Floral traits in relation to breeding system in *Emex australis* Steinh.

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***Emex australis* Steinh. is a monoecious winter annual which has assumed the status of an obnoxious weed in some countries. In India, there are three reports on its occurrence which date back to the 1980s. Since then nothing has been reported about its life history, spread and control. Plants bear male and female sexes in separate flowers. Being axillary, the male flowers are aggregated in a raceme whereas female are solitary borne in clusters of 4–6 below the male. Small size, herbaceous nature, structure and arrangement of flowers favour self-pollination. However, at a closer look a number of evidences such as protandry, male-biased sex ratio, high P/O ratio and wind pollination indicate cross-pollination. The species, therefore, exhibits facultative xenogamy. This conclusion is supported by the data on pollen–ovule and sex-allocation ratios, results of pollination experiments and reproductive outputs thereof.**

Keywords: *Emex australis*, facultative xenogamy, male : female biomass, P/O ratio, reproductive output, wind pollination.

EMEX belonging to the family Polygonaceae is a small tropical genus represented by only two monoecious species; *E. australis* Steinh. and *E. spinosa* (L.) Campd[1]. *E. australis*, a native of South Africa[2], is widespread in distribution having assumed an aggressive nature only in South Africa and Australia. Consequently, the literature is flooded with extensive studies carried out in those regions[3–11]. In India, the genus is distributed very scarcely. There are only three reports on its occurrence, two on *E. spinosa*[12,13] and one on *E. australis*[14]. Except for these three reports, no information is available on the breeding and meiotic systems, seed-to-seed cycle, spread and control of the genus in India even though the reports date back to the 1980s. Of the two species, *E. australis* grows luxuriantly at many places in and around Jammu district and is likely to spread to larger areas. During our collection trips, we have noticed these plants growing in groups in those localities where they were previously not found. Even in our campus (University of Jammu), the plants which used to grow in two to three patches are now forming small, semi-continuous belts. By extending its distribution ranges, it is likely to attain obnoxious status in near future. This fear is based upon the plant's ability to grow fast, produce ample fruit and seed[15]. Fruits are hardy, three-spined having highly dormant seeds which can persist for as long as 8 years in soil[7]. Data on its spread, aggressiveness and reproductive efficiency therefore need to be collected and consolidated first, and then appropriate remedial measures sought. The main objective of this study was to evaluate the reproductive potential of this species by studying its breeding system.

Plants of *E. australis* Steinh. form dense populations in the wild from December to May at Jammu when diurnal temperature fluctuates between 20°C and 40°C and the relative humidity ranges between 95% and 56%. Plant body is initially a rosette of leaves which later on differentiates shoots at the base. Shoots are prostrate, dichotomously branched and grow indeterminately until the end of the season when their terminal ends start turning brown (Figure 1 *a*). From the prostrate shoots, arise subsequent branches which grow in a semi-erect manner away from the ground.

The plants were collected from two sites in the University of Jammu Campus. Separated by a distance of about 1 km, the two locations vary in plant density, soil type and intensity of light. Plants at both these sites were exposed to different degrees of trampling and clearing. Seedlings ($n = 60$) at 3–4 leaf stage were uprooted and transplanted in the experimental beds (5×11 sq. ft) of the botanic garden at the university during December 2006. All the 60 seedlings survived, adapted well to the garden conditions and differentiated more leaves within a month of transplantation. Flowering of the plants so raised commenced in the first week of January and continued till May. Of these 60 plants, 20 served as control for fruit set and the remaining 40 were used to generate data on floral morphology, phenology and pollination.

The two populations that were studied differ in all morphological features in the field (natural) conditions. However, when they were transplanted to the experimental beds, the differences in the morphology expected on the basis of soil type and different light availability became less and were not statistically significant [$t_{(18)} = 1.47$; $p > 0.01$]. Therefore, the information collected on the two populations was pooled.

Fifteen mature male and female flowers ($n = 60$ each) randomly collected per day were examined under a stereomicroscope (Olympus OIC) and the different floral parts were counted. And their morphometry was carried out with calibrated ocular and stage micrometres using a compound microscope (Olympus OIC).

The sex ratio was calculated according to Willson[16] from 20 plants at two levels (branch and plant) using the formula

$$\frac{\text{Av. no. of male flowers per inf.} \times \text{Av. no. of inf. per branch (or plant)}}{\text{Av. no. of female flowers per branch (or plant)}}$$

where, Av., average; no., number; inf., inflorescence.

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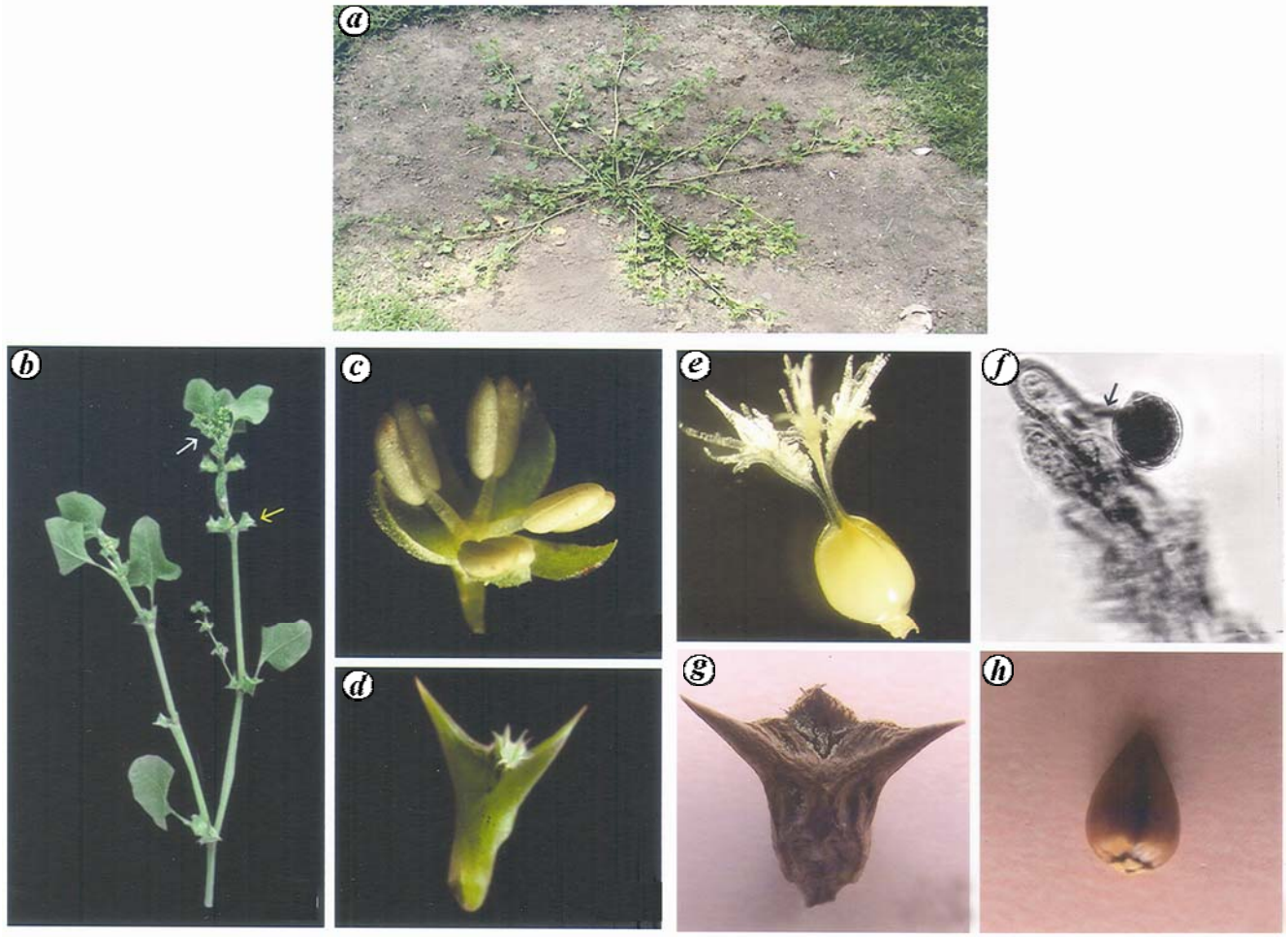

Figure 1. *Emex australis*. ***a***, A single plant showing prostrate habit. ***b***, A flowering twig showing arrangement of male (white arrow) and female (yellow arrow) flowers. Stereophotomicrographs of a male flower (***c***) and a female flower (***d***). ***e***, An excised pistil with three feathery stigmatic lobes. ***f***, Photomicrographs of germinating pollen grain (see a long pollen tube entering stigmatic papilla). ***g***, Mature fruit and ***h***, seed.

Time of anthesis and anther dehiscence was recorded from 60 randomly tagged flowers. Stigma receptivity was checked by bagging and manually pollinating 20 unopened flowers of different ages and their microscopic examination at timely intervals to record pollen germination.

Pollen (P) and ovule (O) counts were estimated by the method given in Kaul *et al.*[17]. In *E. australis*, pollen count was calculated at different hierarchical levels of the plant, viz. inflorescence, branch and plant. Pollen count at the level of inflorescence was calculated by multiplying the averages of number of pollen grains per flower and number of flowers per inflorescence. Similarly, the pollen count at branch and plant levels was calculated by multiplying pollen grains per inflorescence with the average number of inflorescences per branch and per plant respectively.

As *E. australis* is monoecious, the P/O ratio was calculated by dividing the number of pollen grains per male flower with the number of ovules per female flower[18]. The female flowers are invariably uniovulate. Thus, the P/O ratio per flower is equivalent to the pollen output of male flowers. However, as the number of female flowers per branch and plant varies, it leads to a difference in the number of ovules (and hence P/O ratio) per branch and per plant. Therefore, P/O ratio at different hierarchical levels was also calculated. This bears a direct relationship to the number of pollen grains available to a branch and/or plant for siring the ovules of its own female flowers.

To determine the extent of resources expended on male and female functions, the dry biomass method was applied[17,19]. For this purpose, mature pre-anthesis floral buds, male as well as female, were collected in lots of 10 (n = 10 lots), and separated into tepals, stamens and pistils; oven-dried at 60°C for 24 h and weighed on an electronic balance (Ohyo MR-200) to obtain dry biomass estimates of individual floral parts. Sex allocation ratio (dry wt of androecium/dry wt of gynoecium) was calculated with an aim to see how far it complements P/O ratio in determining the breeding system of the species. Male–female allocation ratio at the level of plant was calculated as follows.

$$\text{Plant} = \frac{A \times B \times C}{D \times E},$$

where A, average number of ♂ inflorescences/plant; B, average number of ♂ flowers/inflorescence; C, mean dry wt of ♂ flower; D, average number of ♀ flowers/plant, and E, mean dry wt of ♀ flower.

The two types of experiments undertaken to study the pollination system of the plant were: (i) Hanging slide experiments to ascertain the role of wind in affecting pollination. The slides smeared with Mayer's albumen (filtered egg albumen and glycerine in the ratio of 1 : 1 and a pinch of sodium salicylate) were suspended from 20 cm long T-shaped stands at a distance of 25 and 50 cm from plants in experimental beds for 24 h. These slides were then removed, microscopically examined and scored over an area of 18.75 sq. cm for trapped pollen grains of *E. australis*. (ii) Bagging entire twigs and denying access to insect visitors. Twigs ($n = 20$) were enclosed in bags made of net (pore size = 0.5 mm) to restrict the access of insects to anthers and stigma and record fruit set.

To determine the type of breeding system operative in study species, flowers were subjected to four pollination treatments.

Unassisted selfing: Bagging entire twigs ($n = 20$) with butter paper bags to estimate unassisted selfing or geitonogamy.

Open pollination: Of the 20 plants which were left undisturbed, one twig per plant was tagged before anthesis and left for pollination to take place as it does in nature.

Apomixis: Twigs rendered female by removing all male flowers were denied pollination by bagging them with butter paper bags to check for non-pseudogamous apomixis.

Manual pollination experiments: Fresh twigs rendered female as given above were pollinated with either self (pollen from the same plant) or cross (pollen collected from other plants of a different population) pollen.

For fruit set, a single branch at maturity was collected randomly from each of the 10 plants of both the populations and the number of female flowers (if any) and fruits counted. Fruit set was determined separately for the plants raised in experimental beds in the same way. As the fruit and seed are shed as a single unit, fruit set is equivalent to seed set.

One-way analysis of variance (ANOVA)[20] was applied to determine the effect of experimental and non-experimental (natural) conditions on percentage of fruit set and different pollination treatments on percentage of fruit set. This was done to see if anthropogenic stress in terms of trampling and deweeding plays a significant role, in reducing fruit/seed set in non-experimental conditions, and whether type of pollen impacts reproductive efficiency.

Self-compatibility and auto-fertility indices were also calculated following Jacquemart[21] and Kaul and Koul[22]. Self-compatibility refers to the ability of the plant to produce embryos through self-pollination relative to that by out-crossing and auto-fertility measures the ability of flowers to practise autogamy without the intervention of pollinators. A value of 1 indicates complete self-compatibilty and values greater than 0.75 are indicative of partial self-compatibility[21].

Plants of *E. australis* are monoecious bearing small, herbaceous, unisexual (staminate and pistillate) and actinomorphic flowers devoid of any nectar and odour, a feature characteristic of many wind pollinated/self-pollinated taxa[23]. Flowers are borne at two sites; at the base and on secondary and tertiary shoots. Both the flower types are axillary, male in the form of an inflorescence and female solitary in clusters of 4–6 (Figure 1 *b*, Table 1). The number of flowers differentiating at the two sites varies; those at the base are almost half less than those on the cauline stems. This difference is more pronounced in the male flowers. The sex ratio (male to female flowers) is therefore very high being male-biased both at branch and plant levels (4♂ : 1♀) (Table 2). This male-biased sex ratio favours cross-pollination. Male flowers are pedicellate consisting of a green perianth enclosing 4–5 stamens. Each stamen consists of a large dull yellow anther held on a small delicate filament (Figure 1 *c*, Table 3). Female flowers although green are sub-sessile and larger than male (Figure 1 *d*, Table 3). The gynoecium comprises a feathery, trifid stigma, reduced style and a white trigonous ovary (Figure 1 *e*, Table 3). The ovary is unilocular with a single basal and orthotropous ovule. In *E. australis*, male

Table 1. Details of floral and fruit count per branch and per plant

Character	Mean ± SE (range)
No. of ♂ inflorescences per	
Branch	4.7 ± 0.72 (1–11.4)
Plant	24.7 ± 4.58 (1–80)
No. of ♂ flowers per inflorescence	
Aerial	26.02 ± 1.075 (10–42)
Basal	16.5 ± 0.46 (12–24)
No. of ♀ flowers per	
Branch	20.3 ± 2.28 (11.7–42.5)
Plant	100.7 ± 14.63 (35–277)
No. of aerial achenes per	
Branch	13.5 ± 1.76 (1.7–28.7)
Plant	65.9 ± 10.19 (5–201)
No. of basal achenes per plant	6.9 ± 0.53 (3–10)

Table 2. Comparative male and female investment

Character	Flower	Plant
Pollen count	11,968	7,889,497
Ovule count	1	173.4
Pollen–ovule ratio	11,968	45,472.6
Sex ratio	–	3.7
Sex allocation ratio	1.2	4.2

Table 3. Morphological details of male and female flowers

Floral feature	Mean ± SE
Male flower	
Tepal no. per flower	4.4 ± 0.06 (3–5)
Pedicel length	2.27 ± 0.09 (0.9–4.12)
Large tepal	
Length	2.51 ± 0.06 (1.76–4.03)
Width	1.08 ± 0.02 (0.69–1.37)
Small tepal	
Length	2.18 ± 0.04 (1.5–3.1)
Width	0.83 ± 0.07 (0.39–1.33)
No. of anthers per flower	4.6 ± 0.09 (3–6)
Filament length	0.63 ± 0.02 (0.39–1.2)
Anther	
Length	1.25 ± 0.02 (1.03–1.59)
Width	0.95 ± 0.02 (0.56–1.45)
Female flower	
Pedicel length	1.4 ± 0.06 (0.5–2.0)
Perianth length	6.9 ± 0.08 (5.0–8.0)
Stigma length	2.1 ± 0.06 (1.5–3.0)
Ovary length	1.8 ± 0.06 (1.0–2.0)

n = 60, measurements in mm.

flowers are regularly placed above the female with a spatial separation of 3.0 cm (raceme length at maturity 2.9 cm). This spatial arrangement of sexes allows self-pollen deposition on the stigmas. Similar condition is found in *Zea mays*[24] and some grasses. The separation of the sexes in space is further accentuated by their temporal separation.

Flowering in *E. australis* starts during the first week of December. Flowering in those plants transplanted in the botanical garden of Jammu University, is delayed by one month. Basal flowers are first to differentiate followed three weeks later by aerial cauline flowers. Male flowers open first in acropetal succession along a raceme. A single flower takes about 22 h and the entire inflorescence 18.9 days on an average to open completely. The anthers dehisce along a longitudinal slit, usually after but sometimes in synchrony with anthesis. An individual anther takes 5 min to extrude all the pollen grains that are dispersed by short wind currents. Anthers dehisce in two groups of two each – one group dehisces 1.5–2 h before the second group. Within each group, the two anthers dehisce in quick succession.

Female flowers at the base appear after the dehiscence of 4–7 male flowers, whereas on the secondary and tertiary shoots female flowers appear 5–10 days after the emergence of first male flower. In female flowers, the perianth is strongly adpressed to the ovary so that anthesis is marked by the emergence of stigmatic lobes. Results of manual pollination experiments reveal that stigmatic lobes are receptive even when only their tips have extruded such that anthesis, i.e. emergence is accompanied with receptivity (Figure 1 *f*). Peak receptivity is found when stigmatic lobes have extruded completely and flowers of half the male inflorescence have already dehisced[25]. These events lead to effective temporal separation and hence pronounced protandry which ensures cross-pollination for a brief and initial period of flowering. Thereafter, the two sexual phases overlap and become simultaneous increasing the chances of self-pollination[25]. Thus floral structure, placement of male distal to female, male-biased sex ratio and floral phenology supports self- as well as cross-pollination in the species under study.

Evidences in favour of both the pollination types operative in this species have been recorded. Pollen output of different anthers of a single flower does not vary (2602 ± 112.01). It, however, varies among the flowers of a plant as well as between different plants of a population. Plants are high pollen producers with an average P/O ratio of 43303 : 1 and 45473 : 1 at branch and plant levels respectively (Table 2). These figures are quite high and belong to the xenogamous category of Cruden[18].

Similarly, the dry weight of accessory and essential parts of male and female flowers varies. The ratio between dry weight of androecium and gynoecium averages 1.21 on a one-to-one flower basis. At the other hierarchical (branch and plant) levels of the plant, the ratio is highly and consistently male-biased (Table 2). The increase in magnitude at the branch and plant levels is understandable in view of the high male-biased (4♂ : 1♀) floral sex ratio and its wind-pollinated nature. Sex allocation and P/O ratios support these observations.

Further hanging slide experiments confirm the incidence of wind pollination in this species. The slides smeared with Mayer's albumen and hung around the plants at distances of 25 and 50 cm, when scanned under microscope, were found to carry considerable amount of *E. australis* pollen (66.68 ± 7.73 (35–188) and 44.4 ± 2.39 (33–54) respectively). The possibility of pollinators causing pollination has been ruled out completely as flowers enclosed in bags made of net and denied access to insects were capable of setting good fruit ($\bar{x}$ = 84.2%). This means that flowers are getting pollinated either by self- or by cross-pollen made available by the wind currents. Hence, in conclusion, production of inconspicuous, colourless, odourless and nectar-less flowers, copious quantity of small, dry- and smooth-walled pollen grains and feathery extruded stigma well above the level of perianth and uniovulate condition specific to *E. australis* make it anemophilous.

The results of the different pollination experiments augment the occurrence of both self- (geitonogamy) and cross-fertilization (xenogamy) in this species indicating *E. australis* to be facultative xenogamous. Fruit set resulted in all the four pollination experiments (unassisted selfing ($\bar{x}$ = 57.9%), open pollination ($\bar{x}$ = 63.4%), manual self-pollination ($\bar{x}$ = 83.05%) and manual cross-pollination ($\bar{x}$ = 76.43%)), being highest in manual self-pollination. Despite these differences, fruit set did not vary significantly following manual self and manual cross-

pollination treatments ($F_{(1,24)} = 0.63$; $p > 0.01$). Similarly, the fruit set did not vary significantly in unassisted selfing and open pollination ($F_{(1,18)} = 0.07$; $p > 0.01$). However, results of one-way ANOVA applied to all the four treatments, reveal the differences to be significant indicating the importance of pollen type in causing fruit set ($F_{(3,24)} = 4.38$; $p < 0.01$). No fruit was ever recorded in emasculated and bagged twigs ruling out the possibility of non-pseudogamous apomixis.

Self-compatibility and auto-fertility indices on fruit set exceed 1 and 0.75 respectively, confirming *E. australis* to be self-compatible and capable of setting fruit in the absence of pollinating agents.

Fruits are small, one-seeded, brown, indehiscent achenes with very hard persistent perianth (Figure 1 *g*). Fruit set under experimental and non-experimental conditions differ significantly ($F_{(1,18)} = 25.99$; $p < 0.01$ and $t_{(18)} = 1.78$; $p < 0.01$). In nature, i.e. under non-experimental conditions, fruit set per branch averages 32.5%. It is likely to be an underestimate on account of several reasons which include trampling, deweeding and fruit fall in nature on its own. Under experimental conditions, fruit set following unassisted selfing is 57.9% and on open pollination averages 63.4%. Less fruit set in the former is expected because the flowers are monoecious, separated in time and space, and pollination is subject to the falling of pollen on to the extruded stigmas below.

As the female flowers are uniovulate, the seed set is commensurate with fruit set. Seed set per branch is, therefore, 60.6% while that per fruit is 100%. Seeds, although small, trigonous with a broad base and pointed tips (Figure 1 *h*) are never shed independently. In contrast, fruit and seed disperse as a single unit. Dispersal is largely brought about by humans (pers. obs.) and to some extent by animals[15]. Seeds exhibit maximum germination and emergence during the first autumn. Thereafter, germination declines[10] and seeds enter into a period of dormancy referred to as secondary dormancy by Panetta and Randall[26], which may extend up to 8 years[7]. This leads to the formation of persistent seed banks in the soil[27] making it increasingly difficult to eradicate the weed completely.

Thus, facultative xenogamy and good reproductive efficiency coupled with prolonged seed dormancy are some of the factors responsible for the spread and aggressiveness of this species[15,28,29]. Although different chemical and biological methods are available for controlling its growth and spread[30–36], none is sufficient to eradicate the weed completely. We recommend manual de-weeding of the plant at the seedling stage.

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