

Review Article

Reproductive Biology of Several *Garcinia* Species of Agricultural Importance in Malaysia

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ABSTRACT

The *Garcinia* genus belongs to the Clusiaceae or Guttiferae family, comprising 350 species. *Garcinia* is a large genus, and it is widely distributed in tropical environments, especially in the Southeast Asia region. Despite their wide distribution in Malaysia, information on their reproductive biology is still lacking. This overview highlights the distribution and the reproductive system of several *Garcinia* species in Malaysia, which are *Garcinia mangostana* var. *mangostana*, *Garcinia celebica*, *Garcinia mangostana* var. *malaccensis*, *Garcinia prainiana*, *Garcinia cowa*, *Garcinia atroviridis* and *Garcinia parvifolia*. Apomixis, specifically agamospermy in *Garcinia* species, is widely acknowledged by previous research. Apomixis develops a distinctive mechanism in gametophytic and sporophytic types, and it is molecularly triggered either by hybridisation or polyploidisation. *G. mangostana* var. *mangostana* is classified under obligate apomict due to male sterility caused by the alteration of tapetum during pollen development. On the other hand, the occurrence of male trees, male fertility and pollen viability are the important features that consider *G. celebica*, *G. mangostana* var. *malaccensis*, *G. prainiana*, *G. cowa*, *G. atroviridis* and *G. parvifolia* to be facultative apomict. Besides, the seeds of *Garcinia* species are recalcitrant and possess low

resistance to desiccation. The size and moisture content of the seeds can influence germination ability. The overall information of this review can help explore the life cycle of *Garcinia* trees to facilitate conservation programs along with the agricultural benefits.

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INTRODUCTION

Garcinia species are mostly agamospermy, either facultative or obligate (Richards, 1990a). Scientifically, agamospermy is a form of apomixis in which seed is produced asexually rather than sexually (Ha et al., 1988). In the common condition of most angiosperms, the facultative apomixis plant undergoes both sexual and asexual fertilisation to produce embryos. According to Richard (1990b), most *Garcinia* species are facultative apomixis, including *Garcinia celebica*, *Garcinia mangostana* var. *malaccensis*, *Garcinia cowa* and *Garcinia atroviridis* with the occurrence of male trees. Another species, *Garcinia prainiana*, is a potential facultative apomict, proved through genetic variation analysis (Rohani et al., 2021). On the other hand, obligate apomixis undergoes adventive embryo development (Kant & Verma, 2012) that occurs asexually within the tissue of ovules. *G. mangostana* var. *mangostana* is an obligate apomict that potentially bears no morphological and genetic variation (Mansyah et al., 2010). It can be inferred that all of the offspring of *G. mangostana* var. *mangostana* are identical to their mother plant.

The reproductive biology of *Garcinia* species is another study area with significant research gaps. *Garcinia* species has ecological and economic importance, yet there is limited understanding of many aspects of its reproductive biology. Plant reproductive biology serves as primary knowledge to identify reproduction types and capabilities through a sexual and asexual mechanism. This understanding can improve plant conservation and agricultural technology in conventional and non-conventional breeding, such as genetic selection, mutation, somaclonal variations, genomic sequence-based application and physical maps (Ahmar et al., 2020), especially on the common cultivated and rare *Garcinia* species. Some *Garcinia* species are economically important in the agricultural sector, such as *G. mangostana* var. *mangostana*. In contrast, the others might be critically endangered due to the loss of biodiversity, especially *G. cowa*. The failure of conservation of the threatened plants in nature due to lack of regeneration success can be avoided by employing the knowledge of reproductive biology (Marbaniang et al., 2018). The underutilised species, such as *G. celebica*, *G. atroviridis* and *G. parvifolia*, perhaps are important for commercial development and local uses (Khoo et al., 2010).

This review aims to provide the available research documentation on the reproductive biology of several *Garcinia* species that encompass morphologies of flowers and fruit, the occurrence of apomixis, pollen viability and seed germination ability. The overall information regarding the distribution and the reproductive system of *G. mangostana* var. *mangostana*, *G. celebica*, *G. mangostana* var. *malaccensis*, *G. prainiana*, *G. cowa*, *G. atroviridis* and *G. parvifolia* will be brought to light for identification of the reproductive capability for agricultural interest and plant conservation.

CULTIVATION OF *GARCINIA* SPECIES

As proposed by Yaacob and Tindal (1995), *G. mangostana* var. *mangostana* is native to Southeast Asia. Due to its pleasant taste, *G. mangostana* var. *mangostana* is a well-known tropical fruit that locals highly prefer. Malaysia, Indonesia, Thailand and the Philippines are the major cultivating countries of *G. mangostana* var. *mangostana*. *G. mangostana* var. *mangostana* is scattered in other tropical regions, namely Northern Australia, South America and Tropical Africa (Cruz, 2001). Furthermore, the growth and cultivation of *G. celebica* occur in Malaysia, Thailand, Vietnam, Cambodia, Borneo, Andaman, Nicobar Island, Kerala and Tamil Nadu, India (Lim, 2012b; Nazre, 2010; Nazre et al., 2018). *G. prainiana* is usually found in Malaysia, specifically in Pahang, Kelantan, Terengganu and Perak (Azuan et al., 2015). The information on the cultivation areas of *G. mangostana* var. *malaccensis*, *G. cowa*, *G. atroviridis* and *G. parvifolia* is scarce.

ECOLOGY OF *GARCINIA* SPECIES

Plant reproductive traits are important in the correlation studies between ecological interactions and evolutionary change. The environmental diverseness in abiotic climate conditions highly regulates the extent of sexual dimorphism in the dioecious system (Puixeu et al., 2019). In addition, the ecological well-being of plants is affected by climate change (Pareek et al., 2020) and soil (Bitew & Alemayehu, 2017). The breeders need to consider these factors for cultivation purposes in the agriculture sector and plant conservation. *Garcinia* species are commonly distributed in lowland tropical areas, and most of the species occur in a particular region, especially in Southeast Asia (Sweeney, 2008). Table 1 shows the overall ecological and cultivation description of *G. mangostana* var. *mangostana*, *G. celebica*, *G. mangostana* var. *malaccensis*, *G. prainiana*, *G. cowa*, *G. atroviridis* and *G. parvifolia*.

A prolonged drought followed by rain in July-August led to increased leaf flushing rather than flowering, limiting fruit production of *G. mangostana* var. *mangostana* in Thailand (Apiratikorn et al., 2012). Unfavourable conditions also will cause slow growth and the contamination of yellow latex on fruit. According to Mansyah et al. (2003), heavy rainfall and higher relative humidity will lead to more yellow latex within the fruit's endocarp. Moreover, the level of yellow latex is also affected by the calcium concentration in the soil (Martias et al., 2021). According to Lim (2012a), *G. mangostana* var. *mangostana* grows better on organic-rich soils such as sandy loams and moderately lateritic and volcanic soils with proper drain conditions.

Garcinia celebica is known as seashore mangosteen or “beruas” in Malaysia. The name of seashore mangosteen is based on its tropical distribution from the seaside region and morphological resemblances with *G. mangostana* var. *mangostana* (Nazre, 2010). *Garcinia celebica* is native to Malaysia, Cambodia, Thailand, and Vietnam (Lim, 2012b)

and has largely spread from coastal to highland regions in tropical countries (Nazre, 2018). Due to its nature, *G. celebica* can adapt to sandy, rocky and acid clay soils, heavy rainfall, and drought environments and is salt-tolerant (Lim, 2012b). *Garcinia mangostana* var. *malaccensis* is regarded as one of the possible ancestors of *G. mangostana* var. *mangostana* (Richards, 1990b). *Garcinia mangostana* var. *malaccensis* is native to Peninsular Malaysia, Sumatra and Brunei and is found in lowland and highland tropical forests (Lim, 2012c; Nazre et al., 2018). *Garcinia mangostana* var. *malaccensis* is well-adapted to organic-rich soils and has a tropical climate with hot and wet conditions (Lim, 2012c). The study of the reproductive biology of *G. celebica* and *G. mangostana* var. *malaccensis* is essential due to their significant role in determining the ancestor of *G. mangostana* var. *mangostana*.

Garcinia prainiana (cerapu), or button mangosteen, is believed to be indigenous to Peninsular Malaysia and Thailand (Mohd Khairuddin et al., 2018). Besides, *G. prainiana* and *G. mangostana* var. *mangostana* share a similar condition for growth, which is in lowland and hill areas where it needs well-distributed rainfall, warm temperature, well-drained and porous soils and fairly acid clay loams that are rich in organic matter (Lim, 2012d). The current status of *G. prainiana* under the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (April 2024) is registered as lower risk. *G. prainiana* is an underutilised species (Azuan et al., 2015), resulting in limited agricultural yield and research studies. The potential of underutilised species remains largely untapped due to limited scientific understanding, especially concerning their reproductive biology. The reproductive biological study of underutilised species encompasses their potential and incorporates them into mainstream agriculture and conservation.

Garcinia cowa Roxb. known as kandis in Malaysia, is natively from Southwest India, East India, Nepal, Andaman and Nicobar Island, Yunnan in China, as well as Southeast Asia including Myanmar, Thailand, Laos, Vietnam, and Northern Peninsular Malaysia (Lim, 2012e). Like other *Garcinia* species, *G. cowa* commonly occurs in tropical evergreen, sand, and dry deciduous forests, especially in Thailand. The current status of *G. cowa* corresponds to *G. prainiana* under the IUCN Red List of Threatened Species (April 2024). Based on the assessment by Deepu and Geethakumary (2020), *G. cowa* is listed as one of the endangered species mainly caused by deforestation and habitat destruction; for endangered species like *G. cowa*, effective conservation strategies might require a deep understanding of its reproductive biology.

Garcinia atroviridis Griff. ex T. Anderson is locally known as “asam gelugor” in Malaysia. *G. atroviridis* is an indigenous species from Peninsular Malaysia, Thailand, Myanmar, and India, and it is found in humid weather in lowland and highland rainfall regions (Lim, 2012f). *G. atroviridis* is widely distributed and essential to Indonesia’s forest (Bayu, Lestami et al., 2018). *G. parvifolia* (Miq.) is native to tropical regions: Thailand, Malaysia, Sumatra, Java, Brunei, Kalimantan, Sulawesi, Maluku Islands and New Guinea

(Lim, 2012g). *G. parvifolia* or cherry mangosteen is also locally known as “asam kandis” or “takob akob”, especially in Sabah and “asam kundong” in Sarawak (Hassan et al., 2013). In the agroecological part, the distribution of wild *G. parvifolia* is favourable toward humid tropical areas such as peat swamp and lowland forests through submontane with hillsides and ridges as well as well-drained, alluvial sites and along rivers (Lim, 2012g; Hassan et al., 2013). Both *G. atroviridis* and *G. parvifolia* have agricultural benefits. It is necessary to acknowledge the reproductive biology of these *Garcinia* species to enhance productivity, sustainability, and resilience in the agricultural system.

REPRODUCTIVE BIOLOGY OF *GARCINIA* SPECIES

The reproduction process is an important phase in the life cycle of an organism, and it also can be a fundamental aspect of the evolutionary system (Li et al., 2018). The sexual reproduction cycle in most angiosperm involves the development of an embryo (embryogenesis) and endosperm as an outcome of the fusion of a male gamete (sperm) and a female gamete (egg cell) together with the combination of two polar nuclei and a male gamete in the embryo sac respectively (Ao, 2020).

Apomixis is closely related to sexual reproduction; however, the embryo undergoes (1) the exclusion of meiosis throughout embryo sac development (apomeiosis), (2) the development of the embryo out of an unfertilised egg cell (parthenogenesis) and (3) the development of endosperm either through fertilisation or non-fertilisation (Hand & Koltunow, 2014). The change of epigenetic regulatory pathway determines Apomixis as an outcome of polyploidisation and hybridisation that can generate unreduced female gametophytes (Hojsgaard & Hörandl, 2018) as most of the natural apomictic individuals are polyploids and hybrids (Barke et al., 2018). Polyploidy disintegrates genetic self-incompatibility (SI) by initiating a reproductive block on the diploid progenitor, and hence, pseudogamous apomictic plants can be self-fertile (Hojsgaard & Hörandl, 2018).

Apomixis is classified into two types: (1) sporophytic and (2) gametophytic (apospory and diplospory). The reproduction in sporophytic apomixis occurs concurrently with normal sexual reproduction (Figure 1). However, the adventive embryo emerges somatically from the integumental or nucellus tissue through mitotic division. As a result, multiple embryos or polyembryony in sporophytic apomixis are developed. The formation of polyembryony in sporophytic apomixis is prevalent in Rutaceae, such as *Citrus* species (Yuantao et al., 2021). Brukhin (2017) stated that the maturation of diploid adventive embryos is competitive, and it relies on sexually-originated endosperm to gain nutrients by repressing sexual embryos. Occasionally, the endosperm can autonomously evolve independently of fertilisation. This condition is termed autonomous apomixis (Cardoso et al., 2018).

Meanwhile, in gametophytic apomixis, both apospory and diplospory share a similar pathway where the unreduced embryo sac is developed via mitosis with suppression

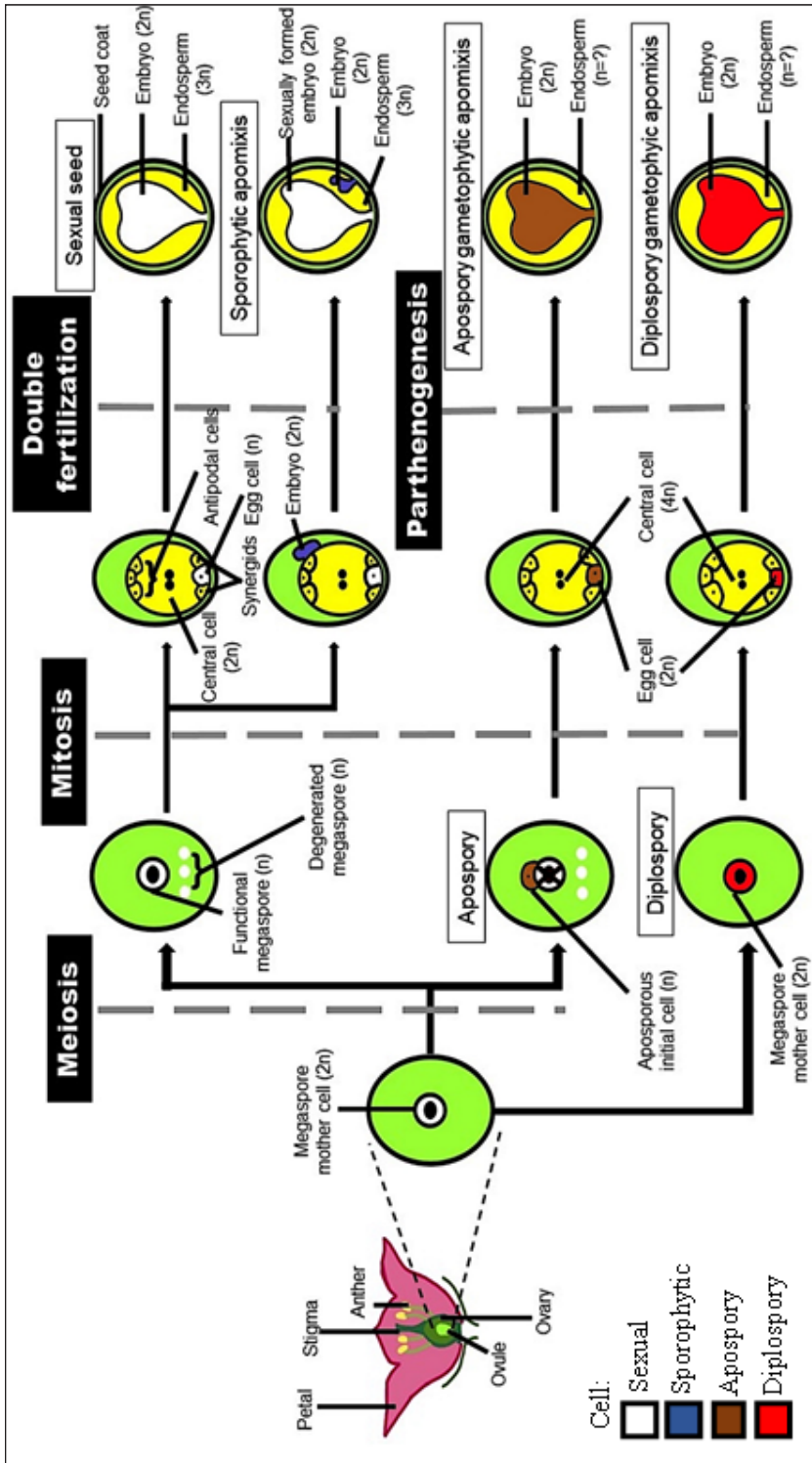


Figure 1. Process of sexual and apomixis seed development. The illustration is based on the description from Hand and Koltunow (2014) with slight modifications. A dashed line represents the processes and pathways. Colours represent cells that develop the embryo: sexual (white), sporophytic (blue), apospory (brown), and diplospory (red). The ploidy level of cells (n) is displayed as a question mark

of meiosis (apomeiosis) in the absence of double fertilisation and later undergoes parthenogenesis to form a diploid embryo (Hand & Koltunow, 2014). Parthenogenesis occurs synergically with apomeiosis and autonomous endosperm formation (absent or present of central cell fertilisation) (Vijverberg et al., 2019). Functional megaspore mother cells from meiosis division in apospory degenerate, leaving only diploid somatic apospory initial cells to further develop mitotically into the embryo (Figure 1). Meanwhile, the megaspore mother cell in the diplospory develops into the embryo sac through mitotic division during the whole process. The development of endosperm in gametophyte apomixis differs in the ploidy level of cells (n) with or without the occurrence of fertilisation.

Obligate Apomixis

Generally, obligate apomixis occurs without the fusion of female and male gametes, which might be caused by altering certain components during the reproductive phase. The reproduction system of *G. mangostana* var. *mangostana* is categorised under obligate apomixis, as confirmed by Lim (1984) and Richard (1990a), due to the absence of male trees (Whitmore, 1973). Male *G. mangostana* var. *mangostana* was last spotted by Idris and Rukayah (1987), and it is uncommon due to the cultural actions of the locals that chop down the trees because they believe male trees are non-beneficial (Nazre, 2014). Thus, the progenies of apomictic *G. mangostana* var. *mangostana* should be genetically identical to the mother plant (Koltunow et al., 1995) because no depletion of chromosome number and egg fertilisation occurred to form an embryo (den Nijs & van Dijk, 1993). It also results in a lack of genetic variability. However, in some cases, a morphological variation of *G. mangostana* var. *mangostana* happens depending on its locality. In addition, the mechanism of male flowers in terms of morphology and pollen development of *G. mangostana* var. *mangostana* has been described (Awachare & Upreti, 2019; Nazre, 2014; Sutthinon et al., 2019).

***Reproductive System of Garcinia mangostana* var. *mangostana*: Flowers, Fruits, and Seeds**

A large flower of *G. mangostana* var. *mangostana* consists of four fleshy petals, yellowish green in colour and pinkish or reddish toward the margin, and it also bears infertile staminodes (Awachare & Upreti, 2019; Lim, 2012a; Sulassih et al., 2013; Yuniastuti, 2010). In the report of Nazre et al. (2018), the calyx of *G. mangostana* var. *mangostana* is thicker than other *Garcinia* species with ovate to obovate or concave in shape (Table 2). The female flowers consist of a large sessile or subsessile discoid stigma (Richards, 1990b; Te-chato, 2007) and blunt star-shaped or broadly ovoid ovary with 4–8 chambers, and the inflorescence is usually in triads (Nazre et al., 2018; Yuniastuti, 2010). A male flower has a fungiform pistillode with basal encircled by 4-angled stamen bundles (Nazre, 2014).

Most wild species have a long flowering cycle, and the flowering period takes place more than once a year. In the case of *G. mangostana* var. *mangostana*, the flowering period occurs in March–April and July–September (Te-chato, 2007). The flowering begins after the vegetative growth flushes depending on the environmental states, the total flushes and post-dry weather (Awachare & Upreti, 2019). As Yuniastuti (2010) reported, the average time taken for a flower of *G. mangostana* var. *mangostana* (Jogorogo, East Java province, Indonesia) to bloom perfectly was 24–25 days. The flower has a perfectly functional female part but has male sterility due to male reproductive degradation (Awachare & Upreti, 2019; Sobir & Poerwanto, 2007; Suthhinon et al., 2019).

During the initial stages of flowering in *G. mangostana* var. *mangostana*, the development of stamens is stunted and aborted (Awachare & Upreti, 2019). It has been discussed that the male sterility of *G. mangostana* var. *mangostana* experienced pollen abortion during micro gametogenesis due to alteration of tapetum (Shi et al., 2010), which resulted in microspore degradation and failed formation of male gamete (Suthhinon et al., 2019). Specifically, cellular deprivation due to a slight accumulation of starch on disintegrated microspore and degenerated microspore mother cell has caused early cell death of tapetum with acutely shape alteration of mitochondria (Suthhinon et al., 2018a; Suthhinon et al., 2019). It was stated that the microspore mother cell in *G. mangostana* var. *mangostana* contained insufficient Golgi apparatus and vesicles together with unusual callose wall build-up that resulted in unsystematic cytoplasm (Suthhinon et al., 2019). Furthermore, microspore degeneration occurs at all stages of development (Suthhinon et al., 2019) but precisely during meiosis at stage VI (Yapwattanaphun et al., 2008). The microspore tetrads alongside total callose depositions were infrequently detectable (Suthhinon et al., 2018b). Few persistent free microspores initiated from meiosis were noticeable, with an unusual shape during the late microspore development stage but completely degenerated later during vacuolate and bicellular stages (Nuanjungkong & Meesawat, 2010). Besides, the pollen viability (0.1-1%) was extremely low (Te-chato, 2007), which strongly justifies the male sterility theory on *G. mangostana* var. *mangostana*.

The fruits are globose in shape, smooth surface and large, thick with dark purple or red pericarp, which contains a sweet and sour taste, and fleshy and snowy white aril (Nazre, 2014; Sulassih et al., 2013; Techato, 2007; Yuniastuti, 2010). Yuniastuti (2010) mentioned that the fruits also contain more than one light brown seed and are ellipsoid in shape. *G. mangostana* var. *mangostana* also displays certain variations in fruits. Based on the report from Mulyono et al. (2021), six varieties of *G. mangostana* var. *mangostana* in Indonesia named “Kaligesing”, “Puspahiyang”, “Wanayasa”, “Ratu Kamang”, “Ratu Tembilihan”, and “Lingsar” exhibited different fruit traits in terms of size, shape, weight and flavour. It was concluded that all varieties may adapt differently in the same environmental state. The differences in the morphological features of fruit in *G. mangostana* var. *mangostana*

(taper and round flat downside in shape), aril (cream-coloured and pure-white), seed (ellipse, oval, long and irregular in shape) were reported in Langkat region, North Sumatra, Indonesia (Syahputra et al., 2021). Meanwhile, in the Philippines, the fruit characteristics of *G. mangostana* var. *mangostana*, including shape, size, pericarp thickness and ripened taste between two territories, namely Quezon in Luzon Island and Davao-Zamboanga in Mindanao Island, were highly comparable to each other. These characteristics also nearly resembled *G. mangostana* var. *malaccensis* from different geological areas (Berame et al., 2020).

The fruits of *G. mangostana* var. *mangostana* are likely to mature in the absence of crossbreeding (Richards, 1990a; Te-chato, 2007). The time for *G. mangostana* var. *mangostana* to begin fruiting is relatively slow. Fruiting was rare before the age of 12 (Lim, 1984), but it started to fruit regularly at 18 to 20 (Richards, 1990b). Te-chato (2007) also reported that developing unfertilised ovaries into mature fruits took 4 to 6 months. The fruit of *G. mangostana* var. *mangostana* also has a few locules that formed completely developed ovules with liquid endosperm residuals consisting of plant growth hormones (auxin, cytokinin, gibberellin, abscisic acid and jasmonic acid), while the remaining locules contained a deflated ovule that will cease to growth (Yapwattanaphun et al., 2014). Besides, the fertility of apomictic seeds of *G. mangostana* var. *mangostana* is sustainable, as Yuniastuti claims (2010). The apomictic seeds appear to be polyembryony (Suhendra & Mustamu, 2018), which means multiple seedlings can emerge from one seed.

A long interval of seed dormancy before germination is one of the common traits in the agamospermy plant (Ha et al., 1988). However, in the report of Normah et al. (2016), the mean germination time (MGT) in *G. mangostana* var. *mangostana* was reported to be 24 days along with *G. celebica* (22.2 days), *G. atroviridis* (25 days) and *G. prainiana* (47 days). A short germination time in *G. mangostana* var. *mangostana* is likely caused by the high level of moisture content that could accelerate the germination ability even though the seeds have short-term viability (Oliveira & Valio, 1992). The moisture content (61.12% of fresh weight) in the larger seed (length:width=1.9 ± 0.03 cm: 1.3 ± 0.03 cm) of *G. mangostana* var. *mangostana* was the highest; however, due to desiccation, the moisture content constantly decreased beyond 30% after 72 hours which dropped its germinability drastically (Normah et al., 2016). Besides, the seeds from *Garcinia* species, especially *G. mangostana* var. *mangostana*, are recalcitrant (Yuniastuti, 2010), which means the seeds are susceptible to losing viability during cold storage together with low survivability on desiccation (Normah et al., 2016).

Seed sizes and nutrient reservation also play a role in seed germination. The variation in seed size possesses distinct levels of starch and energy reservation that could enhance germination expression and primary development of seedlings (Steiner et al., 2019)—in the case of *Garcinia* species, *G. mangostana* var. *mangostana*, *G. celebica*, *G. atroviridis* and

G. prainiana similarly contained a large amount of lipid and calcium oxalate despite being different in sizes and moisture content, except for the high level of starch which was found in *G. mangostana* var. *mangostana* only (Normah et al., 2016). The high accumulation of energy metabolites could increase *G. mangostana* var. *mangostana* germinability. As stated by Goh et al. (2019), the seeds can germinate easily upon imbibition along with the optimum level of seed metabolism, unlike other *Garcinia* species that need a period of dormancy breaking, such as *G. cowa* (Liu et al., 2005).

Facultative Apomixis

Facultative apomixis is very common in an angiosperm plant where both apomixis and sexual reproduction are concurrent in the presence of male plants. The level of residual sexuality in facultative apomicts is highly varied, which enhances the heterogeneity of genotypic and phenotypic (Majeský et al., 2017). As mentioned before, *G. celebica*, *G. mangostana* var. *malaccensis*, *G. prainiana*, *G. cowa*, *G. atroviridis* and *G. parvifolia* are considered facultative apomixis based on the reproductive system reported by previous studies.

Reproductive System of Garcinia celebica: Flowers, Fruits and Seeds

The female flowers of *G. celebica* are solitary, axillary, borne singly, lack staminode and yellowish-green petals (Sulassih et al., 2013), with a large fungiform stigma and globose or ovoid ovary (Table 2). The male flowers are axillary in fascicle, slightly smaller, sessile and borne vertically in clusters, thinly coriaceous sepals, usually aromatic, cream in colour with numerous 4-lobed stamens connected at the base of pistillode on top of the petals (Nazre et al., 2018; Richards, 1990c).

Unlike *G. mangostana* var. *mangostana*, *G. celebica* is considered a facultative apomixis when it bears fertile female and male flowers. As reported by Richards (1990c), female inflorescence buds produce one or two flowers and reach anthesis six days following bud initiation, whereas male inflorescence developed earlier by producing three to seven flowers that open consecutively over four days, followed by pollen release on two straight mornings. In addition, the flowering period of *G. celebica* is longer, occurring from January to June (Richard, 1990c). Besides, the increase in chances for sexual reproduction in *G. celebica* is likely due to a high number of male flowers compared to female flowers (Nazre et al., 2018).

In a previous study reported by Suthhinon et al. (2019), during an anthesis phase, the complete flower of *G. celebica* gives rise to a standard male gametophyte with normal development of microspore mother cell containing packed cytoplasm and plentiful Golgi apparatus as well as vesicles that lead to the effective pollen yield. Unlike the premature cell death of tapetum that occurred in *G. mangostana* var. *mangostana*, the degradation of

tapetum for *G. celebica* occurred after meiosis II, which is parallel with the total enclose of callose wall surrounding microspore tetrads (Sutthinon et al., 2018b). A normal starch build-up occurs primarily at the microspore cell stage and reaches its highest peak during the unicellular microspore phase (Sutthinon et al., 2018a). It is consistent with the outcomes where *G. celebica* provided 68% viability and 68% germination through tetrazolium test (TTC) assay and in vitro germination (Sutthinon et al., 2018b). Pollen viability and development can justify the functionality of *G. celebica* as a perfect and fertile male plant.

The fruits of *G. celebica* have thin pericarp, deep red when matured, sub-globose to ellipsoid, and smooth surface with creamy white and sour aril (Sulassih et al., 2013) (Table 3). The recalcitrant seeds of *G. celebica* were found to be the largest in terms of seed length (2.5 ± 0.05 cm) and seed width (1.4 ± 0.04 cm) and obtained the second-highest moisture content (51.52% of fresh weight) from the study conducted by Normah et al. (2016). The seed size and moisture content could affect the percentage of seed germination. The higher rate of germination is comparable to the larger seed size (Yousif, 2010); a similar case happened in *G. mangostana* var. *mangostana*. The bigger seeds of *G. celebica* reserved relatively 20%–60% moisture content at 96 hours desiccation with 95.6% germination, which was the highest, followed by *G. mangostana* var. *mangostana* (75.6%), *G. atroviridis* (57.3%) and *G. prainiana* (48.9%) (Normah et al., 2016).

***Reproductive System of Garcinia mangostana* var. *malaccensis*: Flowers and Fruits**

The male flowers of *G. mangostana* var. *malaccensis* have pinkish-red petals, pistillode fungiform but sometimes can be absent, and long and slender stamen is slightly 4-angled or comical-cylindrical, whereas the female flower has a corrugated surface stigma (Nazre, 2014; Nazre et al., 2018) (Table 2). The fruits are reddish pink to dark purple, ovoid to globose, corrugated surface with snowy white and sour taste of aril (Sulassih et al., 2013; Nazre, 2014) (Table 3). In addition, the size of its mature fruit is smaller than *G. mangostana* var. *mangostana* but similar to *G. celebica* (Taher et al., 2012). There is no data concerning the specific details of pollen viability and *G. mangostana* var. *malaccensis* seed germination. According to Nazre (2014), the previous studies of *G. mangostana* var. *malaccensis* done by Ha et al. (1988) and Richards (1990a) were not properly documented due to species misidentification.

***Reproductive System of Garcinia prainiana*: Flowers, Fruits, and Seeds**

Garcinia prainiana is regarded as a dioecious plant whereby the male and female flowers are situated on different plants, as stated by Rohani et al. (2021). The flowers of *G. prainiana* are axillary in dense clusters, consisting of five rounded sepals with green to pink in colour and five rounded petals with rose pink to yellow; male flowers have compacted stamens with yellow anthers, whereas female flowers are large and no stamens were found (Azuan

et al., 2015; Rohani et al., 2021) (Table 2). Like *G. celebica*, *G. prainiana* exhibits viable pollen from the male plants. To justify this, Rohani et al. (2021) have revealed the high pollen viability ($77.6 \pm 9.68\%$) and germination ($60.95 \pm 15.87\%$) of *G. prainiana*. Hence, it shows that *G. prainiana* is a facultative apomictic with both functional male and female plants with well-evolved ovules (Rohani et al., 2021). In addition, most of the sexual pollination in plants will rely on biotic and abiotic approaches to ensure the proper dispersal of pollen. A group of insects were found on the male flower of *G. prainiana*, assuming that the pollination probably occurred between male and female plants (Rohani et al., 2021).

The fruits of *G. prainiana* are yellowish-orange in colour, rounded but rather flattened soft and thin rind; the pulp is orange in colour, 4–7 segmented, and acidic sweet taste (Azuan et al., 2015; Mohd Khairuddin et al., 2018) (Table 3). For seed development, based on the study by Normah et al. (2016), *G. prainiana* contained a smaller size (length:width= 1.1 ± 0.02 cm: 0.9 ± 0.01 cm) and thickest testa (147.35 ± 1.24 μ m) with 47 days mean germination time which was the slowest compared to *G. mangostana* var. *mangostana*, *G. celebica* and *G. atroviridis* (22 to 25 days). The slow germination of *G. prainiana* is probably due to the test itself. Testa in higher plants protects the embryo against biotic and abiotic conditions during seed storage by limiting water permeability or mechanically restricting the radicle protrusion (Debeaujon et al., 2000).

Reproductive System of Garcinia cowa: Flowers, Fruits, and Seeds

The flowering period of *G. cowa* usually occurs from July until September, similar to *G. mangostana* var. *mangostana* (Te-chato, 2007). *G. cowa* also develops distinctive features for flower morphology. It bears male flowers consisting of four yellow petals with clustered stamens, with four unified fascicles developing an innermost capitate quadratic clump of 40 to 50 anthers. In contrast, female flowers are solitary, axillary with fused staminodes in the lower half, and the surrounding ovary base consists of an ovoid ovary and four to eight radiate ridged and papillate stigma (Te-chato, 2007; Lim, 2012e) (Table 2). As reported by Richards (1990a), *G. cowa* is likely to be facultative apomixis due to the occurrence of the male plant. Besides, pollen of *G. cowa* exhibited 96%–100% of viability (Te-chato, 2007), which strongly supported the claim by Richards (1990a).

In addition, according to Lim (2012e), the fruits of *G. cowa* are subglobose to globose and oblique in shape, green when unripe, and the matured fruits turn to yellow or pale orange with five to eight furrows close to the top, and remaining stigma lowered on the small black persistent calyx. The young fruit has an elongated oval shape and changes into a round shape during maturation (Roy et al., 2010) (Table 3). Moreover, the seeds of *G. cowa*, immersed in dull orange and sour pulp, are great in size and trigonous. Due to their large size, the matured seeds of *G. cowa* provided moisture content roughly at 50% fresh weight (Liu et al., 2002), and the seeds were desiccation-tolerant. However, they

immediately decreased seed viability under 4°C and died almost at 17% of moisture content (Liu et al., 2005). Hence, the seeds of *G. cowa* might be regarded as tropical recalcitrant due to low endurance to desiccation and chilling imbibition. Seed dormancy is a common phenomenon in all plants that affect germination ability. To break dormancy and promote germination, seed pre-treatment, such as scarification, is required by providing water permeability through the seed coat and initiating imbibition (Ardiarini et al., 2021). In the case of *G. cowa*, the seeds have long dormancy up to 8–11 months with 252 days of MGT, and unsuccessful germination was reported after the dispersion at 30°C for 120 days (Liu et al., 2005). The removal of the seed coat of *G. cowa* resulted in the decline of MGT to 13 days at 30°C (Liu et al., 2005).

Reproductive System of Garcinia atroviridis: Flowers, Fruits, and Seeds

The flowering period of *G. atroviridis* occurs from July to September, usually five to six years after planting (Pangsuban et al., 2009; Te-chato, 2007). The flowers of *G. atroviridis* are terminals and pedicellate, consisting of four yellow, spreading spherical and concave sepals as well as dark red or crimson, obovate, and fleshy petals with yellowish colour at the edge (Bayu, Febrianti, & Damanik, 2018b; Lim, 2012f) (Table 2). Male flowers are in small, flowered racemes with various stamens in whorls around the pistillode. In contrast, the female flowers are solitary, large, and have 8–16 celled ovoid ovaries with deep red pileate, sub-tetragonal, convex, or sessile stigma with corrugated surface, and staminode connected to an annulus (Te-chato, 2007; Lim, 2012f).

Garcinia atroviridis is gynodioecious that carries both female and hermaphrodite flowers, and it depicts a female-biased ratio when the hermaphrodite flower produces less to no fruit while the female flower contains a bigger ovule that develops a bigger fruit with more seeds (Pangsuban et al., 2009). On top of that, the clustered hermaphrodite flowers have a long filament and plenty of fertile pollens, but they encounter early drops compared to female flowers (Bayu, Febrianti, & Damanik, 2018b). *G. atroviridis* is presumably classified as facultative apomixis, although male trees are rare (Richards, 1990a). The pollen viability of *G. atroviridis* was reported to be 3%–5% (Te-chato, 2007) owing to its influence on the female-biased ratio. Besides, based on the *in vitro* germination evaluation, *G. atroviridis* showed high pollen viability (79.5%) a day after anther dehiscence but gradually lost about 50.0% (17 days) due to pollen half-life and then followed by non-germinated pollen grains prior to 25 days after dehiscence (Pangsuban et al., 2009).

The immature green fruits of *G. atroviridis* turn to vivid yellow when matured with sunken globose in shape, widely lowered hollow apex that consists of 12–16 ribs, slightly grooved, segregated segments, sustained calyx and corolla, thick husk as well as contain flattened seeds encircled by sour and bright orange arillode (Lim, 2012f; Te-chato, 2007) (Table 3). Based on the study by Pangsuban et al. (2009), the apogamy treatment (bags

without pollination) on *G. atroviridis* resulted in a high fruit drop ratio, less and smaller fruit production, and low quantity and quality of seeds compared to open and hand pollination treatments. Regardless, this apogamy treatment on *G. atroviridis* carried out the asexual development of fruit (17.5%) and seed with a 2.82 ± 0.99 (7) average number per ripe fruit based on the data obtained from the same study. In addition, the smaller recalcitrant seeds (Length:width= 1.3 ± 0.03 cm: 0.6 ± 0.01 cm) of *G. atroviridis* showed 57.3% of germination and 25 mean germination time (Normah et al., 2016). A small seed will likely have a rapid moisture content loss that causes low desiccation resistance (Wen & Cai, 2014). In the case of *G. atroviridis*, the moisture content was reported to be 34.92% in fresh weight and rapidly dropped at 96 hours of desiccation (Normah et al., 2016).

Reproductive System of Garcinia parvifolia: Flowers, Fruits, and Seeds

The flowers of *G. parvifolia* are unisexual, bisexual, polygamous, pedicellate, solitary, or axillary in fascicles (2–12) with four yellow to dull orange sepals, large petals, the male flower has no pistillodes, whereas the female flower consists of 7–12 staminodes (Lim, 2012g) (Table 2). *G. parvifolia* is shown to be facultative apomixis, and the reproduction behaviour depicts gametophytic apomixis, while *G. mangostana* var. *mangostana* and *G. celebica* reproduce through sporophytic apomixis (Dike et al., 2020).

The young dull green fruit turns to yellow or orange when matured, depressed globose in shape that comprises a sunken top with a persistent small stigma, thin peel, and small seed surrounded by white and moderately acidic arils (Lim, 2012g) (Table 3). *G. parvifolia* exhibits apomixis behaviour when seed germination occurs without males, parthenogenesis happens, undeveloped proembryos are actuated as well as single embryos can generate many seedlings (Ha et al., 1988; Richards, 1990a). The seed germination was revealed to be a *Garcinia* type when the emergence of plumule and radicle occurs in two opposite ways, similar to *G. mangostana* var. *mangostana*, *G. celebica*, *G. atroviridis* and *G. prainiana* (semi-*Garcinia*), as documented by Normah et al. (2016).

Table 1
The overall description of the distribution of selected *Garcinia* species

<i>Garcinia</i> species	Ecological aspects		
	Origin	Cultivation	Climate
<i>Garcinia mangostana</i> var. <i>mangostana</i>	Southeast Asia (Yaacob & Tindal, 1995)	Malaysia, Indonesia, Thailand, Philippines, Northern Australia, South America and tropical Africa (Cruz, 2001)	Non-seasonal wet tropical and hot and humid weather (Richard, 1990b; Junior et al., 2019)
<i>Garcinia celebica</i>	Malaysia, Cambodia, Thailand and Vietnam. (Lim, 2012b)	Malaysia, Thailand, Vietnam, Cambodia, Borneo, Andaman, Nicobar Island, Kerala and Tamil Nadu, India (Lim 2012b; Nazre 2010; Nazre et al., 2018)	Tropical (Lim, 2012b)
<i>Garcinia mangostana</i> var. <i>maltaccensis</i>	Peninsular Malaysia, Sumatra and Brunei (Lim, 2012c)	NI	Tropical. Hot and wet condition (Lim, 2012c)
<i>Garcinia pratiniana</i>	Peninsular Malaysia and Thailand (Mohd Khairuddin et al., 2018)	Pahang, Kelantan, Terengganu and Perak (Azuan et al., 2015)	Tropical (Lim, 2012d)
<i>Garcinia cowa</i>	Southwest India, East India, Nepal, Andaman and Nicobar Island, Yunnan (China), Myanmar, Thailand, Laos, Vietnam, and Northern Peninsular Malaysia (Lim, 2012e; Richard, 1990)	NI	Tropical (Lim, 2012e)
<i>Garcinia atroviridis</i>	Peninsular Malaysia, Thailand, Myanmar and India (Lim, 2012f)	NI	Humid weather in lowland and highland rainfall region (Lim, 2012f)
<i>Garcinia parvifolia</i>	Thailand, Malaysia, Sumatra, Java, Brunei, Kalimantan, Sulawesi, Maluku Islands and New Guinea (Lim, 2012g)	NI	Tropical. Humid conditions such, as in peat swamps and lowland forests (Hassan et al., 2013; Lim, 2012g)

Note. NI indicates that no information

Table 2
The summary of the flower parts of selected *Garcinia* species

<i>Garcinia</i> species	Flower parts						
	Inflorescence	Petal	Sepal	Stamen	Pistillode	Stigma	Ovary
<i>Garcinia mangostana</i> var. <i>mangostana</i>	Inflorescence triads (Nazre et al., 2018)	Fleshy Yellowish green and pinkish toward the edge (Awachare & Upreti, 2019; Sulassih et al., 2013; Yuniasututi, 2010)	Ovate to obovate or concave Thick (Nazre et al., 2018)	4-angled (Nazre, 2014) Pollen viability = 0.1-1% (Te-chato, 2007)	Fungiform (Nazre, 2014)	Large sessile or subsessile Discoid (Osman & Milan, 2006; Richards, 1990b; Te-chato (2007)	Blunt star-shaped or broadly ovoid 4-8 chambers (Yuniasututi, 2010)
<i>Garcinia celebica</i>	Solitary, axillary (female) Axillary, borne singly (male) (John et al., 2008; Nazre et al., 2018; Richards, 1990c)	Yellowish green (Sulassih et al., 2013)	Thinly coriaceous (John et al. 2008; Nazre et al., 2018; Richards, 1990c;)	4-lobed (Nazre et al., 2018) Pollen viability and germination = 68% (Sutthinon, Samuels, & Meesawat, 2018a)	NI	Large Fungiform (John et al., 2008; Nazre et al., 2018; Richards, 1990c;)	Globose to ovoid (John et al., 2008; Nazre et al., 2018; Richards, 1990c;)
<i>Garcinia mangostana</i> var. <i>malaccensis</i>	NI	Pinkish red (Nazre, 2014)	NI	Long and slender 4-angled or comical-cylindrical (Nazre, 2014; Nazre et al., 2018)	Fungiform (Nazre, 2014)	Corrugated surface (Nazre, 2014)	NI

Table 2 (Continue)

<i>Garcinia</i> species	Flower parts						
	Inflorescence	Petal	Sepal	Stamen	Pistillode	Stigma	Ovary
<i>Garcinia prainiana</i>	Axillary in clusters (Azuan et al., 2015; Rohani et al., 2021)	Five rounded Rose pink to yellow (Azuan et al., 2015; Rohani et al., 2021)	Five rounded Green to pink (Azuan et al., 2015; Rohani et al., 2021)	Compacted (Azuan et al., 2015; Rohani et al., 2021) Pollen viability and development = 77.6±9.68 and 60.95±15.87%, respectively (Rohani et al., 2021)	NI	NI	NI
<i>Garcinia cowa</i>	Solitary or axillary (female) (Lim, 2012e)	Yellowish (Te-chato, 2007, Lim, 2012e)	NI	Clustered Pollen viability = 96%–100% (Te-chato, 2007)	No pistillodes (Lim, 2012e)	Radiate ridged and papillate stigma (Lim, 2012e)	Ovoid (Lim, 2012e)
<i>Garcinia atroviridis</i>	Terminal and pedicellate Racemes (male) Solitary (female) Clustered (hermaphrodite flower) (Bayu, Febrianti, & Damanik, 2018b; Lim, 2012f)	Dark red or crimson, obovate and fleshy petals with yellowish colour on the edge (Bayu, Febrianti, & Damanik, 2018b; Lim, 2012f)	Four yellow, spreading spherical and concave sepals (Bayu, Febrianti, & Damanik, 2018b; Lim, 2012f)	Stamens in whorls round (Te-chato, 2007; Lim, 2012f) Pollen viability = 3-5% (Te-chato, 2007), 79.5% (a day after anther dehiscence), 50.0% (17 days), no pollen germinated (25 days) (Pangsuban et al., 2009)	Pistillodes present (Lim, 2012f)	Deep red plicate, sub-tetragonal, convex or sessile stigma with corrugated surface (Lim, 2012f; Te-chato, 2007)	Ovoid (Lim, 2012f)

Table 2 (Continue)

<i>Garcinia</i> species	Flower parts						
	Inflorescence	Petal	Sepal	Stamen	Pistillode	Stigma	Ovary
<i>Garcinia parvifolia</i>	Pedicellate, axillary or solitary in fascicles (Lim, 2012 g)	Large (Lim, 2012 g)	Four in total and yellow to dull orange (Lim, 2012 g)	Female flower consists of 7–12 staminodes (Lim, 2012 g)	No pistillodes (Lim, 2012 g)	NI	NI

Note. NI indicates that no information

Table 3
 The summary of the fruit parts of selected *Garcinia* species

<i>Garcinia</i> species	Fruit parts				
	Shape	Colour	Taste	Aril	Seed
<i>Garcinia mangostana</i> var. <i>mangostana</i>	Globose (Nazre, 2014; Richards, 1990b; Sulassih et al., 2013; Te-chato, 2007; Yuniastuti, 2010)	Dark purple or red (Nazre, 2014; Richards, 1990b; Sulassih et al., 2013; Te-chato, 2007; Yuniastuti, 2010)	Sweet and sour (Nazre, 2014; Richards, 1990b; Sulassih et al., 2013; Te-chato, 2007; Yuniastuti, 2010)	Fleshy Snowy white (Nazre, 2014; Richards, 1990b; Sulassih et al., 2013; Te-chato, 2007; Yuniastuti, 2010)	Light brown Ellipsoid (Yuniastuti, 2010) Recalcitrant Large <i>Garcinia</i> -type of germination Germination rate=75.6% (24 days; Normah et al., 2016)
<i>Garcinia celebica</i>	Sub-globose to ellipsoid (John et al., 2008; Sulassih et al., 2013)	Deep red (John et al., 2008; Sulassih et al., 2013)	Sour (John et al., 2008; Sulassih et al., 2013)	Creamy white (John et al., 2008; Sulassih et al., 2013)	Recalcitrant Large <i>Garcinia</i> -type of germination Germination rate = 95.6% (22 days) (Normah et al., 2016)
<i>Garcinia mangostana</i> var. <i>malaccensis</i>	Ovoid to globose (Nazre, 2014; Sulassih et al., 2013)	Reddish pink to dark purple (Nazre, 2014; Sulassih et al., 2013)	Sweet and sour (Nazre, 2014; Sulassih et al., 2013)	Snowy white (Nazre, 2014; Sulassih et al., 2013)	NI

Table 3 (Continue)

<i>Garcinia</i> species	Fruit parts			
	Shape	Colour	Taste	Seed
<i>Garcinia pratiniana</i>	Rounded but rather flattened (Azuan et al., 2015; Mohd Khairuddin et al., 2018)	Yellowish orange (Azuan et al., 2015; Mohd Khairuddin et al., 2018)	Acidic sweet (Azuan et al., 2015; Mohd Khairuddin et al., 2018)	Recalcitrant Small Thick testa
<i>Garcinia cowa</i>	Subglobose to globose and oblique (Lim, 2012e; Roy et al., 2010)	Yellow or pale orange (Lim, 2012e)	Sour (Lim, 2012e)	Semi <i>Garcinia</i> -type of germination Germination rate = 48.9% (47 days; Normah et al., 2016) Trigonous* Recalcitrant Large Mean germination time = 252 days (without scarification) and 13 days (with scarification) (Liu et al., 2002; Liu et al., 2005)

Table 3 (Continue)

<i>Garcinia</i> species	Fruit parts				
	Shape	Colour	Taste	Aril	Seed
<i>Garcinia atrovirens</i>	Sunken globose, widely lowered hollow apex that consists of 12–16 ribs, slightly grooved and segregated segments (Lim, 2012f)	Vivid yellow (Lim, 2012f)	Sour (Lim, 2012f; Te-chato, 2007)	Bright orange (Lim, 2012f)	Flattened (Lim, 2012f) Recalcitrant Small <i>Garcinia</i> -type of germination Germination rate = 57.3% (25 days; Normah et al., 2016)
<i>Garcinia parvifolia</i>	Depressed globose and sunken top (Lim, 2012 g)	Yellow or orange (Lim, 2012 g)	Moderately sour (Lim, 2012 g)	White (Lim, 2012 g)	Small <i>Garcinia</i> -type of germination (Vogel, 1980)

Note. NI indicates that no information

CONCLUSION

This present overview has provided an insight into the reproductive system of *G. mangostana* var. *mangostana*, *G. celebica*, *G. mangostana* var. *malaccensis*, *G. prainiana*, *G. cowa*, *G. atroviridis* and *G. parvifolia*. To summarise, a tropical environment provides well-distributed *Garcinia* species, perhaps due to suitable ecological conditions such as temperature, weather and soil properties. On top of that, apomixis is a valuable discovery as it can alter normal sexual reproduction. Based on previous findings, *G. mangostana* var. *mangostana* is reported to be an obligate apomict due to male sterility resulting from a cellular alteration in tapetum that gives rise to abnormal pollen development. Meanwhile, a male flower of *G. celebica* is functionally fertile due to normal pollen development and viability similar to *G. prainiana* and *G. cowa* which these species display a facultative apomixis together with *G. atroviridis* and *G. parvifolia*. Moreover, the seed size, moisture content, and vulnerability towards desiccation are the key factors that could influence the viability and germinability of *Garcinia* species in this overview study. This available information could perhaps serve to further understand plant conservation and breeding approaches to improve the quality and yield of *Garcinia* plants.

To date, several comprehensive studies of reproduction are yet to be documented. There is limited information on the timing and duration of flowering periods and how environmental factors influence these. Effective conservation strategies for *Garcinia* species are scarce, especially endangered ones with restricted distributions. Pollen development and viability studies can further determine male fertility, particularly in *G. mangostana* var. *malaccensis* and *G. parvifolia*. In addition, more studies regarding seed development and germination capability are required on these two species. The influence of seed scarification, especially on *G. prainiana*, can be evaluated for future research since the seeds require a long period to germinate. These recommendation studies could help ascertain a possible solution to fulfil agricultural and plant conservation demands.

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