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# ECAP coordinates upstream and downstream ABA signaling during seed germination in Arabidopsis

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## Abstract

Abscisic acid (ABA) is a major phytohormone that regulates seed dormancy, germination, and plant adaptation to environmental stresses. Recent studies identified the EAR motif-containing adaptor protein ECAP as a central regulator of ABA signaling in Arabidopsis. ECAP coordinates ABA receptor complex assembly, PP2C inhibition, and *ABI5*-mediated transcriptional activation, thereby integrating upstream signal perception with downstream transcriptional responses controlling seed germination and stress adaptation.

**Keywords:** ABA; Seed; Phytohormone; Adaptation; Transcription

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## Main text

Abscisic acid (ABA) is a major phytohormone that plays a pivotal role in regulating seed dormancy, inhibiting seed germination, promoting stomatal closure and mediating adaptation to environmental stress in plants. Over the last two decades, the basic ABA signaling pathway of PYR/PYL receptors, type 2C protein phosphatases (PP2Cs), SnRK2 kinases, and downstream transcription factors like *ABSCISIC ACID INSENSITIVE 5 (ABI5)* has been extensively studied [1]. However, how ABA signal perception is coordinated with downstream transcriptional regulation remains incompletely understood. Recently, two independent studies by Li*, et al.* [2], Li*, et al.* [3] found that ECAP, a member of the EAR motif-containing adaptor protein family, serves as a key link between ABA perception and ABI5-mediated transcriptional activation. These studies collectively greatly expand our understanding of ABA-mediated control of germination and stress responses in *Arabidopsis*.

### Advances in technical and mechanistic aspects of the ECAP-mediated ABA signaling

Most previous studies focused on ECAP function as a transcriptional adaptor and its roles in jasmonate signaling, salt stress response, anthocyanin accumulation and developmental regulation [4]. Recent papers, however, have revealed that ECAP is a multipurpose regulator in the ABA pathway. Li et al. (2026a) showed that *ecap* mutants exhibit decreased ABA sensitivity during germination and cotyledon

greening, whereas ECAP overexpressors exhibit increased ABA sensitivity. Substantial overlap between ECAP-regulated genes and ABI5 regulated genes was also observed in transcriptomic analyses, including *EM1*, *EM6*, *RAB18* and *RD29B*, which are ABA-responsive genes. The genes that ECAP can modulate are tightly linked to genes known to be responsive to ABA and to genes involved in stress adaptation and developmental arrest under adverse environmental conditions.

The study showed that ECAP physically interacts with ABI5 in multiple independent ways, including yeast two-hybrid, split-luciferase complementation, bimolecular fluorescence complementation, pull-down, and co-immunoprecipitation assays. ECAP ECAP enhances ABI5 promoter activity and promotes ABI5 transcript accumulation, thereby further boosting ABA-responsive transcriptional programs, thereby further boosting ABA-responsive transcriptional programs. Moreover, ECAP interacts with the *ABI5* promoter via as-yet-unknown transcription regulators, establishing a positive regulatory feedback loop in ABA signaling. These findings were corroborated by genetic analyses, which showed that overexpression of ABI5 partially complemented the ABA-insensitive phenotype of *ecap* mutants, while the *ABI5* mutants were more tolerant of ECAP-mediated ABA hypersensitivity.

A complementary study Li et al., (2026b) significantly expanded these results by introducing ECAP upstream of the known canonical ABA signaling pathway. In this work, the authors showed that ECAP directly binds to PYR1/PYLs and the PP2C phosphatases ABI1 and ABI2, which interact with the ABA receptor. ECAP induces *PYR/PYL–ABA–PP2C* receptor complex assembly and dose-dependently inhibits *ABI1/2* phosphatase activity through these interactions. As a result, *SnRK2* kinases escape PP2C-mediated repression, leading to increased ABA signaling outputs, including seed germination inhibition, stomatal closure, and drought tolerance.

Biochemical and cellular assays supported this mechanism. Both direct ECAP associations with ABI1 and ABI2 were confirmed in vitro and in planta using multiple protein-interaction experiments. Importantly, ECAP was found to assemble receptors with high efficiency and directly inhibit the phosphatase activity of *ABI1/2*, indicating that ECAP is a positive regulator of ABA signal amplification and a signaling scaffold. The combination of these activities enhances signaling efficiency and could allow plants to coordinate developmental responses to stress quickly.

## ECAP is an integrative hub for signaling

What is becoming clear from these studies is that ECAP serves as an integrative signaling hub at multiple regulatory levels of the ABA pathway. Upstream, ECAP stabilizes ABA receptor complexes and inhibits PP2C phosphatase activity. At the same time, downstream at the transcriptional level, ECAP promotes the accumulation and activation of the protein ABI5. This dual activity provides a direct mechanistic link between ABA signal sensing and the plant's germinative response to ABA.

Of particular significance for the studies presented here is the fact that they contradict the notion of transcriptional repression for proteins containing EAR motifs. Despite the presence of a canonical EAR motif in ECAP linked to repression, studies showed that ECAP can act as a transcriptional activator when interacting with different partners and under certain signaling conditions. The EAR motif was not required for the ECAP–*ABI5* interaction, indicating that the C-terminal region of ECAP may attract other regulatory proteins to stimulate transcriptional activation. This functional versatility underscores the increasing complexity of transcriptional co-regulators in hormonal signaling pathways.

## Emerging complexity in ECAP-mediated ABA regulation

The following studies also identified two possible mechanisms of action for ECAP: the *ABI5*-dependent and ABI5-independent pathways. We observed that the ecap abi5 double mutant is more tolerant to ABA than every single mutant, indicating that there are other targets downstream of ECAP. Many other transcription factors that are associated with ABA signaling, such as *ABI3, ABI4, ABF3, HY5, AGL21* and *RAV1*, may also interact with ECAP to control *ABI5* transcription and other ABA-responsive networks [2, 3].

Moreover, no obvious DNA-binding domain is annotated in the ECAP sequence, suggesting that interaction with other transcription factors is likely required to recruit ECAP to target promoters. Future studies using yeast two-hybrid screening, co-immunoprecipitation followed by mass spectrometry, ChIP-seq, and proximity labeling approaches will be important for identifying these interacting partners and clarifying ECAP-mediated transcriptional regulation. Furthermore, it is not well understood how the temporal dynamics of complex assembly are affected by environmental changes in the presence of ECAP. The mechanism by which ECAP regulates signaling during drought, salt and temperature stress could have broader implications for this protein's other functions beyond its role as a regulator of seed germination.

## Discussion

We believe that the core contribution of these studies lies in redefining ABA signaling coordination from receptor activation to transcriptional output. ECAP is not a transcription adaptor or signaling accessory factor, but rather acts as a scaffold that brings together multiple components of receptor complex assembly, phosphatase inhibition, kinase activation and ABI5-mediated transcription regulation. The integrated regulatory mechanism greatly extends the current model of ABA signaling in seed germination and stress adaptation.

The findings are especially relevant to agriculture, as ABA-mediated seed dormancy and ABA-mediated germination control are closely related to crop establishment, drought resistance, and the avoidance of preharvest sprouting. Targeting ECAP-mediated regulatory pathways could thus offer novel opportunities to improve stress resilience and seed performance in crops. Moreover, since many ABI5 homologs and components of the PP2C-mediated ABA signaling pathways are also well conserved across plant species, the mechanistic insights gleaned from *Arabidopsis* could be highly translatable to cereal and horticultural crop improvement.

Despite these developments, there are still some key gaps to be addressed. So far, the molecular factors that recruit ECAP to the *ABI5* promoter remain unknown. Furthermore, while the ability of ECAP to boost ABA signaling is apparent, the systemic effects of ECAP-regulated signaling in more complex environments should be studied. Future insights into the integration of hormonal signalling may come from structural analyses of protein complexes containing ECAP, and from genome-wide characterization of ECAP-dependent transcriptional networks.

In brief, these studies place ECAP in a new category of central components of ABA signaling, connecting upstream perception of the signal with downstream transcriptional activation. ECAP significantly extends current knowledge of the hormonal regulation of seed germination and stress response in plants by coordinating receptor complex assembly and the control of *ABI5* gene expression.

## Data availability

Not applicable

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## Conflict of interest

The authors declare that they have no conflict of interest.

## Author Contribution

The author(s) confirm contribution to the paper as follows: AMT: study conception and design, draft manuscript preparation, reviewed the results and approved the final version of the manuscript.

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