POLLINATION BIOLOGY OF *ERIOLAENA HOOKERIANA* WIGHT & ARN. (STERCULIACEAE), A RARE TREE SPECIES OF EASTERN GHATS, INDIA

A.J. Solomon Raju¹, P. Hareesh Chandra², K. Venkata Ramana³ & J. Radha Krishna⁴

^{1,2,3,4} Department of Environmental Sciences, Andhra University, Visakhapatnam, Andhra Pradesh 530003, India ¹ ajsraju@yahoo.com (corresponding author), ² hareeshchandu@gmail.com, ³ vrkes.btny@gmail.com, ⁴ jrkrishna30@gmail.com



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Abstract: Eriolaena hookeriana is a rare medium-sized deciduous tree species. The flowering is very brief and occurs during early wet season. The flowers attract certain bees such as Apis dorsata, Halictus sp., Anthophora sp., Xylocopa latipes, and also the wasp, Rhynchium sp. at the study sites. These foragers collect both pollen and nectar during which they contact the stamens and stigma and effect self- or cross-pollination. Nectar depletion by thrips during bud and flower phase and the production of few flowers daily at tree level drive the pollinator insects to visit conspecific plants to gather more forage and in this process they maximize cross-pollination. The hermaphroditic flowers with the stigmatose style beyond the height of stamens and the sticky pollen grains do not facilitate autogamy but promote outcrossing. The study showed that pollinator limitation is responsible for the low fruit set but it is, however, partly compensated by multiseeded fruits. Bud and anther predation by beetles also affects reproductive success. Explosive fruit dehiscence and anemochory are special characteristics; these events occur during the dry season. The plant is used for various purposes locally and hence the surviving individuals are threatened. The study suggests that the rocky and nutrient-poor soils, the pollinator limitation, bud and anther predation, establishment problems and local uses collectively contribute to the rare occurrence of E. hookeriana in the Eastern Ghats.

Keywords: Eriolaena hookeriana, bees, wasps, thrips, entomophily, anemochory.

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Author Contribution: AJSR has conceived the concept, ideas, plan of work and did part of field work and prepared the paper. PHC, KVR and JRK did field work compiled the field observations and results reported in the paper.

Author Details: PROF. A.J. SOLOMON RAJU is Head of the Department of Environmental Sciences, Andhra University, Visakhapatnam. He is the recipient of several national and international awards. He has more than 250 research papers in international and national journals. He is on the editorial board of several international journals. He is presently working on endemic and endangered plant species in southern Eastern Ghats forests with financial support from MoEF and CSIR. P. HAREESH CHANDRA is working as senior research fellow in the MoEF research project under Prof. A.J. Solomon Raju. He has published five research papers. J. RADHA KRISHNA is working as Junior Research Fellow in the MoEF research project under Prof. A.J. Solomon Raju. He has registered for PhD under Prof. A.J. Solomon Raju. He has published four research papers. K. VENKATA RAMANA is a research associate working in the CSIR Research project under Prof. A.J. Solomon Raju.

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INTRODUCTION

Eriolaena is a genus of the family Sterculiaceae with arborescent deciduous tree and shrub species distributed in India, Southeast Asia and southern China (Kubitzki & Bayer 2003). It has about 10 species distributed in India, Southeast Asia and southern China. It is placed in the tribe Eriolaeneae (Hutchinson 1967) but recent molecular studies suggest its placement in the subfamily Dombeyoideae (Bayer et al. 1999; Bayer & Kubitzki 2003; Whitlock et al. 2001). The identified species include E. candollei, E. spectabilis, E. quinquelocularis, E. kwangsiensis, E. glabrescens, E. wallichii, E. stocksii, E. lushingtonii and E. hookeriana. E. candollei occurs in open forests on slopes at 800-1400 m in Guangxi, southwestern Sichuan, southern Yunnan in China, Bhutan, India, Laos, Myanmar, Thailand and Vitenam. It flowers during March-April. This species has been studied for male and female gametophytic development to evaluate the systematic affinities of *Eriolaena* within the Malvaceae. E. spectabilis occurs in open forests and bush lands at 500-1300 m in the northwestern Guangxi, South Guizhou, South and Southeast Yunnan in China, Bhutan, India and Nepal. E. quinquelocularis occurs in open forests and savannas at 800-1700 m in South Yunnan in China. It flowers during May. In India, it occurs in the deciduous forest of Mudumalai Wildlife Sanctuary, Tamil Nadu State, where it is associated with dominant tree species, Tectona grandis, Anogeissus latifolia, Lagerstroemia microcarpa and Terminalia crenulata. The flowering occurs here during the dry season and is pollinated by bees. E. kwangsiensis is endemic to China where it occurs in dense valley forests or scrubs at 800-1200 m in Guangxi, southern Yunnan; it flowers during June-August. E. glabrescens occurs on mountain slopes and valleys at 800-1300 m in southern Yunnan, and also in Thailand and southern Vietnam; it flowers during August-September (Shu 2007; Murali & Sukumar 1994). E. wallichii grows at 1300-1400 m in Yunnan, and also in India and Nepal. E. stocksii is distributed in western peninsular India (Kubitzki & Bayer 2003). The flowering period of both E. wallichii and E. stocksii has not been documented. E. lushingtonii is an endemic and endangered deciduous tree species of southern peninsular India where it is restricted to open slopes of moist deciduous forests at 350-900 m (Hutchinson 1967; Kubitzki & Bayer 2003; Rao & Pullaiah 2007; Tang et al. 2007). The chronology of field collection of E. lushingtonii in peninsular India has been noted by Rao & Pullaiah (2007). In Andhra Pradesh, the type collection was made by Lushington during pre-independence time from the Nallamalai Hills in Kurnool District. After a lapse of about 70 years, Ellis collected it from Chelama Reserve Forest of Kurnool District on 05 July 1963 and adjacent locality Rollapenta on 16 August 1972 in the Nallamalais. In Tamil Nadu, it was collected from the South Srivilliputhur Reserve Forest on 24 July 1965 by E. Vajravelu. Malick (1993) noted the distribution of this species in Karnataka and Kerala. Recently, Raju et al. (2013) reported details of floral ecology and pollination of this species from the southern Eastern Ghats of Andhra Pradesh. Parrotta (2001) stated that E. hookeriana is commonly found in cleared slopes in full sun at 750-1000 m in central and southern India. Meena & Yadav (2010) reported that E. hookeriana naturally grows on Bhakar Hill, Rajasthan and it is surrounded by trees such as Anogeissus latifolia, Ficus benghalensis and Lannea coromandelica. Nayar & Sastry (2000) included these plants in the Red Data Book of Indian Plants. Jayasuriya (1996) noted that E. hookeriana also occurs at 300-500 m in Galleletota Other State Forest in the Ratnapura District, Sri Lanka. Chetty et al. (2008) recorded that the flowering and fruiting events in E. hookeriana occur during January-October. Different authors have documented the economic and medicinal values of this tree species (Pullaiah & Chennaiah 1997; Parrotta 2001; Meena & Yadav 2010; Gnananath et al. 2011). All plant parts are ethnobotanically important. Fruits are eaten by birds, bears and monkeys. The mucilage from the bark is mixed with water and given as a cure for stomach aches. Strong wood is used for agricultural implements and axe handles. Fresh leaves are fed to cattle once in a time to increase fat in the milk content. The root extracts contain certain phytochemicals such as alkaloids, flavonoids and phenolic compounds which have effective antimicrobial properties. Gnananath et al. (2011) stated that this species is available in most parts of Andhra Pradesh State but no scientific study was conducted on this medicinal plant while Tang et al. (2009) has also mentioned that only scant information is available for the entire genus Eriolaena. Keeping this state of information in view and also due its rarity, E. hookeriana has been studied for its floral ecology and pollination and the same is presented and discussed in this paper.

MATERIALS AND METHODS

Eriolaena hookeriana located at Tirumala forest (13°40'N & 79°19'E, elevation 745m) in the southern Eastern Ghats and at Galikonda forest area (17°59'N

& 82°35'E, elevation 727m) near Ananthagiri in the northern part of Eastern Ghats of Andhra Pradesh were observed for the aspects studied during 2011-2013. The soil samples were collected from this area for pH, organic carbon, nitrogen, potassium and phosphorous. The soil analysis was done by the Central Research Institute for Dry land Agriculture, Hyderabad. Galikonda site was used to record anthesis and anther dehiscence schedules. Twenty-five tagged mature buds were followed for recording the time of anthesis and anther dehiscence; the mode of anther dehiscence was also noted by using a 10x hand lens. Five flowers each from 10 trees selected at random at each site were used to describe the flower morphology such as flower sex, shape, size, colour, odour, sepals, petals, stamens and ovary. The pollen output was determined separately for both the study sites. Ten mature but undehisced anthers were collected from five different plants at each site and placed in a petri dish. Later, each time a single anther was taken out and placed on a clean microscope slide (75x25 mm) and dabbed with a needle in a drop of lactophenol-aniline-blue. The anther tissue was then observed under the microscope for pollen, if any, and if pollen grains were not there, the tissue was removed from the slide. The pollen mass was drawn into a band, and the total number of pollen grains was counted under a compound microscope (40x objective, 10x eye piece).

This procedure was followed for counting the number of pollen grains in each anther collected. Based on these counts, the mean number of pollen produced per anther was determined. The characteristics of pollen grains were also recorded. Five flowers each from five trees at each study site were used for testing stigma receptivity. It was tested with hydrogen peroxide from mature bud stage to flower drop as per Dafni et al. (2005). Hydrogen peroxide when applied to stigma does not stain but produces bubbles as a result of catalase (peroxidase) presence. The period of bubble production was taken as the duration of stigma receptivity. The duration between fruit initiation and maturation and dispersal was recorded by conducting field visits at weekly intervals. Fruit set rate was recorded at tree level since the number of fruits produced were few in number. The fruit and seed characters were recorded in the field itself. Seed dispersal event was also observed in the field to record the mode of dispersal. Field observations were made on seed germination and seedling establishment rates at both the study sites to the extent possible since the terrain is sloppy and risky to do the work during rainy season.

Regular field visits were conducted to observe the

foraging activity of insects at both the study sites. A total of 120 man hours each were spent in 2011 and 2012 exclusively for this aspect. The insects were observed with reference to the mode of approach, landing, probing behaviour, the type of forage collected, contact with essential organs effecting pollination and inter-plant foraging activity in terms of cross-pollination. Based on the preliminary field observations on the presence of thrips in buds and flowers, a sample of buds and flowers, 50 each for each site was used to calculate the percentage of infestation by thrips. A beetle (unidentified) was a consistent voracious pollen feeder and completely emptied the flowers that it fed. It also sucked the sap from the growing buds due to which the latter wilted without reaching to flower stage. A sample of 75 flowers was observed at both the study sites for recording the percentage of such pollen-free flowers. Another sample of 50 buds at both the study sites was observed for recording the percentage of wilted buds due to sap collection by the beetle. The plant habit, flowers, fruits, and insect foragers at flowers were photographed with Nikon D40X Digital SLR (10.1 pixel).

RESULTS

E. hookeriana is a deciduous medium-sized tree species (Image 1a,b). It occurs naturally on hill slopes characterized by rocky or rubble mixed with brown or red soils. The soil is principally transported from other areas during rainy season in areas of its occurrence. The phenological events occur one after the other: leaf shedding during November-February, leafless state during March-May, leaf flushing during June-July (Image 1c-e), and flowering during August only (Image 1f, 2a,b). A few individuals extend flowering into 1st week of September. An individual tree flowers for three weeks. The flowers are borne in 2-3 flowered cymes borne in the leaf axils; they are pedicellate and hang downwards or positioned at right angles to the axis. They are large, yellow, mildly fragrant, hypogynous, actinomorphic and bisexual. The calyx is composed of five linear to lanceolate sepals which are pale green with light brown tinge. The sepals bear stellate-hairs on the outside and villous on the inside. The corolla has five free petals and arranged alternate to sepals; they are golden yellow, reflexed, and have thickened, densely pubescent claws. The staminal column is elongate and antheriferous throughout. Filaments arise from the entire length of the staminal column and each filament is tipped with fertile anthers which are bilocular, tetrasporangiate



Image 1. Eriolaena hookeriana. a - Habitat, b - Trunk, c - Partial leaf flushing, d - Complete leaf flushing, e - Fully developed foliage, f - Flowering phase.

with parallel locules (Image 2I,m). The ovary is sessile, globose, stellate-pubescent and 7-9 celled; it extends into prominent style and tipped with 7–9 stigma lobes. Normally, the ovary is 8 or 9-loculed and stigma is 8 or 9-lobed (Image 2o–q). The stigmatose style is far beyond the length of staminal column. Each locule contains 5–8 ovules only (Image 2r).

The floral morphometrics differed significantly between Tirumala and Galikonda sites. The flowers collected at Tirumala site are a bit smaller than the flowers collected from the Galikonda site. Accordingly,

the flower parts measured differently. The Tirumala site flowers are 2.78±0.16 cm long, 3.34±0.26 cm wide; sepals are 2.29±0.21 cm long, 0.6cm wide at and 0.3cm at apex, petals 1.84±0.15 cm long, 0.4cm wide, staminal column 0.6±0.2 cm long, stamens 0.4–1.0 cm long, the number of stamens per flower 103±9, ovary 1.96±2.15 cm long, style and stigma 1.4±0.06 cm long, the number of ovules per locule 6–8 and the number of ovules per flower 51±4.69. The Galikonda site flowers are 3.13±0.2 cm long, 3.98±0.14 cm wide; sepals are 2.87±0.04 cm long, 0.5cm wide at and 0.3cm at apex, petals 3.03±0.1

cm long, 0.5–0.6 cm wide, staminal column 1.6 \pm 0.2 cm long, stamens 0.4-1.2 cm long, the number of stamens per flower 96 \pm 11, ovary 2.68 \pm 0.12 cm long, style and stigma 2.3 \pm 0.07 cm long, the number of ovules per locule 5–6 and the number of ovules per flower 47 \pm 7.8. The chronological events of floral and fruiting events are mentioned in Table 1.

The mature buds open at 0700-0800 h and at the same time anthers also dehisce by longitudinal slits. The stages of internal growth and development of buds and flowers are shown in Image 2c-k. The sepals and petals unfold and reflex backwards exposing the entire length of staminal column and style and stigmatic lobes. The pollen output per anther is 759±32 and per flower 78,177; and pollen-ovule ratio is 1,533:1 in case of Tirumala site. The corresponding values for Galikonda site are 734±35; 70,464±3,387 and 1,499:1. The pollen grains are spherical, echinate, panporate, sticky and 75µm in size on equatorial axis (Image 2n). The stigmas extend 3mm beyond the staminal column during bud stage and 6mm beyond the staminal column during flower stage. They attain receptivity soon after anthesis, show peak activity during 0900-1100 h and a gradual decline in receptivity occurs towards the end of the day. During this period, the stigmatic lobes are semi-wet and pubescent. The receptivity is absent in the remaining period of flower life. A flower produces 1.8±0.3 µl of nectar at the base of the ovary, which is firmly held by the pubescent hairs and the nectar glistens against sunlight. The flowers remain in place for five days and

Table 1. Floral, breeding and fruiting aspects of Eriolaena hookeriana

Floral event	E. hookeriana		
Anthesis	0700-0800 h		
Anther dehiscence	During anthesis		
Sepals	Five		
Petals	Five		
Stamens	96–103		
Stigma receptivity	Day 1 with peak during 0900-1100 h		
Pollen output/flower	70,464–78,177		
Pollen-ovule ratio	1,499–1,533:1		
Nectar volume/flower (μl)	1.8±0.3		
Pollination system	Entomophily		
Pollinators	Bees and butterflies		
Breeding system	Self-compatible		
Fruit set in open pollinations (%)	27% but 9% abort subsequently		
Fruit maturation time	6–7 months		
Seed dispersal mode	Anemochory		

petals and stamens fall off thereafter while sepals drop off 10 days after anthesis.

In both the sites of study, the buds and flowers were found with several individuals of thrips. On average, 5-9 thrips were found in both buds and flowers. The bud and flower infestation rates were 35% and 68% at Tirumala site; the corresponding values for Galikonda site were 42% and 72%. In such flowers, nectar was almost absent while those that were not found with thrips had normal nectar volume. The nectar free-flowers were considered to be compelling the flower-visiting insects to make multiple visits to the same or different conspecific plants in order to guench their nectar thirst. Such a foraging activity appeared to be promoting crosspollination. The flowers were foraged by the same species of bees, wasps, and butterflies during daytime during the entire flowering season at both the study sites (Table 2). The individuals of each insect species visiting the flowers at any given time of observation were 1 or 2 only. Their foraging activity schedules were also almost similar at the two sites and hence their foraging activity schedules and hourly foraging visits were combined and hence were not presented separately. The bees were Apis dorsata (Image 3a,b), Halictus sp. (Image 3c), Anthophora sp.(Image 3d,e) and Xylocopa latipes (Image 3f). Their foraging activity started at 0700h, gradually

Table 2. List of insect foragers and forage collected from the flowers of *Eriolaena hookeriana*

Order/ Family	Scientific name	Common name	Forage sought	
			Nectar	Pollen
Hymenoptera				
Apidae	Apis dorsata F.	Rock bee	+	+
	Apis cerana F.	Indian Honey bee	-	-
	Apis florea F.	Dwarf bee	-	-
	Trigona iridipennis Smith	Stingless bee	-	-
	Anthophora sp.	Miner bee	+	+
	Xylocopa latipes Drury	Carpenter bee	+	-
	Xylocopa pubescens	Carpenter bee	-	-
Halictidae	Halictus sp.	Sweat bee	+	+
Vespidae	Rhynchium sp.	Potter wasp	+	+
Thysanoptera				
Thripidae	Thrips (unidentified)		+	+
Lepidoptera				
Lycaenidae	Jamides bochus Stoll	The Dark Cerulean	+	-
	Lampides boeticus L.	Pea Blue	-	-



Image 2. *Eriolaena hookeriana* a&b - Flowering branches, c–e - Different stages of maturation of flower bud, f&g - Open flowers, h&k – Inside view of developing stamens, ovary, style and stigmas, I - Staminal sheath with anthers, m - Anthers, n - Pollen grain, o - Ovary, p - twisted stigma lobes, q - unfolded stigma lobes, r - Ovules.

rose towards noon, thereafter declined and ceased by 1400/1500 h (Fig. 1). They collectively made 77% of total foraging visits (Fig. 3). Their prominent foraging activity during forenoon period was due to availability of fresh nectar and pollen; all these bees collected both pollen and nectar during their flower visits. These bees exhibited two different approaches, the first included approach of the bee in upright position from the side bypassing the stamens and stigmas for probing the

ovary base directly for nectar collection while the second included approach of the bee in upright position via the stamens and stigmatic lobes for collecting nectar from the ovary base. In both the approaches, the pollen collecting bees after nectar collection ascended to the place of stamens for pollen collection; sometimes these bees first collected pollen and then descended unto the ovary base for nectar collection. All the bees had contact with the stamens and stigmatic lobes while



Image 3. Eriolaena hookeriana
a&b - Apis dorsata collecting nectar, c - Halictus sp. collecting nectar, d - Anthophora sp. collecting pollen, e - Anthophora sp. collecting nectar, f - Xylocopa latipes collecting nectar, g - Rhynchium sp. collecting nectar, h - Rhynchium sp. collecting pollen, i - Jamides bochus collecting nectar, j - Beetle (unidentified) feeding on pollen and sap of growing buds.

collecting nectar and/or pollen in the same or different visits; such a contact was considered to be resulting in pollination. The production of a small number of flowers at tree level was found to be driving the bee foragers from one plant to the other to seek more forage and such a foraging behavior was considered to be resulting in cross-pollination. The wasp, *Rhychium* (Image 3g,h) was almost a day-long forager but it was relatively more inconsistent nectar and pollen feeder; it also foraged during the same period as bees did (Fig. 2). It made 23% of total foraging visits (Fig. 3). The wasp approached always in upright position but it bypassed the sex organs while collecting nectar but contacted the sex organs while collecting pollen. It usually collected both floral rewards in the same visit and occasionally either

pollen or nectar in a single visit. The nectar collection activity did not result in effecting pollination while pollen collection activity did always effect pollination. It was a fast flier, collected the forage very quickly from individual flowers and frequently foraged the flowers of different conspecific plants due to production of a few flowers daily by individual plants. The lycaenid butterfly, Jamides bochus (Image 3i) was an occasional forager. It collected nectar always from the flower base without any contact with stigma and hence was not involved in effecting pollination. A beetle (unidentified) (Image 3j) was a regular and consistent flower visitor at both the study sites but it collected pollen voraciously and also sap from growing buds. Its foraging activity was found to be emptying the flowers of pollen and causing wilting

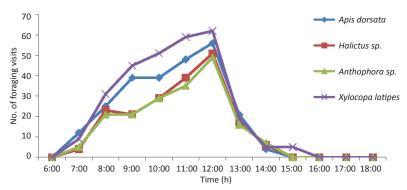


Figure 1. Hourly foraging activity of bees on *Eriolaena hookeriana* (average of foraging visits recorded on three different days Tirumala and Ananthagiri sites in 2011 and 2012



Image 4. Eriolaena hookeriana a&b - Fruiting phase, c - Initial stage of fruit, d - Well developed fruit, e - Mature and dry fruits ready for seed shedding by explosive dehiscence.

of growing buds. The percentage of pollen-free flowers was 31% at Tirumala site and 45% at Galikonda site. Further, 54% of buds sampled at Tirumala site and 63% of buds at Galikonda site were wilted without reaching to flower stage due to sap collection by the beetle. The pollen feeding from flowers and sap feeding from growing buds by this beetle were considered to be affecting the reproductive success of the plant.

In fertilized flowers of *E. hookeriana*, the ovary gradually bulges, transforms into fruit and produces seeds. The total duration from fruit initiation to maturation and dispersal is 6–7 months (Image 4a–d). A tree produces 31–43 fruits. The fruit is a 2.5–3 cm long 8–9 valved ellipsoid-ovoid capsule with 4-5 seeds which are 1.2–1.6 cm long and winged at apex. The mature, dry capsules dehisce loculicidally a bit explosively liberating

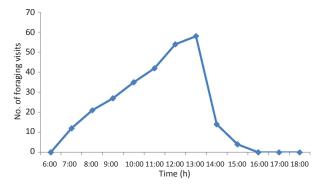


Figure 2. Hourly foraging activity of *Rhynchium* wasp on *Eriolaena hookeriana* (average of foraging visits recorded on three different days Tirumala and Ananthagiri sites in 2011 and 2012

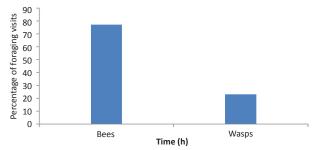


Figure 3. Percentage of foraging visits of bees and wasps on Eriolaena hookeriana

apically winged seeds into the air (Image 4e). The seeds thus released are driven away by the prevailing wind during February–March.

The Tirumala site is rocky with in situ and migrated soil while the Galikonda site is characteristically rugged terrain with mostly migrated soil. The results of soil analysis for the Tirumala site for texture, major nutrients, pH and organic carbon indicated that it is brick brown sandy loamy soil consisting of 4.56% silt, 19.04%

clay and 76.4% sand. The soil pH was 4.9 and organic carbon 8.5% (high). The nitrogen (N), phosphorous (P) and potassium (K) values for this soil were 144.21 kg/ ha (low), 8.51kg/ha (very low) and 268kg/ha (very low) respectively. The soil analysis for the Galikonda site is sandy loam clay soil consisting of 4.56% silt, 21.04% clay and 74.4% sand. The soil pH was 6.689 and organic carbon 1.75% (high). The nitrogen (N), phosphorous (P) and potassium (K) values for this soil were 156.75kg/ ha (low), 15.32kg/ha (low) and 166.21kg/ha (very low) respectively. The soil characters for both the study sites indicated that the soils are mostly migratory during rainy season and are nutrient-poor; the soil is moderately acidic in case of Tirumala site while it is near optimal in case of Galikonda site. Field observations indicated the occurrence of a few seedlings ranging from 27-43 in the surroundings down the slope in both the study sites during mid-June-late July. The accessible seedlings were handpicked and confirmed with the surviving seedlings of the previous years. Further, the surviving seedlings were found to be growing very slowly due to rocky and nutrient-poor soils in both the study sites.

DISCUSSION

Eriolaena is a genus distributed exclusively in dry or moist deciduous open forest. In India, Murali & Sukumar (1994) reported that E. quinquelocularis occurring in a dry forest of Mudumalai in southern India exhibits leaf flushing and flowering events successively within the dry season. E. lushingtonii is a dry deciduous open forest species but shows leaf flushing in late dry season while flowering in early wet season (Raju et al. 2013). Tang et al. (2007) reported that the flowers of all Eriolaena species are characteristically yellow. E. quinquelocularis, a dry deciduous species distributed in and outside India bears yellow flowers which are more conspicuous due to its flowering during dry season when the herbaceous plants disappear and tree species remain leafless (Murali & Sukumar 1994). E. lushingtonii is also a producer of yellow flowers (Raju et al. 2013). E. hookeriana, a dry deciduous species confined to India and Sri Lanka also produces yellow flowers. Chetty et al. (2008) noted that in E. hookeriana, flowering and fruiting events take place during January-October. On the contrary, the present study shows that E. hookeriana displays leaf flushing during early wet season, flowering for a brief period in August and fruit maturity and seed dispersal during February-March. It also produces yellow flowers in axillary cymes daily at tree level and the flowers do not stand out very prominently against the foliage and hence could go unnoticed by the flower visitors due to the flowering pattern characterized by the production of a few flowers per day at tree level and emergence of herbaceous flora and leaf flushing in deciduous tree species following rainfall in early June. Such flowering pattern and flower position appear to be disadvantageous for the plant to attract a wide array of flower visitors, especially in the presence of other simultaneously flowering plant species in the area. The co-occurring and co-flowering nectariferous and polleniferous herbaceous plant species, Bidens pilosa, Vernonia cinerea (Asteraceae), Borreria hispida, Spermacoce pusilla (Rubiaceae) and Triumfetta rhomboidea (Tiliaceae) with common occurrence, gregarious flowering and very conspicuously present grouped flowers against the foliage attract a variety of insects comprising of bees, wasps and butterflies while E. hookeriana receives foraging visits of certain bees (Apis dorsata, Halictus sp. and Xylocopa latipes), the wasp Rhynchium and the lycaenid butterfly Jamides bochus. The flower visiting rate of these insects has been found to be related to the level of standing crop of nectar and pollen during forenoon and afternoon period. All the co-flowering plant species and E. hookeriana produce minute amount of nectar; the latter species produces high amount of pollen. Bidens and Vernonia with capitulum inflorescence type bearing numerous flowers in clusters are copious producers of pollen while the other co-flowerers produce moderate amounts of pollen from individual flowers. Their profuse flowering pattern, the floral arrangement and their occurrence in extensive mats appear to be playing a key role in enabling them to compete well with E. hookeriana for flower visitors.

In *E. hookeriana*, significant variation has been recorded in floral morphometrics in the plants studied at two different sites. The Tirumala site being a habitat typical of rocky boulders intermingled with sparse growth of herbaceous flora accumulates less migratory soil while the Galikonda site relatively accumulates more migratory soil due to the covering of habitat with diverse herbaceous flora by the time of onset of flowering in *E. hookeriana*. The variations recorded in floral morphological characters appear to be reflective of the soil nutrient environment existing during flower phase. Further, the variations noted in pollen output and pollen-ovule ratios at the study sites are relatable to the number of stamens and ovules per flower.

Murali & Sukumar (1994) reported that *E. quinquelocularis* is insect-pollinated in the Mudumalai

deciduous forest. Raju et al. (2013) stated that E. lushingtonii occurring in the Nallamalai deciduous forest is melittophilous but pollination limitation exists due to inconsistent foraging visits of pollinator bees. In the present study, E. hookeriana with morning anthesis, exposed dehisced anthers presenting pollen and exposed flower base presenting nectar after anthesis indicates that it is adapted for day-active flower foragers for pollination. In line with this, certain bees, the wasp and the lycaenid butterfly visit the flowers for forage, the bees and the wasp for both pollen and nectar while the butterfly for only nectar. The bees and the wasp fly between conspecific plants for more forage collection and in the process contribute to both self- and crosspollination. The production of a small number of flowers at tree level and nectar depletion by thrips in buds and flowers drive them to fly between plants to collect as much forage as possible for meeting their needs. Such foraging activity by them contributes to the maximization of the cross-pollination rate. The flowers with stigma receptivity only, on the day of anthesis, facilitate pollination on the same day only, although they remain in place for five days. The long life of flowers certainly enhances attraction of the plant to some extent to the foragers and also the pollen available in the flowers becomes available for cross-pollination to be effected by pollinating insects. The butterfly recorded in the study is not a pollinator since it does not contact the sex organs of flowers while collecting nectar. The floral characteristics of E. hookeriana as detailed above conform to the entomophilous pollination syndrome (Faegri & van der Pijl 1979). Sharma (1967) reported that Eriolaena pollen grains are stenopalynolous and described the pollen grain characteristics of Eriolaena species, E. wallichii, E. spectabilis and E. hookeriana. These three species exhibit similar pollen morphology and hence have been referred to as E. wallichii type by him. The panporate and spinulate characters typify this type of pollen grains. He considered the panporate condition as a climax in the line of apertual evolution. The pollen grain characters observed in this study for E. hookeriana conform to his findings. Further, the pollen grains are sticky and there is no possibility for their dissemination into the air during wet season. The sticky and echinate nature of the grains in this species is an adaptive feature for entomophily and is also advantageous for the bees and wasps to collect and transport them to their nest (Gottsberger 1989).

E. hookeriana with hermaphroditic sexual system and weak protandry facilitates both self- and cross-pollination. The ability to fruit through both modes

of pollination is adaptive but it is essentially insectdependent since the extension of the stigmatose style beyond the height of stamens and the sticky nature of pollen grains which is further dampened by the high humidity during wet season preclude the occurrence of autogamy. The study indicates that the pollinator limitation appears to be playing a considerable role for the low fruit set and the fruit number per tree in the entire population stands below 45. However, the low fruit set is partly compensated by the production of 4–5 seeds per fruit. The seed set rate could be attributed to the number of fertilized ovules and to the nutrient status of the soil. Further, the bud and flower feeding activity of a beetle at both the study sites affects the reproductive success of the plant as the buds and flowers fed by it do not take participation in sexual reproduction. Murali & Sukumar (1994) reported that in E. quinquelocularis, the fruits mature in a short duration and this reason could be the investment of more resources in flowers. Further, the fruit dehisces explosively to disseminate seeds into the air and hence the seeds are characteristically wind-dispersed for which the dry season is very effective because of low humidity at that time. All the reproductive events, flowering, fruiting and seed dispersal of this plant occur within the dry season only. In E. hookeriana, the leaf flushing and flowering events occur during wet season, fruit growth and development during late wet season and entire winter season, and seed dispersal during dry season. The fruits dehisce explosively liberating winged seeds into the air and then the latter are dispersed effectively by wind due to dry ambient conditions; and hence the plant is anemochorous (Maury-Lechon & Curtet 1998). The seeds germinate during rainy season depending on their viability and soil nutrient environment. Since the dry season with high winds contribute to top soil erosion in the absence of all herbaceous flora on the slopes, the germinated seeds in the early rainy season struggle to establish and in effect, a few eventually establish and grow slowly. Further, the high organic carbon in the soils of both the study sites might lead to a situation in which it ties up the micronutrients in unavailable forms (Sarwar et al. 2010). The successful establishment and the continuous growth of the seedlings of E. hookeriana into new plants could be related to the existence of some pockets of deep soils within the rocky habitat. The areas where the plants established have deep soil which enables them to penetrate gradually through crevices and cracks of rocks. The study suggests that the soil layer and its composition have a great bearing on the build-up of population of E. hookeriana. Further,

the various local uses as mentioned in the introduction section are additional factors affecting the surviving individuals. Therefore, the rocky and nutrient-poor soils, the pollinator limitation, bud and anther predation, establishment problems and local uses collectively contribute to the rare occurrence of *E. hookeriana* in the Eastern Ghats. These aspects are to be taken into account while framing effective conservation and management measures as well as the recovery of the population of *E. hookeriana*.

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