Flower Visitors and Potential Major Pollinator of Diospyros blancoi A. DC. in Taiwan

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At least eight arthropod species belonging to five taxa as flower visitors of Diospyros blancoi A. DC. were investigated in terms of their visiting frequency, activities on the flowers and pollen-bearing capacity. The main results of this study are as follows: First, thrips particularly Thrips hawaiiensis (Morgan) (Thysanoptera: Thripidae), and ants showed the highest visiting frequency. Second, the long pollination distance and the fruit-set on single female trees isolated by water barriers indicate that arboreal ants were not pollinators. Third, thrips species other than T . hawaiiensis were not observed in this study. Fourth, male flowers provided shelter (flower tube) and food (pollen) for T. hawaiiensis. Fifth, T. hawaiiensis visited both blooming and non-blooming female flowers. Finally, pollen was found only on thrips visiting either male or female flowers. Our results suggest that T . hawaiiensis is the major pollinator of *D. blancoi* in Taiwan.

Key Words: Diospyros blancoi A. DC., entomophily, flower-dwelling thrips, flower visitor, mabolo, pollination, Thrips hawaiinensis (Morgan) (Thysanoptera: Thripidae)

INTRODUCTION

Evolving and radiating from the Philippines, Diospyros blancoi A. DC. (Synonyms: D. discolor, D. philippinensis, etc.) has now extended northward to as far as the southern and eastern regions of Taiwan (Li et al. 1994). Its wood is considered as top quality ebony. Moreover, large, fragrant, edible D. blancoi fruits (commonly known as mabolo or velvet apple) have been traditionally consumed by aborigines. Analysis on the nutrients in mabolo conducted in the Philippines and India show the fruit as an excellent source of iron, calcium, and vitamin B complex (Morton 1987). Recent findings also confirmed that mabolo is rich in aroma compounds and nutrients (Hung et al. 2015a). At present, due to the advancements made in selection and breeding, D. blancoi fruits have become of high economic value (Hung et al. 2007, 2009 and 2015a, b).

Diospyros blancoi is a dioecious arbor plant, and its flowers, including inflorescences, are either axillary, sympetalous, campanulate (♀) or tubular (σ) in shape. Male inflorescences consist of up to four flowers. In fully opened male flowers, the flower tube is almost completely filled with a large number of filaments and anthers, but anthers are not exserted from the tube (Fig. 1A). The inside of the male flower tube is quite crowded, and nectarines appear to be absent. When the mature anther dehisce, a large amount of pollen is scattered, filling the flower tube. Although the pollen is dry and powdery, it does not get carried in the wind but often forms small aggregates. Female plants produce only a single solitary flower inside a

Fig. 1. Thrips hawaiiensis in male and female Diospyros blancoi flowers. The arrows show (A) T . hawaiiensis coming out from the male flower tube, and (B) T. hawaiiensis visiting the female flower.

leaf axil. Flowers have a single pistil, and stigma with four tapered ends. In mature flowers, the pistil stretches out slightly beyond the tube (Fig. 1B). Unlike in the male flower, the inside of the female flower tube is quite empty. Due to the apparent absence of nectaries and dry pistil base, it seems to produce no nectar or only a small amount of nectar. D. blancoi has strongly scented flowers with complex scents (Pan et al. 2008), related to biotic pollination (Farre-Armengol et al. 2015). According to aeropalynological studies, in the habitat of D. blancoi in the Pingtung area of southern Taiwan, D. blancoi pollen does not exist in the air during the flowering period in April (Huang 1998). However, according to the flower and pollen characteristics of D. blancoi, the flowers are not anemophilous, but rather match the characteristics of entomophilous flowers. Fletcher (1942) stated that wind may also contribute to pollination in *D. virginiana*, but did not give evidence.

Flower visitors of D. blancoi are rarely observed in nature, but the average seed number of one mabolo, according to our preliminary investigation, is more than seven (Table 1). The pollinators of the genus Diospyros have not been previously investigated, except for those of D. kaki and D. virginiana. The potential pollinators of D. kaki include bees, wasps and flies (Free 1993), while D. virginiana is generally pollinated by bees (Fletcher 1942). Although these three groups of insects of flower visitors are abundant in *D. blancoi* habitats in Taiwan, they are rarely (even not) found to visit the flower of D. blancoi.

The appearance of mabolo is similar to that of persimmon and is characterized by parthenocarpy. Our preliminary test showed that seedless fruits can be obtained by using either "flower bagging" or "stigma removal" method on the eve of blossom; however, we found even after such manipulations, a few seeds can be formed in some fruits. Without considering the possibility of apomixis, this suggests that prior to stigma removal or bagging, early pollination had taken place (Hung et al. 2015b), and the pollinator (s) should be very small. In fact, apomixes in Ebenaceae were never reported. This study therefore aimed to investigate the flower visitors and identify the major pollinator of D. blancoi.

MATERIALS AND METHODS

Overview of Habitat of D. blancoi Sample Tree

All the sample trees in this study were found in nature or semi-nature forest instead of orchards in Taiwan, including Kenting (21° 57' 37" N, 120° 48' 41" E), in Dulan, Taitung (22° 53' 16" N, 121° 14' 19" E), in Zhongpu, Chiayi (23° 22' 54" N, 120° 31' 41" E), and Taipei (25° 01' 56" N, 121° 30' 33" E) from 2010 to 2012. Maximum and minimum monthly average temperature (°C), annual average temperature (°C), annual rainfall (mm), daylight hour and relative humidity (%) in Kenting were 20.7 (January), 28.4 (July), 25.1, 1779.6, 1727.8 and 74.1; 19.5 (January), 28.9 (July), 24.5, 2022.4, 2233.8 and 75.2 in Dulan, Taitung; 16.5 (January), 28.6 (July), 23.1, 1774.3, 2066.7 and 80.6 in Zhongpu, Chiayi; 16.1 (January), 29.6 (July), 23.0, 2405.1, 1405.2 and 76.6 in Taipei.

Observations of D. blancoi Flower Visitors with the Naked Eye

The first step of this study was to observe flower visitors of D. blancoi with the naked eye during daytime. Observation was conducted on scaffolding beside the sample tree where the whole canopy was visible. When necessary, flower visitors were captured and identified. Because we had to wait and observe under sun exposure, the observation period was divided into six sessions during the flowering period. The six sessions were: 06:00–08:00, 08:00–10:00, 10:00–12:00, 12:00–14:00, 14:00–16:00, and 16:00–18:00. Three male and three female trees were observed in each session. Therefore, the total duration of observations per tree gender was 36 h, which is equivalent to three daytimes. In total,

Table 1. Rates of fruit set and seed set of mabolo (Diospyros blancoi) by nature.

	Distance from Target Female Tree to Closest Male Tree (m)						
Status	10	$10 - 50$	$50 - 100$	100-1000			
Fruit set rates ($n = 100$)		68	70	80			
Seedless rates							
Average seed no. ^x	7.04 ± 0.88 ^a	7.17 ± 0.92 ^a	7.10 ± 0.94 ^a	7.13 ± 0.9^a			

^aThe same superscript letter "a" indicates non-significant LSD difference comparisons of paired data, $P > 0.05$.

 x The maximum seed number in one mabolo is 8.

observation time of the two genders was 72 h, which is equivalent to six daytimes. During each session, we identified flower visitors to the species level or higher taxa and recorded the frequency they appeared. In addition, we randomly selected 20 flowers to check smaller-sized flower visitors at close distance. Each flower was observed for more than 2 min. This observation was conducted in the flowering period in 2010, spanning approximately 30 d. Observation was conducted in Kenting, southern Taiwan.

Flower Collection for the Identification of Pollinators of D. blancoi

We pruned the leaves on the branches where flowers were to be collected during the next day to avoid impediment of flower collection. Flowers or inflorescences were encased in resealable bags, then quickly removed from the branches and sealed. These bags were frozen for at least 4 h, and then defrosted. A small amount of silica desiccant was placed in the resealable bag to avoid moisture buildup. After defrosting, flower visitors in the bag, as well as flowers were microscopically examined (dissecting microscope) for species identification and bearing of pollen. We sampled 30 female flowers (15 flowers from 3 trees, 5 flowers per tree in Kenting; 5 flowers from 1 tree in each source in Dulan in Taitung, Zhongpu in Chiayi, and Taipei) and 18 inflorescences including 40 male flowers (9 inflorescences from 3 trees and 3 inflorescences per tree with a total of 20 flowers in Kenting; 3 inflorescences from 1 tree with a total of 7 flowers in Dulan, Taitung; 3 inflorescences from 1 tree with a total of 6 flowers in Zhongpu, Chiayi; 3 inflorescences from 1 tree with a total of 7 flowers in Taipei) day and night.

Continuous Video Recording

The branches with target flowers were fixed to avoid losing focus due to wind disturbance and to keep them within the range of the video cassette recorder. The macro camera with the infrared night vision function was tuned to focus on flowers, which were on the eve of blooming. Recording continued until the flower fell and fruit set for male and female flowers, respectively. The video recording continued until the end of the flowering period. In total, eight female flowers from two trees and five male inflorescences from two trees were completely recorded during two consecutive years (two flowering periods). All images of flower visitors and video material collected in the Kenting area were viewed and analyzed.

Data Analysis

Preliminarily data were summarized in MS Excel. Statistical analysis (LSD difference comparisons of paired data) was performed in CoStat (CoHort software, website: http://www.cohort.com/ coplot.html). Data were tabulated in MS Excel.

RESULTS

Observations of D. blancoi Flower Visitors with the Naked Eye

The arthropod visitors of *D. blancoi* flowers are presented in Table 2. Ants were the major flower visitors observed in both male and female flowers. A total of three ant species were observed: Crematogaster sp., Aphaenogaster sp., and one unidentified species (body length 10–1.5 mm). The paper kite butterfly (Idea leuconoe) rarely visited D.

^xExcept for large-size visitors (e. g., Lepidoptera and Coleoptera), data about smaller-size visitors were collected by close inspection on flowers (selecting flowers to check at random).

blancoi flowers and was only observed in female plants. The skipper (Suastus gremius) showed occasional flower-visiting behavior, often appearing at twilight and was observed in both male and female plants. The flower-visiting frequency of beetles (Coleoptera) and spiders (Araneae) was also low. Meanwhile, Thrips hawaiiensis, a small and active insect, was observed in high numbers (Fig. 1, 2). They entered the flower tube (σ) and/or touched the stigma (♀) more frequently than other flower visitors. Less frequently, this behavior was also observed in ants; however, it was rarely observed in other flower visitors (Table 2).

Flower Collection for the Identification of Pollinators of D. blancoi

The flower visitors caught from flower sampling are shown in Table 3. Thrips hawaiiensis was the most abundant insect found at/in female flowers, followed by ant species. Small beetles, spiders and small lepidopteran larvae were also observed, but in smaller numbers. Thrips hawaiiensis was also the most abundant visitor found at/in male flowers, followed by ant species, small beetles, spiders, and small larvae. Thrips hawaiiensis collected in both male and female flowers could adhere to the pollen (Fig. 2C, 2D). Ants of Crematogaster sp. collected from male flowers were also found to adhere to pollen, although less frequently than T. hawaiiensis. After pattern comparison and germination testing,

Fig. 2. The lifecycle of Thrips hawaiiensis in the Diospyros blancoi male flower tube (all stages of development except non-feeding pre-pupa and pupa stage). (A) A T. hawaiiensis egg under the subsurface of a petal (about 50 µm long, 25 µm wide.); (B) A T. hawaiiensis larva (body length about 0.8 mm); (C) Pollen attached to fringe hair, as indicated by the arrow (body length about 1.1 mm); (D) A large amount of pollen attached to the antennae, as indicated by the arrow (body length about 1.2 mm).

these sampled pollens were found mostly to be D. blancoi pollens with germination ability.

Continuous Video Recording

The images showed that ant Crematogaster sp. was very active and exhibited similar behavior towards the male and female plants. Most of the time

A

Table 3. Arthropods collected from four habitat-sources of Diospyros blancoi flowers.

^x The number of flowers per test $^\mathrm{y}$ The number of individuals with pollen / the total number of individuals observed

 z L1, L2 – Larva stage 1 and larva stage 2, respectively

Crematogaster sp. walked along the branches, leaves and flowers, and occasionally walked into the flower tube ($\sigma \&$?), but then came out immediately. We observed an interesting hair-collecting behavior in Crematogaster sp. The hairs of both male and female D. blancoi leaves or sepals are possibly used by ants as one of the materials to build formicaries. We observed that ant Aphaenogaster sp. spent most of the time moving around, and occasionally entered the flower tubes ($\sigma \& 9$). We observed that Aphaenogaster sp. ran away when encountering Crematogaster sp. Another unidentified little ant species was rarely observed on D. blancoi.

Thrips hawaiiensis were also very active due to their ability to fly. Often, they suddenly appeared on the petals, crawled and entered the flower tube, or crawled out and went away. They were also found inside and outside the gaps between petals of mature but non-blooming female flower buds. Ants and thrips can be found day and night, and Crematogaster sp. and T. hawaiiensis were observed in almost every flower. In addition, skippers also visited D. blancoi flowers, but only thrice. The results of insect video observations are shown in Table 4 and Fig. 3. All the eight videotaped female flowers set fruit successfully, and formed more than seven seeds each fruit.

DISCUSSION

Ants and (or) Thrips are Possible D. blancoi Pollinators

Many different D. blancoi flower visitors were observed in this study, but ants and thrips were the most frequent flower visitors (Tables 2, 3, and 4).

The other creatures such as skippers, paper kite butterfly, beetles, spiders and small larvae were rarely seen (Tables 2, 3, and 4). The high percentage of seed setting suggests that such arthropod groups were not the main pollinators of D. blancoi. Idea leuconoe and S. gremius, drawing nectar with their long mouth parts, were not D. blancoi pollinators. Although lepidopteran insects, bees and bumblebees are abundant in Kenting (Chu et al. 1986; Starr 1992) and are considered to have strong pollination ability (Faegri and van der Pijl 1971; Crane and Walker 1984; Mand et al. 2002; Klein et

Table 4. Frequency level of flower (or inflorescence) visitors on Diospyros blancoi during the flowering process.

	Observation of Flower Visitors						
Observed Insects	Flower Visiting Frequency Level ^x		Rate $(\%)^y$		Frequency Level of Flower Visitors Entered the Flower Tube or Touched the Stigma ²		
Hymenoptera							
Crematogaster sp.			100	100			
Aphaenogaster sp.			75	80			
Little ant (not identified)	R	R	25	20			
Lepidoptera							
Suastus gremius	R	R	25	20	А		
Thysanoptera							
Thrips hawaiiensis			100	100	A		

Complete flowering process was observed for eight female flowers and five male inflorescences.

X Frequency level of visited flowers (or inflorescences). If the time difference between two consecutive visits was less than 3 min, these two visits were counted as one visit. Average times: $>$ 10 = very often (V); 5–10 = often (O); 2–4 = sometimes (S); 0–1 = rare (R).

Frequio between the visited flowers (or inflorescences) and all observed flowers (or inflorescences).

 2 Frequency level: 100% = always (A); 60–100% = often (O); 20–60% = sometimes (S); < 20% = rare (R).

al. 2007; Michener 2007; Kwon 2008), their visiting frequency on *D. blancoi* was very low or none. These insects were only observed occasionally in D. blancoi flowers (Tables 2 and 4). It is possible that the nectar production of D. blancoi flower is low or even none, so butterfly, bees and bumblebees were not attracted by *D. blancoi* nectar but flower fragrance or color occasionally.

Gametis forticula (Tables 2 and 4), little beetles (Table 3) and spiders (Tables 2 and 3) were occasionally found, but their visiting frequency was also very low. Although beetles are known as primitive pollinators (Jolivet 2005), they were not found to pollinate D. blancoi flowers. Spiders have hairs that can probably aid pollen transport, but they did not carry *D. blancoi* pollen; moreover, we found spiders in female flower tubes, but never in male flower tubes. Therefore, neither beetles nor spiders were pollinators of *D. blancoi*. Possibly, spiders were hiding inside the flowers and/or were opportunistic predators. While little beetles were likely hiding inside the flowers during a short period of time for other purposes, Gametis forticula stayed just for a short rest. Therefore, flower visitors must visit male and female flowers frequently in order to become major pollinators. Only ants and thrips had high visiting frequency and were possible D. blancoi pollinators.

Ants are Not Pollinators of D. blancoi

Ants are considered nectar thieves that eat parts of the flower and cause organ damage in plants (Cerda et al. 1992; Weiser 2002; Blancafort and Gomez 2005), expel or kill pollinators (Blancafort and Gomez 2005). Also, ants are not conducive to plant pollination (Hickman 1974; Schubart and Anderson 1978; Guerrant and Fiedler 1981; Haber et al. 1981). In addition, many characteristics of ants, as explained by the "antibiotic hypothesis" (Beattie et al. 1985; De Vega et al. 2009), reduce their capability to assist in plant pollination. However, examples of ant pollination can be found in a number of literatures (Hickman 1974; Weiser 2002; Liu et al. 2008; Wang et al. 2008; De Vega et al. 2009). Hickman (1974) described 10 botanical characteristics that make plants attractive to ant pollinators, but none of them matched D. blancoi.

Ants may often visit D. blancoi flowers, but were not considered potential pollinators in the dioecious plant. The distance between male and female trees can be more than a few hundred meters or even a

few kilometers. In addition, male and female trees can be isolated from each other by water barriers; but in this case, the pollination of D. blancoi was not hindered. As an example, a single D. blancoi female tree on Turtle Island can produce normal seeds, even though the distance between Turtle Island and Taiwan is about 9.1 km. We observed two arboreal ant species that occasionally left D. blancoi trees but stayed in the vicinity of a tree. These ants could not overcome the long distance over land and water to assist D. blancoi pollination. In addition, D. blancoi pollen was not found in ants present in female plants. Only one Crematogaster sp. individual from a male plant was found carrying pollen (Table 3). Therefore, these findings suggest that ants have no contribution to pollen transportation and therefore cannot be regarded as a D. blancoi pollinator.

Thrips hawaiiensis as the Most Probable Major Pollinator of D. blancoi

Thrips hawaiiensis is a flower-dwelling insect species that causes production loss in many crops, and is most severe in such crops as bananas (Pinese and Piper 1994; Chao et al. 1997), citrus (Srivastava and Bhullar 1980; Chiu et al. 1991), mango (Lee and Wen 1982), gladiolus (Chen and Lo 1987), and roses (Wang 1982) to name a few. Spending most of their lives inside flowers, thrips have many fine hairs to carry pollen. Thrips often trapped pollen by the setae on their legs, wings, abdomen, thorax, head, or antennae, with the greatest load on the ventral edges of the abdomen and on the thorax around the mouth parts (Norton 1984). Therefore, although thrips could damage plants, their activities and morphological characteristics may help in plant pollination (Ananthakrishnan et al. 1981; Kirk 1985; Saxena et al. 1996; Williams et al. 2001). Norton (1984) suggested that thrips could pollinate plants with small, shallow, and clustered flowers lacking bright colors.

The pollination ability of thrips was first found in sugar beet (Shaw 1914). In recent years, thrips are also described as pollinators of palm (Syed 1981 and 1979; Tay 1981; Listabarth 1993; Barfod et al. 2011), cycad, Arisaema (Aroideae) (Rust 1980; Gibernau 2003), Cosmos bipinnatus (Varatharajan et al. 1982), Lantana camara (Mathur and Mohan Ram 1978), and many other species. Megalurothrips distalis was shown to assist pollination of Chloranthus holostegius (an endemic plant in China) through crosspollination (Wang et al. 1998). Thrips as a plant

pollination assistant may have started from the Mesozoic Era (about 105 to 110 million years ago). The direct fossil evidence proving this hypothesis was found in 2012. Two species of Melanthripidae thrips assisted cycads in pollination, and thrips larvae possibly fed on pollen (Penalver et al. 2012).

All of the T. hawaiiensis larvae and adults collected from male flowers and two of the six adults collected from female flowers were carrying pollen (Table 3). In addition, regardless of flower gender, as shown in Table 4, T. hawaiiensis visited a single flower very often (V), visited all the observed flowers (100%), and inevitably entered the flower tube in a single visiting event (A). Furthermore, only T. hawaiiensis is small enough to enter the flower tube and carry pollen to reach D. blancoi stigma before flower opening. Therefore, it can be concluded that the pollination of D. blancoi in Taiwan is probably mainly assisted by T. hawaiiensis.

Life History of T. hawaiiensis is Closely Related to Male D. blancoi

Thrips development involves five instar stages. First and second larvae correspond to the feeding stage. The pre-pupa and pupa correspond to the nonfeeding stage, followed by adulthood (Lewis 1973). Thrips hawaiiensis from male D. blancoi were found across different life stages (egg, larva, and adult) (Fig. 2). Pre-pupa and pupa stages were not found. Possibly, non-feeding pre-pupae were hiding until the emergence of adults (Proter-Morgan 2007). We observed that the flower tube of male D. blancoi was filled with filaments and anthers. Following anther dehiscence, a large amount of pollen was scattered covering the internal portion of the flower tube, where thrips were active and present in high numbers (more than 20 larvae and adults could be found) (Table 3).

Thrips suck the contents from plant cells (Heming 1993; Mound 2005), and leave scars on the plant tissue. The presence of scars on bananas and citrus peel reduces their price in the commodity market (Srivastava and Bhullar 1980; Chiu et al. 1991; Pinese and Piper 1994; Chao et al. 1997). Petals are expected to be the most delicate parts of the flowers; however, no large number of feeding traces on D. blancoi petals was found. Female flowers, unlike the male flowers, did not contain thrips larvae. As a result, the petals of female flowers did not have feeding traces. The outer part of D. blancoi female ovary is covered with bushy hair (Fig. 4). Thrips cannot break through this barrier easily, which saves *D. blancoi* fruits from damage during early maturity development. Therefore, T. hawaiiensis could not be regarded as a D. blancoi pest.

Plants attract insects (or other animals) to aid in their pollination by providing foods and/or roosting sites, and this is called a symbiotic relationship. Sakai (2001) proposed that thrips pollination is based on the symbiosis between herbivorous insects and plants. Macaranga hullettii, similar to dioecious *D. blancoi*, is pollinated by thrips. The bracteoles of M. hullettii provide shelter to propagating thrips and supply food to thrips in the form of nectar (Moog 2002). Similarly, during blossoming in D. blancoi, the male flower tube provides a hiding place as living premises for thrips and the pollen as a food source attracts T. hawaiiensis to visit male flowers. Many previous studies also pointed out that pollen represents an important food source for flower thrips (Kirk 1985; Trichilo and Leigh 1988; Murai 2001; Williams et al. 2001; Hulshof and Vanninen 2002). However, what attracts T. hawaiiensis visiting female flowers? There is a strong possibility that D. blancoi flowers attract T. hawaiiensis by aroma components. In addition,

Fig. 4. A longitudinal section of Diospyros blancoi fruitlet. Dense fluff covers the ovary wall and the developing seeds. The fruitlet diameter is about 1 cm.

white and yellow colors can also attract thrips (Vernon and Gillespie 1990; Hoddle et al. 2002; Lu et al. 2011). Although aroma ingredients analysis of both male and female D. blancoi flower have been done (Pan et al. 2008), the key aroma ingredient(s) that attracts T. hawaiiensis and the effect of D. blancoi petal color to attract T. hawaiiensis need further research.

CONCLUSION

Based on the high frequency of flower visitation and pollen-carrying behavior, not shared by other flower visitors, we arrived at the conclusion that the pollination of D. blancoi in Taiwan is assisted mostly by T. hawaiiensis, although more in-depth studies should be done to further strengthen this claim. Another interesting subject to study is the identification of main pollinators of D. blancoi in other geographic locations such as the Philippines, or Europe and America. Nonetheless, we hypothesize that if the main pollinator of D. blancoi is proved to be T. hawaiiensis, T. hawaiiensis must be segregated from female *D. blancoi* during flowering period in order to produce seedless mabolo, making all-female D. blancoi cultivation in an artificial facility a good approach.

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