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Flowering and Pollination in Sago Palms (*Metroxylon sagu* Rottb.): A Review

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Inflorescence development

The sago palm (*Metroxylon sagu* Rottb.) is hepaxantic and produces a huge inflorescence at its terminal. Towards the end of its vegetative growth, newly emerged fronds are increasingly erect and smaller, and eventually become bract-like just before the emergence of the inflorescence (4). This is followed by trunk elongation and the emergence of a torpedo shaped inflorescence structure at its terminal. As the inflorescence develops, first-order (a × 1), second-order (a × 2) and third-order (a × 3, rachilla or spike) flowering axes are produced and spread out at the terminal of the sago palm. Flower buds are produced in spiral rows on the rachillae. Each pair of buds is enclosed in a cup-like scale called bracteole (1). Globose fruits covered with imbricate scales develop on the bracteole upon fruit set.

In studies carried out in West Java (9), each palm produces an inflorescence consisting of 5–6 a × 1, 9–10 a × 2 and about 12–16 rachillae per a × 2, with 200–240 flower buds per rachilla. In Sarawak (4), each sago palm inflorescence consists of 15–19 a × 1, 173–334 a × 2 and 1313–3427 rachillae. The average number of flower buds per rachilla ranges from 121 to 273 and the maximum number of buds in a rachilla just before anthesis is over 400.

In *M. vitiense*, around 917,280 flower buds are estimated in its inflorescence. The number is probably doubled in *M. sagu* due to its larger size and greater number of flowering branches (5). In *M. sagu*, each flower spike is covered with 24 to 28 spirals of 9 to 10 pairs of flowers. The number of flowers is estimated at 120,960 to 376,320, which is capable of producing about 2500 mature fruits (3). The estimated number of flowers in *M. rumphii* Martius, *M. Sylvester* Martius *and M. longispinum* Martius range from 856,000 to 2,074,000 (7). In West Java, a total of 108,000–232,400 flower pairs in a palm have been reported (9) whereas in Sarawak (Malaysia), the estimated number of flower buds in an inflorescence just before anthesis is between 276,000 to 864,000 (4).

Flower development prior to anthesis

In *Metroxylon* Rottb, two types of flowers are found in a pair enclosed in a bracteole and they are externally similar. One is the staminate (male) and the other hermaphrodite in appearance but physiologically female or pseudo-hermaphrodite (1). In a mature specimen of *Metroxylon vitiense*, the flower pair consists of a staminate and a hermaphroditic flower rather than a pseudo-hermaphrodite as the stamens on both flowers appears identical (5). Uhl (1987) reports that the hermaphroditic flowers are similar to the staminate in their calyx, corolla and the stamens. However, the hermaphroditic flowers are somewhat flatter and their filaments are fused proximally to form an androecial tube surrounding the ovary. In *M. rumphii* Martius, *M. Sylvester* Martius *and M. longispinum* Martius, staminate and hermaphroditic flowers are present (7). In West Java, sago palm flowers are arranged in pairs, one (staminate) with under-developed pistil but functional stamens and the other 'female flower' with under-developed stamen but functional pistil (9).

The floral biology of nine sago palms has been followed more closely in Sarawak (4). In a developing rachilla, flower buds are formed in a pair partially embedded in each bracteole. During flower bud development, abscission of buds occurs continuously until flowering. One of the flower buds in a pair

abscises and is pushed out of the bracteole, probably to give sufficient space for the development of the other. The abscised can either be a staminate or a hermaphroditic flower bud and can be from either side of the flower pair. Abscission of flower buds is near completion at anthesis. At this stage, a bracteole usually contains a single mature bud and paired flower buds (1, 3, 5, 7, 8, 9) are uncommon on a rachilla. Abscission of both staminate and hermaphroditic flower buds in one bracteole is also common, leaving empty bracteoles on some parts of the rachilla (4). The time taken from the appearance of the first a × 1 to anthesis of its flowers is about six to nine months.

Modes of flower opening and pollination

(*a*) *Time course of flower opening*

Flowers of *Metroxylon* are monoecious[1] and proterandrous[2] (= protandrous) on the same spike and female flowers open only after the fall of all the staminate flowers. The female flowers are likely to be pollinated after the disappearance of all the staminate flowers (1). Studies on three sago palms in West Java (9) indicate that they are monoecious and self-pollinated. In these palms, insects may play an important role in fruit set as rachillae covered with wire gauze produce 1–4 full-sized fruits and those uncovered rachillae produce 3–15 fruits (no mention of seed set). The insects caught are *Apis indica, Ttrigona iridipennis, Rygchium haemorrhoida, Anomala breviceps* and drosophila melanogaster. The timing and the number of visiting insects are positively correlated with the time of abundance of nectar secretion. *Trigona* species are the most common visitors in sago palm inflorescence (4) and they are also reported to visit other palms inflorescence (2).

In Sarawak (4), two different types of flowers are encountered during flower opening of *M. sagu*. One is denoted by the presence of both normal staminate and hermaphroditic flowers on the same palm (andromonoecious) whereas the other by the presence of normal staminate and a mixture of normal and abnormal hermaphroditic flowers. In the latter, the initial flower opening is irregular, with most of the abnormal hermaphroditic flowers and a small pulse of normal hermaphroditic flowers opening before or concurrently with the opening of the staminate flowers. The overlap in the opening of the staminate and hermaphroditic flowers indicates that they are not strictly protandrous. In West Java (9), overlapping of flower opening within the rachilla, branches and inflorescence are also reported. The duration of flower opening in a branch is 120–150 days (9) as compared to 50–100 days in the entire sago palm inflorescence in Sarawak (4).

In two of the sago palms studied in Sarawak, the staminate flowers open 3–4 weeks earlier than the hermaphroditic flowers. These flowers have relatively larger and conspicuous orange to yellow anthers on extended filaments. In general, both staminate and hermaphrodite flowers open successively from the lower to the upper a × 1. The time separation in the initial flower opening from the proximal to the distal a × 1 is about 3 weeks for staminate and 2 weeks for hermaphroditic flowers. In most of the a × 1, the intensity of flower opening is low at the start but accelerates steadily there after. Within two weeks, the mid-point of flower opening (50%) is attained. Fruits are set 3–4 days after the opening of the hermaphroditic flowers. Overlapping in the opening of staminate and hermaphroditic flowers occurs between the a × 1 but the peak opening period in each a × 1 are mostly separated.

In another two palms, most of the hermaphroditic flowers open prematurely, possessing under-developed anthers. In one of these palms, the abnormal hermaphroditic flowers have short and under-developed stamens consisting of pale anthers and short filaments. The opening of each flower bud is very slow, extending from a few weeks to over a month, as compared to about 30 minutes in a normal mature flower bud. The initial opening of staminate and abnormal hermaphroditic flowers overlaps in all the a × 1. However, the peak of fruit set is about 1 month later than the opening of abnormal hermaphroditic flowers, indicating that these flowers opened prematurely. A small proportion of normal hermaphroditic flowers is also present on the inflorescence and

[1] with unisexual flowers borne on the same plant
[2] stamen shedding pollen before the stigma is receptive

they open in two small pulses, one at the beginning of staminate flower opening and the other at the end of anthesis in the inflorescence, about a week before main fruit set.

In another palm, the duration of the abnormal hermaphroditic flowers opening stretches over three months. All the under-developed stamens in the abnormal hermaphroditic flowers turn brown and die during the lengthy opening period. Only about 1% of the flowers in this palm is staminate flowers and they open about two months after the commencement of the opening of abnormal hermaphroditic flowers.

In both palms, infertile (seedless) fruits are set and developed normally from both the normal and abnormal hermaphroditic flowers. These abnormal hermaphrodite flowers secrete no visible nectar and very few insects are present during their lengthy opening. Some fruits are formed prior to the opening of staminate and hermaphroditic flowers. A few fruits and flowers of different development stages are commonly found in the same a × 2 and rachillae. However, most of the fruits are set after the opening of the hermaphroditic flowers.

In yet another palm, a smaller number of staminate and hermaphroditic flowers open concurrently at the beginning. However, the peak opening of staminate and hermaphrodite flowers in the inflorescence occurs at 9–14 and 23–30 days respectively from the initial opening. A wave of peak flower opening progresses gently upward from the lower to the upper a × 1, with slight overlap in peak flower opening between the proximal and distal a × 1. The sequence of flower opening in a single a × 1 is similar to that of the inflorescence, with peak opening of staminate and hermaphrodite flowers separated by about 16 days. As about 70–80 % of the flowers is hermaphrodite, their peak opening is much more prominent than those of the staminate flowers. Apart from the fusion of filaments at the proximal end, the stamens of newly opened hermaphroditic flowers are identical to those of staminate flowers. The hermaphroditic flowers also open in a similar manner to the staminate flowers. This is similar to the flower pairs described by Tomlinson (1971, 1990) and Uhl and Dransfield (1987) but different from the pseudo-hermaphrodite flowers described by Beccari (1918) and Utami (1986).

From various studies, it appears that three biological types of flower combinations are found in the sago palm, namely: (i) staminate and pseudo-hermaphrodite (1, 7 and 9); (ii) staminate and hermaphrodite (4 and 5); (iii) staminate and abnormal hermaphrodite that opens prematurely (4). Type (i) could be a mild form of type (iii) where the stamens are apparently healthy but physiologically non-functional. Type (ii) can be found in individual palm and type (iii) is found in combination with type (ii) in the same inflorescence.

(b) Opening of staminate flowers

In West Java, the staminate sago palms flowers open first and last 3–4 days. Only the staminate flowers produce nectar (2 cm^3 per flower), from 1030–1700 hours, with a peak at 1300 hours. Most of the nectar falls to the ground with a small portion sucked up by visiting insects (9). In spineless sago palms in Sarawak (4), the staminate flowers start to open at about 1030 hours. The sepals split at the point of fusion and gradually move apart. The anthers then emerge from the opened flower and extend above and away from the center of the flower. They are light purple and burst open slowly to expose the pollen before the filaments are fully extended. Within about 30 minutes, the anthers are fully exposed and spread out on top of the sepals. They turn from purplish to orange and then yellow in the next few hours.

The peak of opening is about 1100 to 1200 hours. About 5–10% of the total flower buds in a rachilla is open, in a rather random manner in most of the intensely flowering rachillae. Nectar appears gradually at around 1130 hours and gradually forms a droplet drowning the center cavity of the opened flower by 1200–1230 hours. Some nectar droplets may fall to the ground especially when the flowering axes are agitated by wind.

Visiting insects (mainly stingless bees like *Trigona itama* and *Trigona apicalis*) gather around the inflorescence before flower opening. By 1000 hours, they increase to over a thousand and an hour later, the

number of sting-less bees appear doubled, with warps (*Vespa tropica*) joining the crowd. Insects move from one opened flower to another and wasps are sucking up the nectar droplets. Some honeybees (*Apis dorsata*) arrive at about 1230 hours to suck up nectar droplets. By 1500 hours, the honeybees have mostly disappeared but the population of other insects remain steady. Some nectar is still present on late-opening flowers but in most other flowers, wilting of the anthers have occurred. After 1700 hours, most anthers have withered and only a few insects remain foraging on them.

At 0800 hours on the next day, most of the opened staminate flowers in the previous day have fallen off from the rachillae. They are abscised completely with the calyx and sepals, and are pushed out of the bracteoles. A few flowers with soggy anthers still remain on the rachillae but are abscised before noon. Observations on the following days confirm the similar sequence of flower opening and insect visits.

(*c*) *Opening of hermaphroditic flowers*

In West Java, the female sago palm flowers open on the last day of the opening of staminate flower in the flower pair, and last 3–4 days. The duration of flower opening on a rachilla is about one month and on each branch, 4–5 months (9). In *M. sagu* in Sarawak (4), partial opening of a few hermaphroditic flowers is observed from 0700 to 1000 hours. Purplish anthers are visible but the filaments have not elongated. Opening picks up after 1000 hours. Partially opened flowers as well as new flowers open up in a similar manner as described for the staminate flowers. The appearance and shape of the anthers are similar except that the newly opened anthers are less purplish than those of the staminate flowers.

The most active opening of hermaphroditic flowers occurs at 1100–1200 hours. They open rather randomly in each of the a × 2 and rachilla. At peak opening in a single rachilla, the percentage of flower opening in a day is between 20–50%. Nectar is secreted in most of the opened flowers by about 1130 hours, in a similar manner as described in the staminate flowers. Within half an hour, nectar overflows from the center of the flower and starts to drop down to the ground. Nectar secretion from opened flowers continues in the next hour although a few flowers are still in the process of opening.

Stingless bees are present as early as 0700 and gradually increase in number as more flowers open. From 1000 to 1200 hours, the number of stingless bees increases to a few thousands, joined by other unidentified flies and insects and about a hundred wasps. Shortly after 1200 hours, a swamp of honeybees arrives to suck up nectars from the opened flowers. Within 20 minutes, all the nectar droplets are consumed in the estimated 50,000 newly opened flowers in the entire inflorescence. The honeybees and wasps appear to gather and feed on pollen too. Pouches full of pollen are seen on the pollen baskets of many stingless bees. The number and types of insects are constant in the next hour and no new flower opening or nectar droplets are detected as the nectar is consumed as soon as it is secreted.

The honeybees start to leave at about 1415 and are completely vanished within 15 minutes. Most other insects remain although the anthers of opened hermaphroditic flowers appear withered and curled up. By 1530 hours, nectar oozes out and fills up the center cavity again in many flowers. Some nectar overflow from the flowers although the number of nectar secreting flowers is greatly reduced. Each flower is estimated to secret around 0.05 to 0.1 cm^3 of nectar. Most insects are leaving by 1630 and only a few stingless bees are still around by 1800 hours.

Similar events of flower opening and insect visits are observed in the following two days. In the morning, anthers of the flowers that opened in the previous day appear soggy and pale brown although the filaments remain extended. Un-germinated pollens are present on the stigma of all the flowers that opened in the previous day. Those flowers that opened two or three days earlier have collapsed filaments and the anthers are resting or hanging loosely outside the opened flowers. Abscission of opened hermaphrodite flowers and secretion of nectar is not found in flowers opened in the previous days. Developing fruits are visible at about three to four days after flower opening.

The secretion of nectar by the newly opened hermaphroditic flowers is in contrast to the report that only the staminate flowers secrete nectar (9). Probably, those 'female' flowers possess nonfunctional stamens and are unable to secrete nectar, similar to the inability of nectar section from the prematurely opened abnormal hermaphroditic flowers found in Sarawak.

(*d*) *Controlled and assisted pollination*

When hermaphroditic flowers in a × 2 are bagged prior to anthesis until after fruit set, the number of fruits set in the bagging and control treatments are similar (4). Totally seedless fruits are set in both the bagged and control treatments. In a different bagging experiment on abnormal hermaphrodite flowers in which the anthers die prematurely, fruits are set without pollination. This proves that sago palms fruits can be formed parthenocarpically.

In assisted self and cross-pollination carried out separately in four palms using apparently healthy pollen from the same palm for selfing and nearby palms for crossing, seedless fruits are set in all the treatments (4). In fact, all the fruits in the entire inflorescence of the 3 palms are seedless although they are visited by numerous insects. This suggests that the pollens or stigmas in these palms are either naturally or physiologically defective or some kinds of incompatibility exist between these pollens and pistils.

In a separate trial, several a × 2 in a palm are bagged prior to and throughout the flower-opening period (4). Half of the bagged a × 2 are opened to allow insect visits during anthesis. Totally seedless fruits are formed in the bagged a × 2 but 0–14% of the fruits are successfully fertilized when the pollination bags are opened during anthesis. This provides strong evidence that seeds are only set through cross-pollination and insects play an important part in carrying the compatible pollens for fertile seed set. In this palm, 5.1% of the total 6675 open pollinated fruits are seeded. Pollens from staminate and hermaphrodite flowers are sticky and succulent in appearance, which are characteristics of pollens in insect-pollinated flowers. Less than 1% of the pollens collected from the hermaphrodite flowers are capable of germinating in 10% sucrose solution. As the pollens are collected from un-bagged flowers, it cannot be certain whether the germinated pollen is from the same palm or brought in by insect pollinators. More studies need to be done on pollen viability from bagged staminate and hermaphrodite flowers. Nonetheless, it is obvious that vast majority of the pollens collected from the hermaphrodite flowers are unable to germinate. It is thus postulated that the presence of insect pollinators together with concurrent flowing palms producing compatible pollens at the vicinity is essential to enhance fertile seed set

Fruit set and duration of fruit growth

Kiew (1977) reports that the flowering period in *Metroxylon* lasts about two months and the time taken from inflorescence development to fruit maturation is about two years. Jong (1995) finds that during fruit development, successive abscission of developing fruits occurs, probably due to over-crowding. Two months after fruit set, most rachillae in both bagged and control experiments contain 20–50 fruits. After 16 months when the fruits are approaching maturity, an average of 0.8 to 2.3 full-sized fruits is left per rachilla.

The growth of the fertile and infertile sago palm fruit follows a normal curve. A mature fruit in Sarawak has a width (diameter across the center) of about 35 to 50 mm as contrasted to some fruits with a width of about 80 mm in the Solomon Islands. The duration of fruit growth from anthesis to complete fruit drop varies from 19 to 23 months. The total number of matured fruits produced in each palm ranges from 2174 to 6675 and vast majority are seedless.

Conclusions

In *Metroxylon*, both staminate and hermaphrodite flowers are found in the same inflorescence and the flowering axes. The staminate flowers constitute only about one to thirty percent of the total flowers in the inflorescence. Some palms produce normal staminate and abnormal hermaphrodite flowers (pseudo-hermaphrodite or physiologically female) with de-

fective anthers and premature flower opening. A combination of staminate with a mixture of normal and abnormal hermaphrodite flowers is also found in some palms. The sago palms are largely but not strictly protandrous as overlaps in the opening of staminate and hermaphrodite flowers often occurs to a small extent. Parthenocarpic fruit develop without pollination is common and the fruits formed are seedless. The sago palms are cross-pollinated and insects play a vital role in pollination. Studies in Sarawak indicate that the sago palms are self-incompatible and for seeds to be set, cross-pollination with compatible pollens is essential.

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