Open Access

Journal of Plant Science and Phytopathology

Heighten Science PUBLICATIONS Corporation
ISSN
2575-0135

Mini Review

Common transcriptional regulation of ABA and ethylene

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Submitted: 21 December 2017
Approved: 02 January 2018
Published: 03 January 2018

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_2H_4 inhibits ABA-induced promotion of seed dormancy	ABA promotes seed dormancy	Arc et al. (2013)
Seed germination	C_2H_4 promotes seed germination	ABA delays/inhibits seed germination by enhancing seed dormancy	Linkies et al. (2009); Zhu et al. (2009)
Seedling development	C_2H_4 affects glucose signalling and promotes post-germination seedling development	ABA inhibits the promoted role of C_2H_4 of seedling development	Leon & Sheen (2003)
Submergence-induced root epidermal cell death	C_2H_4 induces programmed cell death of root epidermal cells	ABA inhibits the promoted role of C_2H_4 of cell death	Steffens & Sauter (2005)
Glucose-induced repression of RBCS	C_2H_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_2H_4 inhibits/limits ABA promotion of stomata close	ABA promotes stress-induced stomata close	Chen et al. (2013); She & Song (2012)
Petiole angle	C_2H_4 positively regulates petiole angle	ABA negatively regulates petiole angle in both C_2H_4-independent and dependent ways	Polko et al. (2013); Benschop et al. (2007)
Root quiescence center (QC) cell division and differentiation	C_2H_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_2H_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_2H_4 promotes LR emergence	ABA inhibits LR emergence	Jung & McCouch (2013)

How to cite this article: Valluru R. Common transcriptional regulation of ABA and ethylene. J Plant Sci Phytopathol. 2018; 2: 001-005. https://doi.org/10.29328/journal.jpsp.1001013

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.

Acknowledgements

The views expressed by the author were derived from the project that was financially supported by the Consultative Group on International Agricultural Research (CGIAR) Research Program (CRP-WHEAT, SI-6) through the CIMMYT.

References

1. Drury RE. Interaction of plant hormones. Science. 1969; 164: 564-565. **Ref.:** https://goo.gl/KdVwwT
2. Chang KN, Zhong S, Weirauch MT, Hon G, Pelizzola M, Li H, et al. Temporal transcriptional response to ethylene gas drives growth hormone cross-regulation in Arabidopsis. eLife. 2013. **Ref.:** https://goo.gl/3CD9vv
3. Arc E, Sechet J, Corbineau F, Rajjou L, Marion-Poll A. ABA crosstalk with ethylene and nitric oxide in seed dormancy and germination. Front Plant Sci. 2013; 4: 63. **Ref.:** https://goo.gl/uLFyL9
4. Li Z, Zhang L, Yu Y, Quan R, Zhang Z, et al. The ethylene response factor AtERF11 that is transcriptionally modulated by the bZIP transcription factor HY5 is a crucial repressor for ethylene biosynthesis in Arabidopsis. The Plant Journal. 2011; 68: 88-99. **Ref.:** https://goo.gl/sB4miV

5. Robles L, Stepanova A, Alonso J. Molecular Mechanisms of Ethylene-Auxin Interactions. Mol Plant. 2013; 6: 1734-1737. **Ref.:** https://goo.gl/Eq2d1y

6. Santner A, Calderon-Villalobos LI, Estelle M. Plant hormones are versatile chemical regulators of plant growth. Nat Chem Biol. 2009; 5: 301-307. **Ref.:** https://goo.gl/jnDspC

7. Muday GK, Rahman A, Binder BM. Auxin and ethylene: collaborators or competitors? Trends in Plant Science. 2012; 17: 181-195. **Ref.:** https://goo.gl/rHRKXc

8. Weiss D, Ori N. Mechanisms of Cross Talk between Gibberellin and Other Hormones. Plant Physiol. 2007; 144: 1240-1246. **Ref.:** https://goo.gl/NyyMW7

9. Lewis DR, Negi S, Sukumar P, Muday GK. Ethylene inhibits lateral root development, increases IAA transport and expression of PIN3 and PIN7 auxin efflux carriers. Development. 2011; 138: 3485-3495. **Ref.:** https://goo.gl/FMdvmL

10. Xu W, Jia L, Shi W, Liang J, Zhou F, et al. Abscisic acid accumulation modulates auxin transport in the root tip to enhance proton secretion for maintaining root growth under moderate water stress. New Phytologist. 2013; 197: 139-150. **Ref.:** https://goo.gl/TFmDCC

11. Goda H, Sawa S, Asami T, Fujioka S, Shimada Y, et al. Comprehensive Comparison of Auxin-Regulated and Brassinosteroid-Regulated Genes in Arabidopsis. Plant Physiol. 2004; 134: 1555-1573. **Ref.:** https://goo.gl/Mfcysd

12. Nemhauser JL, Mockler TC, Chory J. Interdependency of Brassinosteroid and Auxin Signaling in Arabidopsis. PLoS Biol. 2004; 2: 258. **Ref.:** https://goo.gl/nnrF8H

13. Stepanova AN, Yun J, Likhacheva AV, Alonso JM. Multilevel Interactions between Ethylene and Auxin in Arabidopsis Roots. Plant Cell. 2007; 19: 2169-2185. **Ref.:** https://goo.gl/QnR1NJ

14. Chow B, McCourt P. Hormone signalling from a developmental context. J Exp Bot. 2004; 55: 247-251. **Ref.:** https://goo.gl/vrqbyw

15. Nakashima K, Ito Y, Yamaguchi-Shinozaki K. Transcriptional Regulatory Networks in Response to Abiotic Stresses in Arabidopsis and Grasses. Plant Physiol. 2009; 149: 88-95. **Ref.:** https://goo.gl/fu1dRm

16. Manavella PA, Dezar CA, Ariel FD, Chan RL. Two ABREs, two redundant root-specific and one W-box cis-acting elements are functional in the sunflower HAHB4 promoter. Plant Physiology and Biochemistry. 2008; 46: 860-867. **Ref.:** https://goo.gl/Mrb1qn

17. Manavella PA, Dezar CA, Bonaventure G, Baldwin IT, Chan RL. HAHB4, a sunflower HD-Zip protein, integrates signals from the jasmonic acid and ethylene pathways during wounding and biotic stress responses. The Plant Journal. 2008; 56: 376-388. **Ref.:** https://goo.gl/eTK2ba

18. Manavella PA, Dezar CA, Ariel FD, Drincovich MF, Chan RL. The sunflower HD-Zip transcription factor HAHB4 is up-regulated in darkness, reducing the transcription of photosynthesis-related genes. J Exp Bot. 2008; 59: 3143-3155. **Ref.:** https://goo.gl/rKLAzF

19. Manavella PA, Arce AL, Dezar CA, Bitton F, Renou JP, et al. Cross-talk between ethylene and drought signalling pathways is mediated by the sunflower Hahb-4 transcription factor. The Plant Journal. 2006; 48: 125-137. **Ref.:** https://goo.gl/xBsdPb

20. Finkelstein RR, Gampala SS, Rock CD. Abscisic Acid Signaling in Seeds and Seedlings. Plant Cell. 2002; 14: 15-45. **Ref.:** https://goo.gl/XxzDex

21. Licausi F, Ohme-Takagi M, Perata P. APETALA2/Ethylene Responsive Factor (AP2/ERF) transcription factors: mediators of stress responses and developmental programs. New Phytologist. 2013; 199: 639-649. **Ref.:** https://goo.gl/V6uPK4

22. Lingam S, Mohrbacher J, Brumbarova T, Potuschak T, Fink-Straube C, et al. Interaction between the bHLH Transcription Factor FIT and ETHYLENE INSENSITIVE3/ETHYLENE INSENSITIVE3-LIKE1 Reveals Molecular Linkage between the Regulation of Iron Acquisition and Ethylene Signaling in Arabidopsis. Plant Cell. 2011; 23: 1815-1829. **Ref.:** https://goo.gl/uRgffJ

23. Harris JC, Hrmova M, Lopato S, Langridge P. Modulation of plant growth by HD-Zip class I and II transcription factors in response to environmental stimuli. New Phytologist. 2011; 190: 823-837. **Ref.:** https://goo.gl/xQuFB7

24. Lin Z, Hong Y, Yin M, Li C, Zhang K, et al. A tomato HD-Zip homeobox protein, LeHB-1, plays an important role in floral organogenesis and ripening. The Plant Journal. 2008; 55: 301-310. **Ref.:** https://goo.gl/6h7tJX

25. Lin Z, Zhong S, Grierson D. Recent advances in ethylene research. J Exp Bot. 2009; 60: 3311-3336. **Ref.:** https://goo.gl/gXGmJB

26. Ariel F, Diet A, Verdenaud M, Gruber V, Frugier F, et al. Environmental Regulation of Lateral Root Emergence in Medicago truncatula requires the HD-Zip I Transcription Factor HB1. Plant Cell. 2010; 22: 2171-2183. **Ref.:** https://goo.gl/aXpRg8

27. Brady SM, Sarkar SF, Bonetta D, McCourt P. The ABSCISIC ACID INSENSITIVE 3 (ABI3) gene is modulated by farnesylation and is involved in auxin signaling and lateral root development in Arabidopsis. The Plant Journal. 2003; 34: 67-75. **Ref.:** https://goo.gl/yzDkgd

28. Aoyama T, Dong CH, Wu Y, Carabelli M, Sessa G, et al. Ectopic Expression of the Arabidopsis Transcriptional Activator Athb-1 Alters Leaf Cell Fate in Tobacco. The Plant Cell. 1995; 7: 1773-1785. **Ref.:** https://goo.gl/kNj6iP

29. Guzmán P, Ecker JR. Exploiting the triple response of Arabidopsis to identify ethylene-related mutants. Plant Cell. 1990; 2: 513-523. **Ref.:** https://goo.gl/s3mWZc

30. Zhang Z, Zhang H, Quan R, Wang XC, Huang R. Transcriptional Regulation of the Ethylene Response Factor LeERF2 in the Expression of Ethylene Biosynthesis Genes Controls Ethylene Production in Tomato and Tobacco. Plant Physiol. 2009; 150: 365-377. **Ref.:** https://goo.gl/iZA5UK

31. Cheng MC, Liao PM, Kuo WW, Lin TP. The Arabidopsis ETHYLENE RESPONSE FACTOR1 Regulates Abiotic Stress-Responsive Gene Expression by Binding to Different cis-Acting Elements in Response to Different Stress Signals. Plant Physiology. 2013; 162: 1566 -1582. **Ref.:** https://goo.gl/sfDpP4

32. Himmelbach A, Hoffmann T, Leube M, Höhener B, Grill E. Homeodomain protein ATHB6 is a target of the protein phosphatase ABI1 and regulates hormone responses in Arabidopsis. EMBO J. 2002; 21: 3029-3038. **Ref.:** https://goo.gl/vGFsSq

33. Deng X, Phillips J, Bräutigam A, Engström P, Johannesson H, et al. A Homeodomain Leucine Zipper Gene from Craterostigma plantagineum Regulates Abscisic Acid Responsive Gene Expression and Physiological Responses. Plant Mol Biol. 2006; 61: 469-489. **Ref.:** https://goo.gl/RaQCUH

34. Leung J, Merlot S, Giraudat J. The Arabidopsis ABSCISIC ACID-INSENSITIVE2 (ABI2) and ABI1 Genes Encode Homologous Protein Phosphatases 2C Involved in Abscisic Acid Signal Transduction. The Plant Cell. 1997; 9: 759-771. **Ref.:** https://goo.gl/YjTtXG

35. Gago GM, C Almoguera, J Jordano, DH Gonzalez, RL Chan. Hahb-4, a homeobox-leucine zipper gene potentially involved in abscisic acid-dependent responses to water stress in sunflower*. Plant Cell & Environment. 2002; 25: 633-640. **Ref.:** https://goo.gl/NT8QYy

36. Li Z and Huang R. The reciprocal regulation of abscisic acid and ethylene biosyntheses. Plant Signal Behav. 2011; 6: 1647-1650. **Ref.:** https://goo.gl/Wiopz3

37. Wang Z, Cao H, Sun Y, Li X, Chen F, et al. Arabidopsis Paired Amphipathic Helix Proteins SNL1 and SNL2 Redundantly Regulate Primary Seed Dormancy via Abscisic Acid–Ethylene Antagonism Mediated by Histone Deacetylation. Plant Cell. 2013; 25: 149-166. **Ref.:** https://goo.gl/6G9XbW

38. Lee J, He K, Stolc V, Lee H, Figueroa P, et al. Analysis of Transcription Factor HY5 Genomic Binding Sites Revealed Its Hierarchical Role in Light Regulation of Development. Plant Cell. 2007; 19: 731-749. **Ref.:** https://goo.gl/3X9ur1

39. Grzenda A, Lomberk G, Zhang JS, Urrutia R. Sin3: Master scaffold and transcriptional corepressor. Biochimica Biophysica Acta. 2009; 1789: 443-450. **Ref.:** https://goo.gl/C84fzu

40. Kucera B, Marc Alan Cohn and Gerhard Leubner-Metzger. Plant hormone interactions during seed dormancy release and germination. Seed Science Research. 2005; 15: 281-307. **Ref.:** https://goo.gl/RjbqbS