



Mini Review

Common transcriptional regulation of ABA and ethylene

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Plant hormones are versatile chemical regulators of plant growth. The concept of hormone 'interaction' [1] has gained much importance and several key players of hormonal network are uncovered for major plant hormones. The fact that hormones are structurally unrelated and their interaction elicits different genomic and non-genomic responses suggest hormone interaction involve co-regulation at multiple levels [2]. Recent studies suggest that hormonal interaction involves control over biosynthesis genes [3-6], key components of signalling pathways [7,8], hormone distribution [9,10], and interaction at the level of gene expression [11-13]. The spatial and temporal changes in hormone sensitivity add further complexity as they are developmental stage-dependent [14]. Understanding how these mechanisms are integrated would allow us to manipulate hormone interaction-regulated growth response under environmental changes. One such prominent emerging hormone interaction is ethylene and abscisic acid (ABA) in several growth processes. In this short review, I discuss some of the common transcriptional regulators of ethylene and ABA.

ABA and ethylene interaction regulates a multitude of plant developmental processes (Table 1). Many developmental processes have been observed to be antagonistically

Table 1: Functional roles of ethylene and ABA in several developmental processes.

Trait	Ethylene	ABA	References
Seed dormancy	C ₂ H ₄ inhibits ABA-induced promotion of seed dormancy	ABA promotes seed dormancy	Arc et al. (2013)
Seed germination	C ₂ H ₄ promotes seed germination	ABA delays/inhibits seed germination by enhancing seed dormancy	Linkies et al. (2009); Zhu et al. (2009)
Seedling development	C ₂ H ₄ affects glucose signalling and promotes post-germination seedling development	ABA inhibits the promoted role of C ₂ H ₄ of seedling development	Leon & Sheen (2003)
Submergence-induced root epidermal cell death	C ₂ H ₄ induces programmed cell death of root epidermal cells	ABA inhibits the promoted role of C ₂ H ₄ of cell death	Steffens & Sauter (2005)
Glucose-induced repression of RBCS	C ₂ H ₄ inhibits ABA promotion of sugar-induced repression of RBCS and increases Rubisco levels	ABA promotes sugar-induced repression of RBCS and decreases Rubisco levels	Tholen et al. (2007); Acevedo-Hernandez et al. (2005)
Stress-induced stomatal closure	C ₂ H ₄ inhibits/limits ABA promotion of stomata close	ABA promotes stress-induced stomata close	Chen et al. (2013); She & Song (2012)
Petiole angle	C ₂ H ₄ positively regulates petiole angle	ABA negatively regulates petiole angle in both C ₂ H ₄ -independent and dependent ways	Polko et al. (2013); Benschop et al. (2007)
Root quiescence center (QC) cell division and differentiation	C ₂ H ₄ promotes QC cell division	ABA suppresses QC stem cell differentiation	Zhang et al. (2010); Ortega-Martinez et al. (2007)
Auxin transport in the root	C ₂ H ₄ induces both acropetal and basipetal auxin transport by activating PIN3, 7 and PIN1 & AUX1 expression, respectively	ABA induces basipetal mode of auxin transport by activating AUX1 & PIN2 expression	Xu et al. (2013); Lewis et al. (2011)
Lateral root (LR) emergence	C ₂ H ₄ promotes LR emergence	ABA inhibits LR emergence	Jung & McCouch (2013)

regulated by ABA and ethylene. Plants must therefore need to integrate information provided through ABA- and ethylene-signalling pathways that are largely achieved through transcription factors (TFs), which repress or activate suits of genes to modulate growth responses [15]. Several components identified in ABA and ethylene pathways may act as nodes to connect multiple pathways/signals of endogenous developmental and exogenous environmental signals. Recently, these molecular nodes appear to be commonly, often oppositely, regulated by several TFs [4,16-19]. Although a plethora of TFs are identified as targets of ABA and ethylene signalling [4,20-23], here, HD-Zip (homeodomain-leucine zipper), bZIP (basic leucine zipper) and AP2/ERFs (APETALA2/Ethylene Response Factor) that are recently shown to interfere with both ABA and ethylene signalling are discussed. These proteins play roles in regulating plant adaptation under changing environmental conditions [23-25] by binding to specific DNA sequences and HD-Zip's have the ability to form a large number of interacting complexes affecting hormone-related and developmental functions in vivo [25].

A class 1 HD-Zip TF of tomato, *LeHB1*, which plays an important role in floral organogenesis and ripening, can transcriptionally activate the expression of tomato *LeACO1*, a biosynthetic gene of ethylene [24]. *LeHB1* binds to *LeACO1* promoter sequence with dyad symmetry. Down-regulating *LeHB1* via virus-induced gene silencing significantly reduced *LeACO1* expression, suggesting *LeHB1* transcriptionally activate *LeACO1* and thus promote ethylene responses [24]. Any ABA interference in *LeHB1* overexpressing lines is unknown, however, a *Medicago truncatula* HD-Zip, *MtHB1*, acts as a positive regulator of ABA signalling in lateral root emergence [26]. When *MtHB1* was overexpressed in the roots, it suppressed LOB-binding domain 1 (LBD1) resulting in longer primary root while reduced lateral root (LR) emergence, which involved *MtHB1* repression of auxin-induced ABI3, a ABA-responsive TF, that is important for LR primordia [27] suggesting ABA sensitivity can override auxin response mediated by *MtHB1*. Interestingly, when ectopically overexpressed, *AtHB1* overrides the etiolation response of dark-grown *Arabidopsis* seedlings [28]. Considering the fact that *AtHB1* shares 69% and its HD-Zip domains share 92% similarity to *LeHB1* [24] and the triple response is typical to ethylene [29], it is possible that HB1 can act as a positive regulator of ABA response and a negative regulator of ethylene signalling. However, this needs to be experimentally tested.

Ethylene Response Factors of tomato and tobacco, *LeERF2* and *TERF2*, respectively, have shown to involve in the feedback loop of ethylene synthesis [30]. *ERF2* belongs to the family of AP2/ERF TFs carrying a single AP2 domain in which acidic N-terminal and/or C-terminal regions act as activation domains [21]. Both *LeERF2* and *TERF2* activate ethylene biosynthesis genes, *ACO* and *ACS*, by binding to GCC box and DRE/CRT cis-elements and participates in ethylene production. Interestingly, plants overexpressing *LeERF2/TERF2* germinated twice as high as that of wild types in the presence of ABA [30]. Similarly, ABA failed to decrease *ERF1* expression in an ethylene hypersensitive mutant *ctr1* [31]. These studies suggested that *ERF1* and *ERF2* act as negative regulators of ABA response. However, such negative response was decreased under high ABA levels and salt-induced *ERF1* expression was indeed significantly lower in ABA-hypersensitive *abi1* and *abi2* knockout mutants [31], suggesting the dominance of ethylene response over ABA sensitivity might be dependent on ABA levels. Low concentrations of endogenous ABA levels may not necessarily affect ERFs expression, however, under stress conditions, which induces higher ABA levels, ABA or its dominant mutational components might modify ERFs expression and antagonize ethylene responses [31]. Supporting evidence also comes from a dominant negative allele *ABI1*, which transcriptionally interact and activate a HD-Zip TF of *Arabidopsis* *AtHB6* that act as a negative regulator of ABA inhibition of stomata closure under drought stress [32,33], a reminiscent of ABA-insensitive mutants *abi1* and *abi2* [34].

These studies highlight the cross-talk between ABA and ethylene responses need further studies using a common experimental platform, where TF promoters carry

motifs necessary for binding of genes of both ABA and ethylene pathway. A *Helianthus annuus* HD-Zip, *HaHB4*, represent such an excellent resource, which carry two redundant root-specific ABA response elements (ABREs, one ABRE is ABA-responsive and the other is NaCl-responsive) and one W-box cis-acting element [16], and is strongly induced by water deficit and ABA [35]. Plants overexpressing *HaHB4* was shown to act as a negative regulator of ethylene signalling, while its role in ABA signalling was not reported. Nevertheless, these plants might serve as an excellent resource to study how TFs might regulate both ABA and ethylene signalling in a common experimental platform.

The differential regulation of ABA and ethylene responses is further shown by bZIP TFs. A bZIP factor, *HY5* (Long Hypocotyl5) was recently reported to act as a molecular link between ABA and ethylene signalling [4,36]. *HY5* was shown to form a part of crucial transcriptional cascade in ABA-modulated ethylene responses. ABA-induced *HY5* binds to the G-box of *AtERF11* to activate its transcription, which in turn binds to the DRE of, and repress, *ACS2* and *ACS5* genes, thus attenuating the ethylene biosynthesis [4], suggesting *HY5* act as a positive regulator of ABA response and a negative regulator of ethylene response. However, the mechanism how ABA-induced *HY5* activates *ERF11* is unknown; presumably it may occur through the histone modifications to *ERF11* [37]. Alternatively, given the fact that the ethylene biosynthesis gene (e.g. *ACS8*) contains cis-element for *HY5* binding [38], it is equally possible *HY5* could also directly transcriptionally regulate *ACS* gene expression. Taken together, numerous transcriptional factors appear to be acting as common regulators, but oppositely operating, potentially interfering with both ABA and ethylene signalling pathways.

In addition to TFs, amphipathic helix proteins, SNL1 and SNL2, were recently shown to form another cross-link point of ABA and ethylene signalling [37]. They belong to SWI-INDEPENDENT3 (SIN3)-LIKE protein family, which play roles in recruiting histone binding proteins resulting in a transcriptionally repressed state of the chromatin [39]. During Arabidopsis seed dormancy establishment, SNL1 and SNL2, through histone deacetylation, negatively regulates the ethylene pathway while positively regulates the ABA pathway, leading to an increase in seed dormancy. These two proteins regulate key components of ethylene (*ACO1*, *ACO4*, *ERF9* and *ERF112*) and ABA (*CYP707A1 & A2*, and *NCED4*) pathway by modifying their histone acetylation levels, thus promoting the seed dormancy [40]. Interestingly, only *NCED4* gene expression was down regulated in the double mutant *snl1 snl2* (low ABA levels) raising the question whether increased ABA levels would induce SNLs proteins that in turn could repress ethylene signalling is unknown, which deserves further studies.

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