Position and Development of Differentiated Lateral Buds in Sago Palm (*Metroxylon sagu* Rottb.)

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Abstract: During sago palm cultivation, many suckers appear from the mother stem as it grows. Some suckers are thinned out, but the rest are left to grow to be harvested several years later after harvesting of the mother stem (trunk). Proper management of the suckers from the mother stem is important to obtain successive sago trunks from a single transplantation. Nevertheless, little scientific knowledge exists about the sucker growth, even the development of its primordium. Our objective is to clarify the differentiation position and the development of the sago palm lateral bud, which is the sucker bud. Results show that in sago palm, the sucker bud differentiates inside of the connate part of the leaf petiole, which is opposite to the axil side. Swelling of tissue is first visible inside of the third leaf from the growth point (rbL 3). Sucker bud initiation is visible at almost all leaf positions lower than rbL 5. Furthermore, at each leaf position, one or two (rarely three) buds are observed. Differentiated buds usually elongate exponentially. Some develop more than two times on average. These sucker buds differentiate inside of the connate part of the thin leaf petiole, which split toward the base gradually as new leaves emerge. The differentiation position of the sucker buds and the thin leaf petiole are expected to be related closely to the further growth of the large sucker buds.

Key words: Bud development, Differentiation position, Lateral bud, *Metroxylon sagu* Rottb., Sago palm, Sucker bud.

Sago palms (*Metroxylon sagu* Rottb.), which accumulate large amounts of starch in the trunk, can grow on humid peat soil. They are therefore important as a starch crop, mainly for use as an industrial raw material. Large-scale production at plantations has just begun in Indonesia. An adequate cultivation technique must be developed for future expansion of production.

Sago palm trunks are first harvested ten and several years after transplantation. Many branches, called ‘suckers’, appear from the mother stem during growth. Some of these suckers are thinned out (sucker control), whereas the rest are left to grow to be harvested several years after harvesting of the mother trunk (Nabeya et al., 2013). Consequently, for sago palm cultivation, proper management of the suckers from the transplanted sago plant is important to obtain successive sago trunks from a single transplantation.

For crop cultivation, understanding the developmental behavior of the branch is extremely important to improve crop production. Katayama (1951) reported the relation between the emerging leaves and appearing tillers in rice. Based on that relation, the differentiation and development of rice tillers have been studied (Sekiya, 1958, 1977; Nishikawa and Hanada, 1959). Organization of the relation between leaf emergence and tiller development of rice contributed to the analysis of growth and the theoretical proof of cultivation techniques (Goto, 2003). However, for sago palm, data related to sucker growth and the development of lateral bud primordium are lacking. The lateral bud of sago palm, the sucker bud, differentiates on the side opposite to the axil, different from many plants (Goto et al., 1998), but details of the position and the ratio of differentiated sucker buds have not been clarified. Sucker bud development and the relation between sucker bud development and leaf emergence have not been elucidated. Development of cultivation techniques such as sucker control requires accumulation of basic knowledge about sucker buds. The present study clarified differentiation of the position and the development of differentiated sucker buds.
Materials and Methods

Suckers with a stem diameter mean and SD of 55.5 ± 13.6 mm were collected from two sago gardens in Mukah, Sarawak, Malaysia. We used 37 suckers derived from the spineless type of sago palm, which is widely cultivated in Sarawak.

To investigate the differentiation of sucker buds, we removed the expanding leaves, the spear leaf which was the emerging and unexpanded leaf and the unemerged leaves formed inside of the spear leaf carefully up to the growth point. Then, we designated the leaf position as follows. In the hood-like leaf primordium covering the growth point, the youngest leaf primordium, with tip of hood-like leaf beyond the tip of growth point, was designated L 1 and next lower leaves L 2, L 3, and so on, basipetally. However, this leaf position represents the relative position, not the absolute position. Accordingly, L 1 is referred to as the rbL 1 (relative basipetally Leaf 1) followed by rbL 2, rbL 3, and so on.

We regard the position of sucker bud that differentiated inside of rbL n, outside of rbL n-1, as rbS n. On the leaf position of all leaves attached to the investigated suckers, we checked for sucker buds using a stereomicroscope. For the size of sucker bud, the length from the base to the tip and the width of the part which is the widest near the base were measured.

In sago palm, since a leaf sheath, which is the lower part of the petiole, wraps around the stem, a part of the leaf sheath attached to the stem appears to be a node like a ring after removal of the leaf sheath (Fig. 1a). Therefore, considering the part of leaf attached to be a circle, we measured the diameter of the part of leaf attached to the stem in the circle.

To analyze the position at which the sucker bud was attached in detail, we determined the position at which the sucker bud was attached from the designated reference points. At the connate part of leaf petiole, the vascular bundle travels from petiole to the base, the two bundles fuse into one near the base (Fig. 1a). This part is also the part that is gradually split as new leaves emerge and stem...
enlarges. Assuming this leaf is rbL\(_n\), the position, where the fused vascular bundle attaches to the node, was designated as the reference point of rbL\(_n\). The position at which the buds of rbS\(_n\) attached on the circumference of rbL\(_n\) is shown by the central angle between the reference point and the position of rbS\(_n\). When the sucker bud is located on the right side of the reference point as viewed from the front, the position of attachment of the bud is shown by a positive angle, and when it is located on the left side, it is shown by a negative angle (Fig. 1b).

Sago palm has a phyllotaxis of 4/13 (Jong, 1991) and the leaves are arranged clockwise (Fig. 2) or counterclockwise from an old leaf (rbL\(_n\)) toward younger leaves (rbL\(_n\)-1, rbL\(_n\)-2, ...) from the top view. Therefore, we classified into two groups, clockwise and counterclockwise of leaf arrangement, and analyzed the relationship between the leaf arrangement and the attached position of sucker bud.

## Results

In the investigated suckers, the leaf position of a spear leaf ranged from rbL\(_6\) to rbL\(_9\). About 80% of them were rbL\(_7\) or rbL\(_8\). The diameter of the part of leaf attached on each leaf position is shown in Fig. 3. The diameter increased exponentially at a lower leaf position. The diameter of the part of a spear leaf attached ranged from 6.7 to 18.5 mm, an average of 10.6 mm.

### 1. The initiation position and ratio of sucker bud

In sago palm, sucker bud differentiated near the reference point which is inside of the connate part of leaf petiole (Fig. 1b). This position was on the side opposite the axil across the center of the stem. There was no sucker bud on each leaf position in rbL\(_1\) and rbL\(_2\), and the sign of differentiation was not visible. However, in rbL\(_3\), the swelling of tissue was visible in 13.6% of investigated suckers. In this study, the swelling of tissue was regarded as the initiation of sucker bud. The diagram of the differentiation position of sucker bud at the initiation stage is presented in Fig. 4. Since the tip of hood-like leaf primordium was beyond the tip of growth point, this leaf primordium was assumed rbL\(_1\) (Fig. 4a). The swelling of tissue inside rbL\(_4\) was visible in 77.3% of investigated suckers (Fig. 4b). The initiation of sucker bud inside rbL\(_5\) was visible in all investigated suckers, and the sucker bud was visible at almost all leaf positions after rbL\(_5\). Additionally, multiple buds were observed at each leaf position. At leaf positions lower than rbL\(_6\), where the number of differentiated bud was definitely identified, the rate at which one, two and three sucker buds differentiated at each leaf position was 30.1, 68.1, and 1.8% respectively (Fig. 5).
2. The development of sucker bud

Fig. 6a and 6b show diagrams of the development of one sucker bud and two sucker buds differentiated, at each leaf position, respectively. The diagrams of rbS 5 in Fig. 6a and 6b are those of sucker bud developed from the swelling of rbS 4 shown in Fig. 4b. In Fig. 6a, the swelling increased, and the top became slightly hollow, while, in Fig. 6b, the development of new organization was visible on both sides of the swelling. The diagram of rbS 6 in Fig. 6a shows the hollow of top part and the organization on both sides of the swelling is more developed in Fig. 6b. In the diagrams of rbS 7 the sucker buds have already begun to elongate.

The length and the width of sucker buds from rbS 6 to rbS 13 are shown in Fig. 7a and 7b, respectively. The vertical axis of the figures is logarithmic scale. Thus, both length and width increased exponentially. At the leaf position lower than rbS 11, some sucker buds developed markedly in length and width (Fig. 8). The size of all sucker buds from rbS 11 to rbS 13 were 13.0 ± 8.7 mm in length and 1.9 ± 1.7 mm in width on average. The large sucker buds were about 7.0% of all sucker buds from rbS 11 to rbS 13, and the length and the width near the base were 28.7 ± 10.8 mm and 5.5 ± 2.0 mm on average, respectively. They were 2 times the average size. Additionally, such sucker buds were enlarged generally around its base, and it was easy to distinguish the large sucker buds from other sucker buds.

![Fig. 5. Three sucker buds differentiated. The arrow indicates the sucker buds. The triangle denotes the reference point. Bar = 10 mm.](image)

![Fig. 6. Diagram of development of sucker bud. The development of one sucker bud (a), and two sucker buds (b) on each leaf position, respectively. Bar = 1 mm.](image)

![Fig. 7. Size of sucker bud on each leaf position. (a): The length of sucker bud. (b): The width of sucker bud at the base. ○ denotes sucker bud developing greatly. n = 23.](image)
4. The attached position of sucker bud to the reference point

Fig. 11 shows the position at which the sucker buds attached to the reference point on the leaf position of a spear leaf and each expanding leaf where vascular bundles developed and the reference point was visible. In this figure, the circumference of attached part of leaves was arranged concentrically and the position of the reference point was on a straight line. The black circles show the position at which the sucker buds were attached; they were distributed in a fan-shaped from inside to outside in a concentric circle. Fig. 12 shows the frequency distribution of the attached position. The sucker buds were distributed from $-40.5^\circ$ to $37.9^\circ$ to the reference point. Most of the sucker buds were distributed from $-5^\circ$ to $5^\circ$, near the reference point, and about 90% of them were distributed from $-25^\circ$ to $25^\circ$.

5. The relationship between the leaf arrangement and the attached position of sucker bud

To analyze the relationship between the leaf arrangement and the position at which the sucker buds attached to the reference point, we categorized the sucker buds as follows. When one sucker bud differentiated, it was designated $O_{sb}$. When two sucker buds differentiated, the large bud and small bud were designated $L_{sb}$ and $S_{sb}$, respectively, since the two buds were usually different in size. The case of three buds differentiated was excluded from analysis because such a case was rare. Fig. 13 shows the positions at which the sucker buds were attached presented in Fig. 11, with classification of crosswise property, the clockwise or the counterclockwise leaf arrangement sucker. The attached positions were generally one-side toward positive or negative direction from the reference point. Approximated by a straight line, $y = -0.17x + 26.31$ with $R^2 = 0.004$, the line was almost parallel to $x$-axis, indicating that the distance between two sucker buds tend to be more apart from each other at a lower leaf position.

By contrast, some sucker buds with only an increase in length not width were also observed from $rbS\,11$ to $rbS\,13$. Most of these sucker buds elongated meanderingly (Fig. 9).

3. The differentiation position of two sucker buds

In the sucker buds growing to more than 1 mm in length, when two sucker buds differentiated, the differentiation position of two buds was located at a distance. The distance between two buds was less than 1 mm (Fig. 6b). To clarify the relationship of the position of two sucker buds, we examined the central angle subtended by the differentiation positions of two buds at each leaf position (Fig. 10). The central angle from $rbS\,5$ to $rbS\,15$ was $24.9 \pm 7.3^\circ$ on average. Approximated by a straight line, $y$-intercept was $26.3^\circ$ and the line was almost parallel to $x$-axis, indicating that the distance between two sucker buds tend to be more apart from each other at a lower leaf position.
clockwise leaf arrangement sucker, from $-25^\circ$ to $15^\circ$ in the counterclockwise leaf arrangement sucker. $L_{sb}$ buds were distributed near the reference point, $O_{sb}$ buds were distributed slightly distant from the reference point and $S_{sb}$ were distributed at a greater distance in both suckers, though there was difference in right and left.

Discussion

In sago palm, the lateral bud which is called the sucker bud, differentiates inside of the connate part of leaf petiole. This position is the side opposite to the axil. Fisher and Dransfield (1979) reported that the lateral bud of an Arecaceae, *Daemonorops* spp. and *Korthalsia rigida* differentiated on the side opposite to the axil, and named it leaf-opposed bud.

At a leaf position lower than rbL 6, almost all sucker buds were visible. This result was different from the report by Goto et al. (1998). At each leaf position lower than rbL 6, the rate of two sucker buds and three sucker buds was 68.1 and 1.8%, respectively. The presence of multiple vegetative buds differentiated in a leaf position has been reported in *Plectocomia elongata* (Fisher and Dransfield, 1979). In *P. elongata*, one to ten vegetative buds appear as small swellings in a node, and become multiple branches. By contrast, in sago palm, a small swelling occurred (Fig. 4b), then, it differentiated into two sucker buds (Fig. 6b). So far, we have not observed sago palm with both sucker buds developing and appearing from a leaf position.

When two sucker buds differentiated, the two buds were at a distance, which tended to become longer at a lower leaf position. However, the central angle subtended by two buds was constant at $25^\circ$ from rbS 5 onward (Fig. 6), regardless of the leaf position (Fig. 10), indicating that the relative positional relation of two buds at the circumference of attached part was not changed by leaf position. Therefore, the increase of the distance between two buds was attributed to the enlarging of stem and the length of stem circumference with lower leaf position.

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When suckers were classified into two leaf arrangements and into $O_{SB}$, $L_{SB}$ and $S_{SB}$, the position at which each sucker bud was attached to the reference point showed a similar tendency though there was a difference in the crosswise property of leaf arrangement (Fig. 14). In order to analyze the attached position of sucker bud to the reference point in detail, the difference of crosswise property in leaf arrangement was removed as follows. Based on the frequency distribution presented in Fig. 14, in the sucker with the counterclockwise leaf arrangement, the sign of attached position was reversed, and the frequency distribution of counterclockwise leaf arrangement was unified in the clockwise leaf arrangement. Then, the unified frequency distribution of $O_{SB}$, $L_{SB}$, $S_{SB}$ and total buds were approximated by Richard function, and presented in Fig. 15. The peak of frequency distribution of total was 11.5° and it leaned toward the positive direction from the reference point. The peak of $O_{SB}$, $L_{SB}$ and $S_{SB}$ were 9.5°, –6.8° and 20.6°, respectively. In case of one sucker bud, the sucker bud develops at the position where the tissue swells as presented in Fig. 6a. Hence, in the sucker with clockwise leaf arrangement, the differentiated position of sucker bud was considered to be essentially leaned toward positive direction from the reference point. In the case of two sucker buds, sucker buds developed on both sides of the swelling (Fig. 6b). Consequently, it was
considered that the peaks of L<sub>SB</sub> and S<sub>SB</sub> were located on the right and left side of the peak of O<sub>SB</sub>. Furthermore, the central angle subtended by the peaks of L<sub>SB</sub> and S<sub>SB</sub> in Fig. 15 was calculated to be 27.4º. This angle was almost the same as the y-intercept presented in Fig. 10 and the average of the central angle subtended by two buds.

Fig. 16 shows the diagram of the leaf arrangement and the differentiated position of sucker bud. The area of the reference point indicated by arrows is the part where leaf petiole connate and the tissue of leaf sheath around this part becomes extremely thinner than in other parts. Moreover, this part is gradually split toward the base as new leaves emerge and expand. These results suggested that it should be easier for sucker buds in this area to develop and enlarge due to lower physical pressure than in other areas. This characteristic in the area should be closely related to the further growth of the large sucker buds (L<sub>SB</sub>) attached around the reference point.

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