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Shoot Meristem Formation in Vegetative Development

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INTRODUCTION

The majority of the plant body is derived from the activities of groups of specialized cells, known as apical meristems, at the growing tips. In a typical flowering plant, the shoot apical meristem (SAM) gives rise to the bulk of the above-ground portion of the plant, whereas root meristems give rise to the bulk of the subterranean plant body. Of course, not all plants are typical, and numerous exceptions to these broad generalizations are found in nature. For example, aerial roots are a common feature, and rhizomes or other subterranean shoot systems have SAMs that remain beneath the soil. Whether or not a plant is typical, the apical meristems of the plant represent the site at which organs are initiated and the pattern of the shoot and root system is established. In this review, we focus on meristem formation in the vegetative shoots of flowering plants. Although the term "meristem" can be used in a broad sense to refer to any actively growing portion of the plant, we limit our discussion to those portions of the plant that generate new lateral organs.

Shoot and root meristems behave in different ways. The root apical meristem gives rise to the root and root cap but otherwise forms no lateral structures (lateral roots arise endogenously at a distance from the root apex; see Schiefelbein et al., 1997, in this issue). The SAM, by contrast, may adopt one of a variety of different developmental fates. A SAM may become determinate, forming a terminal flower, tendril, or thorn, or it may display an indeterminate pattern of growth, continuously producing vegetative leaves and branches. The types of lateral organs initiated by the SAM vary tremendously as well; modified leaves such as bud scales, leaf tendrils, floral bracts, and petals may all be produced. Moreover, the fate of a SAM may change during development, as, for example, when an indeterminate vegetative SAM becomes an inflorescence meristem or a determinate floral meristem.

Different types of vegetative shoot meristems may be distinguished based on their position in the plant and on the developmental context in which they form (Figure 1). The SAM forms during embryogenesis and can be found distal to the youngest (most recently initiated) leaf primordia during development. Axillary meristems arise in the axils of leaves, although they may give rise to shoots that are indistinguishable from the primary shoot. Adventitious meristems arise de novo from differentiated tissues. These adventitious shoots are common in some species and may appear on leaves (or leaf homologs), stems, or roots (Figure 1).

These different types of meristems all function in the same way in initiating the organs that make up the shoot. To describe our current understanding of meristems and the mechanisms by which they form and function in flowering plants, we summarize some shared features of different shoot meristems and discuss meristem formation in embryonic, axillary, and adventitious positions.

STRUCTURAL FEATURES OF SAMs

Cytological Zonation in SAMs

Externally, the apices of different plants vary greatly in their size and shape and in the pattern in which leaf primordia are formed. The internal organization of most angiosperm apices, however, differs relatively little in structure. Cytohistochemical studies of sectioned meristems from various angiosperms indicate that different meristems of the vegetative shoot share a number of structural features. SAMs have been described in terms of zones, which are based on staining patterns and the number and arrangement of cell divisions (reviewed in Gifford and Corson, 1971; Steeves and Sussex, 1989). Three regions are typically distinguished (Figure 2A), although the boundaries between zones are often indistinct. The central zone (CZ) consists of cells at the summit of the SAM that typically are quite large. CZ cells exhibit prominent vacuoles, and they divide somewhat less frequently than do the surrounding cells. Cell divisions occurring within the CZ serve to maintain a population of indeterminate cells while replenishing the cells that have been incorporated into leaf primordia or stem.

The morphogenetic or peripheral zone (PZ), which consists of smaller, more rapidly dividing cells with inconspicuous vacuoles, is located on the flanks of the SAM (Figure

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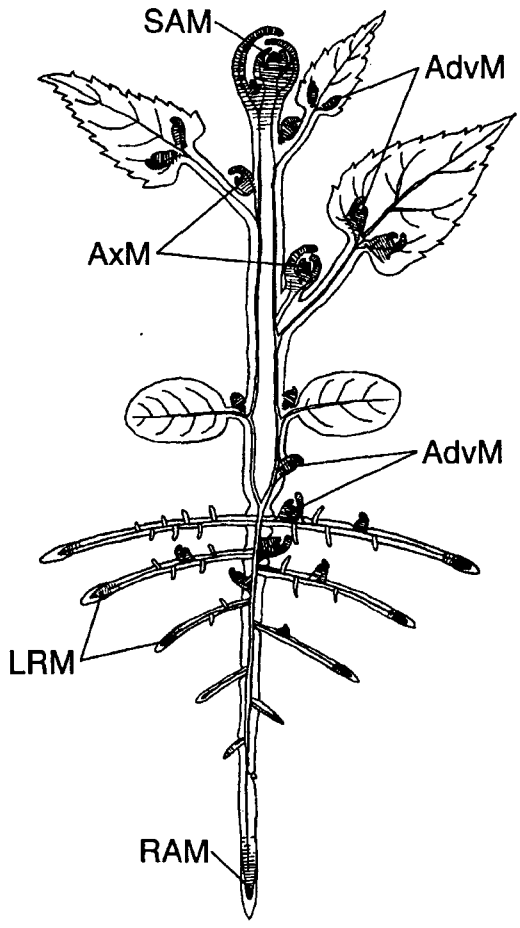

Figure 1. Vegetative Shoot and Root Meristems.

An idealized dicotyledonous plant is shown with adventitious buds forming on leaves, roots, and hypocotyl (redrawn after Foster and Gifford, 1974). AdvM, adventitious meristem; AxM, axillary meristem; LRM, lateral root meristem; RAM, root apical meristem.

2A). The cells of the PZ function as initials, that is, they serve as the major source of new cells in the meristem. The PZ is the region in which the first cell divisions leading to the formation of organ primordia occur. The rib zone (RZ) includes the cells at the base of the SAM, which also divide and expand rapidly. These cells contribute primarily to the tissues of the stem.

The shoot apex comprises the three zones of the SAM and a subapical zone of maturation (ZM) in which the shoot grows considerably in width and primordia enlarge rapidly (Figure 2A). It is thought that no cells occupy permanent positions in the shoot meristem because there is a general basipetal displacement of cells. In smaller apices, the meristem cells appear to undergo more rapid cell division than do those in larger apices, and the proportion of the apex involved in the initiation of each leaf is greater (Gifford and Corson, 1971).

Another structural feature observed in the SAMs of many angiosperms is the stratified appearance of the cell layers (Schmidt, 1924), which is depicted for a maize SAM in Figure 2A. Cells in the outermost layer(s) of the SAM (i.e., the tunica) divide primarily in an anticlinal plane (perpendicular to the surface), whereas periclinal divisions occur largely in the inner apical layers (i.e., the corpus). As a result of their anticlinal divisions, cells within each of the tunica layers maintain a separate lineage from cells above and/or below them. The use of chimeric plants with one complete cell layer that is genetically distinct from adjacent layers (periclinal chimeras) has demonstrated that the layered cellular organization of the meristem tends to be maintained in the stem and lateral organs of the shoot, although invasion of cells from one layer into another occurs frequently (Dermen, 1953; Stewart and Burk, 1970; Stewart and Dermen, 1979). In general, the outermost layer, termed L1, gives rise to the epidermis, whereas the inner layers, L2 and L3, contribute to the central tissues of the leaf and stem. Although the stratified appearance of the SAM allows reasonable predictions regarding the fate of a cell, the study of lineage relationships in plants has shown that position rather than lineage is the most important factor in determining cell fate (Dermen, 1953; Stewart and Burk, 1970; Stewart and Dermen, 1979; see Clark, 1997; Laux and Jürgens, 1997; Poethig, 1997; Schiefelbein et al., 1997, all in this issue).

Despite the apparent consistency of these shared structural features of angiosperm SAMs, care must be exercised in interpreting their meaning. The absence of or change in a particular cytological feature may or may not reflect a real change in the function of the SAM. For example, apical cells of a germinating *Cheiranthus cheiri* seed display characteristics of meristematic tissues in that they appear densely cytoplasmic, lack plastids, and have small vacuoles and enlarged nucleoli (reviewed in Gifford, 1954). After the cotyledons expand, however, the meristematic cells appear to differentiate: vacuoles form, chloroplasts appear, nucleoli diminish in size, and the cells have less chromatic cytoplasm. When growth resumes, PZ cells dedifferentiate in positions at which foliage leaves will appear, resulting in a return of that portion of the apex to a meristematic state. The differences in the cytoplasmic appearance of cells in the different regions of the apex are maintained as the plant grows, that is, cells in the central, uppermost portion of the apex remain vacuolated, and cells at the position of presumptive leaf primordia appear less differentiated.

Meristem-Specific Gene Expression

Recently developed techniques, such as RNA in situ hybridization, immunolocalization, and the transgenic expression of reporter genes, provide molecular tools to study the structure and function of the SAM. Indeed, a number of genes with meristem-related expression patterns have been characterized (Medford, 1992). Most such genes display

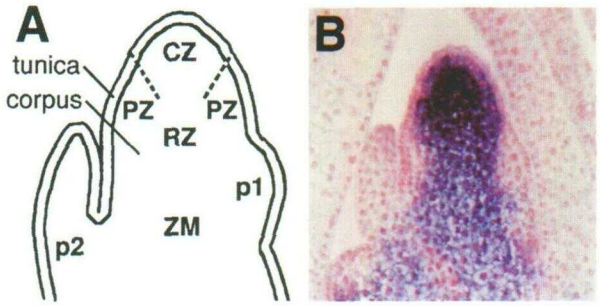

Figure 2. SAM Structure and Gene Expression.

(A) Structural features of shoot meristem organization. The typical apical zonation pattern of the SAM includes a central zone (CZ), peripheral zone (PZ), and rib zone (RZ). Immediately below the SAM is a zone of maturation (ZM). The first leaf primordium (p1) forms as a shoulder on the flank of the SAM. p2 indicates the next oldest leaf primordium. The tunica or histogenic L1 layer is indicated relative to the corpus (L2).

(B) In situ hybridization of the *kn1* homeobox gene in a maize vegetative meristem (Jackson et al., 1994). *kn1* expression disappears from the meristem flank as lateral organ primordia form.

patterns of expression that extend beyond the meristem per se. In fact, many meristem-expressed genes appear to represent basic housekeeping functions that would be expected to be highly expressed in densely cytoplasmic or rapidly dividing cells (Köhler et al., 1992; Fleming et al., 1993).

Nevertheless, some expression patterns reflect the tunica/corpus and apical zonation that are apparent from histological analyses (Fleming et al., 1993; Kelly and Meeks-Wagner, 1995; Lu et al., 1996). Others are beginning to reveal domains within the SAM that are not obviously related to structural features but that may reflect important aspects of meristem function (Smith et al., 1992; Souer et al., 1996). For example, the expression pattern of the maize homeobox gene *knotted1* (*kn1*) has proven to be a useful marker of meristem activity (Figure 2B; Smith et al., 1992; Jackson et al., 1994). *kn1* is expressed throughout the dome of all shoot meristems, in the RZ, and in the expanding stem (Smith et al., 1992). *kn1* is not expressed in cells of leaf primordia or in other determinate lateral organs of the shoot. Within the apical dome itself, *kn1* expression disappears from a portion of the meristem corresponding to the position at which the next leaf primordium will initiate (Figure 2; Smith et al., 1992). The first detectable expression of *kn1* occurs during embryogenesis, before the organized SAM can be detected and before the cotyledon is elaborated (Smith et al., 1995). A closely related gene in Arabidopsis, *SHOOT MERISTEMLESS* (*STM*), has a pattern of expression very similar to that of *kn1* (Long et al., 1996). The expression patterns of *kn1* and *STM* distinguish leaf from nonleaf domains in the PZ, a distinction that is not immediately obvious by examining structural features alone.

A number of class 1 homeobox genes closely related to *kn1* (*knox* genes) have been characterized in maize and in other species (Lincoln et al., 1994; Schneeberger et al., 1995; Hareven et al., 1996; Long et al., 1996). Individual *knox* genes display slightly different patterns of expression within the meristem. In general, they are expressed in the shoot meristem and young stem, but they are not expressed in determinate lateral organs such as leaves (Jackson et al., 1994; Kerstetter et al., 1994). As more genes with meristem-specific expression patterns are characterized and compared, we may gain further insight into the meaningful domains or compartments that contribute to the patterning of the shoot and to early events in lateral organ initiation.

SHOOT MERISTEM FUNCTION

Initiation of Organs

The morphogenetic processes that occur at apical meristems contribute directly to the specification of plant form. Although axillary buds and stem tissue also have their origin in the SAM, leaves or leaflike organs tend to be the most conspicuous products of the SAM. Initiation of a new leaf primordium is marked by a change in the plane of cell division rather than by an increase in division rate (Steeves and Sussex, 1989). Usually a periclinal division in either the L1 or L2 of the tunica represents the first indication that a new leaf primordium is forming. A predictable number of cells are set aside by the SAM to form each leaf. These cells are known as founder cells because they are the initial set of cells from which all subsequent cells of the leaf are derived. One can imagine that a tight control exists over the allotment of founder cells so that the population of indeterminate cells in the SAM is not depleted.

A number of mutations can be interpreted as having a defect in this control. The initation of larger leaf primordia in the *forever young* (*fey*) mutant of Arabidopsis results in depletion of the meristem after a few leaves have formed (Medford et al., 1992; Callos et al., 1994). A less pleiotropic effect on founder cell allotment is seen in maize *narrow sheath* mutants, in which narrow leaves arise from fewer founder cells in the meristem (Scanlon et al., 1996). These authors used a polyclonal antibody that recognizes KN1 and related proteins to show that the zone of leaf founder cells is smaller in *narrow sheath* mutants. Interestingly, the presence of "extra" cells in the meristem did not lead to an increase in leaf number in this mutant.

Phyllotaxy

The position at which the next leaf primordium arises on the SAM relative to previously initiated leaves largely determines

the pattern of lateral organs on the shoot, namely, the phyllotaxy (Steeves and Sussex, 1989; Callos and Medford, 1994). Phyllotactic patterns are of two basic types, spiral and whorled. The angle between initiating leaves in a spiral phyllotactic pattern is highly regular. Within a whorl, there can be a single leaf, as in the distichous pattern of maize, two leaves, as in the decussate pattern of mint, or many leaves, as in *Equisetum.*

The *abphyl* mutation in maize, which conditions two leaves at each node instead of one, specifically affects phyllotaxy without disrupting other meristem functions (Greyson and Walden, 1972). Examination of *abphyl* embryos has shown that the SAM makes up a much larger proportion of the embryo than it does in normal embryos (Jackson and Hake, 1995). Nevertheless, this larger meristem initiates leaf primordia in a regular pattern, rarely forming more than two leaves per node. *abphyl* shoots also can produce twins at any node. However, the phyllotaxy of these twin shoots is distichous, suggesting that the meristem size of each twin shoot reverts back to normal (D. Jackson and S. Hake, unpublished data).

Among its effects on meristem function, the *fey* mutation also alters the phyllotaxy of the vegetative shoot (Callos et al., 1994). Wild-type vegetative rosettes display a spiral phyllotaxy in either a clockwise or counterclockwise direction, with the smallest angle between successively initiated leaves approaching 137.5° (Callos and Medford, 1994). In *fey* mutants, however, leaf primordia arise in abnormal positions, with divergence angles varying from 29° to 176° (Callos et al., 1994). The abnormal positioning of leaf primordia frequently leads to a switch in the rotation of the spiral. In contrast to the *abphyl* mutation in maize, the size of the SAM does not appear to be affected in *fey* mutants, although the size and shape of leaf primordia are abnormal (Medford et al., 1992; Callos et al., 1994).

SAMs Are Self-Regulating

The phyllotactic pattern of normal plants is usually very stable and changes only under certain environmental or developmental stimuli, such as the transition to flowering. This stability is also reflected in the maintenance of meristem size. Destruction of central or peripheral portions of the SAM or bisection of the meristem consistently leads to the same result; the meristem cells remaining after the operation proliferate to reconstitute a meristem of normal size, reestablishing the original pattern of apical zonation and phyllotaxy (reviewed in Sussex, 1989). The regeneration of a complete meristem exemplifies its self-regulating nature and suggests that it is not a mosaic of determined zones committed to different functions.

A number of mutations have been described that disrupt the self-regulating capability of the meristem. Fasciated meristems, which frequently are found in nature (White, 1948), do not have a focused apex but enlarge and grow as a ridge or break into multiple apices. They can be conditioned by a single genetic locus (Mertens and Burdick, 1954; Leyser and Furner, 1992; Medford et al., 1992; Clark et al., 1993, 1995). For example, the *clavata*, *fasciata*, and *fully fasciated* mutations in Arabidopsis condition a phenotype in which the meristem appears to grow unchecked (see Clark, 1997, in this issue). Occasionally, fasciated stems are found in these mutants, but the most consistent defect is a large increase in the number of lateral organs.

Integration of Environmental and Developmental Signals

The meristem also is a site for the integration of environmental cues, such as day length, temperature, and nutritional status, with endogenous signals from other parts of the plant, such as leaf number, physiological age, or distance from the roots. This integration process is most obvious during the transition to flowering, when the shape of the meristem and the phyllotaxy of the shoot can change markedly. However, changes in phyllotaxy and meristem shape may also occur during vegetative phase change, when a plant makes the transition from a juvenile pattern of growth to an adult phase (Poethig, 1990, 1997, in this issue; Marc and Hackett, 1992). Moreover, aquatic or semiaquatic plants may display different patterns of growth when submerged than when growing in air, and at least some of these differences are likely to be regulated at the SAM.

MERISTEM FORMATION IN EMBRYOGENESIS

As discussed above, the vegetative SAMs of flowering plants share a number of structural and functional features, but to understand how meristems function, it is important to examine how they form. The SAM, the cotyledons (embryonic leaves), and the primary root are usually formed during embryogenesis. Thus, mutations in genes involved in organogenesis of the early meristem are likely to lead to defects in the embryo. However, mutations affecting many fundamental biological processes would also be expected to result in embryo defects. Consequently, although a number of mutations affecting embryo meristems have been described (Nagato et al., 1989; Clark and Sheridan, 1991; Mayer et al., 1991), differentiating the defects in organogenesis from those in basic metabolism, cell division, and growth presents a number of challenges.

Analysis of the Arabidopsis *stm* mutation has circumvented these challenges because the defect is specific to the shoot meristem. Severe alleles of *stm* result in the absence of a histologically defined embryonic SAM (Barton and Poethig, 1993). Nevertheless, other embryonic structures, including cotyledons, hypocotyl, and root, do form. Barton and Poethig (1993) place the first detectable difference from wild-type embryonic development at or just before the torpedo stage of embryogenesis, at which time the embryonic meristem takes on a specific tunica–corpus pat-

tern of cell division. Upon germination, *stm* mutant seedlings are readily identified by the absence of any seedling leaves arising from the shoot apex (Barton and Poethig, 1993). However, in some seedlings, leaves form from the hypocotyl (or fused cotyledonary petioles). This formation of leaves has been interpreted as adventitious leaf formation (Barton and Poethig, 1993) or as delayed and limited leaf initiation from meristems formed in the axils of the fused cotyledons (Endrizzi et al., 1996).

Mutant seedings carrying weak alleles of *stm* form a few leaves from an apical position before the meristem fails, at which time an axillary meristem initiates a few leaves, and the cycle is repeated (Clark et al., 1996; Endrizzi et al., 1996). The first leaves appear to initiate from apical precursor cells present at the same position as the shoot meristem in the wild type (Endrizzi et al., 1996).

The interpretation of the strong *stm* mutant phenotype depends largely on how one defines the shoot meristem. If a specific histological pattern must be present, then *stm* mutant embryos clearly lack a shoot meristem (although seedlings of *C. cheiri* may also be so described; see above). If a functional definition of the SAM is applied, however, the top half of the globular embryo may well be considered to comprise the meristem, in which case the cotyledons would represent the first leaves initiated by the embryonic SAM. The expression of *STM* in a few cells at the top half of the globular embryo (Long et al., 1996) may itself be an indication that this tissue has meristem identity. In this light, *stm* mutants may be seen primarily as a defect in the ability of the meristem to renew itself after organ primordia (cotyledons) are formed.

There is ample evidence that cotyledons do, in fact, represent the products of an embryonic SAM. For example, some plant embryos display the apical zonation and cell division patterns of a SAM before cotyledons are initiated (Kaplan, 1969). Moreover, the morphological differences between cotyledons and leaves may be a function of when they initiate during development rather than where or how. Indeed, *Brassica napus* embryos that are germinating precociously in vitro initiate a rosette of cotyledons (Finkelstein and Crouch, 1984). These embryos only begin making leaflike lateral organs at about the time an untreated seed would reach maturity. In *B. napus,* the transition from initiating cotyledons to initiating leaves is accompanied by other changes, such as hypocotyl elongation, that normally are associated with germination of a mature embryo (Finkelstein and Crouch, 1984).

The morphological distinctions between leaves and cotyledons are not inviolable. For example, mutations in Arabidopsis that alter the timing of leaf initiation relative to seed maturation produce cotyledon-like leaves (L. Conway and R.S. Poethig, personal communication), and cotyledons of *leafy cotyledon* mutants display a number of leaflike traits (Meinke et al., 1994; West et al., 1994).

The possibility that meristem initiation and maintenance may represent genetically separable processes also deserves further attention. A number of other mutations with defects in the formation or maintenance of the primary SAM have been described in tomato (Caruso, 1968), petunia (Souer et al., 1996), and Arabidopsis (Medford et al., 1992; Callos et al., 1994; Jürgens et al., 1994; McConnell and Barton, 1995; Laux et al., 1996; Pickett et al., 1996). As these loci are characterized further and the genes responsible are cloned, they promise to provide new genetic and molecular tools for investigating meristem formation in angiosperms.

AXILLARY MERISTEM FORMATION

Regulating the initiation and outgrowth of axillary meristems is an important mechanism for controlling overall plant form. The manner in which axillary meristems arise differs significantly among flowering plant species, although in every case there is a close association with a leaf primordium (Garrison, 1955; Foster and Gifford, 1974). In *Heracleum*, for example, axillary meristems arise from the surface of the leaf primordium (Majumdar, 1942), whereas in Arabidopsis, the axillary meristem appears to be initiated either concurrently with the leaf as part of a common primordium or from the base of a developing leaf (Irish and Sussex, 1992; Hempel and Feldman, 1994). In maize, clonal analysis has shown that the axillary meristems are not associated with the leaf in whose axil they appear; rather, they are associated with the margins of the previously formed leaf (Johri and Coe, 1983).

Axillary Meristem Mutants

Numerous mutants that increase vegetative branching (i.e., that affect axillary meristem initiation) have been identified. These include *teosinte branched* in maize (Doebley et al., 1995), *ramosus* in pea (Arumingtyas et al., 1992), a number of *auxin resistant* mutants in Arabidopsis (Lincoln et al., 1990), and the *decreased apical dominance* mutants in petunia (Napoli and Klee, 1993; Napoli and Ruehle, 1996). It is likely that many of these mutants act by interfering with apical dominance, possibly by interfering with the action of auxin or cytokinin (Sachs and Thimann, 1967; Cline, 1994).

A few mutations that specifically affect axillary meristem formation have also been described. The *lateral suppressor* mutant in tomato prevents the initiation of axillary meristems during vegetative growth (Malayer and Guard, 1964), although axillary buds form normally after flowering. In this mutant, the SAM was shown to be smaller than normal, which may restrict the initiation of axillary bud primordia (Malayer and Guard, 1964). A second mutation in tomato, *torosa-2*, reduces the number of vegetative axillary buds that develop. This defect has been correlated with reduced levels of cytokinin in the mutant plant compared with the wild type (Mapelli and Lombardi, 1982).

Two mutants with defects in axillary bud formation have been described in Arabidopsis, both of which also display

defects in the primary SAM. For example, the *pinhead* mutation reduces the number of buds initiated in the axils of cauline and rosette leaves (McConnell and Barton, 1995) in addition to its effects on the embryonic SAM, where a leaf or pinlike organ appears to terminate the growth of the meristem. Mutations in the *REVOLUTA* gene result in plants with unusually large leaves, stems, and floral organs and reduced numbers of vegetative and floral axillary shoots (Talbert et al., 1995). The premature termination of the primary SAM and the appearance of leaves or filamentous structures in place of axillary shoots in *revoluta* mutants indicate that *REVOLUTA* plays a role in meristem maintenance. However, it is also possible that excessive leaf growth in *revoluta* plants occurs at the expense of axillary bud development (Talbert et al., 1995). This mutant phenotype complements the results of surgical experiments showing that axillary bud growth is enhanced by reducing the size of the subtending leaf primordium (Snow and Snow, 1942; see also Poethig, 1997, in this issue).

Determinate Axillary Meristems

In some axillary meristems, the developmental pattern is altered to produce a distinct structure, such as a flower, a tendril, or a thorn, and the growth of the shoot becomes determinate. The conversion of vegetative apices into inflorescences and flowers has been extensively studied in recent years, but the differentiation of meristems into tendrils and thorns has received little attention. The development of branched tendrils of *Parthenocissus inserta* (Virginia creeper/woodbine) has been followed by Millington (1966), who showed that the tendril essentially develops from an axillary shoot meristem that gives rise to reduced bract leaves with tendril arms in their axils.

Thorns are formed in the axils of leaves in a number of species. In *Ulex europaeus* (gorse), for example, axillary SAMs produce leaf and bud primordia until thorn differentiation is initiated (Bieniek and Millington, 1967). This transition from a vegetative shoot to a thorn begins as cells of the RZ and their immediate derivatives elongate vertically. With elongation, the innermost initials appear to converge to a point, and the shape of the apex shifts from a dome to a sharp cone. Leaf and bud initiation cease, and sclerification of the elongated cells proceeds basipetally. In *Ulex*, the degree of vegetative development preceding thorn differentiation is variable (Bieniek and Millington, 1967), and little is known about the regulation of this process.

ADVENTITIOUS SHOOT MERISTEM FORMATION

In addition to meristems formed during embryogenesis and in the axils of leaves, meristems have been found to organize at other locations on the plant (Figure 1). So-called adventitious shoots form normally on many different organs in a variety of plant species. Examples such as the root-bearing shoots of bindweed (*Convolvulus arvensis*), shoots initiated from the cambial tissue of tree stumps, and vegetative meristems that arise on the hypocotyl of flax seedlings illustrate only a few of the places at which adventitious shoots can form. Most root-borne shoots are thought to arise from the pericycle in a manner analogous to the initiation of lateral roots. Under the appropriate conditions, cells in the pericycle of Arabidopsis roots that normally would form lateral root meristems can be coaxed into forming shoot meristems instead (J. Welsch and I. Sussex, personal communication).

The development of organs or shoots upon a leaf or leaf homolog is known as epiphylly (reviewed in Dickinson, 1978), and there are naturally occurring examples of shoots forming on almost any part of the leaf. Among the more familiar examples are the piggyback plant (*Tolmiea menziesii*), which forms shoots at the junction between the petiole and the blade, and *kalanchoë* (*Bryophyllum*), in which plantlets form along the margin of the blade. The analysis of epiphyllous shoots in naturally occurring species and in transgenic plants may prove informative in the study of meristem formation.

An epiphyllous shoot may represent the fusion or displacement of an otherwise normal axillary meristem or may represent a truly adventitious shoot, occurring without any obvious relationship to either the primary or axillary shoot meristems. Normal axillary buds have been displaced onto the adaxial surface of the subtending leaf, the abaxial surface of the leaf above, and a variety of other stem and leaf positions (Dickinson, 1978). In these situations, meristem formation proceeds as in an axillary meristem, but differential growth alters the position of the meristem relative to the other identifiable plant parts. In one example, the spiny shoots or areoles on the cactus *Coryphantha* are initiated as vegetative meristems in the axils of the leaf but subsequently are carried up onto the summit of the leaf by differential growth on the adaxial side of the leaf base (Boke, 1952).

Many examples of epiphylly, however, cannot be explained by the repositioning of an axillary meristem resulting from differential growth. In cases in which shoots form in the axils of leaflets of a compound leaf, the leaf may have acquired so many characteristics of a shoot that the epiphyllous bud forms in a manner similar to a normal axillary bud (Fisher and Rutishauser, 1990). However, vegetative adventitious shoots often appear to be initiated by the remeristemization of more or less differentiated tissues of mature leaves (Dickinson, 1978). In *kalanchoë*, the epiphyllous shoots are derived from cells of the leaf margin, which precociously stop dividing and remain blocked in the G1 phase of the cell cycle (Brossard, 1973). In the mature leaf, these cells become reactivated to form an undifferentiated meristem that acquires zonation and forms a small shoot (Brossard, 1973). Troll (1939; reviewed in Dickinson, 1978) points out the rela-

tionship between the late maturation of the tissue of the petiole–lamina junction and the occurrence there of epiphyllous shoots in a number of species, including the piggyback plant.

Epiphylly has also been observed in transgenic plants overexpressing different members of the *kn1* class of plant homeobox genes and a cytokinin-synthesizing gene. Transgenic tobacco and Arabidopsis plants that overexpress the maize *kn1* cDNA or related genes show retarded growth, reduced apical dominance, and perturbed leaf development (Sinha et al., 1993; Lincoln et al., 1994). Leaves are thickened and lobed, and in severe cases, shoots arise on the adaxial leaf surface (Figure 3A; Sinha et al., 1993; Chuck et al., 1996). These results indicate that a high level of *kn1* expression is sufficient to induce ectopic meristem formation in transgenic tobacco and Arabidopsis leaves.

Similar experiments with the rice homolog of *kn1*, *OSH1*, expressed in tobacco under the control of a promoter that conditions expression only in the SAM and very young leaf primordia, yield the same spectrum of phenotypes as *OSH1* and *kn1* expressed under the control of the cauliflower mosaic virus 35S promoter (Sato et al., 1996). This result suggests that only a brief window occurs during which expression of *OSH1* is phenotypically relevant in leaves. Analysis of plants overexpressing the related gene *KNAT1* in Arabidopsis showed that ectopic shoots form only in a restricted region of the leaf blade (Chuck et al., 1996). Transgenic *KNAT1* plants form shoots in the sinuses of the basal-most lobes of the leaf blade in a region considered to be the least differentiated (Chuck et al., 1996). Figure 3B shows a section through an Arabidopsis leaf overexpressing *KNAT1* and bearing an ectopic SAM.

A dominant mutation in the homolog of the *kn1* gene in barley, *HvKnox3*, leads to ectopic expression in a determinate lateral organ, the awn, and results in the formation of floral meristems on the awn surface (Müller et al., 1995). This spontaneously occurring example of epiphylly illustrates the ability of a *kn1*-like gene to establish meristem identity in a normally determinate organ. The phenotype is similar to that observed when the maize *kn1* gene is expressed in transgenic barley (R. Williams, Y. Lie, S. Hake, and P. Lemaux, unpublished data).

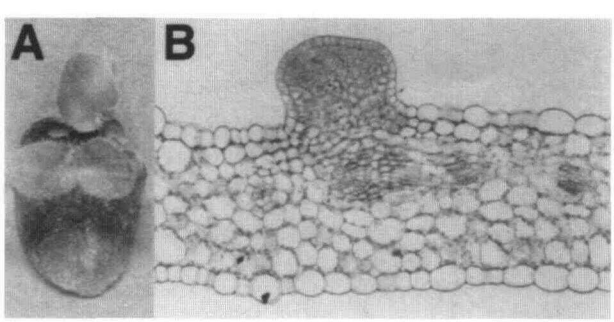

Figure 3. Adventitious Meristems Form on the Adaxial Surface of Leaves Overexpressing *kn1*-like Homeobox Genes.

(A) A reduced transgenic tobacco leaf expressing the maize *kn1* cDNA under the control of the cauliflower mosaic virus 35S promoter bears shoots on the adaxial surface (Sinha et al., 1993).

(B) A median longitudinal section through an epiphyllous shoot meristem on a transgenic Arabidopsis leaf overexpressing the Arabidopsis *KNAT1* cDNA under the control of the cauliflower mosaic virus 35S promoter (Chuck et al., 1996).

Overexpression of a bacterial gene involved in cytokinin synthesis, *isopentenyltransferase* (*ipt*), in transgenic tobacco plants also leads to the formation of shoots from the adaxial surface of the leaf blade (Estruch et al., 1991; Li et al., 1992; Hewelt et al., 1994). Interestingly, the *ipt* gene was not expressed in all of the epiphyllous buds (Estruch et al., 1991), indicating that adventitious bud formation may also be triggered by cytokinin synthesized in other parts of the plant. Moreover, not all leaf cells exhibited the same potential to form adventitious shoots. For example, the buds formed preferentially on the adaxial surface of the leaf in proximity to veins, either at the leaf tip (Estruch et al., 1991) or on the leaf base and petiole (Li et al., 1992). The striking similarity between the phenotypes of tobacco plants expressing either *ipt* or *kn1*-like genes raises the possibility that they affect the same developmental pathway. Thus, overexpression of *kn1* may mimic overproduction of cytokinin.

In a discussion of SAM formation, the ontogeny of compound or dissected leaves deserves some attention. Although compound leaf primordia are initiated from the PZ, just like simple leaves, and exhibit dorsoventral characteristics from their inception, compound leaf primordia display some basic features normally associated with the shoot meristem (Kaplan, 1983; Sattler and Rutishauser, 1992). For example, the compound leaf primordium gives rise to lateral organ primordia (leaflets) in a regular pattern (phyllotaxy). Moreover, a *kn1* gene of tomato (*TKN1*), a plant with compound leaves, was found to be expressed in young leaf primordia as well as in the SAM (Hareven et al., 1996). Expression of *TKN1* in leaf primordia may indicate that leaflet initiation occurs in much the same way as does leaf initiation from the SAM. When *kn1* was overexpressed in tomato, the degree of leaf dissection increased dramatically.

Another connection between the dissected leaf and the SAM can be drawn from the dominant leaf shape mutation *Lanceolate* (*La*) in tomato. A single dose of *La* transforms the compound tomato leaf into a simple lanceolate leaf (Mathan and Jenkins, 1962). *La* homozygotes show a spectrum of phenotypes, the most severe of which is a failure to reach the heart-shaped stage of embryonic development (Caruso, 1968). Cells at the shoot apex lose their meristematic character and fail to initiate cotyledons or leaves (Caruso, 1968). Thus, a single dose of the *La* mutation disrupts the shootlike qualities of the compound leaf primordium, and two doses disrupt the function of the SAM itself. It will be interesting to determine whether other mutations that affect compound leaves also affect SAM functions.

CONCLUSIONS

SAMs are formed in a number of different locations in the plant, display different degrees of activity, and acquire a variety of different fates during development. As a result, significant attention has been given to elucidating the properties of SAMs in flowering plants. Nevertheless, a concise and universal definition of the term SAM remains elusive. What constitutes a SAM? The totipotency and plasticity demonstrated by the ability of differentiated plant cells to dedifferentiate and organize adventitious shoot meristems may suggest that virtually any living cell or group of cells in the plant has the potential to form a meristem, given the appropriate conditions or signals. Most cells, however, do not normally form meristems, and many of the conditions or signals that are required to organize a SAM remain to be discovered. Characterizing mutant phenotypes that disrupt normal meristem function, uncovering patterns of gene expression that mark functional domains within the meristem, and inducing ectopic meristem formation are a few of the recent approaches that are helping to elucidate the mechanisms by which SAMs form, maintain themselves, initate organ primordia, and pattern the shoot system.

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