

**STYLE MORPH DISTRIBUTION IN NEW WORLD POPULATIONS OF
EICHHORNIA CRASSIPES (MART.) SOLMS-LAUBACH (WATER
HYACINTH)**

S.C.H. BARRETT

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

I.W. FORNO

Division of Entomology, CSIRO, Long Pocket Laboratories, Brisbane, Queensland Q4068 (Australia)

(Accepted for publication 16 December 1981)

ABSTRACT

Barrett, S.C.H. and Forno, I.W., 1982. Style morph distribution in New World populations of *Eichhornia crassipes* (Mart.) Solms-Laubach (Water Hyacinth). *Aquat. Bot.*, 13: 299–306.

Eichhornia crassipes (Mart.) Solms-Laubach (Water Hyacinth) exhibits the rare genetic polymorphism tristily. Populations of tristylous species usually contain three floral morphs which differ in style length and stamen height. In a survey of style morph representation in 196 New World populations, 77.0% were monomorphic, 18.4% were dimorphic and 4.6% were trimorphic. The three floral morphs were found in Brazil and Argentina. The short-styled morph predominated in the Amazon Basin and Mato Grosso of Brazil but was absent from North and Central America and the Caribbean. The mid-styled form predominated in the introduced range of the species and in parts of the native range. The long-styled form rarely gains ascendancy over the other style morphs and occurred less frequently in both the native and introduced ranges. The patterns of style morph distribution suggest Amazônia as the centre of origin of *E. crassipes*, with natural spread from there to other areas of the South American continent and introduction by man to North and Central America and the Caribbean.

INTRODUCTION

Eichhornia crassipes (Mart.) Solms-Laubach (Water Hyacinth) is a free-floating perennial aquatic in the monocotyledonous family Pontederiaceae. During the past century it has spread, with man's aid, from its native range in lowland tropical South America to become one of the world's most serious aquatic weeds (Sculthorpe, 1967; Holm et al., 1977). *Eichhornia crassipes* possesses prolific powers of clonal propagation which constitute the major factor contributing to its success as a weed of lakes, reservoirs and canals. Sexual reproduction occurs in seasonal habitats, particularly in the native range of the species, where frequent water level fluctuations provide suitable

ecological conditions for seed germination and seedling establishment (Barrett, 1977a, 1979, 1980a,b).

The Pontederiaceae is one of three angiosperm families in which tristily is known to occur (Ganders, 1979). Populations of tristylous species usually contain three floral forms or morphs, which often occur in equal proportions (Dulberger, 1970; Halkka and Halkka, 1974; Barrett, 1977b). The morphs are distinguished by style length, stamen height and pollen size. Tristily and the more widespread distily are floral mechanisms which promote insect-mediated cross-pollination among floral morphs (Darwin, 1877; Ganders, 1979).

Since Müller (1871, 1883) and Darwin (1877) described long- and mid-styled forms of *E. crassipes*, there has been considerable discussion on whether the species is distylous or tristylous (Haldane, 1960; François, 1964; Ornduff, 1966). Due to insufficient evidence for the existence of the short-styled form, workers have considered the species to be distylous (François, 1964; Faegri and van der Pijl, 1971; Mulcahy, 1975). However, in 1974 the "missing" short-styled form of *E. crassipes* was discovered in the Lower Amazon Basin of Brazil, demonstrating that the species is tristylous (Barrett, 1977a).

The purpose of this report is to draw attention to the occurrence of tristily in *E. crassipes* and to present the results of a geographical survey of style morph representation in New World populations of *E. crassipes*. An attempt is then made to explain the unusual patterns of style morph distribution in the native and introduced range of the species.

MATERIALS AND METHODS

One hundred and ninety-six populations of *E. crassipes* in tropical and temperate regions of the New World were sampled between 1974–1980 to determine the representation of style morphs in each (Fig. 1). Inflorescences were gathered at random from populations and the style forms recorded. In populations with less than 200 inflorescences all were sampled. In floating populations sampling was facilitated by use of a boat or an inflatable air mattress. For the purpose of the survey, a population was considered to be a colony of plants separated spatially from other such colonies by a minimum distance of 1 km.

Locality and habitat data, as well as various aspects of the reproductive biology of populations surveyed from California, south eastern U.S.A., Costa Rica and the Lower Amazon, are presented elsewhere (Barrett, 1977a, 1979, 1980). Populations from the Caribbean were sampled from drainage ditches and streams in Jamaica, Dominican Republic, Puerto Rico and Trinidad. Those in Venezuela were sampled from flooded marshlands of the Llanos, Gúarico state and Lake Suata and Lake Taiguaiguay, Aragua state and in Guyana from lowlands near Georgetown. In Paraguay, populations were sampled in the Paraguay river near Asuncion and in flooded marshlands near Encarnacion. Populations in Argentina were sampled in the northern states of Misiones, Corrientes and Chaco and also in the States of Santa Fé and Entre

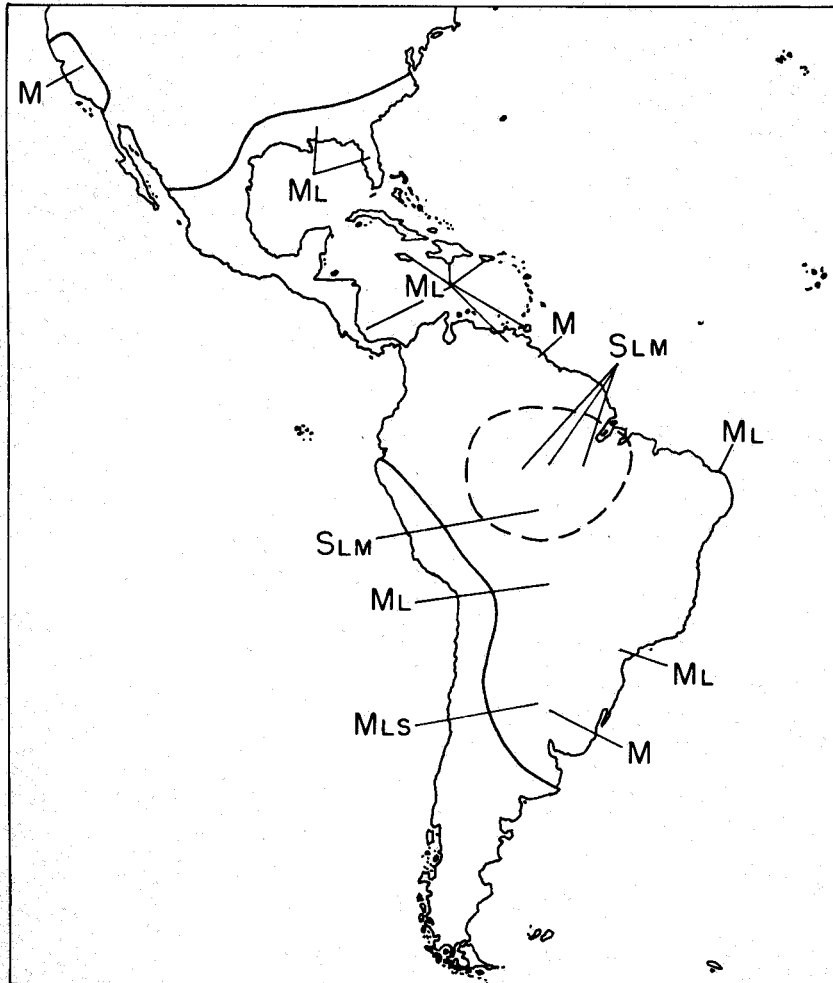


Fig. 1. Distribution of *Eichhornia crassipes* in the New World with regions sampled for style morph presence. The predominant form in a given region is indicated by a large letter (S, short-styled morph; M, mid-styled morph; L, long-styled morph). Less frequent forms are in smaller letters. The probable area of origin of *E. crassipes* is marked by the dashed line.

Rios. In Uruguay flowering populations were found at only two sites, Montevideo and Lake Sauce.

Sampling in Brazil was extensive. Eighty-two populations were sampled in Amazônia from the river systems of the Solimões, Amazon, Tapajós and Jari rivers in the vicinity of Manaus, Itacoatiara, Santarem and Boca de Jari respectively as well as from a small dam at Belém. A further 25 populations were sampled on the coast between Maruim, Sergipe state and Taim, Rio Grande do Sul state, eight in the Paraguay river and the Pantanal of Mato Grosso do Sul state and the remaining eight were from sites scattered throughout the catchment of the Paraná river in São Paulo and Paraná states.

TABLE I
Representation of style morphs in a survey of New World populations of *Eichhornia crassipes*

Region	Total no. of populations surveyed	Monomorphic		Dimorphic		Trimorphic	
		n	Style morph ¹	n	Style morph	n	Style morph
North America							
S.E. USA	16	12	10M, 2L	4	3M>L ² , 1L>M	0	—
California	4	4	4M	0	—	0	—
Caribbean	16	14	10M, 4L	2	2M>L	0	—
Central America	6	4	3M, 1L	2	2M>L	0	—
Venezuela	15	13	10M, 3L	2	2M>L	0	—
Guyana	2	2	2M	0	—	0	—
Paraguay	4	2	2M	2	1M>L, 1L>M	0	—
Argentina	8	4	3M, 1S	2	1M>L, 1S>M	2	2M>L>S
Uruguay	2	2	2M	0	—	0	—
Brazil							
Amazônia	82	61	43S, 2M, 16L	18	16S>L, 2S>M	3	3S>M,L
East Coast	25	24	24M	1	1M>L	0	—
Mato Grosso do Sul	8	1	1S	3	2L>M, 1S>M	4	4S>M,L
Inland São Paulo & Paraná states	8	8	8M	0	—	0	—
Total (%)	196	151 (77.0)	80M, 45S, 26L	36 (18.4)	12M>L, 16S>L 4S>M, 4L>M	9 (4.6)	7S>M,L 2M>L>S

¹ Abbreviations: S, short; M, mid; L, long.

² Three populations in which mid predominated over long.

RESULTS

Of the 196 populations sampled, 151 (77.0%) were monomorphic for style morph, 36 (18.4%) were dimorphic and 9 (4.6%) contained all three style morphs (Table I). In all dimorphic populations, a single style morph predominated and generally the minority component represented less than 10% of the inflorescences sampled. However, a population at Wallisville, Texas was composed of 69.6% long-styled morphs and 39.6% mid-styled morphs ($n=483$) and a population at Palo Verde, Guanacaste Province, Costa Rica contained 80.2% mid-styled morphs and 19.8% long-styled morphs ($n=1272$).

Few trimorphic populations were encountered in the survey, seven in Brazil and two in Argentina. In Amazônia three populations were found on beaches along the Solimões and Amazon rivers. The populations were composed of scattered terrestrial plants which had become stranded following the seasonal fall in water levels. A trimorphic population alongside the River Solimões contained 150 short-styled plants, nine mid-styled plants and 30 long-styled plants. A population at Itacoatiara was composed of 26 short-styled plants, one mid-styled plant and two long-styled plants. Four trimorphic populations on beaches of the Paraguay river in the Pantanal region of Mato Grosso do Sul also exhibited a predominance of short-styled plants. However, the mid-styled morph predominated in two trimorphic populations sampled near Corrientes and Barranqueras in Argentina.

In populations from North and Central America, the Caribbean and Venezuela, the mid-styled morph predominated with the long-styled morph occurring occasionally. In Guyana, Uruguay and along the east coast of Brazil only the mid-styled morph was observed except at Pelotas in southern Brazil where one long-styled inflorescence was found in a sample of 1000 inflorescences. This pattern of mid-styled morph predominance is in striking contrast to the situation in Amazônia and Mato Grosso where the short-styled morph, when present, was always dominant (Table I). There was no significant difference in the number of monomorphic populations occurring in Brazil compared with the remainder of the areas sampled (Brazil 94, remaining areas 57, $X^2 = 0.02$, $df 1$, $P > 7.9$).

DISCUSSION

The tristylous breeding system of *E. crassipes* is largely non-functional as an outcrossing mechanism due to population structure. Rapid clonal propagation associated with the high mobility of free-floating plants results in populations which are often composed of a single floral morph. Where polymorphic populations occur, a single style morph usually predominates. The absence of suitable ecological conditions for seed germination and seedling establishment in many floating populations further restricts the opportunity for the build up of genetic diversity (Barrett, 1982). Hence populations of *E. crassipes* are frequently composed of a single clone.

The results of this survey and limited observations of style morph distribution published elsewhere (Haldane, 1960; Mulcahy, 1975; Bir Bahadur, 1977) indicate that in most of the introduced range of *E. crassipes*, the mid-styled morph predominates with the long-styled morph occurring less frequently. The short-styled morph is apparently restricted to the native range of *E. crassipes* (Barrett, 1977a). The absence of the short-styled morph of *E. crassipes* from the introduced range of the species is probably due to chance. Short-styled genotypes were apparently not among the introduction(s) to North and Central America and the Old World. Since mid- and long-styled morphs cannot segregate the short-styled morph, a separate introduction would be necessary to allow colonization of the introduced range (Barrett, 1977a).

It is often stated in the literature that *E. crassipes* is native to the Neotropics. However, the results of this study suggest that *E. crassipes* may be introduced to parts of the continent (see Sculthorpe, 1967, p. 461). Surveys of natural populations and herbarium specimens from Central America, the Caribbean, Guyana, Venezuela and limited observations in Colombia, Paraguay and Uruguay failed to locate the short-styled morph. The short-styled morph was common in the Amazon basin and Mato Grosso. These data are consistent with the suggestion that *E. crassipes* is native to lowland tropical South America and, in particular, the Amazon basin of Brazil (Holm et al., 1977; Barrett, 1979).

The three floral morphs were observed in lagoons near the confluence of the Paraguay and Paraná rivers in Argentina. It seems highly probable that populations in Argentina originated by natural dispersal of plants south in the Paraguay river from Mato Grosso. It is also possible that plants may have spread by natural means from the Amazon basin to the lowland areas of Mato Grosso and the Paraguay river since a portion of the catchment area of the Paraguay and Tapajós rivers is closely associated in a region with no obvious geophysical barriers. Hence it is suggested that the centre of origin of *E. crassipes* is probably in Amazônia and that the species spread naturally south and perhaps north to northern South America. The species was then introduced to North and Central America and the Caribbean by man.

Of the 82 populations of *E. crassipes* sampled from Amazônia, 64 were monomorphic for the short-styled morph or contained a predominance of this form. This finding was unexpected since surveys of style morph in related tristylous taxa, native to Amazônia, [*Eichhornia azurea* (Swartz) Kunth and *Pontederia rotundifolia* Linnaeus] failed to detect a pattern of style morph dominance (Barrett, 1977b, 1978). One explanation is that the predominance of the short-styled morph in the areas sampled does not reflect a regional pattern but merely local concentrations of this form. Surveys conducted for us by W. Junk (I.N.P.A., Manaus, Brazil) and M. Mathias (U.C.L.A., Los Angeles, U.S.A.) in lakes associated with the river Solimões (Middle Amazon) and at Leticia (Upper Amazon) revealed a predominance of short- and mid-styled morphs respectively. In other parts of Brazil the mid-styled morph

predominated except in Mato Grosso where short- and long-styled morphs were most frequently encountered. In addition, Müller's early observations from southern Brazil (1871, 1883) mention only the mid- and long-styled morphs. In view of the great powers of dispersal of the free-floating habit, it is not clear how a single morph gains ascendancy over extensive areas within the native range. The high mobility of floating populations might be expected to result in a more random distribution of style morphs.

An alternative explanation for the apparent predominance of the short-styled morph in parts of Amazônia is that there are ecological differences among the style morphs under Amazonian conditions. The short-styled morph may exhibit a greater fitness, in some Amazonian environments, than the other two morphs. This could be manifested by superior cloning ability, or by higher reproductive capacity. In this context it is worth noting that in controlled pollinations of the three floral morphs, the seed production of the short-styled morph from the Lower Amazon was 44–75% higher than that of mid- and long-styled morphs (Barrett, 1977a, 1980a). Clearly further surveys are necessary to reveal the pattern of style morph distribution throughout the native range of *E. crassipes*. In addition, comparative studies of the growth and reproductive performance of clones may aid in providing an explanation for the curious geographical distribution of style morphs in the native range of *E. crassipes*.

ACKNOWLEDGEMENTS

The authors thank H.G. Baker, S.D. Price and S.G. Weller for advice and W. Junk, N. Smith and J. Velasquez for providing logistical support in Amazônia and Venezuela. This research was funded in part by grants from the Natural Sciences and Engineering Research Council of Canada and the Connaught Committee of the University of Toronto.

REFERENCES

- Barrett, S.C.H., 1977a. Tristyly in *Eichhornia crassipes* (Mart.) Solms (water hyacinth). *Biotropica*, 9: 230–238.
- Barrett, S.C.H., 1977b. The breeding system of *Pontederia rotundifolia*, a tristylous species. *New Phytol.*, 78: 209–220.
- Barrett, S.C.H., 1978. Floral biology of *Eichhornia azurea* (Swartz) Kunth (Pontederiaceae). *Aquat. Bot.*, 5: 217–228.
- Barrett, S.C.H., 1979. The evolutionary breakdown of tristyly in *Eichhornia crassipes* (Mart.) Solms (Water Hyacinth). *Evolution*, 33: 499–510.
- Barrett, S.C.H., 1980a. Sexual reproduction in *Eichhornia crassipes* (Water Hyacinth) I. Fertility of clones from diverse regions. *J. Appl. Ecol.*, 17: 101–112.
- Barrett, S.C.H., 1980b. Sexual reproduction in *Eichhornia crassipes* (Water Hyacinth) II. Seed production in natural populations. *J. Appl. Ecol.*, 17: 113–124.
- Barrett, S.C.H., 1982. Genetic variation in weeds. In: R.C. Charudattan and H. Lynn Walker (Editors), *Biological Control of Weeds with Plant Pathogens*. Wiley, New York, in press.

- Bahadur, Bir., 1977. Heterostyly in *Eichhornia crassipes* (Mart.) Solms. J. Ind. Bot. Soc., 56: 299—306.
- Darwin, C., 1877. The Different Forms of Flowers on Plants of the Same Species. John Murray, London, 361 pp.
- Dulberger, R., 1970. Tristyly in *Lythrum junceum*. New Phytol., 69: 751—759.
- Faegri, K. and van der Pijl, L., 1971. The Principles of Pollination Ecology (2nd edn.). Pergamon, Oxford, 291 pp.
- François, J., 1964. Observations sur l'hétérostylie chez *Eichhornia crassipes* (Mart.) Solms. Acad. R. Sci. Outre-Mer (Brussels) Bull. Séances, 1964: 501—519.
- Ganders, F.R., 1979. The biology of heterostyly. N.Z. J. Bot., 17: 607—635.
- Haldane, J.B.S., 1960. The water hyacinth — an appeal for information. J. Bombay Nat. Hist. Soc., 57: 243.
- Halkka, O. and Halkka, L., 1974. Polymorphic balance in small island populations of *Lythrum salicaria*. Ann. Bot. Fenn., 11: 267.
- Holm, L.G., Plucknett, D.L., Pancho, J.V. and Herberger, J.P., 1977. The World's Worst Weeds: Distribution and Biology. Univ. Press Hawaii, Honolulu, 609 pp.
- Mulcahy, D.L., 1975. The reproductive biology of *Eichhornia crassipes* (Pontederiaceae). Bull. Torrey Bot. Club, 102: 18—21.
- Müller, F., 1871. Ueber der Trimorphismus de Pontederien. Jena. Z. Med. Naturwiss., 6: 74—78.
- Müller, F., 1883. Einige Eigenthümlichkeiten der *Eichhornia crassipes*. Kosmos, B: 297—300.
- Ornduff, R., 1966. The breeding system of *Pontederia cordata* L. (Pontederiaceae). Bull. Torrey Bot. Club, 93: 407—416.
- Sculthorpe, C.D., 1967. The Biology of Aquatic Vascular Plants. Edward Arnold, London, 610 pp.