Floral device for obligate selfing by remote insect activity and anemochory in *Wrightia tinctoria* (Roxb.) R.Br. (Apocynaceae)

*Wrightia tinctoria* is a deciduous tree with milky latex. It has medicinal and economic importance. Its flowers and seeds yield a yellow dye which is useful as an adjuvant in dyeing. The seeds are also useful in flatulence and bilious affections. They are also reported to be having aphrodisiac and anthelmintic properties. Further, the dry wood which is white and even-grained is used in making toys and household items. Despite these multiple uses, *W. tinctoria* has not been studied thoroughly for its reproductive biology. The present study was contemplated to describe the sexual system, pollination mechanism, pollinators and seed dispersal in *W. tinctoria*. These aspects have been studied during 2003 and 2004 for *W. tinctoria* occurring in the Andhra University campus and the surrounding areas in Visakhapatnam, Andhra Pradesh, India. Sixteen trees were used for making field observations and experimentation on the aspects described here.

Flowering period and floral characteristics were observed for their relationship with the pollinator fauna. Twenty bagged flowers were used to measure nectar volume and sugar concentration at different times of the day. Sugar concentration was observed using a Hand Sugar Refractometer (Erma, Japan). Pollen production per flower was determined according to Dafni. Fifty mature buds intended for autogamy were bagged and followed for fruit set. Twenty panicles with 2400 flowers on five trees were tagged and followed until pod set to determine the natural fruit set and seed set rates. Flower visitors were observed during daytime from the time of anthesis to the late evening of the day over a period of three weeks during each year of study. They were observed for their flower-probing behaviour and pollination role in *W. tinctoria*. Fruit dehiscence and seed dispersal mode were carefully observed.

*Figure 1. Wrightia tinctoria: a, Mature bud; b, Flower; c, Connivent stamens with sagittate arrangement of anthers, enveloping the stylar head; d, Style and stigma inside the connivent stamens; e, Fruit (a mericarp with two pendulous, green follicles fused at the tip); f, Seed with a tuft of white silky hairs.*
*W. tinctoria* flowers during dry season from the second week of April to the first week of June. It shows sparse flowering occasionally during the rainy season from the second week of July to the second week of August. It produces bisexual flowers on terminal panicles. The flowers are creamy-white, fragrant, actinomorphic and hypogynous. The calyx consists of five small, green-coloured sepalas. The corolla has a short cup-shaped tube at the base around the ovary, and is divided into five elaborate petals. Hairy appendages arise from the inner side of the throat of short corolla tube and are arranged in 2–3 series. The stamens are five, connivent with sagittate arrangement of anthers and inserted near the base of the short corolla tube. They are arranged in a whorl forming a cone-shaped structure enclosing the style and stigma (Figure 1 c). The filaments are not fused with each other and there is a wide gap at their insertion point, and this gap is gradually narrowed towards the tip (Figure 1 d). The narrow gap between the filaments facilitates the passage of sunlight only (Figure 2 a). Anthers dehisce introrsely by longitudinal slits. Pollen grains are creamy white and sticky throughout the flower life. A flower produces 4235 ± 53 pollen grains which are 35.69 ± 3.80 μm in size. Every flower has two carpels, each with one free ovary; but both ovaries have a common style and stigma which are situated slightly below the level of the anthers and completely concealed by the corollal filaments. The style is simple, but the stigma is highly viscid and massively thickened with a ring below. The ring has tiny grooves that run parallel to and intersect with the narrow gap between the filaments (Figure 1 d). In effect, the stigma region is completely sealed-off from the rest of the conical part of the stamens and the flower (Figure 2 b). Each ovary produces 38 to 62 ovules, but on an average, 97 ± 14 ovules are produced per flower. A flower produces 6.5 ± 0.69 μl of nectar in the short corolla tube around the ovary. The nectar sugar concentration is 19% at anthesis and it gradually increases to 32% through the day. The mature buds open daily during 0300–0400 h (Figure 1 a and b). The nectar is available at anthesis. When this nectar was removed manually, there was no further secretion indicating that the flower does not produce nectar following its removal by insect visitors. The sticky pollen grains and concealed anthers indicate that there is no possibility for pollination by wind. Wind causes swinging of flowers on their pedicels, but it does not cause any disturbance to the stamens to result in self-pollination. The flowers covered with porous butter-paper bags intended for unmanipulated autogamy showed no fruit set, indicating that wind has no role in effecting self-pollination. According to Renner, wind-pollination and wind seed dispersal almost never co-occur. This appears to be completely true in *W. tinctoria*, which is anemochorous.

*W. tinctoria* flowers with concealed anthers provide only nectar as a reward to the insect visitors. The flowers with their fragrance and creamy white colour of the corolla and filaments attract different insects. Bees (*Apis cerana indica, A. florea, Trigona iridipennis* and *Ceratina similima*) were found collecting nectar almost never co-occur. This appears to be completely true in *W. tinctoria*, which is anemochorous. The nectar is of a concentration 19% at anthesis and it gradually increases to 32% through the day. This may be attributed to a gradual increase in temperature, occurrence of a small percentage of the rewarding flowers and non-secretion of nectar following its removal by them. Wasps (*Delta coideus* and *Rhynchium metallicum*) and butterflies (*Catopilia pyramide, Anthes lat poopae and Cerata narissa*) were also found feeding on nectar occasionally from 0800 to 1700 h. Ants (*Camponotus sp. and Crematogaster sp.*) were resident foragers and collected nectar during sunlight hours. All these insects visited the flowers in an upright position, landed on the petals and hairy appendages, and inserted their proboscis through the wide openings between the staminal filaments at the base to collect nectar. While leaving the flower, the proboscis of the insects often got stuck in the narrow space between the filaments towards the apex. In this act, the filaments do not bend or become stiff after the departure of the foragers. In effect, such insects struggled to release their proboscis, but their attempts were mostly futile; some left the flower without the proboscis and some others died in the flower subsequently. In a sample of 400 flowers collected at the end of the day, 94 contained the proboscis or ants (sometimes even two in a flower) inside the staminal cone and bees in the hairy appendages of the corolla. The struggling insects caused disturbance and/or vibrations to the staminal filaments, which in turn made the dehisced anthers with sticky pollen grains to contact the wet and viscid stigma. In effect, pollen transfer takes place from the anthers to the stigma. This results in self-pollination without any bodily contact between insects and the anthers and stigma, suggesting that *W. tinctoria* has evolved...
a remote device to achieve self-pollination with the aid of nectar-feeding insects. However, this pollination mechanism is a silent killer of insects.

Reddi et al. have not reported thrips as flower visitors of W. tinctoria. We found that thrips (Thrips hawaiiensis and Haplothrips tardus) were the resident and common visitors to the flowers of W. tinctoria. They were found to feed on nectar only, as there is no access to the anther-stigma chamber to collect pollen and stigmatic secretions. Their nectar-feeding activity does not contribute to effecting self-pollination, because they are tiny insects and do not get stuck in the narrow space between the filaments to cause disturbance to the filaments and result in self-pollination. This suggests that the thrips deplete the nectar crop that is required by pollinating insects. The occurrence of thrips in large colonies on W. tinctoria indicates that the latter seems to be the host plant for its reproduction during dry season, and its flowers with short corolla tube surrounded by hairy apicules may serve as oviposition sites. The fragrant odour and creamy white colour of the flowers collectively attract thrips. Further, the sticky pollen, nectar and stigmatic exudates present in the flowers serve as food for the thrips. But, the thrips act as pests if they feed on the stigmatic exudates and sticky pollen in W. tinctoria flowers. In effect, the plant might have evolved a protective device to conceal the anthers and stigma with the staminal filaments to avoid thrips from eating them and also to prevent them from drying up. But, this mechanism involving concealment of the sex organs from all the foraging insects is useful to achieve only self-pollination within the flower, as there is no possibility for the foraging insects to access the sex organs for pollen transfer to effect geitonogamy and cross-pollination. Therefore, this pollination mechanism seems to have evolved in response to the feeding behaviour of thrips. It suggests that the flower–insect adaptations evolve continuously as the dynamics of pollen transfer mechanisms is closely related to the behavioural characteristics of the pollinators.

W. tinctoria produces mericarp fruits, each with a pair of pendulous follicles joined at the tips (Figure 1e). The natural fruit set is 3.7% only and the seed set 72.76%. The low fruit set rate is attributable to the random occurrence of self-pollination by insects during their struggling behaviour and the energy resources available to the plant during dry season. However, it is compensated by the higher seed set rate. The fruits are green initially and brown when mature. They mature during the dry season itself and dehisce longitudinally, liberating the seeds into the air. The seeds are 15 to 18 mm long, pointed at the ends, linear, light greyish-brown, light and crowned with a tuft of white silky hairs (Figure 1f). These constitute aerodynamic traits of anemochorous tree species, suggesting that W. tinctoria is anemochorous and evolved these expensive morphological structures for effective seed dispersal. Further, plant height and wind speed also contribute to long-distance dispersal. However, seed dispersal by wind is often considered to be inefficient because it is involved with expensive morphological structures and indiscriminate placing of seeds in every type of habitat, causing failure of seed germination or seedling mortality in unfavourable situations.

But, the seed characteristics in W. tinctoria suggest that it is imperative for this plant to use wind for dissemination of its seeds. Therefore, W. tinctoria exhibits entomophily and anemochory for the success of its sexual reproduction.

1. Thammanna and Narayana Rao, K., Medicinal Plants of Tirumala, Department of Gardens, Tirumala Tirupati Devasthanams, 1990.

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