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Sumoylation and abscisic acid signaling

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The conjugation of small ubiquitin-related modifier (SUMO) to substrates (sumoylation) is one of post-translational modification systems in eukaryotes. Sumoylation plays an important role in the regulation of environmental stress response, biotic stress response, and flowering control in plants. Covalent SUMO conjugation requires an E1/E2/E3 enzyme, and SUMO E3 ligase SIZ1 is essential for these regulations. This addendum summarizes our recent study in which it has been established that in Arabidopsis, SUMO E3 ligase SIZ1 negatively controls abscisic acid (ABA) signaling through the sumoylation of ABI5. The conjugation of SUMO to ABI5 represses its activity and also prevents ABI5 from undergoing degradation.

Key words: seed germination, seedling growth, SUMO, sumoylation, SIZ1, signal transduction

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Many biochemical pathways are reversible; this allows the creation of on and off states, which are essential for biological regulation. A reversible system has the advantage of quick initiation and termination of a biological response that needs to be precisely regulated. SUMO modification is an example of a reversible system that is controlled by a series of on-and-off enzymes.[1,2] Sumoylation is catalyzed by E1-activation, E2-conjugation and E3-ligation enzymes, whereas SUMO proteases contribute to deconjugation of SUMO from substrates.[3,4]

On the basis of genetic analysis and biochemical evidence, it has been established that sumoylation and desumoylation are functionally linked to ABA signaling,[5] phosphate-starvation response,[6] thermotolerance,[7] cold acclimation,[8,9] drought and salt tolerance,[10,11] defense against phytopathogens,[12] growth[13] and flowering.[14-16] SIZ1 (SAP and Miz), the principal SUMO E3 ligase in Arabidopsis,[6,13] plays an important functional role in most of these processes.[6-8,11-14] Recently, HPY2/MMS21 (high proidy2/methyl methanesulfonate sensitive21) has been identified as another SUMO E3 ligase that modulates cell cycle progression and meristem maintenance.[17,18] Cells having the *hpy2* mutation had high ploidy and caused severe growth defects.[17] On the basis of ploidy and the expression of CDKB, it has been reported that SIZ1 and HPY2 may play different roles in mediating plant growth.[17]

Arabidopsis SIZ1 is the plant ortholog of yeast SIZ and mammalian protein inhibitor of activated STAT (PIAS) proteins.[2] SIZ/PIAS proteins perform several functions, including repression or activation of transcription factors to control signaling.[19] SIZ/PIAS proteins are also reported to function as transcriptional co-regulators, controlling subnuclear relocalization of substrates and interactions of transcriptional coregulatory complexes.[1,19,20]

Plant sumoylation appears to be important for ABA signaling. Our research shows that in Arabidopsis, ABA signaling is negatively regulated by SIZ1 SUMO E3 ligase-mediated sumoylation of ABI5.[21] The loss-of-function *siz1* mutation facilitated ABA-mediated inhibition of seed germination and root growth, which were restored by introduction of Pro_{SIZ1}*:SIZ1:GFP* into *siz1-2* mutants (**Fig. 1**). Furthermore, overexpression of AtSUMO1 or AtSUMO2 attenuates and co-suppression of AtSCE1 accelerates ABA-mediated inhibition of root growth;[5] therefore, the SUMO reaction contributes to the regulation of ABA responses.

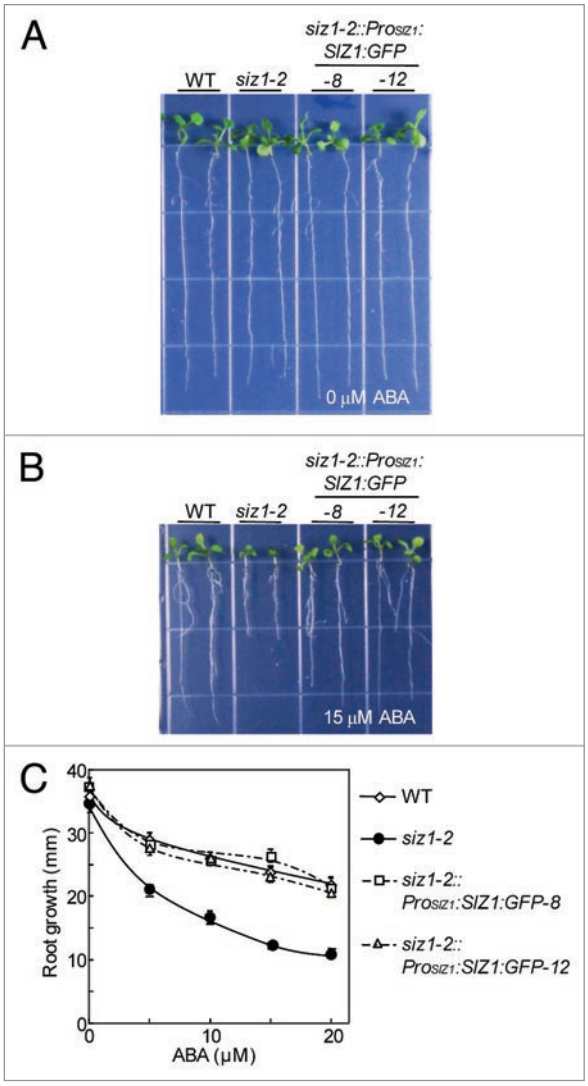

Figure 1. The *siz1-2* mutation increases ABA inhibition of primary root growth in a seedling, and this mutation is complemented by transformation of the wild-type *SIZ1* gene. Three-day-old seedlings were transferred onto media containing various concentrations of ABA. Pictures show representative wild-type, *siz1-2* and *siz1-2* transformed with Pro_{SIZ1}*:SIZ1:GFP*, seven days after transfer onto the media containing 0 (A) or 15 μM (B) ABA. (C) Root growth values are expressed as mean ± SE (n = 12). *siz1-2*::Pro_{SIZ1}*:SIZ1:GFP-8* and *siz1-2*::Pro_{SIZ1}*:SIZ1:GFP-12* are representative lines illustrating that *SIZ1:GFP* driven by the promoter of *SIZ1* was transformed into *siz1-2*,[14] and genetically complemented the mutation.

ABI5 is an important basic leucine zipper (bZIP)-type transcription factor that controls ABA response and ABA-responsive genes.[22-24] SIZ1-mediated sumoylation of ABI5 negatively regulates ABA signaling and responses.[21] Furthermore, sumoylation of ABI5 blocked proteasome-mediated degradation that was facilitated by AFP (ABI five binding protein). These findings indicate that SIZ1-mediated sumoylation of ABI5 is an important regulatory process in ABA signaling and responses and in the prevention of degradation of ABI5.

Sumoylation may play an important role in the precise regulation of ABI5 activity. Unlike the proteasome-mediated degradation of ABI5 that is facilitated by AFP,[25] sumoylation/desumoylation system is a reversible mechanism. ABI5 may be stored in the inactive form by sumoylation; subsequently, it is released by desumoylation, if necessary. Phosphorylation of ABI5 may play a role in the activation of the transcription factor because SnRK2.2 and SnRK2.3 phosphorylate ABI5 in response to ABA.[26] These posttranslational modifications are required for controlling ABI5 activity precisely.

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