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Polypeptide signaling molecules in plant development

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Intercellular communication mediated by small signaling molecules is a key mechanism for coordinating plant growth and development. In the past few years, polypeptide signals have been shown to play prominent roles in processes as diverse as shoot and root meristem maintenance, vascular differentiation, lateral root emergence, and seed formation. Signaling components such as CLV1 and the IDA-HAE/HSL2 signaling module have been discovered to regulate distinct developmental processes in different tissues. Recent studies have also uncovered novel polypeptide–receptor interactions, intracellular components and downstream target genes, adding complexity to our picture of polypeptide signaling networks. Finally, new families of plant polypeptides, such as the GLV/RGF/CLEL and ESF factors, are being identified, the functions of which we are only beginning to understand.

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Introduction

In multicellular organisms, the coordination of growth and development programs within cell communities relies on cell-to-cell interactions. Research has shown that small polypeptide signaling molecules play prominent roles in short-range intercellular communications. Multiple families of small polypeptide signaling molecules are known in plants, encoding two structurally different classes: small post-translationally modified polypeptides (5–20 amino acids) that are cleavage products of larger precursor proteins, and cysteine-rich polypeptides (approx. 50 aa) that form disulfide bonds during their maturation process. Both classes of polypeptides are thought to act extracellularly, moving through the apoplast where they are perceived by transmembrane receptors of neighboring cells and regulate signal transduction pathways [1]. Therefore, polypeptide action is described as mostly non-cell autonomous. The Arabidopsis genome encodes more than 1000 putative small signaling molecules [2] and over 600 putative receptor-like proteins [3], yet only a few polypeptides have been functionally characterized. However, recent studies have described the functions of several new signaling modules in plant development as well as new functions for previously characterized signaling components [4•,5,6•,7•,8]. This review will highlight some of the most recent discoveries in the field, emphasizing those pathways for which multiple components are known. For brevity, we omit studies on the RALF polypeptide family [9,10], the C-TERMINALLY ENCODED PEPTIDE (CEP) family [11–14] and the EPIDERMAL PATTERNING FACTOR (EPF) family [15–17].

CLV3-dependent signal transduction in shoot meristem maintenance

In the above-ground meristems of flowering plants, the fine balance between stem cell maintenance and organ differentiation is orchestrated by a negative feedback loop comprising the stem cell-restricting 12 aa glycopeptide CLAVATA3 (CLV3) [18,19], the receptors CLV1, CLV2-CORYNE and RPK2/TOAD2 [20–23], and the stem cell-promoting homeobox transcription factor WUSCHEL (WUS) [24,25] (Figures 1 and 2A). Although this signaling module is well described [1,26], the intracellular signal transduction components downstream of CLV1 and CLV2 are largely unknown. A recent study, however, describes the involvement of COMPACT PLANT2 (CT2), a Gα subunit of a predicted heterotrimeric G protein, in a maize CLV3-dependent signaling pathway [27••]. *ct2* plants exhibit a wide range of shoot apical meristem (SAM) phenotypes resembling those of maize *clv* mutants. Phenotypic analysis indicates that *CT2* and *FASCIATED EAR2* (*FEA2*), which encodes the maize orthologue of *CLV2* and maps to a QTL for kernel row number [28], act in a common genetic pathway. Consistently, co-immunoprecipitation experiments demonstrate the physical interaction of CT2 with FEA2 *in vivo* [27••]. In addition, CLV3 peptide treatment inhibits wildtype but not *ct2* embryonic meristem activity [27••], indicating that CT2 may transmit a CLV3-dependent signal to control shoot stem cell proliferation. Interestingly, no genetic interaction occurs between *ct2* and the *CLV1* orthologue *thick tassel dwarf1*; thus CT2-mediated signal transduction may only contribute to a subset of shoot meristem maintenance pathways.

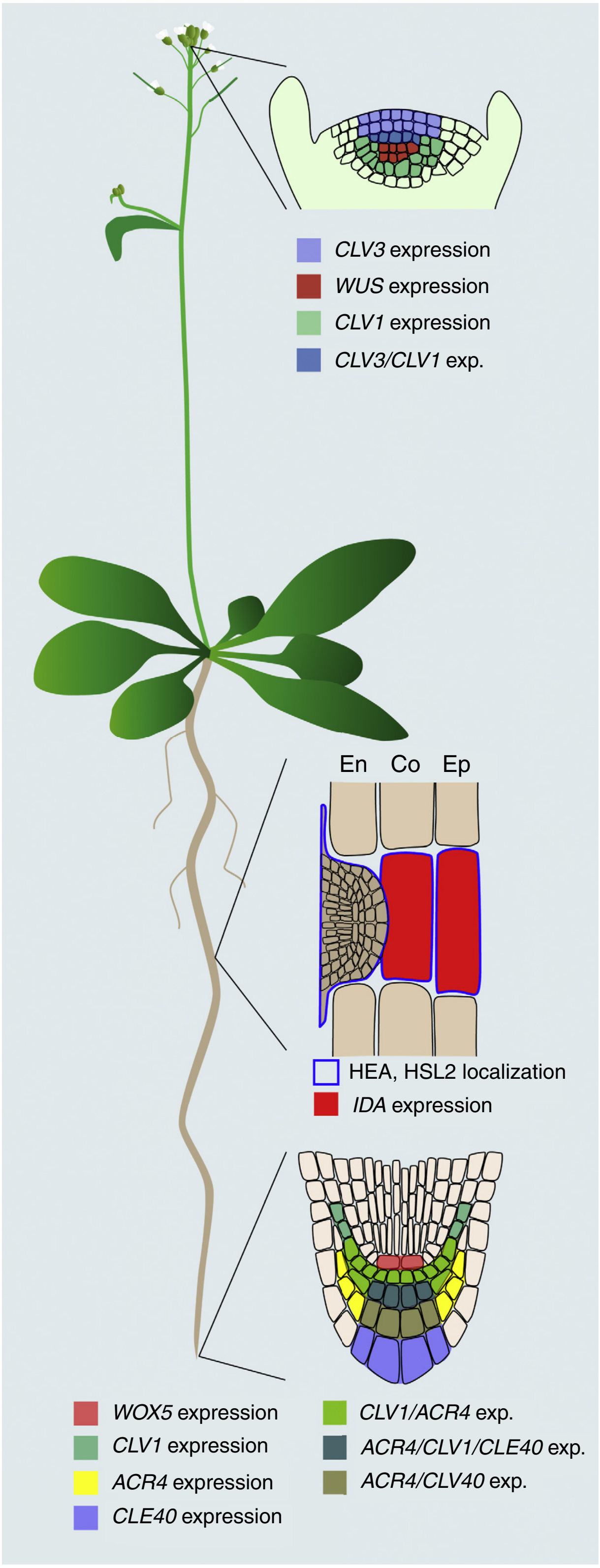
Roles of small polypeptides in root development

Regulation and maintenance of the root apical meristem

The root system in higher plants originates from the activity of a root apical meristem (RAM) at the growing tip. A negative feedback loop involving the CLV3-related protein CLE40 and WUSCHEL-RELATED HOMEOBOX5 (WOX5) is required to maintain the columella stem cell (CSC) population in the Arabidopsis RAM [8], establishing a parallel with the CLV3–WUS module in the SAM (Figure 2B). However, in contrast to CLV3, CLE40 protein is generated in differentiated cells and is perceived by the receptor-like kinase ARABIDOPSIS CRINKLY4 (ACR4) [8]. A recent study reports that *CLV1* is also expressed in the RAM and partially overlaps with the *ACR4* expression domain [29•] (Figure 1). Mutational analysis indicates that CLV1 contributes to CLE40-dependent stem cell restriction, but is not necessary when CLE40 peptide is in excess. CLV1 and ACR4 form homomeric and heteromeric complexes *in planta*, with the proportions of the different complexes depending on the local concentrations and differential subcellular localization of the two receptors in the plasma membrane and plasmodesmata [29•]. Thus the CLV1 receptor-like kinase functions in stem cell signaling complexes not only in the shoot meristem but also in the root meristem, where it promotes columella cell differentiation.

Peptides other than CLE family members are also involved in RAM maintenance. The ROOT MERISTEM GROWTH FACTOR (RGF), CLE-like (CLEL) or GOLVEN (GLV) family of polypeptides was identified in independent *in silico* studies [30–32], and comprises 11 members in Arabidopsis. The 13-aa polypeptide RGF1 (GLV11) was identified based on its ability to suppress the formation of extra quiescent center (QC) cells in *tpst* mutant roots [30]. The tyrosylprotein sulfotransferase (TPST) enzyme catalyzes the post-translational tyrosine sulfation of peptides in Arabidopsis, including RGF1 [33]. *RGF1*, and the closely related

Figure 1



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Expression of polypeptide signaling module components during Arabidopsis shoot and root development. The expression domains of genes encoding polypeptides, receptors and downstream targets in developing shoots and roots are illustrated. *CLV3* is expressed in the stem cell reservoir overlying the expression domains of the *CLV1* receptor kinase gene and the *WUS* target gene in the organizing center of the shoot apical meristem. Expression of the *IDA* polypeptide and localization of the *HAE/HSL2* receptors is illustrated at stage V of lateral root primordium formation [61]. *IDA* expression is induced in the cortical and epidermal cells by local auxin accumulation, and the peptide is perceived in the same cell files by HAE and HSL2 receptor kinases. *CLE40* is expressed in the distal columella cells of the root tip. The *ACR4* receptor gene is expressed in the CSCs, columella cells, the adjacent lateral root cap and epidermis initials. The *CLV1* receptor gene is expressed in the CSCs, in the adjacent layer of columella cells and in epidermis root cap initials. The *WOX5* target gene is expressed in the quiescent center of the root apical meristem. En, endodermis; Co, cortex; Ep, epidermis.