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Morphological and Anatomical Observations of Adventitious and Lateral Roots of Sago Palms

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Abstract : Sago palm (*Metroxylon sagu* Rottb.), which produces starch in large quantities in its trunk, could become one of the most important nutritious food resources in the near future. Although its root functions are thought to be very important for the enormous shoot growth, the morphological and anatomical studies are limited. This study investigates external and internal structures of sago roots with reference to their functions to distinguish two types of roots in each plant; i.e., large (about 6-11 mm diameter) and small (about 4-6 mm diameter) roots. Large roots were adventitious roots whose primordia were formed just inside the epidermis in the stem, emerged from the trunk surface and grew downward into the soil. Small roots were lateral roots whose primordia were formed on large roots running horizontally or on other small roots, grew not only downward and obliquely in both deep peat and mineral soils, but also right above in deep peat soils. Anatomical observations revealed that both large and small roots had the same internal structures containing epidermis, exodermis, suberized sclerenchyma cells, cortex and stele, with only differences in their sizes or cell numbers. Both roots had characteristic development of schizogenous or lysigenous aerenchyma, but seem to have different functions. Root primordia were formed successively throughout the trunk. Root primordia in the lower trunk had a large diameter, while density of root primordia per unit trunk surface area was high in the upper trunk.

Key words : Adventitious root, Lateral root, Lysigenous aerenchyma, *Metroxylon sagu* Rottb., Root primordia, Sago palm, Schizogenous aerenchyma.

Sago palm (*Metroxylon sagu* Rottb.) is a monocotyledon of the family Palmae. It is widely distributed in tropical rain forest climate zones located between lat. 10° N and S with high temperature, humidity, and solar radiation (Flach, 1977). The plant possesses great plant length (more than 10 m) and fresh weight (more than 1000 kg for the whole body) and accumulates much starch (100-600 kg) in the trunk (Flach, 1980; Jones, 1994; Ehara et al., 1995; Yamamoto, 1998). Sago palm could become one of the most important nutritious food resources in the 21st century because it is the only plant allowing growth even in extensive areas (about 20-30 million ha (Kyuma, 1992)) of strong acid peat soils in southeast Asia (Fukui, 1984) as well as producing starch with small amounts of fertilizers (Yamamoto, 1998).

Although the sago palm is a monocotyledonous plant, the trunk grows to be quite tall, thick (about 30-50 cm diameter), and heavy (about 500-2000 kg). Therefore, great attention is focused on the root structure and function that support such great shoot growth. In this paper, we describe the morphological and anatomical structures of sago palm roots and discuss the functions related to their structures.

Materials and Methods

1. Research sites and sampling methods

We carried out three researches at two sites with different soil types. In July 1996, root systems exposed along a ditch wall about 1 m in soil depth at 50 cm distance from palms were investigated under mineral and deep peat soils in Mukah, Sarawak, Malaysia. In April 1997, several root system parts, about 50 cm in soil depth and 50 cm distance from the palms, were investigated under deep peat soil (plantation of PT. National Timber and Forest Product Co.) in Selatpanjang, Riau, Indonesia. The water table was quite high (20 cm under the ground surface) and some ground surface areas near the palms were flooded.

2. Preparation of scanning electron microscopy

Root portions of various thickness and running habits roots were taken from several root system parts in Dec. 1999 in Selatpanjang, stored in water, and brought to Japan. Three days after sampling, roots were cut into

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Abbreviations : SEM, scanning electron microscope.

5 mm sections and frozen rapidly with slush nitrogen (−210°C) followed by vacuum freeze drying (−60°C, 10^{-3}Pa, OTD-5SF-S, Oka Science Co., Japan) (Zakaria et al., 2000). Cross sections of dried material cross sections were made with a razor blade and then coated with platinum so that the dissected surfaces were exposed. Specimens were viewed with a scanning electron microscope (SEM) (JSM6301F, JEOL Co., Japan).

Results

1. External morphology of roots

(1) Deep peat soil

Roots emergent from the trunk surface grew toward right under the soil surface; most were emerged from the trunk surface up to about 30 cm from the ground surface (Fig. 1).

In root systems, two types of roots were distinguished in all plants : large roots about 6-11 mm in diameter and small roots of about 4-6 mm in diameter (Fig. 2). The former ones were adventitious roots whose primordia (root tip tissues including their own original meristem) were formed just inside the epidermis in the stem, emerged from the trunk surface and grew downward into the soil. The latter ones were lateral roots whose primordia were formed on large roots running horizontally or on other small roots (Fig. 2). Though both large and small roots were distributed in the 0-30 cm soil layer, there were many more small roots than large roots (Fig. 2). Also, about half the number of small roots were observed to grow right above : from the deep soil layer to the ground surface. Below the 30 cm soil layer, the number of large roots was greater than that of small roots (Fig. 2).

Moreover, in the submerged ground area around the trunk, some small roots grew right above and exposed themselves to the air up to about 10 cm above the water (Fig. 3). Meanwhile, trunks in moist air and low radiation conditions due to covering by leaf sheathes and other plant organs had large roots growing directly toward the ground surface (Fig. 4).

On lower trunk surfaces, emergence of small roots was also observed (Fig. 5). Most of these roots grew upward just after emergence from the trunk surface. Root lengths were 10-15 cm. They had round root caps and node-like white portions along the root axis. There was slight branching at their tips. Anatomical observations revealed that a small protuberance was produced on the large root primordia, and then the protuberance made an upright elongation to be a small root, indicating that the small roots were branches of large roots.

(2) Mineral soil

Similar to the deep peat soil, both large (about 6-11 mm in diameter) and small (about 4-6 mm in diameter) roots were observed in mineral soil, although there were many more large roots than small roots. Formations of primordia of both roots were also the same as in deep peat soil. There were no submerged areas in mineral soil fields, so no small roots growing right above were observed.

2. Internal morphology of roots

Figs. 6a, 6b, 7a and 7b show SEM micrographs of cross sectional views of large and small roots, respectively. In large roots, the outermost layer was the epidermis, which had no hairs (Fig. 6a). The pericycle was the outermost layer of the stele (Fig. 6b). Several cortex layers were observed between the epidermis and pericycle (Fig. 6a and b). Outermost two layers of cortex were exodermis with thin cell walls (Fig. 6a). Just inside the exodermis, there were 4 to 6 suberized sclerenchyma

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Explanations of figures

Fig. 1. A part of root system at the trunk base. Most roots originate from the trunk surface up to about 30 cm from the ground surface.

Fig. 2. Root system at 0-30 cm soil layer. Large and small roots are shown. Arrow indicates branching portion of small root growing right above from large root.

Fig. 3. Some small roots grow right above and are exposed to the air up to about 10 cm above the water near the trunk.

Fig. 4. Large roots grow right under and up to the ground surface in conditions of wet air and low radiation due to covering by leaf sheathes and other plant organs.

Fig. 5. Surface view of lower trunk. Small roots, bearing round root caps and node-like white portion along the root axis, grow upward just after emergence.

Fig. 6. Cross sectional view of a large root (SEM micrograph). a : outer portion, b : inner portion. Bar : 100 μm.

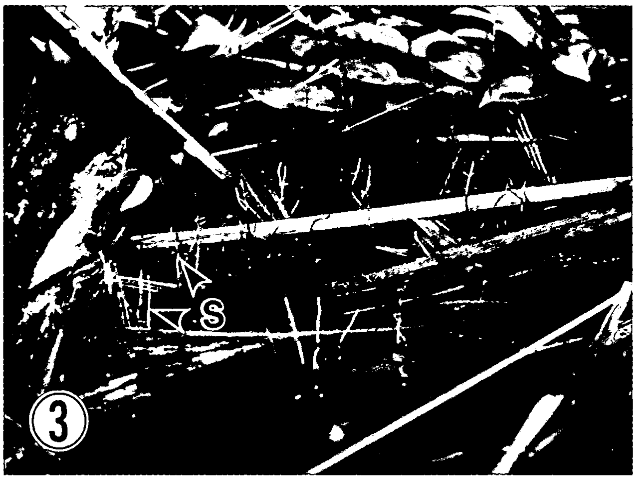
Fig. 7. Cross sectional view of small root (SEM micrograph). a : outer portion, b : inner portion. Bar : 100 μm.

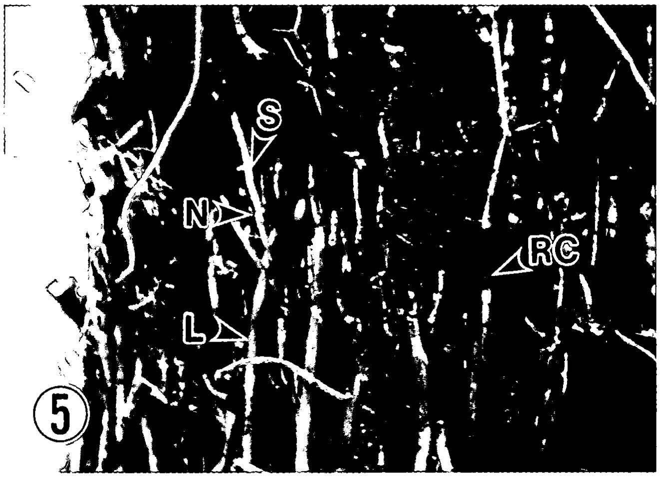
Fig. 8. Surface view of lower trunk just inside the leaf sheath. Emerged root and root primordia (indicated by arrow) are observed.

Fig. 9. Surface view of upper trunk from which leaf sheathes are removed. Emerged root and root primordia (indicated by arrow) are seen.

Abbreviations on figures

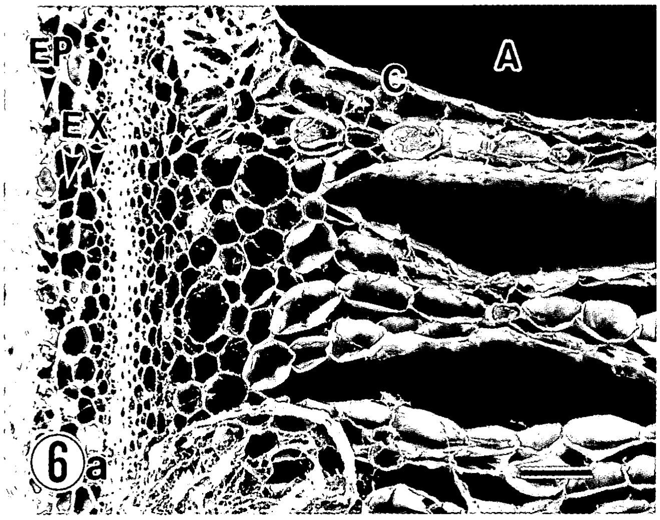
A, schizogenous or lysigenous aerenchyma; C, cortex; EN, endodermis; EP, epidermis; EX, exodermis; L, large root; N, node-like white portion; PE, pericycle; PH, phloem; RC, root cap; S, small root; X, xylem.

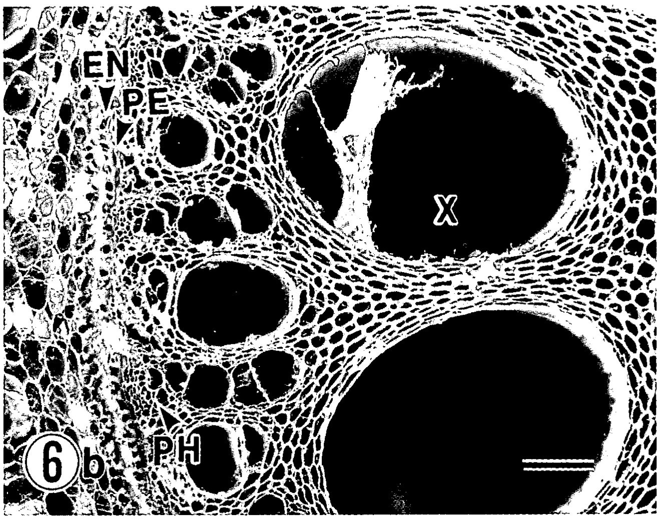


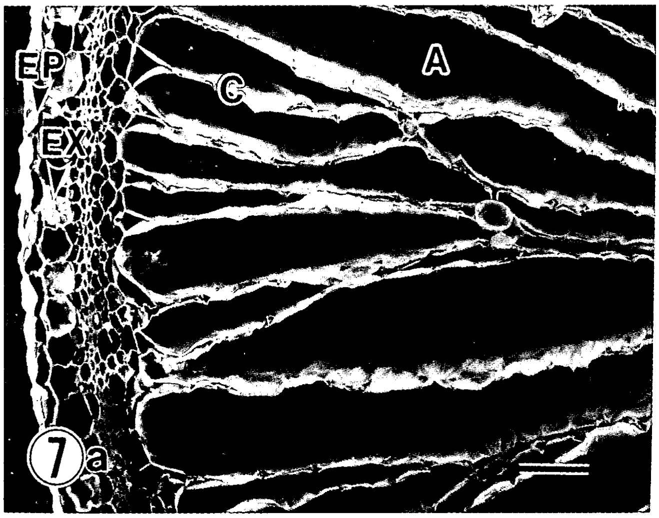


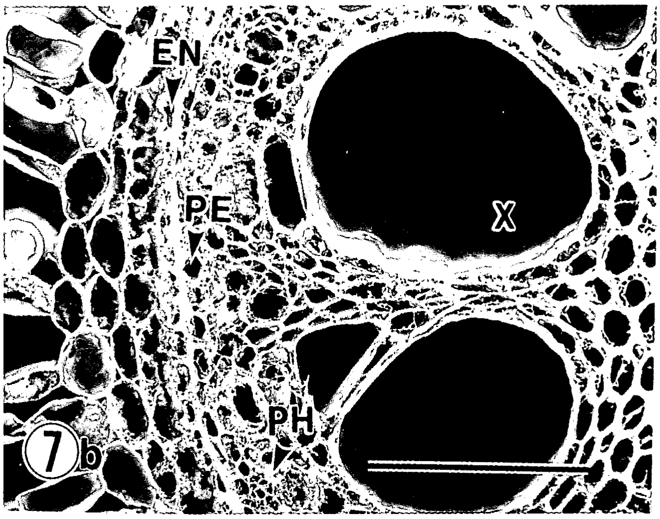
cells (Fig. 6a). Most cell walls of 30 to 40 layers of cortex were collapsed in on themselves or separated from each other so that a few radial walls remained and air spaces were made. These air spaces were schizogenous or lysigenous aerenchyma (Fig. 6a). The innermost layer of cortex was the endodermis whose inner tangential and radial walls had been thickened (Fig. 6b). In the sample in Fig. 6b, stele, consisting of vascular bundles, had twelve large xylems with a diameter of about 400-600 μm. Outside layers of large vascular bundles, small xylems and phloems were arranged in the stele periphery (Fig. 6b).

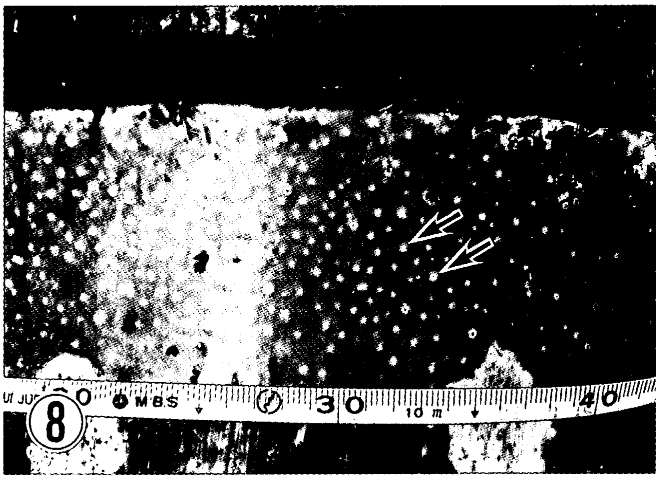
Small roots had a diameter of about 3.5 mm including the 0.8 mm stele diameter; cortex was about 1.0 mm in thickness. The outermost layer was the epidermis, which had no hairs (Fig. 7a). One exodermis layer was observed just inside the epidermis; inside of it, 3 to 4 suberized sclerenchyma cells were seen (Fig. 7a). Cortex layers, consisting of 20 to 30 cells, also had schizogenous or lysigenous aerenchyma similar to large roots (Fig. 7a). There were large xylems, 100-200 μm in diameter, surrounded by small xylems and phloems (Fig. 7b).

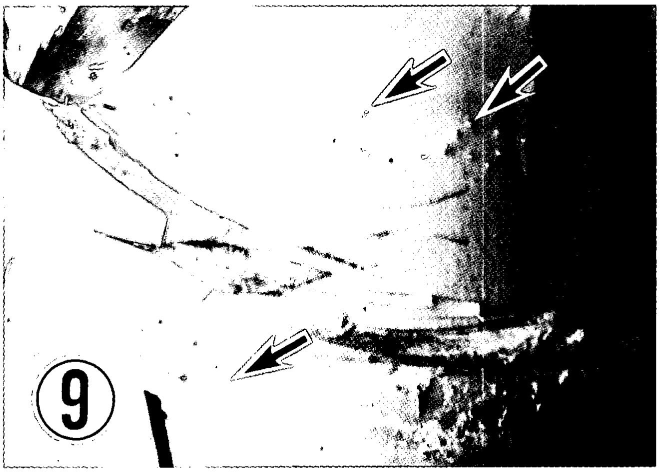












3. Formation and growth of roots

(1) Formation of root primordia

After the trunk formation stage, the emerged roots or root primordia were easily observed on trunks just inside the leaf sheath in sago palms (Fig. 8). Emerged roots or root primordia were formed not only in the basal portion, but also in the upper portion of the trunk surface, which was wrapped by several leaf sheathes (Fig. 9). Accordingly, it was revealed that root primordia were formed along the entire trunk surface, even in the top portion. Root primordia grew and emerged from the trunk surface except in the upper trunk portion, where root primordia were observed in a protuberant shape (Figs. 8 and 9). Moreover, roots growing inside the leaf sheath were only small roots and not large ones.

(2) Thickness and number of root primordia

Root primordia diameter was larger in lower logs than in upper logs irrespective of trunk age (Table 1). Difference in diameters between lowest and uppermost logs was larger in 7-yr-old trunks (1.7 mm) than in 5- (0.3 mm) or 2-yr-old (0.7 mm) trunks, indicating that the difference in diameter within a trunk increases when

Table 1. Diameter of root primordia (mm).

	Estimated yrs after trunk formation		
Log position[1]	7	5	2
Uppermost	1.8 ± 0.1 (9)	2.9 ± 0.1 (5)	2.9 ± 0.1 (4)
Middle	2.6 ± 0.1 (5)	2.9 ± 0.1 (3)	3.2 ± 0.1 (3)
Lowest	3.5 ± 0.1 (1)	3.2 ± 0.1 (1)	3.6 ± 0.1 (1)
Whole	2.7 ± 0.1	3.0 ± 0.0	3.3 ± 0.0

1 : Fallen trunks were cut into 90 cm long sections (log) from the base. The number of each log was counted from the base; then the log positions were determined.
Values are means±S.E.
Numerals in parentheses show numbers of log position counted from the base.

Table 2. Distribution density of root primordia (/100 cm^2).

	Estimated yrs after trunk formation		
Log position[1]	7	5	2
Uppermost	202.9 (9)	159.4 (5)	124.5 (4)
Middle	175.0 (5)	139.0 (3)	69.0 (3)
Lowest	108.2 (1)	85.1 (1)	56.9 (1)
Whole	162.0	127.8	84.5

1 : Fallen trunks were cut into 90 cm long sections (log) from the base. The number of each log was counted from the base; then log positions were determined.
Values are means.
Numerals in parentheses show number of log position counted from the base.

trunk length is so long in a later stage near the harvest time (about 10-yr-old after trunk formation) (Table 1).

The density of root primordia per unit surface trunk area was higher in upper logs than in lower logs irrespective of trunk age (Table 2). In lowest log areas, root primordia density was higher in 7-yr-old trunks (108.2), followed by 5-yr-old trunks (85.1), and 2-yr-old trunks (56.9) (Table 2). Average root primordia density was higher in uppermost, middle and lowest logs in 7-yr-old trunks (162.0), followed by 5-yr-old trunks (127.8), and 2-yr-old trunks (84.5), indicating that the density of root primordia positively correlated with trunk age (Table 2).

Discussion

1. External morphology of roots

Two types of roots with different thickness were distinguished in sago root systems: large roots (about 6-11 mm in diameter), whose primordia were formed just inside the epidermis in the stem, emerged from the trunk surface and grew downward into the soil. The running features of large roots were different among soil types: running mainly downward in mineral soils, while running downward in 0-30 cm soil layer and horizontally in below 30 cm soil layers in deep peat soils. On the other hand, small roots (about 4-6 mm in diameter), whose primordia were formed on large roots running horizontally or other small roots, grew not only downward and obliquely in both deep peat and mineral soils, but also to right above in deep peat soils.

Thus, one important feature of sago roots is that they are classified into large and small roots by their diameters and occurrence positions. Kasuya (1996) investigated root systems immediately surrounding sago palms and reported running of three types of roots: large roots (more than 5 mm in diameter) which had few branches, small roots (less than 2 mm in diameter) which had many branches, and intermediate ones. Detailed morphology of these three root types has not been clarified. However, the features of root systems in large and small root classes agree with our results. Further studies of deep soil layers are needed because Kasuya (1996) investigated only 0-40 cm soil layers and our experiments addressed only the 0-1 m soil layer. Still, it is very difficult to research into deep soil layers since the water table is high in most sago growing areas.

Another important feature of sago roots is their running right above the surface up to the air such that some roots are exposed in the air. Such aerial roots are also observed in mangroves, appearing to have the function of conducting air into the plant body (Esau, 1977; Komiyama, 1995).

2. Internal morphology of roots

Our anatomical observations revealed that both large and small roots had the same internal structures containing epidermis, exodermis, suberized sclerenchyma cells, cortex and stele, with only differences in their sizes or cell numbers. These structures have features similar to those of rice (Hoshikawa, 1989). Besides, both roots had characteristic development of schizogenous or lysigenous aerenchyma. Former studies have also shown that development of lysigenous aerenchyma was observed in wetland plants such as rice (*Oryza sativa* L.), barnyard millet (*Echinochloa utilis* Ohwi et Yabuno), common reed (*Phragmites australis* Cav.) and mat rush (*Juncus decipiens* Nakai) (Tatsumi, 1998) as well as in field crops such as maize (*Zea mays* L.) (Arikado, 1975), wheat (*Triticum aestivum* L.) (Dunn, 1921), and barley (*Hordeum vulgare* L.) (Bryant, 1934). The main function of lysigenous aerenchyma is thought to be conductance of air from roots to shoots because of remarkable development in wetland plants (Arikado, 1975). Sago roots we reported here also seem to have the function of conducting air by development of schizogenous or lysigenous aerenchyma, illustrated best by bubbling occurring from roots in submerged ground when someone walked on it.

3. Morphogenesis of roots

Root primordia in the sago palm, which have their own original meristem root tissues, are made just inside the epidermis in the stem. Roots that are members of root systems grow out from the trunk surface up to about 30 cm from the ground surface. However, formation features of root primordia and emergence along all through the trunk surface should be investigated to clarify their morphogenesis. In this study, we investigated morphology of root and/or root primordia along the trunk surfaces with several trunk ages.

Our study revealed that root primordia of large roots were formed all through the trunk surface, from the base to the top, successively. Nitta and Yamamoto (1998) mentioned that in gramineous crops the root primordia were formed only near the nodal portion in both elongated and non-elongated stems. In elongated rice stems, it was noted that roots emerged just only near the node, which was a very restricted portion of the stem (Nitta et al., 1998, 1999). In the sago palm, it is not clear whether the trunk portion corresponds to the node or internode in gramineous crops. However, if the trunk portions with leaf traces or attached portion of leaf sheath are regarded as nodes, and if the trunk portions between leaf traces or leaf sheath are regarded as internodes, root primordia are formed all through the trunk axis successively in both nodal and internodal portions. These features of root primordia formation in the sago palm are similar to those of unelongated stems of gramineous crops.

Diameters of root primordia are larger in lower logs irrespective of trunk age. Root primordia of the lower trunk differentiate and grow earlier than in the upper ones, hence the age of root primordia of the lower trunk is greater than that of the upper ones. Diameter of root primordia in the lowest logs shown in Table 1 were around 3.2 to 3.6 mm irrespective of trunk age, indicating that these values are almost the thickest ones of final growth. Moreover, since root primordia in the lowest logs even in 2-yr-old trunks seemed to finish their growth (Table 1), thickness of root primordia appeared to finish their thickening growth within 2 yrs after trunk formation.

High densities of root primordia measured in upper logs irrespective of trunk age (Table 2) may be related to the compensation for the small diameter.

4. Function of sago roots

As mentioned above, two distinct types of roots were distributed in each sago root system. One is the large root and the other is the small root. Large roots are formed just inside the epidermis in the stem and run vertically in the mineral soil and 0-30 cm soil layer of deep peat soil or horizontally below about 30 cm soil layer of deep peat soil. Large roots seems to be a suitable structure for air conduction and transport of nutrition and water.

On the other hand, small roots are formed on the large roots running horizontally or on other small roots growing not only downward and obliquely in both deep peat and mineral soils, but also right above in deep peat soils. Since the internal structure of this root is suitable for air exchange and this root body is exposed in the air, the function of this root seems mainly to be air transportation from the root to the shoot rather than transport of nutrition or water. Thus, the functions and roles of large and small roots seem to be different in each sago root system.

Also, root primordia were formed successively all through the trunk surface in our investigation. Root primordia formed on the trunk surface more than several meters from the ground surface, however, never elongated up to the soil and became members of the root system. Therefore, great attention is focused on the function and role of these higher root primordia. Our observations of root emergence from the higher trunk of lodged sago palms, from the higher node of lodged maize (*Zea mays* L.), sorghum (*Sorghum bicolor* Moench) and floating rice (*Oryza sativa* L.) suggest that, in sago palms during lodging, some roots would emerge from the higher trunk and may have active functions for propping up the shoot body and/or nutrition uptake.

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*In Japanese.

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***In Japanese with English abstract.