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The pillars of land plants: new insights into stem development

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In spite of its central importance in evolution, plant architecture and crop improvement, stem development remains poorly understood relative to other plant organs. Here, we summarise current knowledge of stem ontogenesis and its regulation, including insights from new image analysis and biophysical approaches. The stem initiates in the rib zone (RZ) of the shoot apical meristem, under transcriptional control by DELLA and BLH proteins. Links have emerged between these regulators and cell proliferation, patterning and oriented growth in the RZ. During subsequent internode elongation, cell wall properties and mechanics have been analysed in detail, revealing pectin modification as a prominent control point. Recent work has also highlighted signalling to coordinate growth of stem tissues with different mechanical properties.

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Introduction

Development of a vertical shoot axis capable of bearing organs above the ground was one of the key steps in the evolution of land plants. The shoot of modern land plants is thought to derive from the sporophyte of a bryophyte-like ancestor, which acquired indeterminate growth maintained by apical initial cells [1,2]. These apical initials were the precursors of the shoot apical meristem (SAM), and the first organ they produced was likely the equivalent of the stem in seed plants. Indeterminate growth and branching of the shoot axis set the stage for the evolution not only of overall shoot architecture, but also of leaves and probably roots [1,2]. Therefore, development of the main axis of the shoot, represented in seed plants by the stem, is an ancient and fundamental aspect of plant development.

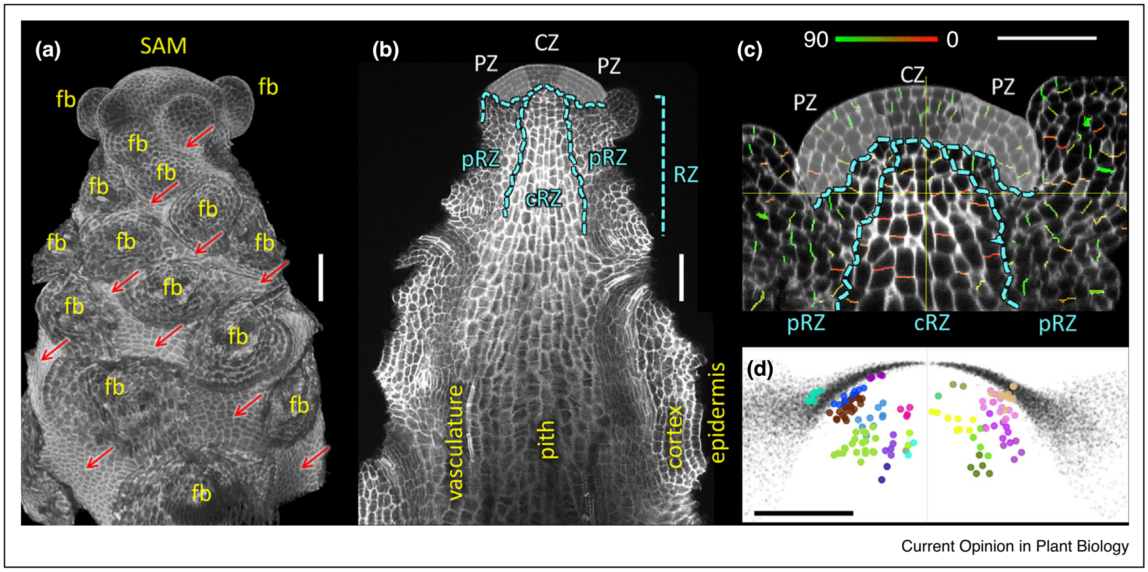
The control of stem elongation is also of great importance in crop improvement. Apart from the direct use of stems in the production of fibres, yarns, paper, wood and biofuels [3,4], changes in stem height and architecture have been a key factor for increases in grain yields the last 50 years [5]. Semi-dwarf mutants played a key role in the 'green revolution' that averted a food security crisis in the 1960–70s and continue to be important in commercial varieties. The yield gain associated with shorter stems is attributed to an increase in harvest index (yield relative to total crop biomass) and to decreased lodging (falling over) caused by wind and rain [6]. Not all effects of these mutations, however, are advantageous for crop productivity. The regulatory genes affected control a large number of genes and processes and consequently their mutations have pleiotropic, undesired effects, for example, on seed size or seedling establishment [7,8]. More precise genetic tools for modifying stem growth and architecture are needed to increase crop yield.

In spite of its basic and strategic importance, stem development has been relatively neglected, partly because ontogenesis of the stem is not as easily imaged as that of roots and lateral organ primordia, and perhaps because, at least externally, stems lack the attractive morphological complexity of leaves and flowers. Here, we review recent insights on stem ontogenesis and its regulation. We focus primarily on the initiation of stem tissues and on internode elongation, as secondary growth of the stem has been recently reviewed [9,10].

Initial stages of stem development: rib zone function

Like all other post-embryonic shoot organs, the stem is initiated at the SAM. Lateral organs, such as leaves and floral buds, are initiated in the SAM peripheral zone (PZ), which is replenished by the descendants of stem cells present in the central zone (CZ) [11]. In seed plants, the stem originates from the sub-apical region of the SAM, named the rib zone (RZ) because of its characteristic pattern of oriented cell divisions (Figure 1). The RZ includes a central region, which produces the pith of the stem, and a peripheral region that is continuous with the overlying PZ and gives rise to the stem epidermis and cortex; the stem vasculature develops at the boundary between both regions [12]. The lower boundary of the RZ is not anatomically clear, but the zone of active cell

Figure 1



Early stages of inflorescence stem growth. **(a)** Three-dimensional (3D) view based on a stack of confocal images, showing the Arabidopsis inflorescence apex with most floral buds removed; SAM: shoot apical meristem; fb: position of floral buds; red arrows indicate the proliferating internode epidermis. **(b)** Longitudinal section through the image in (a), with the central zone (CZ), peripheral zone (PZ) and rib zone (RZ) indicated; the RZ is subdivided into central (cRZ) and peripheral (pRZ) regions; different stem tissues are indicated in yellow. **(c)** Close up of a SAM section similar to (b), with different SAM regions indicated as in (b); planes of recent cell divisions are coloured according to their orientation in 3D (the colour bar above the image shows angles between the stem main axis and the vector normal to a plane fitted to the new cell wall; red indicates divisions perpendicular to the main axis, green marks divisions at a low angle to the main axis). **(d)** Clonal analysis showing growth patterns in the SAM; each set of coloured dots indicates the position of cells descended from a single cell that had been genetically marked three days before imaging; clones were imaged in different apices, which were aligned and overlapped based on the position of floral buds; grey dots correspond to the position of epidermal cells in each of the overlapped apices. Bars: 50 μm. For details of methods used in (c) and (d), see [14••].

division typically extends to at least 1–2 cm from the apex [12].

In monocotyledons, stem elongation is also promoted by intercalary meristems (IMs) located at the base of each internode. Although located differently, the IMs are functionally comparable to the RZ in dicots and are subject to similar regulation. For example, both the RZ and IMs are the main sites where stem growth is stimulated by gibberellin (GA) [12,13] and both are regulated by closely related BEL1-like (BLH) transcription factors, represented in Arabidopsis by REPLUMLESS (RPL) (also known as BELLRINGER, PENNYWISE, LARSON, VAAMANA and BLH9) and in maize by BLH12 and BLH14 [14••,15•].

Early work showed that cell division in the RZ is stimulated by GA [12,16]. This hormone acts by promoting the degradation of DELLA proteins [17], which modulate the activity of a wide set of proteins to integrate environmental and endogenous signals in plant growth. Recent work in both dicotyledons and grasses revealed the links between GA function and other hormones that regulate stem growth, particularly brassinosteroid (BR) and abscisic acid (ABA) [18–21]. DELLAs were known to control cell division in the stem by binding and inhibiting the activity of class I TCP (TEOSINTE BRANCHED 1, CYCLOIDEA, and PROLIFERATING CELL FACTOR) transcription factors, which activate genes controlling cell cycle progression [22]. More recently, a direct link emerged between DELLAs and cell proliferation in the RZ, through activation of the cell-cycle inhibitor KRP2 (CDK/Kip-Related Protein2). Surprisingly, this revealed that control of cell division by DELLAs in the RZ affects not only stem elongation, but also the size of the overlying SAM and consequently the rate of floral bud production [23•].

KNOX-family transcription factors are central regulators of shoot meristem function in combination with BLH proteins [24]. Some of these, such as RPL in Arabidopsis, are particularly important for RZ development. RPL has been found to maintain RZ function by repressing the expression of organ boundary genes; in *rpl* mutants, ectopic expression of the *LSH4* (*LIGHT-DEPENDENT SHORT HYPOCOTYL 4*) boundary gene disrupted the distinct patterns of oriented cell division that distinguish the central and peripheral regions of the RZ (Figure 1) and inhibited stem elongation [14••]. Recent work highlighting the importance of oriented divisions in plant