Moving on up - controlling internode growth

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Moving on up – controlling internode growth

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Summary

Plant reproductive success depends on making fertile flowers but also upon developing appropriate shoot internodes that optimally arrange and support the flowering shoot. Compared to floral morphogenesis, we understand little about the networks directing internode growth during flowering. However, new studies reveal that long-range signals, local factors, and age-dependent micoRNA-networks are all important to harmonize internode morphogenesis with shoot development. Some of the same players modulate symplastic transport to seasonally regulate internode growth in perennial species. Exploring possible hierarchical control amongst symplastic continuity, age, systemic signals and local regulators during internode morphogenesis will help elucidate the mechanisms coordinating axial growth with the wider plant body.

I. Introduction

The first land plants developed simple upright axes. More recently derived flowering plants segment their verticle axis into nodes of lateral growth separated by cylindrical internodes (Harrison & Morris, 2018). Changing internode length allows plants to vertically shift the distribution of their leaves and buds attached at nodes, which can profoundly change plant form. For instance, many species develop short internodes when vegetative but spectacularly elongate their internodes at flowering, changing their growth habit from compressed to caulescent (Fig. 1a). Benefits of internode elongation at flowering include inflorescence escape from soilborne pests, outcompeting neighbours, and potential for diversified pollination and wider seed dispersal. However, increased internode elongation brings costs, such as synthesis of a new cuticle, epidermis, vasculature and other internal tissues, during which axial integrity and transport is preserved. Internode growth also controls grain yield in cultivated cereals, famously demonstrated by improved resistance to lodging in the Green Revolution semi-dwarf varieties. Despite its importance, following the pioneering studies by Roy Sachs and others, axial growth became overlooked as a feature of reproductive development; however, new interest is reversing this trend (McKim, 2019). Here, I first describe axial organogenesis, and then recent insights which shine light on how internode growth is coordinated with developmental stage.

II. Different ways to grow up

All aerial organs in seed plants originate from indeterminate, renewing meristem cells and their proliferating daughter cells at the shoot tip. Lateral organs and buds develop off the periphery of the apical meristem. Transversely dividing cell files from the inner rib meristem

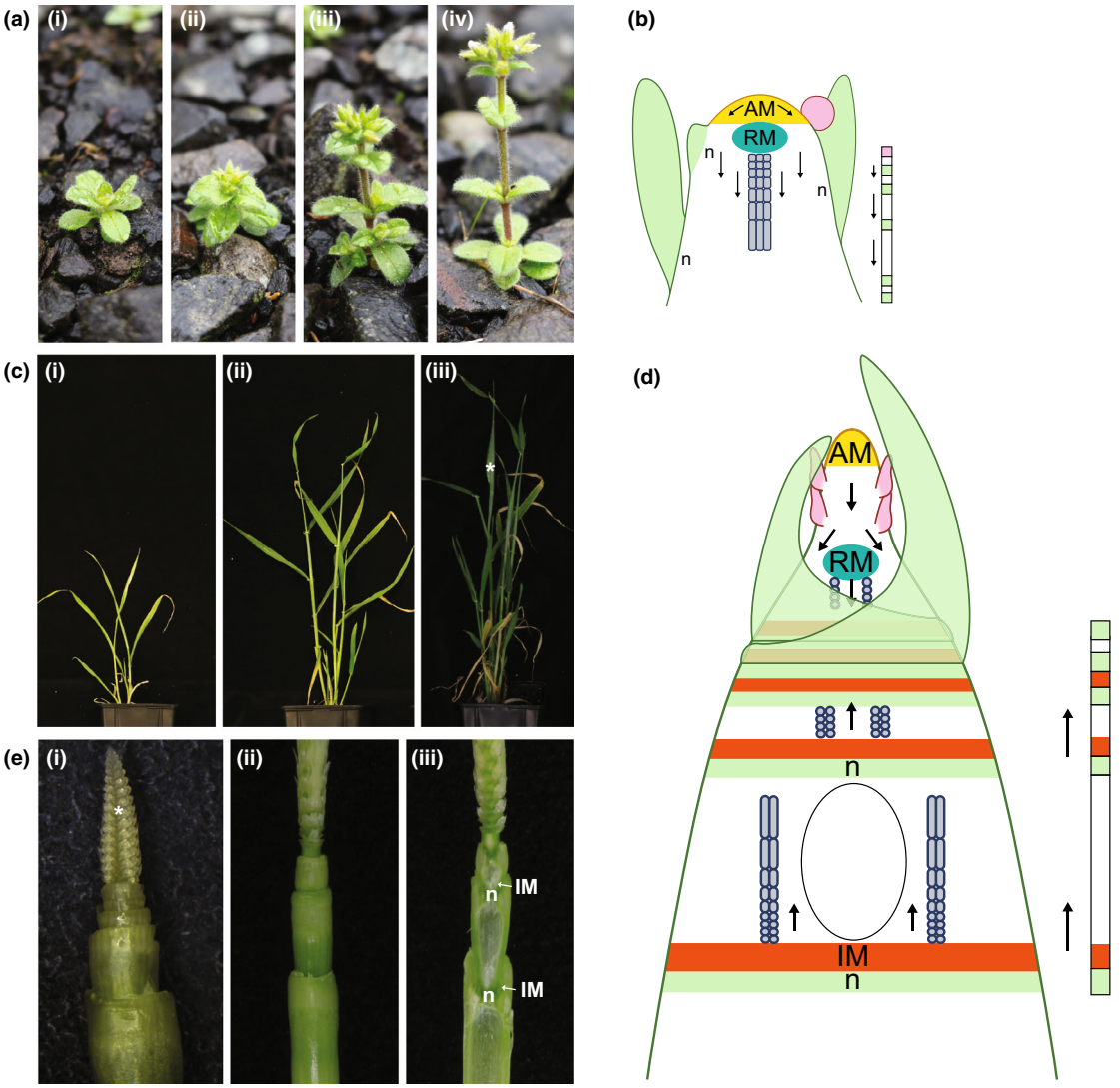

Fig. 1 Axial elongation at flowering in rosette dicots and monocots. (a) From left to right: (i) sticky mouse-ear chickweed rosette showing short internodes between vegetative leaves; (ii-iv) at flowering, internodes immediately below the inflorescence lengthen. (b) Model based on flowering rosette in (a). Leaf primordia (green) and floral bud (pink) develop off the flanks of the apical meristem (yellow). Enhanced activity in the rib meristem (teal) drives increased internode elongation in internodes in a top-down developmental gradient. Bar on side shows alternating nodes (green) and internodes (white). (c) From left to right: (i–iii) barley stalks dramatically lengthen to raise the barley inflorescence (asterisk) on top of a long stalk. (d) Model based on barley. Internodes elongate due to activation of intercalary meristems (orange) between vegetative nodes (green), elongating the internode from the bottom-up in an acropetal pattern as spikelets (pink) differentiate. Bars on side show alternating nodes (green), intercalary meristems (orange) and internodes (white). The youngest two leaves are shown; the rest are omitted for clarity. (e) From left to right: (i) young barley plant with inflorescence (*) transitioning from initiation to floral development, and little internode elongation; (ii) elongating internodes on an older barley stalk; (iii) same stalk as in (ii) but sliced open transversely. AM, apical meristem; RM, rib meristem; IM, intercalary meristem; n, node.

expand downward to extrude the stem, displacing the apex upward (Sachs, 1965; Fig. 1b). At flowering, rosette plants increase the length and activity of their rib meristems to lengthen the internodes forming underneath and between the floral buds (Sachs, 1965). Monocots also dramatically elongate their internodes during flowering (Fig. 1c) but do so primarily by activating determinate intercalary meristems above each node (Fig. 1d). Intercalary proliferation displaces expanding cells upward to regenerate a single, often hollow, internode from the bottom-up, while supported by the enclosing leaf sheath (Fisher & French, 1976). Internodes lengthen in an acropetal succession, vertically distributing the leaves and exposing the inflorescence (Fig. 1d,e). Plants must coordinate rib and/or intercalary cell renewal with daughter cell proliferation/differentiation and inflorescence development, so that flowers emerge at the optimum time, height and developmental stage.

III. Compress and release

Signals orchestrating increased axial growth with inflorescence maturation likely modify gibberellin (GA) hormone concentrations and/or responsiveness (Fig. 2). GA promotes cell division and expansion during internode growth (Sachs, 1965) by degrading DELLA growth-suppressing transcription factors (Sun, 2008).

Elevated GA signalling causes precocious and ectopic internode elongation in rosette plants and cereals (Rood *et al.*, 1990; Ikeda *et al.*, 2001). Similar GA-dependent phenotypes of photoreceptor mutants (Devlin *et al.*, 1996; Peng & Harberd, 1997; Mazzella *et al.*, 2000; Iwamoto *et al.*, 2011) suggest that photoreceptor signalling may suppress the GA pathway to limit internode growth in vegetative plants. The Arabidopsis BELL-like homeodomain (BLH) transcription factor ARABIDOPSIS HOMEODOMAIN1 (ATH1) is a promising player in this putative pathway. A photoreceptor pathway induces *ATH1* expression (Quaedvlieg *et al.*, 1995) and *ATH1* transcripts accumulate in the rib meristem and leaf-stem boundaries where it suppresses both rosette internode elongation (Gómez-Mena & Sablowski, 2008) and the floral transition (Proveniers *et al.*, 2007), possibly by limiting GA (Zhang *et al.*, 2018). Like other BLH proteins, ATH1 can interact with KNOTTED-Like homeoboxes (KNOXs) that promote GA catabolism in the meristem (Jasinski *et al.*, 2005; Bolduc & Hake, 2009), potentially contributing to ATH1 suppression of vegetative internode growth.

Flowering signals counteract vegetative internode growth suppression (Fig. 2). In fact, GA itself acts as a flowering signal across species (Sun, 2008). Increased GA in the leaf vasculature and apex promotes flowering, often in a photoperiod-dependent manner (Pearce *et al.*, 2013; Andrés *et al.*, 2014; Boden *et al.*, 2014). Leaf GA also translocates to the apex to induce flowering (Kanno *et al.*, 2016; Tal *et al.*, 2016). We do not know if mobile 'floral GA' promotes internode elongation during its transport. However, movement of leaf-derived GA in tobacco likely induces GA biosynthesis and elongation in adjacent internodes (Dayan *et al.*, 2012). Also, GA appears actively mobilized to intercalary regions based on the accumulation of GA transporters in phloem sieve elements of activated intercalary meristems in sorghum (Milne *et al.*, 2017). Furthermore, expression of a GA catabolic gene is strikingly downregulated in nascent internodes of rice at flowering, potentially increasing local GA concentrations (Sakamoto *et al.*, 2001). Taken together, changes in GA metabolism as well as its long-distance transport and delivery may be important regulatory targets to alter internode growth during flowering.

Increased GA is often linked to florigens, systemic signals which terminate vegetative growth and promote morphological events associated with reproduction. In Arabidopsis, the florigen FLOWERING LOCUS T (FT) moves from the leaves to the rib meristem where it increases local GA by repressing the gene encoding the SHORT VEGETATIVE PHASE (SVP) transcription factor that normally inhibits GA biosynthetic gene expression (Andrés *et al.*, 2014). We now know that florigens also control GA signalling in intercalary regions: in their exceptional new paper, Gómez-Ariza showed that two FT-like rice florigens inhibit the intercalary expression of the C2H2 transcription factor-encoding gene *PREMATURE INTERNODE ELONGATION1* (*PINE1*) in order to increase internode GA responsiveness and synchronize axial elongation with the flowering transition (Gómez-Ariza *et al.*, 2019). Whether florigens enter the intercalary meristem to regulate targets such as *PINE1* remains a crucial question relevant to intercalary autonomy.

However in dicots, florigens were recently demonstrated to move directly into internodes to influence their development. Shalit-Kaneh and colleagues showed that grafts overexpressing the tomato

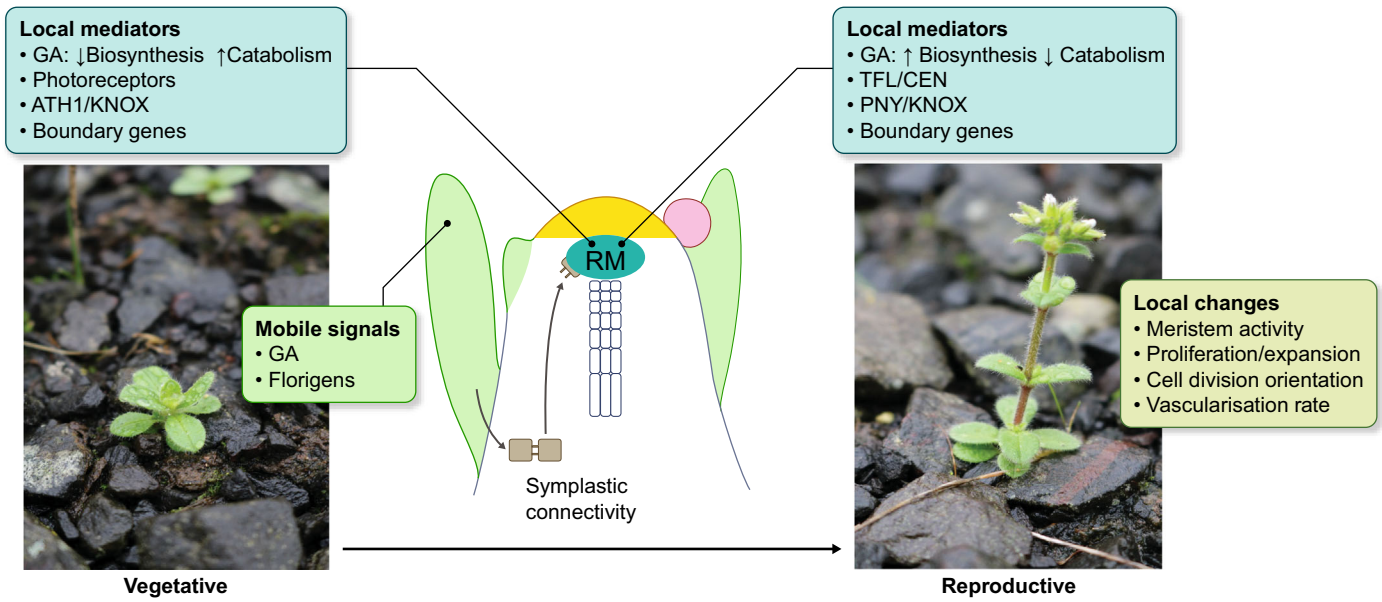

Fig. 2 Orchestration of internode elongation and flowering. Dicot model shown but some players act in intercalary meristems as well (see text). In the vegetative phase, pathways downstream of photoreceptors minimise gibberellin (GA) signalling to repress internode elongation between rosette leaves. The BELL-like homeodomain (BLH) ARABIDOPSIS THALIANA HOMEODOMAIN1 (ATH1) also represses rosette internode elongation. Floral induction leads to mobile florigens and GA which promote the floral transition at the apex. Phloem unloading of mobile signals in the rib meristem depends on symplastic conductivity. GA signalling at the apex also increases, sometimes due to florigens, associated with increased rib meristem size and activity. TERMINAL FLOWER (TFL)/CENTRORADIALIS (CEN) expression antagonizes florigen promotion of floral and rib determinacy in the apex. The BLH PENNYWISE (PNY) promotes transverse cell division orientation by excluding boundary gene expression from the central rib region. BLH and florigen control of vascularization rate influences the extent of internode elongation. RM, rib meristem.

FT orthologue, *SINGLE FLOWER TRUSS* (*SFT*), accelerated vascular maturation in recipient stems, making them shorter and thinner (Shalit-Kaneh *et al.*, 2019). This phenotype is consistent with the involvement of florigens in terminal fate, and with *FT* overexpression in multiple species leading to short stems. Florigen action is normally spatially and temporally tempered across plants via related CENTRORADIALIS/TERMINAL FLOWER1-likes (CEN/TFL1s) proteins induced at flowering, which preserve both apical and rib meristem indeterminacy (Périlleux *et al.*, 2019). Local TFL antagonism may help balance GA-driven flower and internode differentiation with stem cell renewal. Boundaries also may be important to balance differentiation and proliferation in internodes. Typically, meristematic regions high in cytokinin are separated by a boundary from proliferating and differentiating lateral organs high in GA (Hepworth & Pautot, 2015). Although rib and intercalary meristems lack a clear histological boundary from their daughter cells, it is possible that localized micro-domains of elevated GA are established distal to the cytokinin-accumulating stem cells to promote internode growth while preserving subapical indeterminacy.

In support of this model, regulation of boundary gene expression appears crucial for internode growth, *ATH1* expression progressively declines in both nodal boundaries and the rib meristem during floral induction in Arabidopsis (Gómez-Mena & Sablowski, 2008). In parallel, expression of another BLH-encoding gene, *PENNYWISE/ REPLUMLESS/ BELLRINGER/ VAAMANA* (*PNY*) increases in the rib meristem (Andrés *et al.*, 2015). PNY helps reduce and confine the transcripts of *ATH1*, *LIGHT DEPENDENT SHORT HYPOCOTYLS4* and *BLADE-ON-PETIOLE1/2* (all boundary genes) to the base of floral buds and the internode periphery, excluding them from the central rib meristem in order to promote both photoperiodic flowering and axial elongation (Ragni *et al.*, 2008; Andrés *et al.*, 2015; Khan *et al.*, 2015; Bencivenga *et al.*, 2016). Intriguingly, peripheral exclusion of boundary genes by PNY does not enhance proliferation *per se*, but increases the proportion of transverse cell divisions in the central rib region (Bencivenga *et al.*, 2016). A similar effect was observed following GA treatment of rice intercalary meristems (Sauter *et al.*, 1993), suggesting that regulatory pathways target cell division orientation in both rib and intercalary-mediated elongation. PNY also limits axial vascular development (Smith & Hake, 2003), and two BLHs in maize maintain intercalary activity and internode length by preventing premature and ectopic internode vascularisation (Tsuda *et al.*, 2017). Thus, BLHs such as PNY may help foster extensive axial growth by constraining the development of boundary and vascular tissues, potentially linked to controlling cell division orientation. PNY likely works by interacting with specific KNOXs to limit lignification (Khan *et al.*, 2012) and promote meristematic function and cytokinin accumulation (Byrne, 2003; Yanai *et al.*, 2005), the latter module being necessary for axial elongation in both flowering plants and moss (Coudert *et al.*, 2019).

IV. Independence

SINGLE FLOWER TRUSS control of stem growth was independent from its promotion of flowering in tomato (Shalit-Kaneh *et al.*, 2019). In fact, differences in rib and intercalary activity are not obligate outcomes of floral fate since these events, including those mediated by DELLAs, can be separated genetically and by responsiveness to seasonal cues (Mazzella *et al.*, 2000; Serrano-Mislata *et al.*, 2017; Gómez-Ariza *et al.*, 2019; Kemi *et al.*, 2019). Differential control of the rib meristem in part explains how perennial species cycle between dormancy and growth. At the end of the growing season, trees form a compressed stack of leaves, internodes and axillary buds on their branch tips, collectively called the terminal bud, which remains dormant until spring. In poplar, terminal buds form in response to reduced *FT2* expression in shorter days (Bohlenius, 2006). The rib meristem then arrests due to downregulation of *CENTRORADIALIS-LIKE1* (*CENL1*) (Ruonala *et al.*, 2008), reinforcing a key role for CEN/TFLs in rib proliferation. Dormancy sets in as abscisic acid-dependent expression of the *SVP-like* gene *SVL* promotes GA breakdown and closure of plasmodesmata, isolating the dormant bud from activating signals (Ruonala *et al.*, 2008; Singh *et al.*, 2018, 2019; Tylewicz *et al.*, 2018). Prolonged low winter temperatures in turn downregulate *SVL*, causing local upregulation of *FT1*, which initiates axillary floral buds, and increased GA biosynthesis. Elevated GA concentrations restore symplastic connectivity enabling the rib meristem to perceive long-distance leaf-derived cues such as FT1 and GA produced later in spring to drive bud break (Hsu *et al.*, 2011; Rinne *et al.*, 2011; Singh *et al.*, 2018; Miskolczi *et al.*, 2019). Thus, perennial species manipulate symplastic connectivity and use FT1 and FT2 florigens in different seasons to selectively control rib meristem activity in response to seasonal change.

Although annuals, barley and wheat also undergo separate stages of inflorescence maturation: first, 'inflorescence initiation' when compressed reproductive units bearing floret primordia called spikelets develop, and second, 'floral development' when floret primordia differentiate and internodes lengthen (Fjellheim *et al.*, 2014). Autumn-sown winter cereals will only undergo inflorescence initiation in early spring after exposure to winter temperatures (vernalization). Subsequent floral development also is dependent on vernalization but requires the long photoperiods of spring (Fjellheim et al., 2014). Spikelet initiation is independent of photoperiod and advanced by FT3, long photoperiods elevate FT1 and GA to advance floral development, and the TFL1-like *CEN* antagonizes both FT1 and FT3 (Boden *et al.*, 2014; Digel *et al.*, 2015; Mulki *et al.*, 2018; Bi *et al.*, 2019). Plasmodesmata constrict in wheat over winter (Jian & Wang, 2004), suggesting a seasonal regulation of symplastic continuity in cereals which could influence perception of florigen and CEN/TFL signals. Differentiation of nodal vasculature is concomitant with elongation of the overlying internode in barley (S. M. McKim, pers. obs.). It is tempting to speculate that nodal boundaries or vasculature, and their symplastic connectivity, could gate perception of leaf or apically-derived dormancy-breaking signal(s), such as FT1 and/or GA, potentially regulating seasonal control and/or the acropetal pattern of internode growth in cereals.

V. Not so fast

Antagonism between two miRNAs also modulates internode growth. MiR156 and miR172 drive developmental transitions across plant species with miR156 promoting vegetative juvenile characteristics and miR172 advancing adult, reproductive traits, by targeting transcripts encoding the SQUAMOSA-PROMOTER-BINDING-LIKE (SPL) and APETALA2 (AP2)-likes, respectively (Wang *et al.*, 2009). In cereals, internode growth follows different phases from intercalary proliferation, to coupled proliferation-expansion and to a final expansion stage (Patil *et al.*, 2019). A miRNA172-resistant allele encoding an APETALA2 (AP2)-like transcription factor in barley delayed the transition to floral development (Houston *et al.*, 2013), prolonged a less active intercalary proliferation stage and led to premature vascularization in the internode, blocking final expansion, causing dwarfism (Patil *et al.*, 2019). This overexpression of *AP2* reduced GA responsiveness, but also elevated jasmonate (JA) phytohormone-related gene expression, and exacerbated a JA-mediated block of floral progression and internode elongation (Patil *et al.*, 2019). As JA antagonizes GA-promoted growth (Guo *et al.*, 2018), miR172-limitation of AP2 may help dampen the JA pathway to facilitate rapid GA-promoted internode elongation at flowering (Patil *et al.*, 2019). Stress accelerates poplar bud dormancy, associated with lower expression of JA signalling repressors, suggesting a role for JA-related growth suppression in bud dormancy (Hsu *et al.*, 2011). Taken together, JA and the miRNA-regulated aging pathway could be important interacting factors in seasonal control, floral progression and internode development.

VI. Conclusion

For many plants, internode development is a critical part of reproductive maturation. We are just starting to understand the signalling pathways directing phase-associated changes to axial growth. However, this research reveals some central themes: (1) localized control of GA signalling is sensitive to the reproductive phase and responds to long-distance signals; (2) cell division orientation, boundary gene expression patterns and vascularization are important regulatory targets during reproductive internode morphogenesis; (3) control of axial growth can be uncoupled from the floral transition; and (4) phase-specific regulators may exploit JA to modulate developmental growth switches in the apex and internode. Looking forward, a convergence of genetic, 'omic' and imaging approaches may reveal additional and deeper insights about internode growth control. It will be particularly satisfying to learn whether BLHs interact with meristem regulators, seasonal cues and phytohormone signalling to control cell division orientation and vascularization rate, and whether ATH1 uses similar mechanisms to suppress internode elongation in vegetative rosettes. We should precisely examine the molecular and phytohormone zonation within the rib and intercalary regions and determine how these change during developmental transitions and in response to external cues. Defining how developmental phase, age and seasonal signals interact with vascular connectivity also may help explain the switches from quiescence, maintenance and activity across intercalary, rib and floral meristems. These comprehensive approaches to understand the wider axial system also may reveal mechanisms which preserve axial transport while the internode undergoes morphological change.

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