[Plant Signaling & Behavior 4:5, 1-2; May 2009]; ©2009 Landes Bioscience

Article Addendum

DOR

A link between an F-box protein and guard cell ABA signaling

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Key words: DOR, F-box protein, guard cell, ABA signaling

Guard cells are a model system for studying signal transduction. F-box proteins, representing one of the largest gene families in Arabidopsis, have been shown to be involved in many developmental and physiological processes, including stress responses. However, it is unclear if there is a direct link between an F-box protein and the guard cell ABA signaling. DOR is a guard cell-preferential F-box protein, and our results suggested that it likely forms two negative feedback regulatory loops for the ABA-induced stomatal closure under drought conditions in Arabidopsis. These findings have a potential impact on genetically modifying drought stress responses in plants.

Introduction

Plant hormone abscisic acid (ABA), also known as "stress hormone", plays vital roles in regulating plant responses to drought stress. Guard cells control plant water balance, and a better understanding of ABA signal transduction in guard cells is important for the goal of engineering crops with improved drought tolerance.

ABA Signaling in Guard Cells

ABA signal transduction in guard cells is a highly complex process. In an effort to provide genome-wide information on gene expression in a single cell type, Leonhardt et al.[1] identified a number of transcripts expressed in Arabidopsis guard cells which appeared to be regulated by ABA. This study reveals that ABA modulates many known guard cell ABA signaling components at the transcription level, including both the positive regulators OST1, ROS and GCA2 and the negative regulators ABI1, ABI2, ERA1 and AtP2C-HA for the ABA responses. Moreover, with the advent of systems biology techniques, a dynamic model for induction of stomatal closure by drought and ABA has been developed.[2]

Although much progress has been made on the guard cell ABA signaling, little is known about proteins or sets of proteins that are preferentially expressed in guard cells. In a recent attempt, Zhao et al.[3] have applied proteomics tools to examine guard cell function by isolating guard cells and determining their protein composition. Interestingly, their guard cell proteome suggested that phosphorylation serves as one of the main posttranslational modifications in guard cells, which is consistent with previous results showing the importance of phosphorylation to light and ABA signaling in guard cell.[4-7]

Proteolysis is important for regulating developmental and physiological processes.[8] F-box proteins found in SCF (SKP1/Cullin/F-box) complexes are known to provide the specificity when deciding on which substrate to degrade. The Arabidopsis genome is predicted to encode a large number of F-box-containing proteins,[9,10] indicating that this class of genes play important roles in Arabidopsis. Many F-box proteins have been shown to be involved in plant responses to at least four major phytohormones: auxin, jasmonate (JA), gibberellin (GA) and ethylene.[11,12] In most cases, substrate phosphorylation is one common prerequisite for F-box protein target recognition. For example, DELLA protein SLR1 is phosphorylated in response to GA treatment,[13] and the F-box protein SLY1 also appears to associate with the phospho-DELLA protein better in vivo.[14] These results indicate that plants mediate GA responses in a phosphorylation-dependent manner. Nevertheless, it is unclear if there is a direct link between an F-box protein and the guard cell ABA signaling.

DOR likely Forms Two Negative Feedback Regulatory Loops for the ABA-Induced Stomatal Closure

Recently, we identified a novel negative regulator of guard cell ABA signaling, DOR (DrOught tolerance Repressor), in *A. thaliana*. The DOR gene encodes a putative F-box protein, a member of AtSFL (S-locus F-box-Like) family related to AhSLF-S_2 and specifically interacting with ASK14 and CUL1,[15] indicating that it may function as a subunit of the SCF E3 ligase in the ubiquitin/26S-mediated proteolysis pathway.[16]

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Submitted: 03/19/09; Accepted: 03/24/09

Previously published online as a *Plant Signaling & Behavior* E-publication: http://www.landesbioscience.com/journals/psb/article/8546

Addendum to: Zhang Y, Xu W, Li Z, Deng XW, Wu W, Xue Y. F-box protein DOR functions as a novel inhibitory factor for abscisic acid-induced stomatal closure under drought stress in Arabidopsis. Plant Physiol 2008; 148:2121–33; PMID: 18835996; DOI: 10.1104/pp.108.126912.

The F-box protein DOR is preferentially expressed in guard cells and suppressed by ABA treatment. As a guard cell-preferential protein, how is DOR involved in ABA signaling? Our results found that *abi1-1* is epistatic to *dor*, indicating that the *dor* locus acts upstream of the *abi1-1* locus.[16] Moreover, we found that the stress-induced ABA reduces *DOR* expression and could in turn enhance the ABA biosynthesis. Thus, they could form a negative feedback regulatory loop for ABA in the guard cells under drought stress. Taken together, our results demonstrate that DOR acts as a regulator of ABA signaling by at least forming two negative feedback loops to mediate the guard cell ABA responses (Fig. 1), revealing two novel pathways for modulating the ABA-induced stomatal closure under drought conditions in Arabidopsis.

Perspective

Although the guard cell expressed F-box protein DOR was not detected in the guard cell proteome,[3] possibly due to its low abundance, our findings suggest that it could target an unknown factor(s) in the guard cells for regulating the ABA signaling pathway. Thus, modulation of DOR or its target(s) could provide an avenue to genetically modify the plant tolerance to drought stress.

Acknowledgements

This work was supported by the Natural Science Foundation of China (grant no. 30870216).

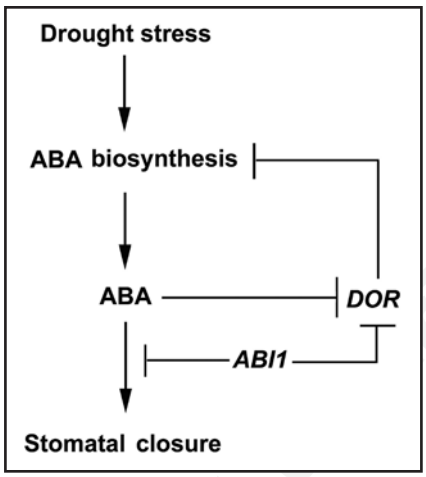

Figure 1. Model for DOR in mediating ABA-induced stomatal closure under drought stress. Arrows indicate the ABA signaling pathway for inducing stomatal closure in response to drought stress. *DOR* functions as a negative regulator of ABA biosynthesis and ABA further reduces the *DOR* expression. *ABI1* acts as a negative regulator for both ABA-induced stomatal closure and *DOR* expression. *DOR* likely forms two negative feedback regulatory loops for ABA-induced stomatal closure.

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