Sexual Reproduction in Eichhornia crassipes (Water Hyacinth). II. Seed Production in Natural Populations

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SEXUAL REPRODUCTION IN *EICHHORNIA CRASSIPES* (WATER HYACINTH)

II. SEED PRODUCTION IN NATURAL POPULATIONS

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SUMMARY

(1) A total of nineteen populations in two tropical regions (Lower Amazon and Costa Rica) and two temperate regions (California and southern U.S.A.) was surveyed to assess the levels of natural seed production and the occurrence of sexual reproduction in *Eichhornia crassipes.*

(2) Of 7750 flowers sampled, 45·9% produced capsules with an average of 44·2 seeds per capsule. Seed production was twice as great in tropical populations as in temperate populations. This difference is probably associated with higher levels of insect visitation to flowers of *E. crassipes* in tropical regions. Seedlings growing in saturated soil were observed in three of the nineteen populations.

(3) The seasonal pattern of seed production during 1976 was estimated for a population at Stockton, California. Seed production was low at the beginning and end of the flowering season (June–November) but reached a peak in September.

(4) Controlled field pollinations showed that seed set was sub-maximal throughout the season. The foraging behaviour of the honey bee (*Apis mellifera*) largely determined the seasonal levels of seed production at Stockton, California.

(5) The major factors limiting sexual reproduction in *E. crassipes* are low and 'inefficient' pollinator service, which limits fecundity, and the absence of suitable ecological conditions for seed germination and seedling establishment.

INTRODUCTION

Controlled pollination studies on clones of *Eichhornia crassipes* (water hyacinth) demonstrate that a high degree of seed fertility accompanies the well documented capacity for vigorous clonal propagation (Mulcahy 1975; Barrett 1977b, 1979, 1980). However, observations made throughout the range of *E. crassipes* by botanists and agriculturalists indicate that only limited sexual reproduction occurs in natural populations.

This suggests that environmental factors play a major role in limiting sexual reproduction under field conditions. Although several workers have suggested environmental factors which might limit sexual reproduction in *E. crassipes*, e.g. scarcity of pollinators (Müller 1883; Penfound & Earle 1948), unfavourable climatic conditions preventing seed formation (Agharkar & Banerji 1930; Parija 1934; Tag el Seed & Obeid 1975) and the absence of suitable sites for seed germination and seedling establishment (Hitchcock *et al.* 1949, 1950) there have been few field studies which have attempted to determine the relative importance of these factors.

Eichhornia crassipes currently has a widespread distribution, occurring in both tropical and temperate regions. Therefore, environmental factors which influence sexual

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reproduction are likely to vary in different parts of the species' range. In order to provide an opportunity for assessing the importance of sexual reproduction in *E. crassipes*, populations in both tropical and temperate areas of the New World were surveyed. In each population, measurements of seed production and observations of pollinators and seedling establishment were made. In addition, a detailed investigation of the seasonal pattern of seed production and factors limiting sexual reproduction was made in California, at the northern limit of the range of the species.

MATERIALS AND METHODS

Survey of sexual reproduction

A total of nineteen populations in two tropical regions (Lower Amazon and Costa Rica) and two temperate regions (California and southern U.S.A.) was examined between 1974 and 1976. In each population, the style form, the presence and type of pollinators and seedling occurrence were recorded. Infructescences were gathered at random from each population and used to obtain several measures of fecundity. The numbers of flowers, capsules and seeds per infructescence were recorded. The percentage capsule set and average numbers of seeds per capsule as well as seeds per flower were also estimated for each population.

Seasonal pattern of seed production at Stockton, California

A population at Stockton, California was selected for an investigation of seed production during the summer of 1976. The population has only mid-styled plants, is probably composed of a single clone and is located in Bacon Island Slough, 8 km west of Stockton adjacent to Highway 4. Associated species growing with *E. crassipes* in the remnant freshwater marsh community (Munz & Keck 1973) include *Scirpus acutus* Muhl., *Typha latifolia* L., *Ludwigia peploides* (H.B.K.) Raven ssp. *peploides* and *Azolla filiculoides* Lam.

At monthly intervals between June and October, three different pollination treatments were conducted on plants chosen at random from the population. One group of plants was artificially self-pollinated in the field with the aid of forceps. In the majority of cases all flowers on inflorescences in the population opened on the same day. Inflorescences bearing flowers of different ages were not utilized in the pollination programme and only newly opened flowers were pollinated. All field pollinations were completed before insect activity commenced. Plants of the second group were marked several hours prior to anthesis and were not artificially pollinated. Any seed produced by these plants resulted from natural or 'open' pollination. Jewellers' tags were used for marking plants in these two groups. The third group of plants, due to flower the following day, was removed from the population and taken to a heated tropical glasshouse at the University of California, Berkeley, where they were artificially self-pollinated. Plant collection and pollination were facilitated by the use of an inflatable air mattress and plants were transported to Berkeley in 30-litre plastic tubs. Between 18 and 25 days after pollination, the numbers of capsules and seeds produced by infructescences were recorded. Observations and subjective estimates of pollinator abundance were made on 3 days in each month during the flowering season. Meteorological records for June–October were obtained from the nearest weather station, located approximately 5 km from the study site.

Field germination

In order to assess the potential for seed germination and seedling establishment under field conditions in California, four plastic trays (25 cm^2) filled to 4 cm depth with soil, were floated on separate mats in the Stockton population during September 1976. The seed used in the germination test had been collected from the same population during September 1975. Fifty seeds were scattered on the surface of soil of each tray. Holes in the bottom of each tray allowed the soil to remain permanently saturated during the germination test. The number of seedlings in each tray was recorded after 28 days.

RESULTS

Survey of sexual reproduction

Eichhornia crassipes was found to occupy a wide range of natural and man-made aquatic habitats. Mats of floating plants occurred most commonly in the populations sampled. In nine of the populations, some individuals occurred in more terrestrial situations and were rooted to the substrate. Seedlings were observed at three of the nineteen populations (Missouri City and Wallisville, Texas; Palo Verde, Costa Rica). In all cases seedlings were growing on wet soil at the periphery of dense stands of *E. crassipes* and no seedlings were observed on floating mats. Insect visitors to flowers of *E. crassipes* were observed at nine of the nineteen populations surveyed; no insects were observed at the remaining populations (Table 1). Insect activity was greatest at the Stockton, Gibson, Palo Verde and Jari (canal and stream) populations. The introduced honey bee (*Apis mellifera L.*) was the predominant insect visitor at the first three populations.

Of a total of 7750 flowers sampled from all populations in the survey, 45·9% produced capsules with an average of 44·2 seeds per capsule. Capsule and seed production varied greatly among populations although all populations produced seed (Table 2). There were no consistent differences among style forms in the levels of capsule and seed production. Although the mean number of flowers per inflorescence varied greatly among populations (range 5·3 to 22·8), there were only small variations within populations (Table 2). There was no clear relationship between percentage capsule set and the numbers of flowers per inflorescence or seeds produced in a capsule (Fig. 1).

The most striking pattern to emerge from the survey is derived from a comparison of the seed fecundity of temperate and tropical populations. There were no significant differences between populations in the two regions in the numbers of flowers produced on an inflorescence. However, the number of capsules produced on an inflorescence and the percentage capsule set in a population were twice as great in the tropics as in temperate regions. The average number of capsules on tropical inflorescences was 5·8 compared to 2·9 in temperate regions ($F = 7{\cdot}48$, $P < 0{\cdot}025$). Of the 3629 flowers sampled in the tropics, 64·6% produced capsules compared to 29·3% ($n = 4121$) in temperate regions ($\chi^2 = 967{\cdot}4, P < 0{\cdot}001$). Although capsule set was twice as great in the tropics, there was no significant difference between populations in the two regions in the number of seeds set per capsule.

Seasonal pattern of seed production at Stockton, California

Flowering commenced in the Stockton population of *Eichhornia crassipes* at the end of May. In early June open pollinated plants set very few capsules and seeds compared to the two artificial pollination treatments (Table 3). Although 72·3% of the flowers pollinated under field conditions set capsules, seed set per flower averaged 74·1 compared with 178·9 in flowers pollinated the following day under glasshouse conditions. In July, capsule and seed production of open pollinated plants was also low, but the productivity of field pollinations increased to levels similar to those obtained from glasshouse pollinations in

TABLE 1. Style form, insect visitors and seedling occurrence in a survey of New World populations of *Eichhornia crassipes*

Locality	Habitat	Sample date	Style form	Insect visitors and rewards*	Seedlings observed†
Temperate populations.					
Clarksburg, Calif., U.S.A.	Slough	Sept. 1976	Mid	None observed	–
Stockton, Calif., U.S.A.	Slough	Sept. 1975	Mid	*Apis mellifera* (P, N) Syrphidae (P)	–
Merced, Calif., U.S.A.	River	Sept. 1976	Mid	None observed	–
Centerville, Calif., U.S.A.	Pond	Sept. 1978	Mid	None observed	–
Missouri City, Texas, U.S.A.	River	Aug. 1976	Long	Apioideae (?) Lepidoptera (N)	+
Wallisville, Texas, U.S.A.	Marsh	Aug. 1976	Long Mid	*Melissodes* spp.	+
Abbeville, Louisiana, U.S.A.	Canal	Aug. 1976	Mid	Apioideae (P, N)	–
Berwick, Louisiana, U.S.A.	River	Aug. 1976	Mid	None observed	–
Gibson, Louisiana, U.S.A.	Borrow pit	Aug. 1976	Mid	*Apis mellifera* (P, N)	–
Lake Okeechobee, Florida, U.S.A.	Lake	July 1976	Mid	None observed	–
Andytown, Florida, U.S.A.	Canal	July 1976	Mid	None observed	–
Tropical populations.					
Boca de Jari, Amapa, Brazil	Stream	Nov. 1974	Short	*Trigona* (P) Halictidae (P)	–
Boca de Jari, Amapa, Brazil	Canal	Sept. 1974	Short	*Ancyloscelis gigas* (P, N) Megachilidae (P, N)	– –
Boca de Jari, Amapa, Brazil	Marsh	Nov. 1974	Short	*Trigona* (P)	–
Boca de Jari, Amapa, Brazil	Pool	Nov. 1974	Long	None observed	–
Arenal, Guanacaste, Costa Rica	River	Nov. 1975	Mid	Halictidae (P)	–
Palo Verde, Guanacaste, Costa Rica	Marsh	Nov. 1975	Mid Long	*Apis mellifera* (P, N) Meliponidae (P)	+ +
Aranjuez, Guanacaste, Costa Rica	Pond	Nov. 1975	Long	None observed	–
Turrialba, Cartago, Costa Rica	Lake	Nov. 1975	Mid	None observed	–

* Pollen (P), Nectar (N).

† – No seedlings observed, + Few seedlings, + + Many seedlings.

Table 2. Capsule and seed production in New World populations of *Eichhornia crassipes*

Locality	No. of flowers sampled	No. of flowers producing capsules	% capsule set	$\bar{x}$ flowers inflorescence^{-1} ± s.e.m.	$\bar{x}$ capsules inflorescence^{-1} ± s.e.m.	$\bar{x}$ seeds inflorescence^{-1} ± s.e.m.	$\bar{x}$ seeds capsule^{-1} ± s.e.m.	$\bar{x}$ seeds flower^{-1} ± s.e.m.
Temperate populations								
Clarksburg	286	78	27·3	9·5 ± 0·3	2·6 ± 0·4	129·5 ± 29·5	49·8 ± 4·4	13·6 ± 1·8
Stockton	786	384	48·9	7·9 ± 0·1	3·8 ± 0·3	238·8 ± 21·2	62·2 ± 2·4	30·4 ± 1·6
Merced	205	31	15·1	10·3 ± 0·7	1·6 ± 0·3	72·9 ± 15·9	47·0 ± 7·9	7·1 ± 1·7
Centerville	145	25	17·2	8·1 ± 0·4	1·4 ± 0·3	50·5 ± 11·5	36·4 ± 6·1	6·3 ± 1·5
Missouri City	482	147	30·5	14·2 ± 0·7	4·3 ± 0·7	176·0 ± 46·2	54·0 ± 4·4	13·4 ± 1·6
Wallisville	626	47	7·5	8·5 ± 0·2	0·6 ± 0·2	20·4 ± 6·3	32·1 ± 3·8	2·4 ± 0·4
Abbeville	149	58	38·9	7·8 ± 0·5	3·1 ± 0·6	75·1 ± 17·0	27·0 ± 2·4	9·4 ± 1·5
Berwick	263	53	20·2	11·4 ± 0·6	2·3 ± 0·4	38·4 ± 7·8	16·7 ± 1·5	3·4 ± 0·5
Gibson	267	147	55·1	13·4 ± 0·6	7·4 ± 0·6	223·3 ± 26·1	30·4 ± 1·7	16·7 ± 1·3
Lake Okeechobee	442	220	49·8	18·4 ± 0·7	9·2 ± 0·9	397·9 ± 108·2	51·9 ± 4·9	22·7 ± 3·0
Andytown	470	19	4·0	9·8 ± 0·4	0·4 ± 0·1	12·3 ± 3·2	30·9 ± 3·7	1·3 ± 0·3
Tropical populations								
Jari, river	328	123	37·5	17·2 ± 0·9	6·5 ± 1·3	115·9 ± 35·3	17·9 ± 1·7	6·7 ± 0·8
Jari, canal	346	295	85·3	18·2 ± 1·4	15·5 ± 1·6	663·6 ± 102·1	42·6 ± 2·3	36·4 ± 2·1
Jari, marsh	297	263	88·6	22·9 ± 1·8	20·2 ± 1·5	510·0 ± 69·7	25·3 ± 1·7	23·5 ± 1·6
Jari, pool	237	134	56·5	15·8 ± 0·8	8·9 ± 1·4	263·7 ± 51·1	29·5 ± 2·0	17·8 ± 1·5
Arenal	193	121	62·7	9·7 ± 0·4	6·1 ± 0·7	186·5 ± 35·1	30·8 ± 2·3	19·3 ± 1·8
Turrialba	640	470	73·4	18·3 ± 0·5	13·4 ± 0·7	617·9 ± 62·5	43·2 ± 2·4	32·9 ± 2·1
Palo Verde	1218	934	76·7	5·3 ± 0·1	4·1 ± 0·1	229·9 ± 13·3	61·0 ± 1·8	43·2 ± 1·6
Aranjuez	370	5	1·4	6·7 ± 0·2	0·1 ± 0·04	0·9 ± 0·4	9·6 ± 0·4	0·9 ± 0·4

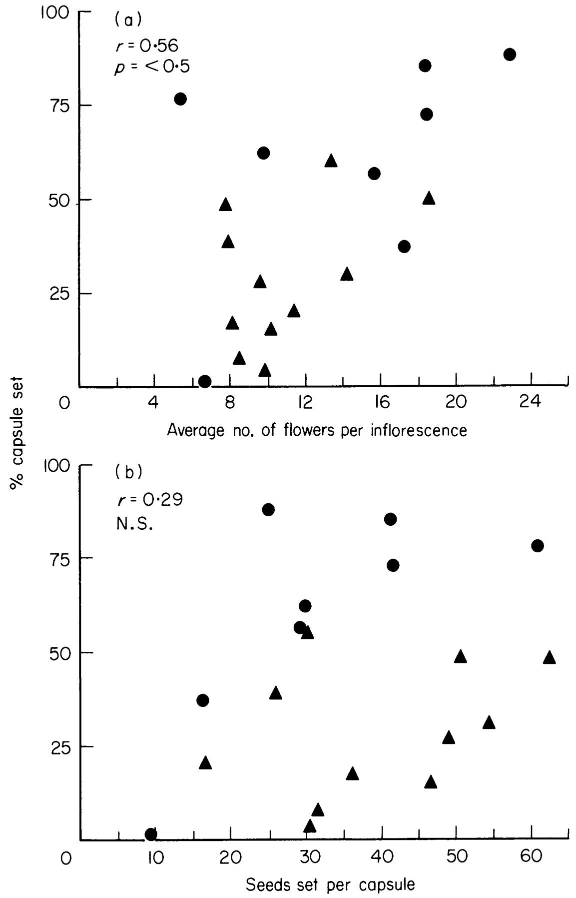

FIG. 1. The relationships between capsule production and (a) the number of flowers per inflorescence, (b) the number of seeds per capsule. ● tropical population, ▲ temperate population.

June and July. During the rest of the season, field and glasshouse pollinations gave near maximal capsule set (Fig. 2(a)). Throughout the season, average seed set per flower in the two controlled pollination treatments ranged from 152–189, with the exception of the glasshouse pollinated plants of July and August, which averaged 130·3 and 134·5 seeds per flower respectively (Fig. 2(b)). The cause of reduction in seed productivity is not known, but may be related to high temperatures (30–35 °C) in the glasshouse where pollinations were undertaken.

Open pollinated plants showed a substantial increase in capsule production during August (Fig. 2a). However, seed production was still only 19·0% of that obtained from field pollinated flowers. The seed fecundity of the population at Stockton reached a peak during September with 68·7% of the open pollinated flowers sampled producing capsules with an average of 40·8 seeds per flower. In October, capsule and seed production fell to levels similar to those obtained in August. Flowering declined at the end of October and in November very few flowers were available for sampling. It was possible to obtain data only for open pollinated flowers during that month. Seed production in November was substantially lower than in August, September and October.

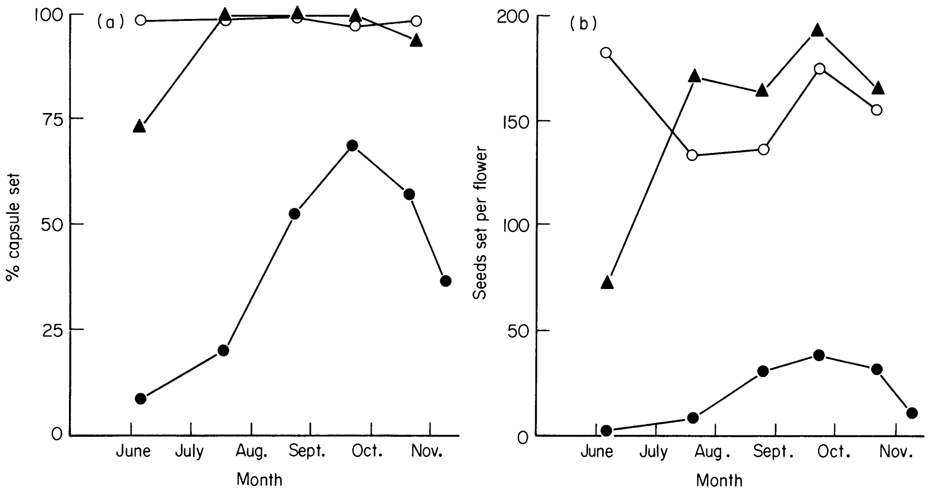

Fig. 2. Seasonal pattern of seed production in a population of *Eichhornia crassipes* at Stockton, California during 1976. (a) Capsule production of open, field and glasshouse pollinated flowers. (b) Seed set per flower of open, field and glasshouse pollinated flowers. ● open pollinated, ▲ field pollinated, ○ glasshouse pollinated.

Table 3. Open and artificial pollinations of *Eichhornia crassipes* at Stockton, California during the summer of 1976

Pollination	Total no. of flowers sampled	Total no. of flowers producing capsules	% capsule set	$\bar{x}$ seeds flower^{-1}	s.e.m.
Open pollination					
June	198	16	8·1	3·1	1·2
July	347	62	17·9	6·0	1·4
August	418	224	53·6	31·2	2·8
September	485	333	68·7	40·8	3·4
October	436	253	58·0	32·9	3·0
November	168	62	36·9	12·5	2·2
Field pollination					
June	119	86	72·3	74·1	9·0
July	242	242	100·0	168·1	5·7
August	178	178	100·0	163·8	6·5
September	225	225	100·0	188·7	9·3
October	265	253	95·5	159·1	5·8
Glasshouse pollination					
June	90	89	98·9	178·9	7·7
July	159	158	99·4	130·3	3·9
August	79	79	100·0	134·5	8·5
September	187	180	96·3	171·8	8·8
October	252	248	98·4	151·9	8·8

During June and July, no insects were observed visiting flowers of *E. crassipes* (Table 4). During August, honey bees (*Apis mellifera*) began visiting *E. crassipes* and for the rest of the flowering season they were the predominant insect visitors to flowers. Observations of the foraging behaviour of *A. mellifera* indicate that pollen and possibly nectar were obtained from flowers of *E. crassipes*. Although bees tended to visit most flowers on an inflorescence, three different foraging patterns were observed. Individual bees tended to

Table 4. Sample dates and details of climate, flowering and insect activity at a population of *Eichhornia crassipes* at Stockton, California, 1976

	Climate			
Pollination	Day of pollination	Monthly average	Time of flower opening on pollination day	Insect activity during month
4 June	Warm, cloudy Max. 28·9 °C Min. 10·6 °C	Av. max. 31·3 °C Av. min. 13·9 °C R.H. 23–63%	12.00–13.00 hours	Small numbers of *Apis mellifera* on *Ludwigia peploides*
18 July	Warm, sunny Max. 30·6 °C Min. 15·0 °C	Av. max. 33·9 °C Av. min. 15·9 °C R.H. 27–65%	09.30–10.00 hours	Small numbers of *Apis mellifera* on *Ludwigia peploides*
21 August	Warm, sunny Max. 30·6 °C Min. 17·8 °C	Av. max. 30·8 °C Av. min. 15·9 °C R.H. 31–67%	09.30–10.00 hours	Moderate numbers of *Apis mellifera* on *Eichhornia crassipes* and *Ludwigia peploides*
18 September	Warm, sunny Max. 32·8 °C Min. 14·4 °C	Av. max. 30·9 °C Av. min. 15·6 °C R.H. 36–75%	10.00–10.30 hours	Large numbers of *Apis mellifera* on *Eichhornia crassipes*
17 October	Warm, sunny Max. 29·4 °C Min. 10·0 °C	Av. max. 28·0 °C Av. min. 11·7 °C R.H. 32–74%	12.00–13.00 hours	Large numbers of *Apis mellifera* on *Eichhornia crassipes*.

forage in one manner only. The most frequent behaviour involved the bee hovering near and sometimes alighting on the long-level anthers in order to collect pollen. No nectar was collected and the likelihood of pollen being transferred to the mid-level stigmas was low. In the other methods of foraging, *A. mellifera* landed on either the nectar guide or on the mid-style. In these cases, bees collected pollen and probed for nectar. Only by the last method of foraging was *A. mellifera* effective as a pollinator of *E. crassipes*. A few small syrphid flies were observed collecting pollen from the long anther level; no flies were observed contacting the stigma.

Field germination

After 28 days, the four trays used in the germination test were found to contain 40, 47, 46 and 42 seedlings respectively. This demonstrates a high rate of seed germination (87·5%) and seedling establishment under field conditions.

DISCUSSION

The reproductive potential of *E. crassipes* coincides well with the expectations of Salisbury (1942) and Baker (1965) for colonizing plant species. Vegetative and sexual methods of reproduction occur and both are characterized by the potential for production of large numbers of individuals in a short period of time. In the Sudan, Batanouny & El-Fiky (1975) report that a single plant of *E. crassipes* can produce forty-three daughter rosettes in 50 days. Further, they estimate that clonal growth by these plants and their offspring would result in a total of 3 418 800 plants being produced over a 200 day period. Earlier studies by Penfound & Earle (1948) in Louisiana also report striking rates of clonal growth.

In addition, certain features of flowering and seed production enhance the reproductive potential of *E. crassipes*. Flowering may take place 10–15 weeks after germination, a relatively short period for a perennial species. An inflorescence with twenty flowers can produce over 3000 seeds and up to four inflorescences can be produced by a single rosette during a 21 day period (S. Barrett unpublished data). The flowering season lasts for 5–9 months in North America and large numbers of inflorescences are produced during spectacular periods of mass flowering. Despite these reproductive traits, which give *E. crassipes* an enormous potential for seed production, the majority of individuals in natural populations are probably produced by clonal growth.

Seed production occurred in all of the nineteen populations surveyed in this study, but seedlings were observed in only three of them. In these populations, seedlings occurred on saturated soil at the periphery of colonies. Most colonies of *E. crassipes* occurred as dense mats floating on deep water. In these circumstances, any seeds produced either sink to the bottom, being heavier than water, or accumulate in the organic debris of the mat. Low temperatures and light levels prevent seed germination in deep water and shading by dense foliage inhibits germination on mats of *E. crassipes* (Haigh 1936; Hitchcock *et al.* 1950). At the Stockton population, foliage of *E. crassipes* was cut back and 'safe sites' (Harper, Williams & Sagar 1965) in the form of trays with saturated soil were provided. This method resulted in the production of high levels of seed germination and seedling establishment during September on floating mats. These results indicate that climatic conditions in the San Joaquin delta of California, where *E. crassipes* reaches its northern limit (Bock 1968; Baker 1972), would allow sexual reproduction during some periods of the year if appropriate ecological conditions for germination and seedling establishment were available. The slough at Stockton has steep banks; saturated soil and shallow water are absent from the habitat.

The failure to observe seedlings in sixteen of the nineteen populations surveyed suggests that sexual reproduction is not occurring in them. In some populations, further evidence of the absence of sexual reproduction can be provided by observations of the types of style form present in the population and genetic analysis of this character. Studies of the inheritance of style form in plants obtained from Stockton and Jari (canal, marsh, and river) populations indicate that these plants are heterozygous for genes controlling style length (Barrett 1977a). Both mid- and long-styled forms segregated from self-pollinations of mid-styled plants from the Stockton population, and short- and long-styled forms were obtained from self-pollinations of short-styled plants from the Jari populations. If sexual reproduction was occurring in these populations, long-styled plants should be present. However, these four populations were monomorphic for style form.

Although limited sexual reproduction in *E. crassipes* appears to be largely a result of the absence of suitable ecological conditions for germination and establishment, low levels of seed production in many populations must also reduce opportunities for sexual reproduction. Moderate amounts of seed were produced in some populations sampled in this study. Nevertheless, the seed production of populations was substantially lower than that obtained in a controlled pollination programme with eight clones under glasshouse conditions (Barrett, 1980). Artificially pollinated flowers (n = 2546 flowers) gave 94·7% capsule set with an average of 143·3 seeds per capsule. In contrast, of the 7750 flowers sampled from all natural populations surveyed, 45·9% produced capsules with an average of 44·2 seeds per capsule. The large disparity between open and artificially pollinated flowers suggests that fecundity under field conditions is probably sub-maximal in many populations of *E. crassipes*. Results from the study at Stockton also support this conclusion.

Some insight into the causes behind the low fecundity of natural populations can be gained from a comparison of capsule and seed production in tropical and temperate populations. Percentage capsule set was twice as great in the tropics as in temperate populations. This is probably due to higher levels of insect visitation to flowers of *E. crassipes* in the New World tropics. Observations of insect activity in the two regions support this view. With the exception of the Stockton and Gibson populations, where large numbers of *Apis mellifera* were observed, very few insects were seen visiting flowers of *E. crassipes* in North American populations. Penfound & Earle (1948) commented on the paucity of insect visitors to flowers of *E. crassipes* in the southeastern U.S.A. Where insects were observed in tropical populations they were represented by large numbers of individuals. Since *E. crassipes* is native to the New World tropics, it would seem reasonable to expect a larger and more highly adapted pollinator fauna there than in North America where the species was introduced less than a century ago. The difference in seed production between the two regions may also be associated with a more favourable environment for fertilization and seed development in tropical regions.

Seasonal variations in pollinator activity may influence the amount of seed produced at certain times of the year in some regions. The flowering season of *E. crassipes* at Stockton lasts from the end of May to the beginning of November. During this period, levels of seed production changed markedly, low seed production was recorded at the beginning and end of the season, and peak seed set occurred during September. Data from field pollinations and observations of insect activity indicate that the seed fecundity of the Stockton population is largely determined by the foraging activity of honey bees (*Apis mellifera*) in the community. In June and July no insects were observed visiting flowers of *E. crassipes*. The small amounts of seed produced by the population during these months probably resulted from autogamy (Barrett 1979). During August, September and October, moderate to large numbers of honey bees visited flowers of *E. crassipes* to collect pollen and nectar, and seed production increased substantially compared with the early part of the season.

Ludwigia peploides is the only other entomophilous plant to occur to any extent in the community at Stockton. The species has large, showy, yellow flowers which are produced from early May to mid September. Large floating mats of *E. crassipes* and *L. peploides* cover most of the open water in the slough. During June and July, honey bee activity was confined to *L. peploides* despite the presence of flowers of *E. crassipes*. However, in August, bees were observed visiting both species, although individual bees generally confined their foraging activity to one species only. Similar patterns of honey bee foraging involving species constancy are reported elsewhere (Bateman 1951). During September and October honey bees were observed only on flowers of *E. crassipes*. During August and September the size of floating populations, and hence the number of inflorescences of *E. crassipes*, increased substantially as a result of clonal growth, whereas in *L. peploides* blooming declined during this period. It is possible that the change in patterns of insect visitation from *L. peploides* to *E. crassipes* during mid summer may be related to the flowering phenology of the two species. Whatever the cause of changes in pollinator preference, it is clear that the foraging behaviour of the honey bee largely determines the seasonal pattern of seed production of *E. crassipes* at Stockton.

These studies indicate that populations of *E. crassipes* can produce large quantities of seed. Furthermore, where warm, shallow water or saturated soil are present, seed germination and seedling establishment can occur. Current management techniques employed for aquatic weed control in various parts of the world (e.g. southeastern U.S.A.) include the removal of water from infested lakes and reservoirs during certain periods of the year. The draining of these areas results in the destruction of vegetative parts through desiccation. However, these practices also provide an opportunity for seed germination and the establishment of seedlings of *E. crassipes*, particularly if rains allow the soil to remain wet during the drainage period. Large numbers of seedlings are produced annually following the practice in Louisiana and Florida.

Future control measures for *E. crassipes* should take into account the fact that seed is usually produced in natural populations. If suitable conditions for seed germination and seedling establishment occur, sexual reproduction could be a potential problem resulting in the reinfestation of cleared areas.

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