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SHORT COMMUNICATION

Interplay between miRNA regulation and mechanical stress for *CUC* gene expression at the shoot apical meristem

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ABSTRACT
The shoot apical meristem is the central organizer of plant aerial organogenesis. The molecular bases of its functions involve several cross-talks between transcription factors, hormones and microRNAs. We recently showed that the expression of the homeobox transcription factor *STM* is induced by mechanical perturbations, adding another layer of complexity to this regulation. Here we provide additional evidence that mechanical perturbations impact the promoter activity of *CUC3*, an important regulator of boundary formation at the shoot meristem. Interestingly, we did not detect such an effect for *CUC1*. This suggests that the robustness of expression patterns and developmental programs is controlled via a combined action of molecular factors as well as mechanical cues in the shoot apical meristem.

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Throughout their lifetime, plants are exposed to a number of external mechanical perturbations, such as wind or touch. This leads to changes in mRNA level of many genes, and long-term developmental responses such as stem thickening and flowering delay [5] In addition to these external factors, plants are also constantly affected by intrinsic tensile stresses, notably because plant cells are under high turgor pressure. There is now accumulating evidence that these internal stresses are affecting many aspects of the cells, thus channeling growth in the long term.[14]

The shoot apical meristem (SAM) is the central organizer of plant aerial organogenesis. Initiation of new organs and maintenance of SAM is achieved through the concomitant action of multiple regulatory pathways. Genetic screens have identified many key players, including transcription factors, hormones, and microRNAs.[38,48,53,55] In addition to these biochemical factors, mechanical forces are also present within the meristem. In particular, the boundary domain that separates newly emerging organ from the meristem is under highly anisotropic tensile stresses.[4,15,32] A key question for the future is the analysis of the interplay between mechanical forces and the molecular regulators of meristem function (Fig. 1A).

In a recent article,[26] we showed that a master regulator of meristem maintenance, the homeodomain protein SHOOT MERISTEMLESS (STM) is expressed at a higher level in the boundary domain, and that this local increase in promoter activity can be related to mechanical stress: mechanical perturbations are sufficient to induce *STM* expression in the meristem. Interestingly, mechanical perturbations do not affect all boundary-expressed genes in the same way. For instance, the promoter activity of the *PINOID* gene, which is also increased in the boundary domain, is not affected by mechanical perturbations.[26]

Here we focus on the most canonical genetic markers of boundary identity, the *CUP SHAPED COTYLEDON (CUC)* genes. CUC1, CUC2 and CUC3, belong to a group of NAC domain transcription factors and show a high level of functional redundancy. They play an essential role in shoot meristem initiation through the regulation of *STM* expression.[1,9,19,29,34,45,49] Recently it has been reported that *CUC1* and *CUC2* are also required for formation and stable positioning of the carpel margin meristems.[23] Depletion of these genes leads to defects in cotyledon separation, organ fusions and cup-shaped cotyledons.[19,49] Although functionally connected, the expression of *CUC1, CUC2* and *CUC3* genes is regulated through different pathways. This is also reflected by their expression profiles, which are not identical in the SAM,[25,34,45] Fig. 1B

In addition to transcriptional control, CUC1 and CUC2 are subjected to post-transcriptional regulation through the microRNA pathway.[2,27,37,39,42] In plants, miRNAs are produced from larger RNA precursor transcripts that contain a self-complementary structure allowing the formation of a hairpin. After transcription, the miRNA precursor is being recognized by a protein complex that induces its cleavage and further maturation of an active miRNA. miRNAs are short (20 - 22 nt) single stranded molecules, that are predominantly associated with AGO1 and target mRNAs to cleaveage or translational repression in a sequence-dependent manner.[3,20,22,28,30,51] Based on sequence similarity of the mature miRNA and the target specificity, the miRNAs are grouped to several (over 90) families (http://www.mirbase.org/; [6,7,24,36,39] The mRNA of CUC1 and

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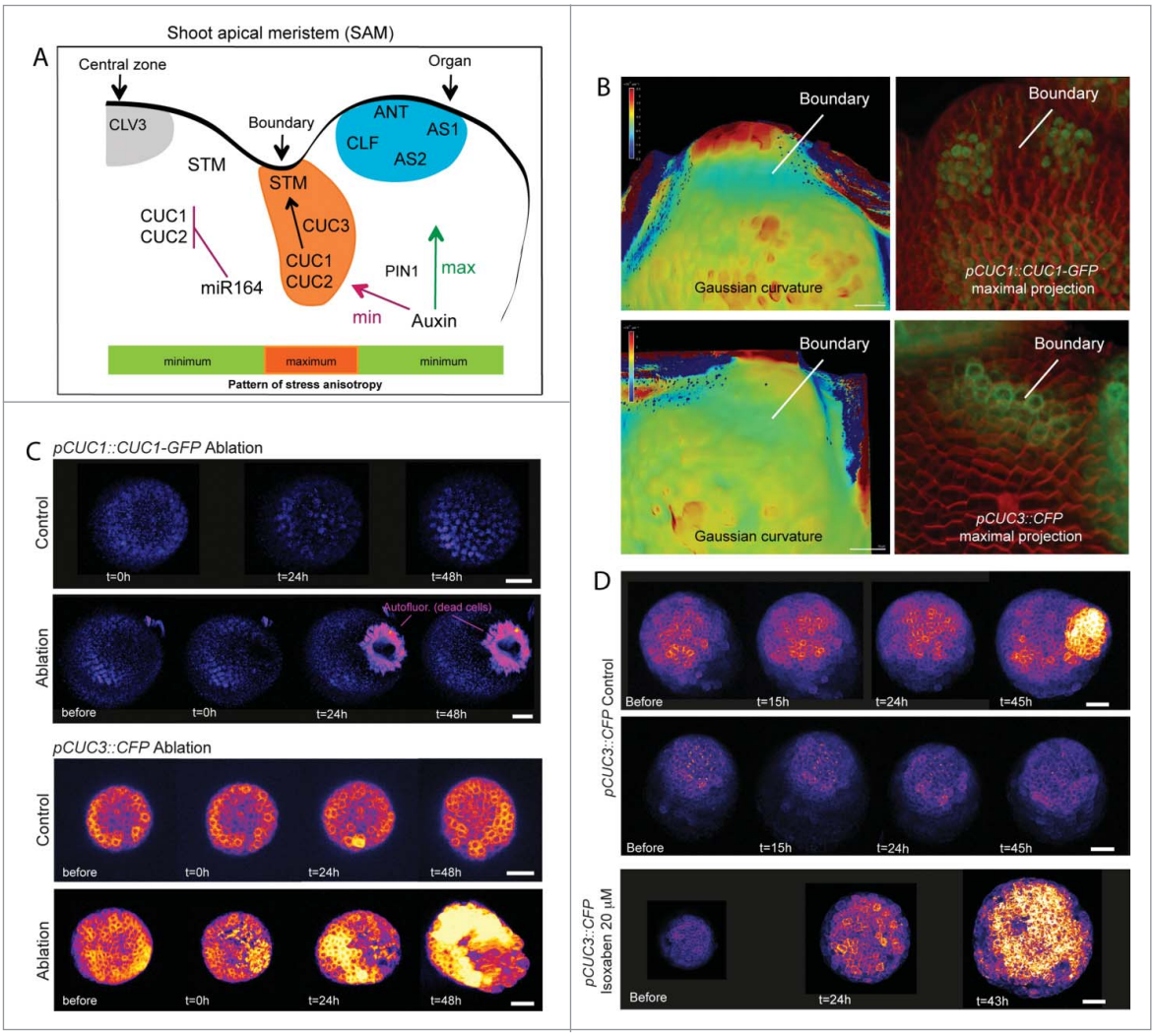

Figure 1. Interplay between molecular and mechanical regulators at the shoot meristem boundary. (A) Shape changes at the meristem is accompanied by the expression of specific genes.[52,46] Among those are *ANT, CLF, AS1, AS2* that are expressed mainly in the growing organ and, *CUC*1, 2 and 3, the expression of which is restricted to the boundary domain.[43,46,52,54] The pattern of stress anisotropy is represented by color bar with green corresponding to the regions with lower stress anisotropy (central zone and organ) and orange in the boundary domain where stress anisotropy is maximal. This stress and gene expression pattern correlates with the distribution of the plant hormone auxin that has its local maximum where new organ initiates and its local minimum at the organ boundary.[8,17,38] Acting in a PIN1-dependent manner, auxin may promote organ emergence, notably through the repression of *KNOX* genes,[11,16,41] whereas in the boundary, it may negatively regulate the axillary meristem formation.[50] (B) *CUC1* and *CUC3* expression pattern at the boundary in meristems from greenhouse-grown plants: Signal intensity (right panels) and Gaussian curvature (left panels) of *pCUC1::CUC1-GFP* and *pCUC3::CFP* in representative SAM. Membranes were labeled with FM4–64. Gaussian curvature is extracted using the level set method and MorphoGraphX. Representative images highlighting the differences between *pCUC1::CUC1-GFP* and *pCUC3::CFP* signal intensities in young boundaries, as revealed by the curvature map. Scale bars: 10 μm. (C) Expression of *pCUC1::CUC1-GFP* (upper panels) and *pCUC3::CFP* (lower panels) in meristems from *in vitro* grown plants, before and after ablation. Expression is shown using the Fire lookup table in ImageJ, with the threshold of 5 in the Fire representation. No significant induction of signal is observed for *pCUC1::CUC1-GFP;* only an increase of autofluorescence in dead cells can be detected 24 hour after ablation. In contrast, *pCUC3::CFP* expression (lower panels) is induced 24 hours after ablation, when compared to control. Scale bar, 20 μm. (D) Expression of *pCUC3::CFP* in meristems from *in vitro* grown plants, before and after treatment with 20 μM isoxaben. The two upper panels display representative untreated *pCUC3::CFP* meristems with induction only when an organ emerges (upper panel). In contrast, after the isoxaben treatment the intensity of *pCUC3::CFP* signal is induced everywhere in the meristem, when compared to control. Scale bar, 20 μm.

CUC2 is targeted for cleavage by the miRNAs of the miR164 family, comprising 3 isoforms - *miR164a*, *miR164b* and *miR164c*.[2,27,31,39,42,43] Plants, with the miR164-resistant versions of CUC1 or CUC2 have been shown to have severe defects in the organ boundary formation and organ separation during both vegetative and reproductive development.[2,27,31,33,35] The elimination of miR164 activity leads to enlargement of the *CUC1* and *CUC2* expression domains in the inflorescence meristem, supporting a scenario in which miR164 acts in spatio-temporal regulation of expression of these genes, preventing the fluctuations and contributing to the robustness of developmental programs.[35,43] Interestingly, the CUC3 mRNA does not contain the microRNA targeted site, yet it displays a robust boundary specific expression,[12,46,52] Fig. 1B.

We recently showed that mechanical perturbations in the form of ablation in the SAM is sufficient to induce *CUC3* expression in the SAM, while *CUC1* expression profile remains largely unaffected in the same conditions.[26] Here we further confirm this result: No significant induction of signal or change in signal patterning was detected in the *pCUC1::CUC1-GFP* line after ablation (Fig. 1C upper panels). This suggests that *CUC1* expression at the boundary is unlikely to be controlled through mechanical cues. In contrast, the *pCUC3::CFP* line exhibited a strong induction of the signal

in meristem (here represented at 24 hours after ablation (Fig. 1C lower panels).

To further investigate the effect of mechanical perturbation of *CUC3* expression, the *pCUC3::CFP* reporter line was treated with isoxaben and the impact on CFP signal intensity was analyzed over time. Isoxaben is a well-known inhibitor of cellulose synthesis; such a treatment is supposed to weaken and increase tensions in cell walls. We detected an increase of the CFP signal intensity in the regions of tissue folding in the treated meristems (Fig. 1D).

This rather supports a scenario in which mechanical stress may impact *CUC3* expression, and channel its expression in the boundary domain of the meristem, while *CUC1* would rely on miRNA activity to achieve such specificity. Needless to say that other factors, and notably auxin depletion at the boundary, may very well add another layer of regulation to these expression patterns.

Altogether, this work illustrates how the members of a small gene family can be regulated by different cues, despite having redundant functions. It also shows how mechanical cues and miRNA activity can differentially channel molecular inputs into specific outputs. As the molecular bases of meristem functions are now well described, elucidating further such interplays represents a major challenge for the future of plant development.

Material and methods

Plant lines and growth conditions

The *pCUC1::CUC1-GFP* and *pCUC3::CFP* lines have recently been described.[12]

"Greenhouse-grown plants" were initially grown in short-day conditions (8 hr/16 hr light/dark period) for one month and then transferred to long-day conditions (16 hr/8 hr light/dark period). Stems were cut and the SAM was dissected when the inflorescence meristem was visible, i.e. between the appearance of the first flower to the appearance of first silique (stages 13 to 17 [44] and transferred on a half MS medium with vitamins and 0.125 μg/μL of BAP for imaging as already described.[10]

"*In vitro* grown plants" were grown in a phytotron in long day conditions on *Arabidopsis* medium (Duchefa) supplemented with 10 μM NPA to inhibit flower initiation and generate naked meristems. NPA-treated in vitro grown plants were transferred to a medium without NPA as soon as naked meristems were formed as already described.[13] Meristems were then imaged from 24h to 48h after transfer on the NPA-free medium.

Confocal laser scanning microscopy and image analysis

Dissected meristems and plants grown *in vitro* were imaged in water using a SP8 confocal microscope (Leica, Germany) or a LSM780 microscope (Zeiss, Germany) to generate stack of optical sections with an interval of 0.25, 1 or 2 μm between slices. In some cases, membranes were stained with FM4-64.

The maps of meristem curvature, *pCUC1::CUC1-GFP* and *pCUC3::CFP* signals at cellular levels were obtained using the MorphographX software (www.morphographix.org). The curvature maps were generated by plotting the mean Gaussian curvature on non-segmented meshes with a neighboring of 15 μm.

Ablations and isoxaben treatment

Each experiment was performed on at least 2 independent sets of plants, and with at least 4 independent plants in each set. In all experiments, the t = Xh time point corresponds to X hours after the beginning of treatment. Controls and assays were analyzed in parallel (same growth conditions, same imaging conditions). The ablations and isoxaben treatments that were carried out on WT plants were performed on plants previously grown *in vitro* NPA and transferred in a medium without NPA 0 to 24h before the beginning of the experiment.

The ablations were performed with a needle as already described.[15,47]

The isoxaben treatments were conducted by immersing the plants in aqueous solutions of 20 μM of isoxaben overnight (for 12 to 14 hours,[18,47]). Controls were obtained by water immersion with an equivalent volume of Dimethyl Sulfoxide (DMSO). The presence of isoxaben in the meristem could be confirmed by its impact on meristem and cell size.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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