

## Inflorescence and flower development in Thai aromatic coconut

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### Abstract

Basic information on the inflorescence and flower development of Thai aromatic dwarf coconut was developed. Histology of inflorescences of the Thai dwarf aromatic coconut, 'Nam Hom', was compared to that of a typical tall-type coconut. Both types had the same stages of inflorescence and flower development. 'Nam Hom' had the same or greater number of inflorescences than did the tall type at any of the developmental stages. During two years of reproductive development, floral morphogenesis took about one year, while sex determination occurred in 3-4 months before spadix opening. Despite the difference in number of bunches per year observed in the two coconut types, their inflorescence and flower development were not different in the length of time and in the time of occurrence.

**Key words:** *Cocos nucifera* L., dwarf coconut, floral morphogenesis, flower initiation, histology, palm

### Introduction

The fruit of the coconut palm (*Cocos nucifera* L.) has long been recognized as a valuable source of calories, nutrients and biomaterials, consumed both flesh and water (Foale, 2003). Globally, 60.8 million tonnes of coconuts are produced in 80 countries from 12 millions ha of land, often in marginal regions unsuitable for agriculture (Arunachalam *et al.*, 2001; Foale, 2003; FAOSTAT, 2014). Historically, the coconut was grown and used in small tropical communities (Foale, 2003), but a recent and rapidly increasing interest worldwide in the health properties of the coconut is transforming production and export sales in many Asian economies (PARDI, 2011; Mahr, 2012; Prades *et al.*, 2012).

Generally, coconut can be divided into two types/groups, *i.e.*, tall type and dwarf type. The tall type is the most extensively grown on a plantation scale around the world. The tree can reach 20-30 meters in height. It starts to bear fruit at six to seven years after planting and is usually productive for 60-70 years. Cross-pollination is required for the success of fertilization and fruit set. The tall type coconut is usually grown for mature fruit consumption. There are many cultivars, such as 'Bali' (Indonesia), 'Laguna' (Philippines), 'Tahiti' (Tahiti), 'West African Tall' (Ivory Coast) (Ohler, 1984), and 'Pak Jok' (Thailand) (Yotpanya, 2001). The dwarf type, on the other hand, is smaller, only about 12-15 meters in height. The dwarf coconut starts to bear fruit earlier, around 3-4 years after planting and has a shorter productive life of about 30 years. Unlike the tall type, the dwarf coconut does not require cross-pollination for the success of fertilization and fruit set (Menon and Pandalai, 1958). The dwarf coconut produces more bunches (16-18 bunches per year) than does the tall type (10-12 bunches per year). There are many cultivars being grown, such as 'Yellow Malayan' (Malaysia, Ivory Coast) (Ohler, 1984), Tahiti Red Dwarf, Brazilian Green Dwarf, and Madang Brown Dwarf (Bourdeix *et al.*, 2005). In Thailand, the main cultivar of the dwarf type for young coconut production is 'Nam Hom' (Yotpanya, 2001). This cultivar consists of aromatic

compound, 2-acetyl-1-pyrroline (2-AP), in the water and flesh of the fruit; therefore it is also called young aromatic coconut (Luckanatinvong, 2015). In 2015-16, Thailand exported fresh young aromatic coconut approximately 80,000 tonnes per year or 61 million US dollars in value (Office of Agricultural Economics, 2017). Even though the export market for this aromatic dwarf coconut is expanding, one of its main production problems in Thailand is the significant decrease of yield during summer months (Siriphanich, 2017). Empirical study on inflorescence and flower development of the cultivar is a basis to understanding the problem.

In tall type coconut, the inflorescence and flower development has been comprehensively studied (Patel, 1938; Perera *et al.*, 2010). The development process takes over two years with floral morphogenesis being the longest event taking about one year and sex determination, a rapid process occurring within a month (Perera *et al.*, 2010). With the distinction of growth habits between the aromatic dwarf coconut and the normal tall type coconut, as described above, differences involving inflorescence and flower development are expected. To our knowledge, the inflorescence and flower development of the aromatic dwarf coconut has not yet been studied. The overall goal of this study, therefore, was to develop basic information of the inflorescence and flower development of Thai aromatic dwarf coconut.

### Materials and methods

**Plant materials:** All inflorescence materials were collected from coconut trees (*C. nucifera* L.) grown in an Experimental Field of the Department of Horticulture, Kasetsart University, Kamphaeng Saen Campus, Thailand. Two 22-year-old coconut trees, one *C. nucifera* 'Nam Hom' or Thai aromatic dwarf coconut tree and one tall type tree, were felled in October 2013. All the inflorescences at different stages were taken carefully from the tree to observe their morphological characteristics following the method done by Perera *et al.* (2010). Briefly, the first stage, numbered zero (0),

refers to the oldest inflorescence of which the spathes just opened. The younger inflorescence immediately above inflorescence 0 was numbered -1, and the ones next to it were called -2, -3, -4, and so on. The youngest stage at which inflorescence was possibly isolated by naked eye was called shoot apical meristem (SAM). The whole sample without removing any parts of inflorescence -14 to -33 (aromatic dwarf) or -11 to -24 (tall type) and SAM were directly fixed. For inflorescences -5 to -13 of the aromatic dwarf or -5 to -10 of the tall type, a rachilla without peduncular bract and prophyll was dissected from each inflorescence and fixed. For inflorescence -4 to 0 of both dwarf and tall types, male and female flowers were dissected individually from the center and at the base of rachis, respectively, and fixed.

### Histology of inflorescences

**Fixation of samples:** The plant tissues were fixed in 100 mL of 50 % formalin-acetic acid-alcohol (FAA; 10 mL of 38 % formaldehyde, 5 mL of 99.9 % of glacial acetic acid, 50 mL of 95 % ethanol and 35 mL of distilled water) for 4-5 days. After that, the water was removed from the cell via tert-butyl alcohol (TBA) series (50, 70, 85 and 100 % v/v) for 12 h at each concentration.

**Preparing sample for sectioning and light microscopy:** After the samples were dehydrated throughout the TBA series, they were embedded in paraffin (Gurr™, BDH, VWR International Ltd.) and sectioned to a 10-12 µm thickness using microtome (HM 335E, MICROM International GmbH, Germany). After sectioned, samples were double-stained with Safranin-O and Fast green. Finally, they were observed for the development under the light microscope (Axiostar plus, Carl Zeiss, Germany) using the 5× power.

## Results

**The comparison of general characteristics of inflorescence between Thai aromatic dwarf and tall type coconut:** A photograph indicating the composition of coconut palm

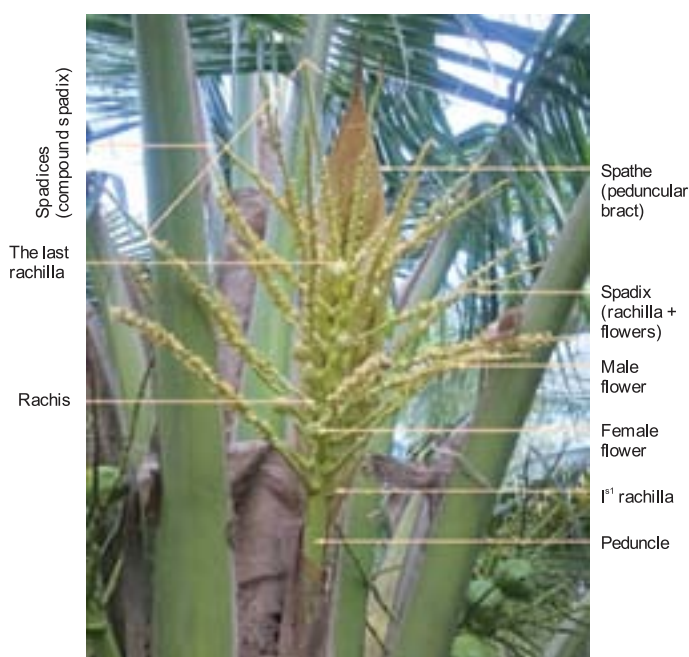


Fig. 1. The composition of a compound spadix inflorescence of coconut palm (*C. nucifera*). The inflorescence consists of a peduncle, an elongated axis, a number of rachillae, sessile flowers, and an enveloping spathe

inflorescence is presented in Fig. 1. The inflorescence is a compound spadix consisting of a peduncle, a number of rachillae on a rachis, sessile flowers on the rachillae, and a spathe. The spathe was one of the two spathes enclosing the inflorescence with the other one smaller and located on the adaxial side over this large one. On each inflorescence, there were 42 rachillae in the case of the Thai aromatic dwarf ('Nam Hom') coconut or 35 rachillae in the case of the tall type coconut (Table 1). The length of the spathe at the inflorescence opening stage was 84 cm for the 'Nam Hom' coconut and 104 cm for the tall type coconut. The length of the peduncle measured from the base to the first rachilla was 24 cm in 'Nam Hom' and 35 cm in the tall type coconut. However, the rachis length measured from the first rachilla to the last rachilla at the tip of the inflorescence of 'Nam Hom' coconut was similar to that of the tall type coconut (34–38 cm at maturity). The rachillae were arranged spirally around a central rachis. The length of the rachillae in 'Nam Hom' coconut was 24 cm, which was shorter than that of the tall type coconut (35 cm) (Table 1). Each rachilla in 'Nam Hom' coconut contained 200 male flowers from the tip to the base and 0–6 female flowers at the base depending on the time of the year (unpublished data).

**Histology of coconut inflorescence:** The development process of the inflorescence from initiation to maturation in 'Nam Hom' and tall type coconut took over 2 years. These inflorescences were completely enclosed at the base of the subtending leaf for most of this time. The comparison of reproductive development between 'Nam Hom' and tall type coconuts is represented in Fig. 2, which details all stages of inflorescence development (see also Online Resource 1). Depending on the tree condition, 'Nam Hom' coconut produced about 36 inflorescences, whereas tall type coconut produced approximately 24 inflorescences.

Based on the stage of flower initiation and development following the description in Perera (2010), seven stages, including (i) formation of prophyll and peduncular bract, (ii) initiation of rachilla bract, (iii) formation of rachilla, (iv) floral bud initiation, (v) formation of floral organ, (vi) sex determination and (vii) flower maturation, could be determined. The present work would only focus on the comparison of those developmental stages between 'Nam Hom' and tall type coconuts. The details of basic cellular organization and key feature distinguishing each developmental stage were fully described previously (Adam *et al.*, 2005; Perera *et al.*, 2010). Surprisingly, the comparison between each stage of the two type coconuts revealed that both types had similar pattern of inflorescence and flower development in the time of occurrence.

**Formation of rachis:** The earliest stage at which developing inflorescence of both 'Nam Hom' and tall type coconuts could be visible by light microscopy was stage -27 and -21, respectively. At this stage, the rachis was initiated and the prophyll and peduncular bract were started to develop (Fig. 3a and data not shown). The rachis still looked like a dome entirely enclosed by the peduncular bract and the prophyll (Fig. 3b). For both 'Nam Hom' and tall type coconuts, this rachis initiation process including the developing of prophyll and peduncular bract event took about 6 months, which occurred 19 to 24 months before inflorescence opening (Table 2).

**Initiation of rachilla bract:** During subsequent development, the production of rachilla bracts, each of which subtending an axillary

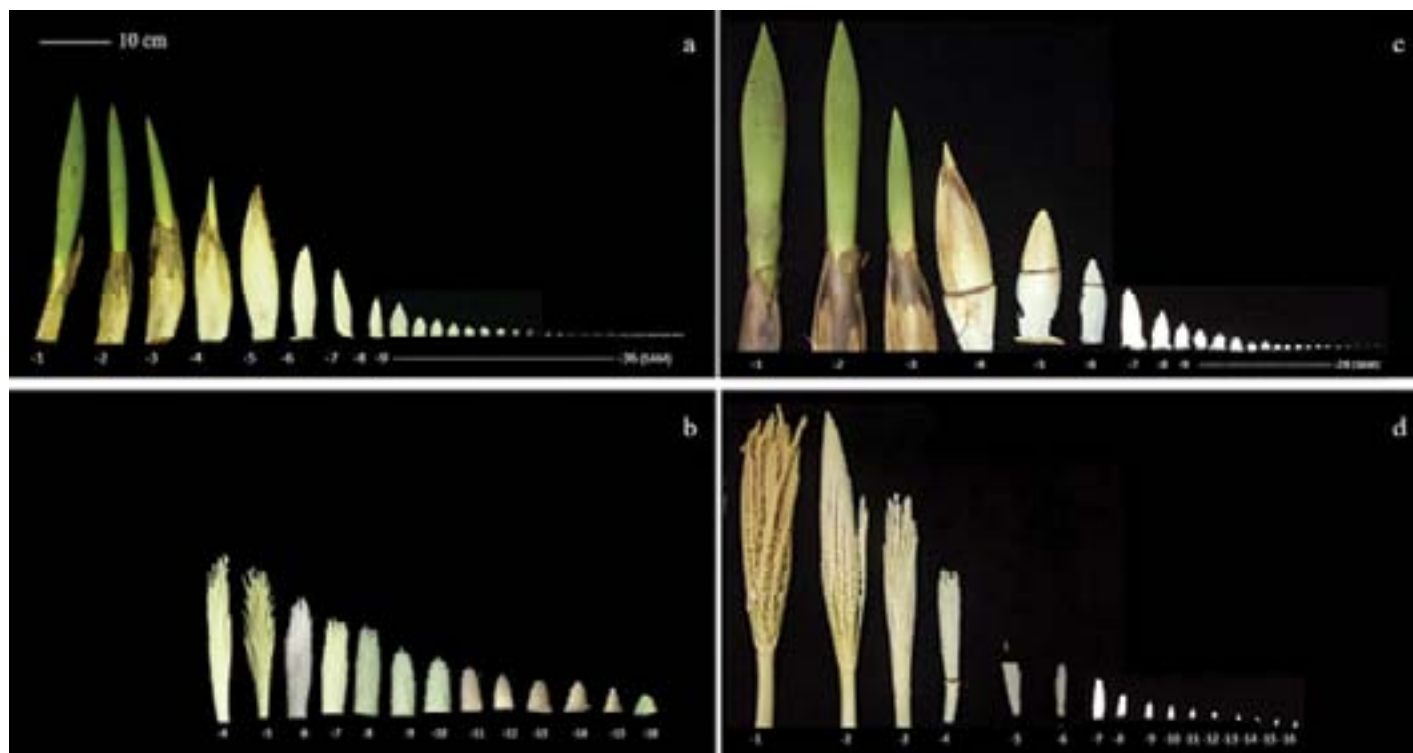


Fig. 2. A series of the inflorescences of Thai aromatic dwarf coconut (*C. nucifera* ‘Nam Hom’; a and b; see also Online Resource 1) and *C. nucifera* tall type coconut (c and d). The oldest unopened spadix or inflorescence was -1. The ones next to this stage were called -2, -3, -4, and so on. The youngest stage at which inflorescence can possibly be isolated with the naked eye was called shoot apical meristem (SAM). The whole spadices without removing any parts were collected from -1 to -36 in ‘Nam Hom’ (a) and from -1 to -24 in tall type coconut (c). Spadices without peduncular bract and prophyll were collected from -1 to -16 in ‘Nam Hom’ (pictures of -1 to -3 spadices were not shown) (b) and from -1 to -16 in tall type coconut (d)

rachilla, was initiated. Every part of the inflorescence—prophyll, rachis, and rachillae bract — developed rapidly (Fig. 4). All the organs were still covered under the peduncular bract. The initiation of the rachilla bract next to the dome of rachis meristem was visible at stage -25 and -18 in ‘Nam Hom’ and tall type coconuts, respectively (Fig. 4a and c). The elongation and development of rachilla bracts of ‘Nam Hom’ and tall type coconuts continued up to stage -21 and -16, respectively. This initiation of rachilla bract event in both coconut types took about 3

months and occurred 16 to 18 months before inflorescence opening (Table 2).

**Formation of rachilla:** The fully developed rachilla bract and rachilla primordia initiation at the bases of each rachilla bract were clearly visible at stage -20 and stage -15 in ‘Nam Hom’ and tall type coconuts, respectively (Fig. 5a and d). The rachilla developed slowly at stage -17 in ‘Nam Hom’ coconut and stage -14 in tall type coconut (Fig. 5b and e), and clearly outgrew the rachilla bract at stage -15 in ‘Nam Hom’ coconut and stage -11 in tall type coconut (Fig. 5c and f). The initiation of rachilla and following development event took about 5 months and occurred 11 to 15 months before inflorescence opening (Table 2).

**Floral initiation:** Each rachilla produced a series of floral bracts and initiated floral primordium subtended by a floral bract at stage -14 to -10 and stage -10 to -8 in ‘Nam Hom’ and tall type coconuts, respectively (Fig. 6a and b, and data not shown). The floral initiation and floral bracts development took approximately 3–4 months and occurred 7 to 10 months before inflorescence opening (Table 2).

**Formation of floral organ:** The initiation of the reproductive

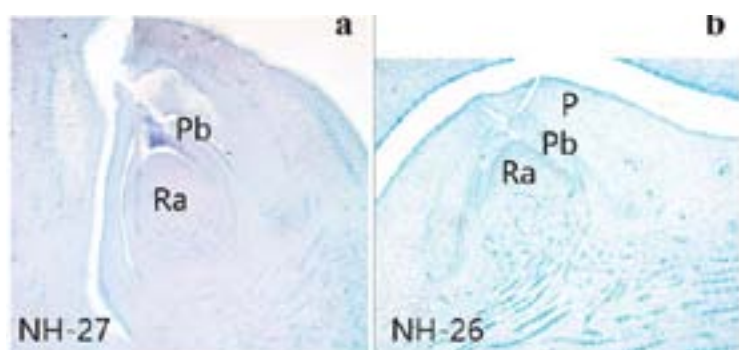







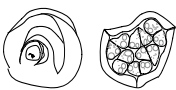


Fig. 3. Histological illustration of the development of rachis in Thai aromatic coconut (*C. nucifera* ‘Nam Hom’) inflorescence (5×) from stage -27 (a) and -26 (b) (19-24 months before inflorescence opening). Ra, rachis, Pb, peduncular bract and P, prophyll

Table 1. Some characteristics of a compound spadix of *C. nucifera* ‘Nam Hom’ and tall type coconuts

Characteristics of a compound spadix	‘Nam Hom’	Tall type
Length of spathe (cm)	88	104
Peduncle length measured from the base to the first rachilla (cm)	24	35
Rachis length measured from the first rachilla to the last rachilla at the tip (cm)	38	34
The number of rachillae per inflorescence	42	35
The length of rachilla (cm)	29	35

Table 2. Schematic diagram comparison between inflorescence development of *C. nucifera* 'Nam Hom' and tall-type coconuts from initiation of inflorescence up to maturation of individual flowers

Flower initiation and development		Months before inflorescence opening	Inflorescence number	
			'Nam Hom'	Tall type
S A M		24	-34 to -32	-24
Formation of prophyll and penducular bract		23	-31	-23
		22	-30	-22
		21	-29	-21
		20	-27	-20
		19	-26	-19
			-25	
Rachilla bract initiation		18	-24	-18
		17	-23	-17
		16	-22	-16
Formation of rachillae			-21	
		15	-20	-15
		14	-19	-14
		13	-18	-13
		12	-17	-12
Floral initiation		11	-15	-11
			-14	
		10	-13	-10
		9	-12	-9
		8	-11	-8
Formation of floral organs		7	-10	-7
			-9	
		6	-8	-6
Sex determination		5	-7	-5
		4	-6	-4
Flower maturation		3	-5	-3
			-4	
		2	-3	-2
		1	-2	-1
		-1		
		0	0	0

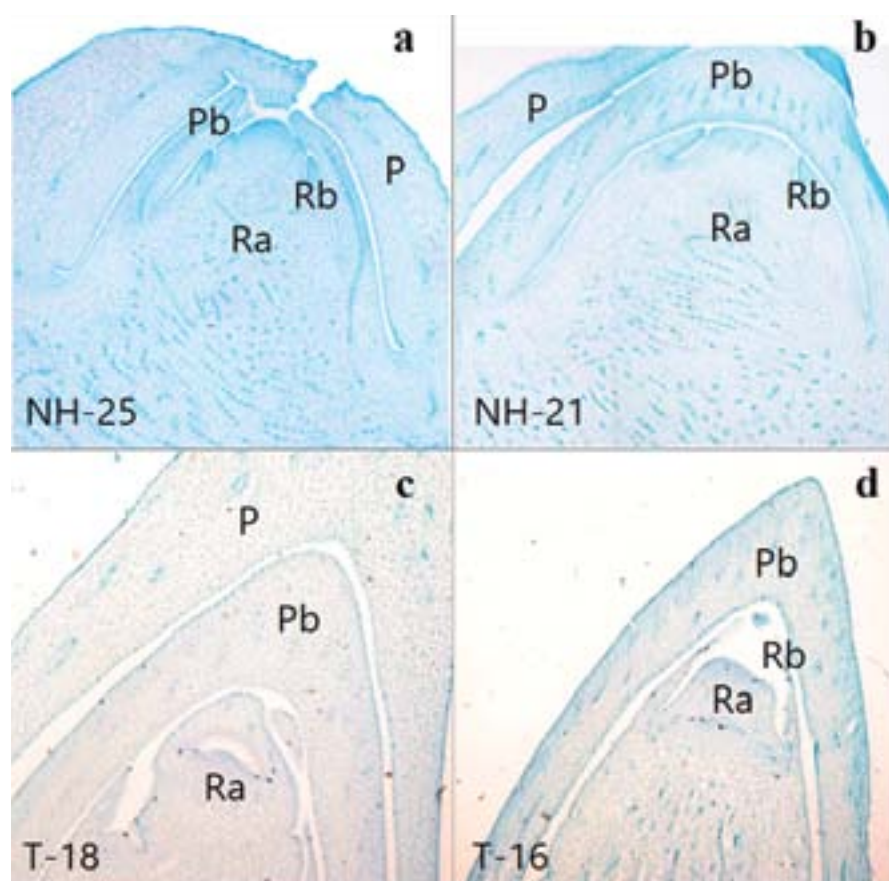


Fig. 4. Histological illustration of the development of rachis (5 $\times$ ) from inflorescence stage -25 and -21 (a and b) in *C. nucifera* 'Nam Hom' coconut (NH) or stage -18 and -16 (c and d) in *C. nucifera* tall type (T), which occurred 16-18 months before inflorescence opening. Ra, rachis, Rb, rachilla bract, Pb, peduncular bract and P, prophyll

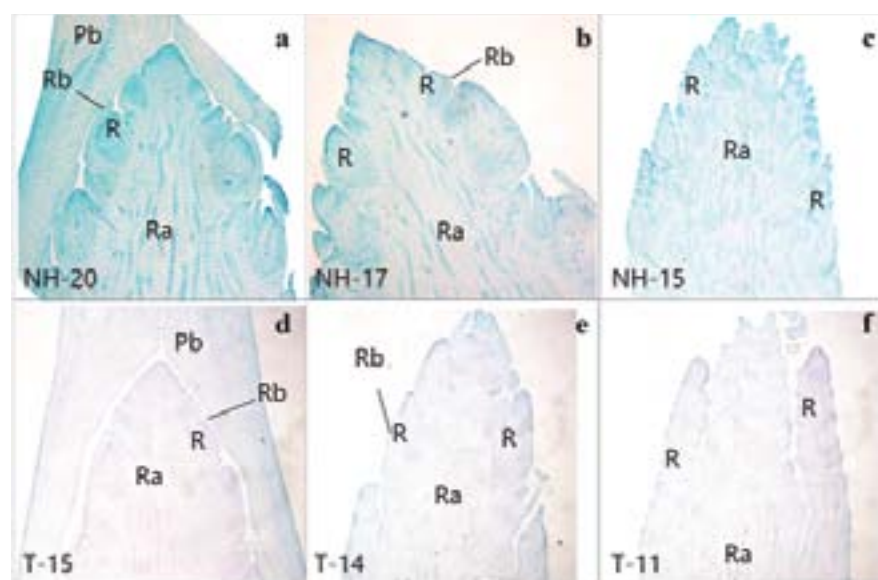


Fig. 5. Histological illustration of the formation of rachillae and the development of rachilla bract (5 $\times$ ) from inflorescence stage -20 to -15 in *C. nucifera* 'Nam Hom' (NH) coconut (a-c) or stage -15 to -11 in *C. nucifera* tall type (d-f). Ra, rachis, Rb, rachilla bract, R, rachilla and Pb, peduncular bract

organ or floral primordium occurred in both male and female flowers at stage -9 in 'Nam Hom' coconut (Fig. 7a) or stage -7 in tall type coconut (Fig. 7c). The development of some floral whorls, *i.e.*, sepals and petals, was also clearly visible at stage -8 or -6 in 'Nam Hom' or tall type coconuts, respectively (Fig. 7b and d). However, no difference was visible between male and female flower at this stage. The floral organ initiation and took approximately 2 months and occurred 5 to 6 months before inflorescence opening (Table 2).

**Sex determination:** The differences of male and female flower were visible at stage -6 in 'Nam Hom' (Fig. 8a and b) and stage -5 in tall type (T) coconut (Fig. 8c and d). In male flower, the meristematic potential of the stamen continued further to form anther and filament, whereas the development of the pistil (female part of the flower) was diminished and appeared as a pistillode. The petals elongated rapidly and completely enveloped the meristematic zone of the stamen, limiting the sepals to the base of the flower (Fig. 8a, c, e, and g). The polyphenol accumulation was visible at the anthers and pistillodes of the male flower (Fig. 8a, c, e, and g). In female flower (Fig. 8b, d, f, and h), the meristematic potential of the ovary was present in the reproductive organ primordia whereas the meristematic potential of the stamen is diminished, resulting in a staminode (Fig. 8d and f). Three free carpels were joined at their bases with the accumulation of polyphenol around the female flower (Fig. 8d, f, and h). The flower sex determination stage took approximately 2 to 3 months and occurred 3 to 4 months before inflorescence opening (Table 2).

**Flower maturation:** The staminate or male flower of both coconut types containing six stamens in two whorls was visible at stage -3 (Fig. 9a and c) and became fully developed at stage -1 (Fig. 9b and d). Each stamen is composed of a bilobed anther with a filament in the middle. Each lobe carries a pair of pollen sacs, resulting in a group of four pollen sacs in each stamen. (Fig. 9b and d). For the pistillate or female flower of 'Nam Hom' coconut, the perianth segment, integuments and ovule were clearly observed at stage -3 (Fig. 10a). At stage -1, the embryo sac and nucellus were visible (Fig. 10b and c). Due to the technical sampling, the staminode inside the pistillate flower could not be found in this study. However, the staminodes should be present inside the female flower at this stage as described by Menon and Pandalai (1958). The polyphenol inside the flower could also be seen clearly in dark pink color at stage -1 (Fig. 10b and c). The flower maturation stage took approximately 2 months and occurred 2 months before inflorescence opening (Table 2).

## Discussion

**No difference in the time of occurrence in inflorescence and flower developmental stages:** Temporal differences in inflorescence and flower development between cultivars have been observed in some crop species. For example, different accessions of apple,

including wild species and hybrids, have different seasonal bloom time and floral development (Gottschalk and van Nocker, 2013). Floral initiation and development of nine Japanese plum cultivars differ on time. Progressing through the same developmental stages, ‘Gulfruby’ has 70 % floral initiation in May, whereas others have only 50 % a month later (Jeengool, 2003). This varietal difference, however, is not observed in pineapple. Even though two groups of pineapple, the Queen (‘Trat See Thong’) and the Cayenne group (‘Pattavia’) requires different lengths of time after chemical flower induction for the inflorescence to be emerged, the two groups have similar inflorescence and flower development period afterward (K. Leungwilai, unpublished data). Given the difference in

number of bunches per year (or spadices during the flowering stages) between the dwarf and tall-type coconuts, temporal differences in inflorescence and flower development between the coconuts were expected. However, the present study revealed no difference.

Usually, dwarf-type coconut produces 16-18 bunches per year, *i.e.*, there is an interval time of about 20 days between each one. The 36 spadices or inflorescences found within a ‘Nam Hom’ coconut tree in this work revealed that the inflorescence development, from floral initiation to maturation, took about two years. In the tall-type coconut, 24 spadices were obtained suggesting the same length of time for the inflorescence development given the average of 10-12 bunches per year it generally produces. In “Sri Lanka Tall” coconut, the inflorescence developmental process takes over two years (Perera *et al.*, 2010), which is similar to that of the African oil palm, another palm in the same tribe Cocoseae (Adam *et al.*, 2005), with 26 and 27 inflorescences of different stages observed within a corresponding palm tree, respectively. Even though the ‘Nam Hom’ and tall-type coconuts produced inflorescence at a different frequency, both types initiated flowering two years in advance.

Analysis of the data in the present work also indicated that each developmental stage of the inflorescence in ‘Nam Hom’ coconut took place at the same age and was morphologically similar to that of the tall-type coconut. The time course of the inflorescence and floral development of the coconuts studied here is as followed (Fig. 11; Table 2). At the age of five months after SAM appearance, the inflorescence main rachis meristem became determined and developed in the rachilla bracts in three months. The inflorescence went on to produce rachilla at age 13 months, then initiated the floral primordial at age 14 months and formed a floral organ, *i.e.*, sepals and petals, at age 18 months from the SAM appearance. The floral organ development took about two months before a sex determination stage was determined at age 20 months from SAM initiation. At this stage, the ontogenesis and structure of male and female organs were developed for

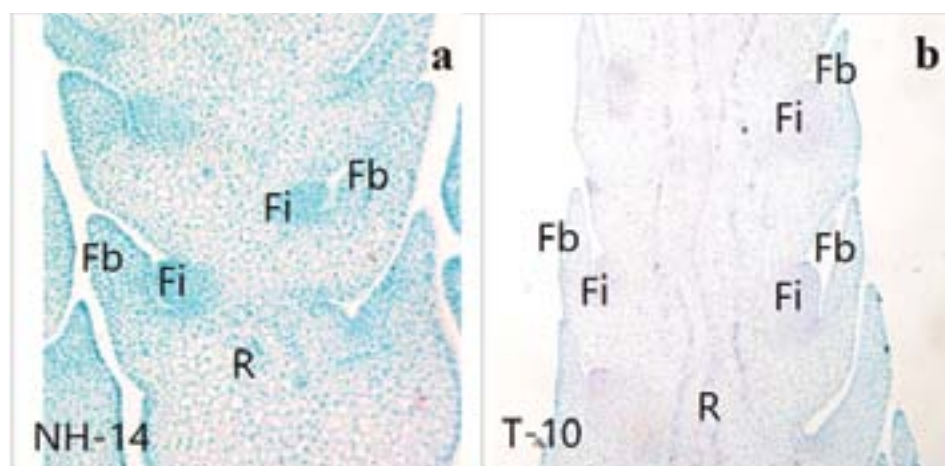


Fig. 6. Histological illustration of the floral initiation. Inflorescences were taken from stage -14 in *C. nucifera* ‘Nam Hom’ (NH) (a) or stage -10 in *C. nucifera* tall type (T) coconut (b). R, rachilla, Fb, flower bract and Fi, floral initials

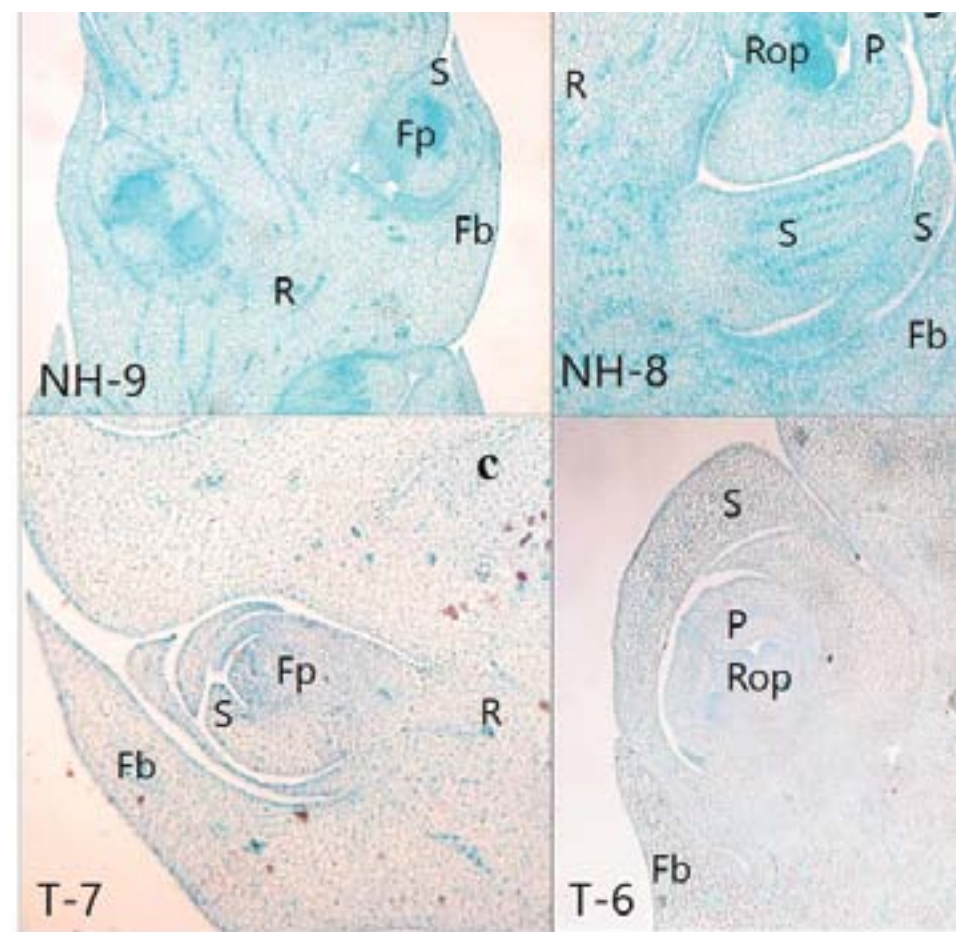


Fig. 7. Histological illustration of the floral organ initiation. Inflorescences were taken from stage -9 (a) to stage -8 (b) of *C. nucifera* ‘Nam Hom’ (NH) or stage -7 (c) to stage -6 (d) of *C. nucifera* tall type (T) coconut. R, rachilla, Fb, flower bract and Fp, floral primordia, S, sepals, P, petal, Rop, reproductive organ primordia

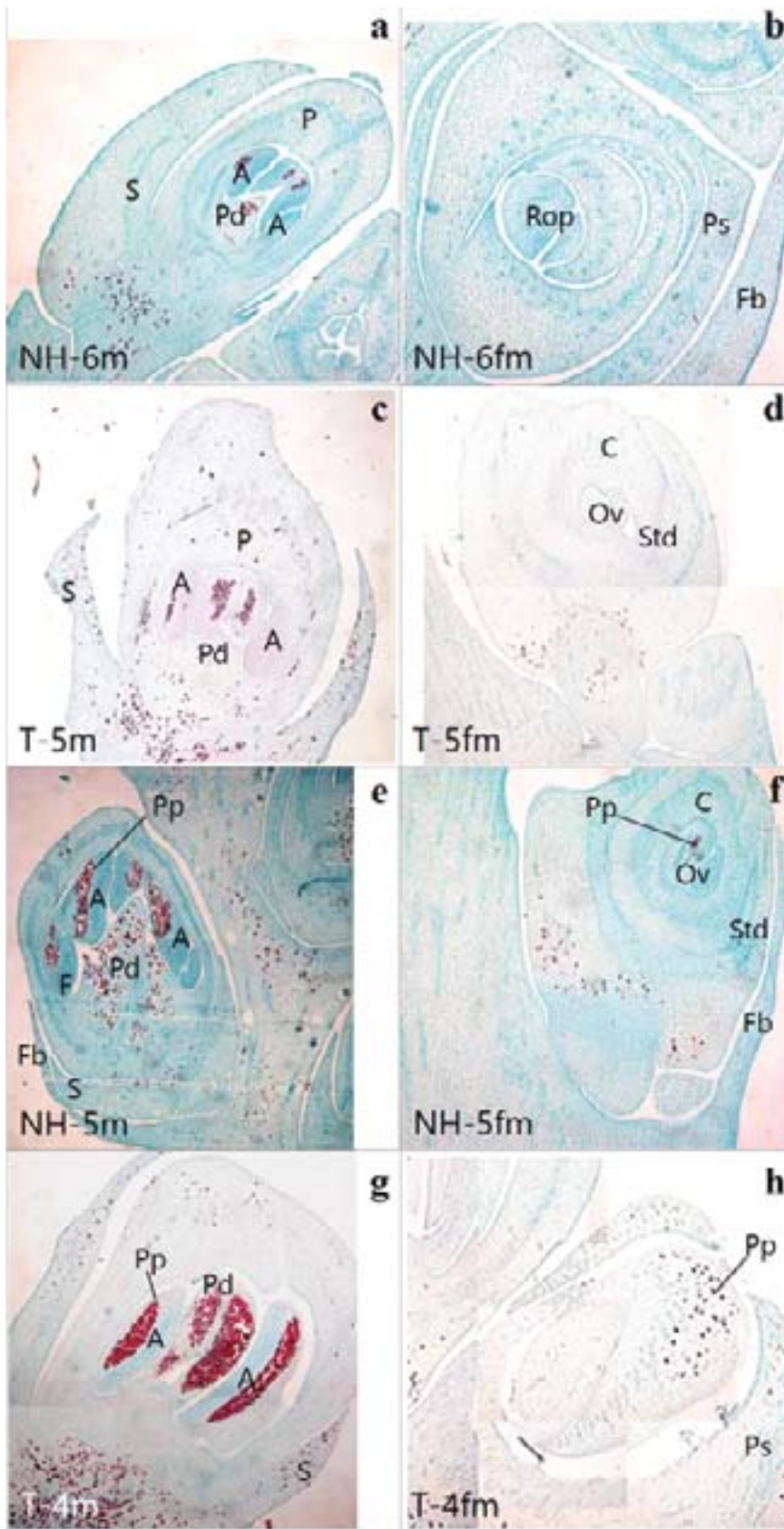


Fig. 8. Histological illustration of the determination and development of male and female flowers. Inflorescences were taken from stage -6 (a and b) to stage -5 (c and d) to stage -4 (g and h) of *C. nucifera* 'Nam Hom' (NH) or stage -5 (c and d) to stage -4 (g and h) of *C. nucifera* tall type (T) coconut. Male flower (a, c, e and g) and female flower (b, d, f, and h) were observed. Fb, flower bract, S, sepals, P, petal, A, anther, Pd, pistillode, Ps, perianth segment, Rop, reproductive organ primordia, Std, staminode, Pp, polyphenol, F, filament, C, carpels, Ov, ovules

three months to become maturation at age 22 months from SAM initiation or 2 months before inflorescence opens (Fig. 11; Table 2). Although, during a certain stage, inflorescences of both coconut types were at the same age, the number of inflorescences might differ. For example, during the sex determination stage, there were five and three inflorescences in 'Nam Hom' and tall-type coconuts, respectively (Table 2). This is in accordance with the difference in the frequency of leaf emergence between the two types. Once start flowering, an inflorescence would emerge from the axil of every mature leaf (Prabhakaran Nair, 2010). With the leaf emerging more frequently, the dwarf type has greater number of inflorescences than does the tall type at the same developmental stage.

**Inflorescence morphology and mode of pollination:** One of the differences between tall-type and dwarf-type coconuts is the mode of pollination, cross- vs. self-pollination, respectively. The key floral biology determining this characteristic is the flowering pattern involving male and female phases. Four types of coconut flowering pattern were classified based on whether the male and female phases are overlapped or not and whether such overlap is within the same inflorescence (intra-spadiX), between different inflorescences (inter-spadiX), or mixed, as reviewed by Thomas and Josephraj Kumar (2013). The phase overlap means the mature male flower is still releasing pollens while the female flower starts to be receptive. The overlap could be less than a day to 10 days. In general, most tall-type cultivars have the flowering patterns with no intra-spadiX overlap, but may be with inter-spadiX overlap (Thomas and Josephraj Kumar, 2013). Hence, most tall-type cultivars perform cross-pollination, albeit possible self-pollination in cultivars with inter-spadiX overlap. For dwarf-type cultivars, the flowering patterns could have intra-spadiX phases overlap or both the intra- and inter-spadiX overlaps (Thomas and Josephraj Kumar, 2013). Either of the patterns would promote self-pollination in the dwarf-type cultivars.

The morphological characteristics of the inflorescence that could be related to mode of pollination of the 'Nam Hom' (a dwarf-type cultivar) and the tall-type coconut in this study were the number of rachillae per inflorescence and the frequency of inflorescence emergence. The greater number of rachillae per spadix (Table 1) could be a reason to why 'Nam Hom' coconut has a longer male phase than that in the tall-type. In 'Nam Hom' coconut, the male flowers start to open right after the opening of

the inflorescence and continue to open in succession of individual flowers for about 25 days (Thongnueaha, 2016), whereas, in tall-type coconut, this male phase is shorter lasting 16-22 days after the inflorescence opened (Thomas and Josephraj Kumar, 2013). Besides, the female phase starts earlier in 'Nam Hom' coconut with the female flower opening 18-19 days after the inflorescence opened and being receptive for about 1-3 days (Thongnueaha, 2016), compared to that in tall-type which begins 22 days after the inflorescence opened (also after its male phase ends) and lasts 5-7 days (Thomas and Josephraj Kumar, 2013). This earlier female phase couples with the longer male phase in 'Nam Hom' coconut suggest the occurrence of intra-spadix male/female phase overlap. In addition, the higher frequency of inflorescence emergence in 'Nam Hom' would encourage the inter-spadix

overlap between the female phase on the older inflorescence and the male phase on a younger, subsequent inflorescence. The tall-type coconut could also have the inter-spadix overlap, but with a longer interval time between subsequent inflorescences, the overlap period, if any, might not be as long as the 'Nam Hom' might have. Information on flowering pattern regarding male and female phases of 'Nam Hom' coconut would be essential in recognizing its self-pollination habit and would be useful for its pollination enhancement in the fruit production.

In conclusion, the length of the period of flower initiation and development of the Thai aromatic coconut counted as months before inflorescence opening is the same as in the tall type coconut, *i.e.*, about 24 months. The total number of inflorescences inside one palm was about 32-33 inflorescences, which is greater than the approximately 24 inflorescences found in the tall-type. The rachilla bract of the aromatic coconut was found in stage -25 to -21 or 18-16 months before inflorescence open. The rachilla was observed at stage -20 to -15 while the flower was observed at stage -14 to -10. Formation of floral organ started 5-6 months, while sex determination started 4 months, before the opening of inflorescence.

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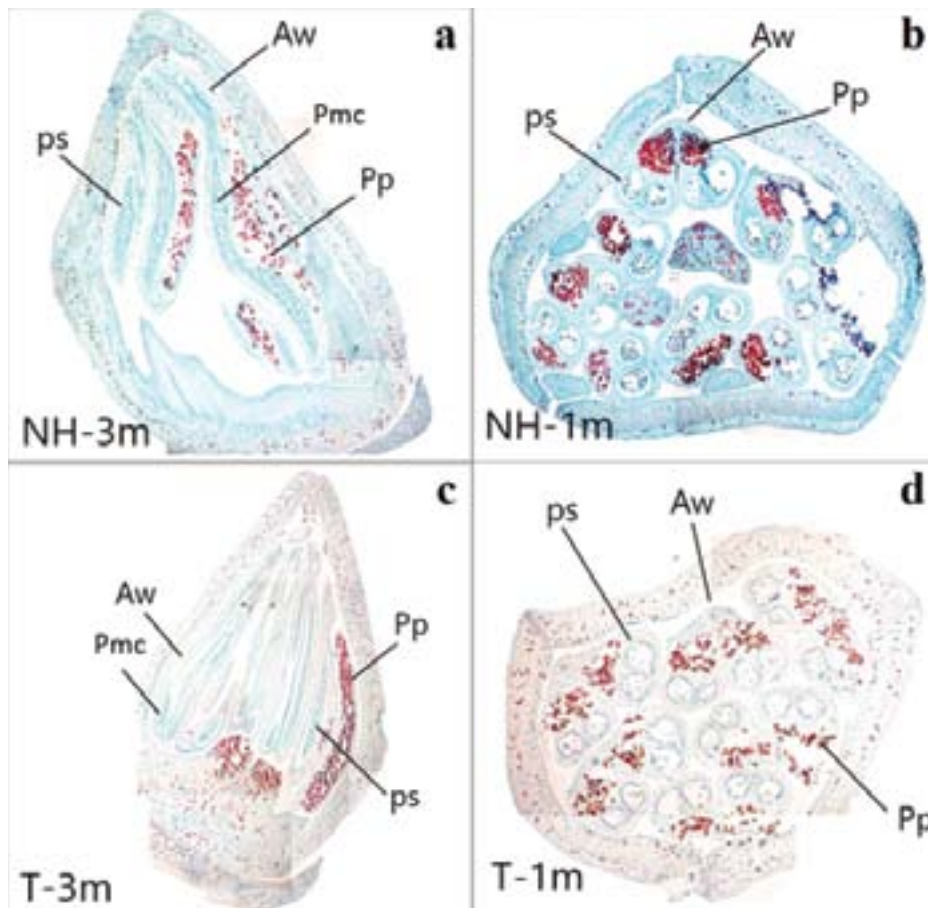


Fig. 9. Histological illustration of the maturation of staminate or male flower. Inflorescences were taken from stage -3 (a and c) to stage -1 (b and d) of *C. nucifera* 'Nam Hom' (NH) and tall type (T) coconuts, respectively. ps, pollen sac, Aw, anther wall, Pmc, pollen mother cells, Pp, polyphenol

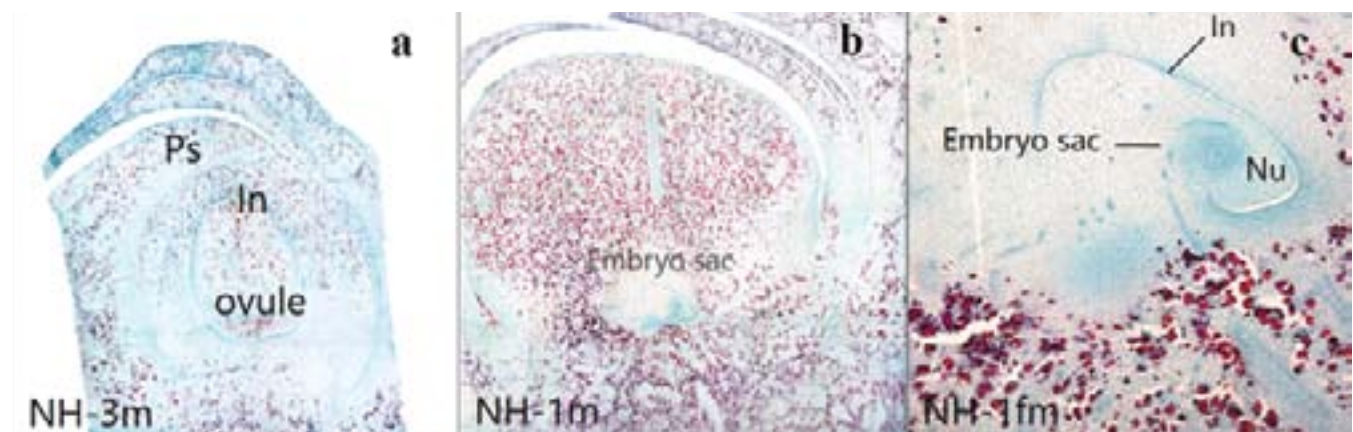


Fig. 10. Histological illustration of the maturation of pistillate or female flower. Inflorescences were taken from stage -3 (a) and stage -1 (b and c) of *C. nucifera* 'Nam Hom' (NH) coconut. The higher magnification (10 $\times$ ) of ovule (c) was taken from the same sample as stage -1 (b). Ps, perianth segment, In, integuments, Nu, nucellus



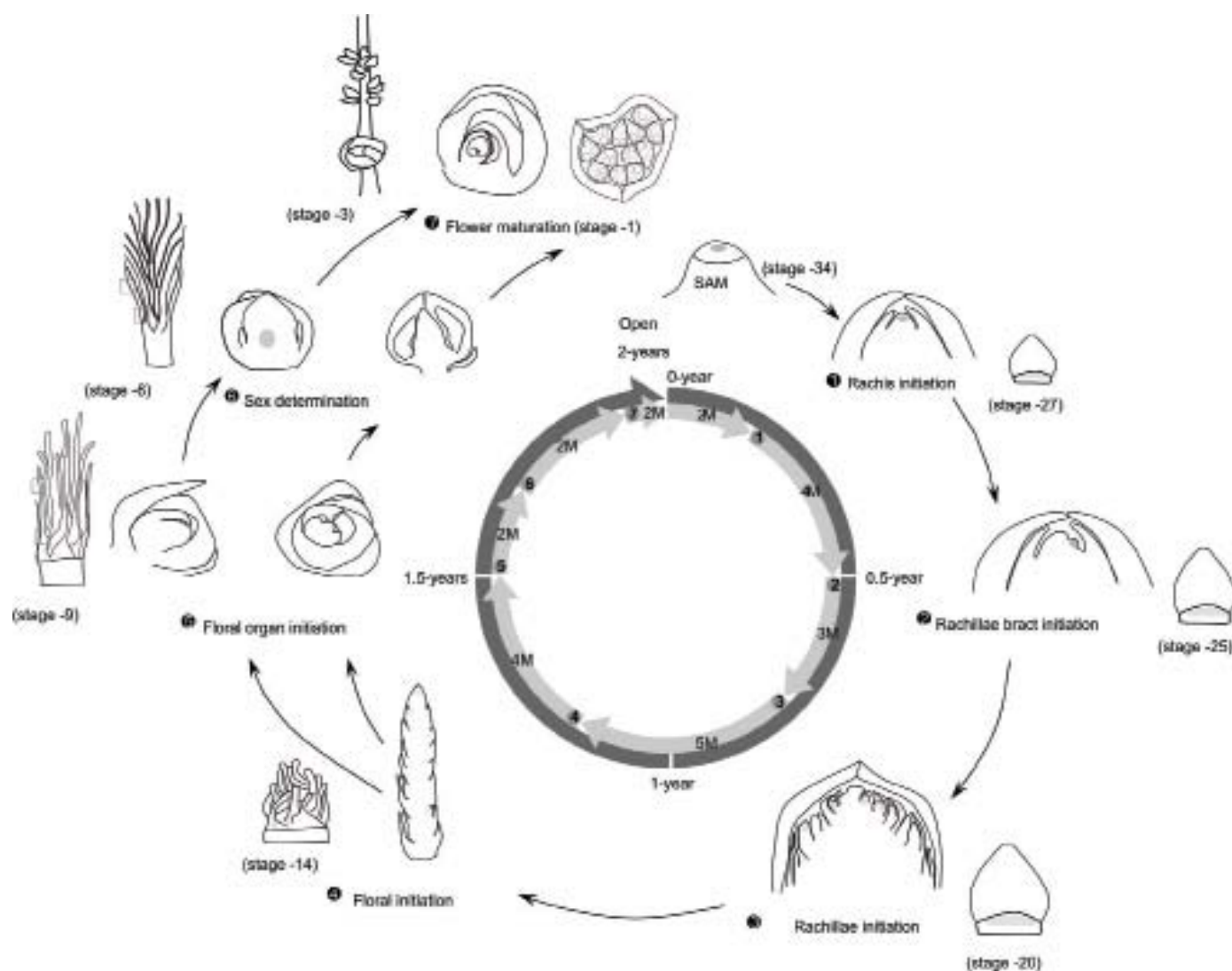


Fig. 11. Schematic diagram of inflorescence development of *C. nucifera* 'Nam Hom' coconut from initiation of inflorescence up to maturation of individual flowers

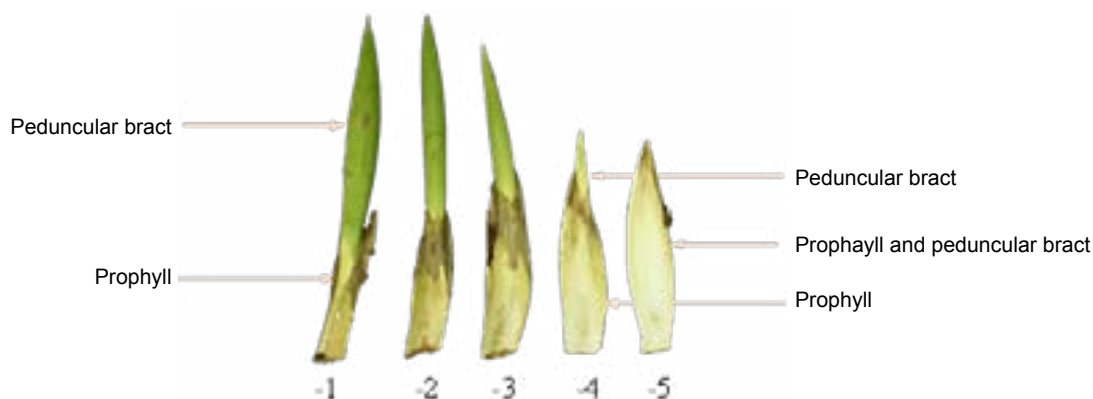
## References

- Adam, H., S. Jouannic, J. Escoute, Y. Duval, J.L. Verdeil and J.W. Tregear, 2005. Reproductive developmental complexity in the African oil palm (*Elaeis guineensis*, Areaceae). *Am. J. Bot.*, 92: 1836-1852.
- Arunachalam, V., B.A. Jerard, M. Elangovan, M. Ratnambal, R. Dhanapal, S.K. Rizal and V. Damodaran, 2001. Unexploited diversity in coconut palm (*Cocos nucifera* L.). *Plant Genet. Resour. Newsl.*, 127: 39-43.
- Bourdeix, R., J.L. Konan and Y.P. N'Cho, 2005. *Coconut: A Guide to Traditional and Improved Varieties*. Editions Diversiflora, Montpellier, France.
- FAOSTAT, 2014. *Crop Production*. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Foale, M. 2003. *The Coconut Odyssey: The Bounteous Possibilities of the Tree of Life*. ACIAR Monograph No. 101. Australian Centre for International Agricultural Research, Canberra.
- Gottschalk C and S. van Nocker, 2013. Diversity in seasonal bloom time and floral development among apple species and hybrids. *J. Amer. Soc. Hort. Sci.*, 138(5): 367-374.
- Jeengool, N. 2003. *Floral Initiation and Development of Japanese Type Plum at the Angkhang Royal Agricultural Station* (in Thai). M.S. Special Problem, Kasetsart University, Thailand, 2003. 25 pp.
- Luckanatinvong, V. 2015. Effect of pre- and post-harvest factors on aroma developing and quality of aromatic coconut (*Cocos nucifera* L.) (in Thai). Ph.D. Diss., Kasetsart University, Thailand, 2015.
- Mahr, K. 2012. *The Coconut Craze*. Time Magazine. Time Inc., New York, New York. <http://content.time.com/time/subscriber/article/0,33009,2130967-1,00.html>.
- Menon, K.P.V. and K.M. Pandalai. 1958. *The Coconut Palm: A Monograph*. Indian Central Coconut Committee, Erakulam, South India.
- Office of Agricultural Economics, 2017. Itemized Agricultural Economics Information 2017. Office of Agricultural Economics, Ministry of Agriculture and Cooperatives, Bangkok, Thailand. <http://www.oae.go.th/assets/portals/1/files/ebook/commodity60.pdf>.
- Ohler, J.G. 1984. *Coconut, tree of life*. Food and Agriculture Organization of the United Nations, Rome.
- PARDI, 2011. *Coconut Value Chain Review*. Australian Centre for International Agricultural Research, Queensland, Australia.
- Patel, J.S. 1938. *The Coconut: A Monograph*. Government Press, Madras.
- Perera, P.I.P., V. Hoher, L.K. Weerakoon, D. Yakandawala, S.C. Fernando and J.L. Verdeil, 2010. Early inflorescence and floral development in *Cocos nucifera* L. (Areaceae: Arecoideae). *S. Afr. J. Bot.*, 76: 482-492.
- Prabhakaran Nair, K.P., 2010. The Coconut Palm (*Cocos nucifera* L.). In: *The Agronomy and Economy of Important Tree Crops of the Developing World*, K.P. Prabhakaran Nair (ed.). Elsevier, London, UK. <https://www.sciencedirect.com/science/article/pii/B9780123846778000035>. p. 67-109.

- Prades, A., M. Dornier, N. Diop and J.P. Pain, 2012. Coconut water preservation and processing: a review. *Fruits*, 67: 157-171.
- Siriphanich, J. 2017. Opportunity and obstacle of Thai young aromatic coconut in World market. (in Thai). *Postharvest Newsletter*, 16(1): 5-7. Postharvest Technology Innovation Center, Chiang Mai, Thailand. <http://www.phtnet.org/2017/03/165/>.
- Thomas, R.J. and A. Josephraj Kumar, 2013. Flowering and pollination biology in coconut. *J. Plant. Crops*, 41: 109-117.

- Thongnueaha, P. 2016. Effect of temperature on pollen viability and pollen germination of aromatic coconut (in Thai). M.S. Diss., Kasetsart University, Thailand, 2016. 66 pp.
- Yotpanya, P. 2001. *Coconut: A Multipurpose Plant* (in Thai). Matichon Public Co., Ltd. Bangkok, Thailand.

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Supplementary Fig. 1. A series of spadices from stage -1 to stage -5 of *C. nucifera* 'Nam Hom' coconut. Stage -5, the inflorescence was enclosed by the thin prophyll and thick peduncular bract. Stage -4 the bracts elongated emerging the prophyll. Stage -3 to stage -1, the peduncular bract rapidly elongated through the prophyll