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Minireview

# The Role of Meristematic Activities in the Formation of Leaf Blades

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**Our understanding of the molecular mechanisms responsible for the maintenance and development of shoot apical meristems has been enhanced as a result of recent studies of mutants of the model plant *Arabidopsis thaliana* (L.) Heynh. Leaf primordia also have their own meristematic regions and meristematic activity is maintained in part of the leaf blade, in some case, even after maturation. Transgenic plants have been generated that have proved to be useful tools in the analysis of the behavior of meristematic regions in leaf blades of *A. thaliana*. This review, based on our present understanding of molecular mechanisms for the maintenance and development of shoot apical meristems in *A. thaliana*, summarizes the variations in patterns and functions of meristematic regions in leaf blades focusing, in particular, on the case of indeterminate leaves.**

**Key words: *Arabidopsis thaliana* — Indeterminate leaf — Leaf morphogenesis — Meristem — Shoot apical meristem**

In angiosperms, in particular, in dicots, the leaf is the most diversified, key organ. Studies of leaf morphogenesis have reached in a turning point as a result of the successful application of the techniques of developmental and molecular genetics and exploitation of model plants, such as *Arabidopsis thaliana* (L.) Heynh. Mechanisms responsible for developmental phenomena, such as the establishment of proximo-distal, dorsiventral (dorsoventral), and right/left polarities; formation of the leaf blade; and formation of dissected and/or segmented leaves, have become 'hot topics' (*e.g.*, Hareven *et al.* 1996, Bohmert *et al.* 1998, Kim *et al.* 1998, Waites *et al.* 1998, Sawa *et al.* 1999, Siegfried *et al.* 1999). Current interest in this field is reflected by the fact that many reviews of leaf morphogenesis are now available (*e.g.*, Tsukaya 1995, 1998, Sinha 1997, Goliber *et al.* 1999, Dengler 1999, van Volkenburgh 1999).

Molecular genetic aspects of the maintenance or development of the shoot apical meristem (SAM), from which leaf primordia are formed, have been clarified to some extent, through studies of mutants of *Arabidopsis thaliana* (*e.g.*, Clark and Schifelbein 1997, Fetcher *et al.* 1998, Meyer *et al.* 1998, Moussian *et al.* 1998, Lenhard and Laux 1999, Trotochaud *et al.* 1999). Since the formation of all leaves, with the exception of cotyledons depends on the activity of the SAM, an understanding of the regulation of SAM activity should help us to understand the mechanisms that regulate the initiation of leaf primordia. In this review, we shall focus on meristematic activity in the leaf blade and discuss the importance of an understanding of this activity in our efforts to understand not only leaf morphogenesis but also plant morphogenesis. Other aspects of leaf morphogenesis are discussed in the review papers cited above. Some species generate epiphyllous buds (for review see Dickinson 1978), but we shall omit them from our present discussion since they form shoots rather than leaf blades. We note only, in passing, that such adventitious buds are mostly dependent on the residual cell-proliferative activity in the leaf blade although, in some cases, they appear to be a result of the dedifferentiation of established tissue (see, for example, Okada *et al.* 1999).

*Recent progress in the understanding of the SAM*

Recent molecular genetic and mutational analysis has revealed some important aspects of the mechanisms that regulate the maintenance and development of the SAM (*e.g.*, Clark and Schifelbein 1997, Fetcher *et al.* 1998, Moussian *et al.* 1998, Lenhard and Laux 1999, Trotochaud *et al.* 1999). In *Arabidopsis thaliana*, genes such as *WUS, CLV1, CLV2, CLV3, KAPP,* and *STM* determine whether SAM cells are to remain as stem cells or are to proceed along the pathway for organ formation (Fig. 1). It has been proposed, in particular, that *WUS* and *STM* are critical for the maintenance of stem cells in SAM (Barton and Poethig 1993, Laux *et al.* 1996, Long *et al.* 1996, Schoof *et al.* 2000). By contrast, meristematic cells escape the fate of stem cells by suppressing the functions of WUS, and these cells are located in the peripheral zone of the SAM. It has been proposed that these cells have acquired the capacity to differentiate into organs (Fig. 1). Thus, for example, in *Zea mays*, if the *KNOTTED1* (*KN1*) gene (Vollbrecht *et al.* 1991) is no longer ceased to express in cells that have acquired the capacity to differentiate into organs, the cells become subject to the program for differentiation into lateral organs, such as a single-leaf-type leaf (Smith and Hake 1992, 1994, Jackson *et al.* 1994). Overexpressor of the *KN1* gene or of an ortholog of the *KN1* gene (class I *KNOX* genes), such as *OSH1* of rice or *KNAT1* of *Arabidopsis*, ectopic expression of meristematic activity

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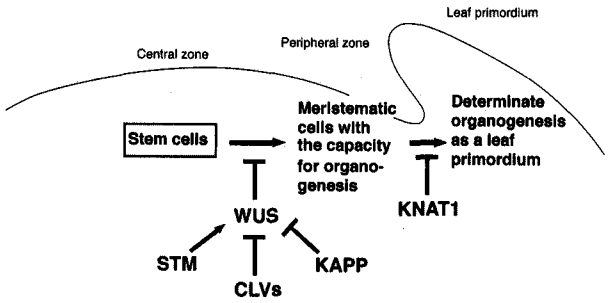



Fig. 1. A simplified model of the genetic regulation of SAM activity. *STM, WUS, CLVs, KAPP* and *KNAT1* are genes whose products function in the SAM of *Arabidopsis thaliana*. See text for details.

occurred in leaf blades (Matsuoka *et al.* 1993, Chuck *et al.* 1996, Williams-Carrier *et al.* 1997). Since the occurrence of adventitious shoots in plants that overexpress the class I *KNOX* gene has only been examined in heterogeneous transgenic systems, the essential aspects of the phenotypes of overexpressors are probably rather moderate. Prolonged proliferation of leaf cells in the lamina is likely to be the true phenotype, as observed in the case of homogeneous overexpressors of the class I *KNOX* in maize, rice and *A. thaliana* (Smith and Hake 1992, Matsuoka *et al.* 1993, Lincoln *et al.* 1994).

The class I *KNOX* genes are also related to mechanisms for the formation of some segmented leaves, which is dependent on the prolonged proliferation of leaf cells in the lamina. Primordia of the segmented leaves of tomato continue to express the tomato homolog of the *KN1* gene (Hareven *et al.* 1996). This phenomenon suggests that the segmented morphology of tomato leaves is the result of prolonged meristematic activity in the leaf blade (Hareven *et al.* 1996, Sinha 1997). We shall bear in mind this simplified explanation of the regulatory mechanisms of the SAM as we consider the meristematic activity in leaf blades.

*The marginal meristem*

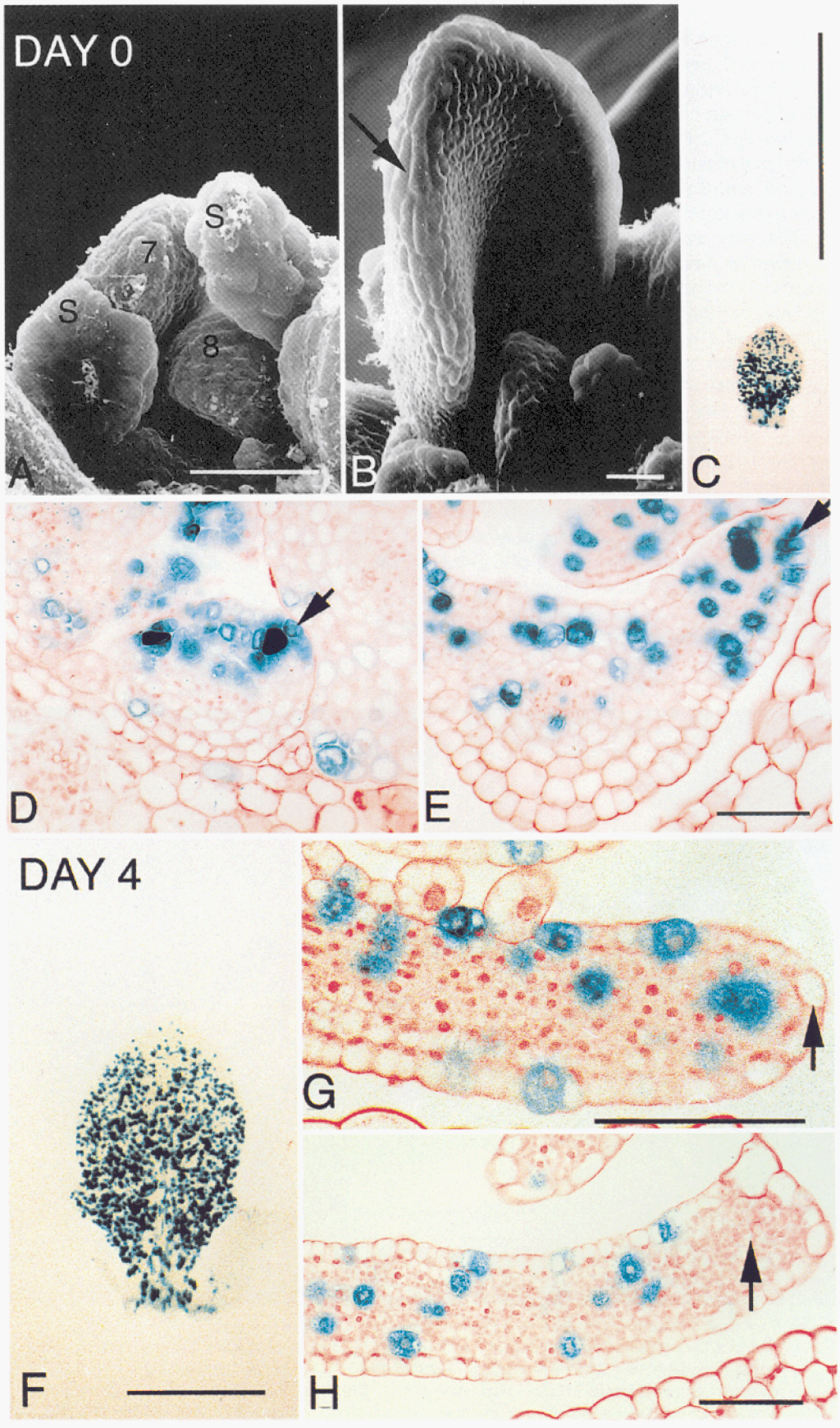
It was believed initially that the establishment of the leaf blade was the result of the activities of marginal meristems (Avery 1933, Hara 1957, 1959). However, some researchers, such as Cusset (1986), questioned the importance of the marginal meristem in the morphogenesis of leaves. Recently, mutants with defects in the establishment of dorsiventrality of leaf blades have been isolated from several species of model plants. All mutants with defects in the dorsiventrality of leaves lack a flat leaf blade, suggesting that the two-dimensional growth of leaves depends on dorsiventrality (for review see Tsukaya 1998). Genes responsible for such mutations have been identified (Bohmert *et al.* 1998, Waites *et al.* 1998, Sawa *et al.* 1999, Siegfried *et al.* 1999). Expression of these genes also exhibits dorsiventrality (*e.g.*, members of the *YABBY/FIL* gene family are expressed only in the adaxial regions of lateral organ [Sawa *et al.* 1999, Siegfried *et al.* 1999]). Specific expression of a gene in the marginal region of the leaf blade exclusively would seem to suggest that the gene might be involved in establishment of the so-called marginal meristem. However, such specific expression has not been reported to this author's knowledge.

Recently Donnelly *et al.* (1999) examined patterns of cell cycling in leaves of *Arabidopsis thaliana* using a marker gene for $\beta$-glucuronidase (GUS) that was driven by the promoter of a gene from *Arabidopsis* for cyclin1 (*cyc1At*) that is expressed at the G2/M phase of the cell cycle. Their analysis showed that the marginal meristem was quite active during the earliest phase of development of leaf primordia, while establishment of tissue layers and expansion of regions of the leaf blade were not dependent on the meristematic activity that was restricted to a particular zone. The marginal meristem ceased to be active during the early stage of development of leaf primordia (Fig. 2). Proliferative cells in the primordia of leaf blades are distributed rather diffusely at the later stages of development. Moreover, Donnelly *et al.* (1999) showed that leaf morphogenesis depended on tissue-specific regulation of the cell cycle. Thus, genetic regulation of such tissue-layer-specific control of the cell cycle remains to be characterized, in spite of the recent accumulation of considerable information about molecular mechanisms of layer-specific control of meristematic activity in the SAM.

*Meristematic activity in the apex of a leaf that supports Meliaceae-type indeterminate leaves*

Let us now examine the various patterns of distribution of meristematic regions in leaf blades. The patterns of meristematic regions in leaf primordia are of several types (Fig. 3). Pinnate, compound leaves appear to be formed by insertion of pinnae in a basipetal manner (Rutishauser and Sattler 1997; Fig. 3, lower row, center). This type of leaf morphogenesis is fundamentally the same as that of a single-leaf-type (Fig. 3, upper row, center) in which meristematic

Fig. 2. Localization of cells at the G2/M stage of the cell cycle in developing leaves of *Arabidopsis thaliana*. Cells at the G2/M phase were stained blue in panels C through H, by histochemical detection of the G2/M-phase-specific expression of *cyc1At::GUS* fusion gene. Arrows indicate the margins of leaf primordia. The upper panels (A through E) show primordia of the eighth foliage leaf on "DAY 0" (just after appearance of the primordia) and the lower panels (F through H) show leaf primordia on "DAY4" (four days after the appearance of the primordia). (A and B), Scanning electron micrographs of primordia of the eighth foliage leaf primordium. In addition to the eighth foliage leaf primordium (8), also the seventh foliage leaf primordium (7) and stipules (S) are shown in panel (A). (C), Cleared leaf of 250 $\mu$m in length. (D), Cross section of the eighth leaf primordia when it was 50 $\mu$m in length at the same stage as that shown in (A). Note the presence of a so-called marginal meristem at the margin of leaf primordia. (E), Cross section of leaf primordium when it was 160 $\mu$m long. Note the dispersed distribution of cells in the G2/M phase. (F), Cleared leaf of 1.2 mm in length. (G and H), Cross sections of leaf primordia of 1.5 mm in length. (G) Section taken from a region 0.38 mm above the leaf base. (H) Section taken 0.75 mm above the base. Note the absence of a so-called marginal meristem in the leaf primordia. Bars, 0.5 mm in (C and F); 50 $\mu$m in all other panels. Modified from Donnelly *et al.* (1999).


DAY 0
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activity remains at the base of the leaf blade. The restriction of the meristematic zone to the base of leaf blade, in particular in members of Gramineae, is an extreme case of localization of the meristematic region in a leaf blade.

Some primordia of pinnate compound leaves have meristematic activity at their tips, which is organized for acropetal differentiation of the primordia of leaflets (Sattler and Rutishauser 1992, Lacroix and Sattler 1994; Fig. 3 upper row, right). In such cases, meristematic activity seems to remain at the leaf apex or just below the terminal leaflet. Indeterminate compound leaves of members of the genera *Chisocheton* and *Guarea*, in the family Meliaceae, are fundamentally of the same type, but these indeterminate leaves can develop indeterminately as a result of the activity of the leaf apical meristem, which can function very similarly to an authentic SAM (Fisher 1992, Fisher and Rutishauser 1990, Steingraeber and Fisher 1986: Fig. 4). The leaf tip continues to differentiate primordia of leaflets (pinnae) eternally and autonomously (Fisher 1992) just as the SAM continues to differentiate leaf primordia, and some species in the genus *Chisocheton* can even differentiate inflorescences on the leaf axis (Fisher and Rutishauser 1990, Mabberley *et al.* 1995). The anatomical structure of leaf tip mimics that of a SAM, with the exception that former exhibits dorsiventrality (Fig. 4B). The leaf apical meristem also has a tunica-corpus-like structure (Fig. 4B). Thus, the leaf apical meristem might maintain stem cells just as the authentic SAM maintains such cells (Fig. 3; the Meliaceae-type indeterminate leaf; bottom row, right).

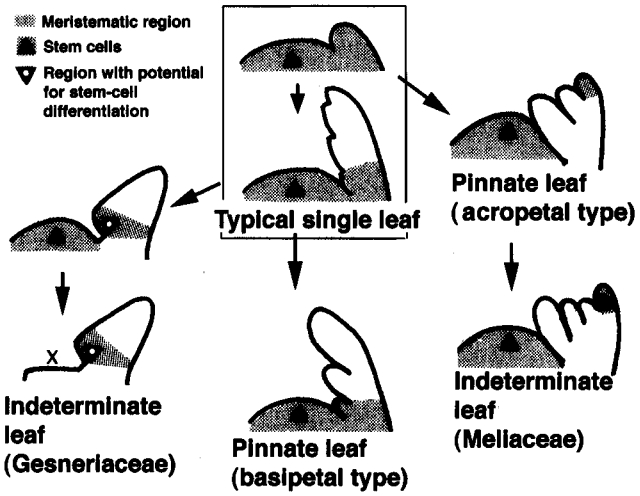



Fig. 3. Models showing the localization of meristematic tissues and stem cells in leaf primordia and SAMs. See text for details.

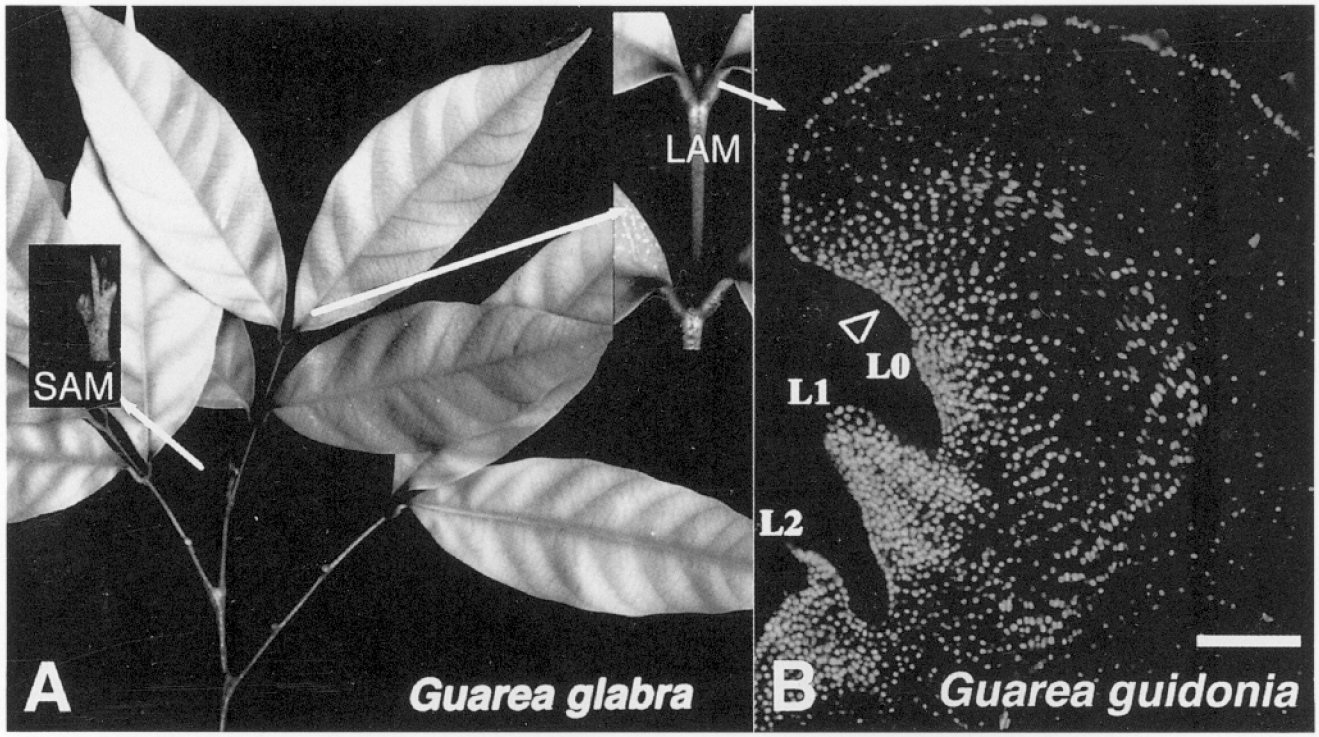
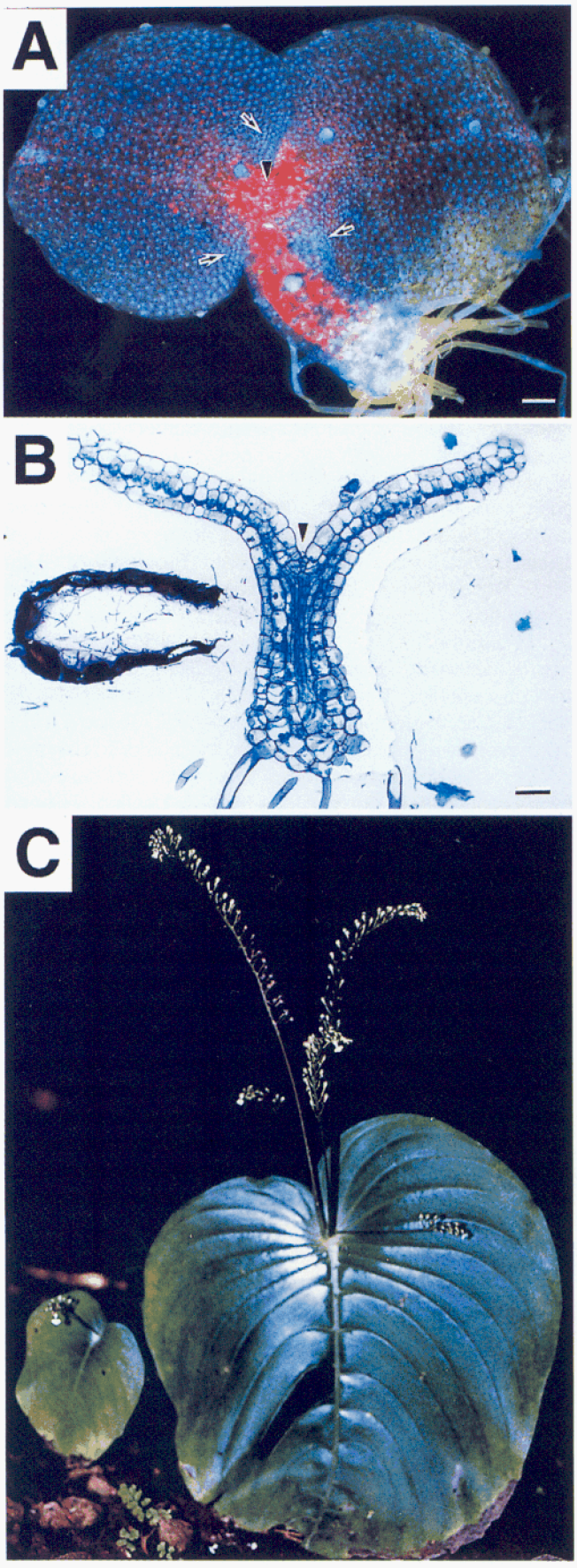



Fig. 4. Indeterminate leaves in Meliaceae. Photographs of two species in the genus *Guarea* are shown. (A), Part of a twig of *G. glabra*, cultivated at the University of Tokyo. Insets show areas around the shoot apical meristem (SAM) and the leaf apical meristem (LAM). (B), Longitudinal section of a leaf apical meristem of *G. guidonia*. Nuclei were stained with DAPI and emitted fluorescence. Notice the presence of a SAM-like structure at the apex (indicated by an arrowhead). L0, L1 and L2 indicate primordia of leaflets from the youngest to the oldest in sequence. Bar, 100 $\mu$m.




*Meristematic activity at the base of the leaf blade that supports development of a Gesneriaceae-type indeterminate leaf*

One-leaf plants, namely, all species in the genus *Monophyllaea* (Gesneriaceae) and some species in the genus *Streptocarpus*, have a unique system, the "phyllomorph" (Jong and Burtt 1974), which is composed of a single leaf blade and a single "petiolode" or stalk-like structure. The single phyllomorph of plants in *Monophyllaea* is derived from the meristematic region of one of two cotyledons (Chifflot 1909, Oehlkers 1923, Hill 1938, Jong and Burtt 1975, Tsukaya 1997; Fig. 5). Plants in *Monophyllaea* and one-leaf-type *Streptocarpus* cannot differentiate a SAM. However, inflorescence meristems are formed at the base of leaf blades (Oehlkers 1923, Jong and Burtt 1975, Weber 1975 and 1976, Cronk and Möller 1997, Tsukaya 1997; Fig. 5). It has been suggested that the development of the phyllomorph is maintained by the activity of three kinds of meristem that appear to be located around the junction of the leaf blade and petiolode (Jong and Burtt 1975).

In a study of *Monophyllaea*, treatment with various combinations of phytohormones stimulated the formation of adventitious, additional phyllomorphs (Tsukaya 1997). However, no shoot apical meristems were recognized at the apices of the additional phyllomorphs. Thus *Monophyllaea* seems to lack some system for the induction of the developmental program that is required for SAM activity in shoots (Tsukaya, submitted). Instead, the meristems of phyllomorphs can be considered to be equivalent, in terms of function, to the SAMs of standard angiosperms. These meristems differentiate not only leaf blades but also axis-like petiolodes and inflorescences.

The one-leaf morphogenesis of *Monophyllaea* might be derived from the standard type of shoot morphogenesis as a result of loss of activity in the SAM region. In *Arabidopsis thaliana*, various mutants, such as *stm* and *wus* mutants, have defects in the organization of the SAM and completely lack SAM activity just after germination (Barton and Poethig 1993, Laux *et al.* 1996, Long *et al.* 1996; Fig. 6), as do seedlings of *Monophyllaea.* If models for the mechanisms that regulate SAM activity in *Arabidopsis* are generally applicable to seed plants, we can interpret the organogenesis of phyllomorphs in *Monophyllaea* as follows. Plants in *Monophyllaea* lacks the gene(s) required for expression of SAM-related genes at appropriate positions at the

Fig. 5. Development of the cotyledons of *Monophyllaea horsfieldii* into a phyllomorph. (A), A seedling just after expansion of cotyledons. Nuclei were stained with DAPI and emitted blue fluorescence. Notice a cluster of small cells with meristematic activity at the base of both cotyledons (indicated by arrows). No shoot apical meristem is present between the two cotyledons (indicated by an arrowhead). (B) Cross section of a seedling at the same stage as that shown in (A). Notice the absence of a shoot apical meristem, as indicated by an arrowhead. (C) Adult plants of *M. horsfieldii.* The base of the phyllomorph, which was derived from one of the cotyledons, has differentiated an inflorescence. Bars in (A) and (B), 100 $\mu$m. Modified from Tsukaya (1997).

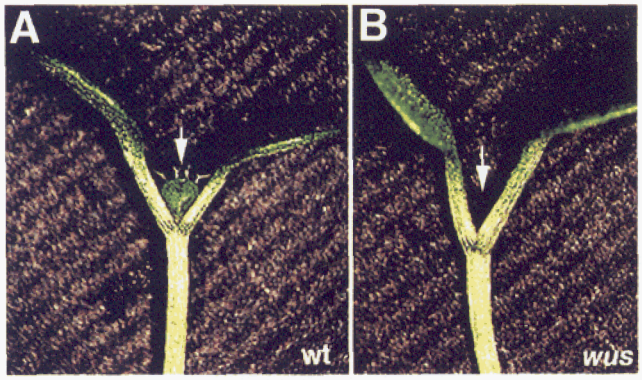



Fig. 6. Seven-day-old seedlings of wild-type *Arabidopsis* and *wuschel* (*wus*) mutant. Young foliage leaves are visible in the wild type (A), while the *wus-1* mutant (B) do not show any activity of shoot apical meristem. Shoot apex is indicated by an arrow. Modified from Laux *et al.* (1996). Courtesy of Dr. Thomas Laux and Dr. Heiko Schoof, ZMBP-Center of Plant Molecular Biology, Entwicklungsgenetik, Univ. Tübingen, Tübingen, Germany.

vegetative stage. Instead, the cotyledons of *Monophyllaea* express ectopically, at the base of the cotyledons, those genes whose products function in the peripheral zones of authentic SAMs. Moreover, after transition from the vegetative to the reproductive stage, part of the phyllomorph meristem expresses genes that are required for establishment and maintenance of stem cells, such as homologs of the *WUS* and *STM* genes of *A. thaliana*, since inflorescence meristems develop in a similar way, with typical shoots differentiating on the phyllomorph.

Imaichi *et al.* (in press) analyzed meristematic regions in the phyllomorph of an other one-leaf plant, *Streptocarpus grandis.* Anatomical analysis suggested that meristems of the phyllomorph in *Streptocarpus grandis* might be a result of embryonic meristematic activity that remains in the SAM region and the cotyledons. We can apply our original hypothesis in this case too, even though we do not yet understand the molecular background of the meristematic activities in the phyllomorph. Further molecular studies, such as isolation and characterization of genes homologous to *STM* and *WUS* in one-leaf plants, should provide clues to a better understanding of what is a leaf and what is a shoot at the molecular level (Cronk and Möller 1997).

*Concluding remark*

Variations in the morphology of leaf blades are, in particular in dicots, quite considerable as a consequence of flexibility in the activity and patterns of distribution of meristematic regions in leaf blades. In extreme cases, we cannot even judge whether organs are leaves, kinds of shoot or something else. Such "fuzzy" morphology has confused botanists for many years (*e.g.*, Lacroix and Sattler 1994, Rutishauser 1995, 1999). However, most of the fuzziness of strange leaf-stem intermediates depends on the unusual activity of meristematic regions in leaf blades with the occurrence of branches, indeterminacy, radial growth or sequential development (Sattler and Rutishauser 1990). Thus the fuzziness might be resolved if we could interpret the form of each leaf blade in terms of the meristematic activity of the leaf blade, exploiting the roles of cell expansion in the enlargement and polarized expansion of leaves (Tsukaya 1998). We discussed two types of indeterminate leaf in this review as examples that can be considered from of such a perspective. An understanding of molecular mechanisms that regulate the functions of meristematic tissues should lead us to the realization that even fuzzy morphology only represents modified leaf morphology.

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