

FLOWER DEVELOPMENT OF MALE AND FEMALE INFLORESCENCE OF OIL PALM, *Elaeis guineensis* Jacq.

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Abstract: Oil palm (*Elaeis guineensis* Jacq.) is a monoecious plant that relies on cross-pollination to ensure the production of viable seeds and prevent parthenocarpy. Understanding the phenology of *Elaeis guineensis* flower development enables planters to optimise the timing of assisted pollination and harvesting. The aim of this study is to describe the development of male and female inflorescence of oil palm *Elaeis guineensis* var. Tenera. The frequency of observation of development was daily, starting from pre-anthesis until post-anthesis for female inflorescence and spikelet degradation for male inflorescence. The flower developments were coded according to the Biologische Bundesanstalt Bundessortenamt und Chemische Industrie (BBCH) scales. The anthesis period for male inflorescence occurs around four to five days. A male inflorescence consists of spikelets that accommodate almost 30% of the rachis. Spikelets are full of yellow flowers and contain millions of pollen grains in the form of dust particles during anthesis. Spikelets are arranged in a spiral around the rachis in one direction and are fully elongated and exposed. The size of the spikelet is between 102 mm and 215 mm in length. Female flowers are fully receptive for three to four days where rachillae are elongated and fully exposed. The total number of rachillae covers 36% of the rachis length. Each rachilla is composed of eight to 25 flowers in a female inflorescence. The anthesis phase of male inflorescence is longer than female inflorescence. The phenological information about inflorescences can be used to enhance pollination techniques and optimise fruit formation.

Keywords: *Elaeis guineensis*, spikelet, rachilla, anthesis, oil palm.

Introduction

Oil palm belongs to the family of Arecaceae and to the genus *Elaeis*, which is commonly cultivated in Southeast Asia. The oil palm is a monoecious and dichogamy plant species. It was commercially introduced in Malaysia in 1917, and to date, more than 100 billion in revenue was generated from the export of palm oil and oil palm products in 2021 (Parveez *et al.*, 2022). These indicate that palm oil is a source of products for human use that are in high demand in the global food industry. In addition, palm oil has also been used in many inedible products. For example, high-value oleochemicals to greater primary biomass-derived substances such as paper and plywood (Suleiman *et al.*, 2012; Murphy, 2014).

Investigating the flower dimorphism of oil palm (*Elaeis guineensis*) is a great interest to understanding the efficiency of palm pollination and plant-pollinator interaction. *Elaeidobius kamerunicus* was first introduced in Malaysia in 1981 and successfully established in oil palm plantations in Malaysia to improve pollination and increase fruit set (Basri *et al.*, 1987). The plant uses the wind, earwigs, Lepidopterans and other vertebrates to assist with the pollination of oil palm (Basri & Norman, 1997; Nor Zalipah *et al.*, in press). The structures of its flora, such as its pollen morphology in male inflorescence and the number of rachillae in female inflorescence have improved the effectiveness of pollinators to reach and pollinate the flower (Appiah &

Agyei, 2013). Insects are attracted to female inflorescences when nectar production and the scent is released during anthesis. Insects transfer the pollen from male to female flowers when foraging for food. Small insects are good pollinators because their mouthparts and bodies are fixed well with the receptive stigma of *Arecaceae* (Copete *et al.*, 2018; Zamudio *et al.*, 2021).

Various pollination techniques have been established in Malaysia including open pollination, hand pollination and assisted pollination (Gintoron *et al.*, 2023). The two later methods require a fundamental understanding of the pollination time relative to the flowering period. Thus, the aim of this study is to describe the development of male and female inflorescence of oil palm, *Elaeis guineensis*. The findings of the study will provide knowledge of floral structures and the development of *E. guineensis* var. *Tenera*, which will help to improve pollination techniques and optimise fruit set formations.

Materials and Methods

Study Site

This study was conducted in TDM Plantation Jerangau, Hulu Terengganu, Terengganu (4°56'09.2"N 103°12'23"E) in from January 2019 until March 2019. Development and morphological studies were conducted on six-

to eight-year-old oil palms (*E. guineensis* var. *Tenera*). The oil palm seedlings were originally obtained from Sime Darby Seeds and Agricultural Services (serial number GH500). The seedlings have been planted at BLOK PM2012A/1 which features soil of Batang Merbau series (Geotanih, n.d). Mean temperature and relative humidity during the experimental period were $25.54 \pm 2.69^{\circ}\text{C}$ and $84.7 \pm 11.36\%$, respectively.

Characterization of Flower Development of Oil Palm

The characterisation of the flower's development was recorded by selecting five male and female inflorescences from five oil palm trees every month. The development of male and female inflorescence was monitored daily throughout their growth stages. Each male and female inflorescence was tagged, starting from pre-anthesis I, where the peduncular bract is tearing off (less than 10 cm) on the centre of inflorescence (Forero *et al.* 2012). The duration of phenological stages for flower development was measured using the general Biologische Bundesantalt Bundessortenamt und Chemische Industrie (BBCH) scale of Bleiholder *et al.* (1991), with modification as described in Forero *et al.* (2012). The flowering stage of oil palm was defined as stage 6 (601-609), and fertilised female flowers were categorised as 701 in the BBCH scale (Forero *et al.* 2012).

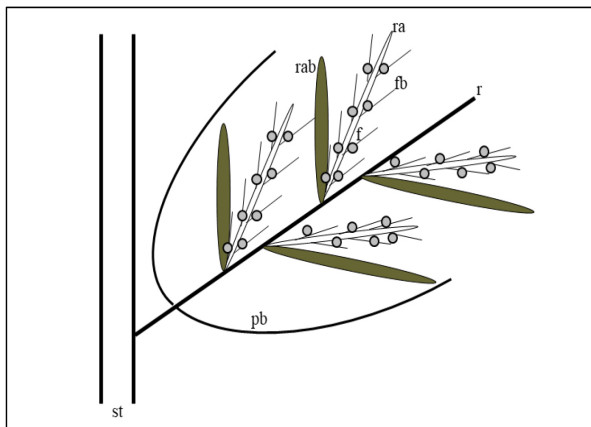


Figure 1: Illustration of oil palm inflorescence structure
Abbreviation: f, flower; fb, flower bract; p, peduncular bract; r, rachis;
ra, rachilla; rab, rachilla bract; s, stem

Measurement of Inflorescence Structure

The number and measurement of inflorescence structure were recorded from five inflorescences per month on the first day of anthesis. The length and number of spikelets and rachilla from the male and female inflorescence, respectively, were taken from 8:00 am until 11:00 am. The number of flowers per rachillae was also recorded from the female inflorescence. Figure 1 shows the illustration of the female inflorescence structure, as modified by Adam *et al.* (2005).

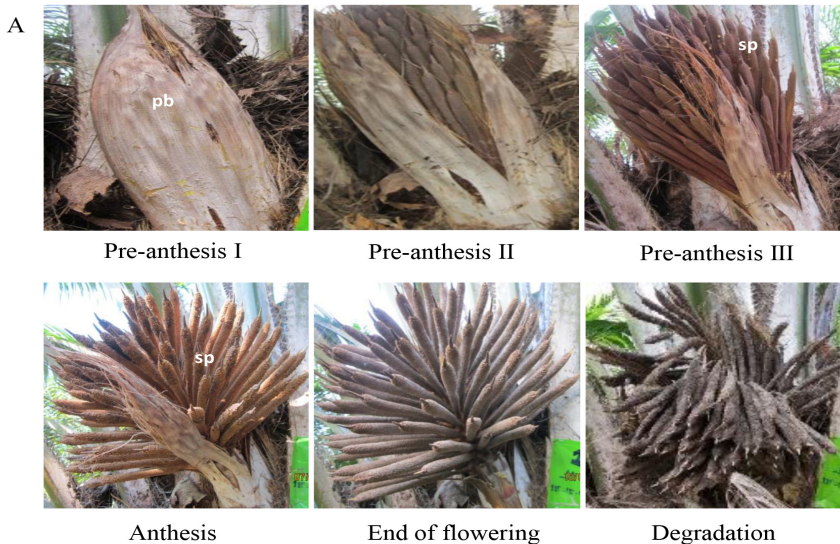
Results and Discussion

The flowering begins when the peduncular bracts tear in the middle of inflorescence. Male and female flowers are clearly distinguishable during this stage, in which the sex of the flowers had been differentiated after the inflorescence initiation (Adam *et al.* 2005).

In male inflorescence, the cylindrical spikelets are displayed in dark brown and tightly bunched in the centre [Figure 2(A)]. This phase is known as pre-anthesis I (stage 601). Following pre-anthesis II (stage 602), approximately 30%

of peduncular bract splits and expose more spikelets. Pre-anthesis III (stage 603) begins when the peduncular bract tears more than 50% and increases the separation of spikelets in the inflorescence [Figure 2(A)]. The flower buds emerge on spikelet surfaces, which the spikelets appear light brown [Figure 2(B)].

The anthesis or stage 607 begins when the peduncular bract has almost entirely detached from male inflorescence [Figure 2(A)]. A male inflorescence consists of spikelets that accommodate almost 30% of the rachis. The flowers are opened from the spikelet base and covered by millions of yellow pollen grains and produce an anise-like scent [Figure 2(B)]. Pollen grains are dust particles and very light. The phase remains around four to five days. A male inflorescence consists of 122 to 140 spikelets and on average, they may elongate an average of 153.7 mm (SD = 15.3). The progressive change of the spikelet colour to white indicates the degradation of spikelet and the end of the flowering phase (stage 609) [Figure 2(A)].



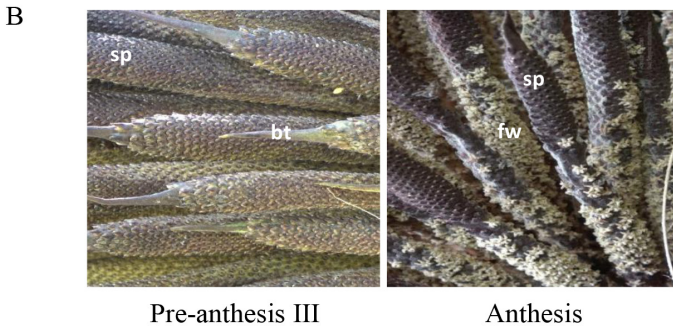


Figure 2: (A) Development stages of male inflorescence of oil palm from pre-anthesis until spikelet degradation. (B) The close-up photos of spikelet of pre-anthesis III (left) and anthesis (right). Mature flowers are apparent on spikelets during anthesis

Abbreviations: fw, flower; pb, peduncular bract; sp, spikelet; bt, bract

In the female inflorescence, tearing of peduncular bracts displays green rachillae and this stage is known as pre-anthesis I (stage 601) [Figure 3(A)]. Rachillae and bracts are tightly bunched together, and flower buds are invisible. During pre-anthesis II (stage 602), the peduncular bracts tear to 30% of their surface and closed flowers covered by whorl bracts are initially observed [Figure 3(A)]. Following pre-anthesis III (stage 603), more than 50% of peduncular bracts are torn and elongation of rachillae and bracts are occurred [Figure 3(A)]. The flowers are fully visible.

The flower development from pre-anthesis to anthesis is estimated to be between 30 and 50 days. The anthesis begins when the stigmatic trilobed is fully opened (stage 607) [Figure

3(A)]. The stigmas are beige in colour [Figure 3(B)]. The sticky stigmatic lobes are ready to receive pollen and emit an anise-like scent. A female inflorescence is composed of 128-143 rachillae, of which 8 to 25 flowers organise spirally on each rachillae. The length of the rachilla is between 7.9 cm and 15.0 cm. The total number of rachillae covers 36% of the rachis length. The receptive stigma can remain around three to four days in the field. Following pollination, the colour of fertilised female flowers changes from beige to purple (stage 609) [Figure 3(A) and 3(B)]. The phase of fruit formation begins when the stigma lobes are hardened and the colour changes to black (stage 701) [Figure 3(A)]. The bracts of floral whorl cover the fruits until ripened [Figure 3(B)].

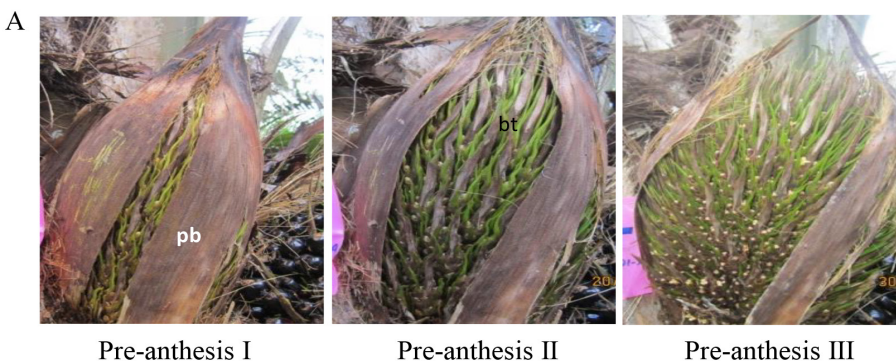




Figure 3: (A) Development stages of female inflorescence of oil palm from pre-anthesis until early fruit formation. (B) Beige stigmatic trilobed are apparent on rachillae bract during anthesis, the purple stigma indicates end of flowering, and the black stigma is fertilized flowers after pollination.

Abbreviations: s; stigma, pb, peduncular bract; ra, rachilla.

During the early phase of flowering development, the inflorescences are covered by a peduncular bract, a protection layer before the inflorescence elongates and is exposed (Adam *et al.*, 2005). In *Arecaceae*, the peduncular bract is not fully open in early development to prevent and limit the access of insects into the flowers (Copete *et al.*, 2018). This mechanism may prevent the insects or other animals from feeding on tissues of reproductive organs. Hence, it minimizes the failure in the development and production of pollen grains. During the observation, the visitation of *E. kamerunicus* increased when the peduncular bract tore off. This is likely because the anise-like scents were already secreted as soon as peduncular bracts exposed the structure of the male flowers. The anthesis period in the male inflorescence of *E. guineensis* commonly occurs

between two to seven days (Tandon *et al.*, 2001; Corley & Tinker, 2003), concurrent with the anthesis period of male inflorescence in TDM plantation. Pollen grains spread out on the first day of anthesis and continue for about one until three days (Corley & Tinker, 2003). Pollen productions end in five days and the viability of pollen decreases toward the end of anthesis. (Corley & Tinker, 2003).

For female inflorescence, a peduncular bract is a barrier of pollinators to access at the most important time for fertilization. However, there are split in the centre on peduncular bract that pollinators can still pass through and go to the stigma for pollen deposited. However, the deposition of pollen grains does not succeed because the stigma is still hidden and covered by bracts in most of the palms (Copete *et al.*,

2018). During the observation, the visitation rate of weevils increased as soon as the peduncular bract tears off. There is a probability that the visitation of weevils is related to the splitting of peduncular bract and secretion of an anise-like scent. While the usual duration of anthesis in the female inflorescence is reported to be two days (Tandon *et al.*, 2001), it is notably longer in TDM plantations. Stigmatic trilobed formed during anthesis phases are highly receptive on day 1 of anthesis. The furrow shape and large surface of stigmatic trilobes encourage a lot in the deposited of pollen grains. In addition, the wet and papillate surfaces of stigmatic trilobed also have a great chance of pollen grains that travel by the air to be deposited (Tandon *et al.*, 2001). The colour changes shown by a flower on a female inflorescence may probably have pollination occurred. When the flower already secretes a reddish-brown substance, the stigma might lose its receptivity. This receptivity loss is due to the formation of anthocyanin that prevents pollen germination (Tandon *et al.*, 2001; Hormaza *et al.*, 2012).

Morphology of male and female inflorescence of *E. guineensis* var. *Tenera* is very different. A rachis of male inflorescence contains from 100 to 300 spikelets (Corley & Tinker, 2003) but a maximum number of spikelets per rachis on oil palm inflorescence in TDM Plantation is 140 spikelets. The number of spikelets and flowers per rachilla of male and female inflorescence, respectively, are affected by water availability (Surhayanti *et al.*, 2020). Spikelets have lengths about 100 to 200 mm (Corley & Tinker, 2003; Montufar *et al.*, 2018), similar size of spikelets in TDM Plantation. Adam *et al.* (2005) reported that spikelets are arranged spirally on the rachis axis. Spikelet contains about 400 to 1500 flowers protected by bract which is smaller than bract in female inflorescence. Each spikelet contains millions of pollen grains (Tandon *et al.*, 2001). However, the male inflorescence of *Elaeis oleifera*, the other commercial oil palm has a shorter spikelet but longer rachis compared with *E. guineensis*, with a length of a spikelet of approximately 50 to 150 mm (Montufar *et al.*, 2018). *Elaeis*

guineensis x *E. oleifera* hybrids produce a lower number of male inflorescences, thus, leading to the low production of pollen formation (Corley & Tinker, 2003).

The morphology of the female inflorescence consists of 150 rachillae and each rachilla contains five to 30 flowers (Adam *et al.*, 2003). According to Corley and Tinker (2003), most of *E. guineensis* has varies number of flowers in one inflorescence. The middle part of the inflorescence has 12 to 30 flowers per rachilla, while the top and bottom parts of the inflorescence has less than 12 flowers per rachilla. However, the number of flowers per rachilla in TDM plantation is lower than most of *E. guineensis* trees. The maximum number of flowers per rachilla is 25 flowers and less in the top and bottom parts of inflorescence. It is likely because oil palm in TDM Plantation has a shorter rachilla and can accommodate a smaller number of flowers on a rachilla. This difference may be due to the age of the palm tree where Corley and Thinker (2003) found that there are around ten flowers per spikelet in three years old palms and this increases up to fifteen flowers after ten years. According to Montufar *et al.* (2018), *E. oleifera* has a persistent peduncular bract where it remains on the inflorescence until the fruit ripens. *Elaeis oleifera* also has longer rachis than *E. guineensis*. Their flowers are embedded between rachillae and do not have bracts that cover flowers like *E. guineensis*. The flowers of *E. guineensis* x *E. oleifera* hybrids are covered by bracts but are longer than *Elaeis guineensis*. This makes the hybrid inflorescence closely resemble both species (Corley & Tinker, 2003).

Pollination of oil palm requires pollinating agents that carry and deposit the pollens from male inflorescence to the stigma of female inflorescence. The different times of anthesis of both male and female inflorescence actively attract the visitation of weevils at different periods. In the TDM plantation, weevils of *Elaeidobius kamerunicus* are introduced as pollinators for *E. guineensis*. They were abundant on both male and female inflorescence

especially when all flowers had opened, and the flowers emitted strong anise-like scents.

Elaeidobius kamerunicus are commonly found on male inflorescence from the 1st day until 5th day of anthesis (Dhileepan, 1994; Nor Zalipah *et al.*, 2023). The weevils' population was abundant from first day until the third day of anthesis, and the population declined from the fourth day onwards (Swaray *et al.*, 2021). Visitation of weevils increases due to opened flowers during the anthesis period (Yue *et al.*, 2015). Visitations of weevils are high on the first day of anthesis of female inflorescence, but this observation is differed from Hala *et al.* (2012) and Yue *et al.* (2015). They reported that the visitations of weevils are higher on the second and third days of anthesis. This is likely due to no reward and no production of an anise-like scent that attracted weevils. The population of *E. kamerunicus* decreased in the monsoon season in Sabah and Sarawak, where assisted pollination is essential to compensate for low fruit yields (Cik Mohd Rizuan *et al.*, 2013; Kamarudin *et al.*, 2018). In contrast, the rainy season increased the population abundance of *E. kamerunicus* per hectare in Pahang, most likely the precipitation was less than 400mm per year (Nurul Fatihah *et al.*, 2019). However, the wet season may lead to reduced fruit set since the rain could wash away the pollen deposited on the bodies of weevil pollinators. Conventional assisted pollination is typically carried out by applying pollen to receptive stigma, but utilising *E. kamerunicus* as pollen distributors has been recently practiced (Yousefi *et al.*, 2020).

Conclusions

Oil palm is a perennial plant that can be harvested continuously. Unlike annual plants, it is challenging to identify a single distinct growth stage once it becomes mature. In the present study, BBCH scores assist in standardising the agronomic activities in TDM plantation such as assisted pollination and harvesting. The findings provide information about the anthesis period of both male and female inflorescence and the

characteristics of flowers during this phase. The phenological data of inflorescence development of *E. guineensis* var. Tenera can be utilised to improve the pollination time and optimise fruit formation.

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References

- Adam, H., Jouannic, S., Escoute, J., Duval, Y., Verdeil, J., & Tregear, J. W. (2005). Reproductive developmental complexity in the African oil palm (*Elaeis guineensis*, Arecaceae). *American Journal of Botany*, 92(11), 1836-1852.
- Appiah, S. O., & Agyei, D. (2013). Studies on Entomophil pollination towards sustainable production and increased profitability in the oil palm: A review. *Elixir Agriculture*, 55, 12878-12883.
- Basri, M. W., & Norman, K. (1997). Role and effectiveness of *Elaeidobius kamerunicus*, *Thrips hawaiiensis* and *Pyroderces* sp. in pollination of mature oil palm in Peninsular Malaysia. *Elaeis*, 9(1), 1-16.
- Basri, M. W., Zulkifli, M., Halim, A. H., & Tayeb, M. D. (1987). The population census and the pollination efficiency of the weevil *Elaeidobius kamerunicus* in Malaysia - A status report, 1983-1986. *Proceedings of the 1987 PORIM International Palm Oil Congress: Progress and Prospects - Agriculture Conference*. Kuala Lumpur.
- Cik Mohd Rizuan, Z. A., Hisham, N. H., & Shamsudin, A. (2013). Role of pollinating weevil (*Elaeidobius kamerunicus*), seasonal effect and its relation to fruit set in oilpalm area of FELDA. *Proceeding of PIPOC 2013 International Palm Oil Congress*. KLCC, Kuala Lumpur, Malaysia.

- Copete, J. C., Florez, D. M., & Nunez-Avellaneda, L. A. (2018). Pollination ecology the *Manicaria saccifera* (Arecaceae): A rare case of pollinator exclusion. In Mokwala, P. W. (Ed.), *Pollination in plants* (pp 23-37). London: IntechOpen.
- Corley, R. H. V., & Tinker, P. B. (2003). *The oil palm* (4th ed.). Hoboken: Wiley.
- Dhileepan, K. (1994). Variation in populations of the introduced pollinating weevil (*Elaeiodobius kamerunicus*) (Coleoptera: Curculionidae) and its impact on fruitset of oil palm (*Elaeis guineensis*) in India. *Bulletin of Entomological Research*, 84(04), 477-485.
- Forero, D. C., Hormaza, P., & Romero, H. M. (2012). Phenological growth stages of African oil palm. *Annals of Applied Biology*, 160, 56-65.
- Geotanih. (n.d). *Soil profile description of common soil series*. Jabatan Pertanian Malaysia. <https://geotanih.doa.gov.my/about/series>.
- Gintoron, C. S., Mohammed, M. A., Sazali, S. N., Deka, E. Q., Ong, K. H., Shamsi, I. H., & King, P. J. H. (2023). Factors affecting pollination and pollinators in oil palm plantations: A review with an emphasis on the *Elaeiodobius kamerunicus* weevil (Coleoptera: Curculionidae). *Insects*, 14(5), 454
- Hala, N., Tuo, Y., Akpessa, A. A. M., Koua, H. K., & Tano, Y. (2012). Entomofauna of oil palm tree inflorescences at La Mé Experimental Station (Côte d'Ivoire). *American Journal of Experimental Agriculture*, 2(3), 306-319.
- Hormaza, P., Mesa, F., Mauricio, E., & Romero, H. (2012). Phenology of the oil palm interspecific hybrid *Elaeis oleifera* x *Elaeis guineensis*. *Scientia Agricola*, 69, 275-280.
- Kamarudin, N., Moslim, R., Mohamad, S. A., & Sulaiman, M. R. (2018). Fruit set and weevil pollination issues in oil palm. 14th NATSEM 2018 Malaysian Plantation Industry (p. 123-135).
- Montúfar, R., Louise, C., & Tranbarger, T. (2018). *Elaeis oleifera* (Kunth) Cortés: A neglected palm from the Ecuadorian Amazon. *Revista Ecuatoriana de Medicina y Ciencias Biológicas*, 3(1), 11-18.
- Murphy, D. J. (2014). The future of oil palm as a major global crop: Opportunities and challenges. *Journal of Oil Palm Research*, 26(1), 1-24.
- Nor Zalipah, M., Tan, H. T., Nurul Izzah, A., Muhammad Haffidzie M. S., Faiq Zulfaqar Z., Muhamad Azrul S. L., Mohamad Idrus A., Shahrul Anuar Mohd Sah Shaipulah, N. F. M., & Basari, N. (2023). Arthropod fauna of oil palm inflorescence (*Elaeis guineensis*), with notes on their ecological roles in a plantation in Terengganu, Malaysia. *Journal of Oil Palm Research*, <https://doi.org/10.21894/jopr.2023.0013>
- Nurul Fatihah, A. L., Fahmi, M., Nasuha, N., Cik Mohd Rizuan, Z. A., Hakim, L., & Ghani, I. (2018). Effect of oil palm planting materials, rainfall, number of male inflorescence and spikelet on the population abundance of oil palm pollinator, *Elaeiodobius kamerunicus* faust (Coleoptera: Curculionidae). *Serangga*, 23(1), 35-45.
- Parveez, G. K. A. Kamil, N. N., Zawawi, N. Z., Ong-Abdullah, M., Rasuddin, R., Soh, K. L., Selvaduray, K. R., Seng, S. H., & Idris, Z. (2022). Oil palm economic performance in Malaysia and R&D progress in 2021. *Journal of Oil Palm Research*, 34(2), 185-218.
- Suharyanti, N. A., Mizuno, K., & Sodri, A. (2020). The effect of water deficit on inflorescence period at palm oil productivity on peatland. *E3S Web of Conferences*, 211, 05005.
- Sulaeiman, O., Salim, N., Nordin, N. A., Hashim, R., Ibrahim, M., & Sato, M. (2012). The potential of oil palm trunk biomass as an alternative source for compressed wood. *BioResources*, 7(2), 2688-2706.

- Swaray, S., Amiruddin, M. D., Rafii, M. Y., Jamian, S., Ismail, M. F., Jalloh, M., Eswa, M., Marjuni, M., Akos, I. S., & Yusuff, O. (2021). Oil palm inflorescence sex ratio and fruit set assessment in *Dura* × *Pisifera* biparental progenies on fibric peat soil. *Agronomy*, *11*(7), 1380.
- Tandon, R., Manohara, T. N., Nijalingappa, B. H. M., & Shivanna, K. R. (2001). Pollination and pollen-pistil interaction in oil palm, *Elaeis guineensis*. *Annals of Botany*, *87*, 831-838.
- Tuo, Y., Koua, H. K., & Hala, N. (2011). Biology of *Elaeidobius Kamerunicus* and *Elaeidobius Plagiatus* (Coleoptera: Curculionidae) main pollinators of oil palm in West Africa. *European Journal of Scientific Research*, *49*(3), 426-432.
- Yousefi, M., Mohd Rafie, A. S., Samsuzana A. A., Syaril Azrad & Abd Razak, A. (2020). Introduction of current pollination techniques and factors affecting pollination effectiveness by *Elaeidobius kamerunicus* in oil palm plantations on regional and global scale: A review. *South African Journal of Botany*, *132*, 171-179.
- Yue, J., Yan, Z., Bay, C., Chen, Z., Lin, W., & Jiao, F. (2015). Pollination activity of *Elaeidobius kamerunicus* (Coleoptera: Curculionidae) on oil palm on Hainan Island. *Journal of Florida Entomologist*, *92*(2), 499.
- Zamudio, F., Gatti, M., Hilgert, N. I., Alvarez, L. J., Mulieri, P., Aguilar, R., & Ashworth, L. (2021). Insects or wind? New findings on the pollination system of *Euterpe edulis* (Arecaceae). *Arthropod-Plant Interactions*, *15*, 503-516.