

# Cultivating potential: Harnessing plant stem cells for agricultural crop improvement

Penelope Lindsay<sup>1,3</sup>, Kyle W. Swentowsky<sup>1,3</sup> and David Jackson<sup>1,2,\*</sup>

<sup>1</sup>Cold Spring Harbor Laboratory, Cold Spring Harbor, NY 11724, USA

<sup>2</sup>National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan, Hubei, 430070, China

<sup>3</sup>These authors contributed equally to this article.

\*Correspondence: David Jackson ([jacksond@cshl.edu](mailto:jacksond@cshl.edu))

<https://doi.org/10.1016/j.molp.2023.12.014>

## ABSTRACT

**Meristems are stem cell-containing structures that produce all plant organs and are therefore important targets for crop improvement. Developmental regulators control the balance and rate of cell divisions within the meristem. Altering these regulators impacts meristem architecture and, as a consequence, plant form. In this review, we discuss genes involved in regulating the shoot apical meristem, inflorescence meristem, axillary meristem, root apical meristem, and vascular cambium in plants. We highlight several examples showing how crop breeders have manipulated developmental regulators to modify meristem growth and alter crop traits such as inflorescence size and branching patterns. Plant transformation techniques are another innovation related to plant meristem research because they make crop genome engineering possible. We discuss recent advances on plant transformation made possible by studying genes controlling meristem development. Finally, we conclude with discussions about how meristem research can contribute to crop improvement in the coming decades.**

**Key words::** meristem, crop improvement, plant transformation, plant breeding, crop yield, gene editing

**Lindsay P., Swentowsky K.W., and Jackson D. (2024).** Cultivating potential: Harnessing plant stem cells for agricultural crop improvement. *Mol. Plant.* **17**, 50–74.

## INTRODUCTION

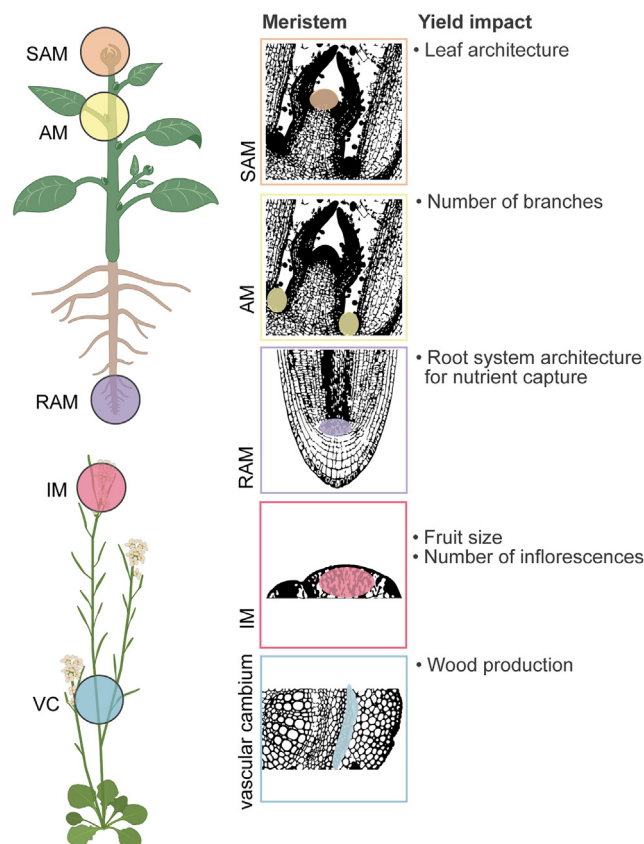
Stem cells are undifferentiated cells that give rise to differentiated tissues and organs (Sablowski, 2004; Heidstra and Sabatini, 2014; Liu et al., 2023a). Short-range intercellular signaling helps maintain a small pool of stem cells in both plants and animals, although the specific molecular players mediating this process are distinct. Plant stem cells, housed in meristems, are unique from animal stem cells in their longevity and their capacity to promote post-embryonic growth. Another remarkable feature of plant developmental trajectories is that many differentiated cell types can de-differentiate. These unique growth characteristics enable plants to grow flexibly depending on abiotic and biotic cues.

Meristems within crop species produce all agriculturally important structures, including harvestable organs such as fruits, leaves, seeds, and tubers as well as supportive tissues like stems and roots. Research on crop species throughout the last century has uncovered how breeding has dramatically altered a wide variety of plants to suit various growing conditions and improve crop productivity. Many crop breeding innovations arose through modifications affecting stem cells. In this review, we will explore the different stem cell types in plants, how stem cell activity is

controlled, and how we have harnessed the knowledge of stem cell regulators to improve several agronomically important traits in plants (Figure 1). Furthermore, we will discuss plant tissue culture and examples of how we may use our knowledge of meristems to further improve crops as we move into a challenging era for crop scientists and breeders.

## SIGNALING PATHWAYS IN THE SHOOT APICAL MERISTEM (SAM)

The shoot apical meristem (SAM) drives primary growth at the shoot apex (Figure 2A). The SAM in many plants is organized in three cell layers: the L1 or epidermal layer, L2 or subepidermal layer, and L3, which will form vascular and stem tissues, although not all plants have this arrangement (Satina et al., 1940). Within the L2/L3 layer lies the organizing center (OC), a group of cells that promote stem cell identity within the SAM. As the shoot grows, lateral organ primordia that will become leaves are produced from the SAM, and an axillary meristem (AM) develops within the axil of each leaf. Both SAMs and AMs



**Figure 1. Meristem types and their impact on yield.**

Circles indicate meristem location. Red, inflorescence meristem (IM); or orange, shoot apical meristem (SAM); yellow, axillary meristem (AM); blue, vascular cambium (VC); purple, root apical meristem (RAM). The highlighted region indicates where meristems are located in section illustrations. Plant illustrations were created with BioRender.

begin development as stem cells that produce vegetative structures (i.e., leaves and leafy branches). Floral induction occurs when florigen is produced and moves systemically through the plant. When florigen reaches meristems, they acquire inflorescence meristem (IM)/floral meristem (FM) identity. In this section, we will first describe the signaling pathways that control SAM and IM organization because many signaling components are shared between the two meristem types. We will then discuss how these signaling pathways have been modified to improve yield traits.

### The CLAVATA signaling pathway

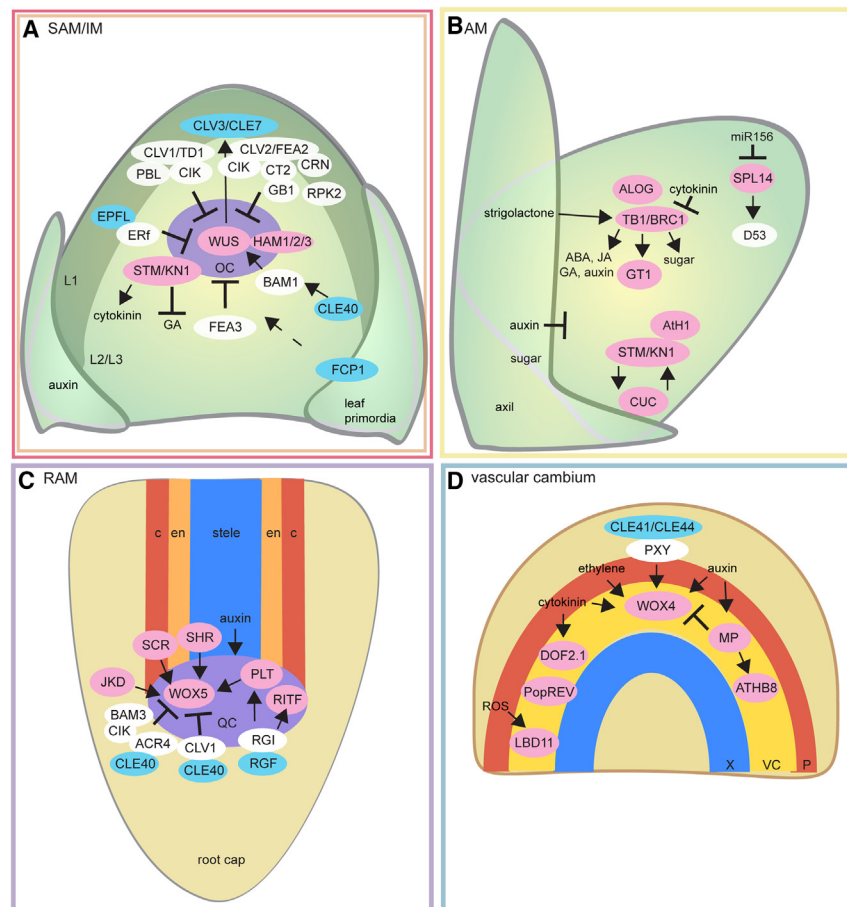
Central to control of shoot and IM maintenance is the *CLAVATA* (CLV) signaling pathway. Cells within the OC express the stem cell-promoting transcription factor *WUSCHEL* (*WUS*), the founding member of a plant-specific transcription factor family called *WOX* (*WUS-RELATED HOMEODOMAIN*). *WUS* protein moves outward toward L1 cells in the shoot apex through plasmodesmata (Yadav et al., 2011; Daum et al., 2014). Here, *WUS* activates expression of *CLV3*, a founding member of the *CLV3/EMBRYO-SURROUNDING REGION* (CLE) peptide family. *CLV3* is cleaved into a short peptide, modified with arabinosyl sugars (Ohya et al., 2009; Xu et al., 2015), and secreted to inhibit *WUS* transcription via perception by a suite of leucine-rich

repeat (LRR) kinases (Somssich et al., 2016). This *CLV3*-*WUS* negative feedback loop ensures a self-renewing population of stem cells while allowing the formation of new tissues and organs. Recent insights into the CLV signaling pathway have expanded the receptor and CLE peptide repertoire required for meristem organization and reveal crosstalk between the CLV signaling pathway with other meristem signaling pathways (Rodríguez-Leal et al., 2019; Su et al., 2020; Liu et al., 2021a; 2021b; Blümke et al., 2021; Wang et al., 2021b; Schlegel et al., 2021; Dao et al., 2022).

*WUS* is essential for meristem maintenance in many plant species. *wus* plants repeatedly produce a set of defective shoots that will make a limited number of leaves and occasionally an incomplete inflorescence with a small, prematurely terminating meristem (Laux et al., 1996). Conversely, when *WUS* is overexpressed, as in the dominant maize *BARREN INFLORESCENCE 3* (*BIF3*) mutant, there is an overproliferation of stem cells that results in a small ball-shaped ear with highly reduced productivity (Chen et al., 2021).

*WUS* promotes stem cell activity through various mechanisms. One primary mechanism is to activate signaling related to the cell division-promoting hormone cytokinin (CK; Leibfried et al., 2005). *WUS* directly regulates the cytokinin response factors *ARABIDOPSIS RESPONSE REGULATOR 5, 6, 7, and 15* (*ARR5, ARR6, ARR7, and ARR15*). Type B *ARRs*, in turn, activate *WUS*, creating a positive feedback loop between cytokinin and *WUS* (Wang et al., 2017; Zubo et al., 2017; Xie et al., 2018). Cytokinin triggers the expression of the MYB transcription factor *MYB3R4*, which promotes mitotic cell division (Yang et al., 2021a). *WUS* also regulates auxin signaling, ensuring the appropriate level of auxin response within stem cells, which is critical because auxin promotes differentiation (Busch et al., 2010; Ma et al., 2019). Beyond binding to transcription factor binding sites to modulate gene expression, *WUS* promotes histone deacetylation, which reduces expression of its target genes in the stem cell niche (Ma et al., 2019; Wang et al., 2022a). Collectively, the diverse targets of *WUS* indicate that control of many cellular processes is necessary for promoting stem cell identity.

CLV receptors and CLE peptides maintain the precise spatial expression of *WUS* and its transcriptional activity, which is key to preserving the balance between stem cells and differentiated tissues. Given that *WUS* induces the expression of *CLV3*, and *CLV3* represses *WUS* expression, how is *WUS* able to be expressed in the OC? One potential explanation involves cooperation between the GIBBERELLIC-ACID INSENSITIVE (GAI)/REPRESSOR OF GAI (RGA)/SCARECROW (SCR) (GRAS) transcription factors HAIRY MERISTEM 1, 2, and 3 (HAM1, HAM2, and HAM3, respectively) and *WUS* (Zhou et al., 2018). HAM interacts with *WUS*, and the presence of HAM in the OC prevents *CLV3* expression. Epidermis-specific microRNAs (miRNAs) block expression of *HAM* in the epidermis, which allows *CLV3* to be expressed there (Han et al., 2020). An alternative explanation for the paradox of *WUS* expression in the OC comes from Perales et al. (2016), suggesting that the activation or repression of *CLV3* by *WUS* depends on *WUS* concentration. Under this model, higher concentrations of *WUS* repress *CLV3*, and lower *WUS* concentrations activate *CLV3*.



**Figure 2. Signaling pathways in plant stem cell niches.**

**(A)** SAM identity is maintained by the mobile transcription factors WUSCHEL (WUS) and SHOOTMERISTEMLESS (STM). WUS and STM have numerous downstream signaling targets, including hormone pathways. WUS induces the expression of *CLAVATA3* (*CLV3*), a small secreted peptide that is perceived by a suite of receptor proteins, including CLAVATA 1 (*CLV1*), CLAVATA 2 (*CLV2*), CIKs, and RPK2. Downstream effectors of CLV receptors include PBL kinases, the pseudokinase CORYNE (CRN), and G alpha protein COMPACT PLANT 2 (*CT2*). WUS activity is also regulated by the receptor-like protein FASCICATED EAR 3 (*FEA3*) and its peptide ligands FCP1, BARELY ANY MERISTEM 1 (*BAM1*) and CLE40 and ERECTA ligands EPFL and Erf receptors. Cytokinin promotes stem cell activity, while auxin promotes differentiation. The OC is denoted by a purple circle.

**(B)** AM activity is initiated by STM/KN1 and AtH1. Boundary formation is maintained by a feedback loop between the transcription factor CUP SHAPED COTYLEDON 2 (*CUC2*) and STM. Dormancy is controlled by the transcription factor TEOSINTE BRANCHED 1 (*TB1*)/BRANCHED 1 (*BRC1*), which is regulated by strigolactone and cytokinin. *TB1* targets include *GRASSY TILLERS 1* (*GT1*), hormone, and sugar pathways. Branching is also regulated by negative feedback by the miRNA *miR156* and transcription factor *SPL14*, which, in turn, regulates *DWARF53* (*D53*).

**(C)** Auxin promotes RAM identity. Stem cell maintenance is promoted by WOX5, PLT, and RITF transcription factors. The RGF-RGI ligand

receptor module controls expression of *PLT* and *RITF*, and CLE40 acts through *CLV1*, *BAM*, *ACR*, and *CIK* to control *WOX5* expression. Differentiation is controlled by the SHOOTROOT (*SHR*) SCARECROW (*SCR*) transcription factor module. C, cortex; en, endodermis; QC, quiescent center.

**(D)** Vascular cambium activity is promoted by *WOX4*, which is induced by ethylene and auxin as well as the phloem-derived CLE peptide-receptor module CLE41/CLE44 and PXY. The vascular cambium is also maintained by the auxin-induced transcription factor MONOPTEROS (*MP*), which, in turn, activates *ATH8*. Cytokinin promotes vascular cambium identity through activation of *WOX4*, and PopREVOLUTA also contributes to vascular cambium maintenance. ROS act through *LBD11* to regulate the vascular cambium. X, xylem; VC, vascular cambium; P, phloem. Blue ovals, peptide ligands; white ovals, receptors; pink ovals, transcription factors.

(Perales et al., 2016). In either case, a regulatory mechanism is in place to ensure that WUS is specifically expressed in the OC.

While *CLV3* is critical for meristem organization, as evident in the enlarged meristems of *clv3* mutants, additional *CLE*s mediate meristem organization with *CLV3* (Je et al., 2016; Rodriguez-Leal et al., 2019; Liu et al., 2021a). For instance, the maize *CLV3* ortholog is *ZmCLE7*, and mutations affecting two additional *CLE* peptides, *FLORAL ORGAN NUMBER 2-LIKE CLE PROTEIN 1* (*FCP1*) and *CLE1E5*, have mild phenotypes on their own but greatly enhance the phenotype of *Zmcle7* (Rodriguez-Leal et al., 2019; Liu et al., 2021a). In tomato, *SICLE9* is dramatically upregulated in the *Siclv3* mutant to actively compensate for a lack of *SICLEV3* (Rodriguez-Leal et al., 2019). In *Arabidopsis*, at least nine other *CLE* genes control meristem size in addition to *CLV3* (Rodriguez-Leal et al., 2019). While *CLE* expression is unchanged in *clv3* mutant inflorescence apices in bulk qRT-PCR experiments, *in situ* hybridization and reporter line expression analyses suggest that *AtCLE16*, *AtCLE17*, and *AtCLE25* are expressed more strongly in *clv3* meristems, which makes it unclear whether other

*Arabidopsis CLE* genes actively or passively compensate for a lack of *CLV3* (Rodriguez-Leal et al., 2019; Dao et al., 2022; John et al., 2023). Thus, while each species has a particular dominant *CLE* peptide that controls meristem size, other *CLE*s can act as a backup to ensure the proper balance of stem cell proliferation and differentiation.

A suite of LRR kinase receptors perceive *CLE* peptides to restrict meristem size, including CLAVATA 1 (*CLV1*), BARELY ANY MERISTEM 1, 2, and 3 (*BAM1*, *BAM2*, and *BAM3*, respectively), and RECEPTOR-LIKE PROTEIN KINASE 2 (*RPK2*) (Clark et al., 1997; DeYoung et al., 2006; Kinoshita et al., 2010). *CLV1* is a negative regulator of stem cell population size; *clv1* mutant meristems are enlarged relative to the wild-type (WT) (Leyser and Furner, 1992; Clark et al., 1993, 1997). Dominant-negative *clv1* alleles are stronger than loss of function, suggesting that multiple receptors are needed to restrict WUS expression (Diévert et al., 2003).

*BAM1*, *BAM2*, and *BAM3* are the LRR kinases most closely related to *CLV1* in *Arabidopsis*. They control diverse processes,



including stem cell proliferation in shoots and roots, anther development, vein development, and the movement of small RNAs (DeYoung et al., 2006; Hord et al., 2006; Rosas-Diaz et al., 2018; Crook et al., 2020). Intriguingly, *bam* mutants have smaller meristems, but *bam1;bam2;clv1* triple mutants have greatly enlarged meristems compared with *clv1* mutants, suggesting that *BAM* genes partially compensate for the lack of *CLV1* (DeYoung et al., 2006; DeYoung and Clark, 2008). This partial compensation is thought to arise from derepression of *BAM* expression in the *CLV1* expression domain (Nimchuk, 2017).

In *Arabidopsis*, *BAM1* promotes *WUS* expression via perception of CLE40, acting in differentiating cells surrounding the meristem (Schlegel et al., 2021). The antagonistic function of *BAM1* and CLE40 in relation to *CLV1* and *CLV3* appears counterintuitive, but this result is consistent with recent studies in the non-flowering plant *Marchantia polymorpha*. The *M. polymorpha* *CLV3* ortholog, *MpCLE2*, promotes stem cell activity when applied exogenously, and *Mpcle2* mutants produce fewer stem cells than WT plants (Hirakawa et al., 2020). Unexpectedly, activity of *MpCLE2* does not depend on the single *WOX* gene present in *M. polymorpha* but instead acts through the NAC transcription factor JINGASA (Hirakawa et al., 2020; Takahashi et al., 2023). *CLV* signaling also mediates stem cell organization independently of *WUS* in the moss *Physcomitrium patens*, suggesting that the ancestral function of the *CLV* signaling pathway is independent of *WOX* activity (Camarata et al., 2022). Further investigation of the *CLV* signaling pathway across the land plant lineage will help us better understand the ancestral relationship between *WOX* transcription factors and *CLV* receptors.

*Arabidopsis* *CLV2* and maize FASCIATED EAR 2 (FEA2) are homologous LRR receptor-like proteins that participate in CLE peptide-mediated signaling independent of *CLV1*. They both perceive multiple CLE peptides to restrict stem cell proliferation (Müller et al., 2008; Je et al., 2018). *CLV2*/FEA2 downstream effectors include the pseudokinase CORYNE (CRN) and heterotrimeric G proteins COMPACT PLANT 2 (CT2) and G protein  $\beta$  subunit (G  $\beta$ ) (Müller et al., 2008; Je et al., 2018; Wu et al., 2020a). FEA3, an additional receptor-like protein first described in maize, is also a negative regulator of stem cell proliferation, restricting *WUS* expression from below the OC (Je et al., 2016). FEA3 perceives the CLE peptide FCP1, but it is not known what other factors interact with FEA3 to limit stem cell proliferation. LRR receptor-like proteins lack a kinase domain, which suggests that they interact with other proteins for signal transduction. The *CLV3* INSENSITIVE RECEPTOR KINASE (CIK) LRR kinases are co-receptors of *CLV1*, *CLV2*, and *BAM1/2/3*, but it is not yet clear whether these proteins may also act as co-receptors for FEA3 (Hu et al., 2018; Zhu et al., 2021).

While many receptor proteins in the *CLV* signaling pathway have been studied, less is known about downstream components that connect CLE peptide perception to *WUS* repression. The protein phosphatase 2C subunits POLTERGEIST (POL) and POL-LIKE 1 (PLL1) act downstream of the *CLV* signaling pathway (Yu et al., 2000, 2003; Song and Clark, 2005; Song et al., 2006; Gagne et al., 2008). Several cytoplasmic kinases interact with *CLV* receptors, including the Pto-interacting (PTI)-like receptor-

like cytoplasmic kinase (RLCK) subfamily VIII MAZZA and RLCK subfamily VII kinases PBS1-like 34/35/36 (PBL34/35/36) (Wang et al., 2021a; Blümke et al., 2021). PBL kinases function redundantly; *pbl34 pbl35 pbl36* triple mutants increase meristem size and carpels per flower, acting through *CLV1*. PBL34 phosphorylates POL and PLL1, connecting these two downstream signaling components (DeFalco et al., 2022). It is not currently known what factors directly modulate *WUS* expression, but MAZZA and related proteins may be involved because they can shuttle between the cytoplasm and plasma membrane via their reversible palmitoylation moiety (Blümke et al., 2021). These findings highlight the challenge of identifying downstream signaling components in the *CLV* pathway due to functional redundancy.

As more is revealed about the *CLV* signaling receptor pathway, how these components coordinate to control stem cell proliferation remains an open question. Existing data emphasize that spatial expression differences of the receptors and their ligands are critical for stem cell maintenance. For example, in *Arabidopsis*, *CLE40* is expressed in a domain complementary to *CLV3* in the shoot meristem and acts antagonistically to *CLV3* but can complement *clv3* when expressed in the *CLV3*-expressing domain (Hobe et al., 2003; Schlegel et al., 2021). Heterogenous receptor complex combinations also fine-tune signal transduction processes. Je et al. (2018) found that downstream interactors of FEA2, the pseudokinase CRN, and G-protein alpha subunit CT2 function additively to restrict meristem size. CRN and CT2 respond to different CLE peptides, ZmFCP1 and ZmCLE7, respectively, supporting the idea that downstream interactors of *CLV* receptors help provide signaling specificity (Je et al., 2018). Ligand binding affinity may also vary among receptors and between different receptor combinations. *CLV3* perception by *CLV1* affects *CLV1* abundance and location at the plasma membrane and may trigger clathrin-mediated endocytosis (Nimchuk et al., 2011). Clathrin-mediated endocytosis of *CLV1* is critical for *CLV3* perception, highlighting the importance of protein abundance and timing in signal transduction (Wang et al., 2023a). Together, an exquisite degree of spatiotemporal fine-tuning of these signaling components ensures robust maintenance of meristem organization.

### The ERECTA (ER) signaling pathway

In parallel to *CLV* signaling receptors and ligands, the ERECTA (ER) receptor family and associated EPIDERMAL PATTERNING FACTOR-LIKE (EPFL) peptides control meristem size (Chen et al., 2013; Shpak, 2013; Uchida et al., 2013; Kosentka et al., 2019; Zhang et al., 2021a). The *Arabidopsis* Landsberg erecta (*Ler*) ecotype carries a weak allele of *er*, resulting in a dwarf phenotype with compact flower clusters. More severe *er* alleles are even shorter and have shorter, wider siliques. *er* and higher-order *er erl* mutants have fewer cells in pedicels compared with WT, indicating that, although *er erl erl2* mutants have enlarged meristems, the dwarf and organ size phenotypes are due to reduced cell proliferation (Shpak et al., 2003, 2004). The ER ligands EPFL1, EPFL2, EPFL4, and EPFL6 are also required for stem elongation, pedicel size, and meristem size and are expressed in the SAM periphery but act non-cell autonomously (Kosentka et al., 2019). In rice, the ER pathway controls panicle architecture through activating a mitogen-activated protein

kinase (MAPK) signaling cascade, and mutating a subset of the EPFL ligands increases panicle branching (Guo et al., 2020, 2023). The ER and CLV signaling pathways are interconnected because *er erl1 erl2 clv3* mutants synergistically increase meristem size compared with *clv3* or *er erl1 erl2*, and *er erl1 erl2* mutants are insensitive to CLV3 peptide (Kimura et al., 2018; Zhang et al., 2021a). *WUS* expression expands laterally in *er erl1 erl2* mutants, and both *WUS* and *CLV3* expression decreases in seedlings treated with EPFL4 peptide, suggesting that ER signaling restricts *WUS* expression laterally in the shoot apex. *ER* genes have *WUS*-independent functions as well, however, because *er erl1 erl2* mutations restore the SAM in the *wus* mutant (Kimura et al., 2018).

### SHOOTMERISTEMLESS (STM)/KNOTTED1 (KN1): Key stem cell identity transcription factors

Additional essential factors in maintaining stem cell identity in the SAM are the orthologous KN1-like homeobox (KNOX) transcription factors *Arabidopsis* STM/maize KN1. Mutants lacking *STM* or *KN1* fail to maintain stem cells in the shoot apex (Barton and Poethig, 1993; Kerstetter et al., 1997). Conversely, ectopically expressing *STM/KN1* results in changes in leaf morphology, which was originally thought to be a result of incorrect specification of stem cell identity (Freeling and Hake, 1985; Sinha et al., 1993; Lincoln et al., 1994; Hay and Tsiantis, 2010). Surprisingly, single-cell pseudotime trajectory analyses comparing the WT and the *KN1-O* dominant mutant demonstrate that ectopic *KN1* expression actually accelerates cell differentiation in the developing maize leaf, which authors propose may be due to increased and ectopic leaf sheath growth (Satterlee et al., 2020). Together, these studies demonstrate that *STM/KN1* are essential for promoting stem cell identity and the timing of cell differentiation.

*KN1* is not transcribed in the L1 layer, but its protein is present there, resulting from intercellular trafficking of both the protein and mRNA through plasmodesmata (Jackson et al., 1994; Lucas et al., 1995; Xu et al., 2011; Kitagawa et al., 2022). *STM* movement is important for its stem cell maintenance function because nonmobile versions do not fully complement the *stm* mutant (Balkunde et al., 2017). Downstream targets of *STM/KN1/KNOX* include gibberellic acid (GA), cytokinin, and auxin hormone pathways (Jasinski et al., 2005; Bolduc et al., 2012). Cytokinin also induces the expression of *STM*, which may provide a feedforward positive feedback loop to reinforce stem cell identity. Conversely, the auxin response factor MONOPTEROS (MP) represses *STM* expression, promoting flower formation (Chung et al., 2019). In addition to its impact on hormone signaling, *STM* interacts with *WUS*, and both *STM* and *WUS* directly induce *CLV3* expression (Su et al., 2020). *WUS* also impacts *STM* expression because inducible overexpression of *WUS* increases *STM* expression in the meristem (Su et al., 2020). Therefore, *STM* and *WUS* promote stem cell identity through separate and overlapping mechanisms.

### Integrating meristem maintenance with environmental cues

Hormones play a critical role in SAM maintenance, and because they are influenced by external stimuli, they can help dictate growth rate in response to the environment. As highlighted

earlier, the key stem cell-promoting transcription factors *WUS* and *STM* modulate plant hormone pathways, notably cytokinin. In addition to cytokinin, auxin plays a pivotal role in stem cell maintenance by promoting cell differentiation, directing the development of new lateral organs, and limiting stem cell proliferation (Smith and Nimchuk, 2023). *CLV* signaling can also act independent of *WUS* through auxin-mediated processes to control flower development (John et al., 2023). Because plant hormones integrate information from multiple cellular processes, including perception of abiotic stresses, they can fine-tune the timing of organ differentiation in response to environmental cues (Jones et al., 2021). Light activates *WUS* expression, likely through cytokinin signaling, and sugar metabolites regulate meristem size through TARGET OF RAPAMYCIN (TOR) kinase, a central integrator of growth with environmental factors (Pfeiffer et al., 2016; Considine, 2018; Janocha et al., 2022). *STM* forms nuclear condensates that increase with salt stress treatment, and salt stress increases AM formation in an *STM*-dependent manner, demonstrating that meristem activity is influenced by abiotic stress (Cao et al., 2023). CLE peptides are also induced by abiotic and biotic stress, providing an additional link between plant growth and the environment (Bashyal et al., 2023). This integration of environmental cues with meristem activity provides essential input about when and how to grow. Because climate change is making environmental conditions less predictable, research linking how abiotic and biotic stress impacts meristem development could substantially improve crop breeding in the future.

### Reactive oxygen species (ROS) signaling

Oxygen and ROS are diffusible signals that impact cell growth and cell division and have recently been implicated in controlling meristem architecture (Zeng et al., 2017; Mhamdi and Van Breusegem, 2018). The superoxide anion promotes stemness through activation of *WUS*, and hydrogen peroxide promotes cell differentiation (Zeng et al., 2017). Glutaredoxins control the oxidation state of the TGACG-binding (TGA) transcription factor FEA4, impacting its ability to control expression of genes important for meristem regulation. Glutaredoxin activity may be triggered by ROS levels, providing an additional way in which ROS mediate meristem signaling (Yang et al., 2021b). Additionally, hypoxia promotes meristem development by preventing degradation of LITTLE ZIPPER 2 (ZPR2), a protein that negatively regulates the activity of homeodomain-leucine zipper (HD-ZIP) transcription factors (Weits et al., 2019; Xu et al., 2019). ROS levels are influenced by environmental stimuli as well as hormone signaling pathways, which provides an additional way to fine-tune meristem activity in response to environmental cues (Waszczak et al., 2018).

### Mechanical feedback

Stem cell organization is influenced not only by genetic and chemical cues but also from mechanical feedback mechanisms (reviewed in Trinh et al., 2021). Plant cell mechanical properties are controlled by the cytoskeleton, cell wall, and turgor pressure. Turgor pressure is heterogeneous among cells in the shoot apex, which impacts growth rate, suggesting that water conductivity regulates meristem architecture (Long et al., 2020). Beyond its role in transcriptional regulation, auxin regulates

SAMs/IMs				
Gene	Species	Class	Type	Citation
<i>BrCLV3</i>	<i>Brassica rapa</i>	CLE peptide	protein coding	Fan et al. (2014)
<i>BnCLV3</i>	<i>Brassica napus</i>	CLE peptide	loss of function	Yang et al. (2018)
<i>ZmCLE7</i>	<i>Z. mays</i>	CLE peptide	Regulatory	Liu et al. (2021a)
<i>SlCLV3 (Fas)</i>	<i>S. lycopersicum</i>	CLE peptide	regulatory	Xu et al. (2015); Wang et al. (2021b)
<i>GhCLV3</i>	<i>Gossypium hirsutum</i>	CLE peptide	regulatory	McGarry et al. (2023)
<i>FIN</i>	<i>S. lycopersicum</i>	hydroxyproline O-arabinosyltransferase (HPAT)	loss of function	Xu et al. (2015)
<i>ZmFEA2</i>	<i>Z. mays</i>	CLE receptor	regulatory, loss of function	Taguchi-Shiobara et al. (2001); Bommert et al. (2013); Trung et al. (2020)
<i>ZmFEA3</i>	<i>Z. mays</i>	CLE receptor	protein coding	Je et al. (2016)
<i>Ppr-CLV1</i>	<i>P. pruinosa</i>	CLE receptor	loss of function	Lemmon et al. (2018)
<i>ZmCRN</i>	<i>Z. mays</i>	CLE receptor	regulatory	Je et al. (2018)
<i>BnCLV1</i>	<i>B. napus</i>	CLE receptor	loss of function	Yang et al. (2018)
<i>BnCLV2</i>	<i>B. napus</i>	CLE receptor	Loss of Function	Yang et al. (2018)
<i>BrCLV1</i>	<i>B. rapa</i>	CLE receptor	protein coding	Chow et al. (2023)
<i>Lc</i>	<i>S. lycopersicum</i>	WUS	regulatory	Muños et al. (2011)
<i>ZmACO2</i>	<i>Z. mays</i>	Ethylene biosynthesis	regulatory, loss of function	(Ning et al., 2021)
<i>KRN2</i>	<i>Z. mays, O. sativa</i>	WD40 protein	regulatory	(Chen et al., 2022c)
<i>KRN4/UB3</i>	<i>Z. mays</i>	SPB transcription factor	regulatory, protein coding	(Liu et al., 2015)
<i>OsCKX2</i>	<i>O. sativa</i>	cytokinin oxidase	regulatory	(Ashikari et al., 2005)
AMs				
<i>TB1</i>	<i>Z. mays</i>	TCP transcription factor	regulatory	Clark et al. (2006)
<i>GT1</i>	<i>Z. mays</i>	HD-ZIP I transcription factor	loss of function	Whipple et al. (2011)
<i>TIN1</i>	<i>Z. mays</i>	C2H2 zinc-finger transcription factor	regulatory	Zhang et al. (2019)
<i>CG1</i>	<i>Z. mays</i>	<i>miR156</i>	duplication	Chuck et al. (2007)
<i>IPA1/WFP</i>	<i>O. sativa</i>	SBP transcription factor	miRNA-binding site	Jiao et al. (2010)
<i>TIN</i>	<i>T. aestivum</i>	cellulose-synthase-like protein	regulatory	Hyles et al. (2017)
<i>TN1</i>	<i>T. aestivum</i>	ankyrin repeat protein	protein coding	Dong et al. (2023)
Inflorescence branching				
<i>S</i>	<i>S. lycopersicum</i>	WOX transcription factor	protein coding	Lippman et al. (2008)
<i>An</i>	<i>S. lycopersicum</i>	F-box protein	protein coding	Lippman et al. (2008)
<i>SITOE1</i>	<i>S. lycopersicum</i>	AP2 transcription factor	loss of function	Sun et al. (2023)
<i>SIFUL1</i>	<i>S. lycopersicum</i>	MADS-box transcription factor	loss of function	Jiang et al. (2022)
<i>SIFUL2</i>	<i>S. lycopersicum</i>	MADS-box transcription factor	loss of function	Jiang et al. (2022)
<i>SIMBP20</i>	<i>S. lycopersicum</i>	MADS-box transcription factor	loss of function	Jiang et al. (2022)
<i>J2</i>	<i>S. lycopersicum</i>	MADS-box transcription factor	loss of function	Soyk et al. (2017)
<i>EJ2</i>	<i>S. lycopersicum</i>	MADS-box transcription factor	loss of function	Soyk et al. (2017)
<i>GN1A</i>	<i>O. sativa</i>	cytokinin oxidase	loss of function	Ashikari et al. (2005)
<i>DEP1</i>	<i>O. sativa</i>	G $\gamma$ subunit protein	protein coding	Huang et al. (2009b)

Table 1. Meristem-related genes with positive effects on agronomic traits.

(Continued on next page)

SAMs/IMs				
Gene	Species	Class	Type	Citation
<i>DST</i>	<i>O. sativa</i>	zinc-finger protein	loss of function	Huang et al. (2009a); Li et al. (2013)
<i>GNP1</i>	<i>O. sativa</i>	GA oxidase	regulatory	Wu et al. (2016)
<i>FZP1</i>	<i>O. sativa</i>	AP2 transcription factor	regulatory	Huang et al. (2018); Wang et al. (2020a)
<i>OsTB1</i>	<i>O. sativa</i>	TCP transcription factor	protein coding	Takai et al. (2023)
<i>IPA1/WFP</i>	<i>O. sativa</i>	SBP-box transcription factor	miRNA binding	Jiao et al. (2010)
<i>Q</i>	<i>T. aestivum</i>	AP2 transcription factor	miRNA binding	Simons et al. (2006); Debernardi et al. (2017); Greenwood et al. (2017)
<i>TaSPL17</i>	<i>T. aestivum</i>	SPB-box transcription factor	regulatory, overexpression	(Liu et al., 2023a; 2023b; 2023c)
<i>OsEPFL6/7/9</i>	<i>O. sativa</i>	EPF ligands	loss of function	(Guo et al., 2023)
<i>OsCKX4</i>	<i>O. sativa</i>	cytokinin oxidase	miRNA	(Wang et al., 2022a)

Table 1. Continued

cell wall properties, which, in turn, impact cell growth (Heisler et al., 2010; Peng et al., 2022). WUS and cytokinin direct anisotropic growth in the meristem, which affects SAM mechanical properties (Banwarth-Kuhn et al., 2022). The interplay of mechanical, chemical, and genetic cues is pivotal in maintaining the delicate balance between stemness and differentiation, but much still needs to be uncovered to understand how these signals are combined to control stem cell activity. Mechanotransduction through receptors and/or secondary messengers that are sensitive to mechanical stimuli is underexplored in meristem maintenance and deserves further attention (Trinh et al., 2021).

### Meristem signaling pathways are targets for crop improvement

Gene families involved in meristem maintenance have expanded during land plant evolution, which may contribute to morphological novelty (Hirakawa, 2022). Due to the expansion of genes controlling meristem organization, genetic manipulation of these genes could alter plant architecture and yield without severely impacting plant growth due to genetic redundancy. Indeed, several recent studies have highlighted how altering components involved in meristem signaling can positively affect yield potential.

Subtle changes to the CLV signaling pathway can positively impact yield traits in maize, tomato, ground-cherry, brassica, and cotton (Muños et al., 2011; Fan et al., 2014; Xu et al., 2015; Xu et al., 2015, 2015; Yang et al., 2018; Chu et al., 2019; Chow et al., 2023; McGarry et al., 2023). For example, reducing *CLE7* and *FCP1* expression by deleting *cis*-regulatory elements (CREs) using CRISPR-Cas9 results in larger meristems, wider ears, and increased productivity in maize. This is in contrast to *cle7-* and *fcp1*-null mutants, which produce misshapen ears with reduced kernel number (Liu et al., 2021a). Furthermore, leveraging weak alleles of genes encoding the receptor-like proteins *FEA2* and *FEA3* can increase kernel row number and, in the case of *FEA2*, increase yield in elite maize varieties (Bommert et al., 2013; Je et al., 2016; Trung et al., 2020). Similar to maize, CRISPR-Cas9-induced mutations of tomato

*S/CLV3* CREs subtly change *S/CLV3* expression, impacting fruit size (Wang et al., 2021b). Furthermore, *CLV1* mutations in the orphan crop species ground-cherry (*Physalis pruinosis*) increase locule number and fruit size (Lemmon et al., 2018), demonstrating how knowledge of meristem signaling can lead to rapid improvement in species that have not been well studied. Together, these studies demonstrate the widespread efficacy of editing the CLV signaling pathway to increase inflorescence size.

Other regulators of meristem size can impact yield. Convergent selection of the domestication allele *KRN2* among two distantly related cereals, maize and rice, positively impacted yield in both species (Chen et al., 2022a; 2022b; 2022c). *KRN2* encodes a WD40 protein that interacts with DUF1644 to control IM size and kernel row number. CRISPR-edited null alleles of *krm2* increase yield by about 10% in both maize and rice without negative impacts on other aspects of plant growth. Therefore, studying evolutionary aspects of domestication can provide novel insights into genes controlling meristem architecture and yield.

Here we describe just a few studies where modifying meristem signaling pathways increases yield, but there are numerous other examples, summarized in Table 1. It should be noted, however, that yield impact is determined by allele strength, genetic background, and the environment, so effects must be thoroughly tested in field trials to determine whether a particular gene modification will increase yield (Khaipho-Burch et al., 2023).

### Axillary meristems

As the shoot tip grows, the flanks of the stem cell niche produce leaf primordia and axillary meristems (AMs, Figure 2B) in the leaf axils. In the early stages of AM development, *STM* expression is maintained at low levels through an interaction between *STM* and *ARABIDOPSIS THALIANA* HOMEODOMAIN GENE 1 (*ATH1*) to maintain meristematic competency (Cao et al., 2020). An auxin minimum in the early-developing AM established by PIN-FORMED (PIN) transporters is necessary for *STM* maintenance (Wang et al., 2014a, 2014b; b).



The acquisition of stem cell identity also requires proper boundary formation between the SAM and developing primordium (reviewed in Žádníková and Simon, 2014). In *Arabidopsis*, the best-known regulators of boundary formation are *CUP-SHAPED COTYLEDON 1–3* (*CUC1–CUC3*), which are expressed in the boundary domain separating the SAM from the developing primordia (Aida et al., 1999). *Arabidopsis cuc* mutant primordia fail to separate from the meristem region, resulting in a singular ring of cotyledon tissue without AMs (Aida et al., 1997). The maize *CUC* homologs, *ZmNAM1* and *ZmNAM2*, fulfill similar roles in maize lateral organ development (Han et al., 2023). *CUCs* act in a signaling pathway with several other transcription factors, *LATERAL SUPPRESSOR* (*LAS*), *REVOLUTA* (*REV*), and *REGULATOR OF AXILLARY MERISTEMS 1* (*RAX1*) to boost *STM* expression in the developing AM when boundary identity is established (Greb et al., 2003; Keller et al., 2006; Raman et al., 2008). Then, a non-cell-autonomous signaling loop between *CUCs* and *STM* establishes the identity of the new AM (Balkunde et al., 2017; Nicolas et al., 2022). At later stages of AM development, CK accumulates in the developing AM, where it activates *WUS* expression and initiates the CLV3-*WUS* feedback loop (Wang et al., 2017).

When an AM is established, it will either be maintained in a dormant state or develop into one of several possible structures, depending on the species and context. In the most simple case, an AM will develop into a branch, in grasses called a tiller. A phenomenon known as apical dominance, which involves communication between the SAM and AM, results in a trade-off between branching and plant height. Apical dominance is an important component of crop yield, and the domestication of most crop species favored a branching pattern that optimizes yield (reviewed in Wang et al., 2018).

Many genetic, hormonal, and environmental factors contribute to the regulation of branch growth. From a hormone standpoint, it is generally understood that auxin produced from the shoot apex travels down and acts as a repressor of branching, while cytokinin produced near the AM and strigolactone moving up from the roots to the AM promotes branching (reviewed in Beveridge et al., 2023). These three hormones (as well as other signals such as abscisic acid [ABA], GA, sugar, and light) control AM dormancy through a well-conserved central regulator transcription factor belonging to the TEOSINTE BRANCHED 1 (*TB1*)/CYCLOIDEA/PROLIFERATING CELL FACTOR (*PCF*) (*TCP*) family. The founding member of this family, *TB1*, is responsible for the change in branching between the highly branched wild progenitor species teosinte (*Zea mays* ssp. *parviglumis*) and single-stalked maize (*Z. mays* ssp. *mays*) (Doebley et al., 1997). *TB1* is a branching repressor, and domestication favored a *TB1* allele with higher expression (Clark et al., 2006). The *Arabidopsis TB1* homolog, *BRANCHED 1* (*BRC1*), regulates branching in response to CK and strigolactone (Braun et al., 2012; Dun et al., 2012). In maize, *TB1* regulates the class I HD-ZIP (HD-ZIP I) transcription factor *GRASSY TILLERS 1* (*GT1*) to control shoot branching (Whipple et al., 2011; Dong et al., 2019). *TB1* directly binds to and regulates at least 268 genes to maintain AM dormancy. Most of these genes are transcriptionally activated by *TB1* and include ones that respond to ABA, jasmonic acid, GA, auxin, and sugar metabolism and transport (Dong et al., 2019). Using a multiomics integrative network

incorporating maize gene and protein expression data, Han et al. (2023) identified the *ALOG* (*Arabidopsis* *LSH1* and *Oryza* *G1*) transcription factors *ZmALOG1* and *ZmALOG2* as regulators of branching suppression and potential interacting partners of *TB1*.

The plant age pathway also regulates AM growth and dormancy, acting upstream of strigolactone signaling. Juvenile plants express *miR156*, a miRNA that targets members of the *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE* (*SBP/SPL*) transcription factor family. A duplication of a *miR156* gene leading to its increased expression causes excessive tillering in the dominant maize mutant *Corngrass1* (Chuck et al., 2007). Consistent with this result, *Arabidopsis spl9 spl15* double mutants have more branches (Schwarz et al., 2008). Likewise, a mutation in the rice *OsSPL14* gene *IPA1/WFP* (*IDEAL PLANT ARCHITECTURE/WEALTHY FARMER'S PANICLE*) disrupts its *miR156* target site, resulting in higher *OsSPL14* levels and fewer tillers (Jiao et al., 2010). *IPA1* binds the promoter of *D53*, a component of the strigolactone perception pathway, to regulate branching (Song et al., 2017), and this module functions similarly in wheat (Liu et al., 2017a).

Sugars also play an important role in activating dormant AMs independent of auxin. Decapitating the SAM rapidly induces axillary bud outgrowth, and this change is temporally correlated with the accumulation of sucrose at dormant AMs in pea and *Arabidopsis*, whereas auxin accumulates later (Mason et al., 2014; Fichtner et al., 2017). Plants perceive local sucrose availability indirectly through trehalose-6-phosphate (Tre6P) (reviewed in Fichtner and Lunn, 2021). Tre6P controls shoot branching independent of the *BRC1* pathway (Fichtner et al., 2021), although the downstream mechanism is still unknown. These recent findings led to a paradigm shift where sugar and not auxin signaling exerts primary control over axillary branching.

The degree of branching significantly influences agronomic traits in nearly all crop species. More branches means a greater canopy area per plant but also reduces the number of plants that can be grown in a given area. In some crop species, notably rice and wheat, shoot branches terminate with the harvestable inflorescence, so branch number and yield can be directly correlated. Branching in domesticated species was and continues to be optimized for each particular crop and cropping system. For example, maize, sorghum, and sunflower domestication strongly favored apical dominance, and this eventually produced modern single-stalked plants that are efficiently grown as row crops. The domestication allele of *TB1* (discussed above) explains most of the differences in branch number between teosinte and maize, but other minor alleles, such as *tiller number 1* (*tin1*), were also selected to reduce tiller number during domestication (Zhang et al., 2019). Selection of apically dominant sorghum favored a particular *SbTB1* allele, suggesting that artificial selection acting on *TB1* was similarly utilized in maize and sorghum (Wu et al., 2022b). In sunflower, the evolution of branch number is more complex. Apical dominance is preferred, but branching was unintentionally re-introduced to sunflower to improve other plant traits, and then additional branching suppressors were subsequently bred in (reviewed in Radanović et al., 2018). Numerous loci for sunflower branch number have been mapped, but the largest effect is the branching locus (*B*) on chromosome 10



(Bachlava et al., 2010; Mandel et al., 2013). Most of these loci are uncharacterized, but one minor-effect branching locus likely corresponds to a sunflower homolog of *MORE AXILLARY GROWTH 2* (*MAX2*), which encodes an F-box protein involved in strigolactone signaling (Mandel et al., 2014).

Conversely, increased branch number is a target of improvement for some crop species. In wheat, where the number of fertile tillers influences yield, many quantitative trait loci (QTLs) for this trait have been identified (Ren et al., 2018; Cao et al., 2020). Two wheat tiller number QTLs have been fine mapped: *TILLER INHIBITION* (*TIM*), which encodes a cellulose synthase-like protein (Hyles et al., 2017), and *TILLER NUMBER1* (*TN1*; distinct from the maize *tin1* locus), which encodes an ankyrin repeat protein that affects ABA biosynthesis (Dong et al., 2023). More tillers are desirable in biomass crops, such as miscanthus and switchgrass. Transgenic switchgrass accessions with moderate *miR156* overexpression yield more biomass, which results in greater biofuel production (Fu et al., 2012; Baxter et al., 2018). These examples demonstrate how developmental regulators can be leveraged to optimize branching for crop performance.

### Stolons, rhizomes, and tubers

AMs can produce additional specialized structures with agricultural significance. Stolons or runners are aboveground shoots that grow parallel to the ground and can propagate plants asexually. The two main crop species that produce stolons are strawberries and mint. In strawberry, the relationship between stolons and berries is complex, and removal of some stolons can either increase or decrease berry weight depending on the variety (Morrison et al., 2018). Thus, optimizing stolon number could be an effective approach to improve strawberry yield.

Rhizomes, similar to stolons, are stems that grow parallel to the ground but below the soil surface and serve as storage organs in perennial species. In recent decades, there has been growing attention toward the development of perennial varieties of cereal crops because these could be more sustainable (Chapman et al., 2022). Because rhizomes are key structures that allow perennial plants to survive dormant periods (e.g., winter freeze or summer drought), researchers have made efforts to understand rhizome development using the perennial rice wild relative *Oryza longistaminata* as a model system. Rhizomes develop from AMs and high concentrations of sucrose can trigger this developmental transition (Fan et al., 2022). It is possible that, in perennial grasses, the large amount of carbohydrates being partitioned into belowground storage organs is sufficient to trigger rhizome development, but more research on how sugars affect rhizome development is needed. The rhizome is also the harvestable organ of ginger and turmeric. Recent work has elucidated how ginger rhizomes expand and soften at the later stages of development by decreasing ABA and CK levels while increasing GA, auxin, and jasmonic acid levels (Chen et al., 2020; Ren et al., 2023), but how the transition from AM to rhizome occurs in ginger is unknown.

Tubers are another shoot-borne belowground storage organ found in several crop species, most notably potato. Tubers differ from rhizomes in that they are typically more swollen and tend to

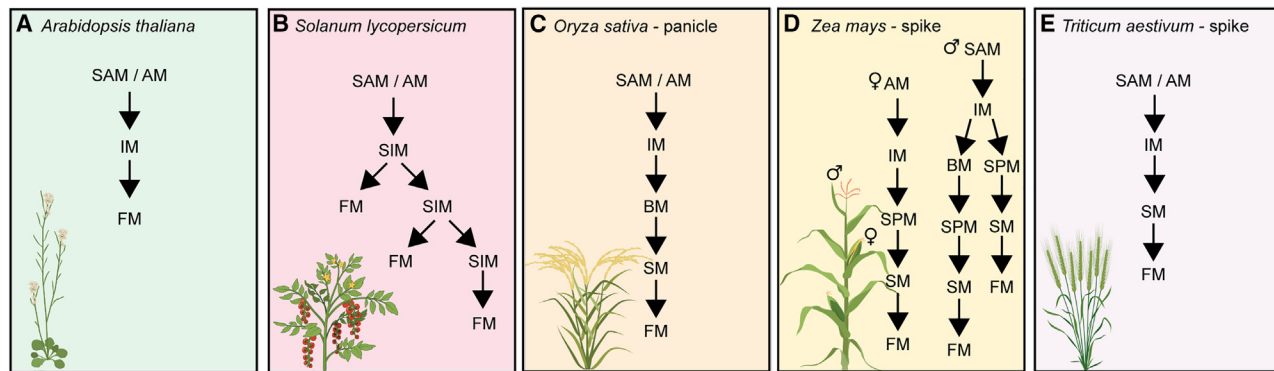
remain at the base of the plant instead of growing horizontally. Tuber development has been extensively characterized in potato due to its agricultural significance (reviewed in Zierer et al., 2021). Potato plants produce belowground stolons that become tuberized in response to photoperiodic cues. Under short-day conditions, a potato FT-like protein, StSP6A, is produced in the leaves and travels to stolons, where it induces tuberization (Navarro et al., 2011; Sharma et al., 2016). StSP6A forms a tuberigen activation complex in stolons with StFDL1 and St14-3-3s, similar to the florigen activation complex that promotes flowering in the SAM (Teo et al., 2017). After stolons have received the tuberization induction cue, tuber development proceeds by modifying hormone and sucrose levels. Nicolas et al. (2022) demonstrated how only belowground AMs develop into tubers while aerial ones do not. They showed that *BRC1b*, one of the two potato *BRC1* paralogs, is expressed only in aerial axillary buds, where it increases ABA levels to lower the number of plasmodesmata connections to these buds. This action reduces the sink strength and prevents StSP6A from entering these buds, allowing it to accumulate only in the belowground stolon buds, where tubers will develop. In addition to potato, FT orthologs influence development of storage organs in onion (Lee et al., 2013), cassava (Adeyemo et al., 2019), and the medicinal herb *Callerya speciosa* (Xu et al., 2016), indicating that storage organs are regulated by common mechanisms in diverse species. Studying stolons, rhizomes, and tubers can help improve crop performance in plants whose storage organs are harvested or an essential component of their survival. Also, introducing storage organs to species that do not naturally produce them could be a significant step in the transformation of annual crops into perennial species.

### Inflorescence branching

The majority of agricultural crop production relies on harvesting inflorescence biomass. Therefore, shaping inflorescence architecture is an effective way of increasing yield. For example, in cereal crop species, QTLs for inflorescence architecture often overlap those for yield, suggesting that inflorescence branching significantly contributes to crop yield traits (Huang et al., 2009a; Yan et al., 2011; Nadolska-Orczyk et al., 2017; Li et al., 2018; Xu et al., 2020; Lin et al., 2021b). However, excessive inflorescence branching may limit yield when resources are limited because this could lead to flower abortion (Stephenson, 1981; Soyk et al., 2017), and in many cases of crop domestication, inflorescence branching has already been optimized to improve yield.

The inflorescence develops from the IM, which shares signaling modules with the SAM, but unique IM components are also involved. AMs grow out from the primary IM, producing inflorescence branches or flowers. There is significant variation in inflorescence organization and development between species, and major differences are observed between fruit and cereal crops (Figure 3). We will discuss these in turn, using tomato as a model for fruit crops and rice and maize for grasses.

Tomato mutations that cause meristem overproliferation by directly or indirectly altering WUS/CLV signaling can also increase inflorescence branch number (Lippman et al., 2008; Xu et al., 2015; Rodríguez-Leal et al., 2017; Chu et al., 2019). Several mutations also alter inflorescence branch number by affecting the timing



**Figure 3. IM architecture varies among plant species.**

**(A)** In *Arabidopsis thaliana*, the SAM or AM transitions into an IM, which, in turn, produces floral meristems (FMs).

**(B)** The compound inflorescence of *Solanum lycopersicum* derives from the sympodial inflorescence meristem (SIM), which repeatedly branches into an FM and additional SIM.

**(C)** In *Oryza sativa*, the SAM or AM transitions into an IM, which, in turn, produces branch meristems (BMs). BMs produce spikelet meristems (SMs), which transition into FMs, which will form rice panicles.

**(D)** In *Z. mays*, the female IM, which produces the ear, derives from AMs. The IM produces spikelet pair meristems (SPMs). Each SPM produces two SMs, and each SM produces two FMs, one of which aborts (not shown). The male IM, which will form the maize tassel, is derived from the SAM and produces BMs but otherwise follows the same developmental trajectory as the female inflorescence.

**(E)** The *Triticum aestivum* IM derives from the SAM/AM. The IM produces SMs, which transition into FMs to form the wheat spike. Plant illustrations were made in BioRender.

of inflorescence maturation. This is a consequence of the sympodial growth form that drives inflorescence growth in tomato, where the IM terminates and produces a specialized AM in its flank called a Sympodial Inflorescence Meristem (SIM). After the original IM terminates, this iterative process continues with new growth from the SIM, which then produces a new SIM that will itself terminate (Figure 3B). Tomato plants carrying *compound inflorescence* (*s*) or *anantha* (*an*) alleles increase inflorescence branching by delaying meristem termination. After each new IM produces another SIM, the original IM retains its ability to generate another SIM instead of terminally differentiating (Lippman et al., 2008; Park et al., 2012). The outcome is a significant increase in inflorescence branching and many more flowers per inflorescence. The highly branching *s* allele is caused by a mutated *SIWOX9* and was likely selected hundreds of years ago to increase tomato yield (Lippman et al., 2008).

Another signaling module in tomato involving *FRUITFULL 1* (*FUL1*), *FUL2*, and *MADS-BOX PROTEIN 10* (*MBP10*) regulates branching by delaying FM development (Jiang et al. (2022). *SITOE1* (*TARGET OF EAT1*) encodes an AP2 transcription factor that regulates *SISTER OF TM3* (*STM3*) (Sun et al., 2023), which, in turn, modulates inflorescence branching by regulating *FUL1* and *JOINTLESS 2* (*J2*) (Wang et al., 2021c, 2023b).

An interaction between tomato *J2* and *ENHANCER OF J2* (*EJ2*), two MADS-box transcription factors homologous to *Arabidopsis* *SEPALLATA4*, also affects inflorescence branching. *j2* mutants lack an abscission zone on their pedicels. Modern tomato breeding favors this mutation because it facilitates mechanical harvestability. The introduction of *j2* into breeding lines in the mid-1900s resulted in overly excessive branching, however, due to an epistatic interaction with *ej2*, which is nearly ubiquitous in tomato, because it increases fruit and sepal size (Soyk et al., 2017). Breeders likely mitigated these adverse epistatic effects

by selecting for unlinked suppressor loci, but these genotypes do not benefit from the yield advantage imparted by moderate branching (Soyk et al., 2017, 2019). When *j2* and *ej2* are combined with *s*, inflorescence branching increases slightly, leading to a higher yield through greater fruit number, demonstrating the potential of this strategy for tomato improvement (Soyk et al., 2017).

Grass inflorescences display unique architectures owing to the arrangement of their spikelets, the grass-specific floral branch units. Each spikelet contains at least one floret, which holds the stamens and pistils. A spikelet also has several subtending bracts that enclose the floral organs until maturity: the palea, lemma, and glumes. In most grass species, inflorescences are categorized either as spikes or panicles. In spikes, such as in maize and wheat (Figure 3D and 3E), florets are directly attached to the rachis, and in panicles, such as in rice (Figure 3C), spikelets are connected to the rachis by branches (Allred, 1982). Because cereal grass species are among the most widely cultivated crops, we have gained significant insights into developmental pathways that regulate these two inflorescence types.

Although inflorescences may appear different across these species, many of the genes and developmental processes that shape overall architecture are conserved. At the early stages of development, a grass spike contains the terminal dome-shaped IM, which can produce branch meristems (BMs) at its base, followed by several rows of spikelet meristems (SMs) along its axis (Figure 3C–3E). In maize, spikelet pair meristems (SPMs) are produced from the IM, which give rise to two SMs (Figure 3D). Branching is controlled by two signaling centers at the SM/SPM: one at the SM/SPM base, where *RAMOSA* genes are expressed, and another at the subtending bract, within the *TASSEL SHEATH 4* (*TSH4*)/*PLASTOCHRON* (*TSH4/PLA*) expression domain (reviewed in Bommert and Whipple, 2018; Kellogg, 2022). The discussion in this review will focus on the genes and

signaling networks of grass inflorescence branching that have particular relevance for enhancing crop production.

A notable feature of maize is its spatially separated male inflorescences (tassels), which terminate the shoot apex, and female (ear) inflorescences borne on axillary shoots. Maize inflorescences also have distinct branching patterns; tassels have multiple long branches at their base, whereas ears are composed of a single spike with numerous rows of spikelets. Conversely, rice produces a single terminal panicle per tiller. During rice domestication and improvement, increased panicle branching has been selected to increase the amount of harvestable grain per plant (reviewed in Li et al., 2021).

Compared with the compact architecture of the maize tassel, teosinte tassels are large, dense, and highly branched (Xu et al., 2017). Maize breeders may have selected for smaller, more compact tassels during domestication and improvement because they intercept less light and use fewer metabolic resources (Grogan, 1956; Duncan et al., 1967; Hunter et al., 1969). We have come to understand the genetic architecture of tassel branching through analysis of mutants with altered branching patterns.

Complex genetic networks regulate maize tassel branching (Eveland et al., 2014; Bommert and Whipple, 2018; Wang et al., 2022b; Kellogg, 2022) and have been integrated into a multiomics regulatory network (Wang et al., 2023c). Many signals that regulate vegetative shoot branching perform a similar role in inflorescence branch development. Given its role in regulating other lateral organs, auxin is unsurprisingly a key regulator of tassel branching. Many tassel branch mutants map to genes encoding auxin biosynthetic enzymes (Gallavotti et al., 2008; Phillips et al., 2011), Aux/IAA co-receptors (Barazesh and McSteen, 2008; Galli et al., 2015), components regulating auxin transport (McSteen et al., 2007; Skirpan et al., 2008; Zhu et al., 2022), and auxin-responsive transcription factors (Gallavotti et al., 2004, 2011; Yao et al., 2019). In rice, the *ospid-4* mutation affects auxin transport, resulting in fewer panicle branches (Wu et al., 2020a; 2020b). OsPID interacts with the transcription factor OsMADS16, suggesting that PINOID proteins, which affect auxin transport by modifying PIN transporters, may also directly affect transcription (Wu et al., 2020a; 2020b).

Genes involved in CK, GA, strigolactone, and ABA signaling are also implicated in maize tassel branch development (Liu et al., 2021b; Wang et al., 2023c), but our knowledge of how these phytohormones contribute is limited. Some of the major genes that affect rice panicle branching modulate cytokinin biosynthesis (Ashikari et al., 2005; Huang et al., 2009b; Li et al., 2013; Guo et al., 2018, 2020) and catabolism (Kurakawa et al., 2007), but how downstream CK signaling affects branching is unknown. *GRAIN NUMBER PER PANICLE 1* (*GNP1*) encodes a GA20ox gene, and higher *GNP1* expression increases CK levels by elevating expression of *KNOX*, which leads to more branched panicles (Wu et al., 2016).

Similar to its role in vegetative axillary branch growth, Tre6P also controls maize inflorescence branching. *RAMOSA3* (*RA3*) encodes a trehalose phosphate phosphatase (TPP) enzyme, and *ra3* mutants have multiple branches at the base of the ear

(Satoh-Nagasawa et al., 2006). TPP enzymes convert Tre6P into trehalose, but Tre6P levels are unaffected in *ra3* ears. Furthermore, a catalytically inactive RA3 partially complements the mutant phenotype, suggesting that RA3 may suppress branching through a non-enzymatic mechanism (Claeys et al., 2019). However, it is unclear whether Tre6P signaling also contributes to inflorescence branching in other cereal grasses.

TCP transcription factors help define lateral organ boundaries to regulate inflorescence branching in grasses. *TB1* is expressed on the flanks of the developing tassel primordium (Hubbard et al., 2002), but it is not known whether *TB1* affects branch number. The closest maize homolog of *TB1* is *BRANCH ANGLE DEFECTIVE 1* (*BAD1*), and tassel branch number is reduced in *bad1* mutants in addition to the primary phenotype of altered branch angle (Bai et al., 2012). This indicates that *BAD1* promotes axillary branching in inflorescences, in contrast to *TB1* and its homologs, which repress vegetative branching. *BAD1* orthologs in sorghum and *Brachypodium distachyon* also promote inflorescence branching. However, the barley ortholog *COM1* is a repressor of inflorescence branching, and selection acting upon this gene contributed to the reduction in spike branch number observed in barley domestication (Poursarebani et al., 2020; reviewed in Koppolu et al., 2022). Another maize *TB1* homolog, *ZmTCP30*, negatively regulates tassel branch number (Kong et al., 2023). In rice, alleles affecting expression of *OsTB1* have a modest effect on panicle branching (Takai et al., 2023). In summary, TCP transcription factor family members can act as both positive and negative regulators of inflorescence branching and have been utilized to modulate meristem and lateral organ boundary formation to generate the diversity observed in grass inflorescence morphology.

The age-related pathway is another important module that regulates tassel branching. Mutants defective in the SBP-box transcription factors *UB2* (*UNBRANCHED 2*), *UB3*, and *TSH4* have fewer tassel branches (Chuck et al., 2010, 2014). The strigolactone signaling component D53 binds to and represses *UB2/UB3/TSH4*, leading to tassel branch growth in the presence of strigolactone (Liu et al., 2021b). *TSH4* is directly suppressed by RA2 in response to the flowering time regulator *ZmELF3.1* (*EARLY FLOWERING 3.1*) to regulate tassel branch number (Xie et al., 2023). *UB2/UB3/TSH4* directly activate expression of large gene networks including a regulator of auxin transport *BARREN INFLORESCENCE 2* (*BIF2*) and *ZmTCP30* to regulate tassel branch number (Kong et al., 2023). In rice, one of the most important genes affecting panicle architecture is *IPA1/WFP*, which encodes an SBP-box transcription factor. The domesticated allele of *IPA1/WFP* contains a mutated *miR156* binding site, which increases panicle branching (Jiao et al., 2010). *IPA1/WFP* modulates panicle branching by directly activating *DENSE AND ERECT PANICLE1* (*DEP1*) (Lu et al., 2013) and *D53* (Song et al., 2017), positioning it upstream of CK and strigolactone signaling. Interestingly, *IPA1/WFP* is also activated downstream of CK signaling, reinforcing a positive feedback loop in the developing IM (Chun et al., 2023).

Several mutants de-repress spikelet determinacy and cause them to become indeterminate branches. In maize and rice, spikelet determinacy is maintained by the orthologous AP2 transcription factors *BRANCHED SILKLESS 1* (Chuck et al.,

2002) and *FRIZZY PANICLE 1* (*FZP1*; Komatsu et al., 2003), respectively. Regulatory variants that moderately decrease *FZP1* expression increase branching, grain number, and yield (Huang et al., 2018; Wang et al., 2020a). Spikelet determinacy is also regulated by the orthologous AP2 transcription factors *INDETERMINATE SPIKELET1* (*IDS1*) and its paralog *SISTER OF IDS1* (*SID1*) in maize (Chuck et al., 1998, 2008) and *SUPERNUMERARY BRACT* (*SNB*) in rice (Lee et al., 2007). Additional spikelets and branches form in *ids1*, *sid1*, and *snb* null mutants, but more subtle expression differences can affect many agriculturally relevant phenotypes. This is highlighted by the major wheat domestication gene *Q*, which encodes a homolog of *IDS1*. A mutated *miR172* binding site in the domesticated *Q* allele increases its expression (Debernardi et al., 2017; Greenwood et al., 2017). This causes the two major *Q* phenotypes that were paramount to wheat domestication: more compact spikelet morphology and increased threshability (Simons et al., 2006).

Some cereal species spontaneously abort some of their spikelets or florets, which can limit yield. For example, many florets of ancient wheat varieties abort, whereas floret abortion is uncommon in modern cultivars. This decline in fertility was caused by selection of alleles that lowered expression of *GRAIN NUMBER INCREASE 1* (*GNI1*), which encodes an HD-ZIP I transcription factor (Sakuma et al., 2019). In barley, pre-anthesis tip degeneration (PTD) causes abortion of apical spikelets. The barley homolog of *GT1*, *HvGT1*, is a major factor that causes PTD, and a gene-edited knockout of this gene decreases PTD and increases spikelet number (Shanmugaraj et al., 2023). Together, these studies highlight how inflorescence branching can be targeted to rapidly improve traits that impact yield.

### Root apical meristems (RAMs)

Roots take up water and nutrients from the soil, provide anchorage, and facilitate interactions with beneficial soil microbes and therefore are critical for plant productivity. As the root apex grows, cells derived from the RAM (Figure 2C) follow a well-defined trajectory to generate all root tissue layers. The RAM stem cell niche is composed of mostly dormant cells called the quiescent center (QC) and its surrounding initial cells, mirroring organization of the SAM. Within the *Arabidopsis* RAM, the transcription factors *WOX5* and *PLETHORA 1–4* (*PLT1–PLT4*) maintain stem cell identity and specify surrounding cell types (Galinha et al., 2007; Sarkar et al., 2007; Burkart et al., 2022). Parallels between SAM and RAM maintenance can be drawn because both stem cell niches use CLE peptides, CLV receptors, CIK co-receptors, and *WOX* transcription factors to regulate meristem activity (Stahl et al., 2009, 2013; Berckmans et al., 2020; Berckmans et al., 2020; Zhu et al., 2021).

ROOT MERISTEM GROWTH FACTORS (RGFs) comprise a family of peptides that act upstream of PLTs to activate RAM fate (reviewed in Shinohara, 2021). These peptides are expressed in the root tip, become tyrosine sulfated, and are secreted (Matsuzaki et al., 2010). RGFs are perceived by the RGF1 INSENSITIVE (RGI)/SOMATIC EMBRYOGENESIS RECEPTOR-LIKE (SERK) membrane co-receptor pair, which activates a YODA-MKK4/5-MPK3/6 phosphorylation cascade to stabilize

PLT1/2 protein and enhance its expression (Matsuzaki et al., 2010; Ou et al., 2016, 2022; Shinohara et al., 2016; Song et al., 2016; Shao et al., 2020). RGF1 also controls root meristem fate by activating *RGF1-INDUCIBLE TRANSCRIPTION FACTOR 1* (*RITF1*), which mediates the distribution of ROS in the root tip (Yamada et al., 2020), but it is unclear whether *RITF1* is connected to the YODA-MKK4/5-MPK3/6 phosphorylation cascade.

Apart from these key regulators of RAM fate, additional signals that regulate cell fate in the layers surrounding the stem cell niche also act non-cell autonomously to control stem cell identity in the RAM. These include *SHORTROOT* (*SHR*), *SCARECROW* (*SCR*), *JACKDAW* (*JKD*), and locally produced auxin (Welch et al., 2007; Brumos et al., 2018; Shimotohno et al., 2018). Due to space limitations, we are unable to discuss the intricacies of stem cell specification and maintenance within the RAM, but this topic is reviewed elsewhere (Drisch and Stahl, 2015; Pardal and Heidstra, 2021).

The shape and size of root systems varies widely, even within a single species or genotype. Root system architecture (RSA) is defined by many underlying traits, such as root thickness, branch angle, and branch number, so control of branching is critical for shaping RSA. Lateral Roots (LRs) are root branches that form at sites where new RAMs are initiated, but the cell types involved in LR initiation differ across species. In *Arabidopsis*, for instance, LRs originate from xylem-pole pericycle cells, while *Medicago truncatula* LR primordia develop from endodermis and cortex cells (Herrbach et al., 2014). In maize and rice, LR primordia initiate from pericycle and endodermis cells opposite the phloem pole (Jansen et al., 2012). Due to the cell type differences that give rise to LRs, it is unclear whether the molecular mechanisms downstream of auxin signaling are conserved.

Auxin signaling is required for LR initiation in all species studied to date. Oscillating auxin pulses through the root generate maxima that become sites of LR development. At these positions in the *Arabidopsis* root, auxin induces a signaling cascade through *INDOLE-3-ACETIC ACID INDUCIBLE28* (*IAA28*) and its co-receptors, *AUXIN-RESPONSE FACTOR 5* (*ARF5*), *ARF6*, *ARF7*, *ARF8*, and *ARF19*. This induces *GATA23* expression in the pericycle cell prior to its anticlinal division that characterizes the beginning of the LR initiation program (De Rybel et al., 2010). LR development is primarily controlled by auxin, but other hormones also contribute through altering auxin levels and signaling in complicated crosstalk networks (reviewed in Liu et al., 2014; 2017b; Zemlyanskaya et al., 2018; Jing and Strader, 2019).

LR development next proceeds with periclinal cell divisions of pericycle cells. The new QC then acquires stem cell identity in response to positional cues from morphogenic regulators. For example, *PLT3*, *PLT5*, and *PLT7* establish inner (closer to the stele) and outer cell layers that are required to establish the new RAM (Du and Scheres, 2017). The inner and outer layers can be distinguished by the expression of *SCR* and *SHR*, respectively, and the new QC forms in several cells in the outer layer (Goh et al., 2016). During the early stages of LR initiation, *PUCHI*, an AP2 transcription factor, is expressed in the boundary domain and suppresses expression of stem cell genes, so only central meristematic cells acquire QC identity (Bellande et al.,



2022). When an LR is established, its RAM is capable of producing all root cell layers and is functionally equivalent to a primary root.

Plants can also form roots from stem tissue. Adventitious roots (ARs) can form naturally at wound sites but can also make up the bulk of the root system in some species. For example, grasses develop ARs from nodes at the base of the stem called crown and brace roots. Embryonic roots in grasses do not persist long after germination, and these ARs make up virtually all of the adult root system. Crown and brace roots originate from ground meristem cells that surround the stele of the stem (reviewed in Gonin et al., 2019). Auxin is a key signal to initiate AR development in stems, and this process closely resembles LR initiation in roots (reviewed in Orman-Ligeza et al., 2013; Gonin et al., 2019).

Fewer molecular details are known about LR development in crop species. Two maize mutants do not produce LRs from embryonic roots, but the shoot-borne roots that comprise the bulk of the maize root system are unaffected (Hochholdinger and Feix, 1998; Hochholdinger et al., 2001; Woll et al., 2005). One of these mutants, *LATERAL ROOTLESS 1* (*LRT1*), encodes a homolog of the DDB1 and CUL4-associated factor (DCAF) protein, which is a component of the CULLIN 4-based E3 ubiquitin ligase complex (Hochholdinger and Feix, 1998; Baer et al., 2023). *LRT1* presumably targets a negative regulator of LR development for degradation, but such a component has not yet been identified. *ROOTLESS WITH UNDETECTABLE MERISTEMS 1* (*RUM1*) mutants do not form seminal roots or LRs from the primary root. This gene encodes an Aux/IAA protein (Woll et al., 2005; von Behrens et al., 2011), consistent with the concept that auxin regulates LR production in both monocots and Arabidopsis. In maize and tomato, members of the *GIBBERELLIC ACID STIMULATED TRANSCRIPT-like* (*GAST-like*) family are also likely involved in LR production (Taylor and Scheuring, 1994; Zimmermann et al., 2010), but the role of GA is not well understood. While not required for LR formation, the Lateral Organ Boundary (LOB) domain gene *ROOTLESS CONCERNING CROWN AND SEMINAL ROOTS* (*RTCS*) is needed to produce crown and seminal roots, indicating that there are some unique components required to produce either LRs or ARs in maize (Taramino et al., 2007).

LR regulation plays a significant role in patterning RSA. Different species often have distinct RSA ideotypes, but most plants can adapt their root system to changes in soil conditions, such as water and nutrient availability and anchorage requirements. For example, in *Arabidopsis*, a high carbon:nitrogen ratio inhibits LR growth (Zhang et al., 2007), and elevated temperatures promote root growth via auxin signaling to seek deeper sources of water (Ai et al., 2023). Relationships between soil conditions and RSA tend to be species specific but can also vary among genotypes within a species (Lynch, 1995; Khan et al., 2016; Morris et al., 2017; Ye et al., 2018; Xiong et al., 2021; LaRue et al., 2022). Intriguingly, several CLEs play a role in shaping RSA in response to changing soil nutrient levels (Araya et al., 2014; Gutiérrez-Alanís et al., 2017). Future work should explore how environmentally responsive CLEs intersect with developmental CLE signaling pathways because these CLE genes could be excellent targets for altering RSA in specific environmental contexts (Bashyal et al., 2023).

The advent of new root imaging technologies has enabled a deeper understanding of RSA dynamics, and researchers have begun to ask how root systems influence agriculturally relevant phenotypes across multiple crops. Unsurprisingly, RSA profoundly affects plant performance, especially under drought and nutrient deficiency stresses. In a study of a panel of 531 elite maize varieties, Sha et al. (2023) found that root traits significantly correlated with aboveground traits, such as flowering time and grain yield. The majority of loci (103 of 115) that are associated with crown root traits overlap domestication-selective sweeps, indicating that crop selection and improvement act upon root traits (Sha et al., 2023). Currently, research on stem cell activity in the RAMs and LRs occurs independent of large-scale RSA studies. Bridging the divide between these two fields could be a promising area for future research and greatly enhance our knowledge of root systems. Comparative single-cell analyses in crop plant roots will also allow us to gain deeper mechanistic insights into how roots are regulated, providing additional targets for improving RSA to optimize nutrient uptake (Ortiz-Ramírez et al., 2021; Guillotin et al., 2023).

### Vascular cambium

The vascular cambium comprises another population of stem cells found within most gymnosperms and eudicots but are absent from most monocots (Figure 2D). The vascular cambium is located between the primary phloem and xylem in shoots and roots. During secondary growth, procambium cells divide and produce secondary phloem and xylem. Secondary xylem is the source of wood, which is grown agriculturally for lumber and paper, making the study of vascular cambium development important for potential advancements in these industries. Some food crops, such as fruit trees, also produce wood, and modifying the vascular cambium could also be beneficial for these species. For instance, viral infections commonly cause stem pitting in perennial woody fruit trees, which impairs vascular cambium function (Sun and Folimonova, 2022).

Our understanding of vascular cambium development comes from studies of leaf and root procambial development in *Arabidopsis* and *Populus* (reviewed in Wang et al., 2021d). Polar auxin transport establishes sites of auxin maxima where the vascular bundles will form (Ibañez et al., 2009). Elevated auxin levels activate MP/ARF5, leading to expression of the HD-ZIP III transcription factor ATHB8, which specifies procambial fate (Donner et al., 2009). In *Populus*, another HD-ZIP III member, *PopREVOLUTA* influences vascular cambium fate in woody stems (Robischon et al., 2011). Components of the auxin signaling pathway work in conjunction with cytokinin signaling components to establish procambial cell identity (De Rybel et al., 2014).

Once established, vascular cambium cell division is tightly regulated to control the balance between cell division and stem cell maintenance. *WOX4* is a central regulator of cambial stem cell fate, and it is transcriptionally regulated by several mechanisms. The auxin-dependent MP/ARF5 represses *WOX4* expression to spatially restrict the vascular cambium (Suer et al., 2011; Brackmann et al., 2018). TRACHEARY ELEMENT DIFFERENTIATION INHIBITORY FACTOR peptides encoded by *CLE41* and *CLE44* are secreted from phloem and perceived by

PHLOEM INTERCALATED WITH XYLEM (PXY) to activate *WOX4* in the procambium during vegetative growth and to induce procambium cell division (Hirakawa et al., 2010; Kucukoglu et al., 2017). Cytokinin and ethylene also promote cell division within the vascular cambium through *WOX4* (Smet et al., 2019; Yang et al., 2020). ROS also regulate both cambial cell proliferation and differentiation through the LOB domain transcription factor LBD11 (Dang et al., 2023). Manipulating expression of *WOX4* or its related signaling molecules could potentially influence wood production or alter vascular cells for agricultural benefits.

### Meristem induction for plant propagation and transformation

Plant cells possess the amazing ability to de-differentiate into stem cells under particular conditions. This remarkable property was first theorized by the Austrian botanist Gottlieb Haberlandt in the early 1900s, and later experimentally confirmed by others (Bonner, 1936). The innovation of regenerating plants by tissue culture was one of the most significant agricultural breakthroughs of the 20th century (Melnyk, 2023). Many crop varieties are impossible or impractical to propagate sexually. For example, this can be due to cytogenetic abnormalities such as triploidy (e.g., banana, seedless watermelon, and mandarin) or in cases where it is difficult to generate large numbers of seeds (e.g., potato, sugarcane, some medicinal plants). In these cases, micropropagation by tissue culture is employed to generate large numbers of genetically uniform, disease-free plants. Tissue culture is also necessary to develop transgenic or genetically engineered crops and has become a rate-limiting component for CRISPR-Cas9-based gene editing in many species because transformation efficiency varies greatly between species and cultivars. Immature embryos, nodes containing a meristem, and leaves as a source of either protoplasts or calli are common starting materials for tissue culture. Many of these techniques use cytokinin and auxin to initiate SAM and RAM production, respectively.

Several studies have begun to probe the molecular mechanisms of regeneration in tissue culture (reviewed in Chen et al., 2022a). Application of the synthetic auxin 2,4-dichlorophenoxyacetic acid during somatic embryogenesis causes global changes in chromatin structure that affects expression of auxin signaling components and developmental regulators (Wang et al., 2020b; Lardon et al., 2020; Lin et al., 2021a). *LEAFY COTYLEDON1* (*LEC1*) and *LEC2* are key downstream targets of auxin that are important for somatic embryogenesis (Lotan et al., 1998; Wójcikowska et al., 2013; Wang et al., 2020b). In later steps, cytokinin activates *WUS* expression to form a new SAM (Zhang et al., 2017; Wu et al., 2022a). Mechanical forces between progenitor cells help determine cell polarity necessary for SAM formation in calli (Varapparambath et al., 2022). Recent transcriptome and epigenome-wide studies of regenerating calli in wheat have identified monocot-specific contributors to regeneration and identified TaDOF5.6 and TaDOF3.4 as additional components that boost regeneration (Liu et al., 2023c).

Applying our knowledge of developmental regulators has expanded the number of transformable species and ease of transformation (reviewed in Chen et al., 2022a). Overexpressing the maize developmental regulators *Babyboom* and *Wuschel2* improves transformation efficiency, allowing transformation of

genotypes and species that were previously recalcitrant (Lowe et al., 2016, 2018; Jones et al., 2019; Wang et al., 2023d). A similar approach using a synthetic chimeric protein combining wheat GROWTH-REGULATING FACTOR 4 (GRF4) with GRF-INTERACTING FACTOR 1 (GIF1), termed GRF-GIF, also improves transformation efficiency in wheat and citrus (Debernardi et al., 2020). Expressing *BBM* with *GRF-GIF1* improves maize transformation rate and decreases tissue culture time (Chen et al., 2022b). The application of plant developmental regulators has led to exciting advances in plant tissue culture that will likely continue to revolutionize this field and facilitate crop improvement.

Although *WUS* promotes SAM formation, and overexpression of *WUS2* increases regeneration efficiency, its homolog *WOX13* negatively regulates SAM initiation in *Arabidopsis* calli (Ogura et al., 2023). Additionally, a group of *Arabidopsis* *CLE* genes, *CLE1–CLE7*, inhibit callus regeneration (Kang et al., 2022). It remains to be seen how the CLV signaling pathway functions in the calli of crop plants and to what extent our knowledge of SAM signaling pathways can be leveraged to improve plant transformation. Additional comparative analyses between permissive and recalcitrant crop varieties can provide further insights into the mechanisms underlying regeneration capacity.

## CONCLUDING REMARKS AND FUTURE PERSPECTIVES

Developmental genetics has provided a solid foundation to understand how meristems produce plant organs and how we may alter meristem architecture to improve crop performance. Traditional breeding methods have been instrumental in our ability to dramatically alter plant development and physiology. The future of agriculture, however, will rely on innovative strategies to create high-yielding varieties that are resilient to various abiotic and biotic stresses in the face of climate change. Progress in tissue culture techniques across a wide spectrum of species and elite cultivars has been accelerated through a deeper comprehension of developmental regulators and regeneration. Being able to transform a wider variety of plants with gene editing tools will allow us to precisely edit genes in elite cultivars.

Editing CREs within promoters of developmental regulators can impact gene expression, leading to changes in meristem organization with effects on yield (Rodríguez-Leal et al., 2017; Soyk et al., 2017; Lemmon et al., 2018; Liu et al., 2021a). With promoter editing, it becomes possible to precisely target pleiotropic genes—optimizing expression at some developmental stages while maintaining it at others (Hendelman et al., 2021). This concept was recently demonstrated in rice by editing a particular CRE controlling *IPA1* expression in the panicle, increasing panicle size without affecting other traits, including tiller number (Song et al., 2022). Despite the transformative potential of editing CREs, our knowledge of these elements is limited across many species, necessitating the development of new methods to identify and validate CREs within crop genomes (reviewed in Schmitz et al., 2022). This will likely be achieved through the development of new bioinformatic and machine learning tools in the coming decade.

The recent surge in single-cell sequencing and spatial transcriptomic technologies in plants has significantly improved cellular resolution of gene expression, including developmental regulators (Satterlee et al., 2020; Xu et al., 2021; Zhang et al., 2021b; Laureyns et al., 2022; Zong et al., 2022; Shen et al., 2023; reviewed in Xu and Jackson, 2023). Single-cell studies have identified cell-specific regulators and cell types that could be targets for crop improvement. Identifying cell-type-specific expression patterns will allow us to mine novel promoters, which can then be used to drive tissue-specific CRISPR to avoid the pleiotropic effect of knocking out genes with functions in many biological contexts. Combining single-cell data with knowledge of CREs could help design new promoters to drive cell-type-specific gene expression patterns that have targeted and specific effects on plant development.

As climate change continues to threaten crop performance, we will seek new ways to make our crops more resilient to abiotic stresses. Research integrating meristem biology with abiotic stress is only recently emerging (reviewed in Lee, 2018; Mandal et al., 2022), and we believe this area deserves additional attention in the future. While novel alleles that impact plant architecture and yield related traits can potentially increase overall yield, it is imperative that these candidates are thoroughly tested in breeding trials and in genomic selection models in multiple environments to ensure their utility in agricultural settings (Khaipho-Burch et al., 2023).

## FUNDING

This work was supported by funding from National Science Foundation award 2129189 and USDA-NIFA award 2020-67013-30909. P.L. is funded by the NSF Postdoctoral Research Fellowships in Biology Program under grant 2010642, and K.W.S. is funded by the NSF Postdoctoral Research Fellowships in Biology Program under grant 2209124.

## AUTHOR CONTRIBUTIONS

K.W.S. and P.L. wrote the manuscript and developed the framework for the review. P.L. made the figures. D.J. edited the manuscript.

## ACKNOWLEDGMENTS

We thank members of the Jackson lab and Sanchari Ghosh for helpful comments in reviewing the manuscript. D.J. is a consultant for Inari Agriculture, and he is also a named inventor on a number of patents and patent applications directed to related technology.

## DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

During the preparation of this work, the authors used ChatGPT to correct grammatical errors. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Received: October 14, 2023

Revised: December 14, 2023

Accepted: December 18, 2023

## REFERENCES

- Adeyemo, O.S., Hyde, P.T., and Setter, T.L. (2019). Identification of FT family genes that respond to photoperiod, temperature and genotype in relation to flowering in cassava (*Manihot esculenta*, Crantz). *Plant Reprod.* **32**:181–191.
- Ai, H., Bellstaedt, J., Bartusch, K.S., Eschen-Lippold, L., Babben, S., Balcke, G.U., Tissier, A., Hause, B., Andersen, T.G., Delker, C., and Quint, M. (2023). Auxin-dependent regulation of cell division rates governs root thermomorphogenesis. *EMBO J.* **42**:e111926.
- Aida, M., Ishida, T., Fukaki, H., Fujisawa, H., and Tasaka, M. (1997). Genes involved in organ separation in Arabidopsis: An analysis of the cup-shaped cotyledon mutant. *Plant Cell* **9**:841–857.
- Aida, M., Ishida, T., and Tasaka, M. (1999). Shoot apical meristem and cotyledon formation during Arabidopsis embryogenesis: Interaction among the CUP-SHAPED COTYLEDON and SHOOT MERISTEMLESS genes. *Development* **126**.
- Allred, K.W. (1982). Describing the Grass Inflorescence. *J. Range Manag.* **35**:672.
- Araya, T., Miyamoto, M., Wibowo, J., Suzuki, A., Kojima, S., Tsuchiya, Y.N., Sawa, S., Fukuda, H., von Wirén, N., and Takahashi, H. (2014). CLE-CLAVATA1 peptide-receptor signaling module regulates the expansion of plant root systems in a nitrogen-dependent manner. *Proc. Natl. Acad. Sci. USA* **111**:2029–2034.
- Ashikari, M., Sakakibara, H., Lin, S., Yamamoto, T., Takashi, T., Nishimura, A., Angeles, E.R., Qian, Q., Kitano, H., and Matsuoka, M. (2005). Cytokinin oxidase regulates rice grain production. *Science* **309**:741–745.
- Bachlava, E., Tang, S., Pizarro, G., Schuppert, G.F., Brunick, R.K., Draeger, D., Leon, A., Hahn, V., and Knapp, S.J. (2010). Pleiotropy of the branching locus (B) masks linked and unlinked quantitative trait loci affecting seed traits in sunflower. *Theor. Appl. Genet.* **120**:829–842.
- Baer, M., Taramino, G., Multani, D., Sakai, H., Jiao, S., Fengler, K., and Hochholdinger, F. (2023). Maize Lateral Rootless 1 Encodes a Homolog of the DCAF Protein Subunit of the CUL4-Based E3 Ubiquitin Ligase Complex. *New Phytologist* **237**.
- Bai, F., Reinheimer, R., Durantini, D., Kellogg, E.A., and Schmidt, R.J. (2012). TCP transcription factor, BRANCH ANGLE DEFECTIVE 1 (BAD1), is required for normal tassel branch angle formation in maize. *Proc. Natl. Acad. Sci. USA* **109**:12225–12230.
- Balkunde, R., Kitagawa, M., Xu, X.M., Wang, J., and Jackson, D. (2017). SHOOT MERISTEMLESS trafficking controls axillary meristem formation, meristem size and organ boundaries in Arabidopsis. *Plant J.* **90**:435–446.
- Banwarth-Kuhn, M., Rodriguez, K., Michael, C., Ta, C.-K., Plong, A., Bourgain-Chang, E., Nematbakhsh, A., Chen, W., Roy-Chowdhury, A., Reddy, G.V., and Alber, M. (2022). Combined computational modeling and experimental analysis integrating chemical and mechanical signals suggests possible mechanism of shoot meristem maintenance. *PLoS Comput. Biol.* **18**, e1010199.
- Barazesh, S., and McSteen, P. (2008). Barren inflorescence1 functions in organogenesis during vegetative and inflorescence development in maize. *Genetics* **179**:389–401.
- Barton, M.K., and Poethig, R.S. (1993). Formation of the shoot apical meristem in Arabidopsis thaliana: an analysis of development in the wild type and in the shoot meristemless mutant. *Development* **119**:823–831.
- Bashyal, S., Gautam, C.K., and Müller, L.M. (2023). CLAVATA signaling in plant–environment interactions. *Plant Physiol.* **1**:2023.
- Baxter, H.L., Mazarei, M., Dumitrache, A., Natzke, J.M., Rodriguez, M., Gou, J., Fu, C., Sykes, R.W., Turner, G.B., Davis, M.F., et al. (2018). Transgenic miR156 switchgrass in the field: growth, recalcitrance and rust susceptibility. *Plant Biotechnol. J.* **16**:39–49.
- von Behrens, I., Komatsu, M., Zhang, Y., Berendzen, K.W., Niu, X., Sakai, H., Taramino, G., and Hochholdinger, F. (2011). Rootless with undetectable meristem 1 encodes a monocot-specific AUX/IAA



- protein that controls embryonic seminal and post-embryonic lateral root initiation in maize. *Plant J.* **66**:341–353.
- Bellande, K., Trinh, D.C., Gonzalez, A.A., Dubois, E., Petitot, A.S., Lucas, M., Champion, A., Gantet, P., Laplace, L., and Guyomarc'h, S. (2022). PUCHI represses early meristem formation in developing lateral roots of *Arabidopsis thaliana*. *J. Exp. Bot.* **73**:3496–3510.
- Berckmans, B., Kirschner, G., Gerlitz, N., Stadler, R., Simon, R., Morris, E.C., Griffiths, M., Golebiowska, A., Mairhofer, S., Burr-Hersey, J., et al. (2020). CLE40 Signaling Regulates Root Stem Cell Fate. *Plant Physiol.* **182**:1776–1792.
- Beveridge, C.A., Rameau, C., and Wijerathna-Yapa, A. (2023). Lessons from a century of apical dominance research. *J. Exp. Bot.* **74**:3903–3922.
- Blümke, P., Schlegel, J., Gonzalez-Ferrer, C., Becher, S., Pinto, K.G., Monaghan, J., and Simon, R. (2021). Receptor-like cytoplasmic kinase MAZZA mediates developmental processes with CLAVATA1 family receptors in *Arabidopsis*. *J. Exp. Bot.* **72**:4853–4870.
- Bolduc, N., Yilmaz, A., Mejia-Guerra, M.K., Morohashi, K., O'Connor, D., Grotewold, E., and Hake, S. (2012). Unraveling the KNOTTED1 regulatory network in maize meristems. *Genes Dev.* **26**:1685–1690.
- Bommert, P., Nagasawa, N.S., and Jackson, D. (2013). Quantitative variation in maize kernel row number is controlled by the FASCIATED EAR2 locus. *Nat. Genet.* **45**:334–337.
- Bommert, P., and Whipple, C. (2018). Grass inflorescence architecture and meristem determinacy. *Semin. Cell Dev. Biol.* **79**:37–47.
- Bonner, J. (1936). *Plant Tissue Cultures from a Hormone Point of View*. *Proc. Natl. Acad. Sci. USA* **22**:426–430.
- Brackmann, K., Qi, J., Gebert, M., Jouannet, V., Schlamp, T., Grünwald, K., Wallner, E.S., Novikova, D.D., Levitsky, V.G., Agustí, J., et al. (2018). Spatial specificity of auxin responses coordinates wood formation. *Nat Commun* **9**:875.
- Braun, N., de Saint Germain, A., Pillot, J.P., Boutet-Mercey, S., Dalmais, M., Antoniadi, I., Li, X., Maia-Grondard, A., Le Signor, C., Bouteiller, N., et al. (2012). The pea TCP transcription factor PsBRC1 acts downstream of strigolactones to control shoot branching. *Plant Physiol.* **158**:225–238.
- Brumos, J., Robles, L.M., Yun, J., Vu, T.C., Jackson, S., Alonso, J.M., and Stepanova, A.N. (2018). Local Auxin Biosynthesis Is a Key Regulator of Plant Development. *Dev. Cell* **47**:306–318.e5.
- Burkart, R.C., Strotmann, V.I., Kirschner, G.K., Akinci, A., Czempik, L., Dolata, A., Maizel, A., Weidtkamp-Peters, S., and Stahl, Y. (2022). PLETHORA-WOX5 interaction and subnuclear localization control *Arabidopsis* root stem cell maintenance. *EMBO Rep.* **23**:e54105.
- Busch, W., Miotk, A., Ariel, F.D., Zhao, Z., Forner, J., Daum, G., Suzuki, T., Schuster, C., Schultheiss, S.J., Leibfried, A., et al. (2010). Transcriptional Control of a Plant Stem Cell Niche. *Dev. Cell* **18**:849–861.
- Cammarata, J., Morales Farfan, C., Scanlon, M.J., and Roeder, A.H.K. (2022). Cytokinin–CLAVATA cross-talk is an ancient mechanism regulating shoot meristem homeostasis in land plants. *Proc. Natl. Acad. Sci. USA* **119**, e2116860119.
- Cao, S., Xu, D., Hanif, M., Xia, X., and He, Z. (2020). Genetic architecture underpinning yield component traits in wheat. *Theor. Appl. Genet.* **133**:1811–1823.
- Cao, X., Du, Q., Guo, Y., Wang, Y., and Jiao, Y. (2023). Condensation of STM is critical for shoot meristem maintenance and salt tolerance in *Arabidopsis*. *Mol. Plant* **16**:1445–1459.
- Chapman, E.A., Thomsen, H.C., Tulloch, S., Correia, P.M.P., Luo, G., Najafi, J., DeHaan, L.R., Crews, T.E., Olsson, L., Lundquist, P.O., et al. (2022). Perennials as Future Grain Crops: Opportunities and Challenges. *Front. Plant Sci.* **13**:898769.
- Chen, M.-K., Wilson, R.L., Palme, K., Ditetgou, F.A., and Shpak, E.D. (2013). ERECTA Family Genes Regulate Auxin Transport in the Shoot Apical Meristem and Forming Leaf Primordia. *Plant Physiol.* **162**:1978–1991.
- Chen, Z., Tang, N., Li, H., Liu, G., and Tang, L. (2020). Genome-wide transcriptomic analysis during rhizome development of ginger (*Zingiber officinale* Roscoe.) reveals hormone and transcriptional regulation involved in cellulose production. *Sci. Hortic.* **264**, 109154.
- Chen, Z., Li, W., Gaines, C., Buck, A., Galli, M., and Gallavotti, A. (2021). Structural variation at the maize WUSCHEL1 locus alters stem cell organization in inflorescences. *Nat. Commun.* **12**:2378.
- Chen, Z., Debernardi, J.M., Dubcovsky, J., and Gallavotti, A. (2022a). Recent advances in crop transformation technologies. *Nat. Plants* **8**:1343–1351.
- Chen, Z., Debernardi, J.M., Dubcovsky, J., and Gallavotti, A. (2022b). The combination of morphogenic regulators BABY BOOM and GRF-GIF improves maize transformation efficiency. Preprint at bioRxiv.
- Chen, W., Chen, L., Zhang, X., Yang, N., Guo, J., Wang, M., Ji, S., Zhao, X., Yin, P., Cai, L., et al. (2022c). Convergent selection of a WD40 protein that enhances grain yield in maize and rice. *Science* **375**, eabg7985.
- Chow, H.T., Kendall, T., and Mosher, R.A. (2023). A novel CLAVATA1 mutation causes multilocularity in *Brassica rapa*. *Plant Direct* **7**:e476.
- Chu, Y.H., Jang, J.C., Huang, Z., and van der Knaap, E. (2019). Tomato locule number and fruit size controlled by natural alleles of *lc* and *fas*. *Plant Direct* **3**:e00142.
- Chuck, G., Meeley, R.B., and Hake, S. (1998). The control of maize spikelet meristem fate by the APETALA2-like gene indeterminate spikelet1. *Genes Dev.* **12**:1145–1154.
- Chuck, G., Muszynski, M., Kellogg, E., Hake, S., and Schmidt, R.J. (2002). The control of spikelet meristem identity by the branched silkless1 gene in maize. *Science* **298**:1238–1241.
- Chuck, G., Cigan, A.M., Saetern, K., and Hake, S. (2007). The heterochronic maize mutant *Corngrass1* results from overexpression of a tandem microRNA. *Nat. Genet.* **39**:544–549.
- Chuck, G., Meeley, R., and Hake, S. (2008). Floral meristem initiation and meristem cell fate are regulated by the maize AP2 genes *ids1* and *sid1*. *Development* **135**.
- Chuck, G., Whipple, C., Jackson, D., and Hake, S. (2010). The maize SBP-box transcription factor encoded by *tasselsheath4* regulates bract development and the establishment of meristem boundaries. *Development* **137**:1243–1250.
- Chuck, G.S., Brown, P.J., Meeley, R., and Hake, S. (2014). Maize SBP-box transcription factors *unbranched2* and *unbranched3* affect yield traits by regulating the rate of lateral primordia initiation. *Proc. Natl. Acad. Sci. USA* **111**:18775–18780.
- Chun, Y., Fang, J., Savelieva, E.M., Lomin, S.N., Shang, J., Sun, Y., Zhao, J., Kumar, A., Yuan, S., Yao, X., et al. (2023). The cytokinin receptor OHK4/OsHK4 regulates inflorescence architecture in rice via an IDEAL PLANT ARCHITECTURE1/WFP-mediated positive feedback circuit. *Plant Cell*, koad257.
- Chung, Y., Zhu, Y., Wu, M.-F., Simonini, S., Kuhn, A., Armenta-Medina, A., Jin, R., Østergaard, L., Gillmor, C.S., and Wagner, D. (2019). Auxin Response Factors promote organogenesis by chromatin-mediated repression of the pluripotency gene SHOOTMERISTEMLESS. *Nat. Commun.* **10**:886.
- Claeys, H., Vi, S.L., Xu, X., Satoh-Nagasawa, N., Eveland, A.L., Goldshmidt, A., Feil, R., Beggs, G.A., Sakai, H., Brennan, R.G., et al. (2019). Control of meristem determinacy by trehalose



- 6-phosphate phosphatases is uncoupled from enzymatic activity. *Nat. Plants* **5**:352–357.
- Clark, R.M., Wagler, T.N., Quijada, P., and Doebley, J.** (2006). A distant upstream enhancer at the maize domestication gene *tb1* has pleiotropic effects on plant and inflorescent architecture. *Nat. Genet.* **38**:594–597.
- Clark, S.E., Running, M.P., and Meyerowitz, E.M.** (1993). *CLAVATA1*, a regulator of meristem and flower development in *Arabidopsis*. *Development* **119**:397–418.
- Clark, S.E., Williams, R.W., and Meyerowitz, E.M.** (1997). The *CLAVATA1* Gene Encodes a Putative Receptor Kinase That Controls Shoot and Floral Meristem Size in *Arabidopsis*. *Cell* **89**:575–585.
- Considine, M.J.** (2018). Oxygen, Energy, and Light Signalling Direct Meristem Fate. *Trends Plant Sci.* **23**:1–3.
- Crook, A.D., Willoughby, A.C., Hazak, O., Okuda, S., VanDerMolen, K.R., Soyars, C.L., Cattaneo, P., Clark, N.M., Sozzani, R., Hothorn, M., et al.** (2020). *BAM1/2* receptor kinase signaling drives CLE peptide-mediated formative cell divisions in *Arabidopsis* roots. *Proc. Natl. Acad. Sci. USA* **117**:32750–32756.
- Dang, T.V.T., Lee, S., Cho, H., Choi, K., and Hwang, I.** (2023). The LBD11-ROS feedback regulatory loop modulates vascular cambium proliferation and secondary growth in *Arabidopsis*. *Mol. Plant* **16**:1131–1145.
- Dao, T.Q., Weksler, N., Liu, H.M.-H., Leiboff, S., and Fletcher, J.C.** (2022). Interactive CLV3, CLE16 and CLE17 signaling mediates stem cell homeostasis in the *Arabidopsis* shoot apical meristem. *Development* **149**:dev200787.
- Daum, G., Medzihradszky, A., Suzuki, T., and Lohmann, J.U.** (2014). A mechanistic framework for noncell autonomous stem cell induction in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **111**:14619–14624.
- Debernardi, J.M., Lin, H., Chuck, G., Faris, J.D., and Dubcovsky, J.** (2017). *microRNA172* plays a crucial role in wheat spike morphogenesis and grain threshability. *Development* **144**.
- Debernardi, J.M., Tricoli, D.M., Ercoli, M.F., Hayta, S., Ronald, P., Palatnik, J.F., and Dubcovsky, J.** (2020). A GRF–GIF chimeric protein improves the regeneration efficiency of transgenic plants. *Nat. Biotechnol.* **38**:1274–1279.
- DeFalco, T.A., Anne, P., James, S.R., Willoughby, A.C., Schwanke, F., Johannndrees, O., Genolet, Y., Derbyshire, P., Wang, Q., Rana, S., et al.** (2022). A conserved module regulates receptor kinase signalling in immunity and development. *Nat. Plants* **8**:356–365.
- DeYoung, B.J., Bickle, K.L., Schrage, K.J., Muskett, P., Patel, K., and Clark, S.E.** (2006). The *CLAVATA1*-related *BAM1*, *BAM2* and *BAM3* receptor kinase-like proteins are required for meristem function in *Arabidopsis*. *Plant J.* **45**:1–16.
- DeYoung, B.J., and Clark, S.E.** (2008). *BAM* Receptors Regulate Stem Cell Specification and Organ Development Through Complex Interactions With *CLAVATA* Signaling. *Genetics* **180**:895–904.
- Diévert, A., Dalal, M., Tax, F.E., Lacey, A.D., Huttly, A., Li, J., and Clark, S.E.** (2003). *CLAVATA1* Dominant-Negative Alleles Reveal Functional Overlap between Multiple Receptor Kinases That Regulate Meristem and Organ Development. *Plant Cell* **15**:1198–1211.
- Doebley, J., Stec, A., and Hubbard, L.** (1997). The evolution of apical dominance in maize. *Nature* **386**:485–488.
- Dong, Z., Xiao, Y., Govindarajulu, R., Feil, R., Siddoway, M.L., Nielsen, T., Lunn, J.E., Hawkins, J., Whipple, C., and Chuck, G.** (2019). The regulatory landscape of a core maize domestication module controlling bud dormancy and growth repression. *Nat. Commun.* **10**:3810.
- Dong, C., Zhang, L., Zhang, Q., Yang, Y., Li, D., Xie, Z., Cui, G., Chen, Y., Wu, L., Li, Z., et al.** (2023). *Tiller Number1* encodes an ankyrin repeat protein that controls tillering in bread wheat. *Nat. Commun.* **14**:3523.
- Donner, T.J., Sherr, I., and Scarpella, E.** (2009). Regulation of precambial cell state acquisition by auxin signaling in *Arabidopsis* leaves. *Development* **136**.
- Drisc, R.C., and Stahl, Y.** (2015). Function and regulation of transcription factors involved in root apical meristem and stem cell maintenance. *Front. Plant Sci.* **6**:505.
- Du, Y., and Scheres, B.** (2017). *PLETHORA* transcription factors orchestrate de novo organ patterning during *Arabidopsis* lateral root outgrowth. *Proc. Natl. Acad. Sci. USA* **114**.
- Dun, E.A., de Saint Germain, A., Rameau, C., and Beveridge, C.A.** (2012). Antagonistic action of strigolactone and cytokinin in bud outgrowth control. *Plant Physiol.* **158**:487–498.
- Duncan, W.G., Williams, W.A., and Loomis, R.S.** (1967). Tassels and the Productivity of Maize 1. *Crop Sci.* **7**:37–39.
- Eveland, A.L., Goldshmidt, A., Pautler, M., Morohashi, K., Liseron-Monfils, C., Lewis, M.W., Kumari, S., Hiraga, S., Yang, F., Unger-Wallace, E., et al.** (2014). Regulatory modules controlling maize inflorescence architecture. *Genome Res.* **24**:431–443.
- Fan, C., Wu, Y., Yang, Q., Yang, Y., Meng, Q., Zhang, K., Li, J., Wang, J., and Zhou, Y.** (2014). A novel single-nucleotide mutation in a *CLAVATA3* gene homolog controls a multilocular silique trait in *brassica rapa* L. *Mol. Plant* **7**:1788–1792.
- Fan, Z., Huang, G., Fan, Y., and Yang, J.** (2022). Sucrose Facilitates Rhizome Development of Perennial Rice (*Oryza longistaminata*). *Int. J. Mol. Sci.* **23**, 13396.
- Fichtner, F., Barbier, F.F., Feil, R., Watanabe, M., Annunziata, M.G., Chabikwa, T.G., Höfgen, R., Stitt, M., Beveridge, C.A., and Lunn, J.E.** (2017). Trehalose 6-phosphate is involved in triggering axillary bud outgrowth in garden pea (*Pisum sativum* L.). *Plant J.* **92**:611–623.
- Fichtner, F., and Lunn, J.E.** (2021). The Role of Trehalose 6-Phosphate (Tre6P) in Plant Metabolism and Development. *Annu. Rev. Plant Biol.* **72**:737–760.
- Fichtner, F., Barbier, F.F., Annunziata, M.G., Feil, R., Olas, J.J., Mueller-Roeber, B., Stitt, M., Beveridge, C.A., and Lunn, J.E.** (2021). Regulation of shoot branching in *arabidopsis* by trehalose 6-phosphate. *New Phytol.* **229**.
- Freeling, M., and Hake, S.** (1985). Developmental Genetics of Mutants That Specify Knotted Leaves in Maize. *Genetics* **111**:617–634.
- Fu, C., Sunkar, R., Zhou, C., Shen, H., Zhang, J.Y., Matts, J., Wolf, J., Mann, D.G.J., Stewart, C.N., Tang, Y., and Wang, Z.Y.** (2012). Overexpression of *miR156* in switchgrass (*Panicum virgatum* L.) results in various morphological alterations and leads to improved biomass production. *Plant Biotechnol. J.* **10**:443–452.
- Gagne, J.M., Song, S.-K., and Clark, S.E.** (2008). *POLTERGEIST* and *PLL1* are required for stem cell function with potential roles in cell asymmetry and auxin signaling. *Commun. Integr. Biol.* **1**:53–55.
- Galinha, C., Hofhuis, H., Luijten, M., Willemsen, V., Blilou, I., Heidstra, R., and Scheres, B.** (2007). *PLETHORA* proteins as dose-dependent master regulators of *Arabidopsis* root development. *Nature* **449**:1053–1057.
- Gallavotti, A., Zhao, Q., Kozuka, J., Meeley, R.B., Ritter, M.K., Doebley, J.F., Pè, M.E., and Schmidt, R.J.** (2004). The role of *barren stalk1* in the architecture of maize. *Nature* **432**:630–635.
- Gallavotti, A., Barazesh, S., Malcomber, S., Hall, D., Jackson, D., Schmidt, R.J., and McSteen, P.** (2008). *sparse inflorescence1* encodes a monocot-specific *YUCCA*-like gene required for vegetative and reproductive development in maize. *Proc. Natl. Acad. Sci. USA* **105**.

- Gallavotti, A., Malcomber, S., Gaines, C., Stanfield, S., Whipple, C., Kellogg, E., and Schmidt, R.J. (2011). BARREN STALK FASTIGIATE1 is an at-hook protein required for the formation of maize ears. *Plant Cell* **23**:1756–1771.
- Galli, M., Liu, Q., Moss, B.L., Malcomber, S., Li, W., Gaines, C., Federici, S., Roshkovan, J., Meeley, R., Nemhauser, J.L., et al. (2015). Auxin signaling modules regulate maize inflorescence architecture. *Proc. Natl. Acad. Sci. USA* **112**.
- Goh, T., Toyokura, K., Wells, D.M., Swarup, K., Yamamoto, M., Mimura, T., Weijers, D., Fukaki, H., Laplaze, L., Bennett, M.J., et al. (2016). Quiescent center initiation in the Arabidopsis lateral root primordia is dependent on the SCARECROW transcription factor. *Development*, 143.
- Goñin, M., Bergougnoux, V., Nguyen, T.D., Gantet, P., and Champion, A. (2019). What makes adventitious roots? *Plants* **8**, 240.
- Greb, T., Clarenz, O., Schafer, E., Muller, D., Herrero, R., Schmitz, G., and Theres, K. (2003). Molecular analysis of the LATERAL SUPPRESSOR gene in *Arabidopsis* reveals a conserved control mechanism for axillary meristem formation. *Genes Dev.* **17**:1175–1187.
- Greenwood, J.R., Finnegan, E.J., Watanabe, N., Trevaskis, B., and Swain, S.M. (2017). New alleles of the wheat domestication gene Q reveal multiple roles in growth and reproductive development. *Development* **144**.
- Grogan, C.O. (1956). Detasseling Responses in Corn 1. *Agron. J.* **48**:247–249.
- Guillotin, B., Rahni, R., Passalacqua, M., Mohammed, M.A., Xu, X., Raju, S.K., Ramírez, C.O., Jackson, D., Groen, S.C., Gillis, J., and Birnbaum, K.D. (2023). A pan-grass transcriptome reveals patterns of cellular divergence in crops. *Nature* **617**:785–791.
- Guo, T., Chen, K., Dong, N.Q., Shi, C.L., Ye, W.W., Gao, J.P., Shan, J.X., and Lin, H.X. (2018). GRAIN SIZE AND NUMBER1 negatively regulates the OSMKKK10-OSMKK4-OSMPK6 cascade to coordinate the trade-off between grain number per panicle and grain size in rice. *Plant Cell* **30**:871–888.
- Guo, T., Lu, Z.Q., Shan, J.X., Ye, W.W., Dong, N.Q., and Lin, H.X. (2020). ERECTA1 acts upstream of the OsMKKK10-OsMKK4-OsMPK6 cascade to control spikelet number by regulating cytokinin metabolism in rice. *Plant Cell* **32**:2763–2779.
- Guo, T., Lu, Z.-Q., Xiong, Y., Shan, J.-X., Ye, W.-W., Dong, N.-Q., Kan, Y., Yang, Y.-B., Zhao, H.-Y., Yu, H.-X., et al. (2023). Optimization of rice panicle architecture by specifically suppressing ligand–receptor pairs. *Nat. Commun.* **14**:1640.
- Gutiérrez-Alanís, D., Yong-Villalobos, L., Jiménez-Sandoval, P., Alatorre-Cobos, F., Oropeza-Aburto, A., Mora-Macías, J., Sánchez-Rodríguez, F., Cruz-Ramírez, A., and Herrera-Estrella, L. (2017). Phosphate Starvation-Dependent Iron Mobilization Induces CLE14 Expression to Trigger Root Meristem Differentiation through CLV2/PEPR2 Signaling. *Dev. Cell* **41**:555–570.e3.
- Han, H., Yan, A., Li, L., Zhu, Y., Feng, B., Liu, X., and Zhou, Y. (2020). A signal cascade originated from epidermis defines apical-basal patterning of Arabidopsis shoot apical meristems. *Nat. Commun.* **11**:1214.
- Han, L., Zhong, W., Qian, J., Jin, M., Tian, P., Zhu, W., Zhang, H., Sun, Y., Feng, J.-W., Liu, X., et al. (2023). A multi-omics integrative network map of maize. *Nat. Genet.* **55**:144–153.
- Hay, A., and Tsiantis, M. (2010). KNOX genes: versatile regulators of plant development and diversity. *Development* **137**:3153–3165.
- Heidstra, R., and Sabatini, S. (2014). Plant and animal stem cells: Similar yet different. *Nat. Rev. Mol. Cell Biol.* **15**:301–312.
- Heisler, M.G., Hamant, O., Krupinski, P., Uyttewaald, M., Ohno, C., Jönsson, H., Traas, J., and Meyerowitz, E.M. (2010). Alignment between PIN1 Polarity and Microtubule Orientation in the Shoot Apical Meristem Reveals a Tight Coupling between Morphogenesis and Auxin Transport. *PLoS Biol.* **8**, e1000516.
- Hendelman, A., Zebell, S., Rodríguez-Leal, D., Dukler, N., Robitaille, G., Wu, X., Kostyun, J., Tal, L., Wang, P., Bartlett, M.E., et al. (2021). Conserved pleiotropy of an ancient plant homeobox gene uncovered by cis-regulatory dissection. *Cell* **184**:1724–1739.e16.
- Herrbach, V., Remblière, C., Gough, C., and Bensmihen, S. (2014). Lateral root formation and patterning in *Medicago truncatula*. *J. Plant Physiol.* **171**:301–310.
- Hirakawa, Y., Kondo, Y., and Fukuda, H. (2010). TDIF peptide signaling regulates vascular stem cell proliferation via the WOX4 homeobox gene in Arabidopsis. *Plant Cell* **22**:2618–2629.
- Hirakawa, Y. (2022). Evolution of meristem zonation by CLE gene duplication in land plants. *Nat. Plants* **8**:735–740.
- Hirakawa, Y., Fujimoto, T., Ishida, S., Uchida, N., Sawa, S., Kiyosue, T., Ishizaki, K., Nishihama, R., Kohchi, T., and Bowman, J.L. (2020). Induction of Multichotomous Branching by CLAVATA Peptide in *Marchantia polymorpha*. *Curr. Biol.* **30**:3833–3840.e4.
- Hobe, M., Müller, R., Grunewald, M., Brand, U., and Simon, R. (2003). Loss of CLE40, a protein functionally equivalent to the stem cell restricting signal CLV3, enhances root waving in Arabidopsis. *Dev. Gene. Evol.* **213**:371–381.
- Hochholdinger, F., and Feix, G. (1998). Early post-embryonic root formation is specifically affected in the maize mutant *lrt1*. *Plant J.* **16**:247–255.
- Hochholdinger, F., Park, W.J., and Feix, G.H. (2001). Cooperative action of SLR1 and SLR2 is required for lateral root-specific cell elongation in maize. *Plant Physiol.* **125**:1529–1539.
- Hord, C.L.H., Chen, C., DeYoung, B.J., Clark, S.E., and Ma, H. (2006). The BAM1/BAM2 Receptor-Like Kinases Are Important Regulators of Arabidopsis Early Anther Development. *Plant Cell* **18**:1667–1680.
- Hu, C., Zhu, Y., Cui, Y., Cheng, K., Liang, W., Wei, Z., Zhu, M., Yin, H., Zeng, L., Xiao, Y., et al. (2018). A group of receptor kinases are essential for CLAVATA signalling to maintain stem cell homeostasis. *Nat. Plants* **4**:205–211.
- Huang, X.Y., Chao, D.Y., Gao, J.P., Zhu, M.Z., Shi, M., and Lin, H.X. (2009a). A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control. *Genes Dev.* **23**:1805–1817.
- Huang, X., Qian, Q., Liu, Z., Sun, H., He, S., Luo, D., Xia, G., Chu, C., Li, J., and Fu, X. (2009b). Natural variation at the DEP1 locus enhances grain yield in rice. *Nat. Genet.* **41**:494–497.
- Huang, Y., Zhao, S., Fu, Y., Sun, H., Ma, X., Tan, L., Liu, F., Sun, X., Sun, H., Gu, P., et al. (2018). Variation in the regulatory region of FZP causes increases in secondary inflorescence branching and grain yield in rice domestication. *Plant J.* **96**:716–733.
- Hubbard, L., McSteen, P., Doebley, J., and Hake, S. (2002). Expression patterns and mutant phenotype of teosinte branched1 correlate with growth suppression in maize and teosinte. *Genetics* **162**:1927–1935.
- Hunter, R.B., Daynard, T.B., Hume, D.J., Tanner, J.W., Curtis, J.D., and Kannenberg, L.W. (1969). Effect of Tassel Removal on Grain Yield of Corn (*Zea mays* L.) 1. *Crop Sci.* **9**:405–406.
- Hyles, J., Vautrin, S., Pettolino, F., MacMillan, C., Stachurski, Z., Breen, J., Berges, H., Wicker, T., and Spielmeyer, W. (2017). Repeat-length variation in a wheat cellulose synthase-like gene is associated with altered tiller number and stem cell wall composition. *J. Exp. Bot.* **68**:1519–1529.
- Ibañez, M., Fàbregas, N., Chory, J., and Caño-Delgado, A.I. (2009). Brassinosteroid signaling and auxin transport are required to establish the periodic pattern of Arabidopsis shoot vascular bundles. *Proc. Natl. Acad. Sci. USA* **106**:13630–13635.

- Jackson, D., Veit, B., and Hake, S. (1994). Expression of maize KNOTTED1 related homeobox genes in the shoot apical meristem predicts patterns of morphogenesis in the vegetative shoot. *Development* **120**:405–413.
- Janocha, D., Pfeiffer, A., Dong, Y., Novák, O., Strnad, M., Ryabova, L.A., and Lohmann, J.U. (2022). TOR kinase controls Arabidopsis shoot development by translational repression of cytokinin catabolic enzymes Advance Access. Preprint at bioRxiv.
- Jansen, L., Roberts, I., De Rycke, R., and Beeckman, T. (2012). Phloem-associated auxin response maxima determine radial positioning of lateral roots in maize. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **367**:1525–1533.
- Jasinski, S., Piazza, P., Craft, J., Hay, A., Woolley, L., Rieu, I., Phillips, A., Hedden, P., and Tsiantis, M. (2005). KNOX Action in Arabidopsis Is Mediated by Coordinate Regulation of Cytokinin and Gibberellin Activities. *Curr. Biol.* **15**:1560–1565.
- Je, B.I., Gruel, J., Lee, Y.K., Bommert, P., Arevalo, E.D., Eveland, A.L., Wu, Q., Goldshmidt, A., Meeley, R., Bartlett, M., et al. (2016). Signaling from maize organ primordia via FASCIATED EAR3 regulates stem cell proliferation and yield traits. *Nat. Genet.* **48**:785–791.
- Je, B.I., Xu, F., Wu, Q., Liu, L., Meeley, R., Gallagher, J.P., Corcilius, L., Payne, R.J., Bartlett, M.E., and Jackson, D. (2018). The CLAVATA receptor FASCIATED EAR2 responds to distinct CLE peptides by signaling through two downstream effectors. *Elife* **7**, e35673.
- Jiang, X., Lubini, G., Hernandez-Lopes, J., Rijnsburger, K., Veltkamp, V., de Maagd, R.A., Angenent, G.C., and Bemer, M. (2022). FRUITFULL-like genes regulate flowering time and inflorescence architecture in tomato. *Plant Cell* **34**:1002–1019.
- Jiao, Y., Wang, Y., Xue, D., Wang, J., Yan, M., Liu, G., Dong, G., Zeng, D., Lu, Z., Zhu, X., et al. (2010). Regulation of OsSPL14 by OsmiR156 defines ideal plant architecture in rice. *Nat. Genet.* **42**:541–544.
- Jing, H., and Strader, L.C. (2019). Interplay of auxin and cytokinin in lateral root development. *Int. J. Mol. Sci.* **20**, 486.
- John, A., Smith, E.S., Jones, D.S., Soyars, C.L., and Nimchuk, Z.L. (2023). A network of CLAVATA receptors buffers auxin-dependent meristem maintenance. *Nat. Plants* **9**:1306–1317.
- Jones, D.S., John, A., VanDerMolen, K.R., and Nimchuk, Z.L. (2021). CLAVATA signaling ensures reproductive development in plants across thermal environments. *Curr. Biol.* **31**:220–227.e5.
- Jones, T., Lowe, K., Hoerster, G., Anand, A., Wu, E., Wang, N., Arling, M., Lenderts, B., and Gordon-Kamm, W. (2019). Maize transformation using the morphogenic genes Baby Boom and Wuschel2. In *Methods in Molecular Biology*.
- Kang, J., Wang, X., Ishida, T., Grienberger, E., Zheng, Q., Wang, J., Zhang, Y., Chen, W., Chen, M., Song, X.F., et al. (2022). A group of CLE peptides regulates de novo shoot regeneration in Arabidopsis thaliana. *New Phytol.* **235**.
- Keller, T., Abbott, J., Moritz, T., and Doerner, P. (2006). *Arabidopsis* REGULATOR OF AXILLARY MERISTEMS1 controls a leaf axil stem cell niche and modulates vegetative development. *Plant Cell* **18**:598–611.
- Kellogg, E.A. (2022). Genetic control of branching patterns in grass inflorescences. *Plant Cell* **34**:2518–2533.
- Kerstetter, R.A., Laudencia-Chinguanco, D., Smith, L.G., and Hake, S. (1997). Loss-of-function mutations in the maize homeobox gene, knotted1, are defective in shoot meristem maintenance. *Development* **124**:3045–3054.
- Khaipho-Burch, M., Cooper, M., Crossa, J., de Leon, N., Holland, J., Lewis, R., McCouch, S., Murray, S.C., Rabbi, I., Ronald, P., et al. (2023). Genetic modification can improve crop yields — but stop overselling it. *Nature* **621**:470–473.
- Khan, M.A., Gemenet, D.C., and Villordon, A. (2016). Root system architecture and abiotic stress tolerance: current knowledge in root and tuber crops. *Front. Plant Sci.* **7**:1584.
- Kimura, Y., Tasaka, M., Torii, K.U., and Uchida, N. (2018). ERECTA-family genes coordinate stem cell functions between the epidermal and internal layers of the shoot apical meristem. *Development* **145**:dev156380.
- Kinoshita, A., Betsuyaku, S., Osakabe, Y., Mizuno, S., Nagawa, S., Stahl, Y., Simon, R., Yamaguchi-Shinozaki, K., Fukuda, H., and Sawa, S. (2010). RPK2 is an essential receptor-like kinase that transmits the CLV3 signal in Arabidopsis. *Development* **137**:3911–3920.
- Kitagawa, M., Wu, P., Balkunde, R., Cunniff, P., and Jackson, D. (2022). An RNA exosome subunit mediates cell-to-cell trafficking of a homeobox mRNA via plasmodesmata. *Science* **375**:177–182.
- Komatsu, M., Chujo, A., Nagato, Y., Shimamoto, K., and Kyoizuka, J. (2003). Frizzy panicle is required to prevent the formation of axillary meristems and to establish floral meristem identity in rice spikelets. *Development* **130**.
- Kong, D., Li, C., Xue, W., Wei, H., Ding, H., Hu, G., Zhang, X., Zhang, G., Zou, T., Xian, Y., et al. (2023). UB2/UB3/TSH4-anchored transcriptional networks regulate early maize inflorescence development in response to simulated shade. *Plant Cell* **35**:717–737.
- Koppolu, R., Chen, S., and Schnurbusch, T. (2022). Evolution of inflorescence branch modifications in cereal crops. *Curr. Opin. Plant Biol.* **65**:102168.
- Kosentka, P.Z., Overholt, A., Maradiaga, R., Mitoubsi, O., and Shpak, E.D. (2019). EPFL Signals in the Boundary Region of the SAM Restrict Its Size and Promote Leaf Initiation. *Plant Physiol.* **179**:265–279.
- Kucukoglu, M., Nilsson, J., Zheng, B., Chaabouni, S., and Nilsson, O. (2017). WUSCHEL-RELATED HOMEBOX4 (WOX4)-like genes regulate cambial cell division activity and secondary growth in Populus trees. *New Phytol.* **215**:642–657.
- Kurakawa, T., Ueda, N., Maekawa, M., Kobayashi, K., Kojima, M., Nagato, Y., Sakakibara, H., and Kyoizuka, J. (2007). Direct control of shoot meristem activity by a cytokinin-activating enzyme. *Nature* **445**:652–655.
- Lardon, R., Wijnker, E., Keurentjes, J., and Geelen, D. (2020). The genetic framework of shoot regeneration in Arabidopsis comprises master regulators and conditional fine-tuning factors. *Commun. Biol.* **3**:549.
- LaRue, T., Lindner, H., Srinivas, A., et al. (2022). Uncovering natural variation in root system architecture and growth dynamics using a robotics-assisted phenomics platform. *eLife* **11**.
- Laureyns, R., Joossens, J., Herwegh, D., Pevernagie, J., Pavie, B., Demuynck, K., Debray, K., Coussens, G., Pauwels, L., Van Hautegeem, T., et al. (2022). An in situ sequencing approach maps PLASTOCHRON1 at the boundary between indeterminate and determinate cells. *Plant Physiol.* **188**:782–794.
- Laux, T., Mayer, K.F., Berger, J., and Jürgens, G. (1996). The WUSCHEL gene is required for shoot and floral meristem integrity in Arabidopsis. *Development* **122**:87–96.
- Lee, D.Y., Lee, J., Moon, S., Park, S.Y., and An, G. (2007). The rice heterochronic gene SUPERNUMERARY BRACT regulates the transition from spikelet meristem to floral meristem. *Plant J.* **49**:64–78.
- Lee, R., Baldwin, S., Kenel, F., McCallum, J., and Macknight, R. (2013). FLOWERING LOCUS T genes control onion bulb formation and flowering. *Nat. Commun.* **4**:2884.
- Lee, H. (2018). Stem Cell Maintenance and Abiotic Stress Response in Shoot Apical Meristem for Developmental Plasticity. *J. Plant Biol.* **61**:358–365.



- Leibfried, A., To, J.P.C., Busch, W., Stehling, S., Kehle, A., Demar, M., Kieber, J.J., and Lohmann, J.U. (2005). WUSCHEL controls meristem function by direct regulation of cytokinin-inducible response regulators. *Nature* **438**:1172–1175.
- Lemmon, Z.H., Reem, N.T., Dalrymple, J., Soyk, S., Swartwood, K.E., Rodriguez-Leal, D., Van Eck, J., and Lippman, Z.B. (2018). Rapid improvement of domestication traits in an orphan crop by genome editing. *Nat. Plants* **4**:766–770.
- Li, S., Zhao, B., Yuan, D., Duan, M., Qian, Q., Tang, L., Wang, B., Liu, X., Zhang, J., Wang, J., et al. (2013). Rice zinc finger protein DST enhances grain production through controlling Gn1a/OsCKX2 expression. *Proc. Natl. Acad. Sci. USA* **110**.
- Leyser, H.M.O., and Furner, I.J. (1992). Characterisation of three shoot apical meristem mutants of *Arabidopsis thaliana*. *Development* **116**:397–403.
- Li, G., Zhang, H., Li, J., Zhang, Z., and Li, Z. (2021). Genetic control of panicle architecture in rice. *Crop J.* **9**:590–597.
- Li, M., Zhong, W., Yang, F., and Zhang, Z. (2018). Genetic and Molecular Mechanisms of Quantitative Trait Loci Controlling Maize Inflorescence Architecture. *Plant Cell Physiol.* **59**:448–457.
- Lin, G., He, C., Zheng, J., Koo, D.H., Le, H., Zheng, H., Tamang, T.M., Lin, J., Liu, Y., Zhao, M., et al. (2021a). Chromosome-level genome assembly of a regenerable maize inbred line A188. *Genome Biol.* **22**:175.
- Lin, Y., Jiang, X., Hu, H., Zhou, K., Wang, Q., Yu, S., Yang, X., Wang, Z., Wu, F., Liu, S., et al. (2021b). QTL mapping for grain number per spikelet in wheat using a high-density genetic map. *Crop J.* **9**:1108–1114.
- Lincoln, C., Long, J., Yamaguchi, J., Serikawa, K., and Hake, S. (1994). A knotted1-like homeobox gene in *Arabidopsis* is expressed in the vegetative meristem and dramatically alters leaf morphology when overexpressed in transgenic plants. *Plant Cell* **6**:1859–1876.
- Lippman, Z.B., Cohen, O., Alvarez, J.P., Abu-Abied, M., Pekker, I., Paran, I., Eshed, Y., and Zamir, D. (2008). The making of a compound inflorescence in tomato and related nightshades. *PLoS Biol.* **6**:e288.
- Liu, J., Rowe, J., and Lindsey, K. (2014). Hormonal crosstalk for root development: A combined experimental and modeling perspective. *Front. Plant Sci.* **5**:116.
- Liu, L., Du, Y., Shen, X., Li, M., Sun, W., Huang, J., Liu, Z., Tao, Y., Zheng, Y., Yan, J., and Zhang, Z. (2015). KRN4 Controls Quantitative Variation in Maize Kernel Row Number. *PLoS Genet.* **11**, e1005670.
- Liu, J., Cheng, X., Liu, P., and Sun, J. (2017a). miR156-targeted SBP-box transcription factors interact with DWARF53 to regulate teosinte branched1 and barren STALK1 expression in bread wheat. *Plant Physiol.* **174**:1931–1948.
- Liu, J., Moore, S., Chen, C., and Lindsey, K. (2017b). Crosstalk Complexities between Auxin, Cytokinin, and Ethylene in *Arabidopsis* Root Development: From Experiments to Systems Modeling, and Back Again. *Mol. Plant* **10**:1480–1496.
- Liu, L., Gallagher, J., Arevalo, E.D., Chen, R., Skopelitis, T., Wu, Q., Bartlett, M., and Jackson, D. (2021a). Enhancing grain-yield-related traits by CRISPR–Cas9 promoter editing of maize CLE genes. *Nat. Plants* **7**:287–294.
- Liu, Y., Wu, G., Zhao, Y., Wang, H.H., Dai, Z., Xue, W., Yang, J., Wei, H., Shen, R., and Wang, H. (2021b). DWARF53 interacts with transcription factors UB2/UB3/TSH4 to regulate maize tillering and tassel branching. *Plant Physiol.* **187**:947–962.
- Liu, L., Qiu, L., Zhu, Y., Luo, L., Han, X., Man, M., Li, F., Ren, M., and Xing, Y. (2023a). Comparisons between Plant and Animal Stem Cells Regarding Regeneration Potential and Application. *Int. J. Mol. Sci.* **24**, 4392.
- Liu, Y., Chen, J., Yin, C., Wang, Z., Wu, H., Shen, K., Zhang, Z., Kang, L., Xu, S., Bi, A., et al. (2023b). A high-resolution genotype–phenotype map identifies the TaSPL17 controlling grain number and size in wheat. *Genome Biol.* **24**:196.
- Liu, X., Bie, X.M., Lin, X., Li, M., Wang, H., Zhang, X., Yang, Y., Zhang, C., Zhang, X.S., and Xiao, J. (2023c). Uncovering the transcriptional regulatory network involved in boosting wheat regeneration and transformation. *Nat. Plants* **9**:908–925.
- Long, Y., Cheddadi, I., Mosca, G., Mirabet, V., Dumond, M., Kiss, A., Traas, J., Godin, C., and Boudaoud, A. (2020). Cellular Heterogeneity in Pressure and Growth Emerges from Tissue Topology and Geometry. *Curr. Biol.* **30**:1504–1516.e8.
- Lotan, T., Ohto, M., Yee, K.M., West, M.A., Lo, R., Kwong, R.W., Yamagishi, K., Fischer, R.L., Goldberg, R.B., and Harada, J.J. (1998). *Arabidopsis* LEAFY COTYLEDON1 is sufficient to induce embryo development in vegetative cells. *Cell* **93**:1195–1205.
- Lowe, K., Wu, E., Wang, N., Hoerster, G., Hastings, C., Cho, M.J., Scelongo, C., Lenderts, B., Chamberlin, M., Cushatt, J., et al. (2016). Morphogenic regulators Baby boom and Wuschel improve monocot transformation. *Plant Cell* **28**:1998–2015.
- Lowe, K., Rota, M.L., Hoerster, G., Hastings, C., Wang, N., Chamberlin, M., Wu, E., Jones, T., and Gordon-Kamm, W. (2018). Rapid genotype “independent” *Zea mays* L. (maize) transformation via direct somatic embryogenesis. *Vitro Cell Dev. Biol. Plant* **54**.
- Lu, Z., Yu, H., Xiong, G., Wang, J., Jiao, Y., Liu, G., Jing, Y., Meng, X., Hu, X., Qian, Q., et al. (2013). Genome-wide binding analysis of the transcription activator IDEAL PLANT ARCHITECTURE1 reveals a complex network regulating rice plant architecture. *Plant Cell* **25**:3743–3759.
- Lucas, W.J., Bouché-Pillon, S., Jackson, D.P., Nguyen, L., Baker, L., Ding, B., and Hake, S. (1995). Selective Trafficking of KNOTTED1 Homeodomain Protein and Its mRNA Through Plasmodesmata. *Science* **270**:1980–1983.
- Lynch, J. (1995). Root architecture and plant productivity. *Plant Physiol.* **109**:7–13.
- Ma, Y., Miotk, A., Šutiković, Z., Ermakova, O., Wenzl, C., Medzihradsky, A., Gaillochet, C., Forner, J., Utan, G., Brackmann, K., et al. (2019). WUSCHEL acts as an auxin response rheostat to maintain apical stem cells in *Arabidopsis*. *Nat. Commun.* **10**:5093.
- Mandal, S., Ghorai, M., Anand, U., Samanta, D., Kant, N., Mishra, T., Rahman, M.H., Jha, N.K., Jha, S.K., Lal, M.K., et al. (2022). Cytokinin and abiotic stress tolerance -What has been accomplished and the way forward? *Front. Genet.* **13**:943025.
- Mandel, J.R., Nambeesan, S., Bowers, J.E., Marek, L.F., Ebert, D., Rieseberg, L.H., Knapp, S.J., and Burke, J.M. (2013). Association Mapping and the Genomic Consequences of Selection in Sunflower. *PLoS Genet.* **9**:e1003378.
- Mandel, J.R., McAssey, E.V., Nambeesan, S., Garcia-Navarro, E., and Burke, J.M. (2014). Molecular evolution of candidate genes for crop-related traits in sunflower (*Helianthus annuus* L.). *PLoS One* **9**:e99620.
- Mason, M.G., Ross, J.J., Babst, B.A., Wienclaw, B.N., and Beveridge, C.A. (2014). Sugar demand, not auxin, is the initial regulator of apical dominance. *Proc. Natl. Acad. Sci. USA* **111**.
- Matsuzaki, Y., Ogawa-Ohnishi, M., Mori, A., and Matsubayashi, Y. (2010). Secreted peptide signals required for maintenance of root stem cell niche in *Arabidopsis*. *Science* **329**:1065–1067.
- McGarry, R.C., Kaur, H., Lin, Y.T., Puc, G.L., Eshed Williams, L., van der Knaap, E., and Ayre, B.G. (2023). Altered expression of SELF-PRUNING disrupts homeostasis and facilitates signal delivery to meristems. *Plant Physiol.* **192**:1517–1531.



- McSteen, P., Malcomber, S., Skirpan, A., Lunde, C., Wu, X., Kellogg, E., and Hake, S. (2007). *barren inflorescence2* encodes a co-ortholog of the Pinoid serine/threonine kinase and is required for organogenesis during inflorescence and vegetative development in maize. *Plant Physiol.* **144**:1000–1011.
- Melnyk, C.W. (2023). Quantitative regeneration: Skoog and Miller revisited. *Quant. Plant Biol.* **4**:e10.
- Mhamdi, A., and Van Breusegem, F. (2018). Reactive oxygen species in plant development. *Development* **145**:dev164376.
- Morris, E.C., Griffiths, M., Golebiowska, A., et al. (2017). Shaping 3D root system architecture. *Curr Biol.* **27**:R919–R930.
- Morrison, D.M., Blankenship, E.E., Read, P.E., and Paparozzi, E.T. (2018). Stolon Development and Cultural Production Practices of Winter-Grown Strawberries. *Int. J. Fruit Sci.* **18**:138–152.
- Müller, R., Bleckmann, A., and Simon, R. (2008). The Receptor Kinase CORYNE of Arabidopsis Transmits the Stem Cell-Limiting Signal CLAVATA3 Independently of CLAVATA1. *Plant Cell* **20**:934–946.
- Muñoz, S., Ranc, N., Botton, E., Bérard, A., Rolland, S., Duffé, P., Carretero, Y., Le Paslier, M.C., Delalande, C., Bouzayen, M., et al. (2011). Increase in tomato locule number is controlled by two single-nucleotide polymorphisms located near WUSCHEL. *Plant Physiol.* **156**:2244–2254.
- Nadolska-Orczyk, A., Rajchel, I.K., Orczyk, W., and Gasparis, S. (2017). Major genes determining yield-related traits in wheat and barley. *Theor. Appl. Genet.* **130**:1081–1098.
- Navarro, C., Abelenda, J.A., Cruz-Oró, E., Cuéllar, C.A., Tamaki, S., Silva, J., Shimamoto, K., and Prat, S. (2011). Control of flowering and storage organ formation in potato by FLOWERING LOCUS T. *Nature* **478**:119–122.
- Nicolas, A., Maugarny-Calès, A., Adroher, B., Chelysheva, L., Li, Y., Burguet, J., Bågman, A.M., Smit, M.E., Brady, S.M., Li, Y., and Laufs, P. (2022). De novo stem cell establishment in meristems requires repression of organ boundary cell fate. *Plant Cell* **34**:4738–4759.
- Nimchuk, Z.L. (2017). CLAVATA1 controls distinct signaling outputs that buffer shoot stem cell proliferation through a two-step transcriptional compensation loop. *PLoS Genet.* **13**, e1006681.
- Nimchuk, Z.L., Tarr, P.T., Ohno, C., Qu, X., and Meyerowitz, E.M. (2011). Plant stem cell signaling involves ligand-dependent trafficking of the CLAVATA1 receptor kinase. *Curr. Biol.* **21**:345–352.
- Ning, Q., Jian, Y., Du, Y., Li, Y., Shen, X., Jia, H., Zhao, R., Zhan, J., Yang, F., Jackson, D., et al. (2021). An ethylene biosynthesis enzyme controls quantitative variation in maize ear length and kernel yield. *Nat. Commun.* **12**:5832.
- Ogura, N., Sasagawa, Y., Ito, T., Tameshige, T., Kawai, S., Sano, M., Doll, Y., Iwase, A., Kawamura, A., Suzuki, T., et al. (2023). WUSCHEL-RELATED HOMEODOMAIN 13 suppresses de novo shoot regeneration via cell fate control of pluripotent callus. *Sci. Adv.* **9**:eadg6983.
- Ohyama, K., Shinohara, H., Ogawa-Ohnishi, M., and Matsubayashi, Y. (2009). A glycopeptide regulating stem cell fate in Arabidopsis thaliana. *Nat. Chem. Biol.* **5**:578–580.
- Orman-Ligeza, B., Parizot, B., Gantet, P.P., Beeckman, T., Bennett, M.J., and Draye, X. (2013). Post-embryonic root organogenesis in cereals: Branching out from model plants. *Trends Plant Sci.* **18**:459–467.
- Ortiz-Ramírez, C., Guillotin, B., Xu, X., Rahni, R., Zhang, S., Yan, Z., Coqueiro Dias Araujo, P., Demesa-Arevalo, E., Lee, L., Van Eck, J., et al. (2021). Ground tissue circuitry regulates organ complexity in maize and Setaria. *Science* **374**:1247–1252.
- Ou, Y., Lu, X., Zi, Q., Xun, Q., Zhang, J., Wu, Y., Shi, H., Wei, Z., Zhao, B., Zhang, X., et al. (2016). RGF1 INSENSITIVE 1 to 5, a group of LRR receptor-like kinases, are essential for the perception of root meristem growth factor 1 in Arabidopsis thaliana. *Cell Res.* **26**:686–698.
- Ou, Y., Tao, B., Wu, Y., Cai, Z., Li, H., Li, M., He, K., Gou, X., and Li, J. (2022). Essential roles of SERKs in the ROOT MERISTEM GROWTH FACTOR-mediated signaling pathway. *Plant Physiol.* **189**:165–177.
- Pardal, R., and Heidstra, R. (2021). Root stem cell niche networks: It's complexed! Insights from Arabidopsis. *J. Exp. Bot.* **72**:6727–6738.
- Park, S.J., Jiang, K., Schatz, M.C., and Lippman, Z.B. (2012). Rate of meristem maturation determines inflorescence architecture in tomato. *Proc. Natl. Acad. Sci. USA* **109**:639–644.
- Peng, Z., Alique, D., Xiong, Y., Hu, J., Cao, X., Lü, S., Long, M., Wang, Y., Wabnik, K., and Jiao, Y. (2022). Differential growth dynamics control aerial organ geometry. *Curr. Biol.* **32**:4854–4868.e5.
- Perales, M., Rodriguez, K., Snipes, S., Yadav, R.K., Diaz-Mendoza, M., and Reddy, G.V. (2016). Threshold-dependent transcriptional discrimination underlies stem cell homeostasis. *Proc. Natl. Acad. Sci. USA* **113**:E6298–E6306.
- Pfeiffer, A., Janocha, D., Dong, Y., Medzihradsky, A., Schöne, S., Daum, G., Suzuki, T., Forner, J., Langenecker, T., Rempel, E., et al. (2016). Integration of light and metabolic signals for stem cell activation at the shoot apical meristem. *Elife* **5**, e17023.
- Phillips, K.A., Skirpan, A.L., Liu, X., Christensen, A., Slewinski, T.L., Hudson, C., Barazesh, S., Cohen, J.D., Malcomber, S., and McSteen, P. (2011). *vanishing tassel2* Encodes a Grass-Specific tryptophan aminotransferase required for vegetative and reproductive development in maize. *Plant Cell* **23**:550–566.
- Poursarebani, N., Trautewig, C., Melzer, M., Nussbaumer, T., Lundqvist, U., Rutten, T., Schmutzer, T., Brandt, R., Himmelbach, A., Altschmied, L., et al. (2020). COMPOSITUM1 contributes to the architectural simplification inflorescence via meristem identity signals. *Nat. Commun.* **11**:5138.
- Radanović, A., Miladinović, D., Cvejić, S., Jocković, M., and Jocić, S. (2018). Sunflower genetics from ancestors to modern hybrids—a review. *Genes* **9**, 528.
- Raman, S., Greb, T., Peaucelle, A., Blein, T., Laufs, P., and Theres, K. (2008). Interplay of miR164, CUP-SHAPED COTYLEDON genes and LATERAL SUPPRESSOR controls axillary meristem formation in Arabidopsis thaliana. *Plant J.* **55**:65–76.
- Ren, T., Hu, Y., Tang, Y., Li, C., Yan, B., Ren, Z., Tan, F., Tang, Z., Fu, S., and Li, Z. (2018). Utilization of a Wheat55K SNP array for mapping of major QTL for temporal expression of the tiller number. *Front. Plant Sci.* **9**:333.
- Giulini, A., Wang, J., Jackson, D., Zhang, W.L., Jue, D.W., Xing, H.T., Li, H.L., and Li, Q. (2004). Dynamic transcriptome profiling provides insights into rhizome enlargement in ginger (*Zingiber officinale* Rosc.). *PLoS one* **18**. response regulator homologue ABPHYL1. *Nature* **430**:1031–1034.
- Robischon, M., Du, J., Miura, E., and Groover, A. (2011). The Populus class III HD ZIP, popREVOLUTA, influences cambium initiation and patterning of woody stems. *Plant Physiol.* **155**:1214–1225.
- Rodríguez-Leal, D., Lemmon, Z.H., Man, J., Bartlett, M.E., and Lippman, Z.B. (2017). Engineering Quantitative Trait Variation for Crop Improvement by Genome Editing. *Cell* **171**:470–480.e8.
- Rodríguez-Leal, D., Xu, C., Kwon, C.-T., Soyars, C., Demesa-Arevalo, E., Man, J., Liu, L., Lemmon, Z.H., Jones, D.S., Van Eck, J., et al. (2019). Evolution of buffering in a genetic circuit controlling plant stem cell proliferation. *Nat. Genet.* **51**:786–792.
- Rosas-Diaz, T., Zhang, D., Fan, P., Wang, L., Ding, X., Jiang, Y., Jimenez-Gongora, T., Medina-Puche, L., Zhao, X., Feng, Z., et al.

- (2018). A virus-targeted plant receptor-like kinase promotes cell-to-cell spread of RNAi. *Proc. Natl. Acad. Sci. USA* **115**:1388–1393.
- De Rybel, B., Vassileva, V., Parizot, B., Demeulenaere, M., Grunewald, W., Audenaert, D., Van Campenhout, J., Overvoorde, P., Jansen, L., Vanneste, S., et al. (2010). A novel Aux/IAA28 signaling cascade activates GATA23-dependent specification of lateral root founder cell identity. *Curr. Biol.* **20**:1697–1706.
- De Rybel, B., Adibi, M., Breda, A.S., Wendrich, J.R., Smit, M.E., Novák, O., Yamaguchi, N., Yoshida, S., Van Isterdael, G., Palovaara, J., et al. (2014). Integration of growth and patterning during vascular tissue formation in Arabidopsis. *Science* **345**.
- Sablowski, R. (2004). Plant and animal stem cells: conceptually similar, molecularly distinct? *Trends Cell Biol.* **14**:605–611.
- Sakuma, S., Golan, G., Guo, Z., Ogawa, T., Tagiri, A., Sugimoto, K., Bernhardt, N., Brassac, J., Mascher, M., Hensel, G., et al. (2019). Unleashing floret fertility in wheat through the mutation of a homeobox gene. *Proc. Natl. Acad. Sci. USA* **116**:5182–5187.
- Sarkar, A.K., Luijten, M., Miyashima, S., Lenhard, M., Hashimoto, T., Nakajima, K., Scheres, B., Heidstra, R., and Laux, T. (2007). Conserved factors regulate signalling in Arabidopsis thaliana shoot and root stem cell organizers. *Nature* **446**:811–814.
- Satina, S., Blakeslee, A.F., and Avery, A.G. (1940). Demonstration of the Three Germ Layers in the Shoot Apex of *Datura* by Means of Induced Polyploidy in Periclinal Chimeras. *Am. J. Bot.* **27**:895–905.
- Satoh-Nagasawa, N., Nagasawa, N., Malcomber, S., Sakai, H., and Jackson, D. (2006). A trehalose metabolic enzyme controls inflorescence architecture in maize. *Nature* **441**:227–230.
- Satterlee, J.W., Strable, J., and Scanlon, M.J. (2020). Plant stem-cell organization and differentiation at single-cell resolution. *Proc. Natl. Acad. Sci. USA* **117**.
- Schlegel, J., Denay, G., Wink, R., Pinto, K.G., Stahl, Y., Schmid, J., Blümke, P., and Simon, R.G. (2021). Control of Arabidopsis shoot stem cell homeostasis by two antagonistic CLE peptide signalling pathways. *Elife* **10**, e70934.
- Schmitz, R.J., Grotewold, E., and Stam, M. (2022). Cis-regulatory sequences in plants: Their importance, discovery, and future challenges. *Plant Cell* **34**:718–741.
- Schwarz, S., Grande, A.V., Bujdoso, N., Saedler, H., and Huijser, P. (2008). The microRNA regulated SBP-box genes SPL9 and SPL15 control shoot maturation in Arabidopsis. *Plant Mol. Biol.* **67**:183–195.
- SHA, X., GUAN, H., ZHOU, Y., SU, E., GUO, J., LI, Y., ZHANG, D., LIU, X., HE, G., LI, Y., et al. (2023). Genetic dissection of crown root traits and their relationship to aboveground agronomic traits in maize. *J. Integr. Agric.* **2023**.
- Shao, Y., Yu, X., Xu, X., Li, Y., Yuan, W., Xu, Y., Mao, C., Zhang, S., and Xu, J. (2020). The YDA-MKK4/MKK5-MPK3/MPK6 Cascade Functions Downstream of the RGF1-RGI Ligand-Receptor Pair in Regulating Mitotic Activity in Root Apical Meristem. *Mol. Plant* **13**:1608–1623.
- Shanmugaraj, N., Rajaraman, J., Kale, S., Kamal, R., Huang, Y., Thirulogachandar, V., Garibay-Hernández, A., Budhagatapalli, N., Tandon Moya, Y.A., Hajirezaei, M.R., et al. (2023). Multilayered regulation of developmentally programmed pre-anthesis tip degeneration of the barley inflorescence. *Plant Cell* **35**:3973–4001.
- Sharma, P., Lin, T., and Hannapel, D.J. (2016). Targets of the StBEL5 transcription factor include the FT Ortholog StSP6A1[OPEN]. *Plant Physiol.* **170**:310–324.
- Shen, X., Xiao, B., Kaderbek, T., Lin, Z., Tan, K., Wu, Q., Yuan, L., Lai, J., Zhao, H., and Song, W. (2023). Dynamic transcriptome landscape of developing maize ear. *Plant J.* **116**:1856–1870.
- Shimotohno, A., Heidstra, R., Blilou, I., and Scheres, B. (2018). Root stem cell niche organizer specification by molecular convergence of PLETHORA and SCARECROW transcription factor modules. *Genes Dev.* **32**:1085–1100.
- Shinohara, H. (2021). Root meristem growth factor RGF, a sulfated peptide hormone in plants. *Peptides*, 142.
- Shinohara, H., Mori, A., Yasue, N., Sumida, K., and Matsubayashi, Y. (2016). Identification of three LRR-RKs involved in perception of root meristem growth factor in Arabidopsis. *Proc. Natl. Acad. Sci. USA* **113**.
- Shpak, E.D. (2013). Diverse Roles of ERECTA Family Genes in Plant Development. *J. Integr. Plant Biol.* **55**:1238–1250.
- Shpak, E.D., Lakeman, M.B., and Torii, K.U. (2003). Dominant-Negative Receptor Uncovers Redundancy in the Arabidopsis ERECTA Leucine-Rich Repeat Receptor-Like Kinase Signaling Pathway That Regulates Organ Shape. *Plant Cell* **15**:1095–1110.
- Shpak, E.D., Berthiaume, C.T., Hill, E.J., and Torii, K.U. (2004). Synergistic interaction of three ERECTA-family receptor-like kinases controls Arabidopsis organ growth and flower development by promoting cell proliferation. *Development* **131**:1491–1501.
- Simons, K.J., Fellers, J.P., Trick, H.N., Zhang, Z., Tai, Y.S., Gill, B.S., and Faris, J.D. (2006). Molecular characterization of the major wheat domestication gene Q. *Genetics* **172**.
- Sinha, N.R., Williams, R.E., and Hake, S. (1993). Overexpression of the maize homeo box gene, KNOTTED-1, causes a switch from determinate to indeterminate cell fates. *Genes Dev.* **7**:787–795.
- Skirpan, A., Wu, X., and McSteen, P. (2008). Genetic and physical interaction suggest that BARREN STALK1 is a target of BARREN INFLORESCENCE2 in maize inflorescence development. *Plant J.* **55**:787–797.
- Smet, W., Seville, I., de Luis Balaguer, M.A., Wybouw, B., Mor, E., Miyashima, S., Blob, B., Roszak, P., Jacobs, T.B., Boeckschoten, M., et al. (2019). DOF2.1 Controls Cytokinin-Dependent Vascular Cell Proliferation Downstream of TM05/LHW. *Curr. Biol.* **29**:520–529.e6.
- Smith, E.S., and Nimchuk, Z.L. (2023). What a tangled web it weaves: Auxin coordination of stem cell maintenance and flower production. *J. Exp. Bot.* **74**:6950–6963.
- Somssich, M., Je, B.I., Simon, R., and Jackson, D. (2016). CLAVATA-WUSCHEL signaling in the shoot meristem. *Development* **143**:3238–3248.
- Song, S.-K., and Clark, S.E. (2005). POL and related phosphatases are dosage-sensitive regulators of meristem and organ development in Arabidopsis. *Dev. Biol.* **285**:272–284.
- Song, S.-K., Lee, M.M., and Clark, S.E. (2006). POL and PLL1 phosphatases are CLAVATA1 signaling intermediates required for Arabidopsis shoot and floral stem cells. *Development* **133**:4691–4698.
- Song, W., Liu, L., Wang, J., Wu, Z., Zhang, H., Tang, J., Lin, G., Wang, Y., Wen, X., Li, W., et al. (2016). Signature motif-guided identification of receptors for peptide hormones essential for root meristem growth. *Cell Res.* **26**:674–685.
- Song, X., Lu, Z., Yu, H., Shao, G., Xiong, J., Meng, X., Jing, Y., Liu, G., Xiong, G., Duan, J., et al. (2017). IPA1 functions as a downstream transcription factor repressed by D53 in strigolactone signaling in rice. *Cell Res.* **27**:1128–1141.
- Song, X., Meng, X., Guo, H., Cheng, Q., Jing, Y., Chen, M., Liu, G., Wang, B., Wang, Y., Li, J., and Yu, H. (2022). Targeting a gene regulatory element enhances rice grain yield by decoupling panicle number and size. *Nat. Biotechnol.* **40**:1403–1411.
- Soyk, S., Lemmon, Z.H., Oved, M., Fisher, J., Liberatore, K.L., Park, S.J., Goren, A., Jiang, K., Ramos, A., van der Knaap, E., et al. (2017). Bypassing Negative Epistasis on Yield in Tomato Imposed by a Domestication Gene. *Cell* **169**:1142–1155.e12.

- Soyk, S., Lemmon, Z.H., Sedlazeck, F.J., Jiménez-Gómez, J.M., Alonge, M., Hutton, S.F., Van Eck, J., Schatz, M.C., and Lippman, Z.B.** (2019). Duplication of a domestication locus neutralized a cryptic variant that caused a breeding barrier in tomato. *Nat. Plants* **5**:903.
- Stahl, Y., Wink, R.H., Ingram, G.C., and Simon, R.** (2009). A Signaling Module Controlling the Stem Cell Niche in Arabidopsis Root Meristems. *Curr. Biol.* **19**:909–914.
- Stahl, Y., Grabowski, S., Bleckmann, A., Kühnemuth, R., Weidtkamp-Peters, S., Pinto, K., Kirschner, G.K., Schmid, J.B., Wink, R.H., Hülsewede, A., et al.** (2013). Moderation of Arabidopsis Root Stemness by CLAVATA1 and ARABIDOPSIS CRINKLY4 Receptor Kinase Complexes. *Curr. Biol.* **23**:362–371.
- Stephenson, A.G.** (1981). Flower and Fruit Abortion: Proximate Causes and Ultimate Functions. *Annu. Rev. Ecol. Systemat.* **12**:253–279.
- Su, Y.H., Zhou, C., Li, Y.J., Yu, Y., Tang, L.P., Zhang, W.J., Yao, W.J., Huang, R., Laux, T., and Zhang, X.S.** (2020). Integration of pluripotency pathways regulates stem cell maintenance in the Arabidopsis shoot meristem. *Proc. Natl. Acad. Sci. USA* **117**:22561–22571.
- Suer, S., Agusti, J., Sanchez, P., Schwarz, M., and Greb, T.** (2011). *WOX4* imparts auxin responsiveness to cambium cells in arabidopsis. *Plant Cell* **23**:3247–3259.
- Sun, Y.D., and Folimonova, S.Y.** (2022). Location matters: from changing a presumption about the Citrus tristeza virus tissue tropism to understanding the stem pitting disease. *New Phytol.* **233**.
- Sun, S., Wang, X., Liu, Z., Bai, J., Song, J., Li, R., and Cui, X.** (2023). Tomato *APETALA2* family member *SITOE1* regulates inflorescence branching by repressing *SISTER* of *TM3*. *Plant Physiol.* **192**:293–306.
- Taguchi-Shiobara, F., Yuan, Z., Hake, S., and Jackson, D.** (2001). The fasciated *ear2* gene encodes a leucine-rich repeat receptor-like protein that regulates shoot meristem proliferation in maize. *Genes Dev.* **15**:2755–2766.
- Takahashi, G., Kiyosue, T., and Hirakawa, Y.** (2023). Control of stem cell behavior by CLE-JINGASA signaling in the shoot apical meristem in *Marchantia polymorpha*. *Curr. Biol.* **16**:2023.
- Takai, T., Taniguchi, Y., Takahashi, M., Nagasaki, H., Yamamoto, E., Hirose, S., Hara, N., Akashi, H., Ito, J., Arai-Sanoh, Y., et al.** (2023). *MORE PANICLES 3*, a natural allele of *OsTB1/FC1*, impacts rice yield in paddy fields at elevated CO<sub>2</sub> levels. *Plant J.* **114**:729–742.
- Taramino, G., Sauer, M., Stauffer, J.L., Jr., Multani, D., Niu, X., Sakai, H., and Hochholdinger, F.** (2007). The maize (*Zea mays* L.) *RTCS* gene encodes a LOB domain protein that is a key regulator of embryonic seminal and post-embryonic shoot-borne root initiation. *Plant J.* **50**:649–659.
- Taylor, B.H., and Scheuring, C.F.** (1994). A molecular marker for lateral root initiation: The *RSI-1* gene of tomato (*Lycopersicon esculentum* Mill) is activated in early lateral root primordia. *MGG Molecular & General Genetics* **243**:148–157.
- Teo, C.J., Takahashi, K., Shimizu, K., Shimamoto, K., and Taoka, K.I.** (2017). Potato tuber induction is regulated by interactions between components of a tuberigen complex. *Plant Cell Physiol.* **58**:365–374.
- Trinh, D.-C., Alonso-Serra, J., Asaoka, M., Colin, L., Cortes, M., Malivert, A., Takatani, S., Zhao, F., Traas, J., Trehin, C., and Hamant, O.** (2021). How Mechanical Forces Shape Plant Organs. *Curr. Biol.* **31**:R143–R159.
- Trung, K.H., Tran, Q.H., Bui, N.H., Tran, T.T., Luu, K.Q., Tran, N.T., Nguyen, L.T., Nguyen, D.T., Vu, B.D., Quan, D.T., et al.** (2020). A Weak Allele of *FASCIATED EAR 2* (*FEA2*) Increases Maize Kernel Row Number (KRN) and Yield in Elite Maize Hybrids. *Agronomy* **10**.
- Uchida, N., Shimada, M., and Tasaka, M.** (2013). *ERECTA*-Family Receptor Kinases Regulate Stem Cell Homeostasis via Buffering its Cytokinin Responsiveness in the Shoot Apical Meristem. *Plant Cell Physiol.* **54**:343–351.
- Varapparambath, V., Mathew, M.M., Shanmukhan, A.P., Radhakrishnan, D., Kareem, A., Verma, S., Ramalho, J.J., Manoj, B., Vellandath, A.R., Aiyaz, M., et al.** (2022). Mechanical conflict caused by a cell-wall-loosening enzyme activates de novo shoot regeneration. *Dev. Cell* **57**:2063–2080.e10.
- Wang, Q., Kohlen, W., Rossmann, S., Vernoux, T., and Theres, K.** (2014a). Auxin depletion from the leaf axil conditions competence for axillary meristem formation in Arabidopsis and tomato. *Plant Cell* **26**:2068–2079.
- Wang, Y., Wang, J., Shi, B., Yu, T., Qi, J., Meyerowitz, E.M., and Jiao, Y.** (2014b). The stem cell niche in leaf axils is established by auxin and cytokinin in Arabidopsis. *Plant Cell* **26**:2055–2067.
- Wang, J., Tian, C., Zhang, C., Shi, B., Cao, X., Zhang, T.-Q., Zhao, Z., Wang, J.-W., and Jiao, Y.** (2017). Cytokinin Signaling Activates *WUSCHEL* Expression during Axillary Meristem Initiation. *Plant Cell* **29**:1373–1387.
- Wang, B., Smith, S.M., and Li, J.** (2018). Genetic Regulation of Shoot Architecture. *Annu. Rev. Plant Biol.* **69**:437–468.
- Wang, S.-S., Chung, C.-L., Chen, K.-Y., and Chen, R.-K.** (2020a). A Novel Variation in the *FRIZZLE PANICLE (FZP)* Gene Promoter Improves Grain Number and Yield in Rice. *Genetics* **215**:243–252.
- Wang, F.X., Shang, G.D., Wu, L.Y., Xu, Z.G., Zhao, X.Y., and Wang, J.W.** (2020b). Chromatin Accessibility Dynamics and a Hierarchical Transcriptional Regulatory Network Structure for Plant Somatic Embryogenesis. *Dev. Cell* **54**:742–757.e8.
- Wang, X., Aguirre, L., Rodríguez-Leal, D., Hendelman, A., Benoit, M., and Lippman, Z.B.** (2021a). Dissecting cis-regulatory control of quantitative trait variation in a plant stem cell circuit. *Nat. Plants* **7**:419–427.
- Wang, W., Hu, C., Li, X., Zhu, Y., Tao, L., Cui, Y., Deng, D., Fan, X., Zhang, H., Li, J., et al.** (2022). Receptor-like cytoplasmic kinases *PBL34/35/36* are required for CLE peptide-mediated signaling to maintain shoot apical meristem and root apical meristem homeostasis in Arabidopsis. *Plant Cell* **34**:1289–1307.
- Wang, X., Liu, Z., Sun, S., Wu, J., Li, R., Wang, H., and Cui, X.** (2021c). *SISTER OF TM3* activates *FRUITFULL1* to regulate inflorescence branching in tomato. *Hortic. Res.* **8**:251.
- Wang, D., Chen, Y., Li, W., Li, Q., Lu, M., Zhou, G., and Chai, G.** (2021d). Vascular Cambium: The Source of Wood Formation. *Front. Plant Sci.* **12**:700928.
- Wang, H., Tong, X., Tang, L., Wang, Y., Zhao, J., Li, Z., Liu, X., Shu, Y., Yin, M., Adegoke, T.V., et al.** (2022a). *RLB (RICE LATERAL BRANCH)* recruits *PRC2*-mediated H3K27 tri-methylation on *OsCKX4* to regulate lateral branching. *Plant Physiol.* **188**:460–476.
- Wang, Y., Bao, J., Wei, X., Wu, S., Fang, C., Li, Z., Qi, Y., Gao, Y., Dong, Z., and Wan, X.** (2022b). Genetic Structure and Molecular Mechanisms Underlying the Formation of Tassel, Anther, and Pollen in the Male Inflorescence of Maize (*Zea mays* L.). *Cells* **11**.
- Wang, J., Jiang, Q., Pleskot, R., Grones, P., Bahafid, E., Denay, G., Galván-Ampudia, C., Xu, X., Vandrope, M., Mylle, E., et al.** (2023a). *TPLATE* complex-dependent endocytosis attenuates *CLAVATA1* signaling for shoot apical meristem maintenance. *EMBO Rep.* **24**, e54709.
- Wang, X., Liu, Z., Bai, J., Sun, S., Song, J., Li, R., and Cui, X.** (2023b). Antagonistic regulation of target genes by the *SISTER* of *TM3*–*JOINTLESS2* complex in tomato inflorescence branching. *Plant Cell* **35**:2062–2078.
- Wang, X., Li, J., Han, L., Liang, C., Li, J., Shang, X., Miao, X., Luo, Z., Zhu, W., Li, Z., et al.** (2023c). *QTG-Miner* aids rapid dissection of the



- genetic base of tassel branch number in maize. *Nat. Commun.* **14**:5232.
- Wang, N., Ryan, L., Sardesai, N., Wu, E., Lenderts, B., Lowe, K., Che, P., Anand, A., Worden, A., van Dyk, D., et al. (2023d). Leaf transformation for efficient random integration and targeted genome modification in maize and sorghum. *Nat. Plants* **9**:255–270.
- Waszczak, C., Carmody, M., and Kangasjärvi, J. (2018). Reactive Oxygen Species in Plant Signaling. *Annu. Rev. Plant Biol.* **69**:209–236.
- Weits, D.A., Kunkowska, A.B., Kamps, N.C.W., Portz, K.M.S., Packbier, N.K., Nemec VENZA, Z., Gaillochet, C., Lohmann, J.U., Pedersen, O., van Dongen, J.T., and Licausi, F. (2019). An apical hypoxic niche sets the pace of shoot meristem activity. *Nature* **569**:714–717.
- Welch, D., Hassan, H., Blilou, I., Immink, R., Heidstra, R., and Scheres, B. (2007). Arabidopsis JACKDAW and MAGPIE zinc finger proteins delimit asymmetric cell division and stabilize tissue boundaries by restricting SHORT-ROOT action. *Gene Dev.* **21**.
- Whipple, C.J., Kebrom, T.H., Weber, A.L., Yang, F., Hall, D., Meeley, R., Schmidt, R., Doebley, J., Brutnell, T.P., and Jackson, D.P. (2011). Grassy tillers1 promotes apical dominance in maize and responds to Shade signals in the grasses. *Proc. Natl. Acad. Sci. USA* **108**.
- Wójcikowska, B., Jaskóła, K., Gąsior, P., Meus, M., Nowak, K., and Gaj, M.D. (2013). LEAFY COTYLEDON2 (LEC2) promotes embryogenic induction in somatic tissues of Arabidopsis, via YUCCA-mediated auxin biosynthesis. *Planta* **238**:425–440.
- Woll, K., Borsuk, L.A., Stransky, H., Nettleton, D., Schnable, P.S., and Hochholdinger, F. (2005). Isolation, characterization, and pericycle-specific transcriptome analyses of the novel maize lateral and seminal root initiation mutant rum1. *Plant Physiol.* **139**:1255–1267.
- Wu, Y., Wang, Y., Mi, X.F., Shan, J.X., Li, X.M., Xu, J.L., and Lin, H.X. (2016). The QTL GNP1 Encodes GA20ox1, Which Increases Grain Number and Yield by Increasing Cytokinin Activity in Rice Panicle Meristems. *PLoS Genet.* **12**:e1006386.
- Wu, Q., Xu, F., Liu, L., Char, S.N., Ding, Y., Je, B.I., Schmelz, E., Yang, B., and Jackson, D. (2020a). The maize heterotrimeric G protein  $\beta$  subunit controls shoot meristem development and immune responses. *Proc. Natl. Acad. Sci. USA* **117**:1799–1805.
- Wu, H.M., Xie, D.J., Tang, Z.S., Shi, D.Q., and Yang, W.C. (2020b). PINOID regulates floral organ development by modulating auxin transport and interacts with MADS16 in rice. *Plant Biotechnol. J.* **18**.
- Wu, L.Y., Shang, G.D., Wang, F.X., Gao, J., Wan, M.C., Xu, Z.G., and Wang, J.W. (2022a). Dynamic chromatin state profiling reveals regulatory roles of auxin and cytokinin in shoot regeneration. *Dev. Cell* **57**:526–542.e7.
- Wu, X., Liu, Y., Luo, H., Shang, L., Leng, C., Liu, Z., Li, Z., Lu, X., Cai, H., Hao, H., and Jing, H.C. (2022b). Genomic footprints of sorghum domestication and breeding selection for multiple end uses. *Mol. Plant* **15**:537–551.
- Xie, M., Chen, H., Huang, L., O’Neil, R.C., Shokhirev, M.N., and Ecker, J.R. (2018). A B-ARR-mediated cytokinin transcriptional network directs hormone cross-regulation and shoot development. *Nat. Commun.* **9**:1604.
- Xie, Y., Zhao, Y., Chen, L., Wang, Y., Xue, W., Kong, D., Li, C., Zhou, L., Li, H., Zhao, Y., et al. (2023). *ZmELF3.1* integrates the *RA2-TSH4* module to repress maize tassel branching. *New Phytol.*
- Xu, L., Wang, J., Lei, M., Li, L., Fu, Y., Wang, Z., Ao, M., and Li, Z. (2016). Transcriptome analysis of storage roots and fibrous roots of the traditional medicinal herb *Callerya speciosa* (Champ.) ScHot. *PLoS One* **11**:e0160338.
- Xu, X.M., Wang, J., Xuan, Z., Goldshmidt, A., Borrill, P.G.M., Hariharan, N., Kim, J.Y., and Jackson, D. (2011). Chaperonins facilitate KNOTTED1 cell-to-cell trafficking and stem cell function. *Science* **333**:1141–1144.
- Xu, C., Liberatore, K.L., MacAlister, C.A., Huang, Z., Chu, Y.-H., Jiang, K., Brooks, C., Ogawa-Ohnishi, M., Xiong, G., Pauly, M., et al. (2015). A cascade of arabinosyltransferases controls shoot meristem size in tomato. *Nat. Genet.* **47**:784–792.
- Xu, G., Wang, X., Huang, C., Xu, D., Li, D., Tian, J., Chen, Q., Wang, C., Liang, Y., Wu, Y., et al. (2017). Complex genetic architecture underlies maize tassel domestication. *New Phytol.* **214**.
- Xu, Q., Wang, X., Jiang, H., Sun, Y., Li, M., and Xiao, H. (2019). Domain-specific expression of meristematic genes is defined by the LITTLE ZIPPER protein DTM in tomato. *Commun. Biol.* **2**:1–14.
- Xu, X., Zhang, M., Xu, Q., Feng, Y., Yuan, X., Yu, H., Wang, Y., Wei, X., and Yang, Y. (2020). Quantitative trait loci identification and genetic diversity analysis of panicle structure and grain shape in rice. *Plant Growth Regul.* **90**:89–100.
- Xiong, R., Liu, S., Considine, M.J., et al. (2021). Root system architecture, physiological and transcriptional traits of soybean (*Glycine max* L.) in response to water deficit: a review. *Physiologia Plantarum* **2**:405–418.
- Xu, X., Crow, M., Rice, B.R., Li, F., Harris, B., Liu, L., Demesa-Arevalo, E., Lu, Z., Wang, L., Fox, N., et al. (2021). Single-cell RNA sequencing of developing maize ears facilitates functional analysis and trait candidate gene discovery. *Dev. Cell* **56**:557–568.e6.
- Xu, X., and Jackson, D. (2023). Single-cell analysis opens a goldmine for plant functional studies. *Curr. Opin. Biotechnol.* **79**:102858.
- Yadav, R.K., Perales, M., Gruel, J., Girke, T., Jönsson, H., and Reddy, G.V. (2011). WUSCHEL protein movement mediates stem cell homeostasis in the Arabidopsis shoot apex. *Genes Dev.* **25**:2025–2030.
- Yamada, M., Han, X., and Benfey, P.N. (2020). RGF1 controls root meristem size through ROS signaling. *Nature* **577**:85–88.
- Yan, W.H., Wang, P., Chen, H.X., Zhou, H.J., Li, Q.P., Wang, C.R., Ding, Z.H., Zhang, Y.S., Yu, S.B., Xing, Y.Z., and Zhang, Q.F. (2011). A major QTL, Ghd8, plays pleiotropic roles in regulating grain productivity, plant height, and heading date in rice. *Mol. Plant* **4**:319–330.
- Yang, Y., Zhu, K., Li, H., Han, S., Meng, Q., Khan, S.U., Fan, C., Xie, K., and Zhou, Y. (2018). Precise editing of CLAVATA genes in Brassica napus L. regulates multilocular silique development. *Plant Biotechnol. J.* **16**:1322–1335.
- Yang, S., Wang, S., Li, S., Du, Q., Qi, L., Wang, W., Chen, J., and Wang, H. (2020). Activation of ACS7 in Arabidopsis affects vascular development and demonstrates a link between ethylene synthesis and cambial activity. *J. Exp. Bot.* **71**:7160–7170.
- Yang, W., Cortijo, S., Korsbo, N., Roszak, P., Schiessl, K., Gursadyan, A., Wightman, R., Jönsson, H., and Meyerowitz, E. (2021a). Molecular mechanism of cytokinin-activated cell division in Arabidopsis. *Science* **371**:1350–1355.
- Yang, R.S., Xu, F., Wang, Y.M., Zhong, W.S., Dong, L., Shi, Y.N., Tang, T.J., Sheng, H.J., Jackson, D., and Yang, F. (2021b). Glutaredoxins regulate maize inflorescence meristem development via redox control of TGA transcriptional activity. *Nat. Plants* **7**:1589–1601.
- Yao, H., Skirpan, A., Wardell, B., Matthes, M.S., Best, N.B., McCubbin, T., Durbak, A., Smith, T., Malcomber, S., and McSteen, P. (2019). The barren stalk2 Gene Is Required for Axillary Meristem Development in Maize. *Mol. Plant* **12**:374–389.
- Ye, H., Song, L., Chen, H., Valliyodan, B., Cheng, P., Ali, L., Vuong, T., Wu, C., Orlowski, J., Buckley, B., Chen, P., Shannon, J.G., Nguyen, H.T., Xiong, R., Liu, S., Considine, M.J., Siddique, K.H.M., Lam, H.M., Chen, Y., LaRue, T., Lindner, H., Srinivas, A., Exposito-Alonso, M., Lobet, G., and Dinneny, J.R. (2018). A major natural



- genetic variation associated with root system architecture and plasticity improves waterlogging tolerance and yield in soybean. *Plant, Cell & Environ* **41**:2169–2182.
- Yu, L.P., Simon, E.J., Trotochaud, A.E., and Clark, S.E.** (2000). POLTERGEIST functions to regulate meristem development downstream of the CLAVATA loci. *Development* **127**:1661–1670.
- Yu, L.P., Miller, A.K., and Clark, S.E.** (2003). POLTERGEIST Encodes a Protein Phosphatase 2C that Regulates CLAVATA Pathways Controlling Stem Cell Identity at Arabidopsis Shoot and Flower Meristems. *Curr. Biol.* **13**:179–188.
- Žádníková, P., and Simon, R.** (2014). How boundaries control plant development. *Curr. Opin. Plant Biol.* **17**:116–125.
- Zemlyanskaya, E.V., Omelyanchuk, N.A., Ubogoeva, E.V., and Mironova, V.V.** (2018). Deciphering auxin-ethylene crosstalk at a systems level. *Int. J. Mol. Sci.* **19**, 4060.
- Zeng, J., Dong, Z., Wu, H., Tian, Z., and Zhao, Z.** (2017). Redox regulation of plant stem cell fate. *EMBO J.* **36**:2844–2855.
- Zhang, H., Rong, H., and Pilbeam, D.** (2007). Signalling mechanisms underlying the morphological responses of the root system to nitrogen in Arabidopsis thaliana. *J. Exp. Bot.* **58**:2329–2338.
- Zhang, T.Q., Lian, H., Zhou, C.M., Xu, L., Jiao, Y., and Wang, J.W.** (2017). A two- step model for de novo activation of wuschel during plant shoot regeneration. *Plant Cell* **29**:1073–1087.
- Zhang, X., Lin, Z., Wang, J., Liu, H., Zhou, L., Zhong, S., Li, Y., Zhu, C., Liu, J., and Lin, Z.** (2019). The tin1 gene retains the function of promoting tillering in maize. *Nat. Commun.* **10**:5608.
- Zhang, L., DeGennaro, D., Lin, G., Chai, J., and Shpak, E.D.** (2021a). ERECTA family signaling constrains CLAVATA3 and WUSCHEL to the center of the shoot apical meristem. *Development* **148**:dev189753.
- Zhang, T.Q., Chen, Y., Liu, Y., Lin, W.H., and Wang, J.W.** (2021b). Single-cell transcriptome atlas and chromatin accessibility landscape reveal differentiation trajectories in the rice root. *Nat. Commun.* **12**:2053.
- Zhou, Y., Yan, A., Han, H., Li, T., Geng, Y., Liu, X., and Meyerowitz, E.M.** (2018). HAIRY MERISTEM with WUSCHEL confines CLAVATA3 expression to the outer apical meristem layers. *Science* **361**:502–506.
- Zhu, Y., Hu, C., Cui, Y., Zeng, L., Li, S., Zhu, M., Meng, F., Huang, S., Long, L., Yi, J., et al.** (2021). Conserved and differentiated functions of CLK receptor kinases in modulating stem cell signaling in Arabidopsis. *Mol. Plant* **14**:1119–1134.
- Zhu, C., Box, M.S., Thiruppathi, D., Hu, H., Yu, Y., Martin, C., Doust, A.N., McSteen, P., and Kellogg, E.A.** (2022). Pleiotropic and nonredundant effects of an auxin importer in Setaria and maize. *Plant Physiol.* **189**:715–734.
- Zierer, W., Rüscher, D., Sonnewald, U., and Sonnewald, S.** (2021). Tuber and Tuberous Root Development. *Annu. Rev. Plant Biol.* **72**:551–580.
- Zimmermann, R., Sakai, H., and Hochholdinger, F.** (2010). The Gibberellic Acid Stimulated-Like gene family in maize and its role in lateral root development. *Plant Physiol.* **152**:356–365.
- Zong, J., Wang, L., Zhu, L., Bian, L., Zhang, B., Chen, X., Huang, G., Zhang, X., Fan, J., Cao, L., et al.** (2022). A rice single cell transcriptomic atlas defines the developmental trajectories of rice floret and inflorescence meristems. *New Phytol.* **234**.
- Zubo, Y.O., Blakley, I.C., Yamburenko, M.V., Worthen, J.M., Street, I.H., Franco-Zorrilla, J.M., Zhang, W., Hill, K., Raines, T., Solano, R., et al.** (2017). Cytokinin induces genome-wide binding of the type-B response regulator ARR10 to regulate growth and development in Arabidopsis. *Proc. Natl. Acad. Sci. USA* **114**: E5995–E6004.