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Original Article

Pollination ecology of *Litsea glutinosa* (Lour.) C.B. Robinson (Lauraceae): A commercially and medicinally important semi-evergreen tree species

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Abstract

Litsea glutinosa is a semi-evergreen wet season blooming tree species. It is a dioecious plant characterized by separate staminate and pistillate trees occurring in a 3:1 ratio. The inflorescence is a solitary and compound pseudo-umbel consisting of involucral bracts each producing several staminate or pistillate nectariferous florets. The florets display myophilous pollination syndrome and are pollinated by flies as well as other insects. The natural fruit set does not exceed 30%. The *Bruchus* beetle is a fruit pest that causes infestation of 23% of total fruits produced. Fruit dispersal occurs by gravity and by the Indian giant squirrel (*Ratufa indica*).

Keywords: *Litsea glutinosa*, dioecy, myophily, fruit infestation

1. Introduction

Litsea is one of the largest genera of Lauraceae and many species under this genus form an important component of tropical forests. It consists of over 300 species distributed mostly in tropical Asia but with a few species in the Islands of the Pacific, Australia, and in North and Central America (Van der Werff, 2001). Recent revisions of regional flora in tropical Asia indicate that there are 74 species in China (Huang, Jie, Xiwen, & van der Werff, 2008), 35 in Thailand (Ngernsaengsaruay, Middleton, & Chayamarit, 2011), 11 in Nepal (Pendry, 2011), and 45 in India (Bhuinya, Singh, & Mukherjee, 2010). In India, there are 18 endemic species that include *L. assamica, L. beddomei, L. bourdillonii, L. coriacea, L. floribunda, L. ghatica, L. keralana, L. laevigata, L. membranifolia, L. mishmiensis, L. mysorensis, L. nigrescens, L. oleoides, L. oreophila, L. stocksii, L. travancorica, L. venulosa* and *L. wightiana*. Furthermore, 8 species are distributed in China, 12 species in Nepal, 11 species in Bhutan, 6 in Bangladesh and Myanmar, 4 in Sri Lanka, and 2 in Pakistan (Bhuinya, Singh, & Mukherjee, 2010). This genus has 28 species in the evergreen forests of the Himalaya and 25 species in the Deccan Peninsula (Bhatt & Pandya, 2012).

Litsea glutinosa is an evergreen tree species native to India, southern China, Malaysia, Australia, and the Western Pacific Islands (Huang, Jie, Xiwen, & van der Werff, 2008). It was reported to be an endangered species in the Philippines (Rabena, 2010), very rare and vulnerable in Bangladesh (Haque, Uddin, Saha, Mazid, & Hassan, 2014), and critically endangered in Andhra Pradesh State of India (Reddy & Reddy, 2008). The wood of *L. glutinosa* is used to make agricultural tools, the root fiber for ropes and paper pulp, the young leaves for fodder, the aromatic seed oil for candles and soaps, and the seed powder is used to treat skin boils. Its bark is used commercially as a binding agent in tablet formulations, pain relief, aphrodisiac, arrest bleeding, bind fractured limbs, and cure wounds on the neck of bullocks due to frequent friction of yoke with the body (Kirtikar & Basu, 1981; Mishra, Kumar, & Talukdar, 2010; Kumar, 2011; Yoko, Akinobu, Atsushi, & Yoshinori, 2000). In the agarbatti

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(incense stick) industry, the paste of the powdered bark is used as a binding agent to make incense sticks and cones due to its excellent viscosity and adhesive properties which aid in continuous burning. Furthermore, the odorless characteristic of the bark is an added advantage to retain the original fragrance of the perfume in incense sticks. Due to tremendous demand for the bark of *L. glutinosa*, its population has been extensively decimated and as a consequence, this species has become threatened and endangered and the potential loss of the wild germplasm is causing grave concern (Rath, 2003, 2004). In Assam, its bark is extensively harvested and used in the essence stick industry despite a ban on the felling of trees by the Supreme Court of India (Dattagupta & Gupta, 2014). In Eastern Ghats, *L. glutinosa* has become threatened and endangered due to indiscriminate exploitation of its bark (Bakshu & Venkata Raju, 2005). The CSIR-DSIR Annual Report 2012-2013 of the Government of India documented that the dwindling supply of bark of *L. glutinosa* is posing a grave threat to the survival of about 3000 core strong agarbatti industry in India. Therefore, the CSIR-National Innovation Council has initiated a search for alternative ingredients to sustain this industry. Despite the high demand for *L. glutinosa*, it has not been studied for its reproductive biology to understand the sexual system and limitations in reproductive success to take measures for the restoration and expansion of its population. Therefore, the present study aimed to generate information on pollination ecology and examine the limitations in the reproductive success through its sexual system in *L. glutinosa*.

2. Materials and Methods

2.1 Study site

A population of *L. glutinosa* consisted of 40 trees located in the Seshachalam Biosphere Reserve in Chittoor District of Andhra Pradesh in Peninsular India (13°42. 539 N latitude and 079°20. 566 E longitude, and 2,541 ft altitude) was used for the study from January to December 2016. In this area, the bark of this tree was over-harvested until recently (Figures 1a and b) but it is now banned because this entire area was declared to be a Biosphere Reserve.

2.2 Phenology, floral morphology and floral biology

Field trips were conducted at weekly intervals to record the timing of leaf fall, leaf flushing, flowering, and fruiting events. During the flowering season, 20 inflorescences collected randomly from 15 trees were carefully observed in the field and in the laboratory to identify the floral sexual status. After identifying the sexual differences in the flowers of these inflorescences, the trees were classified as staminate and pistillate and then their sex-ratio was enumerated. Ten virgin inflorescences were tagged and followed to record the anthesis schedule and anther dehiscence. Twenty-five fresh involucral bracts that consisted of several florets were collected separately from the staminate and pistillate trees. The bracts were used to record the floral morphological details of the staminate and pistillate florets. The protocol mentioned in Dafni, Kevan, and Husband (2005) was used to record pollen output and stigma receptivity. Measurements of floral parts and pollen output are reported as mean±SD. Inflorescences and florets were examined just at anthesis for thrips and once their presence was noticed, their feeding activity for nectar or pollen or both was observed on both staminate and pistillate trees.

2.3 Insect foragers and pollination

Insects foraging at the inflorescences/florets on both staminate and pistillate trees were observed throughout the day on four days for their foraging behavior and pollination potential. Specifically, foraging visits of insects were recorded for 15 minutes at each hour throughout the day on each of the four days, and the percentage of foraging visits made by each insect species and the percentage of foraging visits of each insect category were calculated. Ten specimens of each insect species were captured from staminate trees during peak foraging period, brought to the laboratory, washed in ethyl alcohol, stained with aniline-blue on a glass slide and observed under a microscope to count the number of pollen grains present. From this, the average number of pollen grains carried by each insect species was calculated to know the pollen carrying efficiency.

2.4 Fruiting behavior

Fifty pistillate florets each of 10 virgin inflorescences each tagged on 10 pistillate trees and exposed to insect activity were followed for two months to record the natural fruit set. Since the pistillate florets produce a single ovule per ovary, the seed set was treated as equivalent to a fruit set. Three hundred and fifty fruits collected randomly from eight pistillate trees were used to record the fruit infestation rate by the beetle *Bruchus* sp. Fruit maturation period and seed dispersal aspects were observed from the initiation of fruit formation to seed dispersal time at 2-day intervals in the field.

3. Results

3.1 Phenology

The *L. glutinosa* is a medium-sized semi-evergreen fast growing dioecious tree with staminate and pistillate trees. The stem forms a well developed trunk with light to dark 10 to 20 mm thick brown bark in mature and aged trees. The branchlets are slender, stiff, minutely tomentose towards the apex. Leaves are spiral, blade variable in shape and size, obovate-oblong, apex acute, and base cuneate. The ratio of staminate and pistillate trees was 3:1 in the study area. In both sexes, leaf fall and flushing events occurred almost simultaneously in April-May (Figures 1c and d). Full leaf flushing occurred by the end of June. The flowering occurred during July-August at the population level but individual plants flowered for about 2-3 weeks only. Inflorescence is a flat-topped, grey, pubescent, pseudo-umbel that consisted of 2-4 pedicellate involucral buds in both staminate and pistillate trees (Figures 1e, and f). Solitary involucral buds also occurred here and there along branchlets, axils of leaves, and at the apex of branchlets. Each involucral bud had four green decussate sepaloid, 5.4±1 mm long and 6.1±0.7 mm wide bracts which enclosed 10.13±1.6 florets in the staminate trees and 8.5±1.4 florets in the pistillate trees. In both sexes, the involucral buds behaved as unified flowers, with all their florets opening together synchronously in a time span of 5-6 h during 07:00 to 12:00/13:00 h daily (Figures 1g and h).

3.2 Staminate and pistillate floret morphology and biology

The florets of both sexes were pedicellate, pale yellow, slightly fetid, and actinomorphic. They were 5.8±0.7 mm long, 7.3±1.6 mm wide in staminate florets (Figure 1i) and 5.9±0.6 mm long, 5.2±0.7 mm wide in pistillate florets. In the involucral buds of both sexes, the peripheral florets usually had 1-3 creamy white, 2-3 mm long, and strongly villose perianth lobes while the inner florets lacked perianth lobes. The stamens varied from 8-16 in staminate florets and likewise, staminodes varied from 8-16 in pistillate florets (Figure 1j). In both sexes, the stamens and staminodes were arranged in four whorls without any fixed number in each whorl. The stamens/staminodes in the outer whorl were the longest while those in the innermost whorl were the shortest and accordingly the length of the filament decreased from the outermost to the innermost whorl of stamens. The filaments were creamy white, villose, and had small stalked fleshy glands as swollen pads of tissue at base. Some filaments had two glands, one on each side, while some others had one gland on one side and still some others none. The total number of glands in a floret varied from 6 to 14 in staminate florets and from 5 to 12 in pistillate florets (Figure 1j). In staminate florets, the anthers were yellow, fertile, introrse, semi-orbicular, and 4-celled. The staminate florets possessed a pistillode which was green, glabrous, and had a well developed ovary without ovule and terminated with residual remains of style and stigma. The pistillate florets had a pistil which was green, glabrous, 5.4±0.7 mm, and consisted of a well developed ovary, style, and stigma. The ovary was ovoid and unilocular with a single ovule (Figure 1k). The style was 3.1±0.5 mm long, filiform, and tipped with a peltate slightly bi-fid papillate, wet, and shiny stigma. The stigma extended beyond the height of the staminodes.

In staminate florets, the anthers did not dehisce on the day of anthesis but dehisced gradually between 08:00 and 12:00 h on the next day by valvular mode in which each anther locule wall opened through a flap of tissue. Then, the pollen was exposed and placed on the upper surface of the flaps and also a small amount of pollen remained in the anther locule. The pollen output was 822.3±59.2 per anther and 9,374.2±675.3 per flower. The pollen-ovule ratio was 132,339:1. The pollen grains were slightly wet during anther dehiscence and become dry and powdery gradually. They were spherical, 56.4±16.9 µm, apolar, and spinulose. In pistillate florets, the stigma became receptive from the beginning of anthesis of involucral bud and ceased receptivity at around noon of the third day. The glands situated at the base of the staminal filaments in staminate florets and staminode filaments in pistillate florets secreted nectar only once immediately after anthesis. Their cuticle broke down and the epidermis disintegrated around the glandular surface just ahead of anthesis. The secretion occurred through the intercellular spaces of the basal tissue and the breakdown of the epidermal cells facilitated the ejection of the sticky secretion to the glandular surface which then appeared as droplets and glistened against sunlight. The volume of nectar per staminate or pistillate floret at anthesis was 1.8±0.67 µL. The involucral bracts, all staminate florets, and un-pollinated pistillate florets fell off on the 4th day.

Figure 1. *Litsea glutinosa*: a. Tree shedding foliage, b. Tree with new foliage, c. Bark harvest by local tribe, d. Scars left after bark harvest, e. Staminate tree with pseudo-umbels, f. Pistillate tree with pseudo-umbels, g. A compound staminate pseudo-umbel just anthesed, h Solitary pistillate umbel just anthesed, i. Staminet floret, j. Pistillate floret with staminodes and stalked fleshy glands around ovary base, k. Ovary with a single ovule

3.3 Insect foraging activity and pollination

Thrips used the involucral buds of both staminate and pistillate florets for breeding. They came out when the involucral buds anthesed. Each bud presented several thrips ranging from 8 to 10. Furthermore, they collected only nectar on the day of anthesis and nectar (if available) and pollen after anther dehiscence on the next day in staminate florets while they collected only nectar in pistillate florets. They remained on the trees, moved within and between inflorescences of the same tree to collect the forage and hence they were treated as forage robbers.

The staminate and pistillate florets were foraged during the day time by the same species of bees, wasps, flies, and butterflies. Bees included *Apis cerana* (Figures 2a, b, and g), *A. florea*, *Trigona iridipennis* (Figure 2h), and *Halictus* sp. The wasp that was recorded was *Vespa bicincta* (Figure 2c). The flies were *Chrysomya megacephala* (Figures 2f, and j), *Sarcophaga* sp., and *Eristalinus arvorum* (Figures 2d, e, and i). The butterflies included two nymphalids, *Precis iphita* (Figure 2k) and *Euploea core* (Figure 2l) (Table 1). Of these, bees and flies were regular and consistent while all others were regular but inconsistent in their foraging visits during the

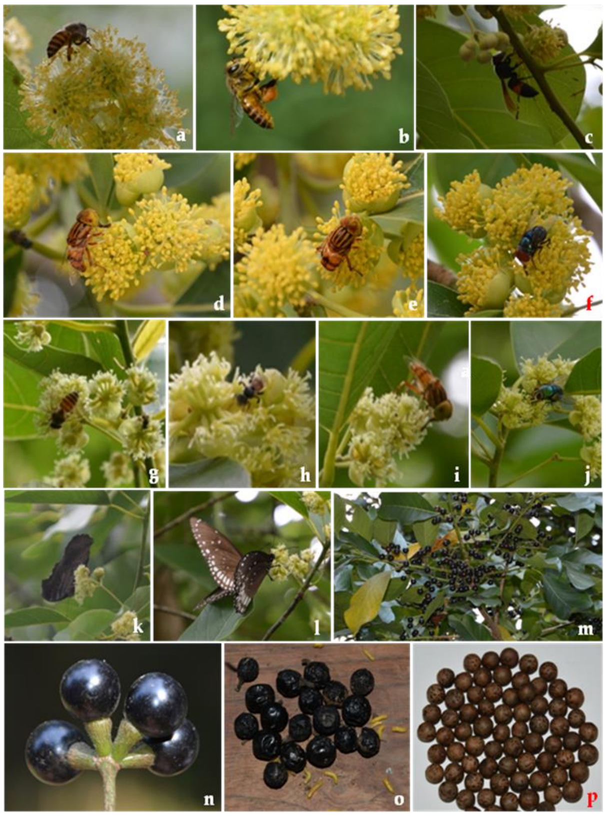

Figure 2. *Litsea glutinosa*: a-f. Foragers on staminate florets- a. *Apis cerana* collecting nectar, b. *Apis cerana collecting pollen, c. Vespa bicincta* collecting nectar, d. *Eristalinus arvorum collecting pollen, e. Eristalinus arvorum* collecting nectar, g-l. Foragers on pistillate florets – g. *Apis cerana* collecting nectar, h. *Trigona iridipennis* collecting nectar, i. *Eristalinus arvorum* collecting nectar, j. *Chrysomya megacephala* collecting nectar, k-l. Nymphalid butterflies collecting nectar – k. *Precis iphita*, l. *Euploea core*, m. Fruiting branch, n. Solitary umbel with 4 ripened fruits, o. Infested fruits, p. Seeds.

entire period of the flowering season. Bees and the fly, *E. arvorum* were both nectar and pollen foragers while all others were nectar foragers only. The foraging visits of all insects began at 08:00 h that gradually reached to a peak at noon and then onwards gradually decreased and ceased by 18:00 h. (Figure 3). The foraging visits in a day were made by bees (41%), flies (32%), butterflies (16%), and wasps (11%) (Figure 4). The body washings of these insects collected from the staminate florets at around noon time showed that all of them were pollen carriers to different extents but pollen recovered from the bees was the highest (Table 2).

In both sexes, the flat-topped pseudo-umbels provided a convenient platform for landing by all these insects. The insects approached the umbels in an upright manner, landed on the umbels, and probed the florets one after the other in a sequential manner to collect the forage. A single visit by insects enabled them to collect the forage from several florets and several umbels with reduced flight distance and search time. The occurrence of several involucral buds at a single point was found to be quite rewarding for the visiting insects in a single visit. Since the staminate and pistillate trees were located closely to each other, these insects made visits to both sexes without any discrimination and this foraging behavior resulted in pollen transfer from the staminate trees to the pistillate trees. The insects that collected only nectar moved fast from one umbel to another on the same tree and to other nearby trees in quest of more nectar. As most umbels were either depleted or emptied of nectar by thrips, the insects, especially flies made quick visits to a number of umbels on the same and different trees in search of nectar which increased the pollination rate in the pistillate trees. In the case of bees, some collected only pollen, some others only nectar and still some others both pollen and nectar. The pollen collecting bees tended to spend more time on the same plant than other categories of bees and such a foraging activity limited pollen transfer to the pistillate trees. The flies visited the umbels of both staminate and pistillate florets in swarms and effected pollination. Therefore, all insect foragers in some way or another effected pollination and hence, this tree has unspecialized flowers which are insect-pollinated.

3.4 Fruiting ecology

Pistillate trees produced 1-8 fruits from a single involucral unified flower. The natural fruit set varied from 21 to 30% on different trees (Figure 2m). The fruits matured within three weeks. They were 1-seeded, 8-10 mm diameter fleshy berries with a persistent apiculate apex seated on a flat disc and supported by enlarged pedicels. They were initially green with white dots but dark purple to black when ripe (Figure 2n). Their surface was glabrous, glossy, and

Table 1. List of insect foragers on *Litsea glutinosa*.

Order	Family	Insect species	Common name	Forage sought
Hymenoptera	Apidae	*Apis cerana* F.	Indian Honey Bee	Pollen + Nectar
		Apis florea F.	Dwarf Honey Bee	Pollen + Nectar
		Trigona iridipennis Smith	Stingless Bee	Pollen + Nectar
	Halictidae	*Halictus* sp.	Sweat Bee	Pollen + Nectar
	Vespidae	*Vespa bicincta* L.	Yellow Banded Wasp	Nectar
Diptera	Calliphoridae	*Chrysomya megacephala* F.	Oriental Latrine Fly	Nectar
	Sarcophagidae	*Sarcophaga* sp.	Flesh Fly	Nectar
	Syrphidae	*Eristalinus arvorum* F.	Hover Fly	Pollen + Nectar
Lepidoptera	Nymphalidae	*Precis iphita* Cramer	Chocolate Pansy	Nectar
		Euploea core Cramer	Common Indian Crow	Nectar

Foragers are the same for both staminate and pistillate trees

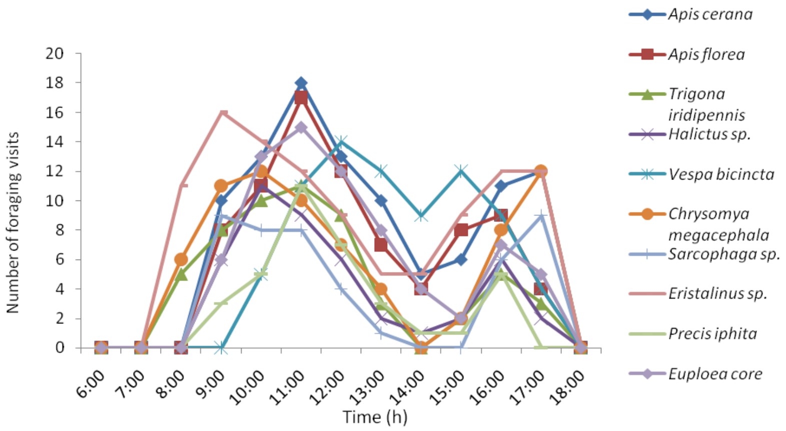

Figure 3. Hourly foraging activity of insect foragers on *Litsea glutinosa*.

Table 2. Pollen recorded in the body washings of insects on staminate trees of *Litsea glutinosa*.

Insect species	Sample size (N)	Number of pollen grains		
		Range	Mean	S.D
Apis cerana	10	41-163	104.6	37.7
Apis florea	10	27-128	86.8	25.8
Trigona iridipennis	10	52-104	77.8	14.6
Halictus sp.	10	18-66	46.2	12.2
Vespa bicincta	10	8-47	30.5	9.6
Chrysomya megacephala	10	10-51	33.9	11.1
Sarcophaga sp.	10	6-38	28.2	8.6
Eristalinus arvorum	10	12-54	34.6	10.3
Precis iphita	10	9-47	31.8	9.6
Euploea core	10	15-60	45.5	12.5

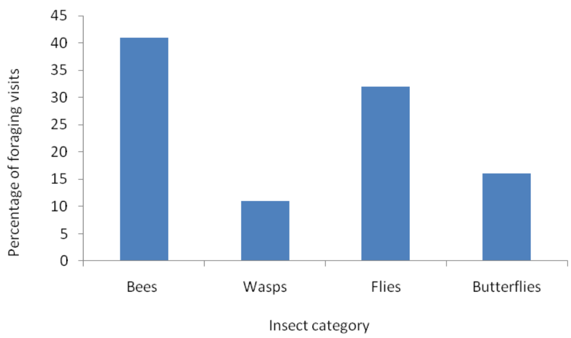

Figure 4. Percentage of foraging visits of different categories of insects on *Litsea glutinosa*.

sometimes glaucous. They are aromatic when crushed. The seeds were brown with dark spots and 7 mm in diameter (Figure 2p). Immature, mature and ripe fruits on pistillate trees showed infestation by the beetle *Bruchus* sp. Infested fruits showed a single larva (Figure 2o). Fruit infestation was 23%. The Indian Giant Squirrel, *Ratufa indica* was found to feed on the fruits regularly during the fruit ripening period. The seed passes through the digestive system of the squirrel and the excreted seed is in its original state but it is softened. The seeds with their small size and smooth surface favor their smooth passage through the digestive system of the squirrel. This squirrel with its swift movements excretes and disperses the seeds in different areas of the forest. Naturally, mature fruits fall to the ground by gravity and the seeds are exposed after the decomposition of fruit pulp. The percentage of seed germination is 17% in the natural habitat.

4. Discussion

Tiwari, Krishnamurthy, Goswami, Pandey, and Singhal (2015) reported that *L. glutinosa* is an evergreen or deciduous polymorphic species with flowering between March and June in Madhya Pradesh. But, the present study showed that it is a fast growing semi-evergreen dioecious species with staminate and pistillate individuals and flowers for a short period during July-August in the Eastern Ghats. Rohwer (1993) stated that all Lauraceae are probably obligate out-breeders, but systematic studies on sexual reproduction of individual species are lacking. In *Persea americana*, the flowers are bisexual and heterodichogamous because each flower opens twice, first functionally as female, then the flower closes and reopens the next day functionally as male (Kubitzki & Kurz, 1984; Rohwer, 2009). In *L. glutinosa*, the involucral bracts act as unified flowers consisting of several florets which have both male and female organs, but functionally they are unisexual, staminate or pistillate indicating dioecy representing an obligate out-breeding system.

Further, the stigma receptivity from the beginning of anthesis to the third day in pistillate florets and anther dehiscence on the second day of anthesis in staminate florets promote obligate out-crossing. The sex ratio is biased in favor of staminate trees which further promotes out-crossing by increased pollen transfer to the pistillate trees via insects. The anthesis of many multi-floreted pseudo-umbels each day and the yellow color of the florets on both the staminate and pistillate trees are well tailored to enhance attraction to insects. The secretion of nectar by specialized glands that occurs only once in the life time of both staminate and pistillate florets seems to be an evolved pattern to discourage repeated visits to the same florets and promote visits between staminate and pistillate trees by insects to maximize the fruit/seed set. Such a nectar secretion pattern was reported in most Lauraceae species with bisexual flowers which open twice in their life time. The first time functions as female during which staminodial glands secrete nectar once and the second time as male during which staminal glands secrete nectar once (Kubitzki & Kurz, 1984; Rohwer, 2009).

Nalini and Nathaniel (2000) stated that Lauraceae members are pollinated by a wide variety of generalist insects such as Hymenoptera, Diptera, and Lepidoptera. Soubadra Devy & Davidar (2006) noted that *Litsea* sp. is dioecious and pollinated by social bees in Kakachi which is a medium elevation wet evergreen forest in the southern Western Ghats of India. Ci, Chen, and Li (2008) noted that *L. szemaois* is insect-pollinated. House (1989) reported that *L. leefeana* with unspecialized flowers was predominantly pollinated by Diptera in a Queensland tropical rain forest. Corlett (2001) reported that *L. glutinosa* was overwhelmingly visited by *Apis cerana* but it paid more visits to the male flowers than the female flowers. The present study showed that the floral characters of *L. glutinosa*, such as light yellow shallow staminate and pistillate florets with slight fetid small and yellow nectar glands, well exposed nectar and actinomorphic symmetry, suggest myophilous syndrome as defined by Faegri and van der Pijl (1979) and Bertin (1989). Accordingly, *L. glutinosa* is pollinated principally by flies although it is pollinated also by other insects. The functionality of myophily in this tree is also in agreement with Armstrong (1979) who stated that fly-pollinated flowers are shallow and unspecialized due to which flies access the nectar with great ease. Myophily, in combination with pollination by hymenopterans evidenced in *L. glutinosa*, has been reported to be a dominating trait among unspecialized entomophilous plants (Jones & Crome, 1990). Therefore, *L. glutinosa* with unspecialized flowers is principally myophilous and pollinated additionally by other insects. Thrips reduce the standing crop of nectar significantly but this situation drives the pollinators to increase foraging visits between staminate and pistillate trees and in effect, the outcrossing rate is enhanced. However, the short flowering season is a drawback for the tree to maximize its fruit and seed set. The recorded fruit set in pistillate trees indicated that myophily is not an efficient pollination syndrome. Further, the *Bruchus* beetle is a pest to fruits as it causes infestation to more than 20% of total fruits produced.

Lauraceae fruits are normally dispersed by frugivorous birds or other animals (Rohwer, 1993). Seed dispersal by birds was reported in *L. cubeba* (Sri-ngernyuang, Chai-Udom, Kanzaki, Ohkubo, & Yamakura, 2003), *L. wightiana*, and *L. mysorensis* (Ganesh & Davidar, 2001). Fruit dispersal by gravity was reported in *L. szemaois* (Ci, Chen, & Li, 2008). In *L. glutinosa*, the fruit dispersal occurs by gravity as well as by the Indian Giant Squirrel (*Ratufa indica*) which disperses seeds through defecation after feeding on the fleshy part of the fruit. Future studies should examine the fate of the seeds dispersed by the squirrel compared to seeds that simply fall from the parent tree. Tiwari, Krishnamurthy, Goswami, Pandey, and Singhal (2015) noted that *L. glutinosa* is able to reproduce vegetatively from root-suckers and in this context we suggest further studies to examine the potential of vegetative mode in addition to propagation by seed.

Figure 5. Percentage of fruit/seed set rate in pistillate trees of *Litsea glutinosa*.

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