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Flowering Behavior in the Sugar Palm, Arenga pinnata

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ABSTRACT

When the sugar palm starts to flower, one of the axillary buds close beneath the apical meristem of the shoot grows into an inflorescence and is followed by the development of other buds in basipetal succession. Meanwhile, the apical meristem ceases functioning and becomes transformed into undifferentiated parenchyma. The inflorescence apex forms 8–9 new bracts in addition to the 6–7 bracts already present in the bud, and flower-bearing branches or rachillae are initiated in the axils of small bracts at its distal end. The uppermost 3–7 inflorescences are pistillate, the rest staminate. On the rachillae, flowers are originally formed in clusters of three. The developmental pattern in both types of inflorescences is similar. At the time of exposure of the rachillae from their ensheathing bracts, triads consisting of two lateral staminate buds and one central, pistillate flower bud are seen. In pistillate inflorescences, the three flower buds grow to a similar size, then the two lateral buds fall off, leaving the central pistillate buds to mature. In staminate inflorescences only the two lateral, staminate flower buds develop and mature. Organogenesis in a pistillate inflorescence shows that the first and second flowers to develop in a cluster are staminate and are initiated in rapid sequence. There is a delay in the initiation and early development of the third flower, the central one which is pistillate.

Flowering types in palms comprise pleonanthy where the stem produces lateral inflorescences throughout its adult life, and hapaxanthy where the stem flowers once only and then dies. Although the pleonanthic method of flowering is much more widespread than the hapaxanthic, the latter method has attracted great attention because of the often spectacular form (Dransfield 1978). In the hapaxanthic tree palm *Corypha*, for instance, the huge terminal inflorescence is a compound structure made up of many lateral inflorescences (Dransfield and Mogea 1984). In another example, the acaulescent *Daemonorops calicarpa*, the flowering axis consists of crowded internodes with short leaves which become smaller and smaller towards the top, the inflorescences in their axils likewise showing a reduction acropetally (Dransfield 1976).

A special type of hapaxanthy is found in the tribe Caryoteae (Arecoideae) where the production of inflorescences is basipetal rather than acropetal (Dransfield 1978). *Arenga pinnata*, which belongs to this tribe, has been known to produce inflorescences basipetally (Heyne 1950). The production of inflorescences starts distally on the stem and development of lateral flowering axes occurs in basipetal sequence from successively older, dormant buds. It has been reported that the vegetative apex of the sugar palm is modified into the first inflorescence at the time of flowering (Sudasrip 1980). Others suspect that inhibition imposed by the vegetative apex upon the growth of the axillary buds into inflorescences is released basipetally when the reproductive phase begins (Moore and Uhl 1982). The present work attempts to fill some gaps in information concerning the flowering behaviour in *Arenga pinnata* by studying the morphological development of the inflorescence.

Material and Methods

Observations were made on sugar palm trees in the neighborhood of the city of Bandung, West Java, situated 800 meters above sea level. Trees approximately 16–20 meters tall and 8–12 years old were examined for one year in 1982 and material obtained from these trees. To identify the nature of the apical meristem and to obtain young pistillate inflorescence buds at the distal end of the tree, a tree was selected which had just commenced flowering. The tree was felled and the apical meristem, the last formed leaf, the young inflorescences, and axillary buds were collected. Older stages of the pistillate inflorescences and growth stages of the staminate inflorescence were obtained from nearby trees. To follow the early development of the individual flowers, various stages of axillary buds and flowers were fixed in FAA (formalin, acetic acid, and alcohol) and processed with the paraffin method (Sass 1958). Serial sections 8–10 μm in thickness were stained with Delafield's haematoxylin and safranin.

Morphology of the Inflorescence and Flower

The sugar palm is a massive solitary palm which grows in the tropical rain forest as well as in semi-cultivation. The tree reaches a height of 20 meters and a diameter of 50 cm. The crown consists of dark green, steeply ascending plumelike leaves usually 3 meters long and 2 meters wide (Fig. 1). All leaves except the last formed subtend an axillary bud. The bud is widened tangentially with respect to the trunk and reaches a width of 8–15 cm and a height of 10–15 cm. At sexual maturity one of the most distal and healthy axillary buds develops into an inflorescence, followed by others in a basipetal sequence. As a rule the distalmost 3–7 inflorescences are pistillate and the rest are staminate. Both types of inflorescence are panicles consisting of a peduncle with flower-bearing branches called rachillae at the end. Using the terminology introduced by Tomlinson and Moore (1968) where the trunk is named ax0, the inflorescence axis would be ax1 and the rachillae are ax2. Staminate and pistillate flowers occur singly on their respective rachillae and pistillate flowers may be found between the two staminate flowers, but as a rule the sexes remain on separate inflorescences.

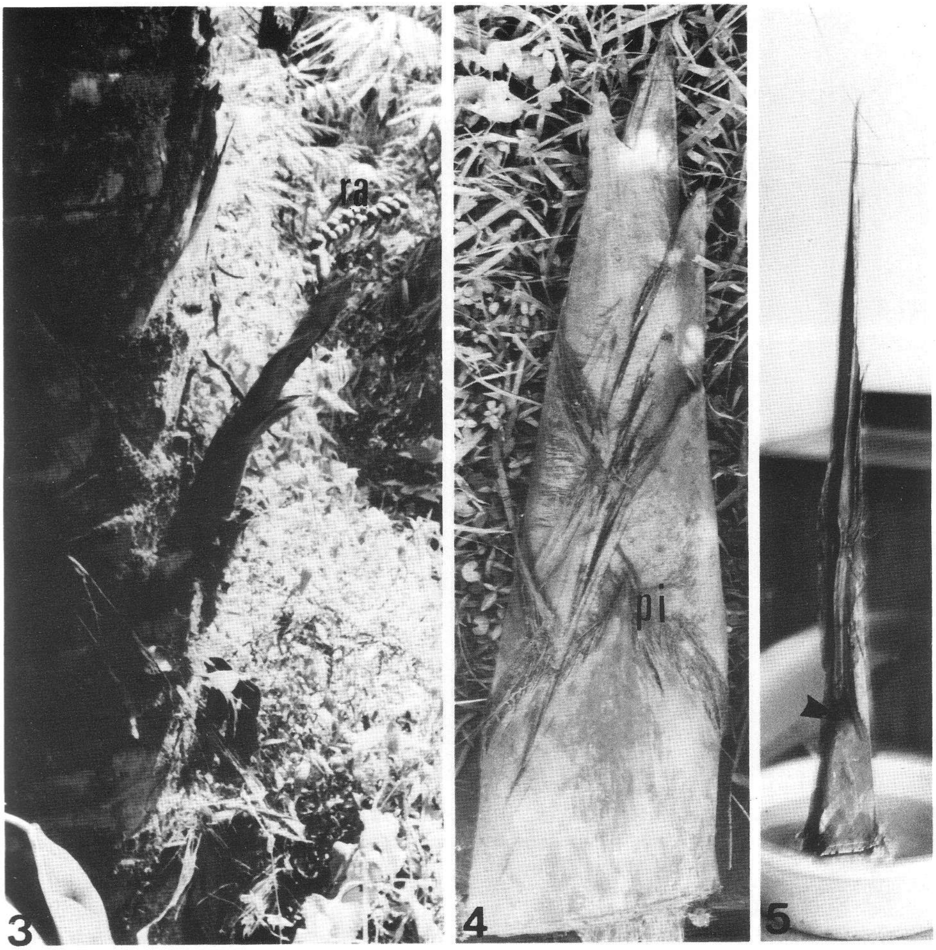
When young inflorescences are developing at the distal end of the trunk it was found that the apical meristem of the stem is a small, flattened, blunt organ consisting of parenchymatic tissue while the last formed leaf is incomplete with a rudimentary sheath, petiole and blade (Fig. 5). Although the basipetal sequence of inflorescence development is the rule, some buds seem to be inhibited or abort and are bypassed. Later, a healthy, bypassed bud may grow into an inflorescence resulting in the occurrence of a younger staminate inflorescence above older ones. This usually occurs halfway down the trunk (Fig. 2). Another irregularity observed was the development of an inflorescence close to the bottom of the tree bearing one rachilla with sterile pistillate flowers and other undifferentiated and smaller rachillae (Fig. 3). On the same tree development of new staminate inflorescences higher up the trunk still occurred.

A mature pistillate inflorescence may reach a length of two meters, the peduncle becoming 80 cm long. There are 35–40 rachillae in one inflorescence each of which may produce 130 individual flowers so that a total of 5,200 flowers may be produced by a single inflorescence. There is a reduction in size of the inflorescences down the trunk; the staminate inflorescences are even smaller. In the pistillate inflorescence the solitary flowers are arranged in a spiral around the axis. A mature pistillate flower consists of three yellowish green colored sepals, three thick valvate petals which are greenish purple on the outside but light green colored on the inside, while the green gynoecium is tricarpellate, trilocular, and triovulate with a sessile tripartite stigma which is somewhat recurved at the end and becomes brownish black at a later stage. A pistillate flower is 14–16 mm high with a diameter of 20–22 mm. During anthesis the pistillate flower emanates a

1,2. *Arenga pinnata*, inflorescences. 1. Tree with two pistillate inflorescences in fruit. The trunk is somewhat hidden by bamboo branches in foreground. 2. Disruption of basipetal development of inflorescences on another tree. A young, pale-colored staminate inflorescence (arrow), 4 days after emergence from its sheaths, is located above older inflorescences, two at the left and one on the right side of the trunk.

soft, fragrant scent and its stigma appears coated with a shiny substance.

A staminate inflorescence located close to the region where pistillate inflorescences are produced may be 150 cm long with a peduncle 50 cm long. There are 40–45 rachillae, each of which may bear 166–244 flowers so that a maximum of 10,980 individual flowers can be found on a single inflorescence. Later formed inflorescences are smaller in size and may be only 70 cm long, including a 30 cm peduncle with 24 rachillae, each approximately 25 cm long. On staminate rachillae, flowers are found in pairs which are also arranged in a spiral around the axis. A mature staminate flower has three yellowish-green imbricate sepals, three leathery, maroonish purple, valvate petals and a large number of yellow stamens. Yellow-colored pollen is produced copiously, feels rather sticky, and tends to clump. A staminate flower in late bud is

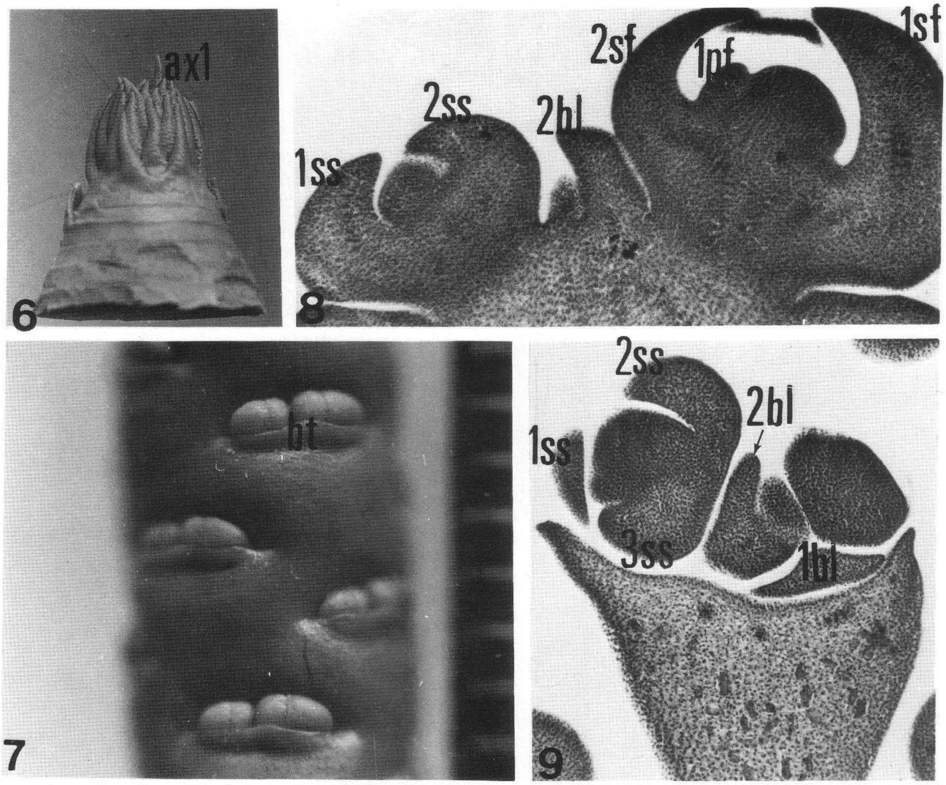


3–5. *Arenga pinnata*, organs. 3. Pistillate inflorescence with only one, 20 cm long rachilla (ra) bearing solitary, sterile flowers is located close to the base of the trunk. 4. A growing, axillary bud 50 cm long showing peduncular bracts each consisting of a short fibrous sheath and a rudimentary petiole (pi). 5. Parenchymatic shoot apex of tree which has started flowering, with the last formed rudimentary leaf. ×⅛.

18–20 cm high with a diameter of 8 mm. Larger flowers are found on vigorous trees and may be 3 cm high with a diameter of 1 cm. At anthesis staminate flowers also produce a scent similar to that of the pistillate flower.

Development of the Inflorescence

An axillary bud consists of a very low domelike apical meristem surrounded by 6–7 bracts, the bases of which are similar in height and together form the base of the bud. The first bract or prophyll is inserted in an adaxial position, is two-keeled, and encloses the bud completely. Subsequent bracts also cover the bud entirely. During inflorescence formation the now active apical meristem produces 8–9 additional bracts, some of the first of these cover the rest of the inflorescence entirely but others reduced in size, do not constitute a complete covering. A bract



6–9. Organogenesis in the flower cluster. 6. Young inflorescence without its bracts showing 1 cm long rachillae (ax1). ×6. 7. Part of a 12 cm long rachilla showing bract (bt) subtending flower cluster and the two first flowers with the younger, smaller flower primordium at the left. ×9. 8. Longisection through a flower pair of Figure 7. Sepal primordia of both flowers have been formed and the first petal primordium of the first flower can be recognized. The third flower is not yet initiated. ×45. 9. Transection through the more distal portion of a 12 cm long rachilla showing a flower cluster somewhat younger than in Figure 8. The bracteole of the first flower is situated parallel to the bract subtending the flower cluster. Bract itself is not shown being situated at some distance above this section. ×45. Details: ax1, inflorescence axis; bt, bract; 1sf, first sepal of first flower; 2sf, second sepal of first flower; 3sf, third sepal of first flower; 1ss, first sepal of second flower; 2ss, second sepal of second flower; 1pf, first petal of first flower; 1bl, bracteole of first flower; 2bl, bracteole of second flower.

can be looked upon as a modified foliage leaf which consists of a blade, a petiole, and a leaf sheath possessing a large tubular ligule narrowing at the distal end (Hidajat and Utomo 1976). The succession of bracts along the peduncle shows a gradual reduction from a bract consisting of a short sheath with a remnant of the ligule and a short petiole (Fig. 4) to a small, scalelike, light green bract distally where rachillae production starts. In total 14–16 bracts including the prophyll are found on the peduncle in a 2/5 phyllotaxy. Bracts do not abscise but dry and remain on the peduncle.

The inflorescence apex forms rachillae acropetally, accompanied by a reduction of the axis diameter which ultimately becomes the last rachilla. Each rachilla except the last is subtended by a small, inconspicuous bract. The full number of rachillae is already formed in a 25 cm long inflorescence bud in which the length of a rachilla is 0.3 cm. Rachillae are oriented vertically and are almost similar in length except the most distal which is the transformed distal end of the axis (Fig. 6). This difference disappears later.

Development of Rachillae and Flowers

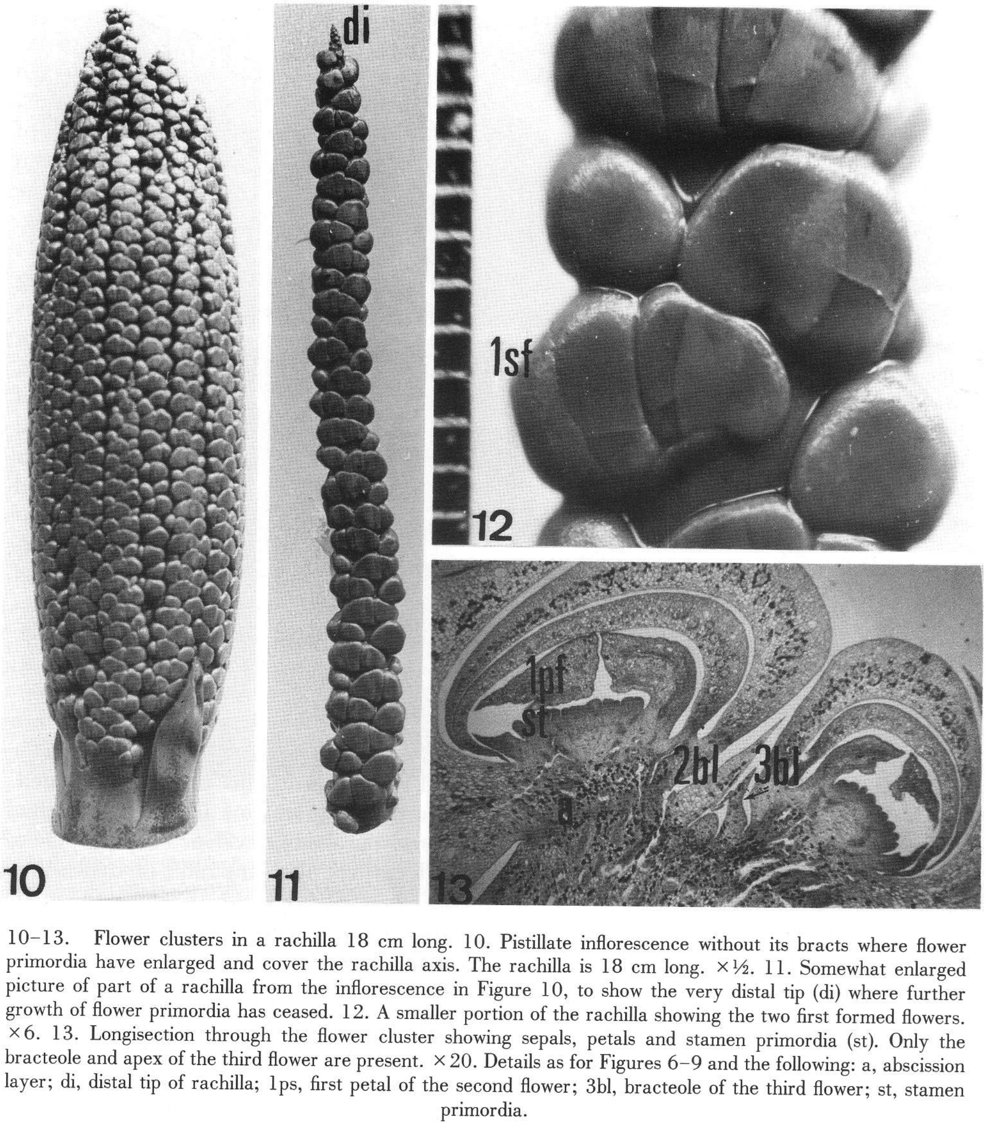
The development of the rachillae and flowers is best understood by following the organogenesis of a pistillate inflorescence. Each rachilla develops bracts in acropetal succession. In the axil of each bract, three flowers are formed consecutively and each flower bud is subtended by a bracteole. When the bracteole of the first flower is formed in the axil of the lowermost bracts, additional bracts are still being formed at the growing rachilla apex. The various growth stages along the length of each rachilla are markedly similar to those of other rachillae of the same inflorescence.

The first two flowers in a flower cluster are initiated in rapid succession producing two flower primordia which do not differ much in size. This size relationship persists during further growth stages (Figs. 7,12). The first bracteole is borne by the first flower and is oriented parallel to the bract subtending the flower cluster. The second bracteole, borne by the second flower, is situated in between the two flower primordia and is oriented perpendicular to the first bracteole.

The shallow side of the second bracteole is facing its flower primordium and indicates whether the primordium is at the right or left side of the first and therefore whether the cluster is right- or left-handed.

Figure 8 shows a longitudinal section through a flower cluster of a 12 cm long rachilla and Figure 9 shows the arrangement of flower parts in a cross section through a somewhat younger cluster of the same rachilla. At this particular stage the three sepals of the first flower are formed and the formation of the first petal in the first flower is visible. The second flower starts to form its first sepal while the third flower is not yet initiated. The place where the third flower will be developed, however, can be detected since its bracteole will face the bracteole of the second flower (Figs. 9,13). It will be noted that the position of the third flower, although it is in between the two lateral flowers is also closer to the proximal side of the flower cluster (Fig. 14).

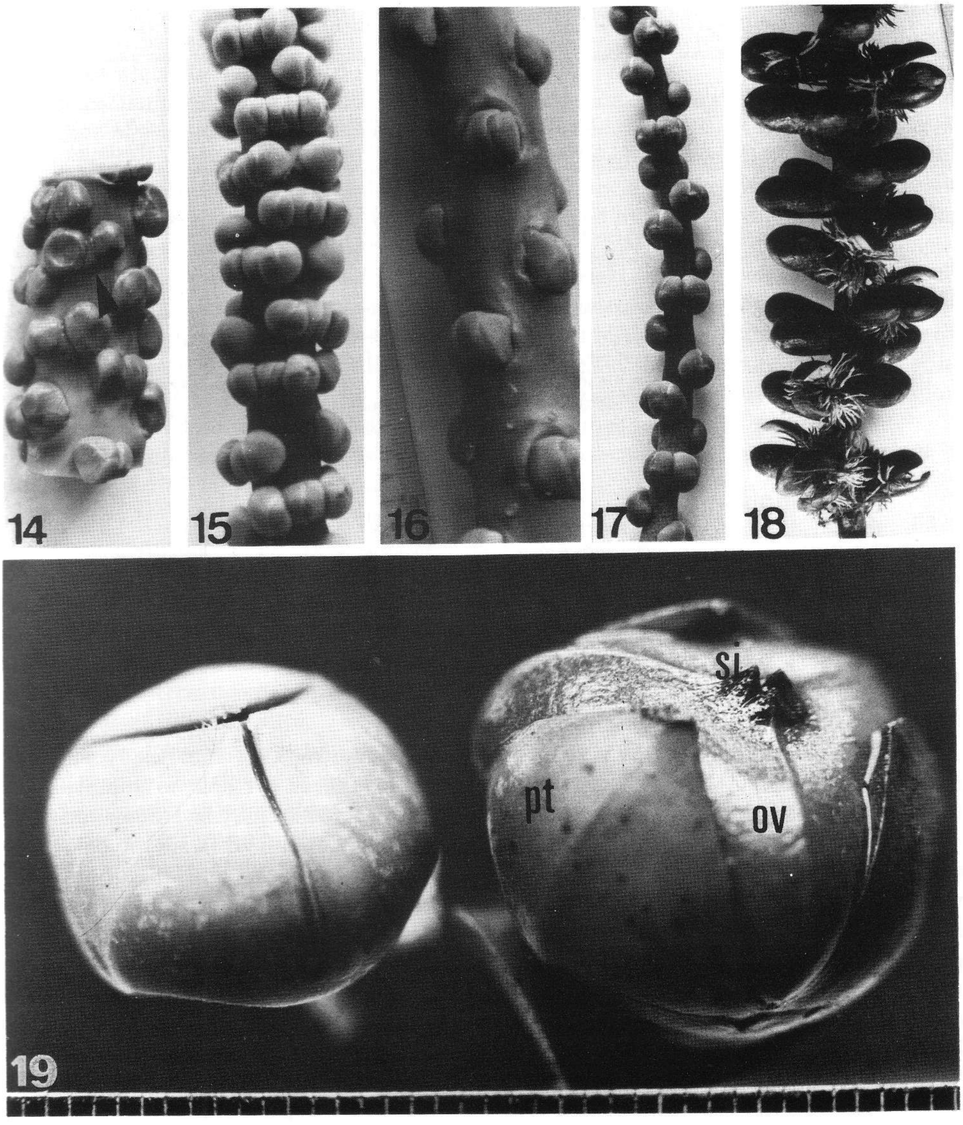
Table 1 shows some of the events during organogenesis of the flowers in a cluster in relation to the length of the respective rachilla. In comparison to the 12 cm stage, at the 18 cm stage sepals and petals of the first and second flower have increased in size. Since the rachilla axis length has not much increased, it seems to be covered by pairs of flower primordia (Fig. 10). At this stage also, the lack of further development of primordia at the distal end of each rachilla is notable (Fig. 11). The bracteole of the third flower has formed (Fig. 13). When the rachilla is 49 cm long, sepals and petals of both the first and second flowers have increased in size and are respectively 2 mm and 1.5 mm in diameter and stamen primordia are being initiated. The third flower, now 1 mm in diameter, has at this stage developed sepals, petals, and carpels, and initiation of ovules has occurred. Further growth before the inflorescence sheath opens involves an increase in the diameter of the flowers along with lengthening of the rachilla axis. Although further development of flower primordia at the distal end of a rachilla seems to be inhibited, this inhibition apparently does not apply to the elongation of the internodes on that portion. At the time of exposure of rachillae from their confining sheaths, the two rounded lateral flower buds are approximately 4 mm in diameter and 2 mm high while in between them the central flower bud is 2 mm in diameter and 1 mm high. Upon exposure its pale yellow color will change first to light green and then to dark green along with further growth of the three flower buds and elongation of the rachilla axis. At the time of



10–13. Flower clusters in a rachilla 18 cm long. 10. Pistillate inflorescence without its bracts where flower primordia have enlarged and cover the rachilla axis. The rachilla is 18 cm long. ×½. 11. Somewhat enlarged picture of part of a rachilla from the inflorescence in Figure 10, to show the very distal tip (di) where further growth of flower primordia has ceased. 12. A smaller portion of the rachilla showing the two first formed flowers. ×6. 13. Longisection through the flower cluster showing sepals, petals and stamen primordia (st). Only the bracteole and apex of the third flower are present. ×20. Details as for Figures 6–9 and the following: a, abscission layer; di, distal tip of rachilla; 1ps, first petal of the second flower; 3bl, bracteole of the third flower; st, stamen primordia.

exposure the rachilla is approximately 60 cm long.

The three flower buds are of similar height and diameter when the rachilla is 90 cm long, forming easily detected triads (Fig. 15). Afterwards, when rachilla length is 100 cm, the two lateral flower buds fall off leaving the central, pistillate flower bud to mature (Fig. 16). Apparently, the abscission layer formed very early in the staminate flower bud (Fig. 13) functions at this moment. Anthesis of the pistillate flowers occurs when the rachilla is 135 cm long. Figure 19 shows a pistillate flower near anthesis and another one some time after anthesis when the stigma has turned dark brown. At the distal end of the pistillate rachilla the development of the pis-



14–19. Further development of the flowers. 14. Part of a 50 cm long rachilla. Early growth of the third flower (arrow) which is located in between, but more to the proximal side of the first (left) and second (right) flower. Natural size. 15. The central flower bud has grown to a similar size as the two laterals. $\times \frac{2}{3}$. 16. After the two lateral flowers have fallen. $\times \frac{1}{2}$. 17. Part of a staminate rachilla showing pairs of staminate flower buds. $\times \frac{1}{2}$. 18. Staminate flowers at anthesis. $\times \frac{1}{2}$. 19. Left, pistillate flower shortly before anthesis; right, early fruit formation. $\times 2$. Details: ov, ovary; pt, petal of the pistillate flower; si, stigma.

tillate flowers remains inhibited. The later staminate flowers do not increase in size as much as elsewhere on the rachilla and fall off together with the others, leaving a portion bare of flowers. Since elongation of the rachilla axis does not seem to be inhibited, the distal bare end may comprise $\frac{1}{5}$th of the rachilla length at maturity.

Table 1. Organogenic events in a pistillate rachilla in relation to its length.

Length of Rachilla (cm)	Events in			
	Rachilla Axis	1st Flower (Staminate)	2nd Flower (Staminate)	3rd Flower (Pistillate)
0.3	bracts formed acropetally	—	—	—
0.5	bracteole of the first flower formed in flower bracts	bracteole of first flower formed	—	—
2.3	all bracts with flower primordia	sepals formed	bracteole 2, initiation of first sepal	—
12	—	first petal initiated	sepals formed	—
18	—	sepals increase in size, all petals formed and stamens initiated	sepals increase in size, all petals formed and stamens are initiated	bracteole 3 formed
49	—	diameter 2 mm	diameter 1.5 mm	sepals, petals, carpels formed, ovules initiated, diameter 1 mm
55	—	diameter 3 mm	diameter 2 mm	diameter 1.5 mm
60*	—	diameter 4 mm	diameter 4 mm	diameter 2 mm
90	—	diameter 7 mm	diameter 7 mm	diameter 7 mm
100	—	falls off	falls off	diameter 8 mm
135	—	—	—	diameter 20 mm, anthesis

* Exposure of rachillae from the sheath.

The staminate rachilla shows a similar mode of development as the pistillate except that the central flower of the triad does not develop at all (Fig. 17). At the time of exposure, the staminate flowers are at the stage of stamen initiation which is similar to that of the staminate flowers in a pistillate inflorescence. The two lateral staminate flowers continue to develop to maturity (Fig. 18). A distal end, bare of flowers, also occurs but is much shorter than in the pistillate rachilla.

Discussion

In the sugar palm the stem apex does not change into an inflorescence as reported by Sudasrip (1980) but remains parenchymatous. Axillary buds are apparently formed in acropetal succession along with their subtending leaves. The last formed leaf, however, does not subtend an axillary bud. This may be due to lack of necessary growth substances usually provided by the apical meristem so that the young leaf primordium is not able to stimulate the initiation of its axillary bud (Snow and Snow 1942, in Cutter 1980). All the buds show a similar structure consisting of an apical meristem surrounded by several bracts indicating that potentially they all may form inflorescences. The stimulus for their further development could be the diminishing amount of certain growth substances due to the absence of young leaf primordia at the apical meristem. Therefore, the inhibition of development of the buds is released basipetally as suggested by Moore and Uhl (1982).

Disruption of the basipetal succession has been reported previously (Dransfield and Mogea 1984). The occurrence of a pistillate rachilla at the trunk's proximal end is another irregularity and others may yet be found. Proximal pistillate flowers, however, are sterile. The fact that fertile pistillate flowers are found only on the distal inflorescences accompanied by the drop of staminate flower buds seems to indicate regulation by balanced amounts of internal substances which are coordinated spatially as well as temporally, and result in the separation of sexes on the respective inflorescences.

Both inflorescences show that at the time of exposure from the ensheathing bracts, staminate flowers have reached the stage of early stamen formation, whereas ovules are in their primordial stage. Protection of ovules, and pollen which are formed later is therefore provided by the perianth as in *Ptychosperma* (Uhl 1976).

The pattern of development in both types of inflorescence is similar. Periods of organ initiation and development are generally uniform for all rachillae within an inflorescence. Flower clusters within a rachilla are usually all right- or all left-handed. Occasionally, however, some of the proximal clusters may show a different direction from the rest as shown in Figures 8 and 9 which were taken from the same rachilla but at different sites. The significance of the delay in the initiation of the third flower in the cluster is not known. Its slow increase in size before exposure may cause misinterpretation during field observation where at first only the two lateral staminate flower buds are easily visible.

The ontogeny of the three flowers in the cluster supports the finding that it is a short axis formed sympodially as was found in *Ptychosperma* (Uhl 1976). Although at later stages of development, the pistillate flower is seen in between the staminate and together form a straight series perpendicular to the rachilla axis, it may be noted that in early ontogeny the central flower is situated close to the abaxial side of the two laterals. In podococcoid palms the pistillate flower is located abaxial to the two staminate (Moore and Uhl 1982). The pattern of flower development involving falling of staminate flower buds before anthesis of the pistillate shows a similarity to that in *Caryota* where staminate flowers open and fall before the anthesis of the pistillate flower (Dransfield and Mogea 1984).

The sugar palm is presumed to be wind pollinated (Miller 1964) but the bright yellow colored stamens, the large amount of yellow, sticky pollen, and the fragrant scent produced by both types of flowers seem to indicate insect rather than wind pollination. Field observations are needed to determine the mode of pollination. Knowledge of histological features could be used to reach a more definite conclusion (Uhl and Moore 1977) about their correlation with either manner of pollination.

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