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ORIGINAL ARTICLE

High yields and bee pollination of hermaphroditic rambutan (*Nephelium lappaceum* L.) in Chiapas, Mexico

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Abstract – Introduction. Many cultivated plants do well with exotic pollinators, and native pollinators can also serve exotic crops. Both can be optimized for agriculture. We studied *Nephelium lappaceum* L. (Sapindaceae), an andro-dioecious Asian plant, in tropical Mexico. The hermaphrodite flowers were not known to shed viable pollen, and outcrossing from male pollinating plants was thought essential for efficient horticulture. **Materials and methods.** We used the locally developed CERI61 variety of rambutan and conducted experiments on pollination and fruit yield. An orchard of 1,000 trees was studied intensively during two flowering seasons in Chiapas, Mexico. Plantation yields were recorded for 10 years. We compared open pollination experiments with pollinator exclusion and 'induced pollination' treatments. We caged some trees with colonies of stingless bees: *Scaptotrigona* and *Tetragonisca*. **Results and discussion.** Caged flowers produced fruit, with no male plant present. Pollen dehisced and was viable on approximately 5% of flowers. Trees caged with pollinators, and open pollination treatments revealed 9.1 times more mature fruit than trees without pollinators. Fruit mass was significantly higher in induced pollination treatments. Yields exceeding 7 t ha^{-1} were obtained during a ten-year test period. *Scaptotrigona mexicana* (Apidae, Meliponini) was the main pollinator, followed by social halictid bees (*Halictus hesperus)*. Feral Africanized honeybees were not strongly attracted to flowers. **Conclusion.** Both stingless bee species in open pollination treatments and within cages showed that fruit production increased nearly 10-fold in this variety of rambutan. Although outcrossing versus selfing did not affect initial mature fruit set, a superior fruit yield, in weight and size, was obtained from selfing mediated by pollinators in caged trees.

Keywords: Mexico / Chiapas / rambutan (*Nephelium lappaceum)* / pollinators / Apidae / bees / selfing

Résumé – Amélioration des rendements et pollinisation par des abeilles du rambutan hermaphrodite (*Nephelium lappaceum* L.) dans le Chiapas, Mexique. Introduction. Beaucoup de plantes cultivées s'accommodent de pollinisateurs importés mais les pollinisateurs naturels contribuent également à la récolte de fruits exotiques. Les deux types peuvent être optimisés pour l'agriculture. Nous avons étudié le rambutan, *Nephelium lappaceum* L. (Sapindaceae), une espèce fruitière asiatique andro-dioïque, dans les conditions tropicales du Mexique. Les fleurs hermaphrodites ne sont pas connues pour libérer du pollen viable, aussi la participation des plantes mâles fécondantes est essentielle en horticulture productive. **Matériel et méthodes.** Nous avons testé la variété CERI61 développée localement en expérimentation agronomique portant sur le rendement en fruits et sur la pollinisation. Un verger de 1000 arbres a été étudié intensivement pendant deux saisons florifères dans le Chiapas. Les rendements fruitiers du verger ont été enregistrés sur 10 années. Nous avons comparé les traitements entre une pollinisation ouverte avec exclusion de tout pollinisateur et une « pollinisation forcée ». Quelques arbres ont été maintenus en cage, avec des colonies d'abeilles sans dard : *Scaptotrigona* et *Tetragonisca.* **Résultats et discussion.** Des fleurs en cage ont produit des fruits en l'absence de toute plante mâle. Le pollen produit était déhiscent et viable sur près de 5 % des fleurs. Les traitements en cage avec des pollinisateurs, et en pollinisation ouverte ont révélé 9.1 fois plus de fruits arrivant à maturité qu'en l'absence de pollinisateurs. La masse de fruits récoltés était significativement plus élevée suite aux traitements d'induction de pollinisation que dans tout autre traitement. Des rendements excédant 7 t ha^{-1} ont été obtenus sur une période-test de dix ans. *Scaptotrigona mexicana* (Apidae, Meliponini) était le pollinisateur principal recensé, suivi par des abeilles halictid sociales (*Halictus hesperus*), alors que les abeilles africanisées sauvages n'ont pas été fortement attirées par

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les fleurs de rambutan. **Conclusion.** L'espèce d'abeille sans dard utilisée tant dans des traitements de pollinisation ouverte que sous cage a contribué à une augmentation proche de 10 fois la récolte de fruits de cette variété de rambutan. Bien que la fécondation croisée n'ait pas affecté la mise à fruit initiale par rapport à l'autofécondation, un rendement supérieur a été obtenu, en poids et en taille de fruits, grâce aux pollinisateurs sur fleurs en cage.

Mots clés : Mexique / Chiapas / rambutan (*Nephelium lappaceum)* / animal pollinisateur / abeilles / autopollinisation

1 Introduction

Rambutan (*Nephelium lappaceum* L., Sapindaceae) is a tropical plant that produces edible fruits and originates from Malaysia and Indonesia. According to FAO data this fruit tree is being developed for commercial exploitation and the market is expanding rapidly. Rambutan is nowadays commercially grown in Southern Asia, Australia, the Caribbean, India, Sri Lanka, Florida, Hawaii and South and Central America [1]. However, there is little information about its pollinators or insect flower visitors. In nature rambutan plants are dioecious with about 50% male and 50% hermaphrodite plants. Therefore, in commercial orchards only hermaphrodite plants are grown, where most of them are functionally female. For example, in the Philippines the cultivars "Maharlika" and "Seematjan" produced about 99.94% and 99.55% hermaphrodite functionally female flowers, respectively [2]. No functional pollen is supposed to be produced by such andromonecious plants, which is being observed in Australia, where isolated trees with low functional male hermaphrodite flowers rarely set fruit satisfactorily [1,3]. In Southeast Asia where rambutan is native, cross pollination by hand increases fruit set 13 times beyond the 1% found in natural conditions whereas bagged flowers fail to set fruits [3]. Recent studies in India find the stingless bee *Tetragonula iridipennis* and Indian honeybee *Apis cerana* dominant foragers on *N. lappaceum* [4].

In our study region, rambutan was introduced during 1950−1970 as an economic alternative to coffee, mango or banana and is now widely cultivated due to favorable agroecological conditions [5–7]. Nonetheless, few studies have examined the pollination system and insect visitors, integral to a sound production technology. We performed studies on pollen and fruit production in a commercially grown variety of rambutan in Chiapas, Mexico, by recording fruit yield, pollen dehiscence and viability, flower visitors and pollinator management in a commercial orchard with a fruit tree population previously believed to be functionally female.

2 Materials and methods

Our studies were performed on a commercial rambutan variety denominated "CERI61" by the Rosario Izapa experiment station, Mexican Institute of Forestry, Agriculture and Livestock Research. In the Soconusco region, rambutan varieties introduced from Malaysia and Indonesia were reproduced by seed and selected from plantations at this station. In subsequent plantings using grafted materials, a genetic uniformity was reached with smaller trees showing a good production and quality for marketing [5]. The CER161 hermaphrodite variety was studied in a 7 ha orchard of approximately 1,000 trees with no male individual trees flowering within the study area or nearby. This orchard at "El Herradero" ranch, in the Metapa de Dominguez municipality, Chiapas, Mexico (14.4948 N, 92.1132 W) is located at 100 m elevation. Two flowering periods were intensively studied, each between January and June in 2001 and 2002. Observations on fruit set (both initial and final), flower visitors and floral characteristics were repeated in 2003–2004. The climate is hot and humid with abundant summer rain [8, 9]. The habitat surrounding the orchard includes orchards of mango (*Mangifera indica* L.). Native secondary vegetation commonly includes *Ficus* spp., *Tabebuia rosea* (Bertol.) DC, *Spondias mombin* L., *S. purpurea* L., *Cybistax donnell-smithii* (Rose) Seibert, *Tecoma stans* (L.) Juss. ex Kunth, *Ceiba pentandra* (L.) Gaertn and *Pachira aquatica* Aubl [9].

To determine the effects of flower visitors on the small (4 mm), apetalous and greenish flowers of rambutan, ten trees with six marked panicles were used for each of three experimental treatments. The control treatment (T1) was open pollination without manipulation, while (T2) excluded all visitors with a 1 mm mesh bag placed over the panicle in bud stage (bagged flowers). The third treatment (T3), called "induced pollination", was simultaneous with the other two. For this we placed cages over trees with buds in the same stage as T1 and T2 and two bee colonies were placed at opposite ends of the $16 \times 16 \times 4$ m cage. The local stingless bees (Meliponini) in wooden hives were *Scaptotrigona mexicana* Guérin-Mélenville and *Tetragonisca angustula* Lat., which maintain colonies with approximately 1000 foragers. They are considered as common flower visitors to rambutan in our region. From the marked panicles in each treatment, final developing fruits were scored and assessed at the time of commercial harvest. In order to estimate the proportion of flowers producing fruit, total flowers were counted in bagged panicles on 10 trees.

Flower visitors were sampled intensively from trees by placing a large net-tent over an entire tree. The net mesh was 1 mm and the tent 3 m on each side. An individual tree was covered, after which insects were collected in tubes containing ethyl acetate. Collections were made, on separate trees at a given hour, between 7 am and 5 pm, every 15 days from February through March 2001 and from February through April 2002. Bees and other insects were identified by using taxonomic keys of Ayala [10] and Michener [11].

3 Results and discussion

Initial fruit set differed nearly ten-fold among the three treatments (ANOVA, $P < 0.001$). Developing and mature fruit per flower were most abundant in the open pollination treatment in both years (Duncan and Tukey tests, $P < 0.001$,

Table I. Fruits produced and fruit mass in three treatments on rambutan, variety CERI61: induced pollination (bee colonies present in cage), open flowers, and bagged flowers with no visitor, at Metapa de Domínguez, Chiapas, Mexico.

Variable	Treatment					
	Induced pollination		Open pollination		Bagged flowers	
	2001	2002	2001	2002	2001	2002
Set Fruit	76.4 ± 27.2^B	71.4 ± 21.2^B	96.8 ± 37.7^A	110.1 ± 46.2^A	7.0 ± 8.0^C	5.6 ± 3.9^C
Mature Fruits	21.2 ± 6.1^A	17.1 ± 6.5^A	22.8 ± 9.3^A	23.1 ± 7.9^A	1.8 ± 3.2^B	3.4 ± 3.3^B
Fruit mass (g)	22.2 ± 2.1^B	28.4 ± 3.2^A	15.5 ± 0.6^C	15.1 ± 0.3^C	13.8 ± 0.5^D	12.6 ± 0.7^E

All treatments included a similar number of flowers ($1,804 \pm 503$ in 2001 and $1,749 \pm 545$ in 2002; $P < 0.05$). Data are means (±standard deviation) of 10 biological replications. Cells with the same letter in a given row are not significantly different (Tukey test, $\alpha = 0.01$).

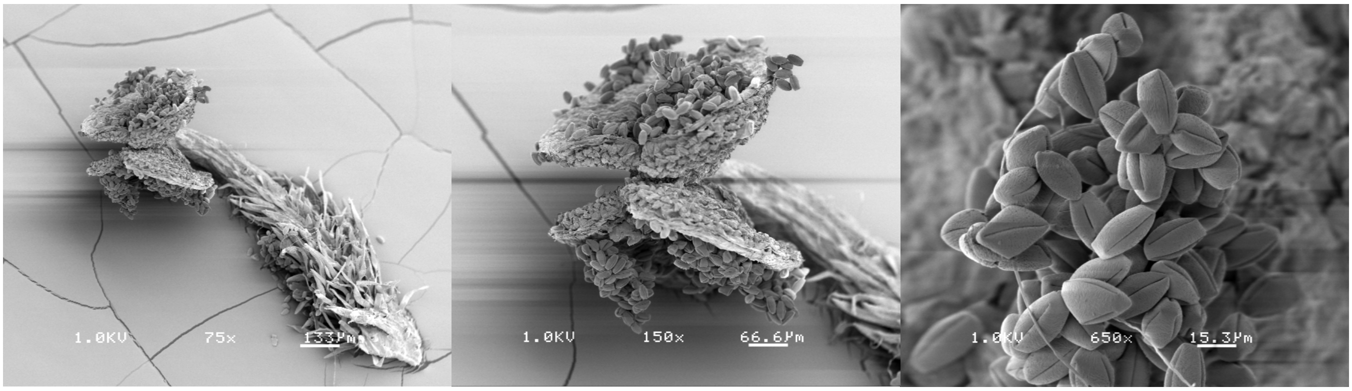

Figure 1. Anther of *Nephelium lappaceum* from hermaphrodite flowers. Left: stamen with opened anther; middle: magnifications of anthers; and right: pollen grains.

table I), but no statistical differences existed between induced pollination (in cages) and open pollination. The fruit mass was significantly greater in induced pollination treatments (*table I*) which also resulted in greater seed mass and fruit length (data not shown). The open pollination treatment of 2001 and 2002 registered the highest fruit set, due to the larger number of flowers present on panicles ($1,804 \pm 503$ and $1,749 \pm 545$ respectively) (*table I*). In contrast, the bagged flowers treatment registered the lowest fruit set (*table I*).

Flowering began early in February and ended in April, reaching a maximum during March. The effective flowering period was 30 ± 5 days. All flowers on panicles were hermaphrodite and approximately 5% of them had pollen on anthers that dehisced and remained present upon stamens up to two days, when the stamens wilted (*figures 1*, *2*).

Many developing fruit dropped during the first four weeks after flowering, with 50% lost, and an additional 15% was lost by the seventh week. By fruit maturity at 11 weeks, little additional loss occurred. With the introduction of stingless bee hives on this ranch from 2000 to 2004, the average yield increased from 3.5 to 7.0 t ha^{-1}.

A total of 28,186 individual bees were collected on flowers, which represented 97.1% of the total insects taken in February–March 2001 and February–April 2002 (*table II*). The peak insect visitation was observed between 10 am and 11 am (468 and 416 in average, respectively). Two bee families, Apidae (*Tetragonisca*, *Trigona*, *Oxytrigona*, *Nannotrigona*, *Apis*, *Exomalopsis*, *Paratetrapedia* and *Scaptotrigona*) and Halictidae (*Halictus*) visited flowers, first collecting a small amount of pollen and nectar, then collecting almost exclusively nectar after 10 am. Visitors carried only small pollen loads on their hind legs. When subjected to microscopic study, pollen loads consisted of Asteraceae, Euphorbiaceae and other flowering plants common in the area. *Scaptotrigona mexicana* dominated flowers during the end of flowering in March–April 2001, with 3,512 individuals and 81.64% of all collected bees. *Halictus hesperus*, a social but not perennial bee, dominated flowers in April 2001 after most flowering had occurred. Our results agree with those Shivaramu *et al.* [2] from India, reporting a stingless bee (*T. iridipennis*) as a predominant forager.

Figure 2. *Scaptotrigona mexicana* on a hermaphrodite flower of rambutan in the Soconusco region.

Rambutan produces hermaphrodite flowers that are traditionally viewed as functionally pistillate [2]. Recent studies in Asia indicate rambutan is a cross pollinated plant and depends on insects for pollination and fruit set [2]. However, Kiew [12]

Table II. Richness and abundance of bees collected in two flowering periods in rambutan flowers at "El Herradero" ranch (Metapa de Domínguez, Chiapas, Mexico).

Bee species	February	March	April	Total	Relative abundance (%)
Apidae: Apinae					
Apis mellifera	3	1	1	5	0.02
Apidae: Apinae					
Scaptotrigona mexicana	2,840	4,819	2,063	9,722	34.49
S. pectoralis	58	49	16	123	0.44
T.(Tetragonisca) angustula	659	171	23	853	3.02
Nannotrigona pelilampoides	204	48	105	357	1.27
Trigona fulviventris	21	21	12	54	0.19
T. nigerrima	27	8	3	38	0.13
Oxitrigona mediorufa	43	–	2	45	0.16
Apidae: Antophorinae					
Exomalopsis sp1	10	4	–	14	0.05
Paratetrapedia sp1	1	2	–	3	0.05
Halictidae					
Halictus hesperus	27	973	13,675	14,675	52.07
Lasioglossum sp1	4	98	1,409	1,511	5.36
Lasioglossum sp2	–	57	555	612	2.17
Lasioglossum sp3	15	15	127	157	0.56
Agapostemon aff. *splendens*	7	5	4	16	0.06
Total of bees	3,919	6,271	17,995	28,185	100.00

stated that rambutan is not bee pollinated but apomictic and parthenocarpic, because hermaphrodite flowers do not release pollen, and male plants are not cultivated because they produce no fruit. In contrast, Nakasone and Paull [3], listing seven cultivars of rambutan used in Thailand, Indonesia and Malaysia, stated that even with no male trees present, mixed plantings, given flowering synchrony, provided acceptable yields. Yields in plantings not meeting such conditions were exceedingly low.

Our data strongly suggest that hermaphroditic flowers can have viable pollen, which must be transferred by a pollinator for the production of mature fruit. The pollen grains dehisced and were fully formed (*figure 1*) on the anther surface, in contrast to deformed pollen found on functionally female but apparently hermaphroditic flowers in *Decaspermum* [13]. In addition, pollen grains kept in a 20% sucrose solution initiated pollen tube growth. Both geitonogamy and outcrossing were possible, but there is no convincing evidence for apomixis in our rambutan variety, because occasional autogamy cannot be discounted. The "induced pollination" treatment, which could only result in geitonogamy, produced significantly lower initial fruit set but equally abundant ripe fruit in both years, compared to the open pollination treatment (*table I*). In contrast, the flowers caged to exclude all pollinators produced almost no fruit, which is not a condition expected if apomixis occurred.

The interpretation that fruit initiation was higher when some outcrossing pollen was deposited on stigmata by bees is consistent with the initial fruit set, but the yield in mature fruit could not reach that provided by full self pollination (*table I*). Any conceivable apomixis was greatly outweighed by geitonogamy, facilitated by pollinators.

In some self-fertilizing plants, fruit set may be strongly increased by the diversity and abundance of flower-visiting bees [14–16]. For example, commercial yield of *Coffea arabica* increased 56% in open pollinated treatments, opposed to autogamous and bagged treatments [17]. Our results agree with these *C. arabica* studies, because rambutan flowers exposed to *S. mexicana* produced 9.1 times more mature fruits than the treatment without pollinators. The bees presumably visited many flowers to obtain a nectar load and are known as group foragers [18]. Small bees are generally thought to favor pollination of small, generalized flowers [19]. Most *Scaptotrigona* had gathered negligible nectar when sampled on flowers and *Apis mellifera scutellata*, present on a few flowers, was not strongly attracted to rambutan, although its flowers occur in dense clusters on large panicles. A small amount of floral nectar reward, scramble competition, or both, likely discouraged this honey bee from greater visitation, despite an unusually high sugar nectar reward, >50% by weight. Although the *Halictus* nested in the ground near the orchard and in the general area [20] it also appeared at rambutan flowers in increasing frequency when numbers increased in tent traps placed over trees [21]. This seasonal, social bee was a significant visitor seen on the flowers and not merely flying into the traps. Other studies also find numerous social bees visiting rambutan [3]. The insignificant production of fruit in their absence indicates this plant depends on the action of small bees to stimulate fruit set and retention. Since *H. hespersus* was active only during late flowering season, it was unable to provide much pollination service in our studies.

This is the first study of which we are aware, in a plant described as dioecious, that implies selfed flowers gain greater maternal investment in fruit than outcrossed flowers. Although we did not experimentally outcross and self flowers on the same plant to test this conclusion, we expect that our open pollination treatments included bees that transported pollen between compatible flowers. If the orchard was essentially a single self-fertile clone, the outcrossing would have little effect, but fruit production in cages, compared to open plants, would not be so large, nor would fruit drop by potentially outcrossed plants be relatively larger than that of strictly selfed plants. In theory, selfing should help to purge lethal alleles [22] and in natural conditions protogyny could offset the tendency of geitonogamy to monopolize maternal resources. The large proportion of dehisced fruits suggests maternal discrimination based upon fruit genotype.

4 Conclusion

Fruit abundance for commercial rambutan is reported to be 10 to 20 per panicle in Costa Rica [23], compared to 21 in the present study, while fruit number in Malaysia is lower [24]. In the latter study and in Chiapas, fruit size was very similar. To the producers of rambutan it is of special interest that the total yield (weight of individual fruit multiplied by fruit retained per panicle) was highest in the induced pollination treatment (in cage). This implies that controlled production in greenhouse, with pollinators, can provide relatively high yields. The yields at our Metapa orchard were over twice that of the leading producers (in Thailand) of *Nephelium lappaceum* [25]. Thailand has approximately the same number and size of stingless bee species as Chiapas, but also possesses five honey bee species. In both hemispheres, increasing productivity through pollinator management seems possible and desirable. Because of the number and availability of pollinators, and particularly the management of *Scaptotrigona* in our Chiapas site, rambutan orchard pollination is likely to be efficient as well as economically sound.

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