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All together now, a magical mystery tour of the maize shoot meristem

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Crop yield improvement requires optimization of shoot architecture, and can be facilitated by understanding shoot apical meristem (SAM) development. Maize, as one of the most important cereal crops worldwide, is also a model system and has significantly contributed to our fundamental understanding of SAM development. In this review, we focus on recent progress and will discuss communication between different meristem regulators, including CLAVATA receptors and ligands, transcription factors, small RNAs and hormones, as well as the importance of communication between different SAM regions.

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Introduction

The maize shoot system is derived from the shoot apical meristem (SAM), a pool of pluripotent stem cells which have the ability of self-renewal, and initiate new leaves and axillary meristems [1]. Due to its importance in determining shoot architecture and its self-organizing capability, the SAM has brought much attention to scientists for more than a century. As in other plants, the maize SAM is formed during embryogenesis, starting from ~7 days post pollination [2]. In contrast to animals, where organogenesis is usually complete during embryonic development, most new tissues and organs are formed during post-embryonic development in plants [3]. During maize embryogenesis, around five leaves are made before the seed matures and the embryo becomes dormant [4]. Upon germination, the SAM becomes active once more, and new leaves initiate continually until the transition stage, when the vegetative SAM transits to an inflorescence meristem (IM) that produces spikelets and flowers. Axillary meristems produced in association with leaf primordia can produce branches (tillers), or ear inflorescence shoots.

The SAM is comprised of different zones, based on their cellular activity. At the tip, the stem cell niche contains a pool of slowly dividing pluripotent stem cells, and is named the central zone (CZ). Surrounding the CZ is the peripheral zone (PZ), where cells divide more rapidly, and will generate leaf or axillary meristem primordia. Lastly, the rib zone (RZ) lies below the CZ, and cells dividing there will form the stem. A small group of cells called the organizing center (OC), sitting between the CZ and RZ was defined more recently based on molecular markers, and is important for communication between different zones (reviewed in [5,6]). A pioneering study showed that in some plants (though not in maize), the SAM can regenerate after the vast majority of cells are surgical removed [7]. This suggests that the SAM is not rigidly programmed, but can reestablish different zones and communication pathways to rebuild the structure of the meristem. Stem cell activity is at the heart of the SAM, and when this is disrupted by specific mutations, plant growth will be abnormal or will cease completely. In contrast, mutants that upregulate stem cell activity lead to bigger meristems with abnormally flattened and split stems and inflorescences, called fasciation. Such mutants have significantly contributed to our understanding of signaling and communication between zones of the maize SAM (summarized in Table 1). Recent progress has been rapid, fueled by advances in genomics, however the picture is still far from complete. In this review, we will synthesize findings from recent studies, focusing on receptor based communication between different zones of the maize SAM and intracellular signal transduction.

The classical CLAVATA (CLV)-WUSCHEL (WUS) model established in *Arabidopsis* is largely conserved in maize

The CLV-WUS model has long been recognized as a key feedback pathway that regulates communication between different zones in the *Arabidopsis* SAM [1]. It relies on communication between a series of receptors, peptide ligands and transcription factors that are expressed in different zones. Central to this complex network is WUS, a homeodomain transcription factor expressed in the OC to promote stem cell fate [8], and CLV3, a small peptide ligand that is secreted from cells in