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How Arabidopsis talks to itself about its water supply

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Abstract. Takahashi et al (2018) report that the peptide CLE25 together with the BAM1, BAM3 LRR receptor-like kinases are involved in root to shoot communication during dehydration stress in Arabidopsis.

Of the many threats facing plants, a reduction in soil water availability is potentially one of the most catastrophic. Depending on the species, and the severity of the drought, plants have evolved numerous adaptations that allow them to withstand periods of reduced water availability. One strategy involves conserving existing water by reducing water loss through the pores on the leaf surface known as stomata. For this to work effectively and efficiently, it requires communication between the roots, which are the site of reduced soil water perception, and the two guard cells that surround the stomatal pore. While much is known about the mechanisms that underpin reductions in stomatal aperture in response to the plant hormone abscisic acid (ABA) that builds up in the leaves during drought (Assmann and Jegla, 2016), we know much less about how reduced soil water availability is perceived in the roots. Similarly, the identity of the signalling molecules responsible for communication between the drying roots and the shoots is not fully understood and has been the subject of hot debate. Over the years, many candidates have been proposed including hydraulic signals, electrical signals, chemical signals including ABA, the pH of the xylem sap, strigolactones and calcium ions (see reviews by Huber and Bauerie, 2016 and Tardieu, 2016). A recent paper by Takahashi et al (2018) adds a new player, the peptide CLE25, to the game.

In plants peptides are involved in the control of growth, development and responses to biotic stress but they have not previously been implicated in systemic signalling of abiotic stress (Matsubayashi, 2014). Takahashi et al. (2018) report that the peptide CLE25 is a long-distance signal induced in the roots in response to dehydration (Fig1A), which accumulates in
the leaves where it stimulates ABA accumulation and this in turn is associated with stomatal closure (Fig 1B). Specifically, Takahashi et al. (2018) found that, in roots, CLE25 expression increased in response to dehydration and that under these conditions CLE25 accumulated in the leaves. When the authors applied CLE25 to leaves they found that this was associated with reductions in stomatal aperture. They next showed that CLE25 induced increased expression of the NCED3 gene, which encodes what is believed to be the rate-limiting enzyme in ABA biosynthesis, and that dehydration-induced ABA accumulation was reduced in cle25 mutants. Because CLE25-induced stomatal closure did not occur in ABA biosynthesis mutants they concluded that CLE25 influences stomatal closure by modulating ABA production.

The authors also investigated candidate CLE receptors from the CLV/BAM LRR-RLK family and found that the bam1-5 bam3-3 putative receptor like kinase double mutant neither showed NCED3 upregulation, nor ABA accumulation in leaves after dehydration. These results suggest that the BAM1, BAM3 pair function as CLE25 receptors in this signalling system (Fig 1C). These results were supported by experiments, which showed that CLE25 application to roots of plants in which WT shoots had been grafted to either WT rootstock or bam1-5 bam3-3 rootstock increased leaf NCED3 expression. Whereas, carrying out the same experiment using plants comprised of bam1-5 bam3-3 shoots grafted to bam1-5 bam3-3 rootstock or bam1-5 bam3-3 shoots grafted to WT rootstock failed to exhibit increased NCED3 expression. Data indicating that root derived CLE25 is capable of modulating NCED3 expression was also obtained using a grafting approach. When WT shoots were grafted to WT rootstock an increase in root dehydration-induced leaf NCED3 expression was observed. In cle25 shoot/WT rootstock grafted plants, dehydration increased NCED3 to 80% of that observed in WT/WT grafted plants. In contrast when roots of plants comprised of the mutant shoot cle25 combined with the mutant rootstock cle25 were dehydrated, no increase in leaf NCED3 expression was observed. Interestingly, in WT shoot grafted to cle25 rootstock, root dehydration resulted in increased leaf NCED3 expression (to 80% of the dehydration levels seen in WT). This indicates that shoot CLE25, in the absence of a functional root CLE25 is capable of increasing NCED3 expression in response to root dehydration. This result would seem to indicate, in root to shoot dehydration signalling, that CLE25 is not the only signal in play. This supports the suggestions made by Tardieu (2016) that root to shoot communication involves multiple, possibly interacting signals.
As with so many studies, the current investigation prompts many further questions. For example, what is the conduit for CLE25 transport from roots to shoots? Plants use their vascular tissues, consisting of xylem water conducting vessels and phloem photosynthetic assimilate translocating tissues, for long distance signalling. Mobile peptides have been detected in the xylem previously, furthermore, their receptors have been found to be predominantly or exclusively expressed in the phloem, implicating a combination of these two tissue types for long distance signalling (Notaguchi and Okamoto, 2015). Further work will be required to clarify the spatial distribution of signalling components, the sites of perception and the sites of ABA synthesis during root to shoot signalling in response to reduced soil water availability. However, this must wait for the future, the important thing at this point is that a new molecule has joined the list of components which likely work together to achieve co-ordinated responses to reduced soil water availability.

References

Figure Legend
Figure 1. The role of the CLE25 peptide in plant drought stress.
Reduced soil water availability increases the expression of CLE25 in root tissue (A). The CLE25 peptide moves from the root to the leaves where it is associated with ABA accumulation and stomatal closure (B). The CLE25 peptide is perceived in the leaves by the BAM1 and BAM3 leucine rich repeat receptors. These induce downstream signalling events that result in up-regulation of the ABA biosynthesis gene NCED3. Increased NCED3 expression in the shoots and leaves leads to ABA accumulation and stomatal closure (C).