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ABSTRACT

A plant's lateral structures, such as leaves, branches and flowers, literally hinge on the shoot axis, making its integrity and growth fundamental to plant form. In all plants, subapical proliferation within the shoot tip displaces cells downwards to extrude the cylindrical stem. Following the transition to flowering, many plants show increased axial elongation with associated increases in subapical proliferation and expansion. However, the stems of grasses, called culms, also elongate due to detached intercalary meristems, which displace cells upwards to elevate the grain-bearing inflorescence. Variation in culm length within species is especially relevant to cereal crops, best exemplified by the high-yielding semi-dwarfed cereals in the Green Revolution. While pathways controlling subapical and intercalary stem growth have been understudied, renewed interest in axial development reveals that control of cell division planes, boundary formation and temporal dynamics of differentiation, are likely critical mechanisms coordinating axial growth and development in plants.

INTRODUCTION

EVOLUTIONARY ORIGINS OF THE LAND PLANT STEM

The central cylindrical axis of land plants is a deeply conserved and ancient feature, shared with their bryophyte-like anctorses and predating roots and leaves. In early land plants, stems were dimunitive stalks for the terminal sporangium acting to aid spore dispersal (Cronk 2009; Ligrone et al. 2012). The advent of lignified vasculature allowed more extensive vertical growth by providing mechanical support and conductive channels for solute transport over long distances. Accessing the higher canopy helped sporophytes better evade soil-borne pathogens and diversify their reproductive strategies. Axial growth also increased photosynthetic capacity in the aerial space which, especially following the evolution of 3D growth, contributed to sporophyte dominance.

STEM MORPHOGENESIS IN VASCULAR PLANTS

Lateral 3D growth from the shoot tip generates leaves and branches which attach to the vertical axis at nodes, segmenting the stem into alternating nodes of lateral organ attachment and intervening internodes. The shoot is thus organised into iterative units called phytomers which comprise a node, its lateral organ, subtending internode and axillary bud (Galinat 1959; Bossinger 2009). All these structures derive from self-renewing indeterminate cells and proliferation at the shoot tip. Thus, unlike the basal intercalary proliferation which lifts the moss sporophyte, the vascular plant stem elongates due to downward displacement of daughter cells to form a “self-extruding cylinder” (Cronk 2009; Harrison and Morris 2018).

Cells in the shoot tip make up the shoot apical meristem which is organised into distinct, functional zones (Figure 1A). The central apical zone consists of a small number of stem cells which is surrounded by the more mitotically-active peripheral zone whose cells are recruited to form lateral organs. The underlying stem grows from two subapical regions: the ‘rib’ meristem basal to the central zone, whose transversely dividing cells form the stem’s central core (pith); and from subapical peripheral cells contributing the stem epidermis and cortex (Vaughan 1955; Sachs et al. 1959b; Sachs 1965; Kwiatkowska 2008; Bencivenga et al. 2016; Greb and Lohmann 2016). Peripheral and central subapical rib regions, including the rib meristem, together constitute the rib zone (Figure 1A; Gaillochet et al. 2015; Bencivenga et al. 2016; Janocha and Lohmann 2018). However, all of these cells have also been called the rib meristem (Perales and Reddy 2012), while sometimes the rib zone is shown separate from the rib meristem (Fletcher 2002). Furthermore, defining the basal borders of the rib zone is challenging since

the axial transition from dividing to differentiating cells lacks an obvious boundary while the length of this region itself varies by species and growth stage (Sachs 1965; Fisher and French 1976). The distinctive phytomeric production in grasses compared to dicots also impacts this subapical zonation (Figure 1B). In dicots, the lateral primordium (leaf or flower bud) bulges from a triangular top flank off the peripheral zone, while in grasses, the leaf primordium remains connected to a basal ring of proliferating founder cells circumnavigating the shoot tip, called the 'disc of insertion' (Sharman 1942). While the leaf blade develops from the lateral primordium growing away from the apex, the upper disc of insertion develops into the leaf sheath while the lower disc of insertion forms the node, internode and axillary bud (Sharman 1942; Johri and Coe 1983; McDaniel and Poethig 1988; Scanlon and Freeling 1997). In this way, the grass stem represents an iterative stack of clonally-related phytomeric units.

SECONDARY AXIAL ELONGATION

Sachs (1965) recognised two phases of stem development: primary stem morphogenesis, which establishes radial patterning and the node-internode arrangement, and secondary elongation, that occurs in some species depending on growth stage and environment. Secondary elongation is distinct from the secondary thickening of dicot stems due to vascular cambium proliferation (reviewed in Sanchez et al. 2012). A classic example of secondary elongation occurs following flowering in the crucifers, Pooideae grasses (including the cereal crops) and other species which undergo extensive internode elongation that shifts their growth habit from compressed to caulescent (often referred to as ‘bolting’; Figure 1C, D; Sachs 1965; Kellogg 2015), elevating the inflorescence into the upper canopy to promote pollen exchange, seed dispersal and evade pathogens. Secondary elongation can influence both the length of extant internodes, as well as those generated after the reproductive transition. For instance, Arabidopsis stems develop long internodes between nodes projecting axillary branches subtended by leaves (cauline paraclades), and then elongated internodes separating solitary flowers, each on their own pedicels, which continually emerge on an exposed inflorescence. In Pooideae grasses, the vegetative internodes elongate and are supported by the leaf sheaths until the final internode extends to push the flowering head out of the final leaf sheath, exposing the developed inflorescence, usually at anthesis. Emergence, called ‘heading’, is critical to harvest the grain-laden inflorescence and must be tightly regulated as overly tall culms are prone to lodge or fall over, thereby leading to lost yeild, making internode elongation a key trait for yeild. Semi-dwarf varieties lodge less, which contributed to the vast yeild improvements during the Green Revolution.

Increased mitotic activity and/or size of cells in the rib zone occurs during secondary axial elongation in both dicots and monocots (Figure 1C, D; Sachs et al. 1959b; Fahn et al. 1963; Jacqmard et al. 2003; Kwiatkowska 2008). However, while not a uniform feature of monocots (Sachs 1965; Fisher and French 1976), individual grass internodes elongate due to intense cell division within an 'intercalary meristem' just above each node: here, transverse divisions displace cells upwards through successive zones of expansion and maturation, lengthening each internode from the bottom up (Figure 1D; Schmalfuss 1930; Evans 1965; Kaufman et al. 1965; Fisher 1970; Fisher and French 1976; Bleecker et al. 1986; Cho and Kende 1997; Martin et al. 2016). Intercalary growth gives rise to most of the cells in the culm, which is typically formed of internal cortex and inner stem tissues of scattered vascular bundles and supporting sclerenchyma, contained within an epidermis of axially arranged cell files, including files of stomata, cork and silica cells (Harting 1845; Grisebach 1943; Kaufman et al 1965). Intercalary meristems are only found in monocots with sheathing leaf bases (Fisher and French 1978) that start elongating before their corresponding internode in an acropetal pattern (Kirby et al. 1994), to provide mechanical support to fragile, meristematic and actively elongating internode tissues both within their own and more apical internodes (Niklas 1990). While the intercalary meristem is still active, internodes in some grass species develop a central cavity or lacuna early during elongation due to comparatively slow pith growth, leading to the characteristic hollow straw of wheat, rice and barley. Internodes in other species remain solid as in maize and sugarcane, or a combination of solid and hollow as in bamboo (Kellogg 2015). However, nodes always remain solid and become thickened with a complex vascular plexus of anastomosed vascular tissue from the stem, leaves and buds (Sharman and Hitch 1967; Kellogg 2015). Thus, an important distinction between bolting of Arabidopsis and internode growth of grasses following flowering is the developmental origin of the internode. In Arabidopsis, cells in the bolting internodes are fueled exclusively cells from the rib meristem after the reproductive transition (Vaughan 1955; Jacqmard et al. 2003) while dividing cells of the grass intercalary meristems either are or quickly become detached from subapical proliferation by differentiating internode tissue. Furthermore, the intercalary meristem, whose activity declines over time (Kaufman et al. 1965), is determinate and generates a single internode. In this way, the intercalary meristem is similar to the leaf plate meristem, a set of parallel cell layers at the base of leaves whose anticlinal divisions contribute to leaf outgrowth; in contrast, the rib meristem usually has an indeterminate nature and continuously divides.

As with other organs, final internode length reflects cell number and the extent of longitundinal cell elongation. GA promotes both intercalary and rib meristem-driven secondary axial elongation through increasing cell division

and cell elongation (Sachs et al. 1960; Sachs 1965; Kende et al. 1998). Interfering with this process leads to varying degrees of dwarfism, which in the cultivated cereals, higher yeilds due to decreased partitioning into vegetative biomass and reduced lodging. For instance, the semi-dwarf rice and wheat of the Green Revolution are altered in GA biosynthesis or perception, respectively (Webb et al. 1998; Peng et al. 1999; Hedden 2003). The *Reduced height* wheat semi-dwarfs show reduced responsiveness to GA (Gale and Youssefian 1985) due to truncated, consistutively-active DELLA transcription factors (Peng et al 1999), negative regulators of GA signalling, normally suppressed by GA (Peng et al. 1997). In rice, the *semidwarf-1* locus encodes a GA 20-oxidase (GA20ox) enzyme critical for GA biosynthesis, which when defective leads to semi-dwarfism (Monna et al. 2002; Sasaki et al. 2002; Spielmeyer et al. 2002). Other semi-dwarfing alleles derive from defects in brassinosteroid (BR) growth hormone biosynthesis or perception/signalling (Chono 2003; Dockter et al. 2014; Hirano et al. 2017). For instance, in barley, the BR insensitive mutant *uzu* has a single nucleotide substitution in the gene encoding the BR receptor, *HvBRI1* (Chono et al. 2003), leading to a temperature-sensitive allele (Dockter et al. 2014). Dockter et al (2014) also described mutant alleles of three BR biosynthetic genes – *HvBRD* (*BR 6-OXIDASE*), *HvCPD* (*BRASSINOSTEROID C-23 HYDROXYLASE*) and *HvDIM* (*DIMINUTO*), which each encode enzymes of the BR pathway, and display similar phenotypes, including erect and small leaves as well as reduced stature. These features of BR semi-dwarfs are usually attributed to reduced cell elongation as opposed to cell proliferation (Szekeres et al. 1996; (Choe et al. 1999; Sun et al. 2010); however, loss of a function of BRI1 in rice leads to shorter internodes associated with improper formation of the IM (Yamamuro et al. 2000). Many roles of BR may reflect molecular and feedback interactions with GA metabolism and signalling to control growth (Bai et al. 2012; Gallego-Bartolomé et al. 2012; Li et al. 2012; Tong et al. 2014) but recent analyses in maize suggest that the extent of interaction between the two hormones depends on the developmental context (Best et al. 2016).

Several reviews comprehensively discuss semi-dwarfing alleles in cereals (Hedden 2003; Dockter and Hansson 2015; Braumann et al. 2018). Unsurprisingly, many other genes whose alleles influence stem elongation are associated with changes in hormone metabolism and/or signalling. An important task is to understand how these alleles participate in the regulatory pathways influencing how, where and when these growth hormones function during primary stem development and secondary stem elongation across plants. In their recent review, Serrano-Mislata and Sablowski (2018) expertly describe how new approaches to study stem organogenesis revealed the importance of oriented growth in the rib zone as well as the role of cell wall mechanics during cell expansion in stem elongation and integrity. Here, I attempt to summarise what we know about the genetic mechanisms controlling the balance between proliferation and differentiation during primary stem development with an emphasis on grass models and Arabidopsis, and discuss the relevance of these mechanisms to secondary intercalary activity,

as well as control of secondary axial elongation. I conclude with outstanding questions deserving attention.

REGULATION OF SUBAPICAL PROLIFERATION

The leaf and subtending internode derive from the same cell population (Jegla and Sussex 1989; Poethig and Szymkowiak 1995). Mutants defective in apex maintenance often exhibit aberrant stem morphology, uneven internode lengths and disturbed phyllotaxis, suggesting a coordination of lateral organogenesis with stem morphogenesis at the shoot tip. Below, I describe several central pathways associated with meristem function and consider their influence on stem development.

Iterative and modular plant growth depends on maintaining a stable meristematic cell population despite continual depletion of daughter cells into new phytomers. The CLAVATA (CLV) – WUSCHEL (WUS) signalling loop is key to this balance, and although best understood in Arabidopsis, the pathway's principles appear broadly conserved across plants (reviewed in Somssich et al. 2016; Figure. 2A). The *WUS* gene encodes a homeodomain whose loss of function leads to arrested growth due to meristem consumption by lateral organogenesis (Laux et al. 1996). This reflects a role of *WUS*, expressed in the rib meristem (a pattern also described as marking an organising centre), to non-cell autonomously promote proliferation and stem cell identity in overlying central cells and restricts expression of differentiation-associated genes to the meristem periphery (Yadav et al. 2014; Gruel et al. 2016). WUS also stimulates the overlying cells to produce CLV3, a mobile peptide ligand, which when perceived by Leucine Rich Receptor (LRR)-receptor complexes surrounding and within the rib meristem, signals repression of *WUS* transcription, thereby completing a negative feedback loop (Schoof et al. 2000; Brand et al. 2002; Muller et al. 2006; DeYoung and Clark 2008; Yadav et al. 2009, 2013; Yadav and Reddy 2011; Snipes et al. 2018). Disruption of CLAVATA function uncouples proliferation from organogenesis, causing expanded/ ectopic *WUS* expression domains and ever-increasing stem cell proliferation. Associated with altered cell division planes, ectopic WUS leads to profound changes in meristem shape and degrees of fasciation (Leyser and Furner 1992; Medford et al. 1992; Clark et al. 1993, 1996; Kayes and Clark 1998; Suzaki et al. 2004; Bommert et al. 2005; Suzaki et al. 2006; Xu et al. 2015; Mandel et al. 2016). Fasciation occurs as the apical meristem progressively widens, flattens and divides into connected meristem ridges, a change in shape and function propagated downwards to form a bundled, fused stem (Cronk 2009). Mutants defective in cell cycle also show fasciation, such as in the maize *tangled* severe dwarf (Smith et al. 1996; Kaya et al. 2001; Suzaki 2004) while altered frequency and orientation of meristematic

cell divisions are also associated with altered *WUS* expression in Arabidopsis (Kaya et al. 2001; Suzaki et al. 2004; Muñoz-Nortes et al. 2014), emphasising the importance of controlling the pattern of WUS expression for proper axial growth. The normal, single central subapical localisation of *WUS* expression is established in the embryo and stably maintained through cytokinin signalling (Leibfried et al. 2005; Gordon and Chickarmane 2009; Chickarmane et al. 2012; Adibi et al. 2016; Meng et al. 2017; Snipes et al. 2018). WUS induction of *HECATE* transcription factor genes, whose activity reduces auxin signalling, is critical for meristem integrity (Schuster et al. 2015; Gaillochet et al. 2018), consistent with reports that both auxin treatment and inhibition of auxin transport cause fasciation (Gorter 1965; Fambrini et al. 2006). Taken together, regulated cell division orientiation associated with a centrally defined *WUS* expression domain and corresponding hormonal balance, are essential for cylindrical axis integrity and coorresponding stem growth.

Fasciated mutants also show aberrant phyllotaxy, uneven internode growth and dwarfing, suggesting that meristem integrity is also key to coordinate stem growth with lateral organ emergence (Smith and Hake 2003; Running et al. 2004; Khan et al. 2012; Pautler et al. 2015). However, these phenotypes are not always present together and can be restricted to a particular growth stage or meristem type, likely reflecting both the context-dependent nature of individual WUS-CLV signalling pathways. Involving multiple CLAVATA3/ENDOSPERM SURROUNDING REGION (CLE) peptides and their CLV-like receptors and co-factors, as well as multiple WUS-like HOMEOBOX (WOXs), these pathways control proliferation in specific contexts, although many intervening steps and exact protein/peptide partners are not completely understood, especially in grasses (Pautler et al. 2013; Somssich et al. 2016; Bommert and Whipple 2018).

For instance, we don’t know whether apical CLV3-like signals control subapical proliferation exclusively through downward displacement of peripheral cells or whether cells subapical or peripheral to the rib meristem themselves emit additional signaling CLEs. In Arabidopsis, several *CLE*s are expressed beneath the *WUS* expression domain, yet none show a loss-of-function phenotype, perhaps due to overlapping expression and functional redundancy (Jun et al. 2010; Gregory et al. 2018). More is known about mechanisms delineating the *WUS* basal boundary in grasses. Rather than sole expression in a central organising or rib meristem, maize vegetative apices transiently express *ZmWUS1* within the lower disc of insertion containing the presumptive node, internode and axillary bud cells (Figure 2B; (Nardmann and Werr 2006). Je et al (2016) showed that perception of a leaf primordium-derived CLE peptide ZmFON2-LIKE CLE PEPTIDE1 (ZmFCP1) by the FASCIATED EAR3 (FEA3) CLV-like receptor, which is expressed below and inside the *ZmWUS1* region, prevents basal expansion of *ZmWUS1*

expression in the transitional inflorescence meristem (Je et al. 2016); however, it is unclear if this mechanism also limits later *ZmWUS1* expression in the developing phytomer. Arabidopsis *fea3* mutants are short and fasciated, while *clv1* mutants in Arabidopsis (*clv1*, Leyser and Furner 1992), maize (*thick dwarf tassel1*, *td1*, Bommert, 2005), rice (*floral organ number1*, Moon et al. 2006) and cucumber (*Csclv1*, Xu et al. 2018) are dwarf; however, neither Arabidopsis *clv3*, *clv2* or maize *fea3* mutants display altered plant height (Clark et al. 1995; Je et al. 2016). Partial expression overlap in the meristem flank and the lateral organ domains *ZmWUS2*, the other *WUS*-like gene in maize, and *TD1*, suggests a possible control of TD1 over the *ZmWUS2* domain, potentially impacting the entire phytomer (Nardmann and Werr 2006). Impaired expression or function of other LRR-like kinase receptors such as BARELY ANY MERISTEMs (BAMs) and ERECTA(ER)/ERL, can enhance *clv* fasciation and dwarfism in Arabidopsis (Yokoyama et al. 1998; DeYoung and Clark 2008), although the function of grass orthologues are unknown. Fine-tuning of receptor complexes via their spatiotemporal levels and interacting partners may integrate diverse peptide signals (Janocha and Lohmann 2018), which possibly explains the severe phenotypes of certain LRR mutants.

In the grasses, a subset of peripheral phytomer founder cells specify a shared marginal domain in the leaf and internode, which when absent leads to narrow leaves, lacking margins and subtending internodes shorter on their side adjacent to the leaf sheath margin (Scanlon et al. 1996). Cloning the *narrow sheath1/2* (*ns1/2*), *narrow leaf2/3* and *narrow leafed dwarf1* mutants in maize, rice and barley, respectively, identified the *WOX3*-like genes as essential to recruit marginal domain founder cells, orthologous to the *PRESSED FLOWER* (*PRS*) gene of Arabidopsis necessary for marginal development in the flower (Figure. 2B; Matsumoto and Okada 2001; Nardmann 2004; Cho et al. 2013; Yoshikawa et al. 2016). However, while neither rice *narrow leaf2* or *3* mutants show differences in plant height, overexpression of *OsWOX3A* in rice led to extreme dwarfism and marginal expansion (Ishiwata et al. 2013), recently associated with downregulation of GA biosynthesis, likely through directly interaction with a GA biosynthetic gene promoter (Cho et al. 2016). Thus, marginal identity must be carefully regulated to recruit sufficient founder cells but balanced with differentiation capacity, which may be related to hormonal homeostasis amongst meristem, founder and differentiating tissues.

Potential partners linking meristem maintence and stem elongation, especially in response to environmental cues, are heterotrimeric G-proteins which interact with CLV signalling (reviewed in Urano et al. 2016). A major dwarfing locus in rice, *DENSE PANICLE1* (DEP1) and barley (*HvDEP1*) encodes a Gγ subunit (Huang et al. 2009; Wendt et al. 2016; Xu et al. 2016) while defective alleles in genes encoding the Gα subunit in rice (‘*daikoku*’ *dwarf1*, Fujisawa *et* al. 1999; Ashikari et al. 1999), barley (*brachytic1*, (Ito et al. 2017; Braumann

et al. 2018b), maize (*compact plant2*, *ct2*, Bommert et al. 2005) and Arabidopsis (*gpa1*, Ullah, 2001) confer compact shoots due to reduced axial proliferation. In rice, *DWARF1* interacts with GA and BR signalling to control height (Ashikari et al. 1999; Oki et al. 2009). In Arabidopsis, the G-protein ß-subunit1 (AGB1) works synergistically with a CLV receptor in meristem maintenance (Ishida et al. 2016), while maize *CT2*, expressed throughout the apex and emerging leaves, signals downstream of FEA2, a CLV2 receptor, as well as independently to control stem cell proliferation (Bommert et al. 2013), highlighting the involvement of heterotrimeric G proteins within the CLV-WUS pathway.

Does a CLV-WUS pathway regulate maintenance of intercalary meristems during secondary stem elongation? Intercalary meristems maintain their integrity prior to their activation and continue dividing for an extended period during internode growth (Kaufman et al. 1965; Bleecker et al. 1986). It is long known that dwarf grass plants usually have fewer cells (Harting 1843), suggesting inadequate intercalary proliferation, as well as the existence of mechanisms ensuring either sufficient founder cell recruitment and/or proliferative capacity in the intercalary meristem. Since expression of *WOX3/PRS* in the nascent internode appears essential for internode growth on the marginal side, these genes could also regulate internode cell recruitment and/ or marginal intercalary proliferation. Another candidate is the *DWARF TILLER* (*DWT*) locus in rice, encoding an *OsWOX* necessary for cell proliferation and elongation and GA signalling; however, loss of function leads to dwarfed tillers only, and *DWT* is not expressed in the internode, suggesting a non-cell autonomous regulation of intercalary growth in tillers (Wang et al. 2014). Other candidates are the *WOX3* clade sister to the narrow leaf *PRS*/*WOX3*'s which arose due to an ancient duplication in grasses (Nardmann et al. 2007). Unlike marginal domain-specific expression domain of *WOX3/PRS* (Nardmann et al. 2004; Shimizu et al. 2009), sister *WOX3*s are expressed in a complete ring around the initiating phytomer which is then restricted to the phytomer base (Nardmann et al. 2007), and in rice, are strongly expressed later on in the intercalary region and nodal vasculature of young internodes (Figure 2C; Angeles-Shim et al. 2012), suggesting subfunctionalisation of the sister *WOX3* clade for the distinctive structures of grasses. However, to date, only the rice sister *WOX3* has been characterised, and reported to control trichome formation (Angeles-Shim et al. 2012; Zhang et al. 2012; Yoshikawa et al. 2016) so the relevance of this expression pattern is unclear.

Overlying the CLV-WUS pathway are the Class I KNOTTED-like homeoboxes (KNOX-I) whose promotion of meristem activity is conserved across vascular plants (Harrison et al. 2005). *KNOX-I* expression (Figure 2C), often used as a marker for meristematic identity, promotes proliferation in meristems by

upregulating cytokinin biosynthesis (Jasinski et al. 2005; Yanai et al. 2005), downregulating GA biosynthesis (Hay et al. 2002) and antagonising expression of differentiation-associated gene (Byrne et al. 2002). Dramatic downregulation of *KNOX-I* marks presumptive primordium cells and is required for lateral organ identity and differentiation (Scanlon 2003). Loss of the marginal domain in maize *ns* mutants is associated with a failure to downregulate *KNOX-I* (Scanlon et al. 1996), suggesting that founder cell recruitment into the emerging internode also depends on *KNOX-I* downregulation. This role is consistent with both the dwarfism caused by the dominant overexpression mutations in maize for *Knotted1* (*Kn1*; Freeling and Hake 1985; Vollbrecht et al. 1991), *Gnarley/KNOX4* (*Gn1*, Foster et al. 1999) and *Rough sheath1* (*Rs1*, Becraft and Freeling 1994) and the direct upregulation of a GA catabolism gene (*ga2ox1*) by KN1 (Bolduc and Hake 2009). However, loss of function *KNOX-I* alleles also lead to dwarfism in rice (*osh15*, Sato et al. 1999); *osh1*, Tsuda et al. 2011), maize (*rs1*, Schneeberger et al. 1995) and Arabidopsis (*brevipeddicellus*, *bp*, Venglat et al. 2002), potentially due to loss of subapical meristematic proliferation. *KNOX-I* show persistent expression in regions forming the stem (Reiser et al. 2000), such as *BP* in the rib meristem and growing stem vasculature of Arabidopsis (Lincoln et al. 1994; Smith and Hake 2003), *Kn1* and *Rs1* in the rib zone and lower disc of insertion of maize, overlapping with *ZmWUS1* (Jackson et al. 1994; Schneeberger et al. 1995; Nardmann and Werr 2006) and similar to *OSH15* localising to the base of growing leaves (Sato et al. 1999), while *Kn1* is expressed throughout intercalary meristems (Tsuda et al. 2017). Coupled with their mutant phenotypes, *KNOX-1* expression patterns suggest important roles in both subapical and intercalary proliferation.

REGULATION OF BOUNDARY IDENTITY AND VASCULAR DIFFERENTIATION

The *osh15* and *bp* mutants also show aberrant, ectopic and/or excessive internode lignification, which may mechanically hamper elongation (Sato et al. 1999; Smith and Hake 2003). While both BP and OSH15 directly inhibit expression of lignin biosynthetic genes (Mele et al. 2003; Yoon et al. 2017), several studies also suggest that antagonistic interactions between *KNOX-I*'s themselves, and interaction with *BEL-LIKE HOMEODOMAIN* (*BLH*) genes (*BLH*s), influence vascular development and boundary positioning. In Arabidopsis, BP physically interacts with the PENNYWISE/REPLUMLESS (PNY/RPL), a BLH whose loss of function resembles *bp*, while double *bp pny* mutants are severely dwarfed with a thick continuous vascular ring in their stems (Smith and Hake 2003). Similar phenotypes occur from overexpression of boundary marking genes, including *KNOX-I* genes *KNAT2*/*6*, the *BLH* gene *ARABIDOPSIS THALIANA HOMEOBOX1* (*ATH1*) and the *BLADE-ON-PETIOLE* genes (Smith and Hake 2003; Norberg et al. 2005; Cole et al. 2006;

Ragni et al. 2008; Gómez-Mena and Sablowski 2008; Khan et al. 2012). *ATH1* is particularly interesting since impaired ATH1 leads to longer internodes and an expansion of the rib zone based on *BP* expression, suggesting that ATH1 represses rib zone proliferation (Gomez-Mena and Sablowski 2008). Ectopic boundary gene expression cauases excess lignification, altered phyllotaxy, dwarfism and uneven internode length in *bp* and *pny* since loss of function boundary gene alleles rescues these phenotypes (Ragni et al. 2008; Khan et al. 2012; Bencivenga et al. 2016). Thus, BP and PNY likely interact to exclude expresion of these boundary genes from the developing internode, limiting their expression to the boundary (Figure 3A). These roles may originate very early during stem morphogenesis (Figure 3A): in their insightful study, Bencivenga et al (2016) showed that loss of *PNY* lead to medial expansion of boundary gene expression from the peripheral to central rib zone region, which decreased transverse cell divisions and correspondingly increased more peripheral-like radial divisions in the central rib zone. Accordingly, PNY may prevent peripheral rib zone encroachment into the central rib region through restricting boundary gene expression to the periphery, similar to PNY's role in defining the boundary between the central and peripheral apical meristem zones (Ung et al. 2011). Since stem vasculature in Arabidopsis develops at the interface between the central and peripheral rib zone regions, Bencivenga et al (2016) speculate that altered cell orientations could influence this positioning, leading to the increased number of vascular strands in *pny*. Altered peripheral and central positiong may also contribute to the thick continuous vascular ring typical of *bp pny* stems.

Regulation of internode elongation by specification and/or proliferation of stem vasculature appears conserved in maize, despite its different proliferation and vascularisation pattern compared to dicots (Figure 3B). Exciting recent work by Tsuda et al (2017) showed that loss of function in *BLH12* and *BLH14* (maize *BLH*s of the *PNY* clade), led to truncated internode elongation, due to earlier arrest of intercalary meristem activity as well as premature vein anastomoses. Since BLH12, BLH14 and KN1 proteins interact and are all detected in the intercalary meristem, suggesting that BLH12/14 and KN1 may work together to maintain intercalary meristems and prevent their precocious differentiation (Tsuda et al. 2017). BLH12 and BLH14 as well as KN1 also accumulate in the provasculature (Tsuda et al. 2017; Jackson et al. 1995), where they slow the timing of the progressive lignification program in internodes. Downregulation of BR via by OSH1 is also important for correct boundary formation and positioning (Tsuda et al. 2014). Since BR also promotes xylem differentiation (Caño-Delgado et al. 2004), it is plausible that increased/ ectopic vascularisation due to loss of KNOX-1, BLH may reflect increased BR leading to premature differentiation and vascularisation. Taken together, work in both dicots and monocots highlight the critical role for

KNOX-I and BLH in coordination of proliferation with vascular development and internode elongation, by controlling temporal and spatial dynamics of cell division and vascular differentiation in the internode.

The master shoot identity regulators, *CLASS III HOMEODOMAIN - LEUCINE ZIPPER* (*HD-ZIP III*) genes are also implicated in the control of stem growth through their effects on proliferation and vascularisation. Expression of the HD-ZIP III *ATHB8* marks preprovascular strands while its overexpression caused precocious vascular differentiation, slower stem elongation and dwarfism (Baima et al. 1995, 2001). In Arabidopsis, *ATHB8* is induced by auxin and negatively regulated by *ACAULIS5* (*ACL5*): a gene which encodes an enzyme synthesising thermospermidine (Kakehi et al. 2008; Baima et al. 2014), whose loss of function *acl5* alleles lead to thicker veins and short stems (Clay and Nelson 2005). In fact, all five *HD-ZIP III* genes affect plant stature in Arbaidopsis, and their higher order mutant phenotypes, which include severe dwarfing, fasciation and increased *WUS* expression, suggest they have redundant roles to ensure radial symmetry, elongation and vascular patterning in the stem (Emery et al. 2003; Prigge et al. 2005; Williams et al. 2005). In rice, these genes are also important for meristem maintenance but also for marginal domain development (Itoh et al. 2008), and can affect height as overexpression of the rice *HD-ZIP III OxHOX32* lead to semi-dwarfism, associated with changes in *YABBY1* (*YAB1*) expression, a gene involved in lateral differentiation and polarity (Li et al. 2016). Less in known about the roles of *Class I HD-ZIP*s; however, *OsHOX4* gene in rice promotes GA degradation and overexpression leads to semi-dwarfism, associated with elevated expression of *YAB1* and a GA catabolism gene, *GA2ox3* (Dai et al. 2008; Zhou et al. 2015). Another *HD-ZIP I* gene, *OsHOX12*, has an opposite function and promotes stem elongation in rice by repressing the expression of *ELONGATED UPPER INTERMODE* (*EUI*, *CYP714D1*), which encodes a GA-deactivating enzyme (Zhu et al. 2006; Gao et al. 2016).

A separate CLV-WUS pathway also influences stem morphology through effects on vasculature proliferation. Overexpression of CLE42 and CLE44 in Arabidopsis led to bushy, dwarf plants (Strabala et al. 2006). These peptides are now known to activate PHLOEM INTERCALLATED WITH XYLEM (PXY) receptors to restrict the expression of vascular proliferation-promoting *WOX4* and *WOX14* to the vasculature, in part through control of cell division orientation (Etchells and Turner 2010; Etchells et al. 2013). Similar to Arabidopsis, *WOX4* in rice (*OsWOX4*) is expressed in the nascent vasculature, in addition to the meristem and leaf primordia, and RNAi-mediated knock-down of OsWOX4 was associated with stunted shoots (Ohmori et al. 2013).

It will be interesting to further unpick the interactions amongst HD-ZIPs, KNOX, BLH and CLE/WOX which control division and vascular differentiation events in elongating internodes in both monocots and dicots. Several transcriptomic datasets describing gene expression along developing grass and Arabidopsis internodes may help construct networks regulating tissue histogenesis and metabolism along this developmental gradient (Ehlting et al. 2005; Cui et al. 2012; Martin et al. 2016; Kebrom et al. 2017). Of particular interest will be comparing these networks to those underlying sporophyte elongation in non-vascular plants, which may reveal the regulatory innovations developed by vascular land plants to balance lignification with proliferation and indeterminacy to both enable axial elongation and apical indeterminacy.

TRANSITION TO SECONDARY STEM ELONGATION

Bolting in Arabidopsis occurs after the reproductive transition (Hempel and Feldman 1994), and similarly, grass culm internode elongation occurs only at specific stages of reproductive spike development across genotypes and environmental conditions (Nicholls and May 1964). Thus, internode elongation may be tuned to an apex-derived signal. In oats, internode elongation was reduced by removal of the inforescence and lost completely when nodes were eliminated, suggestive of an apex-originated signal transported through the nodes (Koning et al. 1977). In pea and tobacco, auxin promoted GA accumulation in stems (Ross et al. 2000; Wolbang and Ross 2001), whereas in barley, inflorescence-derived auxin appears necessary for GA biosynthesis in the internode, suggesting a conserved relationship between apical auxin and GA-driven internode elongation (Wolbang et al. 2004). Furthermore, Arabidopsis, pea and other dicots, and grasses share an acropetal pattern of internode elongation with basal internodes elongating first (Kirby et al. 1994; Pouteau and Albertini 2011). As basal internodes are older, the acropetal pattern could arise if internodes acquire a particular competence for elongation based on developmental stage. Alternatively or additionally, internodes may respond to a signal which itself is acropetally distributed. GA is a promising candidate. Long known to promote both bolting and intercalary elongation when applied to internodes (Sachs 1965; Kaufman 1965; Bleecker et al. 1986), a leaf-derived acropetal GA signal appears important for internode elongation and flowering in tobacco (Eriksson et al. 2006; Dayan et al. 2012). In addition, dicot stems transport GA acropetally through the stems (Binenbaum et al. 2018). Furthermore, internodes in constitutive GA-signalling slender mutants in Arabidopsis, rice and barley concurrently elongate, a similar response observed after saturating GA treatment (Foster 1977; Ikeda et al. 2001; Aoki et al. 2002), suggesting that misregulated GA levels can uncouple the acropetal internode pattern. Interestingly, work in rice suggests differential regulation of GA level and signalling between the basal versus upper unelongated internodes: as suggested by the locus name, the enzyme

encoded by *EUI* described above appears to deactivate GA specifically in the final internode of rice (Zhu et al. 2006), while a gibberellin 2-oxidase, which also deactivates GA, encoded by the *SHORTENED BASAL INTERNODES* gene, is specifically expressed in basal internodes of rice where it prevents basal internode expansion (Liu et al. 2018). Taken together, these data suggest that regulation of GA levels, transport, perception and signalling could influence the acropetal wave of internode elongation along the shoot axis, potentially in response to a basipetal auxin signal. BR is also suggested to move acropetally in wheat and cucumber (Nishikawa et al. 1994) - although not in pea (Symons and Reid 2004) - which may interact with GA to control the elongation pattern.

Recent work by Serrano-Mislata et al (2017) using both Arabidopsis and barley showed that the master negative regulators of GA signalling DELLA proteins control apical meristem size by targeting a cell cycle inhibitor but that this function could be genetically uncoupled from its effects on secondary stem elongation. This work hints that additional DELLA targets and/or partners with a localised function to the elongating stem could be relevant for GA control of bolting growth. DELLA proteins directly interact with Class I TEOSINTE BRANCHED 1 [TB1], CYCLOIDEA [CYC], and PROLIFERATING CELL FACTOR [PCF] (TCP) proteins (Davière and Achard 2013; Davière et al. 2014) which control cell proliferation across plants (Martín-Trillo and Cubas 2010). Class I *TCP14/15* promote proliferation in internodes (Kieffer et al. 2011) and higher order class I *tcp* mutants are severely dwarfed (Davière et al 2014). Interestingly, *tcp14 tcp15* differences originate at the apex, with axial spacing reduced between floral primordia but phyllotaxy normal, suggesting that apical meristem maintenance/size is not hugely altered (Kieffer et al. 2011). Moreover, *TCP14/15* are not expressed in inflorescence meristems and very young floral primordia but strongly expressed in young stems (Kieffer et al. 2011), so the TCPs may be local regulators mediating internode growth, similar to their role in axillary branching in dicots and monocots (Hubbard et al. 2002; Takeda et al. 2003; Aguilar-Martinez et al. 2007).

The grass internode derives from the lower disc of insertion, and remain small and developmentally delayed while the upper disc and primordium differentiate into leaves (Briggs 1978). Intercalary meristems in rice are present by the P3 stage (Kaufman 1959), suggesting that proliferating cells may enter a dormant state upon leaving the apex. The rib meristem itself is known to enter dormant states in other species: in their impressive work, Ruonala et al (2008) describe how bud dormancy in poplar is associated with arrested proliferation in the rib meristem but also callose deposition at plasmodesmata. Short day induced bud break, due to an activated rib meristem capable of inducing callose hydrolysis at plasmodesmata, was later linked to increased GA level, synthesised from an abundant pool of

precursors within the dwarf shoot (Rinne et al. 2016). Thus, the physical properties of the rib meristem may interact with its responsiveness and capacity to elongate which may be relevant to intercalary meristem activation timing and pattern along the stem. Intriguingly, the *Carbohydrate partitioning defective1* dominant mutant in maize is developmentally delayed, dwarf and shows excessive phloem callose plugs and lignification, associated with inability to mobilise starch out of the leaves (Julius et al. 2018). It will be interesting to learn how callose deposition and sugar movement (see below) may relate to intercalary meristem dormancy/ activation.

Transport in and out of the intercalary meristem also influences its activity. The maize *brachytic2* (*br2*) and sorghum *dwarf3* mutants have short, thick internodes caused by defects in a gene encoding an ATP-binding cassette type B1 (ABCB1) auxin efflux transporter (Multani et al. 2003). Knöller et al (2010) showed that *BR2* was expressed in the intercalary meristem and that *br2* mutants showed abnormal nodal vasculature, defective auxin transport out of the intercalary meristem and reduced intercalary proliferation. Thus, proliferative activity in intercalary meristems is likely dependent on proper nodal vasculature supporting auxin export, an intruguing parallel to the role for polar auxin transport out of the bud in promoting axillary bud outgrowth versus dormancy (Domagalska and Leyser 2011). In the case of the axillary bud, this is due to PIN relocalisation dyanmics in the stem and bud vasculature (Balla et al. 2011; Domagalska and Leyser 2011; Shinohara et al. 2013). Determining vascular patterning, auxin fluxes and PIN dynamics in intercalary meristems both before and during activation may be important to understand the relevance of auxin to internode elongation, and how these mechanisms interact with the aforementioned KNOX and BLH functions.

Internodes are adjacent to and develop from same the phytomer as axillary buds. An inverse relationship between internode elongation and axillary bud outgrowth is often observed in cereals. Bud outgrowth in cereals, called tillering, occurs from nodes between basal unexpanded internodes and stops when internode elongation starts (Kirby and Appleyard 1984). Thus, expanding internodes generally do not have tillers, although this relationship is broken in GA constitutive mutants in barley where basal internode elongation occurs concurrently with tillering, and plants adopt an aerial branching habit (Foster 1977), as is also observed in the many-noded dwarf mutants (Harlan and Pope 1922). Another consideration is why tiller buds adjacent to elongating internodes do not grow out. In his recent, intriguing review, Kebrom (2017) postulates that the increased sugar demand from expanding internodes may divert sugar away from their axillary buds, thus promoting dominance of the elongating shoot. Each subsequent internode tends to be longer than its underlying internode (Briggs 1978): i.e. Internodes increase in length with further distance from the outgrowing tillers, potentially

reflecting this interaction. Furthermore, given the role for auxin export from the axillary bud, and a potential role for this movement in intercalary meristem activity (Knöller et al. 2011), the intercalary meristem and the axillary bud rib meristem could also compete for auxin export. Interestingly, strigalactone (SL), which inhibits axillary bud growth by influencing PIN-mediated auxin efflux out of the bud, also promotes internode elongation (de Saint Germain et al. 2013).

CONCLUSION AND OUTLOOK

The Green Revolution heralded the most spectacular increase in food supply in human history (https://ourworldindata.org/). Selection for variation in growth hormone pathways controlling stem elongation was critical to increase yeild, yet also brought some undesirable pleiotropic effects throughout the plant lifecycle, such as reduced seed germination and vigour in GA signalling mutants (Wu et al. 2011; Nagel et al. 2013). Although we know an impressive amount about the downstream molecular mechanisms of these hormones, we are less sure about other components, potentially upstream, which may specifically regulate both primary stem morphogenesis and the secondary stem elongation so critical to yeild. Understanding these regulators may help not only selectively control internode growth compared to other features but gain insight about the pathways controlling upward plant growth, a fundamental activity with profound implications on plant development, diversity and evolution.

Several questions to pursue include:

1) Are there CLV-WUS/KNOX meristem maintenance pathways specific for the rib meristem and/ or intercalary meristem maintenance?
2) Much of our understanding about stem growth is from work in Arabidopsis, pea and the warm weather rice and maize cereals. How conserved are these mechanisms in temperate cereals?
3) How conserved are regulators of intercalary or rib meristem activity compared to other meristems in non-vascular plants which give rise to transverse cell files during sporophyte elevation? How does this reflect the present/absence of lignin between these two groups?
4) Is there an apically-derived signal activating intercalary activity and how is it perceived?
5) How is vascular differentiation in the node, internode and axillary bud regulated and is this relevant to their differential pattern of internode growth within an individual? In particular, how is this timed and relevant to rib meristem function and intercalary dormancy?
6) How are environmental signals perceived at either the rib or intercalary meristem to alter their activity in response to changed conditions during

stem elongation and are these signals more important for proliferation or expansion in the internode?

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Figure 1. Proliferative patterns associated with axial elongation

(**A**) Arabidopsis vegetative shoot apical meristem and rosette. Proliferation in the apical central zone displaces cells into the neighbouring peripheral zones. Leaf primordia form off the peripheral zone. Underlying rib meristem produces files of transversely dividing cells which together with subapical peripheral cells, displace downwards to form the stem. Little internode elongation between nodes leads to a rosette habit. (**B**) Vegetative shoot apical meristem and compressed seedling modelled from maize. Similar to (A), the meristem has central, proliferative and rib zones and produces leaf primordia off its peripheral flank; however, leaf primordia remain attached to the meristem base by a disc of insertion (doi). Clonal analyses shows that the upper doi forms the leaf blade while the lower doi will develop into the node, internode and axillary bud. Little internode elongation between nodes leads to a compressed stacked internodes. (**C**) Bolting Arabidopsis inflorescence and stem. The rib meristem increases in size and activity to fuel acropetal expansion of internodes between secondary axillary buds (paraclade) and later to separate flower-bearing pedicels. (**D**) Grass culm elongation following flowering modelled from barley. Internode elongation occurs in an acropetal pattern up the culm. Division in intercalary meristems displaces cells upwards to expand and mature. The intercalary meristem eventually arrests and all internode cells are expanded. Gray shading indicates the rib zone region of stem morphogenesis. Pale pink shading shows floral meristems produced off the flanks of the inflorescence meristem. Peach colour shows active intercalary meristem fueling grass internode growth. Pale green denotes leaves and leaf primordia. CZ, central zone; rm, rib meristem; im, intercalary meristem; doi, disc of insertion

Figure 2. Pathways and expression patterns assocaited with subapical proliferation and intercalary meristems

(**A**) An Arabidopsis apical meristem. Two overlapping pathways regulate meristem function at the shoot apex. The negative feedback between *WUSCHEL* (*WUS*) expression in the rib meristem and CLAVATA3 (CLV3) peptide production in the overlying cells acts to maintain meristem integrity, size and proliferation rate, thus controlling the cells available for stem morphogenesis. Disruptions in this loop cause stem fasciation, associated with altered cell division orientations and dwarfism. *WUS* expression is reinforced by localised accumulation of cytokinin. The Class-I KNOX genes (*SHOOT MERISTEMLESS* (*STM*), *BREVIPEDICELLUS* (*BP*) and *KNOTTED-like HOMEOBOX2* (*KNOX2*)) promote indeterminacy in the meristem, downregulate GA biosythnesis and are themselves downregulated in emerging lateral primordia. *KNOX2* and *BP* are expressed more strongly at the meristem boundaries and in the rib zone. (**B**) A grass apical meristem modelled on maize. The basal boundary of *ZmWUS1* expression in the central meristem is limited by FEA3 perception of the FCP1 (FON2-LIKE CLE PROTEIN1*), a* CLAVATA3 /ENDOSPERM SURROUNDING REGION (CLE) peptide produced by the leaf primordium. Expression of *NARROW SHEATH* (*NS*) in the marginal domain of the leaf primordium and underling disc of insertion is important to recruit founder cells for leaf margins and internodes. *ZmWUS1* reappears in the lower disc expanding towards the presumptive

axillary bud. *NS* genes in rice repress GA biosynthesis, and may do the same in maize. *Class-I KNOX* genes are expressed in the apical meristem, with *KNOTTED1* (*Kn1*) has the broadest expression through the meristem while *Rough sheath1* (*Rs1*) and *GNARLY1* (*Gn1*) are expressed more predominantly in the disc of insertion. All three remain expressed in the presumptive internode region and vasculature. (**C**) Maize early intercalary meristem. KN1 remains expressed in the intercalary meristem. Rs1 and Gn1 expression has not be examined for intercalary meristem tissue. It is also unknown whether there is a CLE peptide – CLV receptor which regulates intercalary meristem size. Expression of the NS WOX3b sister group is observed in maize and rice.

Figure 3. Control of boundary gene expression in the rib zone and intercalary meristem and internode

(**A**) Arabidopsis rib zone shortly after the reproductive transition. Expression of *PENNYWISE* (*PNY*) in the rib meristem promotes transverse cell divisions and limits expression of boundary genes to the rib zone periphery. PNY physically interacts with BREVIPEDICELLUS (BP) where both act to exclude boundary gene expression from the developing internode and repress lignin biosynthetic gene expression. Gray shading indicates the rib zone region. Pale pink shading shows floral meristems. (**B**) BEL-LIKE HOMEODOMAIN12 (BLH12)/BLH14 are expressed in the intercalary meristem of maize where they are essential to promote meristem maintenance, as well as the internode vasculature (purple stripes) where they prevent premature differentiation and anastomoses. BLH12/14 directly interacts with KNOTTED1 (KN1) which is also expressed in the intercalary meristem and vasculature, although the relevance of this interaction to BLH12/14 function is unknown. Peach colour shows active intercalary meristem.

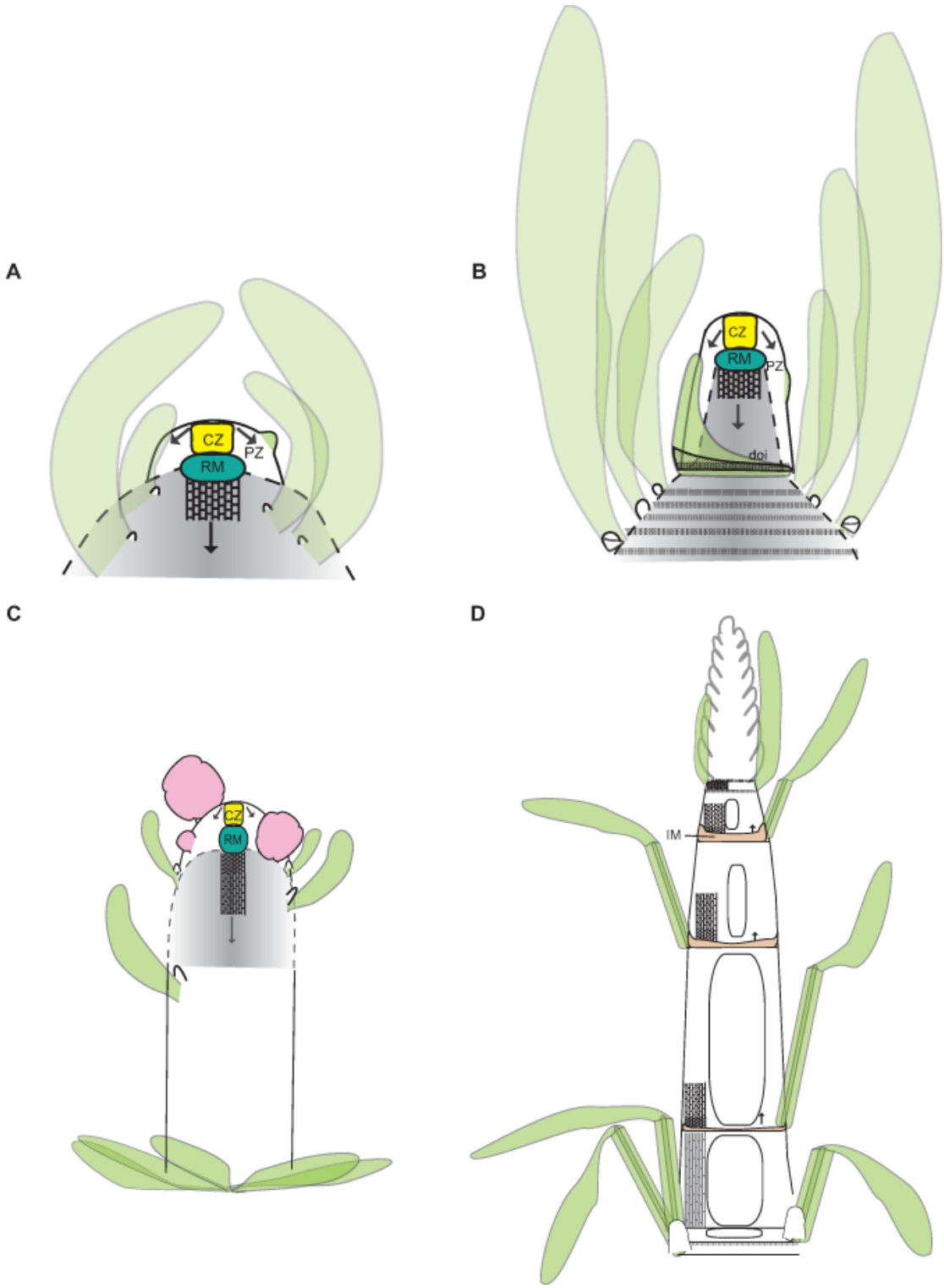

Figure 1

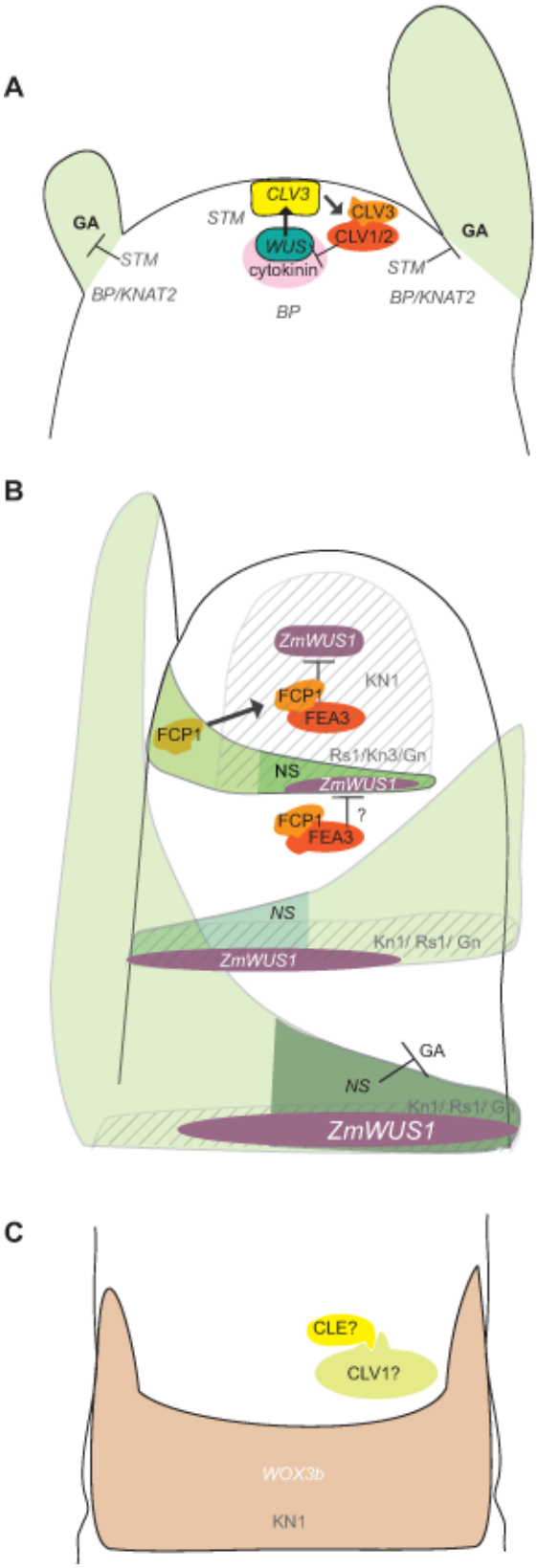

Figure 2

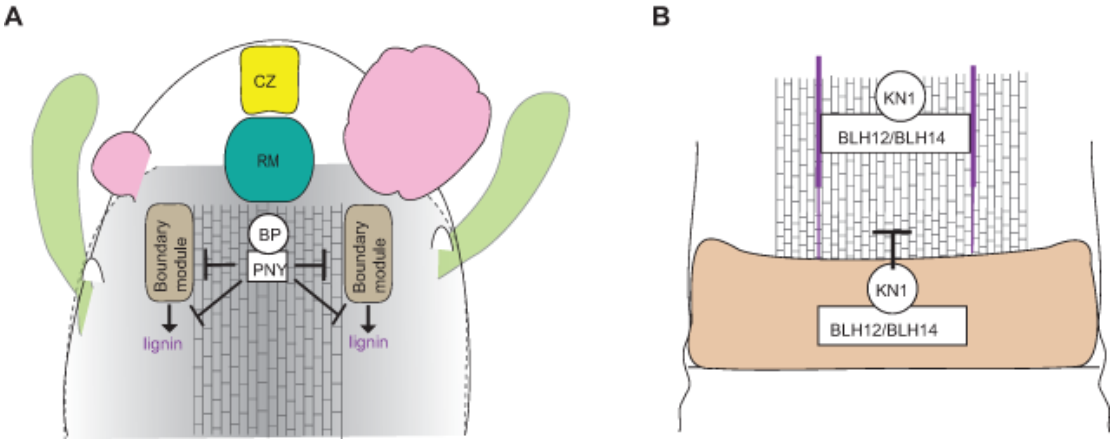

Figure 3