

FLORAL BIOLOGY OF *EICHHORNIA AZUREA* (SWARTZ) KUNTH (PONTEDERIACEAE)

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ABSTRACT

Barrett, S.C.H., 1978. The floral biology of *Eichhornia azurea* (Swartz) Kunth (Pontederiaceae). *Aquat. Bot.*, 5: 217–228.

Since only the long- and short-styled forms of *Eichhornia azurea* (Swartz) Kunth have been observed by botanists, the species has been considered distylous. Populations containing these forms as well as the “missing” mid-styled form are reported from the Lower Amazon, demonstrating that *E. azurea* is tristylous. Strong pollen trimorphism and moderate self-incompatibility accompany floral heteromorphism. The incompatibility behaviour of pollen from the two anther levels of a flower differ markedly. Self-pollination of a long-styled form resulted in 94.3% capsule set with pollen from mid level anthers, whereas only 12.2% of flowers pollinated with pollen from short level anthers produced capsules. A semi-homostylous race of *E. azurea* from Costa Rica is self-compatible, autogamous and possesses dimorphic pollen. *E. azurea* is similar to *E. crassipes* (Mart.) Solms-Laubach in its dispersal both by floating vegetative parts and by seeds. However, its breeding system more closely resembles that of tristylous *Pontederia* species than *E. crassipes*.

INTRODUCTION

Eichhornia azurea (Swartz) Kunth (Pontederiaceae) is a mat-forming aquatic perennial that occurs in marshes, lakes and rivers throughout the Neotropics. It is closely related to the water hyacinth *Eichhornia crassipes* (Mart.) Solms-Laubach (Schwartz, 1927), a serious weed of aquatic habitats in the warmer regions of the world. *E. azurea* and *E. crassipes* are superficially similar in appearance and are confused with one another in botanical collections and in the systematic literature (Hooker, 1829; Standley and Steyermark, 1952).

Due to its showy blue flowers, *E. azurea* (Fig. 1), like *E. crassipes*, has been introduced to various parts of the world, e.g. North America and Africa, for ornamental purposes (Täckholm and Drar, 1950; Shinnars, 1962; Correll and Correll, 1975). In these areas, unlike *E. crassipes*, it shows no tendencies to behave as an aggressive weed. This may seem surprising since both species colonise early stages of neotropical hydrosere (Richards, 1952;



Fig. 1. Inflorescence of a long-styled form of *Eichhornia azurea*.

Taylor, 1963) and *E. azurea* often behaves as a weed in its native range (Standley, 1928; Leiderman and Figueiredo, 1967; Bristow et al., 1972).

Sculthorpe (1967) drew attention to the similarity between the distribution of *E. azurea* and the native range of *E. crassipes*. However, Standley (1928) considered that, while *E. azurea* is native to Central America, *E. crassipes* had been introduced to the region. Schwartz (1927) commented on the similar ranges of the two species but was of the opinion that they were rarely found together in the same habitat.

There has been some disagreement concerning the type of floral heteromorphism present in *E. azurea*. Solms-Laubach (1883) first reported that the species is tristylous. Populations of tristylous species are often composed of three floral forms. One form has long styles and anthers positioned at two levels below the stigmas. The second form has mid length styles with one set of anthers above the stigmas and one set below, and the remaining form has short-styled flowers with two anther levels above the stigmas. The Darwinian interpretation of this floral trimorphism is that it promotes insect-mediated cross-pollination between forms with anthers and stigmas at equivalent levels (Darwin, 1877). In *E. azurea*, a mid-styled form has not been reported and as a result most workers have considered the species to be distylous (Müller, 1883; Hauman-Merck, 1913; Johnston, 1924; Schulz, 1942; Täck-

holm and Drar, 1950; Willis, 1951; Bock, 1966; Bahadur, 1968; Mulcahy, 1975).

The purpose of this paper is to report the discovery of the "missing" mid-styled form as well as a semi-homostylous form of *E. azurea*. In addition, the results of a study of the breeding system and observations of the reproductive biology of natural populations of *E. azurea* in Costa Rica and Amazônia are described.

MATERIALS AND METHODS

Measurements of floral parts were made on ten flowers of *Eichhornia azurea* from different individuals of each style form present in a population from Amazônia (Barrett 1123, Santarém, Pará, UC). 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 anther level of the three floral forms in a population at Boca de Jari, Amapa (Barrett 813, UC).

Five populations from Amazônia were sampled in order to estimate the representation of floral forms in each population. A single inflorescence was gathered from each distinct flowering mat in a population and the style form recorded. A minimum distance of 5 m between mats was utilised during sampling. Due to extensive clonal propagation in *E. azurea*, it is not possible to identify individuals accurately hence data on the representation of floral forms should not be interpreted as indicating genotype frequencies.

A controlled pollination program was undertaken in a pollinator-free glass-house at the University of California, Berkeley, during 1976. The material utilised was a single long-styled clone, reported to be from Brazil, obtained from Van Ness Water Gardens, Upland, California. Self-pollination with pollen from each anther level was undertaken in order to detect the presence of self-incompatibility. All flowers were emasculated and pollen was transferred to stigmas using forceps. Capsules were harvested 20–25 days after pollinations. Autogamy was tested utilising undisturbed inflorescences. Pollen viability and ovule number per flower were also estimated and pollen tube growth was observed by staining styles in lactophenol and cotton blue, eight hours after pollination.

RESULTS

Floral morphology

Measurements of stigmas and anther heights in *Eichhornia azurea* show that three floral forms can be clearly distinguished (Table I). The mean style and stamen lengths are distinct and there is a reciprocal correspondence between the heights of the stigmas and anthers in the three floral forms. The presence of a mid-styled form [Fig. 2(a)] demonstrates that *E. azurea* is tristylous and not distylous as inferred by earlier workers.

TABLE I

Mean height and standard deviation of stigma and anthers in the three floral forms of *Eichhornia azurea*

Floral form	Stigma height (mm)	Anther height (mm)		
		Long stamen	Mid stamen	Short stamen
Long-styled	29.5 ± 1.5		16.1 ± 0.7	7.0 ± 1.1
Mid-styled	17.8 ± 1.4	25.9 ± 1.5		7.8 ± 1.1
Short-styled	8.5 ± 0.7	27.5 ± 0.9	18.5 ± 1.0	

A population of *E. azurea* (Barrett 1053, UC) observed at Lake Arenal (elevation 1200 m), Guanacaste Province, Costa Rica consisted of plants with a floral morphology different to that of the trimorphic forms described above. In these plants, the low level anther is adjacent to the stigma [Fig. 2(b)]. This condition is known as semi-homostyly (Stout, 1925; Lewis, 1954; Ornduff, 1972). The style and lower stamen whorl, measured from the base of the style, ranged from 13 to 15 mm in length whereas the upper stamen whorl ranged from 17 to 20 mm in length. Variability in stamen length is due to differences in the insertion and length of individual filaments.

The flowers of semi-homostylous and tristylous forms differ in other respects. In semi-homostylous flowers, the size and prominence of the yellow nectar guide and the degree of limb expansion of the perianth are much reduced in comparison with tristylous forms. In addition, the synchrony of flowering of inflorescences differs in the two floral types. Individual inflorescences of trimorphic forms take up to five days before the completion of flowering whereas in the semi-homostylous race flowering is completed in 1–2 days. Although inflorescences of the two floral types contain similar numbers of flowers, the axis of the semi-homostylous inflorescence is shorter in length, resulting in a more condensed inflorescence which becomes partially enclosed by a sheathing spathe.

In common with many tristylous species, pollen trimorphism accompanies the differences in stamen and style lengths in *E. azurea* (Table II). In tristylous 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 anther are intermediate, and the smallest pollen is produced by the short anther level. The mean sizes of pollen grains from the two anther levels of each floral form are significantly different. Pollen grains from the mid and short anther levels of different style forms correspond in size. However, pollen from the long anther level of mid-styled plants is considerably larger than pollen from the long anther level of short-styled plants.

Pollen produced by the two anther levels of semi-homostylous flowers differs in size. The average size (μm) of pollen from the lowest anther

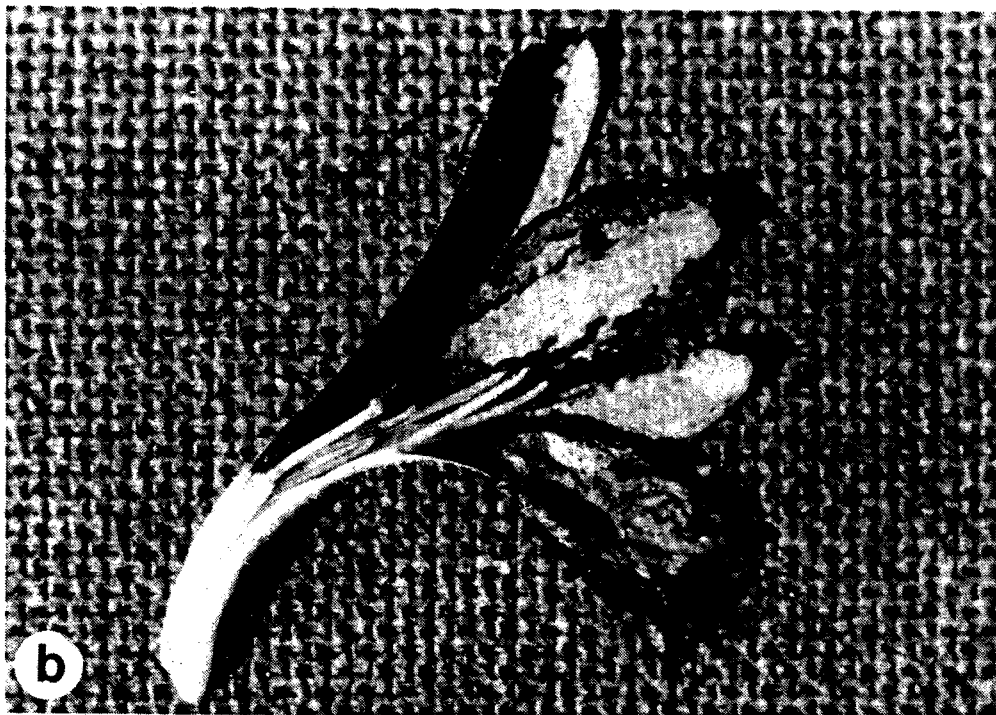


Fig. 2. (a) Mid-styled form of *Eichhornia azurea*, longitudinal section of flower. (b) Semi-homostylous form of *Eichhornia azurea*, longitudinal section of flower.

TABLE II

Measurements of equatorial and polar axes (mean and standard deviation) of pollen grains in the three floral forms of *Eichhornia azurea*

Floral form	Long-level anther		Mid-level anther		Short-level anther		t ^a
	Equatorial axis (μm)	Polar axis (μm)	Equatorial axis (μm)	Polar axis (μm)	Equatorial axis (μm)	Polar axis (μm)	
Long-styled			72.1 \pm 2.3	28.5 \pm 1.3	60.2 \pm 2.8	23.9 \pm 1.4	32.8
Mid-styled	93.0 \pm 4.2	35.3 \pm 1.7			61.4 \pm 3.2	23.7 \pm 1.3	59.9
Short-styled	84.6 \pm 4.5	35.4 \pm 1.9	73.7 \pm 3.6	29.8 \pm 2.0			18.9

^aDifferences between mean pollen size (equatorial axis) of two anther levels of each floral form are all significant ($P < 0.001$).

whorl is $72.3 \pm \text{s.d. } 4.0$ compared with $84.3 \pm \text{s.d. } 4.0$ in the upper anther level. Pollen stainability in both semi-homostylous and tristylous forms exceeded 95%, indicating a high level of viability.

Breeding system

In the large majority of heterostylous plants, floral heteromorphism is associated with a physiological self-incompatibility system (Crowe, 1964; Vuilleumier, 1967). Artificial self-pollination of the long-styled form of *E. azurea* also demonstrates the presence of self-incompatibility. However, the behaviour of pollen from mid and short anther whorls was markedly different in self-pollination. Microscopic examination of styles eight hours after pollination indicated that many pollen tubes had reached ovules when pollen from the mid anther level was utilised. However, very little pollen tube growth occurred in self-pollination using pollen from the short anther level. Seed set resulting from the latter pollination type was low; only 12.2% of flowers pollinated produced capsules whereas 94.3% of the pollination employing pollen from the mid anther level resulted in capsule production (Table III).

The average number of ovules produced by flowers of the long-styled form of *E. azurea* was 38.5 ($n = 10$, s.d. = 6.2). Although capsule production was near maximal in self-pollinations using mid level anthers, less than half of the ovules in pollinated flowers produced seeds. It is probable that greater seed production would result from legitimate cross-pollinations (between stigmas and anthers at equivalent levels) of long-styled plants.

The semi-homostylous race of *E. azurea* is self-compatible and auto-gamous. An undisturbed inflorescence produced abundant seed under pollinator-free glasshouse conditions. Field observations also suggest that the semi-homostyle is self-compatible. The population at Lake Arenal was composed solely of semi-homostylous individuals yet the seed production of isolated plants was substantial. Twenty-three inflorescences, originally contain-

TABLE III

Capsule and seed production in self-pollination of the long-styled form of *Eichhornia azurea*

	No. fls. pollinated	No. caps. produced	% Capsule set	\bar{x} seeds per cap.	s.e.m.	\bar{x} seeds per fl.	s.e.m.
L × m/L ^a	88	82	94.3	14.4	± 1.1	13.4	± 1.1
L × s/L	82	10	12.2	4.3	± 1.1	0.5	± 0.2

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

ing 738 flowers, were sampled from this population. All inflorescences produced seed and an average of 72.2% (s.e.m. ± 3.0) of the flowers in an inflorescence produced seed.

Two monomorphic populations of *E. azurea* in Amazônia, one composed of long-styled plants and the other consisting of short-styled individuals, were sampled for seed production. No seed was found in either population. Undisturbed inflorescences of the long-styled form produced no seed autogamously under glasshouse conditions.

Field observations

Field observations of *E. azurea* and *E. crassipes* contradict the earlier view held by Schwartz (1927) that these species rarely occur together in sympatric populations. I frequently observed mixed populations of the two species in Amazônia, Costa Rica, and Venezuela. No hybrids were ever observed in mixed populations and all attempts at artificial hybridisation of the two species have failed to produce seed.

In Amazônia, populations of *E. azurea* are more commonly encountered in the Lower Amazon region whereas *E. crassipes* is more abundant in Middle and Upper Amazônia. At Boca de Jari and São Raimundo (Lower Amazônia) floating mats of *E. azurea* are a weed problem in the newly constructed irrigation canals and drainage ditches associated with rice cultivation. Although *E. crassipes* occurs in marshlands surrounding these areas, it shows no tendency to colonise these particular artificial aquatic habitats.

Five natural populations of *E. azurea* occurring in Amazônia were sampled to determine the representation of floral forms in each. The three style forms were present in each population although the proportional representation of each form varied among the habitats surveyed (Table IV). A number of monomorphic populations of *E. azurea* were also observed in Amazônia.

The major insect visitors to flowers of *E. azurea* are long-tongued solitary bees (Anthophoridae and Megachilidae) which were observed collecting pollen and feeding on nectar. The bees are large enough for partitioning of the various pollen types on the body surface of the bee and are probably effective pollinators of *E. azurea*. Small pollen-collecting halictid bees were

TABLE IV

The representation of floral forms in natural populations of *Eichhornia azurea* in Amazônia

Locality	Habitat	Long	Mid	Short	Total
Boca de Jari, Amapa	Marshland	30	36	18	84
São Raimundo, Pará	Canal	69	65	27	161
São Raimundo, Pará	Canal	40	41	61	142
São Raimundo, Pará	Ricefield	19	20	55	94
Santarém, Pará	Riverbank	13	11	6	30

also observed feeding on flowers in Amazônia and Costa Rica.

Seedlings were frequently observed in natural populations of *E. azurea*. Young plants and seedlings occurred in shallow water or on wet mud at the periphery of water bodies.

DISCUSSION

There have been no previous experimental studies of *Eichhornia azurea* and little is known of its reproductive biology. In contrast, other tristylous members of the Pontederiaceae, particularly *E. crassipes* and *Pontederia* species, have received considerable attention (Hazen, 1918; François, 1964; Ornduff, 1966; Mulcahy, 1975; Barrett, 1977a, b). The data obtained in this study provide an opportunity to compare the reproductive systems of these taxa with that of *E. azurea*.

Eichhornia azurea and *E. crassipes* possess similar methods of dispersal. Their capacity for vegetative propagation, associated with an ability to float on water, give both species high mobility which aids in the colonisation of new habitats. Seeds of both *Eichhornia* species have limited buoyancy and usually sink in water after approximately 24 h. This is in marked contrast to the seeds of *Pontederia* species which are surrounded by light aeriferous tissue, giving them considerable buoyancy. Schulz (1942) reports a flotation period of 15 days for utricles (fruits) of this genus. Furthermore, *Pontederia* species are generally rooted to the substrate and clonal growth merely increases colony size. Hence, in *Pontederia*, the utricle is the principal dispersal propagule whereas in *E. azurea* and *E. crassipes* the vegetative plant body as well as seeds contribute towards dispersal.

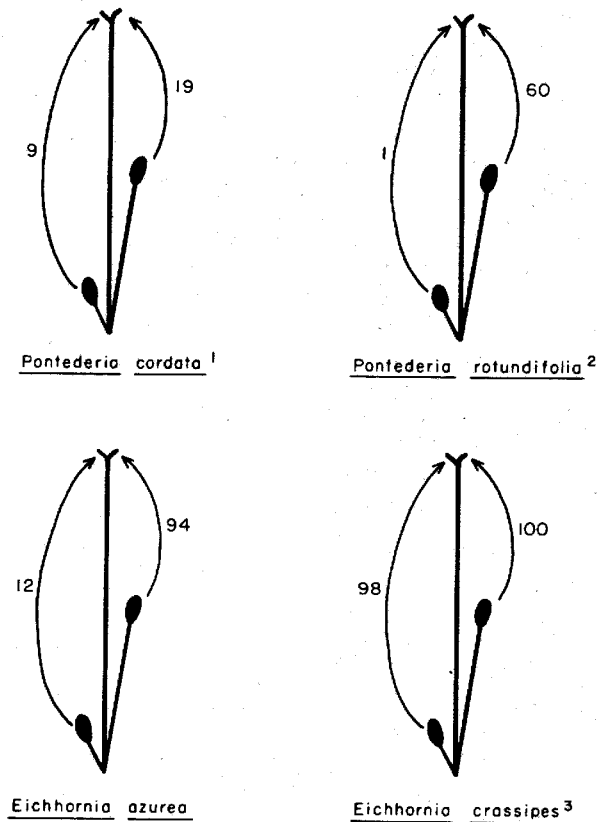
Eichhornia azurea does not exhibit the high degree of specialisation to the aquatic environment which is characteristic of *E. crassipes*. The rosette growth form with inflated leaf bases and numerous plumose roots give young plants of *E. crassipes* considerable buoyancy and complete independence from land. Although mats of *E. azurea* float due to aerenchyma in the stem and leaf bases, vegetative parts which are not anchored to the substrate do not grow and multiply in the same manner as those of *E. crassipes*. Vege-

tative propagation of *E. azurea* is by chance fragmentation of the robust branched stems. In *E. crassipes*, daughter rosettes are formed rapidly on brittle stolons and become separated from floating mats with relative ease. The comparatively slow rate of formation of vegetative propagules in *E. azurea* is perhaps one of the major reasons why it has not become a widespread weed problem.

In some respects, the breeding system of *E. azurea* exhibits more similarities to tristylous *Pontederia* species than to *E. crassipes*. In *E. azurea*, *P. cordata* Linnaeus (Ornduff, 1966) and *P. rotundifolia* Linnaeus (Barrett, 1977a), populations containing mixtures of floral forms are commonly reported. In these circumstances, tristily probably functions to promote some degree of outcrossing. Most populations of *E. crassipes* are monomorphic for style form and tristily is thus rendered non-functional as an outcrossing mechanism (Barrett, 1977b). In common with the two *Pontederia* species, a physiological self-incompatibility system accompanies floral trimorphism in *E. azurea*. Pollen tube growth in long styles of *E. azurea* was inhibited in self-pollination with pollen from the short anther level. In all three species, pollen from the two anther levels of a style form exhibits a striking difference in incompatibility behaviour in self-pollination. For example, self-pollination of long-styled flowers with pollen from short level anthers results in very low seed production, whereas if pollen from mid level anthers is utilised, moderate amounts of seed are produced (Fig. 3). There is no difference in the behaviour of pollen from the two anther levels of *E. crassipes* and both types of self-pollination are highly productive of seed (Barrett, 1977b). *E. azurea* and the two *Pontederia* species possess strong pollen trimorphism with little overlap in the size classes of pollen produced by different anther levels. In contrast, size trimorphism in the pollen of *E. crassipes* is weakly developed (Barrett, 1977b).

The semi-homostylous race of *E. azurea* from Costa Rica is probably derived from an ancestral tristylous race. Homostylous and semi-homostylous races have arisen repeatedly in the majority of heterostylous genera (Stout, 1925; Crosby, 1949; Lewis, 1954; Baker, 1959a; Ornduff, 1972). However, this is the first report of the trait in *E. azurea*. Since homostylous races are generally self-fertilising, they can establish successfully in isolated areas (Baker, 1955, 1967) and, as a result, often occur at the periphery of the range of their heterostylous ancestors (Baker, 1959a, b). The population at Lake Arenal occurs in an isolated volcanic lake in the Cordillera de Guanacaste. No trimorphic populations were found in the area. It is possible that the facility for self-fertilisation as well as vegetative propagation aided in the initial establishment of this population.

Although limited self-compatibility is present in tristylous *E. azurea*, it is probable that in polymorphic populations some degree of outcrossing occurs through the functioning of tristily. In the semi-homostylous race the arrangement of reproductive organs combined with self-compatibility ensure a high level of self-fertilisation. Such a quantum change in breeding system



- 1 Data of Ornduff (1966)
 2 Data of Barrett (1977a)
 3 Data of Barrett (1977b)

Fig. 3. Percentage fruit production in self-pollination of tristylous species of *Eichhornia* and *Pontederia*.

can lead to morphological changes and rapid speciation in some plant groups (Baker, 1961). Accompanying a change from outcrossing to partial self-fertilisation in *E. azurea* may have been a reduction in the size and attractiveness of flowers and the development of a greater synchrony in the opening of individual flowers on an inflorescence. In the majority of heterostylous groups, self-compatibility arises in association with homostyle formation (Crosby, 1949; Lewis, 1954). However, in tristylous *E. azurea*, some self-compatibility is already present. Studies of the compatibility relationships of pollen in the semi-homostylous form would be valuable since it is possible that the evolution of homostyly in *E. azurea* has not been accompanied by a significant change in incompatibility reactions.

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