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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 (Fig1B). 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 (Fig1C). 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.

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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).

