# Pollination Ecology of the Endangered Eremostachys superba Royle ex Benth. (Labiatae)

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ABSTRACT: Pollination ecology of Eremostachys superba Royle ex Benth. (Labiatae) from the Siwaliks of Uttar Pradesh, India, is discussed. The low population strength was found to be responsible for pollinator limitation in the species. This species is adapted for cross-pollination by oligolectic pollinivorous bees, Nomia rustica West and Ceratina heiroglyphica Sm. of the order Hymenoptera. The bees were pollinivorous and eutropic in nature and exhibited floral fidelity behaviour while foraging for pollen. Their visitations to the flowers were ethodynamic, but scanty. The flowers, in turn, were oligophilic and pollination mechanism was sternotribic. A specialized plant-pollinator co-adaptation existed in this critically endangered species which is exposed to a high reproductive bottleneck.

KEY WORDS: Eremostachys superba, Ethodynamic, Monolectic oligophilic, Pollination ecology, Pollinators, Sternotribic.

### INTRODUCTION

The intimate relationship between insects and flowers is synagonistic and is controlled and conditioned by a number of parameters such as the floral modifications, both in colour and form, quality and quantity of floral rewards, population size and flowering phenology of the plant; foraging range, strength of population, availability within plant range and forage storing propensity and capacity of the pollinators. The study of pollination ecology therefore throws light, not only on the mode of pollination, but also on any irregularity in the pollination efficacy of the species. The flowers may be specialized for pollination by different groups of insects (polyphilic/allophilic) or by a specific pollinator (oligophilic / euphilic) (Faegri & Pijl, 1979; Renner & Feil, 1993). Oligophilic flowers offer special rewards (Simpson & Neff, 1981) to their pollinators and possess such morphological adaptations that permit only one or two specific insect species to gain access to these rewards.

The genus *Eremostachys* Bunge (Labiatae) with 27 species is mostly confined to Western and Southern Asiatic regions (Hooker, 1885). *E. superba* Royle *ex* Benth. is the only species in Indian region, which is in a critically endangered state and is restricted to only one locality near Dehra Dun, in Uttar Pradesh (Babu, 1977; Rao & Garg, 1994). The population of the species comprises only 33 ( $\pm$  10) plants. Inspite of a great variety of adaptations in the flower structure for successful entomophilous pollination the population

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size of the species has dwindled to reach extinction. A study on the pollination ecology of this species was therefore undertaken with the aim of ascertaining any abnormality, malfunctioning or failure in pollination efficiency of the species which may serve as a barrier in its multiplication because pollination is an integral stage in the reproductive cycle of plants leading to seed set and multiplication.

## MATERIALS AND METHODS

Four plants of *E. superba* from the natural habitat were grown in the experimental garden at NBRI, Lucknow, in 1993, for *ex situ* study on pollination ecology (The narrow population size did not permit uprooting of more individuals from the natural habitat). Observations were made and data recorded on the nature of the plants under *in situ* and *ex situ* conditions. Flower morphology, phenology and measurements of floral parts were recorded to study plant-pollinator co-adaptation. Phenological events were recorded from opening of first bud till withering of the last flower (13th to 27th March, 1994) at NBRI, Lucknow. Similar observations were made on the flowers under natural conditions in Dehra Dun (from 23rd to 26th March) in the same flowering season.

Visual observations were made on (i) anthesis (ii) insect visits (iii) floral rewards to the pollinators and behaviour of these pollinators on flowers to access these rewards. Time interval and diurnal variations of the insect visitations on sunny and cloudy days were recorded to observe their working efficiency under different light, temperature and moisture conditions. The number of insects working on the flowers and the number of visits made by them at a time, in a day and also during the entire flowering period were also recorded. These observations were made over a stretch of 8 hours per day from 8:00 AM till 5:00 PM both in the experimental garden as well as in the natural habitat.

One each of all kinds of insects that visited the flowers were trapped for identification. Out of these, only two species of insects appeared to be active pollinators, both in the experimental garden as well as in the natural habitat. Pollen morphology of the species was studied. Pollen adhering to the insect's body parts were observed under compound microscope and identified. The pollen collecting apparatus of the pollinators were also studied in detail under Scanning Electron Microscope (SEM) and their pollen contents were examined. For these studies pollen were brushed from the insect's body in glycerine jelly in a drop of safranin on slides and observed under light microscope. Some pollen were also dusted and mounted on brass specimen stubs for SEM photographs. The pollen content per anther and percentage pollen fertility was also recorded. For this purpose, each anther was cut into four equal parts; one part was gently squeezed in about 20 drops of glycerine. One drop was examined under light microscope and pollen contained in the drop were counted. Total pollen content per anther was then calculated. For pollen fertility test, fresh pollen from anther were directly dusted in one drop of acetocarmine (1%) and the total number of stained and unstained pollen were counted.

Seed set under natural pollination was observed to estimate the pollination efficacy of the species.

### RESULTS

E. superba comes to bloom during March when the temperature ranges between 30-32 °C. The plants, both at the experimental garden and in the natural habitat produced basal rosette of leaves and one (or sometimes two) tall, erect, unbranched flowering stalk reaching up to 110 - 160 cm, which terminated in 25 - 30 cm long spikes. The spikes bore successive whorls of 10 flowers arranged in opposite verticillasters of 5 flowers on each side in the axil of a densely woolly bract. The spikes of the ex situ plants were bigger and produced 80 to 100 flowers each, whereas those under in situ conditions were smaller with ca. 30 - 60 flowers in ca. 15 - 25 cm long spikes. The spikes when in bloom were remarkably conspicuous with bright yellow attractive flowers. The sequence of flower maturation was acropetal in the spike and simultaneous in the opposite bracts of each whorl. The central flowers of the whorls matured first with the succeeding side ones (in centrifugal order).

### Flower morphology

Flowers of *E. superba* were zygomorphic, hermaphrodite, aggregated in dense whorls (of 8-10 flowers each) in terminal woolly spikes. The vegetative floral parts were hairy, calyx subcampanulate, broadly 5-lobed, truncate, mouth densely woolly, *ca.* 2 cm long; corolla monopetalous, hypogynous, bright yellow, corolla tube included, 1.4 cm long, 2-lipped, upper lip bi-lobed, erect, hooded, bearded within, lower lip broader, 3-lobed, mid lobe largest. The stamens inserted on the corolla tube, four, didynamous, all perfect, ascending, lower pair largest; upper filaments fimbriate at the base; anthers conniving, cells divaricate; ovary superior, syncarpous, carpels 2, each deeply lobed appearing as four, style simple, 4 cm long, gynobasic (arising from the inner base of the carpel lobes), stigma bifid, thin, delicate (Fig. 1 A-E).

### Phenology

The first flower opened on 14th March and flowering persisted till 27th March of the season. The flowering peak lasted from 19th to 22nd March when more than 70 % flowers were in bloom at a time (Fig. 2). The flowers bloomed for a short span of two to three days after which the zygomorphic, bright yellow corolla started withering and abscised by the 5th day of opening, leaving behind the persistent densely woolly calyx containing the gynoecium which ripens into nutlets.

The anthers dehisced longitudinally within the mature buds prior to opening. Anther dehiscence depended upon the time of flower maturation, which varied with variations in the weather conditions. The flowers opened at a temperature of about 25°C. It was further observed that during days of dry sunny weather the flowers opened around 0930 - 1000 hours while on moist cloudy days they opened around 1130 - 1200 hours. Anthesis occurred simultaneous to flower opening. Pollen production was abundant in the form of moist cream coloured pollen. The pollen adhered loosely to the dehisced anther surface and partly fell on the inner surface of the lower corolla lip which sometimes came in contact with the stigmatic surface during high wind current bringing about some amount of self-pollination.

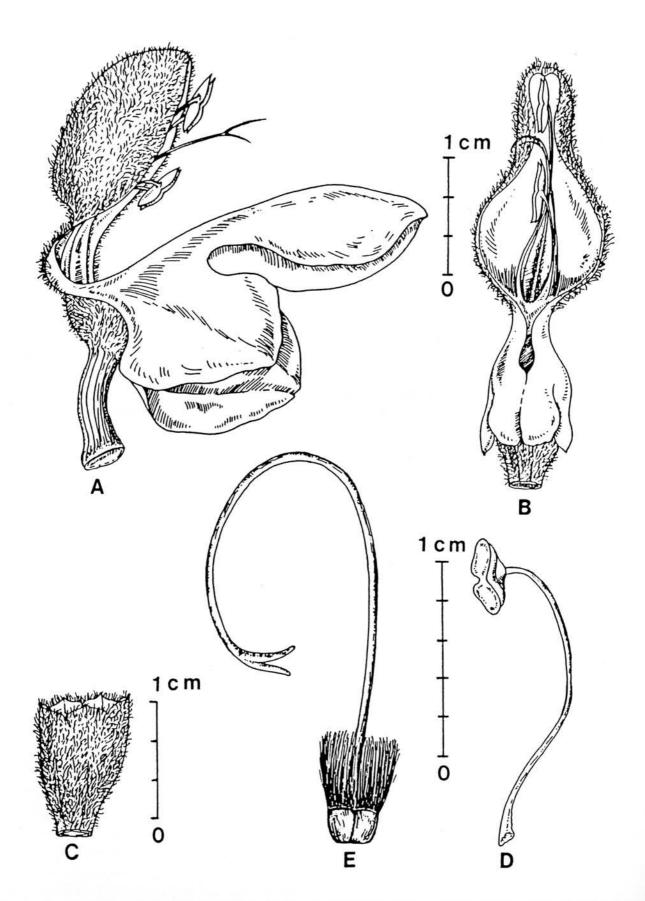


Fig. 1. Flower of *E. superba* and its different parts. A: lateral view showing the arrangement of anthers. B: front view. C: calyx, D: stamen. E: gynoecium showing gynobasic style.

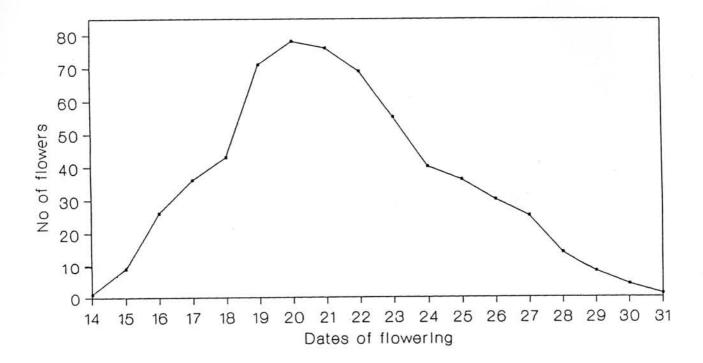


Fig. 2. Floral phenology in E. superba showing the daily floral succession.

### **Insect visits**

Initially, a number of insects were seen to visit the flowers of *E. superba* both in the natural habitat as well as in the experimental garden. These insects belonged to various orders such as Hymenoptera (Halictidae: *Nomia rustica* West.; Apidae: *Ceratina heiroglyphica* Sm.); Diptera (Syrphidae: *Syrphus*) and Hemiptera (Jassidae, Aphididae). Of these, only the two bee species *N. rustica* and *C. heiroglyphica* were observed to be effective pollinators both in the experimental garden and in the natural habitat. The bees repeatedly and actively foraged on the *Eremostachys* flowers. Significantly, their visits were specifically directed towards these flowers neglecting all other, often more attractive and rewarding flowers in vicinity such as Rose, Sunflower etc.

#### Floral rewards

A symbiotic relationship existed between E. superba and its vectors. The bright yellow flowers on the tall conspicuous spikes attract the vectors. The nectarless flowers offer only pollen as rewards to the foragers which in turn aid the plants in transfer of pollen to their female counterparts in the process of pollination. The pollinating bees  $(N. rustica \text{ and } C. heiroglyphica})$  when observed under microscope were found to be dusted with pollen of E. superba. The grains were found to be entangled all over their body hairs and densely packed in the special pollen collecting apparatus of their hind legs. The pollen collecting apparatus consisted of two spur-like projections forming 'V' shaped structure in the first tarsal joint of the bees' hind leg. These projections were surrounded by densely packed bristle-like hairs which entangle the pollen. Morphologically the pollen are 3-colpate with reticulate surface (Fig. 3). The mean pollen production was as high as 33,600 (SD=300) per anther (1,44,560; SD=1200) per flower). Pollen fertility assessed was up to 95%.

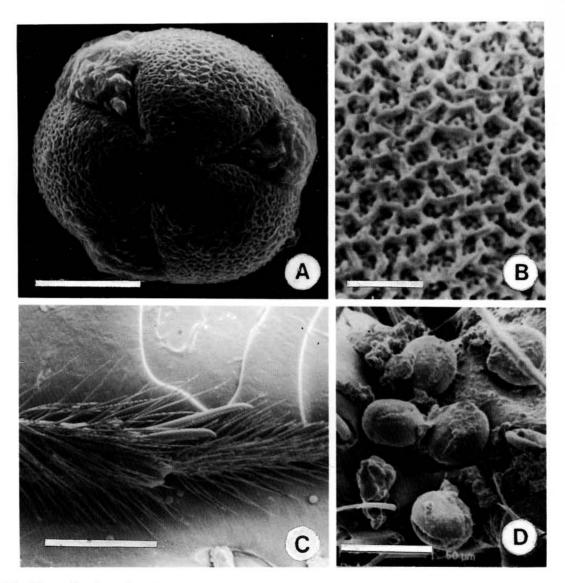


Fig. 3. SEM of A: pollen in polar view showing three colpate condition. B: pollen surface enlarged to show the reticulum. C: bee's (*N. rustica*) hind leg showing pollen collecting apparatus. D: pollen trapped in the setae of the bee's hind leg. Scale lines = A:  $10 \mu m$ , B:  $2 \mu m$ , C: 0.5 mm, D:  $50 \mu m$ .

#### Pollinator behaviour

The pollinator behaviour on the flower depends upon the flower structure and position of its essential organs in relation to the insect's body and mouth parts. The method of pollen collection by the bees was observed to be quite unique and similar for both species. The bee followed a definite pathway on the flowers to gain access to the anthers. This involved the following process: (i) The bee alighted on the lower lip of the corolla (Fig 4A), (ii) crawled inwards towards the corolla tube up to such a distance from where it can cling to the base of the stamens by raising its anterior pair of legs while still resting on the lower corolla lip, (iii) climbed up the stamen in an upside down position (Fig. 4B), and (iv) crawled up to the end of the filament till it reached the lower pair of anthers (Fig. 4C).

Once the bee reached the anthers, it completly abandoned the filament to hang upside down on the lower pair of anthers with the help of its three pairs of legs. Once in firm position, it freed the anterior pair of legs and mouth parts and scraped pollen from the upper pair of anthers. Then it changes its position by turning to almost an angle of 180° in

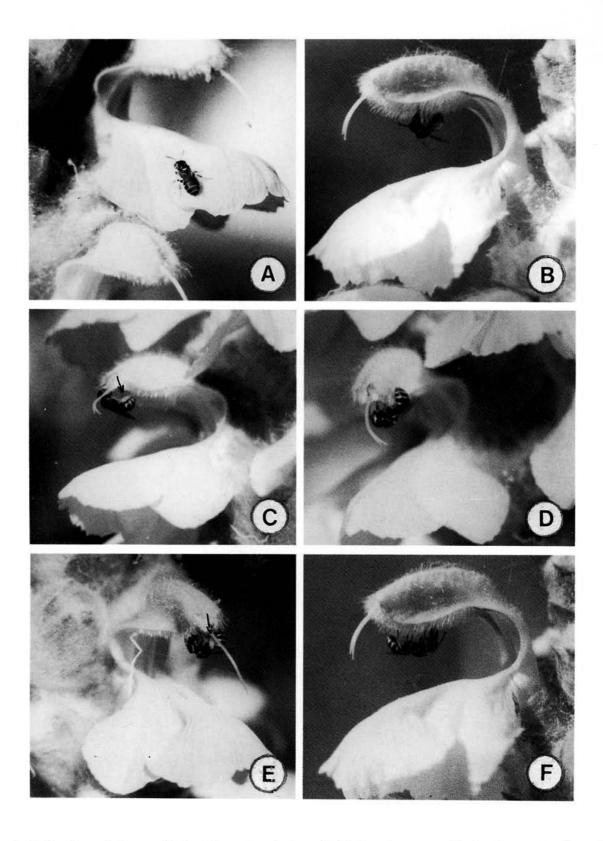


Fig. 4. Pollination of E. superba by N. rustica. A. bee alighted on lower corolla lip. B: moving towards the anthers in upside down position. C: collecting pollen from the upper pair of anthers. D: turning in 180° angle. E, F: collecting pollen from lower pair of anthers. Arrows in fig C & E indicate pollen loads on the bees' hind legs.

order to hold itself from the upper pair of anthers and collect pollen from the lower ones (Fig. 4D-F). The process was repeated many times until the bees' body was fully laden with pollen. From time to time it took short flights to 3-4 flowers thus collecting and exchanging pollen of different flowers, generally on the same spike (bringing about geitonogamous pollination). It also flew to different spike at times (bringing about xenogamous pollination). During this process the bee sometimes reached the stigmatic surface (perhaps mistaking it for an anther). This results in inadvertent transfer of pollen from anthers to the stigma of different flowers by the bees affecting auto-/geitono-/xeno-gamous pollination.

When sufficient quantity of pollen were gathered, these were transferred and packed in their pollen collecting apparatus, also called as pollen basket of the hind legs. In this process the bee used the entire body as a brush. The packing of pollen was a fast and continuous process involving synchronization of movements of the different body parts. The first pair of legs brushed the pollen from the eyes, the antennae and the head. The back of the thorax was brushed by the middle legs and the pollen on the abdomen was swept off by the hind legs. The pollen thus accumulated was continuously passed backwards to the inner side of the hind legs and finally packed as pollen loads. The fully packed pollen became conspicuous as loosely adhering masses of cream coloured pollen loaded on the bees' hind legs (Fig. 4C, E).

The bee collected pollen to her maximum carrying capacity and vanished for 20-30 min. and then it reappeared to repeat the process. The entire foraging process involved an exercise of 15-20 min. Further, the pollen collected by the bees were exclusively of E. superba (unifloral) indicating that the pollinators confine their visits to this species neglecting all other simultaneously flowering plants. Thus they served as monolectic pollinators.

### Time and frequency of insect visits

In case of *E. superba* the time and frequency of insect visits was observed to be governed by fluctuations in day temperature, abundance of flowers, time of pollen release and insect population in the surroundings. The diurnal frequency of pollinator visitations are shown in Tables 1 and 2. During the entire period of observations only one, rarely two and never more than two insects were seen working on the plants in both *in situ* (Table 1) and *ex situ* (Table 2) conditions. On bright and sunny days the pollen was presented around 0930 - 1000 hours with the opening of new flowers and the bees' activity was also at its maximum during this period, whereas on cloudy days under humid conditions the anthesis was around 1130 - 1200 hours simultaneous with the opening of fresh flowers, again coinciding with the time of insect visitations (Table 1, 2). The bee activity and visitations increased with increase in the pollen availability corresponding to the number of freshly opened flowers.

#### Seed set

Only 6.9 % seed set occurred in *E. superba* when left for natural pollination as only 38 ripe seeds (nutlets) were produced against an expected 552 seed output from 138 flowers left for insect pollination.

Table 1. Diurnal frequency of insect visitation to *E. superba* flowers in its type locality (Mohand, Dehra-dun) during March, 1993.

Date	No.of open fls.	Weather condition	Time of visits	No. of visits	Time interval	No. of insects
23rd	50	Rainy with	1400	1	\	1
		frequent showers				
24th	54	Moist cloudy	1200-1500	6	20-30 min	1-2
26th	56	Sunny	1030-1200	5	10-20 min	1

Table 2. Diurnal frequency of insect visitation to E. superba flowers at NBRI during March, 1993.

Date	No.of open fls.	Weather condition	Time of visits	No. of visits	Time interval	No. of insects
16th	26	dry sunny	1000-1230	4	1/2-1hr	1
17th	36	moist cloudy	1130-1330	4	20-30 min	1
18th	43	cloudy	1100-1330	6	20-30 min	1
19th	71	sunny	0940-1300	6	20-60 min	1-2
20th	78	"	1000-1240	4	30-60 min	1-2
21st	76	"	1000-1220	4	40-50 min	1-2
22nd	66	"	1000-1230	5	30-40 min	1
23rd	55	"	0940-1220	3	30-90 min	1
24th	37	"	1040-1200	3	30-40 min	1
25th	36	"	1040-1200	3	30-40 min	1
26th	30	•	1000-1100	3	20 min	1
27th	25	"	1020-1120	2	30 min	
28th	14	"	1030	1		
29th	4	<u>u</u> –	· -	2 <del></del> /2	-	

#### DISCUSSION

E. superba has been regarded as one of the highly endangered species in the Siwaliks of Uttar Pradesh (Rao & Garg, 1994). The species being a member of an advanced family of Angiosperms shows all the advanced features such as a highly specialized hermaphrodite flower with zygomorphic, brightly coloured corolla which is adapted to entomophilous mode of pollination, a gynobasic style, 4 didynamous stamens and nutlets with a tuft of pappus like hairs at the distal end (as in Compositae). Naturally, these traits should have made the species a successful one. But during a short span of the last decade, the population of the species has drastically declined from about 100 plants (Jain & Shastry, 1984) to 33 (± 10) plants (ca. 75% decline). This indicates an acute malfunctioning at some stage during the reproductive cycle of the species. The size of present population is far below the level of minimum effective population size which is essential for survival of any population (Namkoong, 1979; Roche & Dourojeanni, 1984) and therefore it is unable to counteract the demographic pressures which are more prevalent on small populations

(Pollard, 1966; Keiding, 1975). Whether the decline in population is due to insufficient pollination or due to other biotic factors operating upon the species, in the area, is worth further investigation.

The pollination efficacy of plants depends upon their population size, genetic diversity and ability to attract pollinators. In E. superba the elongate raised spikes with conspicuous whorls of bright yellow flowers successfully draws the attention of insects for pollination. Being nectarless, the flowers produce abundant pollen rewards for attracting specific pollen foragers. The distinct bilabiate corolla is another adaptation for insect visitation. Further, the anthers in the flowers are situated at an elevated position with pollen loosely adhering to its surface. Therefore, only two bee species, Ceratina heiroglyphica and Nomia rustica, were found to be effective pollinators of E. superba both in the natural habitat and in the experimental garden. Thus the pollination mechanism in the species was highly specialized one. The flowers were oligophilic (specialised for pollination by one or two insect species) and pollination mechanism was sternotribic (in which pollen is carried on ventral surface of the insect's body) (Faegri & Pijl, 1979). The pollinator visits to the flowers were ethodynamic (the insect purposely and actively approaches the flowers for gathering the floral rewards). A kind of 'Floral fidelity' (floral constancy) was also exhibited by these pollinators as they neglected all the other often more attractive flowers in vicinity. Further, the insects were 'pollinivorous' (visited the flowers with the sole purpose of gathering pollen as nutritive sources) and eutropic (specialized for obtaining the floral rewards) in nature.

Pollinator limitation, which has been investigated in many perennial, obligately outcrossing species with presumed genetic self-incompatibility systems ( Zimmerman & Pyke, 1988), can result from either insufficient or inefficient pollinator visits to the flowers, or due to such visits that provide incompatible sometimes even sterile pollen. The other factors that may be responsible for pollinator limitation are (i) plant dispersal outside the pollinator's geographic range (Spears, 1987), (ii) changes in floral phenology at a time beyond the pollinator's seasonal availability (Schmitt, 1983), (iii) localised interspecific competition for pollinator's service (reviewed in Rathcke, 1983; Wyatt, 1986), and (iv) local pollinator extinction or demographic fluctuations that may cause between-year variation in pollinator availability (Howell & Roth, 1981, Jennersten, 1988), All these factors are more pronounced in species where individual plants have only a single reproductive bout (Stebbins, 1950; Barrett & Eckert, 1990) as is also the case with E. superba. The species is certainly successful in the first stage of attracting its pollinator, which is a prerequisite for entomophilous pollination. The availability of these specific pollinators in the area of the habitat becomes equally important because the species is oligophilic and obligately outcrossing. Absence of the specific pollinator within the plant's geographical range, therefore becomes an important ecological factor limiting the pollination efficiency.

The frequency of pollinator visitation is also a significant aspect which throws light on the efficiency, or otherwise, of a species. In *E. superba* the pollinator visitations are limited to a maximum of 5 - 6 visits in a day. This suggests that the small isolated population of barely two to three individuals flowering simultaneously is not very successful in drawing the attention of many insects. The scanty insect visitations (5 visits in a day, see Tables 1 & 2) indicate that firstly, the nectarless flowers of the species are avoided by most orders of

insects, leaving the species to be visited only by pollinivorous, eutropic insects, and secondly, an imbalance has crept in the phenological co-adaptation between flowering time of the species and abundance of pollinators in the area.

### CONCLUSION

The availability of pollinators is of immense importance for pollination of the endangered *E. superba* which is exposed to a high reproductive bottleneck. Any sort of malfunctioning in the pollination ecology of the species may eventually lead to a decline in seed production by the species. Further, the low population strength of the species has adversely affected the pollinator population upsetting the precise coordination of life cycles of these interdependent organisms and since *E. superba* is oligophilic in nature it is more susceptible to reproductive constraints which may occur due to scarcity of these essentially required pollinators.

On the other hand, it is also observed that the pollinating bees, in turn, are monolectic. Because of this specialized plant-pollinator co-adaptation: (1) Pollen mixing from different species is avoided, (2) The forager gets conditioned with the flower morphology for successful access to the reproductive parts without wasting time and energy in search operations, (3) Since *E. superba* has finite number of ovules even 5-6 effective visits of insects per day can fulfill the pollen transfer, (4) Damage of the delicate stigma and its receptive surface is avoided. This makes oligophily an advantageous adaptation of *E. superba* for successful pollination.

It may therefore be concluded, that although the pollinators of *E. superba* are scanty, but they are not completely lost. They exhibit a specialized plant - pollinator relationship which ensures pollen transfer to the pistil. However, the low seed set (6.7%) calls for investigations on the possibility of existence of discrepancy in post pollination events preceding fertilization because the insects in their ventures are also likely to provide low quality pollination in terms of outcrossing due to their limited interplant movements within the small isolated patch of population of this species which is adapted for out-crossing.

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# 瀕臨絕種的印度沙穗(唇形科)之傳粉生態學

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# 摘 要

本文討論產於印度之Siwaliks,Uttar Pradesh 地區的唇形科(Labiatae)植物:印度沙穗(Eremostachys superba Royle ex Benth.)的傳粉生態學。本植物因傳粉者的限制,反應其脆弱的族群強度。印度沙穗具有適應兩種少食性傳粉蜂: Nomia rustica West.和 Ceratina heiroglyphica Sm. 之他花傳粉,兩者皆屬於膜翅目(Hymenoptera)昆蟲。在自然界中蜂類具有傳粉和依陽光判定方向的能力,並且在找尋及收集花粉時具有對花的忠誠性,採訪花時是群體而非個別行動的。另外本植物花為昆蟲專一性,其傳粉機制為膜版媒的(sternotribic)。對一瀕臨絕種的植物而言,是否有特化的植物傳粉者的共同演化才是其生殖瓶頸。

關鍵詞:印度沙穂,昆蟲動態,昆蟲專一性花,傳粉生態學,傳粉者,膜版媒機制。

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