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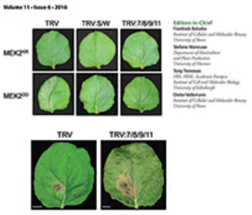

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ARTICLE ADDENDUM

Uprooting an abscisic acid paradigm: Shoots are the primary source

Scott A. M. McAdam[a], Matías Manzi[b], John J. Ross[a], Timothy J. Brodribb[a], and Aurelio Gómez-Cadenas[b]

[a]School of Biological Sciences, University of Tasmania, Hobart, Australia; [b]Ecofisiologia y Biotecnologia, Dept. Ciències Agraries i del Medi Natural, Universitat Jaume I. Castellón de la Plana, Spain

ABSTRACT
In the past, a conventional wisdom has been that abscisic acid (ABA) is a xylem-transported hormone that is synthesized in the roots, while acting in the shoot to close stomata in response to a decrease in plant water status. Now, however, evidence from two studies, which we have conducted independently, challenges this root-sourced ABA paradigm. We show that foliage-derived ABA has a major influence over root development and that leaves are the predominant location for ABA biosynthesis during drought stress.

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Abscisic acid (ABA); root growth; shoot to root signaling; stomata; water stress

Stomatal closure by abscisic acid (ABA) is essential for seed plant survival during water stress and thus an understanding of where plants synthesize this hormone is of paramount importance. Arguably one of the most influential studies investigating this question is that of Zhang et al.[1] The central conclusion drawn from this study was that roots are the primary source of ABA (Fig. 1). This model for ABA biosynthesis has permeated the literature, forming the basis for some of the most widely-cited leaf gas exchange models[2], and leading to the popular practice of measuring xylem sap ABA level in studies of drought responses.[3] However, doubts surrounding the generality of root-sourced ABA were raised by grafting studies with ABA biosynthetic mutants[4,5] as well as evidence for significant ABA biosynthesis in leaves.[6,7] This led our two groups to undertake investigations into the conventional wisdom.[8,9] Our results contrast strongly with the established dogma and together suggest a new paradigm for the ABA biosynthesis and translocation in water-stressed plants (Fig. 1). Using a combination of experimental approaches, including foliar application of labeled ABA, reciprocal grafting between ABA biosynthetic mutant and wild-type plants, as well as stem girdling to inhibit basipetal phloem transport, we found that functional foliage-derived ABA is readily transported to the roots where it is critical for not only maintaining normal root ABA levels but also for determining root architecture and growth.[8,9]

Through reciprocal grafting of ABA biosynthetic mutant and wild-type plants we found that foliar ABA strongly promotes root growth while inhibiting the development of lateral roots, with the overall effect of increasing root biomass investment.[8] This finding is in agreement with earlier studies showing drought-induced root growth through enhanced ABA levels.[10] Foliar ABA levels fluctuate dynamically in response to changes in both atmospheric and soil water status,[11] providing a signal that could link root growth with foliar water stress through the phloem transport of ABA. Thus water limitation sensed in the leaves triggers foliar synthesis of ABA which is transported in the phloem to the roots, promoting root growth to enhance soil water uptake. Furthermore, by observing girdled plants that were exposed to cycles of drought and recovery we found that root ABA accumulation was dependent on a supply of foliage-derived ABA.[9] Contrary to the 'root-sourced' model, droughted plants with roots that are unable to synthesize ABA, either because of an exhaustion of carotenoid precursor reserves or because of a biochemcial inability to synthesize ABA, were found to have normal increases in foliar ABA level and displayed normal stomatal responses to drought.[9]

In conclusion, the results of our two studies provide a new model for ABA synthesis and transport in the plant body. This new 'leaf-sourced model' views foliage-dervied ABA as predominant, determining not only the stomatal response to drought but also root growth and biomass allocation. ABA biosynthesis in roots occurs to a limited extent only.

CONTACT Scott A. M. McAdam smcadam@utas.edu.au; Aurelio Gómez-Cadenas aurelio.gomez@uji.es
Addendum to: McAdam SAM, Brodribb TJ, Ross JJ (2016) Shoot-derived abscisic acid promotes root growth. Plant, Cell and Environment 39: 652-659; doi: 10.111/pce.12669 and Manzi M, Lado J, Rodrigo MJ, Zacarías L, Arbona V, Gómez-Cadenas A (2015) Root ABA accumulation in long-term water-stressed plants is sustained by hormone transport from aerial organs. *Plant and Cell Physiology* 56: 2457-2466.

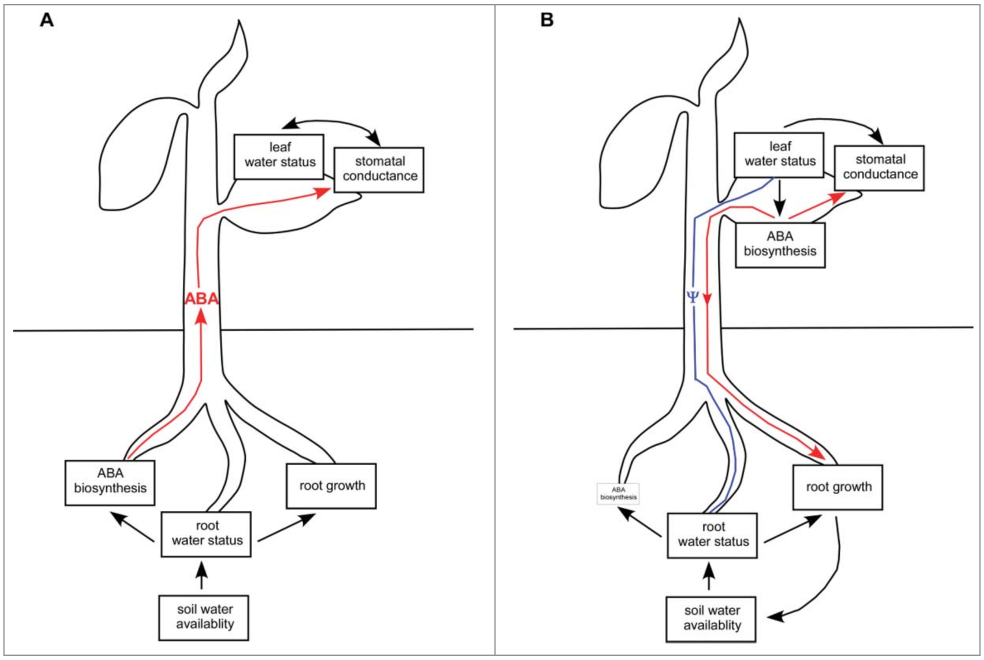

Figure 1. Diagrammatic representations of (A) the classical 'root-sourced' model for ABA biosynthesis and transport (red) in a plant experiencing soil water limitation (adapted from Davies and Zhang[12]) and (B) a schematic synthesis of the findings from our two recent studies.[8,9] We propose a new, 'leaf-sourced' model whereby soil water limitation reduces root water status and thus plant water potential (Ψ, blue). A decline in water potential in the roots provides an instantaneous signal through the internal water column in the xylem to the leaves, directly influencing leaf water status. A decline in leaf water status triggers foliar ABA biosynthesis which in turn closes stomata.[6] Foliage-derived ABA is basipetally transported from the leaves to the roots where it promotes root growth under both well-watered and water-stressed conditions. The promotion of root growth by foliage-derived ABA feeds back on the soil water available to the plant. Root ABA biosynthesis is minimal, scarcely influencing shoot physiology.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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