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Perspective

In vivo action of RNA G-quadruplex in phloem development

Hyunwoo Cho[1,#], *Hyun Seob Cho*[2,#] *& Ildoo Hwang*[2,*]

[1]Centre for Organismal Studies, Heidelberg University, Heidelberg 69120, Germany, [2]Department of Life Sciences, POSTECH Biotech Center, Pohang University of Science and Technology, Pohang 37673, Korea

Phloem network integrates cellular energy status into post-embryonic growth, and development by tight regulation of carbon allocation. Phloem development involves complicated coordination of cell fate determination, cell division, and terminal differentiation into sieve elements (SEs), functional conduit. All of these processes must be tightly coordinated, for optimization of systemic connection between source supplies and sink demands throughout plant life cycle, that has substantial impact on crop productivity. Despite its pivotal role, surprisingly, regulatory mechanisms underlying phloem development have just begun to be explored, and we recently identified a novel translational regulatory network involving RNA G-quadruplex and a zinc-finger protein, JULGI, for phloem development. From this perspective, we further discuss the role of RNA G-quadruplex on post-transcriptional control of phloem regulators, as a potential interface integrating spatial information for asymmetric cell division, and phloem development. [BMB Reports: Perspective 2018; 51(11): 547-548]

In vascular plants, phloem and xylem are responsible for long-distance transport of water, minerals, photosynthates, and diverse signalling molecules. Phloem transports photosynthates from source tissues, mainly leaves, to sink tissues such as roots, flowers, and fruits. Phloem consisting of specialized cells called SEs, functional transport units, is generated by a series of developmental processes tightly associated with hormonal/non-hormonal regulatory networks. The processes including enucleation, clearing of cytosol content, cell wall thickening, and sieve plate formation are prerequisite to fulfill transporting capacity of phloem (Cho H *et al*. (2017) Curr Opin Plant Biol 35, 91-97). Regardless of striking impact on plant life, our current understanding of phloem development is limited. Among limited numbers of genes involved in phloem development, *SMXL4/5* genes play a major role in early phloem development (Wallner ES *et al*. (2017) Curr Biol 27, 1241-1247). Expression starts from the earliest phloem progenitor cell, and the *smxl4/5* mutant reveals a delay in the second tangential cell division to form proto- and meta-phloem strands, resulting in complete lack of mature protophloem in roots; however, how these key regulators are coordinated during phloem development is unclear. A small peptide CLE45 also functions as a key regulator in early phloem development, perceived by its receptor BAM3, and this interaction determines proper timing of protophloem specification and progression of its differentiation (Depuydt S *et al*. (2013) Proc Natl Acad Sci U S A 110, 7074-7079). After onset of early phloem specification, NAC020-APL-NAC045/086-NEN1/2/4 exonuclease module drives formation of functional protophloem following cell wall thickening, nuclear breakdown, cytosolic dilution, and sieve plate formation. Although these regulatory mechanisms highlight the function of transcriptional factors and peptide-receptor interaction, post-transcriptional regulation may be necessary after enucleation, for phloem differentiation as implicated by a significant number of RNA-binding proteins and transporting RNAs in SE. Here, we first revealed post-transcriptional regulation that negatively regulates phloem development, through recognition and interaction of RNA G-quadruplex by a zinc-finger protein (named as JULGI). JULGI (JUL) directly binds to G-rich element of RNAs, and induces formation of RNA G-quadruplex. Especially, JUL-induced RNA G-quadruplex in the 5′UTRs of the *SMXL4/5* suppresses their translation, and inhibits phloem development in vascular plants. Interestingly, JUL deficiency improved phloem transport capacity and significantly enhanced sink strength per seed, suggesting that modulation of JUL-mediated phloem development will be used to develop promising strategy for increasing productivity in various crop plants.

*Corresponding author. E-mail: ihwang@postech.ac.kr
#These authors contributed equally to this work.

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Abbreviations: APL, altered phloem development; BAM3, barely any meristem 3; CLE, clavata3/embryo surrounding region; NEN, nac45/86-dependent exonuclease-domain protein; SE, sieve element; SMXL, supressor of max2-like

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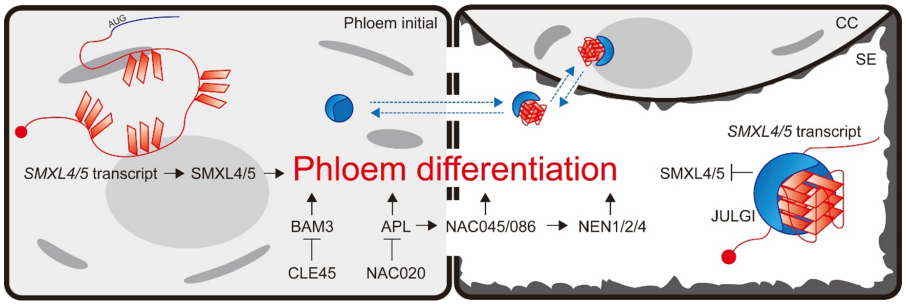

Diagram 1. Regulation of phloem development by *SMXL4/5*-JULGI module. Unstructured G-quadruplex of *SMXL4/5* leads translation, and accumulation of *SMXL4/5* proteins promotes phloem differentiation. Conversely, formation of G-quadruplex in *SMXL4/5* by JULGI suppresses translation, and inhibits phloem differentiation independent of other peptide- or transcription factor-mediated regulation. Blue arrows indicate potential movement of JUL-*SMXL4/5* complex in SE. CC, companion cell; SE, sieve element.

Transport of mRNAs from nucleus to distal parts of a cell is vital for tight control of mRNA distribution during neuronal cell development (Holt CE and Schuman EM, (2013) Neuron 80, 648-657), a prerequisite for local protein synthesis, a key process for relaying rapid changes of distal regions and for lasting local activity. Roles of RNA G-quadruplex in mRNA transport and local protein synthesis in animal studies, inevitably implicate its potential role for long-distance mRNA transport in phloem of plants. In addition to morphological similarity to neurons such as a long continuum of cytoplasm and dense connection with many cell types, functional similarity such as glutamate-based rapid transmission of electric signal (calcium ion fluctuation through phloem conduits) has been reported (Nguyen CT *et al* (2018) Proc Natl Acad Sci U S A 115, 10178-10183) (Toyota M *et al* (2018) Science 361, 1112-1115). Interestingly, JUL-binding to G-quadruplex in *SMXL4/5* inhibits translation by attenuating ribosome assembly at 5′UTR to the transcript, that may enable the transcript to be mobile and loading *SMXL4/5* transcripts into SE (Diagram 1). It is noteworthy that *JUL* expression is up-regulated by sucrose, implying that sucrose level could play a vital role in loading/unloading of *SMXL4/5* transcripts to ensure optimal phloem development. *SMXL4/5* transcripts may be unloaded at specific tissues (lateral root initiation site or axillary bud initiation site, wherein level of JUL and sucrose is low), that subsequently increases *SMXL4/5* translation to initiate phloem development in newly developing sink organs. During post-embryonic development, compared to low translational status of *SMXL4/5* in source tissues, active *SMXL4/5* translation in sink tissues promotes phloem formation. This regulatory unit comprised of sucrose-JUL- SMXL4/5 centers sucrose as a signaling molecule to integrate source-sink relationships into phloem development by controlling local translation of *SMXL4/5*. G-quadruplexes are also identified in several phloem-specific genes, including an exon and an intron in BAM3 and NEN1, respectively, suggesting multiple roles of JUL at post-transcriptional level in phloem development at different developmental stages. Further investigation of JUL functions on these G-quadruplexes would enable us to understand diverse regulatory layers of phloem development.

Based on the role of *SMXL4/5* on asymmetric cell division in phloem formation, JUL potentially optimizes rate of cell division by controlling local translation of *SXML4/5* during early phloem specification in response to sucrose. It is notable that *JUL1*, *SMXL5* and other genes involved in early phloem specification are highly up-regulated during guard cell differentiation, that requires tight control of asymmetric cell division (Bauer H *et al* (2013) Curr Biol 23, 53-57). This observation raises a possibility that JUL-*SMXL4/5* G-quardruplex module may be a core regulatory system underlying asymmetric cell division, integrating systemic signals during plant development.

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