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Cultivating potential: Harnessing plant stem cells for agricultural crop improvement

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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

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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

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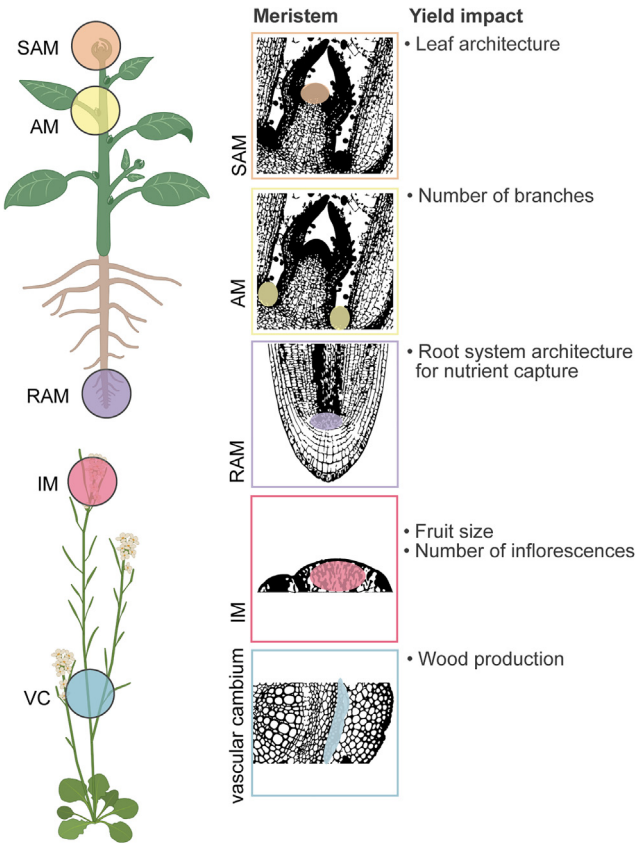

Figure 1. Meristem types and their impact on yield.
Circles indicate meristem location. Red, inflorescence meristem (IM); orange, shoot apical meristem (SAM); yellow, axillary meristem (AM); blue, vascular cambium (VC); purple, root apical meristem (RAM). The highlighted region indicates where meristems 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 HOMEOBOX*). 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 (Ohyama 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 (Rodriguez-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*

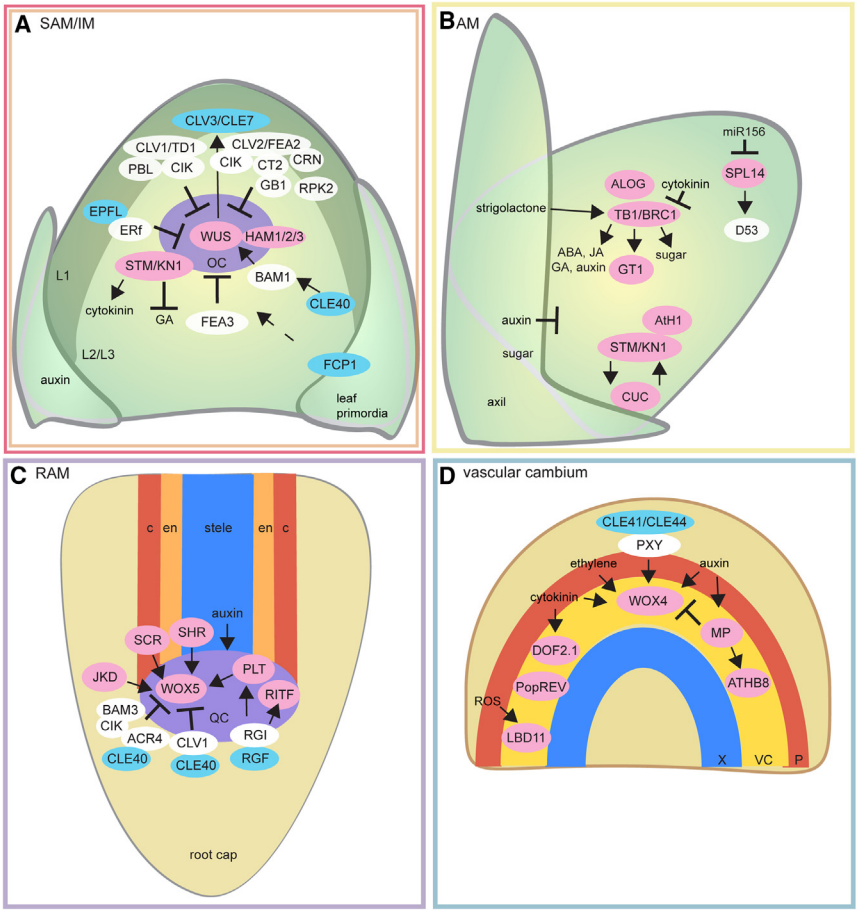

Figure 2. Signaling pathways in plant stem cell niches.

(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 FASCIATED 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 SHORTROOT (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 *CLEs* 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, *SlCLE9* is dramatically upregulated in the *Slclv3* mutant to actively compensate for a lack of *SlCLV3* (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 CLEs 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 (Diévart 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 (Cammarata 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 β subunit (G β) (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 theL1layer, 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**
BrCLV3	*Brassica rapa*	CLE peptide	protein coding	Fan et al. (2014)
BnCLV3	*Brassica napus*	CLE peptide	loss of function	Yang et al. (2018)
ZmCLE7	*Z. mays*	CLE peptide	Regulatory	Liu et al. (2021a)
SlCLV3 (*Fas*)	*S. lycopersicum*	CLE peptide	regulatory	Xu et al. (2015); Wang et al. (2021b)
GhCLV3	*Gossypium hirsutum*	CLE peptide	regulatory	McGarry et al. (2023)
FIN	*S. lycopersicum*	hydroxyproline O-arabinosyltransferase (HPAT)	loss of function	Xu et al. (2015)
ZmFEA2	*Z. mays*	CLE receptor	regulatory, loss of function	Taguchi-Shiobara et al. (2001); Bommert et al. (2013); Trung et al. (2020)
ZmFEA3	*Z. mays*	CLE receptor	protein coding	Je et al. (2016)
Ppr-CLV1	*P. pruinosa*	CLE receptor	loss of function	Lemmon et al. (2018)
ZmCRN	*Z. mays*	CLE receptor	regulatory	Je et al. (2018)
BnCLV1	*B. napus*	CLE receptor	loss of function	Yang et al. (2018)
BnCLV2	*B. napus*	CLE receptor	Loss of Function	Yang et al. (2018)
BrCLV1	*B. rapa*	CLE receptor	protein coding	Chow et al. (2023)
Lc	*S. lycopersicum*	WUS	regulatory	Muños et al. (2011)
ZmACO2	*Z. mays*	Ethylene biosynthesis	regulatory, loss of function	(Ning et al., 2021)
KRN2	*Z. mays*, *O. sativa*	WD40 protein	regulatory	(Chen et al., 2022c)
KRN4/UB3	*Z. mays*	SPB transcription factor	regulatory, protein coding	(Liu et al., 2015)
OsCKX2	*O. sativa*	cytokinin oxidase	regulatory	(Ashikari et al., 2005)
AMs				
TB1	*Z. mays*	TCP transcription factor	regulatory	Clark et al. (2006)
GT1	*Z. mays*	HD-ZIP I transcription factor	loss of function	Whipple et al. (2011)
TIN1	*Z. mays*	C2H2 zinc-finger transcription factor	regulatory	Zhang et al. (2019)
CG1	*Z. mays*	*miR156*	duplication	Chuck et al. (2007)
IPA1/WFP	*O. sativa*	SBP transcription factor	miRNA-binding site	Jiao et al. (2010)
TIN	*T. aestivum*	cellulose-synthase-like protein	regulatory	Hyles et al. (2017)
TN1	*T. aestivum*	ankyrin repeat protein	protein coding	Dong et al. (2023)
Inflorescence branching				
S	*S. lycopersicum*	WOX transcription factor	protein coding	Lippman et al. (2008)
An	*S. lycopersicum*	F-box protein	protein coding	Lippman et al. (2008)
SlTOE1	*S. lycopersicum*	AP2 transcription factor	loss of function	Sun et al. (2023)
SlFUL1	*S. lycopersicum*	MADS-box transcription factor	loss of function	Jiang et al. (2022)
SlFUL2	*S. lycopersicum*	MADS-box transcription factor	loss of function	Jiang et al. (2022)
SlMBP20	*S. lycopersicum*	MADS-box transcription factor	loss of function	Jiang et al. (2022)
J2	*S. lycopersicum*	MADS-box transcription factor	loss of function	Soyk et al. (2017)
EJ2	*S. lycopersicum*	MADS-box transcription factor	loss of function	Soyk et al. (2017)
GN1A	*O. sativa*	cytokinin oxidase	loss of function	Ashikari et al. (2005)
DEP1	*O. sativa*	Gγ 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**
DST	*O. sativa*	zinc-finger protein	loss of function	Huang et al. (2009a); Li et al. (2013)
GNP1	*O. sativa*	GA oxidase	regulatory	Wu et al. (2016)
FZP1	*O. sativa*	AP2 transcription factor	regulatory	Huang et al. (2018); Wang et al. (2020a)
OsTB1	*O. sativa*	TCP transcription factor	protein coding	Takai et al. (2023)
IPA1/WFP	*O. sativa*	SBP-box transcription factor	miRNA binding	Jiao et al. (2010)
Q	*T. aestivum*	AP2 transcription factor	miRNA binding	Simons et al. (2006); Debernardi et al. (2017); Greenwood et al. (2017)
TaSPL17	*T. aestivum*	SPB-box transcription factor	regulatory, overexpression	(Liu et al., 2023a; 2023b; 2023c)
OsEPFL6/7/9	*O. sativa*	EPF ligands	loss of function	(Guo et al., 2023)
OsCKX4	*O. sativa*	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 *SlCLV3* CREs subtly change *SlCLV3* 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 *krn2* 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 HOMEOBOX 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* (*TIN*), 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

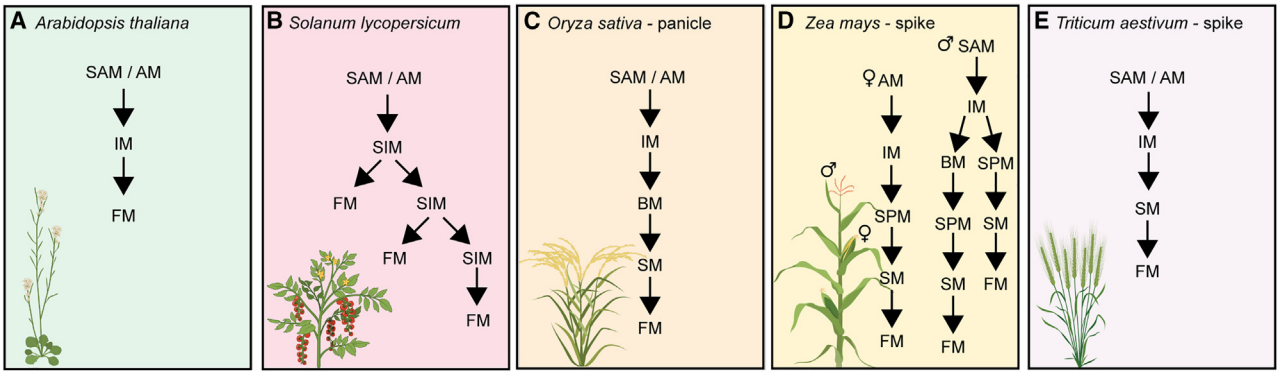

Figure 3. IM architecture varies among plant species.

(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 *SlWOX9* 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 *TASSELSHEATH 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 (Ibañes 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).

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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.

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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.

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