and sunlight are necessary (Haigh 1936, Hitchcock *et al.* 1949, Barton and Hotchkiss 1951). These conditions do not occur in many aquatic habitats in the adventive range, such as canals and reservoirs, and most of the seed produced by floating populations fails to establish seedlings. However, sexual reproduction occurs in certain seasonal habitats where fluctuations in water level provide periods of warm, shallow water (Haigh 1936, Pettet 1964). In its native range *E. crassipes* frequently occupies seasonal lakes, pools, and marshes. In these habitats vegetative parts are often destroyed by fluctuations in water level and desiccation (Junk 1970; Barrett, pers. observ.), and seeds can play an important role in reestablishing populations when conditions become favorable for seed germination and establishment. In the Amazon, changes in water level are a characteristic feature of the aquatic environment (Sternberg

1975), and it is possible that suitable conditions for sexual reproduction often occur.

Most of the seed produced by plants of *E. crassipes* is from self or illegitimate pollinations due to the prevailing monomorphic population structure. In the majority of heterostylous taxa the presence of a physiological self-incompatibility system prevents seed formation in monomorphic populations. However, the high degree of self-compatibility in *E. crassipes* enables seed formation regardless of population structure. Self-compatibility is therefore of considerable importance in habitats favorable for sexual reproduction. Evidence from other heterostylous taxa indicates that when selection favors increased inbreeding, the syndrome of characters associated with heterostyly breaks down (Crosby 1949, Baker 1966, Lèfebvre 1970, Ornduff 1972). This process usually involves relaxation of the strength of self-incompatibility or its eventual replacement by self-compatibility.

Incompatibility systems of varying strengths occur in related tristylous taxa of the Pontederiaceae (Ornduff 1966; Barrett 1977a, b) and in other populations of *E. crassipes* (Mulcahy 1975, Barrett 1977b). This situation suggests that the high levels of self-compatibility currently exhibited by *E. crassipes* are a result of a gradual relaxation in the strength of self-incompatibility. This change in breeding system may be associated with the development of the free-floating habit and rapid methods of vegetative propagation in the species. These traits, particularly the free-floating habit, are well adapted to the annual water-level fluctuations which are a feature of aquatic habitats in the Amazon. However, they have a disruptive effect on the functioning of trimorphic incompatibility, and it is possible that in sexual, monomorphic populations, selection favoring increased self-compatibility has occurred. A gradual weakening in pollen trimorphism may have accompanied the breakdown in strength of self-incompatibility (Baker 1966, Ornduff 1972). An alternative, but perhaps less likely, possibility is that tristily in *E. crassipes* has always been associated with high levels of self-compatibility and weak pollen trimorphism.

The unequal geographical distribution of style forms in *E. crassipes* results from various factors operating in different parts of its range. The absence of the short-styled form in the adventive range is probably due to chance and the genetic determination of style form. Partial information on the inheritance of tristily in *E. crassipes* suggests that a two-locus system (S and M), with S epistatic to M, is involved (François 1964, Barrett 1977b). Since neither long- nor mid-styled forms can segregate short-styled plants,

the only means by which this form could enter the adventive range is by the chance introduction of short-styled plants. Apparently this process has not occurred. The only certainty is that the mid-styled form was introduced to the adventive range. If the mid-style genotype(s) introduced were heterozygous for the M gene, then long-styled forms could be produced by self or cross pollinations. Alternatively, if only homozygous mid-style genotypes were involved, a separate introduction of long-styled form(s) would be necessary to account for their presence in the adventive range. In California (Bock 1966), Malaysia (Backer 1951), and parts of India (McClellan 1922, Brühl and Sen 1927) little or no seed set or seedling establishment has been reported, and thus there are minimal possibilities for the segregation of long-styled plants, assuming that heterozygous mid-styled plants are present in these areas. It is noteworthy that, in these regions, long-styled plants have not been reported.

The dimensions of floral parts in *E. crassipes* are the largest known for a tristylous species, and only relatively large-bodied insects can effectively cross pollinate the three floral forms in the manner suggested by Darwin (1877) for heterostylous species. The long-tongued bee *Ancyloscelis gigas*, the major insect visitor to flowers of *E. crassipes* in the Lower Amazon, is large enough for effective partitioning of the different pollen types on the body surface of the bee. Furthermore, the foraging behavior of *A. gigas* would tend to enhance legitimate pollinations since most visits are to one or two flowers per inflorescence. Although *A. gigas* appears well adapted to the tristylous floral mechanism of *E. crassipes*, the structure of Amazonian populations reduces the likelihood of legitimate pollinations occurring.

In the large, tristylous flowers of *E. crassipes* the anthers and stigmas are separated by 7-11 mm. Due to this separation, the facility for autogamous seed set is limited. In the pollination program, 4.7 percent of flowers which were not artificially pollinated set seed by autogamy. This circumstance indicates that under field conditions where moderate amounts of seed are produced, insects play a major role as pollinating agents. The distance between reproductive organs suggests that the size and behavioral traits of insect visitors are also likely to influence the amount of pollen transferred to stigmas and thus the level of seed set. During observations of short-styled plants, small pollen-collecting bees (*Trigona*) confined most of their activity to the exerted mid and long stamen whorls. As a consequence little pollen was transferred to the deep-seated short styles (fig. 2C), and the seed set of populations visited solely by these bees

was low (pop. 1, stream). Similar foraging activity by *Trigona* on mid- and long-styled plants of *E. crassipes* may result in higher seed set because in these floral forms the stigmas are less concealed. At the canal population (pop. 2) the larger, long-tongued bees were relatively more effective as pollen vectors since the bees contacted the stigmas while entering the perianth tube to feed on nectar. Plants in the canal population produced five times as many seeds per flower as those at the stream population. The most likely explanation for the difference in seed set between the two populations is a result of the size and feeding behavior of the two groups of insects as pollen vectors.

Capsule production was substantial in three of the four populations sampled. However, the number of seeds produced per capsule was considerably lower than obtained from the same plants in the pollination program. Although a high proportion of flowers was pollinated, it appears that the amount of pollen

transferred to stigmas was low. This finding suggests that the fecundity of natural populations of *E. crassipes* in the Lower Amazon is limited by relatively inefficient pollinator service, due to the monomorphic structure of many populations. The results of this study indicate that the occurrence of tristily and vegetative reproduction in *E. crassipes* is an ill-adapted combination of reproductive traits which has probably arisen as a result of the evolution of vigorous clonal propagation in the species.

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