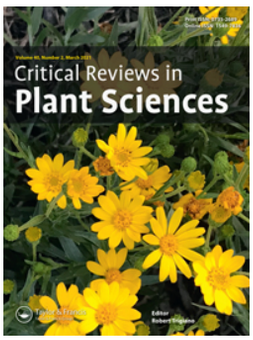

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# Divide and Conquer: The Initiation and Proliferation of Meristems

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**ABSTRACT**

In contrast to animals, which complete organogenesis early in their development, plants continuously produce organs, and structures throughout their entire lifecycle. Plants achieve the continuous growth of organs through the initiation and maintenance of meristems that populate the plant body. Plants contain two apical meristems, one at the shoot and one root, to produce the lateral organs of the shoot and the cell files of the root, respectively. Additional meristems within the plant produce branches while others produce the cell types within the vasculature system. Throughout development, plants must balance producing organs and maintaining their meristems, which requires tightly controlled regulations. This review focuses on the various plant meristems, how cells within these meristems maintain their identity, and particularly the molecular players that regulate stem cell maintenance. In addition, we summarize cell types which share molecular features with meristems, but do not follow the same rules regarding maintenance, including pericycle and rachis founder cells. Together, these populations of cells contribute to the entire organogenesis of plants.

**KEYWORDS**

Founder cells; meristem initiation; meristem maintenance; procambium; root apical meristem; shoot apical meristem

## 1. Introduction

Plants continuously undergo organogenesis during their lifetime; making leaves to collect sunlight for photosynthesis, stems to support growing organs and nutrient transport, floral organs for reproduction, and roots to acquire water, nutrients, and provide anchoring support. Plant growth changes in response to the environment, which results in a variable growth pattern (Kitagawa and Jackson, 2019). Plant organogenesis is attributed to populations of cells known as meristems, which actively divide and differentiate into various cell types to produce mature organs (Clark *et al.*, 1996; Long *et al.*, 1996). Established during plant embryogenesis, plants have two apical meristems: the shoot apical meristem (SAM) and the root apical meristem (RAM), which reside at the shoot and root tips, respectively (Aida *et al.*, 1999; Harada *et al.*, 2003). The SAM is responsible for producing all of the above-ground biomass whereas the RAM produces all of the cell files of the root to drive the root growth into the soil. Plants contain additional meristems that elaborate the plant body and specific cell types with multipotent capabilities to add complexity to various organs. For example, axillary meristems (AMs) are located in the axils of leaves and produce branches (Long and Barton, 2000). While apical and AMs contribute to the longitudinal axis of the plant, meristems, such as the procambium contribute to the radial axis showing that plants have evolved to grow in all directions (Larson, 1976; Swamy and Krishnamurthy, 1980). One defining feature of specific meristematic cells, hereafter referred as initial cells, within the apical meristems is the ability to divide asymmetrically and produce a daughter cell, which has a new identity, and a meristematic cell to replenish the tissue (Dubrovsky *et al.*, 2000; Welch *et al.*, 2007; Goh *et al.*, 2012). In this review, we report on the molecular and cellular factors that contribute to meristem initiation and maintenance, and insight to the molecular players that guide founder cells, which are known to produce new structures without replenishing themselves.

## 2. Apical meristems

### *A. Shoot apical meristem*

The SAM is located at the tip of the shoot and is organized into the following three zones: (1) the central zone (CZ) which contains pluripotent cells that

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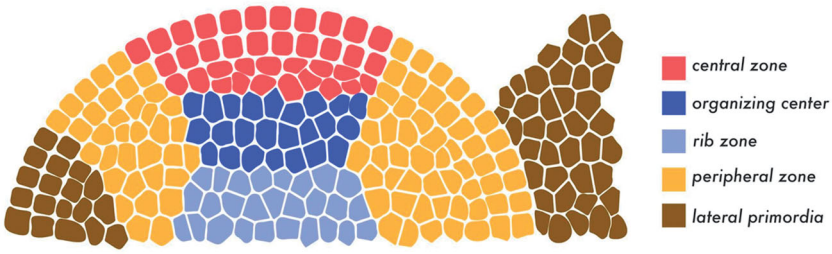


**Figure 1.** The organization of the zones and layers of the SAM. The SAM consists of the central zone (CZ) and rib zone (RZ) which are surrounded by the peripheral zones (PZ). The SAM is further divided into zones L1, L2, and L3. Flanking the PZ are the lateral primordia which form lateral organs.

are self-renewing and have low mitotic activity, (2) the peripheral zone (PZ) which contains cells that are descendants of the CZ cells and contributes to the formation of lateral organs, and (3) the rib zone (RZ) which contributes to the formation of the vasculature and components of the stem (Reinhardt *et al.*, 2003; Yadav *et al.*, 2013) (Figure 1). Subtending the CZ is a small population of cells called the organizing center (OC), which contains some of the molecular players that allow the CZ to maintain pluripotency (Mayer *et al.*, 1998). Within the CZ, there are three layers of cells denoted as: L1, L2, and L3. L1 and L2 make up the surface layers, or tunica, of the SAM, and divide in an anticlinal fashion, where the division plane is perpendicular to the surface, to elongate the cell files and produce the dermal and ground tissue systems (Figure 1). The L3 layer, or corpus, contains the remainder of the cells of the SAM and divides both periclinally, with the division plane parallel to the surface, and anticlinally to produce new cell files and elongate existing ones (Mayer *et al.*, 1998; Traas and Vernoux, 2002).

SAM initiation partially relies on the transcription factor SHOOT MERISTEMLESS (STM) (Clark *et al.*, 1996; Long *et al.*, 1996; Aida *et al.*, 1999). During embryogenesis, STM accumulates at the site of the forming SAM and after germination of the mature seedling, continues to be expressed in mature SAMs (Long *et al.*, 1996). STM regulates the accumulation of cytokinin, a phytohormone required for meristematic cell proliferation (Yanai *et al.*, 2005). Induction of STM results in the rapid accumulation of *ISOPENTENYL TRANSFERASE 7* (*IPT7*) transcripts, which is one of the 9 *IPT* enzymes in cytokinin biosynthesis (Yanai *et al.*, 2005). After SAM initiation, STM acts as a major regulator of meristem maintenance given the coordinated regulation of cytokinin and gibberellins to balance maintenance with differentiation in the SAM, wherein STM positively regulates cytokinin biosynthesis to proliferate the meristematic cells and stimulate the catabolism of gibberellins in the SAM (Jasinski *et al.*, 2005). Mutant analysis of *STM* has implicated its role in both meristem initiation and maintenance as loss-of-function alleles of *STM* are unable to maintain a vegetative SAM and arrest at the seedling stage (Long *et al.*, 1996; Aida *et al.*, 1999). After floral evocation, STM remains in the inflorescence and floral meristems where it regulates meristem size and gynoecium development (Roth *et al.*, 2018). Thus, STM is proposed to function in the maintenance of both the vegetative and floral meristems.

After the SAM undergoes initiation, maintenance between meristematic and differentiated cells is achieved in part by a feedback loop between the transcription factor WUSCHEL (WUS) and the peptide CLAVATA3 (CLV3). WUS accumulates in the RZ of the SAM and migrates to adjacent cell layers (Yadav *et al.*, 2011). Within the OC, WUS functions to specify meristematic cell identity through the repression of transcription factors known to be required in the early stages of leaf development, thus WUS functions to prevent premature differentiation of the cells within the OC (Yadav *et al.*, 2013). WUS is required for meristematic cell proliferation, but in order to prevent over-proliferation of the meristem, WUS acts noncell autonomously to regulate its own expression through the activation of *CLV3* (Mayer *et al.*, 1998). *CLV3* encodes a small peptide which is perceived by the receptor kinase CLAVATA1 and initiates the pathway to repress *WUS* (Clark *et al.*, 1996; Brand *et al.*, 2000). CLV3 signaling determines meristematic cell fate and regulates cell growth rate by ceasing cell division in the PZ (Reddy, 2005)). Thus, the WUSCHEL-CLAVATA pathway is an important regulatory pathway within the SAM to balance cell differentiation with meristem maintenance.

### *B. Root apical meristem*

The RAM plays a primary role in the genesis, growth, and development of the various cell files of the root

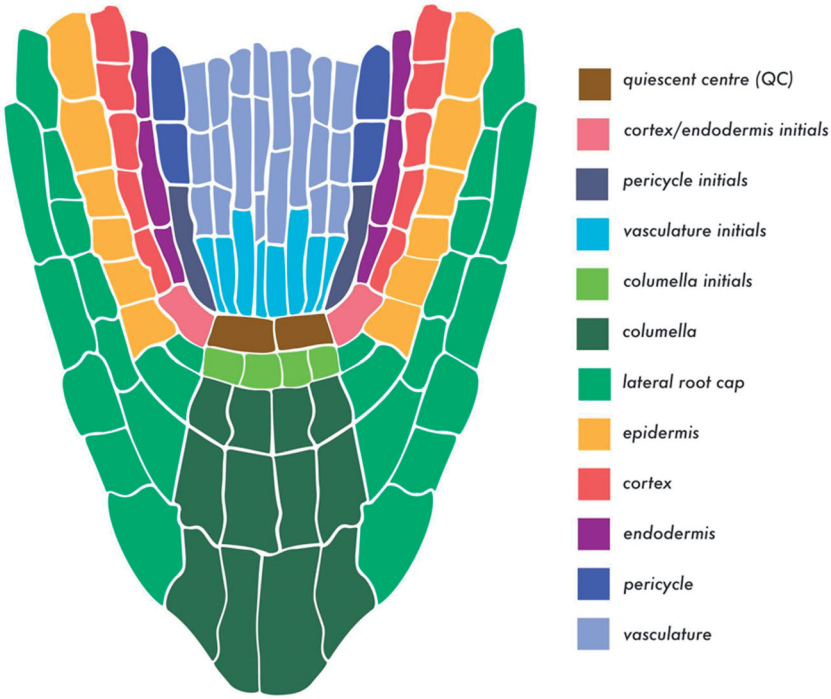


**Figure 2.** The organization of the cell files of the root. Each initial cell in physical contact with the quiescent center (QC) encompasses the RAM.

(Dolan *et al.*, 1993; Kidner *et al.*, 2000) (Figure 2). The RAM resides at the tip of the root, and while it is anatomically dissimilar from the SAM, it contains initial cell populations that divide and undergo differentiation to produce all the root cell files. In *Arabidopsis*, the center of the RAM contains mitotically inactive cells known as the quiescent center (QC) (Figure 2). The cells in direct physical contact with the QC are called initials and make up the stem cell niche (SCN) (van den Berg *et al.*, 1995; Jiang and Feldman, 2005). There are several types of meristematic cells within the RAM: the cortex/endodermal initials (CEIs), which asymmetrically divides to form the cortex and endodermis files, the epidermal/lateral root cap initials (EPi/LRCs) which divides to form the root cap and the epidermis, the columella root cap initials (CSCs) which form the gravity sensing columella cells, and the stele initials which form the xylem, phloem, and pericycle cells in the root vasculature (van den Berg *et al.*, 1995) (Figure 2).

One of the major regulators of meristem cell maintenance is the transcription factor *WUSCHEL-RELATED HOMEOBOX5* (*WOX5*). WOX5 accumulates in the QC and functions in controlling the division rate of the QC (Forzani *et al.*, 2014). *WOX5* mutants contain a mitotically active QC and extra divisions in the surrounding CSCs (Forzani *et al.*, 2014). WOX5 acts in a noncell autonomous manner to maintain the correct number of CSCs through the repression of the transcription factor CYCLING DOF FACTOR 4 (CDF4) by physically interacting with the transcriptional repressors TOPLESS/TOPLESS-RELATED (TPL/TPR) and the histone deacetylase HD19 (Pi *et al.*, 2015). Further, the CSCs subtending the QC rely on WOX5 to repress the premature differentiation of the CSCs into mature columella cells through the negative regulation of the mobile transcription factor SHORTROOT (SHR) (Berckmans *et al.*, 2020; Clark *et al.*, 2020; Van den Broeck *et al.*, 2021). SHR plays major roles in both the radial patterning of the root and maintenance of the root meristem. Specifically, SHR controls the asymmetric division of the CEI cells. SHR is transcribed in the stele and moves into adjacent cells of the QC and CEI where it regulates the transcription factor SCARECROW (SCR) (Gallagher *et al.*, 2004; Clark *et al.*, 2020). SHR and SCR form a protein complex, which is responsible for initiating the division of the CEI into cortex and endodermis through the transcriptional regulation of *CYCD6;1* (Gallagher and Benfey, 2009; Sozzani *et al.*, 2010). The formation of the protein complex prevents the movement of SHR from the endodermis. In *scr* roots, SHR is able to move into the adjacent cell files and cause ectopic periclinal divisions (Cui *et al.*, 2007; Koizumi *et al.*, 2012; Clark *et al.*, 2016). While the role of SHR and SCR has been extensively studied in the ground tissue, their role in the QC is not as clear. New research highlights that their role in the QC is dependent on the concentration

of the protein complex (Clark *et al.*, 2020). High concentrations of the SHR-SCR complex in the CEI promote the formative periclinal division to produce cortex and endodermis, while this concentration level represses divisions in the QC (Clark *et al.*, 2020). Moreover, modeling the concentration dynamics of the SHR-SCR complex and regulatory interactions with other key proteins, such as WOX5 and CYCD6;1, in the QC, CEI, and vascular initials allowed the authors to map QC and CEI division dynamics. Specifically, QC divisions resulted from high SHR/SCR and low WOX5 concentrations, while the rate of CEI divisions resulted from high CYCD6;1 concentrations and was influenced by the QC division (Cruz-Ramírez *et al.*, 2012; Clark *et al.*, 2020; Van den Broeck *et al.*, 2021). This interdependence between CEI and QC divisions was caused by concentration changes due to divisions followed by protein movement between these stem cells (REF QPB). The inclusion of cell-to-cell communication into the model was shown to be crucial to accurately model these division dynamics (REF QPB).

Parallel to the role of WOX5 in the QC, the PLETHORA (PLT) transcription factors are also required to regulate division and differentiation within the RAM (Aida *et al.*, 2004; Santuari *et al.*, 2016). Two PLT transcription factors (PLT1/2) function redundantly to repress cell differentiation (Aida *et al.*, 2004; Galinha *et al.*, 2007). However, while WOX5 has a tight expression pattern within the QC, the PLTs form a concentration gradient within the meristematic region of the root and act in a dose-dependent manner, meaning that the concentration of the PLTs has a major influence on a cell's ability to divide and differentiate (Galinha *et al.*, 2007; Mähönen *et al.*, 2014). High accumulation of PLT1/2 leads to an increase in cell division near the tip of the root or at the meristematic region of the root (Aida *et al.*, 2004; Galinha *et al.*, 2007; Mähönen *et al.*, 2014). Shootward to the meristematic zone contains the elongation and differentiation zone of the root where these cells have ceased dividing and this correlates with a decrease in PLT1/2 accumulation (Mähönen *et al.*, 2014). This demonstrates how crucial both of these pathways are to the maintenance of the RAM.

## 3. Meristems to elaborate the plant's body

While apical meristems are crucial for survival, they are not the sole contributors to a plant's growth. Plants grow in all directions and require additional meristems to achieve this. Branches contribute to the fitness of the plant, producing extra leaves for light capture and flowers for reproduction, thus implicating the importance of AMs. The vasculature system grows in a radial direction, a process which contributes to thickening of the tissues. This type of growth requires a specialized meristem, the procambium, described in detail below.

### *A. Axillary meristem*

The architecture of the plant varies widely between species, and this phenomenon relies on the differential activity of meristematic cells. For example, teosinte has many active AMs, which results in a highly branched plant, whereas the AMs of maize remain dormant, which contributes to maize's apical dominance (Doebley *et al.*, 1995; Dong *et al.*, 2019). AMs reside in the axils of leaves, form post-embryonically, and produce branches that have a lasting impact on the architecture and reproductive success of the plant (Greb *et al.*, 2003; Raman *et al.*, 2008). AMs go through a similar developmental regime as SAMs producing leaves, stems, flowers, and fruits. The formation of branches requires that AMs be first initiated in the leaf axil followed by a break in dormancy to produce the organs which make up the branch (Wang and Jiao, 2018). For AM initiation to occur, cells in the leaf axil require the accumulation of STM, an auxin minimum, and cytokinin to produce a new population of meristematic cells (Long and Barton, 2000; Greb *et al.*, 2003; Balla *et al.*, 2011; Shi *et al.*, 2016). Specifically, before AM initiation begins, auxin accumulation decreases in the developing leaf axil reaching a minimum (Shi *et al.*, 2016). This is followed by an up-regulation of STM in these cells which begins the initiation of AM formation (Shi *et al.*, 2016). In contrast to auxin, cytokinin is necessary to promote bud activation in the leaf axil (Waldie and Leyser, 2018). Plants deficient in endogenous cytokinin or insensitive to cytokinin signaling produce fewer branches when compared to wild type (Müller *et al.*, 2015). Further, auxin has been shown to negatively regulate cytokinin biosynthesis in the leaf axil to repress branching (Tanaka *et al.*, 2006). The initiation and maintenance of branching relies on the antagonistic relationship between auxin and cytokinin as well as STM to accumulate in cells in the leaf axil to maintain an undifferentiated fate. These cells in turn have the potential to either divide and re-populate the axillary meristematic cells or differentiate into the lateral organs which make up branches.

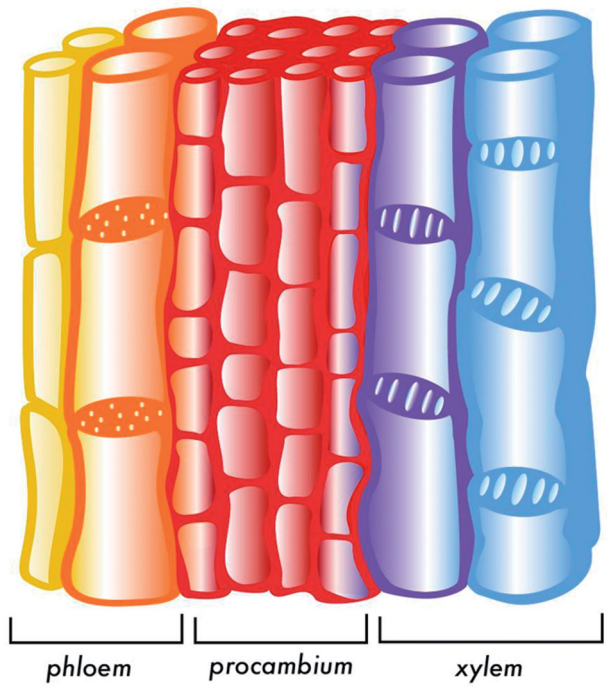


**Figure 3.** The organization of the procambium. A procambial cell divides periclinally to produce a primary phloem cell and a primary xylem cell.

### *B. Procambium*

The vascular system within plants is necessary for long-distance transport of water and nutrients throughout the plant body. Plants utilize a specialized meristem, called procambium, to produce the primary vasculature (Larson, 1976) (Figure 3). The vasculature is made up of xylem and phloem. In the *Arabidopsis* root, the xylem forms a central axis whereas the phloem forms two poles which flank the xylem while stems contain vascular bundles with the primary xylem forming toward the central pith and the primary phloem forming toward epidermis. The cells of the procambium divide periclinaly to produce a xylem cell and a phloem cell (Mähönen *et al.*, 2000) (Figure 3). The procambial cells are established during embryogenesis (Berleth *et al.*, 2000; Yoshida *et al.*, 2014). The establishment of auxin maxima within the forming embryo correlates with the formation of the procambium. The transcription factor MONOPTEROS/AUXIN RESPONSE FACTOR5 (MP/ARF5) plays a major role in procambial identity (Hardtke and Berleth, 1998; Vidaurre *et al.*, 2007). MP/ARF5 accumulates in procambial tissues during embryogenesis and regulates other transcription factors involved in the later stages of vascular development including *TARGET OF MONOPTEROS5* (*TMO5*) (Schlereth *et al.*, 2010). TMO5 is restricted to the xylem precursors in the RAM where it dimerizes with the transcription factor LONESOME HIGHWAY (LHW) to induce periclinal divisions in the procambium (De Rybel *et al.*, 2013). The TMO5-LHW complex initiates cytokinin biosynthesis and subsequent signaling to stimulate procambium cell division (Smet *et al.*, 2019). As similarly described for the apical meristems, the procambium relies on a balance of division and maintenance of the meristematic procambial cells. Procambial cells rely on intrinsic and extrinsic cues for cell division. The peptides CLE41 and CLE44 accumulate in the phloem and function noncell autonomously to stimulate cell division in the procambium (Whitford *et al.*, 2008; Etchells and Turner, 2010). CLE41 and CLE44 are perceived by PHLOEM INTERCALATED WITH XYLEM (PXY), a CLV1-like receptor-like kinase (Etchells and Turner, 2010). Perturbations to either the peptides or receptors results in a disorganized procambium with reduced numbers of vasculature cells and division plane orientation defects (Etchells and Turner, 2010).

The organization of the procambium relies in part on cytokinin signaling (Ohashi-Ito *et al.*, 2014). For example, proliferation of the vasculature is positively regulated by cytokinin (Smet *et al.*, 2019), and when cytokinin is reduced either through signaling or degradation in the procambium, fewer vasculature cells are formed (Smet *et al.*, 2019). Formation of the vasculature is also dependent on cross-talk between cytokinin and auxin (Bishopp *et al.*, 2011a, 2011b). Cells where cytokinin signaling is active have regulatory effects on the localization of two auxin transporters: PIN3 and PIN7 (Bishopp *et al.*, 2011a; Zhang *et al.*, 2011). The transport of auxin by PIN3 and PIN7 route auxin to the xylem where an auxin maxima inhibits cytokinin signaling through the activation of a histidine pseudophospho-transfer encoding gene, *AHP6*, and subsequently induces protoxylem formation (Ohashi-Ito *et al.*, 2014). Additionally, *AHP6* is repressed in forming protophloem by cytokinin signaling (Mähönen *et al.*, 2006). While the organization of the procambium is vastly different from that of the apical meristems, it has an equal reliance on the delicate balance between division and maintenance of cell identity.

## 4. Founder cells

The molecular components that give meristematic cells their identity are also found in other cell types throughout the plant. These cells, denoted as founder cells, differ from their meristematic initials cells because they do not asymmetrically divide in the same manner to replenish themselves. Rather, they divide to produce

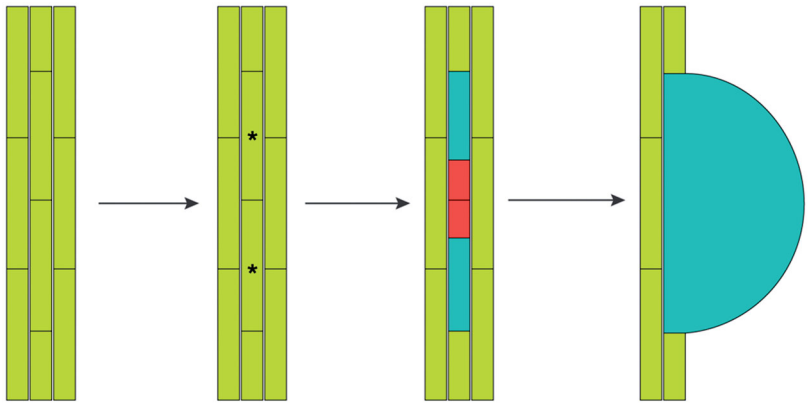

**Figure 4.** The pericycle is a layer of ground tissue associated with the vasculature in the root. Pericycle cells, denoted by an asterisk, adjacent to xylem pole pericycle (XPP) cells acquire a founder cell fate where they divide anticlinally after the perception of an auxin maxima. Following a series of both anticlinal and periclinal divisions a lateral root is formed.

two daughter cells that do not maintain the initial identity (Torres-Martínez *et al.*, 2020).

### *A. Pericycle*

The ability to produce lateral roots increases the surface area of the root system leading to an increase in nutrient uptake and survival. Thus, the formation of lateral roots is crucial to land plant survival and is found throughout the vascular plants. Lateral roots emerge from a specific cell type within the root known as the pericycle, which lies between the stele and the endodermis. In *Arabidopsis*, pericycle cells that are adjacent to the xylem pole, xylem pole pericycle (XPP), are fated to produce lateral roots and acquire founder cell identity (Goh *et al.*, 2012; Torres-Martínez *et al.*, 2020) (Figure 4). The lateral root founder cells are morphologically identical to the surrounding pericycle cells, but are further distinguished by their ability to divide and form lateral roots (Lee *et al.*, 2015; Torres-Martínez *et al.*, 2020). The early patterning of lateral roots relies on auxin signaling in the protoxylem cell files adjacent to the XPP cells. Auxin signaling oscillates every 6 h and following a peak of signaling correlates with the future site of a lateral root (Moreno-Risueno *et al.*, 2010). Auxin induces lateral root formation at all stages of plant development after greening (Xiao *et al.*, 2020). Lateral root formation is redundantly regulated by two transcriptional activators AUXIN RESPONSE FACTOR7/19 (ARF7/19) (Okushima *et al.*, 2007; Goh *et al.*, 2012; Lee *et al.*, 2015). ARF7 and ARF 19 positively regulate the transcriptional activators LATERAL ORGAN BOUNDARIES 16/29 (LBD16/29), which accumulate in the lateral root cells adjacent to the xylem pole and initiate a series of anticlinal divisions to produce a single layer of small founder cells (Goh *et al.*, 2012). Further, auxin signaling in the endodermis is crucial for lateral root initiation in the pericycle (Vermeer *et al.*, 2014). Upon the perception of auxin, yet before cell division, the pericycle founder cell will physically alter its shape and swell, while the adjacent endodermis shrinks, suggesting that a auxin-mediated mechanical force is required to trigger founder cell division (Vermeer *et al.*, 2014). The pericycle relies on the influence of its neighbors to begin the divisions into lateral root primordia (Vermeer *et al.*, 2014). An increase in auxin signaling in the XPP and endodermis results in the proliferation of the pericycle cell and this is the first step in lateral root initiation. Next, the founder cells at the center of this cell file will physically re-orient their division plane to divide periclinally to produce a new cell file (Torres-Martínez *et al.*, 2020). The lateral root founder cells will continue to divide and expand and emerge from the original root.

### *B. Compound leaves*

Cells with meristematic capabilities are not restricted to specific cell types within the roots. In the shoots, compound leaves contain structures called rachises which contain specialized cell types with meristematic capabilities to form complex leaves. In contrast to several well-characterized model organisms (*Arabidopsis*, tobacco, and maize) which form simple leaves, tomatoes, peas, and *Cardamine* produce compound leaves wherein their leaves are composed of several leaflets. In these instances, meristem maintenance and leaf initiation from the SAM is very similar between simple and compound leaves (Long *et al.*, 1996), with the primary differences between simple and compound leaves occurring after organ initiation. For example, in tomato, where compound leaf development has been extensively studied, class 1 KNOTTED-LIKE1 (KNOX1) accumulates in the margins of the leaf

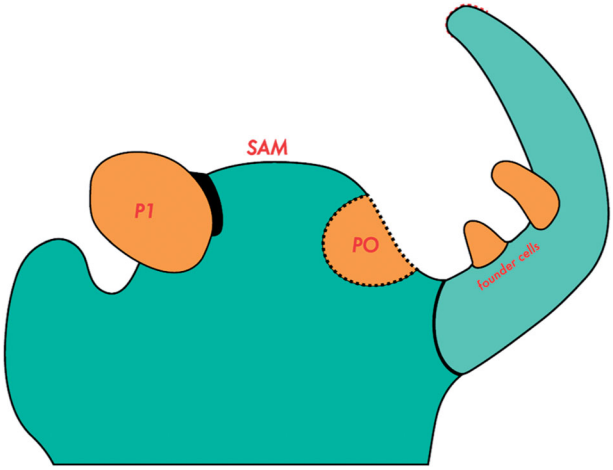


**Figure 5.** Cells on the rachis of a compound leaf regain meristematic identity after leaf initiation. The founder cells on the rachis produce the leaflets of a compound leaf.

primordia of tomato to prevent total differentiation of the leaf and meristematic identity is preserved (Hareven *et al.*, 1996; Chen *et al.*, 1997; Janssen *et al.*, 1998) (Figure 5). The accumulation of KNOX1 is required for leaflet primordia to form. These data are consistent with ectopic expression of *KNOX1* yielding highly compounded leaves and the knock-out of the *KNOX1* ortholog in *Cardamine,* a compound leaf forming species in *Brassicaceae*, reduces the initiation of leaflets within the compound leaf (Hareven *et al.*, 1996; Hay and Tsiantis, 2006). However, in the model legume, *Medicago truncatula*, KNOX1 does not accumulate in the leaf margins. Instead, *SINGLE LEAFLET1* (*SGL1*), the ortholog to the inflorescence meristem identity gene *LEAFY* found in leaf primordia is required for compound leaf development, as mutants lacking *SGL1* have only simple leaves (Wang *et al.*, 2008; He *et al.*, 2020). Further genetic evidence suggests that this holds true for other closely related legume species (Hofer *et al.*, 1997; Champagne *et al.*, 2007). *LFY* control the identity of the floral meristem in *Arabidopsis* and it is ortholog in *Antirrhinum*, *FLORICAULA*, has a similar function, which suggests that the rachis of the compound leaf contains founder cell identity during leaf development.

## 5. Conclusions

Plant meristems are required for highly complex processes, such as the initiation of organs and the elaboration of the plant body whereas founder cells are required to initiate structures and elaborate specific organs. Meristem initiation and maintenance has been studied for decades and has provided valuable knowledge in fundamental plant development, and the advantages to understanding plant meristems have major implications for crop improvement. Current research has suggested that meristems play a role in organ size, either producing larger tomato fruits or increasing the kernel row numbers in the maize infructescence which suggests that these traits can be exploited in other crops (Pautler *et al.*, 2015; Rodriguez-Leal *et al.*, 2019). Other traits regulated by the meristem include branching of both shoots and roots which impacts planting density and nutrient acquisition, respectively (Zhang and Forde, 1998; Zhang *et al.*, 2007; González-Grandío *et al.*, 2013). A greater understanding of the initiation and maintenance of meristems in model organisms will contribute to an abundance of translational plant science to improve the crops used for food and fiber.

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