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Anemophily, anemochory, seed predation and seedling ecology of *Shorea tumbergaia* Roxb. (Dipterocarpaceae), an endemic and globally endangered red-listed semi-evergreen tree species

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Shorea tumbergaia is an endemic and globally endangered, red-listed, semi-evergreen tree species, restricted to the southern Eastern Ghats in Andhra Pradesh and Tamil Nadu. The flowering is ephemeral and also not an annual event. Massive blooming, drooping inflorescence with pendulous flowers, ample pollen production, gradual pollen release as a function of anther appendage, aerodynamic size of the pollen grains with reticulate exine and muri separated by lumina and strong protogyny – all contribute to anemophily. The plant is self-compatible but there appears to be abortion of fruits from selfed-flowers. The fruits are large, winged and anemochorous. The fruits are attacked by an unidentified bruchid beetle prior to dispersal. In healthy fruits, the seed has no dormancy and it germinates as soon as it falls from the tree. The study reveals that non-annual, massive flowering, short flowering period, partial flowering at tree level, seed predation, short-distance seed dispersal, absence of seed dormancy, low rate of seedling establishment and inability of seedlings to compete with other plants collectively contributed to the occurrence of a small population of *S. tumbergaia* in a restricted area of the Eastern Ghats forests and interplay of all these factors might have led to the ‘endangered’ status of this species.

Keywords: Anemochory, anemophily, protogyny, seed predation and seedling ecology, *Shorea tumbergaia*.

THE genus *Shorea* (family Dipterocarpaceae) is native to Southeast Asia, from northern India to Malaysia, Indonesia and the Philippines^{1,2}. It is a tropical genus with 196 species of mainly rainforest trees, out of which 148 species are currently listed in the IUCN Red List; majority of them are listed as critically endangered. Many species are economically important timber trees. Janardhanan³ documented that *Shorea* species are found on the borderline between the moist fertile evergreen forests and the less moist and dry deciduous forests in India. The *Shorea* species found in India are *S. assamica*, *S. robusta*, *S. roxburghii* and *S. tumbergaia*. The last species is an endemic and globally endangered semi-evergreen tree species,

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restricted to the southern Eastern Ghats up to 1000 m, distributed in Seshachalam and Veligonda Hills in Cuddapah, Tirupati Hills in Chittoor District, Andhra Pradesh and North Arcot and Chengalpattu districts, Tamil Nadu. It is more prevalent in drier areas in non-teak mixed deciduous forest vegetation at an altitude of 300 m amsl⁴. The tree trunk is used as flag poles for temples. The stem is a source of resin, which is used as incense and as a substitute in marine yards for pitch. It is also used in indigenous medicine as an external stimulant and a substitute for *Abietis*; *Resina* and *Pix Burgundica* of European pharmacopoeias⁵. The plant extracts are used as a cure for ear-aches and leaf juice is used as ear drops for children⁶. Despite the endemic and endangered status and economic and medicinal importance of *S. tumbuggaia*, there were absolutely no studies made on its reproductive ecology and regeneration problems contributing to restricted distribution and limited population size in the Eastern Ghats of India. Therefore, the present study was undertaken to find out the reproductive ecology, seed predation and seedling establishment rate in *S. tumbuggaia* in its natural distribution areas on Tirupati Hills.

Forty-five individual trees located at an elevation of about 300 m in Akasaganga and Papavinasanam areas of Tirupati Hills in the Eastern Ghats were selected for the study during the flowering and fruiting season of 2007 and 2008. The flowering phenology, and floral structural and functional details were examined following the methods of Dafni *et al.*⁷. Observations on flower visitors and their foraging activity period with reference to pollination were also made by using binoculars. Five mature buds each from five inflorescences were bagged without hand pollination and followed for one month to test self-compatibility and self-pollination. Fruit-set rate, maturation and fruit-fall period, dispersal, seed predation, seed germination and establishment aspects were thoroughly examined to understand the factors responsible for the limited population size of *S. tumbuggaia*. For this purpose, 96 inflorescences with 2018 flowers were tagged and followed until seedling establishment in and around the study area.

S. tumbuggaia trees bear adequate foliage during and after the rainy season (Figure 1a). It has reduced foliage during late winter and early dry season. At the same time, gradual new leaf flushing occurs. The leaf transitional stage characterized by leaf fall and leaf formation is quite prominent during April–May. Flowering occurs during the fourth week of April and first week of May. Of the 45 trees, ten are canopy trees at 12–15 m height, while all other trees are sub-canopy trees at 8–10 m height. Flowering occurred on some branches exposed to sunlight in seven canopy trees (four at Akasaganga and three at Papavinasanam) in 2007 and five canopy trees (three at Akasaganga and two at Papavinasanam) in 2008. During each year, the flowered trees were different at both the study sites. Mass flowering occurred during the short

flowering period and the flowers were covered under the foliage. Inflorescence is a 15–20 cm long, drooping, terminal or axillary racemose panicle with an average of 18 ($R = 15–21$) flowers which anthesise over a period of 7 days ($R = 5–11$). Flowers are horizontal initially and later hang downwards. They are pedicellate, milky-white, fragrant, 1.5 cm long and 2 cm across, bisexual with marked protogyny, zygomorphic, cup-like at the base and star-like terminally. Sepals are five, blunt-lobed, 0.3 cm long, light green, imbricate, basally united into a cup, free terminally and persistent. Petals are five, milky-white with mild fragrance, 1.3 cm long, connate at the base forming a cup-like structure, free terminally. They are slightly twisted in bud and unfold at anthesis; each petal tapers, is wrinkled and faces upwards. Stamens are 42 ± 2 ($R = 40–45$), free, arranged closely in three whorls to the base of the corolla (Figure 1f); the filaments are 0.3 cm long. Their placement is at a much lower level to the height of stigma. Anthers are 0.1 cm long, light brown, dorsifixed but appear to be basifixed, tetrasporangiate and dehisce by longitudinal slits. The connectival part of the filament of each anther extends into a sterile tip to the anther constituting ‘anther appendage’ (Figure 1g). The pollen production per anther is 643 ± 56.42 grains, and per flower is 27,006. The pollen grains are yellow, radially symmetric, tricolporate, 25–30 μm long and have reticulate exine with muri separated by lumina (Figure 1h). Ovary is semi-inferior, syncarpous with three locules, each having two light-yellow ovules. Style is subulate and emerges out in bud stage about a day prior to anthesis (Figure 1b and c); it is semi-wet and extended into a minutely tri-lobed stigma (Figure 1i). The petals, stamens, style and stigma fall off on the third day, while the sepals remain until the fruits drop-off.

The flower opening occurs by 0800 h (Figure 1c–e) and anther dehiscence 2 h after anthesis. The petals unfold and spread upwards gradually giving a star-like appearance. The cup-like flower base with stamens is exposed to the outside environment. The flowers do not secrete nectar. The stigma is receptive prior to anthesis, and remains so for two days by being in a semi-wet state; it is dry and shows signs of withering by the end of the second day. The pollen release from dehiscent anthers was gradual when the flowers were shaken manually. The dehiscent anthers became empty after several shakes manually. Stingless bee, *Trigona iridipennis* was found to collect pollen from the flowers without any difficulty, during which it mostly contacted the stigma. Several bees were found foraging on the same tree during 0800–1600 h. They tended to stay mostly on the same tree to collect pollen.

Three out of 25 mature buds bagged without any hand pollination produced fruits, indicating the presence of self-compatibility and self-pollination. The natural fruit set rate is 15%. Each fruit produces only one seed against the actual number of six ovules. The fruits take about

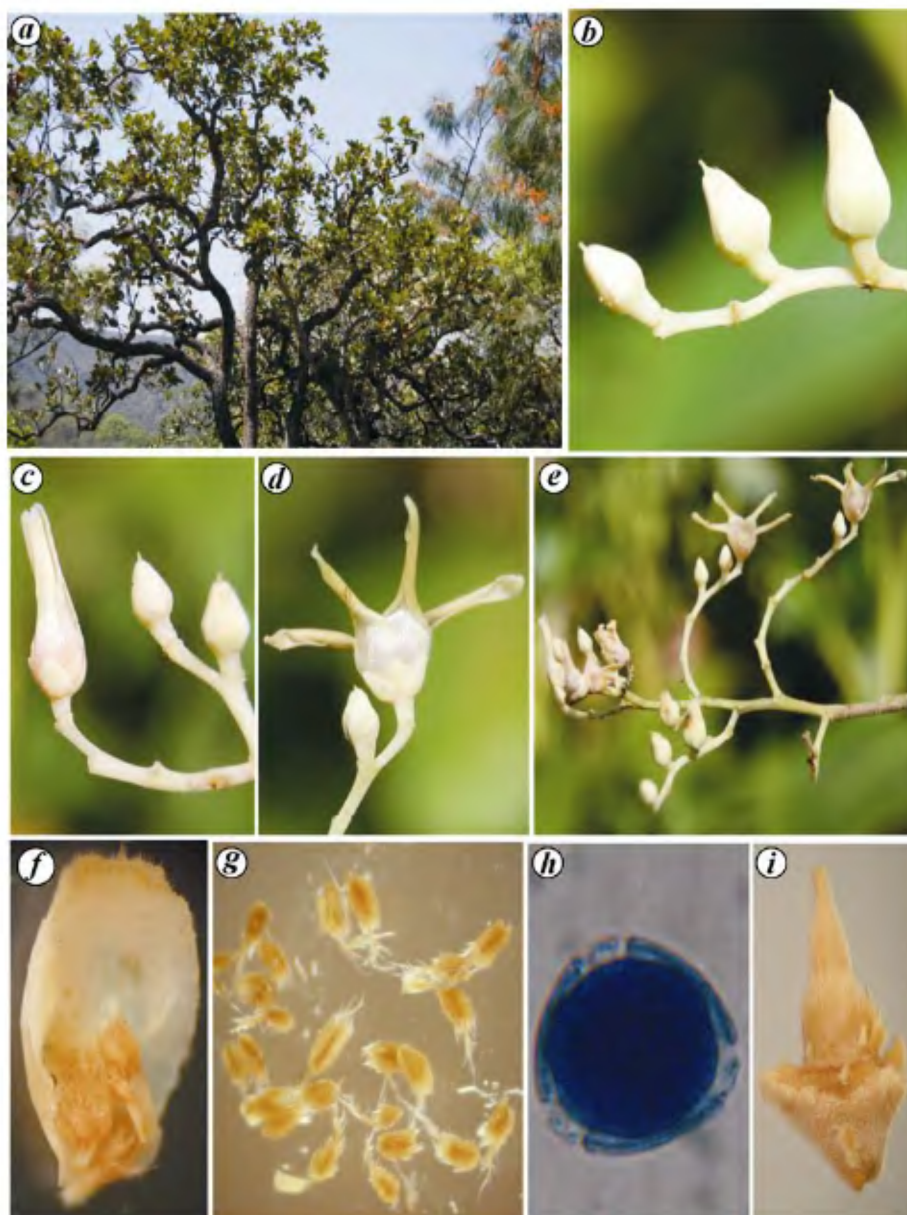


Figure 1. *Shorea tumbergaia*: **a**, Tree habit; **b**, Young buds; **c**, (Left) – Mature bud and (Right) – Young buds; **d**, Flower; **e**, Flowering inflorescence; **f**, Stamen position at the base of the corolla; **g**, Stamens with appendages; **h**, Tricolporate pollen grain; **i**, Ovary with style and minutely tri-lobed stigma.

4 weeks to mature. The sepals are accrescent in that they are thickened, and three of them expand into wings and are larger than the other two sepals (Figure 2 *a* and *b*). The fruit wall is free from calyx, woody, with a thin inner membranous lining invaginated into the folds of cotyledons and split into two parts at the apex. The seed has no dormancy and the embryo is chlorophyllous. It begins germination immediately after the fruit falls to the ground. Seed germination is cryptocotylar, semi-hypogeal and rapid. The hypocotyl is red, long, cylindrical, takes different twists and eventually penetrates into the soil to produce the root system and the leaves (Figure 3 *a–i*).

The fruits were found to be infested with an unidentified Bruchid beetle. It was found at the early stage of

fruit development, had pierced the pericarp and deposited a single egg. When the egg hatched, the young larva burrowed into the developing seed to use it as food source (Figure 2 *c* and *d*). The pierced part from the pericarp into the seed formed a hole throughout and the larva used this hole for exit (Figure 3 *j* and *k*). Fruit fall occurred when the larva was still in its growing stage. The larva left the seed and fruit through the hole after completion of its development and pupated in the soil. The pupal stage was observed for 6 weeks, but there was no emergence of adult; this long period was considered as the dormant stage of the pupa for the emergence of the adult when conditions were favourable in the forest floor. Fruit infestation rate was 70%. In the healthy fruits, seedling establishment rate

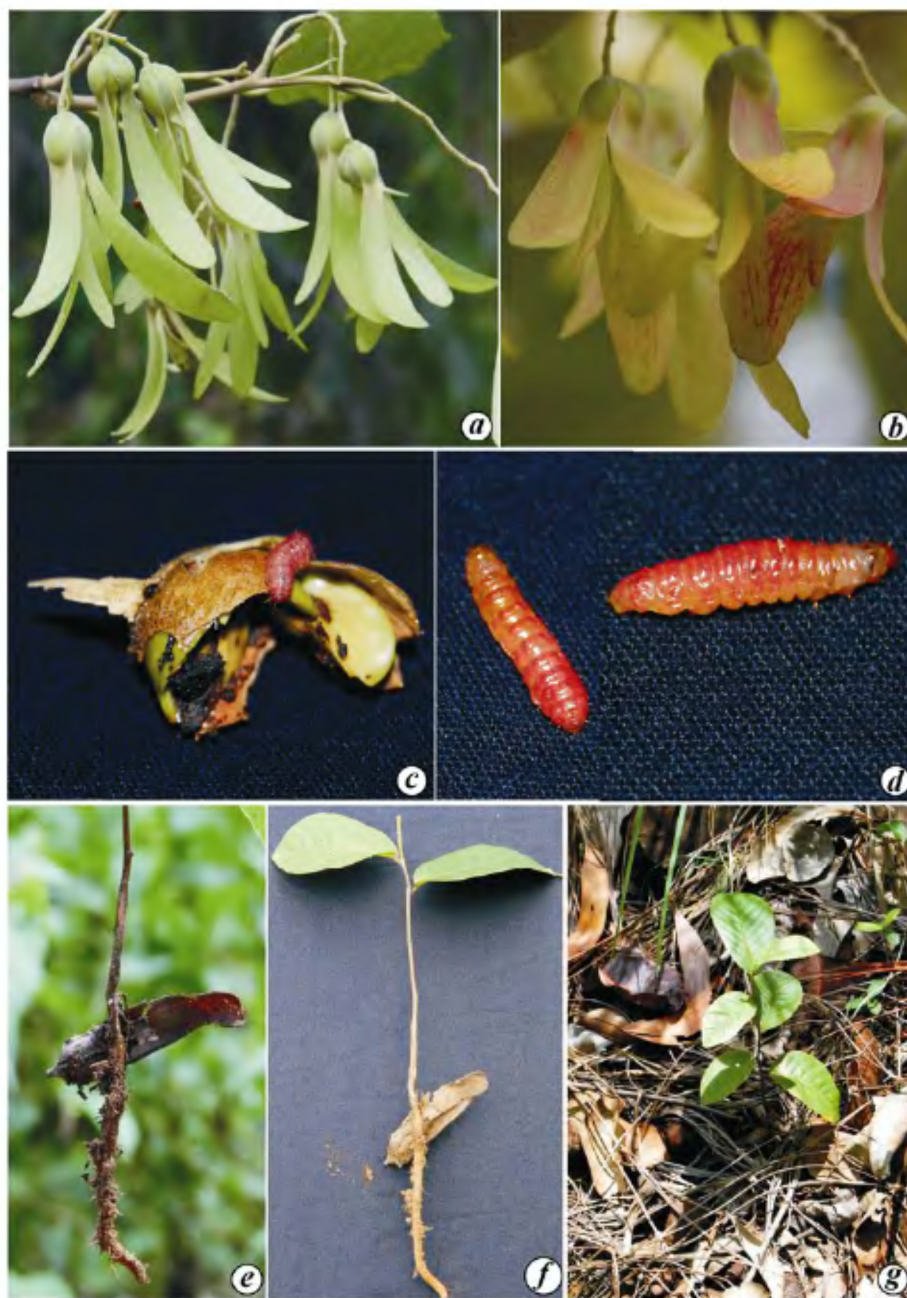


Figure 2. *S. tumbuggaia*: **a**, Healthy, young, hanging winged fruits; **b**, Healthy, maturing hanging winged fruits; **c**, Single red larva inside the fruit; **d**, Well-developed larvae ready for pupation in soil; **e** and **f**, Hypocotyl establishment and production of first leaves while still attached to residual fruit; **g**, Established seedling.

was 48%, but it was only 14% compared to the total fruits produced (Figure 4).

The ripe, dry, winged fruits fell to the ground and dispersed within 10 m area of the tree due to wind action. The floor of the forest in the surroundings of *S. tumbuggaia* was found with a mixture of rocks and soil together with litter and other low-ground herbaceous growth, especially grasses. The forest floor rich in nutrients was found to be good for the seedlings to establish there (Figure 2 e–g); but soon the seedlings were suppressed by competition of other plants.

S. tumbuggaia as a constituent of the seasonal forest in the Eastern Ghats, is semi-evergreen and exhibits leaf transitional stage which is characterized by simultaneous leaf fall and new leaf flushing during April–May. This leaf phenology could be due to drought conditions in the forest and it may provide a stimulus for the onset of flowering. The flowering also occurs exactly during this period. Similar leaf phenology coinciding with flowering has been reported in *Shorea robusta*⁸. In *S. tumbuggaia*, flowering is not an annual event and even in the flowering individuals, it is restricted to branches which are



Figure 3. *S. tumbuggaia* (winged fruits): *a*, green fruit; *b-i*, Different stages of hypocotyl growth from fallen ripe fruits; *j*, Visible hole on young green fruit; *k*, Exit hole for larva from ripe fallen fruit.

exposed to sunlight. The flowering pattern in such branches represents a massive pattern in which more flowers are produced per day for about 2 weeks only^{9,10}. Mass flowering is considered as a property of the individuals of a plant species¹¹, and this pattern of flowering may have evolved among individuals of *S. tumbuggaia* to rapidly utilize the available energy resources during the leaf transitional stage to produce flowers en masse. The new leaf may take up the role of providing energy resources more efficiently to the fertilized flowers to produce fruits.

The occurrence of flowering in *S. tumbuggaia* takes place only in canopy trees. The lack of flowering on the

branches not exposed to sunlight and in sub-canopy trees suggests that sunlight has an important role to provide the necessary stimulus to initiate flowering. However, the flowering seems to be controlled by intrinsic mechanisms and occurs only when it is due, with adequate sunlight falling on the branches during the dry season.

In *S. tumbuggaia*, fruit set observed in bagged flowers is an indication of the presence of self-compatibility and self-pollination. But, the flowers are strongly protogynous as the stigma protrudes out of the bud a day prior to anthesis. The protogyny is a character associated with self-compatible anemophilous flowers to reduce selfing¹².

In *S. tumbuggaia*, the drooping inflorescence, hanging flowers with compactly arranged anthers at the base and held above by anther appendages, and the exposed cup-like flower base collectively aid in the gradual dispersal of pollen by wind. Gradual pollen release occurs when the flowers are manually shaken; it suggests that wind force does not make the anthers release the pollen at once and hence, there is an in-built device for the gradual and economical release of pollen from the oscillating flowers due to wind force. The pollen thus released is carried away and transported to the reception sites of flowers in quick succession. The study site experiences moderate turbulent atmospheric conditions especially during the forenoon period and this favours efficient transport of the entrained pollen¹³. Further, the long-distance transport of pollen and cross-pollination with the aid of wind are most likely to occur with flowering inflorescences in canopy trees of *S. tumbuggaia*. The pollen grain size is a characteristic of a typical aerodynamic particle, which permits effective wind transport and deposition on the stigma through impaction^{14,15}, and the characters such as reticulate exine and muri separated by the lumina may reduce terminal velocity and contribute to the increased dispersal range of pollen¹⁶. Additional adaptations for anemophily are high pollen production at flower level and near synchronous anthesis at tree level. In *S. robusta* also, similar pollen release mechanism and anemophily have been reported¹⁷.

In the study area, bees, wasps, thrips, beetles and butterflies have been found and the foraging activity of these insects has been observed on the co-flowering species, *Boswellia ovalifoliolata*. The Dammer bee, *Trigona iridipennis* is the only species found to collect pollen from the nectarless flowers and effect mostly self-pollination, as it tended to stay mostly on the same tree. This bee also requires nectar for its use, but it is not produced in the flowers. *S. tumbuggaia* with pollen as the only reward is not attractive to insects and hence the flower is not adapted for entomophily. Therefore, any insect activity on the flowers contributes to enhanced pollination.

In *S. tumbuggaia*, protogyny is a system evolved to prevent selfing but the fruit set observed in bagged flowers suggests that self-incompatibility is weak. This is also

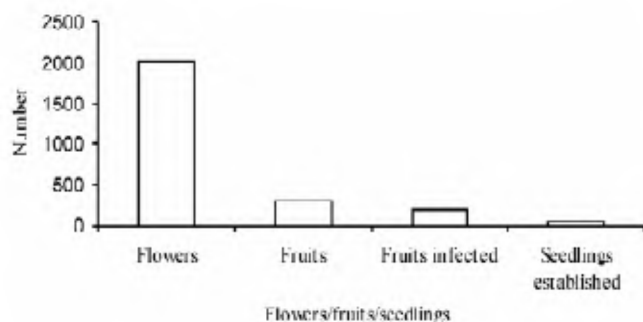


Figure 4. Fruiting and seedling establishment rate in *S. tumbuggaia*.

supported by the natural fruit-set rate which is on the higher side. Further, with mass flowering the protogyny is not effective to prevent self-pollen deposition. However, protogyny with the stigma protrusion from the bud prior to anthesis enables the stigma to capture pollen grains from the air, starting from bud stage onwards and to protect it from self-pollination. The weak self-incompatibility system functional in this species seems to be adaptive to achieve both cross- and self-pollination. Such a sexual system assures fruit set with self-pollination, when cross-pollination fails. A similar sexual system has been reported in *S. robusta*¹⁷.

In *S. tumbuggaia*, the fruits are winged, mature quickly within a month and each fruit invariably produces a single seed with a large chlorophyllous embryo. As the seeds lack dormancy and germinate as soon as they fall from the tree, the large chlorophyllous embryo may aid in better survival in unpredictable habitats with irregular supply of light, nutrients and water during the germination period^{18,19}. Seeds die if moisture content is too low and temperature is too high; they are difficult to store for artificial regeneration and same are often described as 'recalcitrant'²⁰. The winged character of the fruits is seen in most dipterocarps and it is an important adaptation for dissemination by wind¹. The winged structure of the sepals allows the single-seeded fruits to gyrate toward the ground and hence the seed dispersal is anemochorous. The distance of seed dispersal by wing is up to 10 m only due to the semi-closed nature of the canopy cover of the forest. The dispersal of winged fruits takes place much more efficiently by wind if the forest is of open seasonal dry deciduous type²¹. The seeds fallen on the ground have no possibility for further dispersal by sweeping action of the wind due to litter accumulation and grass growth in the study area. But in *S. albida*¹, seed dissemination by wind is up to 2 km.

Different insect species attack the seeds of *Shorea* species during their development²². Insect pests attack at the pre- or post-dispersal stage of the seed; in the pre-dispersal stage, the pest attacks the fruit on the tree before dispersal, while in the post-dispersal stage the pest attacks fruits on the ground²³. Khattua and Chakrabarti²⁴ reported that many Bruchid species spend a dormant stage as pupae in the soil and this holds true in case of the Bruchid pest of *S. tumbuggaia* seeds. They also reported that in India, the seed weevil *Sitophilus (Calandra) rugicollis*, attacks seeds of *S. robusta*, survives as a dormant adult in the forest floor and emerges with the first monsoon rain, which coincides with the commencement of seed fall²⁴.

Mass fruiting appears to favour seed predators, but it can also be a strategy to escape complete seed destruction²⁵. Seed predation can be high, and the crop can be completely wiped out. Natawiria *et al.*²⁶ observed that weevils (Curculionidae) damage 40–90% of the seeds of *Shorea pauciflora*, *S. ovalis*, *S. laevis* and *S. smithiana*. In *S. tumbuggaia*, estimated seed damage was 70% and seed-

ling establishment took place from only about half of the remaining healthy seeds in the forest area. This suggests that seed predation by the Bruchid beetle is the principal limiting factor for the regeneration of *S. tumbuggaia*. Further, the failure of half of the healthy seed crops to germinate indicates that there may be abortion of seeds resulting from self-pollinated flowers, which may be a consequence of the post-zygotic incompatibility system. The existence of such a post-zygotic incompatibility system has been reported for tropical forest trees^{27,28}. With such a system, fruit set in self- and cross-pollinated flowers is initially high, but during development, fruits from self-pollinated flowers suffer from higher abortion rates than those from cross-pollinated flowers^{29,30}. The seed begins germination as soon as it falls to the ground.

The study reveals that non-annual, massive flowering, short flowering period, partial flowering at tree level, seed predation, short-distance seed dispersal, absence of seed dormancy, low rate of seedling establishment and inability of seedlings to compete with other plants collectively contributed to the occurrence of a small population of *S. tumbuggaia* in a restricted area of the Eastern Ghats forests, and the interplay of all these factors might have led to the 'endangered' status of this species.

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