Trends in Genetics

CellPress

Review

# Expanding the Regulatory Network for Meristem Size in Plants

Mary Galli[1] and Andrea Gallavotti[1,2,*]

**The remarkable plasticity of post-embryonic plant development is due to groups of stem-cell-containing structures called meristems. In the shoot, meristems continuously produce organs such as leaves, flowers, and stems. Nearly two decades ago the WUSCHEL/CLAVATA (WUS/CLV) negative feedback loop was established as being essential for regulating the size of shoot meristems by maintaining a delicate balance between stem cell proliferation and cell recruitment for the differentiation of lateral primordia. Recent research in various model species (*Arabidopsis*, tomato, maize, and rice) has led to discoveries of additional components that further refine and improve the current model of meristem regulation, adding new complexity to a vital network for plant growth and productivity.**

## Trends

Recent studies have uncovered the influence of post-translational regulation in controlling the movement of WUS from the OC to the CZ, and the trafficking of CLV1 from the plasma membrane to endosomal compartments, as well as the enzymes responsible for the arabinosylation of CLE peptides.

The regulation of meristem size takes place by a conserved mechanistic framework among various plant species. However, the functions of orthologous members in this regulatory pathway differ between species.

Recent studies have uncovered direct connections between plant hormones and the WUS/CLV pathway, and these help in understanding how environmental changes influence meristems.

New genes and pathways discovered in various plant species have significantly improved our understanding of meristem size regulation. This highlights the importance of research in different species to dissect complex developmental pathways, and paves the way to modify the WUS/CLV pathway for enhanced crop productivity.

## Meristems, The Round-The-Clock Factories Of Plants

If you ever wondered why mowing your lawn does not kill the grass, you would have inadvertently pondered over one of the most fascinating questions in plant biology–how plants adapt their growth in response to the environment, in this case the severing of their organs. In short, this is due to specialized groups of pluripotent stem cells known as meristems. Meristems are tightly regulated and compartmentalized regions with the constant ability to create new organs throughout development. In contrast to their animal counterparts, most plant organs form post-embryonically, allowing plants to initiate new structures (i.e., blades of grass) in recovery from pathogen, herbivore, or zealous gardening attacks, as well as giving rise to the vast array of diverse plant sizes and shapes from a tiny weed to a giant sequoia. There are several types of meristems in plants such as apical, lateral (i.e., cambium), and intercalary meristems. Studies focused on the shoot apical meristem (SAM) and root apical meristem (RAM) that give rise to all above- and below-ground tissues, respectively, have demonstrated that highly-similar organizational and genetic programs underlie both stem-cell systems, with many of the individual genes being encoded by closely related, tissue-specific homologs [1,2]. Furthermore, genetic and molecular data indicate that these unifying principles are conserved across species [3]. This review will focus solely on apical meristems in the shoot: the embryonically formed SAM (which converts to an inflorescence meristem, IM, following the switch to reproductive development), and post-embryonically formed axillary meristems, AMs, which share an identical organization. The SAM is overall responsible for the formation of the shoot, establishing the main axis of growth, whereas AMs form secondary axes of growth such as branches and flowers. Together, the SAM and AMs establish plant architecture (Box 1).

Active throughout the life cycle, apical meristems have essentially two main functions: (i) to maintain an active population of stem cells, and (ii) to form lateral organs and inner tissue (ground tissue and vasculature). These functions are carried out in distinct spatial domains first defined by cytological analysis, the central, the peripheral, and the rib zones (Figure 1, Key Figure). In the central zone (CZ) a small population of stem cells (~35 cells in *Arabidopsis* [4]) is maintained and undergoes

[1]Waksman Institute of Microbiology, Rutgers University, Piscataway, NJ, 08854-8020, USA
[2]Department of Plant Biology and Pathology, Rutgers University, New Brunswick, NJ, 08901, USA

*Correspondence:
agallavotti@waksman.rutgers.edu
(A. Gallavotti).

http://dx.doi.org/10.1016/j.tig.2016.04.001

## Box 1. Plant Architecture

The body plan of a plant shoot is established by primary and secondary axes of growth. The primary axis of growth is determined by the embryonically formed SAM (and subsequently by the IM). AMs form at the axils of true or modified leaves and establish secondary axes of growth such as branches and flowers. Based on their ability to sustain growth, meristems are generally distinguished as indeterminate, when they continuously maintain their structure and reiteratively form lateral primordia (i.e., in the case of branching), or determinate, whereby they terminate in a differentiated structure (i.e., flower). In addition, meristems can become quiescent after forming a few protective leaves (i.e., buds). The SAM is an indeterminate meristem, while IMs and AMs can be either indeterminate or determinate depending on the species and the developmental stage. The number, position, and fate (indeterminate, determinate, or quiescent) of meristems are key determinants of plant architecture and a major source of variability in the architecture of different plant species because they control if, where, and how branches and flowers are formed during both vegetative and reproductive development. Simplified diagrams of the architecture of species mentioned in this review are provided in Figure I.

In *Arabidopsis*, during vegetative development, the SAM forms a rosette of leaves centered around a short stem at the base of the plant. At the transition to flowering, the SAM produces an elongated stem and acquires the identity of an IM that eventually tops the stem and forms a series of regularly arranged FMs (see also Figure 1 in main text). In rice, SAM and AMs form several shoots that are all eventually topped by branched inflorescences. The maize SAM instead forms a single stem that terminates at maturity in its male inflorescence, the tassel, and carries several female inflorescences (ears) at the axils of leaves on short lateral branches (see also Figure 3 in main text). Tomato is characterized by indeterminate shoot development, but upon floral transition determinate apical meristems terminate in a branched inflorescence, and shoot development continues thanks to AMs that generate a new lateral shoot that, after forming three leaves, switches to a determinate apical meristem fate that reiterates inflorescence branching.

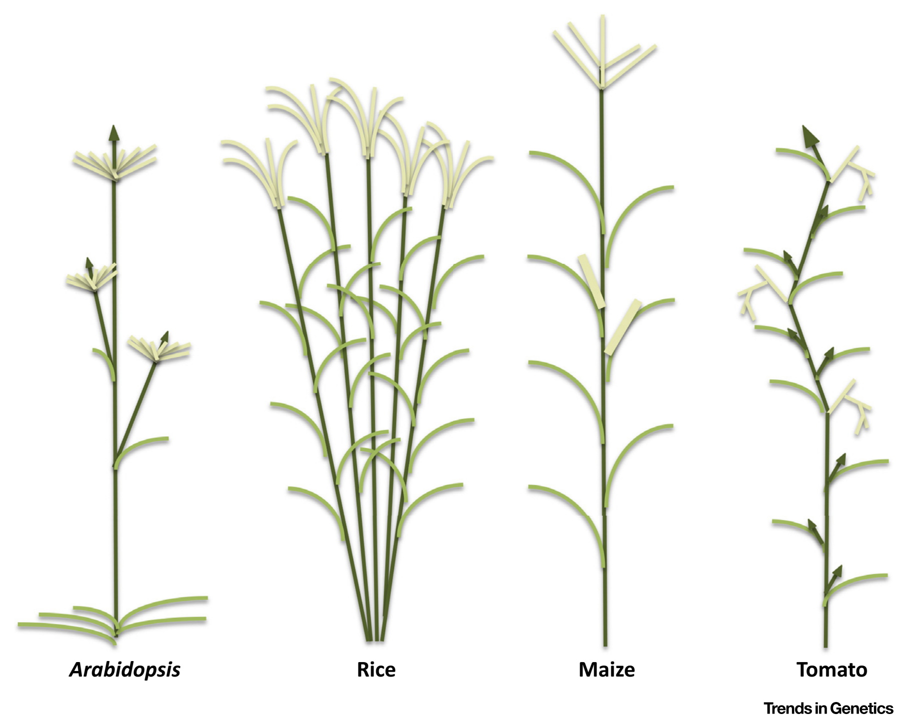

Figure I. Plant Architecture of Different Species. Schematic representations of the mature body plans of *Arabidopsis*, rice, maize, and tomato (not to scale). In dark and light green are represented stems and leaves, respectively, whereas all reproductive structures (branches and flowers) are depicted in yellow. Arrows indicate indeterminate growth.

## Glossary

**Eudicots:** a group of flowering plants (Angiosperms) characterized by the presence of three grooves in pollen grains. The group includes most but not all of the dicotyledon species, characterized by having two embryonic leaves called cotyledons.

**Fasciation:** enlargement of stem and inflorescence diameter as a result of unregulated meristem function.

**Homeobox:** a family of transcription factors characterized by a conserved domain called the homeodomain.

**Monocots:** group of flowering plants characterized by the presence of a single cotyledon.

**Orthologs:** genes in different species that have evolved by speciation from a common ancestor gene.

**Phyllotaxy:** the regular arrangement of lateral primordia around a meristem.

**Plasmodesmata:** channels through the cell wall that connect the cytoplasm of two adjacent cells.

infrequent cell divisions; in the peripheral zone (PZ), cells are recruited to form lateral primordia (e.g., leaves) and are therefore actively dividing cells; and in the rib zone (RZ) meristem cells give rise to the stem. The organizing center (OC, also called the rib meristem), a niche required for the induction and maintenance of stem cells, lies within the CZ and is defined based on the expression