LEAF DEVELOPMENT IN PALMS

D. PADMANABHAN

Department of Botany, Presidency College, Madras

THE plicate lamina of the palm leaf has been the subject of much interest since its ontogeny has been variously interpreted for the last hundred years and we are still far from a solution of the problem. Yampolsky (1922) has already summarized the early literature. Among the more recent works two opposed views have been advocated (Eames, 1953 ; Periasamy, 1962). According to Eames (1953) the plications develop initially as alternating ridges (produced by differential growth) and furrows on both surfaces of the laminal primordium. The ridges of one side oppose the furrows on the other. Subsequently, needle-shaped schizogenous splits originate in the interior of the lamina and extend towards the furrows on the opposite surface. Thus, the lamina is split up into folds (plications). No splitting occurs in the marginal portions (the 'reins') which bind the leaflets. According to Periasamy (1962), the plications originate due to the operation of an unusual type of meristematic activity in the laminal primordium and schizogenous splits do not occur. He interprets that meristematic activity is transferred from the marginal to the submarginal portions and the laminal meristem is resolved into as many intercalary strips as there are plications. My own investigations confirm the occurrence of schizogenous splits in three species of palms—*Borassus flabellifer, Cocos nucifera* and *Phoenix sylvestris.*

The lamina is initiated by the marginal meristematic activity of the leaf primordium. This activity lasts only for a short period. The midrib (which becomes the rachis of the mature leaf) undergoes thickening due to the organization and activity of the adaxial and abaxial meristems (Padmanabhan, 1963). In particular, the widening of the insertion plane of the lamina occurs with the result that the laminal primordium also increases in thickness. At this stage the plications are initiated in the laminal primordium in a basipetal manner, except at its margins which form unplicate strips of tissue (the 'reins' of Eames, 1953). It has been shown (Padmanabhan, 1963) that the plications originate due to the appearance of schizogenous splits on both surfaces of the laminal primordium (Figs. 1-3) at right angles to the midrib (rachis). The lines of splitting on the adaxial surface alternate with those on
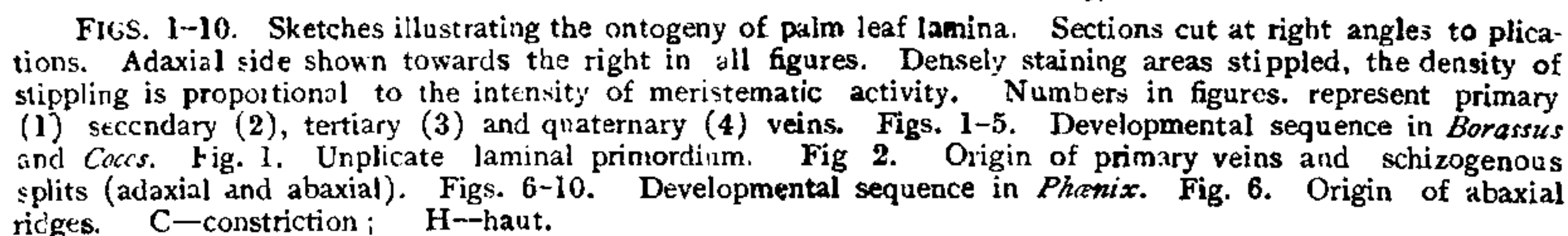
the abaxial surface. The splits start right from the surface and progress inwards and stop short of the opposite surface (Figs. 1-4). The origin and deepening of the splits in the superficial layers results in the initiation of what have been called as 'ridges' and 'furrows' (Eames, 1953 ; Periasamy, 1962). As the splits on the adaxial and abaxial surfaces deepen a series of plications results (Fig. 4).

The description given above applies to *Borassus* and *Cocos. Phoenix* (Figs. 6-10) differs from *Borassus* and *Cocos* in that the adaxial splits do not involve the surface layers and occur deeper in the lamina (Fig. 7) thereby leaving a continuous sheet of laminal tissue on the adaxial side (Fig. 8) (*see* Padmanabhan, 1963 for details). This sheet which incorporates the primary veins of the lamina (Figs. 9, 10) has been interpreted by some authors (Goebel, Eichler, and Deinega ; *see* Yampolsky, 1922) as a secondary product of the lamina—the 'Haut' or the 'Coiffe' (Fig. 10, H). As already pointed out by Yampolsky (1922) the haut is, in fact, a part of the lamina which is cast off when the leaflets unfold.

The plicate lamina further undergoes mechanical tearings (along the abaxial ridges, Fig. 5) which reach the rachis (*Cocos,* compound leaf with reduplicate leaflets) or stop midway between the margin and the rachis (*Borassus,* simple leaf). The extent of tearing varies among the species of the Palmæ which exhibit diverse patterns of leaves. The rachis in *Cocos* elongates considerably thereby separating the leaflets. No marked elongation of the rachis and the consequent separation of the lamina into leaflets occurs in *Borassus.* In *Phoenix,* the leaflets are 'pinched off' from the continuous strip of adaxial tissue (haut) by the close approximation of the adaxial and abaxial splits near the haut (constriction, Fig. 9, C). The rachis elongates and separates the induplicate leaflets and the 'haut' breaks-off when the leaf unfolds.

The lamina of the mature palm leaf shows a large number of parallel veins. There is a gradation in the size of veins correlated with the time of their origin. Commonly, the veins originate in succession, the larger ones differentiating earlier than the progressively smaller ones. Thus, among the early-formed veins four

categories may be distinguished tentatively as follows : the primaries, the secondaries (differentiating in between the primaries), the tertiaries (differentiating in between the secondaries and primaries) and the quaternaries. The veins differentiate in successive groups even while plications are being initiated (Figs. 2-5 ; 6-10). The primary veins occupy the adaxial ridges (Fig. 2) while the secondaries appear nearer to the abaxial ridges (Fig. 4). The tertiaries and quaternaries differentiate subsequent to the primary and secondary veins (Fig. 5). The primaries and secondaries anastomose in the marginal unplicate strip (the 'reins') forming a marginal vein.

(1922). The cells of the lamina become progressively vacuolate from the *original surface* inwards (Figs. 1-4 ; 6-7). The surfaces of the leaflets are actually formed by the cells which originally occupy the interior of the unplicate lamina. This phenomenon which is peculiar to palms has been described by Eames (1953) but refuted by Periasamy (1962).

The 'haut' or 'coiffe' of *Phœnix* has been the subject of much discussion (*see* Yampolsky, 1922). One group of workers considered the 'haut' to be a product of the lamina mostly formed by the approximation of epidermal hairs (*see* Venkataanarayana, 1957). Yampolsky (1922) has already established with overwhelming

FIGS. 1-10. Sketches illustrating the ontogeny of palm leaf lamina. Sections cut at right angles to plications. Adaxial side shown towards the right in all figures. Densely staining areas stippled, the density of stippling is propoitional to the intensity of meristematic activity. Numbers in figures. represent primary (1) seccndary (2), tertiary (3) and quaternary (4) veins. Figs. 1-5. Developmental sequence in *Borassus* and *Cocos*. Fig. 1. Unplicate laminal primordium. Fig 2. Origin of primary veins and schizogenous splits (adaxial and abaxial). Figs. 6-10. Developmental sequence in *Phœnix*. Fig. 6. Origin of abaxial ridges. C—constriction ; H—haut.

Histologically, the unplicate laminal primordium exhibits little internal differentiation excepting the delimitation of protoderm enclosing the inner mass of cells. Following the schizogenous splitting, the inner cells get exposed and a new protoderm is organized quickly as already recorded by Yampolsky

evidence from developmental studies that the 'haut' is a portion of the laminal tissue which is cast off when the leaf unfolds. The present investigation confirms this. The 'haut' in *Phœnix* is seen as a white sheet of parenchymatous tissue enclosing well-developed vascular tissues (the primary adaxial bundles, Fig. 10, H).

Among the palm species studied, two major categories seem to exist—species with leaves developing 'haut' (*e.g., Phœnix, Elœis,* etc.) and those without 'haut' (*e.g., Borassus, Cocos,* etc.).

The interpretation of the palm leaf—whether it is simple or compound—has been an interesting subject. Eames (1953) advanced the view that the palm leaf is simple in nature and the mechanism of leaflet formation is quite different from that in the compound leaf of dicotyledons. In the palm leaf, the leaflets are cut out of the lamina the margin of which is left unaffected holding the leaflets together until unfolding. The leaflets of palms do not have separate

initials nor do they exhibit apical or marginal growth typical of dicotyledonous leaves. The very existence of an exceptional type of development in palm leaves has been the cause of confusion in the literature.

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INDUCED SPHAEROCOCCOID MUTATIONS IN *TRITICUM AESTIVUM* AND THEIR PHYLOGENETIC AND BREEDING SIGNIFICANCE

M. S. SWAMINATHAN, D. JAGATHESAN AND V. L. CHOPRA
Division of Botany, Indian Agricultural Research Institute, New Delhi

THE dwarf Indian wheats with dense ears and spherical grains, described by Howard and Howard[1] as varieties of *Triticum compactum* Host., were assigned specific status by Percival[2] and named *T. sphœrococcum. T. sphœrococcum* differs strikingly from the other hexaploid ($2n = 42$) *Triticum* species in its rigid, erect and abruptly tapering leaves, small dense ears with inflated glumes and hemispherical grains. Its grains have been found in the excavations at Mohenja Daro in Sind.[3] In crosses between *T. œstivum* and *T. sphœrococcum,* the whole constellation of characters peculiar to the latter tends to be inherited as one recessive gene and hence Ellerton[4] postulated that *T. sphœrococcum* probably arose through the deletion of a chromosome segment in *T. œstivum.* Sears[5] showed that the *sphœrococcum* gene *S* is located on chromosome 3 D (XVI). There has been considerable interest among wheat breeders in transferring the spherical grain character of *T. sphœrococcum* to the cultivated bread wheats since a round grain is ideal from the milling point of view.[6] Attempts in this direction have however not been successful.[7] The scope for isolating either spontaneous or induced mutants in *T. œstivum* possessing *sphœrococcoid* grains is hence worth exploring.

In the course of our studies on the frequency and spectrum of mutations occurring in the progenies of several varieties of *T. œstivum* sub-

jected to treatment with different physical and chemical mutagens, we have isolated two different types of *sphœrococcoid* mutants. A mutant having erect and rigid leaves. shorter stature and ears as compared to the control and inflated glumes and hemispherical grains was found in the M_2 generation of the variety N.P. 799 treated with UV (1 hour) and $2 \cdot 5 \mu c$. per seed of S^{35} (Figs. 1 and 2). This mutant is true breeding and possesses the rust resistance and other morphological traits of the parent strain. In crosses between the parent variety and the mutant, a single recessive factor was found to control the mutant phenotype. No segregation for the *sphœrococcoid* complex of characters occurred in the F_2 progenies of reciprocal crosses between the mutant and *T. sphœrococcum,* thereby suggesting that this mutant has the same *S* gene as in *T. sphœrococcum.*

Another type of *sphœrococcoid* mutation giving rise to phenotypic characters resembling closely that of the mutant described recently by Schmidt and Johnson[8] occurred in six different varieties treated with different concentrations of ethyl methane sulphonate (EMS). The earliest to be recorded was in the M_2 progeny of the strain H. 389 treated with 300 p.p.m. of EMS. This mutant had stiff and erect flag leaves with a cup-like ending, long and lax ears, hemispherical glumes and round grains.