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Coordination of seed dormancy and germination processes by MYB96

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The transition between seed dormancy and germination is an important stage that initiates plant life cycle. Hormonal balances of abscisic acid (ABA) and gibberellin (GA) contribute to determining the proper timing to germinate. Here, we demonstrate that the R2R3-type MYB96 transcription factor, a key ABA signaling mediator, coordinates seed dormancy and germination processes through distinct downstream events. This transcription factor controls *ABA-INSENSITIVE 4* (*ABI4*) expression to inhibit seed germination by suppressing breakdown of lipid reserves in embryo. In addition, it also induces seed dormancy by stimulating ABA biosynthesis in an ABI4-independent manner. We propose that MYB96 integrates a multitude of environmental stress signals and acts as a master regulator in the determination of timing for seed germination.

Keywords: ABI4, abscisic acid, *Arabidopsis*, MYB96, seed dormancy, seed germination

Abbreviations: ABA, abscisic acid; ABI4, ABA-INSENSITIVE 4; GA, gibberellic acid; NCED, 9-*cis*-epoxycarotenoid dioxygenase; TAG, triacylglyceride.

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The developmental transition from seed dormancy to germination is intricately regulated to allow plants to grow in favorable seasons.[1] Antagonistic actions of 2 phytohormones, GA and ABA, play a fundamental role in determining proper timing for germination.[2] Consistently, a number of genetic components of GA and ABA signaling pathways are involved in seed dormancy and/or germination.[3-6]

The MYB96 transcription factor is a central ABA signaling mediator that regulates a variety of physiological responses under environmentally unfavorable conditions, such as stress tolerance, root and shoot development, hormone biosynthesis, and cuticular wax accumulation.[7-9] In addition, we recently found that seed dormancy and germination processes are also controlled by MYB96.[10,11]

Seed germination requires lipid oxidation to fuel embryonic growth, but ABA suppresses lipid mobilization particularly in embryos and limits post-embryonic development.[12,13] MYB96 regulates ABA-dependent inhibition of lipid catabolism to determine timing for germination. In the presence of ABA, activation-tagged *myb96-ox* seeds exhibited delayed germination and higher accumulation of triacylglyceride (TAG), whereas *MYB96*-deficient *myb96-1* seeds were hyposensitive to ABA with greater lipid consumption.[11] Notably, MYB96 binds directly to the proximal promoter region of *ABI4*, which is a negative regulator of lipid mobilization during germination process.[14] MYB96 not only confers ABA sensitivity to embryos, but also participates in embryonic lipid mobilization to properly regulate seed germination, similar to the role of ABI4 in seed germination.[11,14] In support of this, genetic analysis revealed that the functions of MYB96 in seed germination and lipid catabolism largely depend on *ABI4*, supporting the epistasis of ABI4 to MYB96.[11]

The ABI4 protein is also implicated in seed dormancy through the metabolic coordination of GA and ABA, rather than lipid metabolism.[15] The *abi4-1* mutant shows shallow seed dormancy with elevated GA levels and reduced ABA contents.[15] Consistently, GA biosynthetic and ABA catabolic genes are up-regulated, while GA catabolic and ABA biosynthetic genes are down-regulated in *abi4* seeds.[15] This coordination is accomplished by direct binding of ABI4 primarily to gene promoters encoding ABA catabolic enzymes, such as CYP707A1 and CYP707A2.[15]

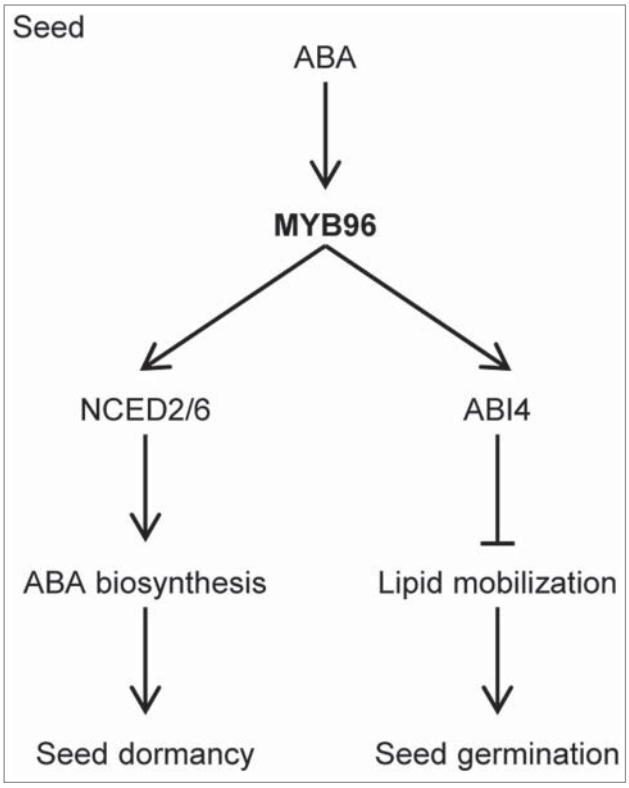

Figure 1. Proposed roles of MYB96 in seed dormancy and germination. The MYB96 transcription factor establishes primary seed dormancy by activating ABA biosynthesis. It is also involved in seed germination process. MYB96 directly binds to the *ABI4* promoter and activates its expression. Consistent with the inhibitory role of ABI4 in embryonic lipid mobilization, MYB96 suppresses lipid catabolism that fuels seed germination.

Since MYB96 is a transcription factor that directly regulates *ABI4*, we assumed that MYB96 also participates in regulating seed dormancy through the ABA catabolism. Without cold stratification, higher germination frequency was observed in *myb96-1* seeds, whereas *myb96-ox* seeds exhibited delayed germination relative to wild-type seeds. However, MYB96 regulation of seed dormancy was independent of *ABI4*.[10] Detailed analysis revealed that MYB96 binds directly to promoters of ABA biosynthetic genes, such as *NCED2* and *NCED6*. The positive feedback regulation of ABA biosynthesis by MYB96-mediated ABA signaling further bolsters ABA responses, especially primary seed dormancy, demonstrating the MYB96 regulation of ABI4-independent signaling in establishing seed dormancy.[10]

Taken together, MYB96 independently regulates both processes of seed dormancy and germination. On one hand, MYB96 confers primary seed dormancy by activating ABA biosynthesis. The *NCED* genes are its primary regulatory targets, and subsequent hormonal metabolic changes may accompany. On the other hand, MYB96 inhibits seed germination through suppression of embryonic lipid catabolism in an ABI4-dependent pathway (**Fig. 1**).

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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