Chapter 12
Morphogenesis of Sago Palm

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Abstract Suckers are normally used for sago palm propagation. The stem of a transplanted sucker elongates in a horizontal direction on the ground, producing leaves in the first 4–5 years after transplanting (the rosette stage). During the rosette stage, transplanted suckers produce large numbers of daughter suckers which develop from lateral buds. The lateral bud of sago palm (sucker bud) differentiates on the opposite side of the axil. In the suckers for transplantation, detailed observation of the differentiation position and the development of the sucker bud showed that the sucker bud differentiates inside near the connate part of the leaf petiole. This is also the part that is gradually split as new leaves emerge and the stem enlarges. In the lower leaf position from rbL 6, which is the sixth leaf from the youngest leaf primordium, there were only one sucker bud and two sucker buds on leaf positions of 30.1% and 68.1%, respectively. Sago palm has reduplicate leaves; however, little has been reported on the leaf formation process of sago palm. The youngest visible leaf, a spear leaf, contains a number of folded leaflets and these open as the plant grows. Observation of the cross section of a spear leaf after trunk formation and the unemerged young leaves during rosette stage showed that the midribs of leaflet are on the adaxial side, and the edges of leaflet are on the abaxial side. When splitting occurs along the abaxial ribs, leaflets that are Λ-shaped in section form. These suggest that splitting would occur along the abaxial ribs in sago palm. An approximately 8-year observation of the stem length in the creeping part of transplanted suckers revealed that the creeping part length increased exponentially from transplantation to around 4 years, thereafter, and gradually increased slowly. As a result of growth analysis for creeping elongation of the sucker stem, the maximum elongation rate was estimated as 0.38 m per year at YAT 3.8.

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12.1 Introduction

Sago palm (*Metroxylon sagu* Rottb.), which accumulates a large amount of starch in its trunk, is a hapaxanthic palm which dies after flowering. Generally, the suckers emerging from the base of stem are used for propagation. The stem of transplanted sucker elongates in a horizontal direction on the ground, producing leaves in the first 4–5 years after transplanting. During this period, called the *rosette stage*, the size of the leaves and stem increases gradually (Fig. 12.1a–c). After the rosette stage, the stem elongates from a horizontal direction to the vertical direction, swelling up at the bottom part with leaves attached (trunk formation), and the trunk (stem) then elongates vertically (Fig. 12.1d, e). The trunk is harvested during the time from just before flower initiation to flowering because the amount of starch accumulated in the trunk decreases thereafter due to the development of the inflorescence and fruit. Although the period for harvest differs by cultivated regions, varieties, and rate of growth, sago palm takes over 10 years from transplantation to the first harvestable trunk. In recent years, sago palm has received much attention as a starch crop for use not only as food but also an industrial raw material; however, the morphogenesis of sago palm is still incompletely understood. This chapter describes recent research on the suckers, leaves, and stem in the morphogenesis of sago palm.

12.2 Suckers

Suckers are normally used for sago palm propagation (Sato et al. 1979). The suckers, cut from mature stems which are creeping horizontally, are grown as seedlings for about 6 months in a nursery and then transplanted into the field. During the rosette stage, transplanted suckers produce large numbers of daughter suckers which develop from lateral buds (Fig. 12.1b). In sago palm cultivation, thinning of daughter suckers in the clump is performed (sucker control) to regulate the density of the suckers. If all of daughter suckers grow well, the clump would become rampant with growth, and the suckers would have a negative influence on each other, resulting in reduction of starch productivity. Nabeya et al. (2013) reported that a farmer in Sarawak, Malaysia, not only has regulated the sucker density in the clump by pruning leaves of daughter suckers to suppress their growth but also has made observations of clumps consisting of suckers at different growing stages, the direction of the creeping growth, and the position of the trunk at harvest time. Yanagidate et al. (2009) suggested that proper cultivation techniques to maintain a suitable trunk density of different trunk lengths (ages) by appropriate sucker thinning should be established to achieve stable annual starch production per unit area, based on investigations in Southeast Sulawesi Province, Indonesia.

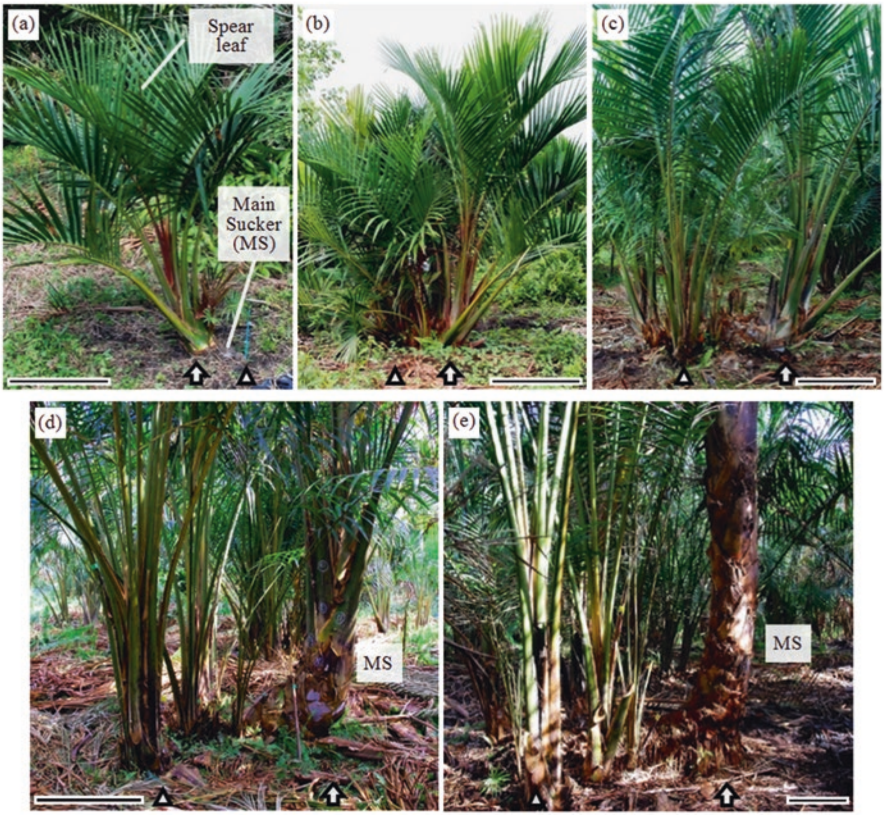

Fig. 12.1 A sago palm without spines. (**a**) 1 year after transplantation (YAT 1), (**b**) YAT 2.9, (**c**) YAT 4.8, (**d**) YAT 5.8, and (**e**) YAT 7.8 in Sarawak, Malaysia. The *triangle* shows the transplanting position. The *arrow* indicates the position of the estimated growth point. The stem length in the creeping part was defined as the horizontal distance from the growth point judged by the appearance to the transplanting position. Bar = 50 cm (**a**, **e**), 1 m (**b**–**d**) (From Nabeya et al. 2015d)

12.2.1 Differentiation of Lateral Sucker Buds

Although utilization and management of suckers are very important in sustainable sago palm cultivation, there are only a few reports about the presence and development of lateral buds from suckers. Goto et al. (1998) described how the lateral bud of sago palm (sucker bud) differentiates on the opposite side of the axil, unlike many plants. Fisher and Dransfield (1979) reported that the lateral bud of rattan palms *Daemonorops* spp. and *Korthalsia rigida* differentiated on the opposite side to the axil and named it a *leaf-opposed bud*.

Nabeya et al. (2015b) reported in detail the differentiation position and the development of the lateral bud of the sago palm sucker for transplantation. In sago palm, since the lower part of the petiole (leaf sheath) wraps around the stem, the part of

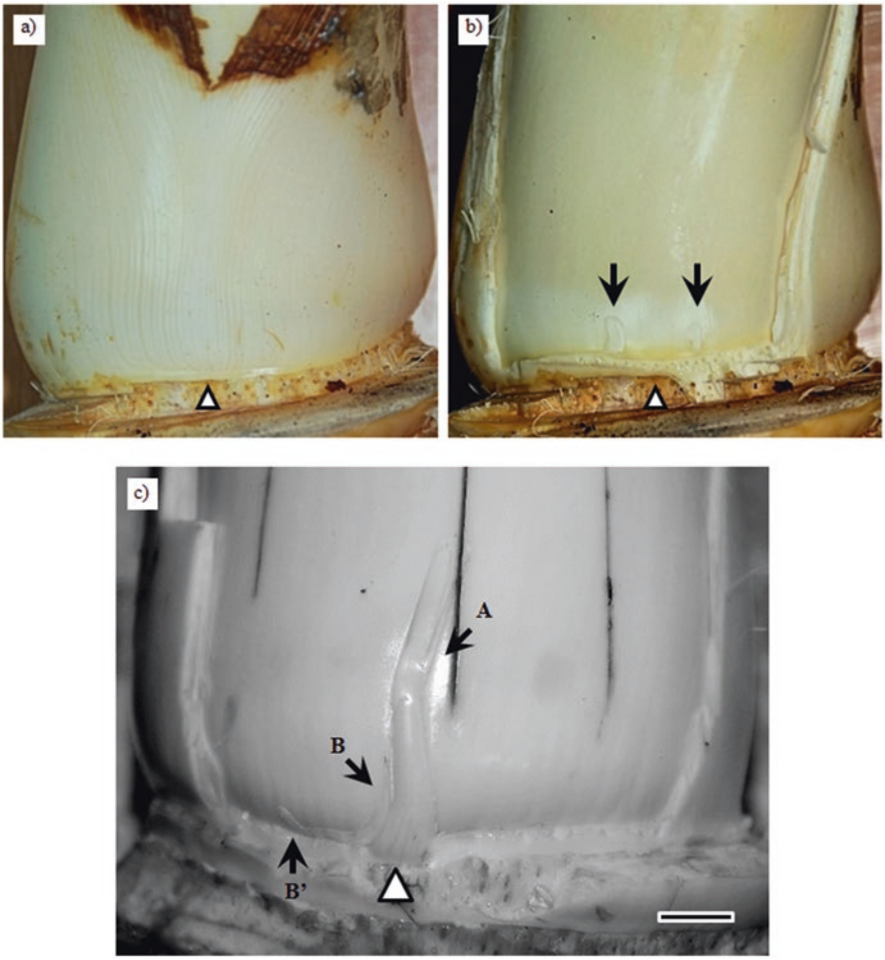

Fig. 12.2 Connate part of both edge of the leaf petiole. (**a**) The connate part of the leaf petiole. (**b**) Sucker removed connate part of the leaf petiole presented in (**a**). The *triangle* denotes the reference point. Two sucker buds differentiated inside of the connate part of the leaf petiole and near the reference point. (**c**) A sucker bud greatly developed. Sucker bud (*A*) differentiated at the reference point and developed greatly. Sucker bud (*B*) differentiated at the position B′ and elongated narrowly. The *triangle* denotes the reference point. Bar = 10 mm (From Nabeya et al. 2015b)

the petiole attaching to the stem appears to be a node-like ring after removal of the petiole (Fig. 12.2a). At the connate part of the leaf petiole, following the vascular bundle along both edges of the petiole to the base, the two bundles fuse into one near the base. The sucker bud differentiates near the reference point which is inside the connate part of the leaf petiole (Fig. 12.2b). This is also the part that is gradually split as new leaves emerge and the stem enlarges. To investigate the differentiation of the sucker bud, the youngest leaf primordium, in which the tip of the hoodlike leaf was beyond the tip of growth point, was assumed to be rbL 1 (relative basipetally Leaf 1) and sequentially rbL 2, rbL 3, and so on (Nabeya et al. 2015b). Sucker buds which differentiated inside of rbL *n*, outside of rbL *n-1*, were regarded as rbS *n*. As a result of investigations, the sign of differentiation of rbS 1 and rbS 2 was not visible, but the swelling of tissue of rbS 3 and rbS 4 was visible in 13.6% and 77.3% of investigated suckers, respectively. The initiation of sucker bud of rbS 5 was visible in all of the investigated suckers; the sucker bud was visible in almost all of leaf position after rbL 5. In the lower leaf positions from rbL 6, only one sucker bud differentiated in a leaf position 30.1%, and there were two sucker buds and three sucker buds on leaf positions of 68.1% and 1.8%, respectively. In *Plectocomia elongata*, the instance of multiple vegetative buds differentiated in a leaf position was reported by Fisher and Dransfield (1979). In *P. elongata*, vegetative buds appear, one to ten, as small swellings in a node, and become multiple branches. By contrast, in sago palm, a small swelling occurred and then differentiated into two sucker buds (Nabeya et al. 2015b). An instance of both sucker buds developing and appearing from a leaf position has not yet been observed in our investigations.

12.2.2 Development of Sucker Buds

It is not clear as to when and how sucker buds develop after differentiation and emerge from the leaf sheath. Nabeya et al. (2015b) reported that both the length and width of sucker buds from rbS 6 to rbS 13 increased exponentially in suckers for transplantation. In the lower leaf position from rbS 11, some sucker buds, greatly developed in length and width, were observed (Fig. 12.2c). 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 and 5.5 ± 2.0 mm on average, respectively. Some sucker buds that only increased in length but not in width were also observed from rbS 11 to rbS 13. Most of these sucker buds elongated in a meandering fashion like the one (B) shown in Fig. 12.2c.

A number of suckers emerge from the stem when it is elongating in a horizontal direction; however, few suckers emerge from the trunk, elongating in a vertical direction. Differentiation and development of sucker buds may be related to gravitational direction. Further studies are required to clarify the development and emergence of sucker buds.

12.3 Leaf

The leaf, which is the distinguishing character of the palm, has three components: a sheathing base (a leaf sheath), a petiole, and a blade (Dransfield et al. 2008; Tomlinson 1990). Palm leaf blades are fundamentally of two types: pinnate or palmate (Dransfield et al. 2008). The sago palm has large compound pinnate leaves which have many leaflets attached to an elongated rachis. The leaflets range in shape from linear lanceolate to narrow lanceolate. The leaf sheath is the extended base of the petiole, which wraps around the trunk and fuses on both ends (Fig. 12.2a). This fused state is observable from the leaf primordium stage, but no morphological boundaries between the petiole and leaf sheath are found on the adaxial or abaxial sides of the petiole (Goto and Nakamura 2004). The leaf sheath has two types: bearing spines on the abaxial surface of the petiole and spineless. The leaf sheath remains attached to the stem (trunk) after the leaf dies (Fig. 12.1c–e).

The youngest visible leaf, which has a pointed stick, forms and emerges along a groove running longitudinally in the petiole of the previous leaf and is called a spear leaf (Fig. 12.1a) (Jones 1995; Tomlinson 1990). A spear leaf contains a number of folded leaflets and these open as the plant grows. When a spear leaf opens, a cord-like tissue connects the tips of leaflets as if to trace the outline of the leaf and then falls away, or breaks up, leaving individual leaflets fully independent (Goto and Nakamura 2004). Sago palm reportedly has a phyllotaxis of 4/13 and a divergence angle of 110.77° (Jong 1991). Sago palm has a dextrorse or a sinistrorse phyllotaxis, depending on the plant.

12.3.1 Leaf Characteristics in the Rosette Stage

Sago palm leaf size increases as the plant grows during the rosette stage (Fig. 12.1). Figure 12.3 exemplifies a sago palm 3.3 years after transplantation and leaf characteristics in the rosette stage (Nakamura et al. 2009). This plant has 16 leaves including a spear leaf and one dead leaf. The spear leaf provides a convenient marker for growth research. The position of the spear leaf, the emerging youngest leaf, is labeled as ebL 1, and the leaves thereafter are labeled basipetally as ebL 2, ebL3, and so on (Fig. 12.3a). Concerning the position of unemerged leaf, the leaf position immediately above (inside) ebL 1 is uL 1, and the positions further up (inside) are labeled acropetally uL 2, uL3, and so on. The leaf length ranged from 2.96 (ebL16) m to 5.37 m (ebL3) (Fig. 12.3b). The leaf length of ebL 2 was shorter than that of ebL3 because the petiole of ebL 2 was elongating and did not reach its final length. The number of leaflets per leaf ranged from 62 (ebL16) to 86 (ebL2). In regard to unexpanded leaves, the leaf blade of uL 2 started to elongate rapidly (Fig. 12.3c) and would reach its final length by the time the position of the leaf becomes ebL2. Although the leaf petiole of ebL 1 could not be measured due to the invisible position at which the lowest leaflet attached, the petiole of ebL 1 would start to elongate rapidly and reach its final length by the leaf position of ebL 3. These results suggested that emergence of a spear leaf (ebL 1) should be attributed to the elongation of the leaf blade and petiole during the rosette stage. After trunk formation, the leaf blade elongated to its final length during the period, from the leaf position of uL 3 to that of ebL 1, and the leaf petiole elongates rapidly at the position of ebL 1 (Nakamura et al. 2015).

12.3.2 Development of Leaflets

The Arecaceae family includes palms with induplicate leaves such as in the date palm and with reduplicate leaves such as in the coconut palm. In leaves with induplicate segmentation, the leaflets are V-shaped in transverse section with the single-fold abaxial; in leaves with reduplicate segmentation, they are Λ-shaped with the single-fold adaxial (Tomlinson 1990). Sago palm has reduplicate leaves (Goto and Nakamura 2004); however, little has been reported on the leaf formation process of sago palm.

Figure 12.4 represents the cross section of the lower part of a spear leaf after trunk formation and unemerged young leaves of the sago palm shown in Fig. 12.3. The midribs of leaflet are on the adaxial side and the edges of leaflet are on the abaxial side (Fig. 12.4a, b). When splitting occurs along the abaxial ribs, leaflets that are Λ-shaped in section form. These suggest that splitting would occur along the abaxial ribs in sago palm. A number of pleats with alternating ridges and furrows are observed in uL2 to uL 4 (Fig. 12.4c, d). The midrib of leaflet might be

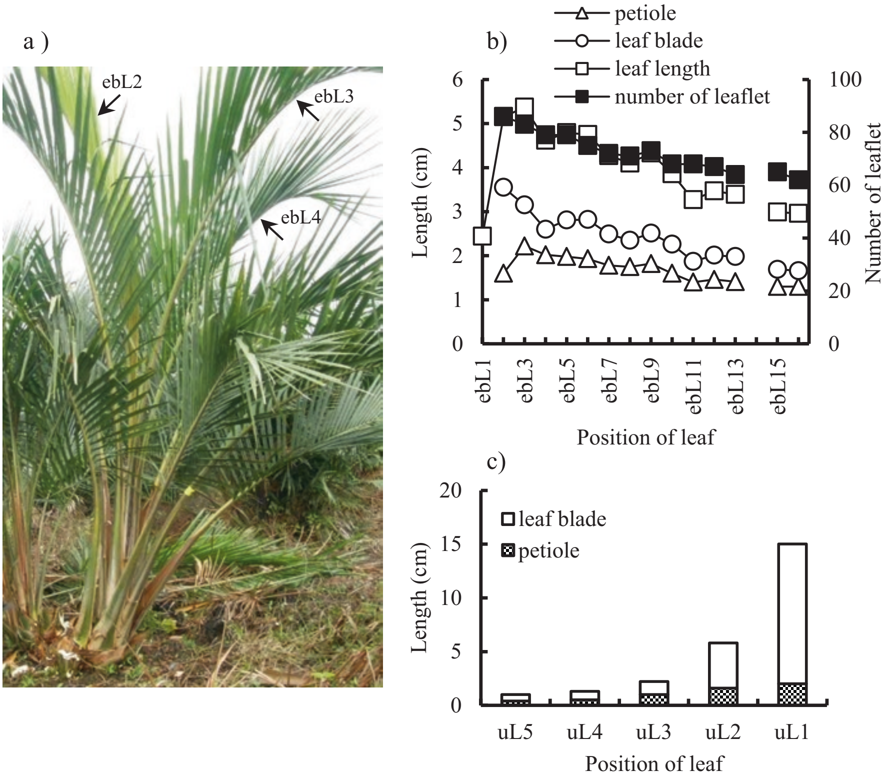

Fig. 12.3 (**a**) A sago palm with no spines 3.3 years after transplantation, (**b**) characteristics of expanded leaves, and (**c**) unexpanded leaves (From Nakamura et al. 2009)

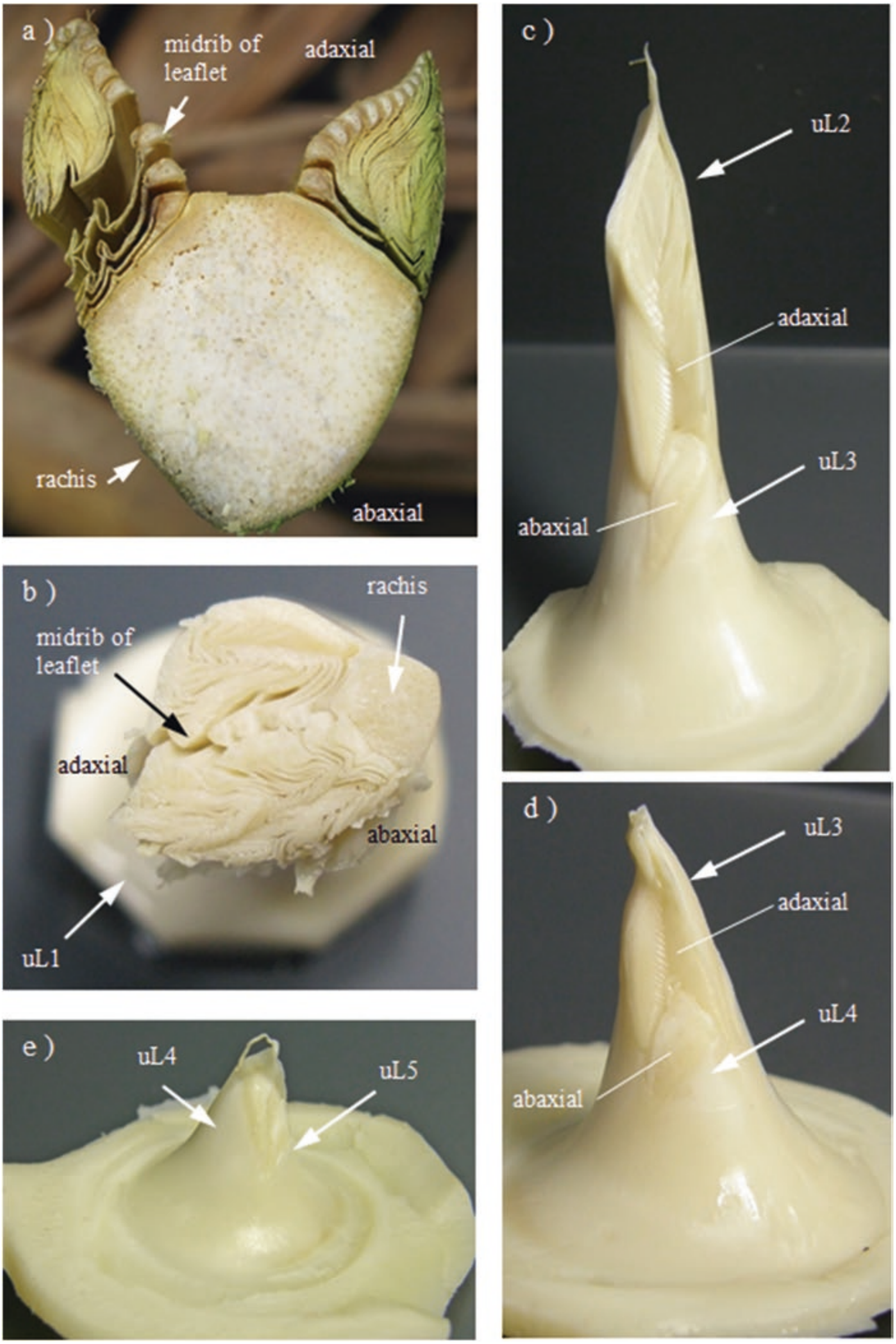

Fig. 12.4 Cross section of the lower part of a spear leaf of plant after trunk formation (**a**) uL1, (**b**) young leaves from uL2 to uL5, and (**c**–**e**) of the sago palm at rosette stage (shown in Fig. 12.3a)

formed in the ridges on the adaxial side. Among the palms with pinnate compound leaves, Dengler et al. (1982) reported on the morphogenetic process in the early stage of leaflet formation in *Chrysalidocarpus lutescens* (=*Dypsis lutescens*). A similar morphogenetic process is expected to occur in sago palm. Further studies are needed for confirmation.

12.3.3 The Number of Unemerged Leaves

An understanding of the number of unemerged leaves is useful for growth analysis of sago palm. Flach and Schuiling (1989) reported that the number of unemerged leaves was 24, which was the same as the number of green leaves in the crown, in the early stage of trunk formation. Nakamura et al. (2015) reported that the number of unemerged leaves of a tree with 15 emerged leaves 4 years after trunk formation was 18 and that of a tree with 17 emerged leaves 8 years after trunk formation was 19. Nabeya et al. (2015a) found that there was a close relationship between the diameter of the attached part of a spear leaf and the number of unemerged leaves of suckers of proper size for transplantation. This result suggests that the number of unemerged leaves inside a spear leaf increases with an increase of the diameter of the attached part of a spear leaf. The diameter of the attached part of a spear leaf may be an indicator of the unemerged leaves; however, further studies are needed on the details of leaf formation.

12.4 Stem

12.4.1 Stem Formation During the Rosette Stage

The stem of a transplanted sucker creeps in a straight line on the ground. The creeping direction remains the same later when the sucker is transplanted. According to observations of the longitudinal section of stem, morphological characteristics such as nodes are not recognized clearly (Nabeya et al. 2015d). Representing the nodal planes, which were estimated as the positions of attached leaves, the nodal planes coincided with an angle of about 40° to the ground (Nabeya et al. 2015d). In other words, during the rosette stage, sago palm stems are formed by the horizontal line of thin disciform internodes with an angle of about 40° to the ground.

12.4.2 Creeping Elongation of Sucker Stems

It is important to know the creeping elongation rate of the stem and the distance from the transplanted position or the attached position to the mother stem to the trunk stand position in order to manage the density of a trunk stand properly. A few studies have focused on this. According to an approximately 8-year observation of the stem length in the creeping part of transplanted suckers by Nabeya et al. (2015c), the creeping part length increased exponentially from transplantation to around 4 years thereafter, and gradually increased slowly, suggesting that the growth curve was sigmoidal. The length from the transplanted position to the trunk stand position ranged from 1.62 to 2.05 m (avg. 1.81 m) 7.8 years after transplantation (YAT 7.8) (Fig. 12.1). As a result of growth analysis for creeping elongation of the sucker stem, the maximum elongation rate was estimated as 0.38 m per year at YAT 3.8.

Nabeya et al. (2015c) also observed the growth of the derivative suckers such as primary suckers from the main sucker and secondary suckers from the primary suckers, finding that the creeping part length from the attached position to main stem to the trunk stand position was about 1.7 m away in the primary suckers which formed trunks. However, the elongation rate of the primary suckers which were in the rosette stage ranged from 0.11 to 0.14 m per year, and the increasing rate of leaf numbers of them was slower than the main suckers. As the main sucker forms a trunk and elongates vertically, the position of the crown is higher, implying that the amount of sunlight that the derivative suckers receives decreases. The low elongation rate and the low increasing rate of leaf numbers of these suckers could be attributed to the low sunlight due to crown shading of main suckers which formed a trunk. Further studies on the growth of not only main suckers but also derivative suckers are needed to establish the sustainable cultivation of sago palm with high starch productivity.

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