

The reciprocal regulation of abscisic acid and ethylene biosyntheses

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Ethylene and abscisic acid (ABA) have compact effects on plant development and stress responses. It is not well understood about the mechanism of ABA modulation in ethylene biosynthesis. In our recent research, HY5-AtERF11 regulon was evidenced to connect the ABA action and ethylene biosynthesis. In this paper, by analyzing the expression of ABA biosynthesis genes and the ABA concentration in ethylene over-production mutants, we demonstrated that ethylene production affected by HY5-AtERF11 regulon targeted gene increased the expression of ABA biosynthesis genes and its contents. In addition, we discussed that HY5 might function as a convergence point of multiple hormones in response to light.

Introduction

Abscisic acid (ABA) plays an important role in seed maturation and dormancy, stomatal closure and adaptation to environmental stress. In addition, ethylene is another stress-induced hormone with fundamental roles in germination, sex determination, leaf abscission, flower senescence, fruit ripening and responses to biotic and abiotic stress,¹ showing that a subset of the functions of ethylene overlaps with those of ABA. Thus the interaction of the ethylene and ABA pathways has been found to be crucial in regulating the development of plants and their responses to environmental stresses.²⁻⁴ Genetic studies on the components of ethylene and ABA pathways have suggested the antagonistic interaction between the two signaling pathways.^{2,3,5} For example, *etr1*, *ein2*, *ein3*, the mutants of ethylene signaling and *aba1*, *aba2*, *abi1*, *abi2*, the mutants of ABA pathway, have been found to regulate antagonistically the expression of defense and stress-responsive genes and subsequently to modulate plant biotic and abiotic stress responses.^{2,3,5,6} Furthermore, growing evidence indicates the antagonistic interaction between the ethylene and ABA pathways in regulating ethylene and ABA production. Arabidopsis ethylene insensitive mutants *ein2/era3* and *etr1* are shown to contain higher level of endogenous ABA, while the ABA deficient mutant *aba2* displays an increase of ethylene production.^{5,7,8} Despite the existence of antagonistic interactions, increasing evidence also strongly suggests a synergistic interaction between the ethylene and ABA pathways in regulating plant development and defense responses. For instance, both ethylene and ABA can inhibit root growth, mutants *ein2* and *etr1* show enhanced resistance to ethylene and ABA, while root growth in the ABA-deficient mutant *abi1* only displays resistance to ABA but not ethylene,^{2,5,9} indicating that ABA-inhibited root growth depends on the ethylene signaling. Hence, the ABA and

ethylene signaling pathways have a close interplay in plant growth, development and stress response. However, it remains unknown whether their respective biosyntheses have any convergent points. In this report we will briefly present an overview on the current knowledge about ABA regulation in ethylene biosynthesis.

ABA Initiates a Transcriptional Cascade of HY5-AtERF11 to Repress Ethylene Biosynthesis

ABA, auxins, cytokinins, ethylene, gibberellins, brassinosteroids, jasmonates and salicylic acid are essential for the regulation of plant growth, development, reproduction and survival. The complex network of cross-communication of hormone signaling pathways controls plant growth, development and defense, and changes in hormone concentration or sensitivity, which can be triggered under biotic and abiotic stress conditions, mediate a whole range of adaptive plant responses.^{10,11} The relationship of ABA and ethylene was extensively discussed in the past years.^{2,3,5,12} Though ABA affects the ethylene production in etiolated seedlings, the roots of the *eto1-1* mutants were highly insensitive to ABA,^{5,13} the mechanism of ABA-modulated ethylene biosynthesis is much less clear. In a recent study, we reported a crucial transcriptional cascade in ABA-modulated ethylene biosynthesis. Our work demonstrated that HY5 binds to the G-box of *AtERF11* to activate its transcription; AtERF11 as an EAR repressor in turn binds to the DRE of ACS genes to repress their transcription, thereby causing a reduction in ethylene emission.¹⁴ Our work evidenced that (1) HY5-AtERF11 as one of crucial transcriptional cascades under ABA action controls ethylene biosynthesis, providing new insight into the integration of ABA and ethylene biosynthesis; (2) the light signaling regulator, HY5 is involved in ethylene biosynthesis, raising interesting questions on the interaction of light signaling and ethylene

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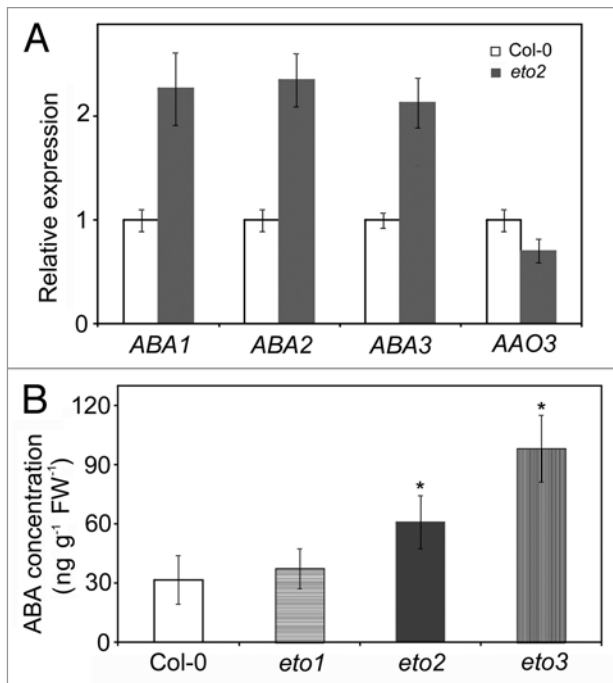


Figure 1. Ethylene overproduction elevates endogenous ABA levels. (A) Transcript levels of ABA biosynthesis genes in Col-0 and *eto2*. Seedlings were grown on MS plates for 4 d under normal growth conditions. After RNA isolation and reverse transcription, Real time PCR analyses were performed. Expression levels were normalized to that of *TUB4*. Each value is the mean \pm SD of three independent biological determinations. (B) ABA content of Col-0 and *eto1*, *eto2* and *eto3*. Seedlings were grown on MS plates for 4 d then subjected to ABA immunoassay. ABA content was measured by the method described by Wu et al.⁴⁷ Each value is the mean \pm SD of three independent biological determinations. The p-value (*eto* mutants vs. Col-0) was determined by a two-tailed Student's t-test assuming equal variances (* $p < 0.05$).

biosynthesis; (3) post-transcriptional regulation of ACS proteins in ethylene biosynthesis process was pivotal for ethylene production, more than one reports showed that transcriptional regulation also played a key role in ethylene biosynthesis, our work evidenced that AtERF11 directly binds to the promoter to negatively regulate the expression of ACS genes, revealing the role of EAR motif containing ERF genes in Arabidopsis ethylene biosynthesis.¹⁴

The Dynamic Balance of ABA and Ethylene is Required for Arabidopsis Development

It is reported that ACS genes have a distinct spatial and temporal expression pattern in different stages of Arabidopsis growth and development, and under various stresses.^{15,16} Most recent study revealed that the mutation of *ACS7* that displayed increased expression of ABA biosynthesis genes and accumulation, enhanced ABA sensitivity.¹⁷ Oppositely, the knockout mutant *acs4-1*, which displayed 40% increase of ethylene,¹⁵ enhanced ABA tolerance in root growth as *eto* mutants in the early seedling stage (data not shown). These differential observations reveal that different expression pattern of each ACS gene in the different developmental stages and organs leads to diverse responses to

ABA, which decides the character of ACS genes in the interaction of ABA with ethylene. However, the deficiency of ethylene mutant *heptuple* results in more tolerant response to ABA in root and shoot growth,¹⁵ indicating a more complex interaction of ethylene and ABA in the regulation of the expression of ACS genes.

Accumulating evidence indicates that the interaction of ABA and ethylene signaling pathways extensively regulates plant growth, development and stress responses, less research was reported in the relationship of ethylene biosynthesis and ABA biosynthesis/metabolic. After checking the microarray data of *eto2* (data not shown), we found that transcript levels of ABA biosynthesis genes (*ABA1*, *ABA2* and *ABA3*, except *AAO3*) in the *eto2* were obviously increased (Fig. 1A). Moreover, the endogenous ABA levels were significantly elevated in the mutation mutants of *ACS5* (*eto2*) and *ACS9* (*eto3*) genes, compared with these in Col. But there were no significantly different ABA contents in Col and an E3 ligase mutation mutant (*eto1*) (Fig. 1B), indicating that the ethylene biosynthesis, triggered at least by HY5-AtERF11 regulon targeted gene,¹⁴ stimulates ABA biosynthesis for balance the hormone through the regulation of specific ABA biosynthesis genes.

Although ethylene plays key roles in seed germination, seedling growth, flowering and seed mature, the increased ethylene also inhibits the growth and development.^{12,18} Additionally, high level of ABA was regarded as a growth inhibitor;⁹ and both ethylene and high level of ABA inhibit the root length, low level ABA, however, promotes root growth by promoting quiescent center quiescence,^{18,19} indicating that the inhibition of root length is the balance of ABA and ethylene hormones. Both endogenous developmental and exogenous environmental signals increased one kind of the hormones, others would be responded. Moreover, the increase of endogenous ABA levels in *eto* mutants might be act as a compensation for high level of ethylene in vivo and endogenous ethylene changes and exogenous ABA stimulation would cause the dynamic balance of the two hormones in plant.

HY5 Participates in Multiple Hormone Biosyntheses and Signaling Pathways

HY5 plays positive regulatory role in photomorphogenesis by controlling the expression of multiple genes including light-responsive and hormone biosynthesis genes.²⁰⁻²³ Also, the phenotype of *hy5* showing longer hypocotyl and lateral roots supports that hormone related genes might be involved in HY5 regulatory network,^{22,24} suggesting that HY5 is an important crosstalk point of gibberellins, cytokinin, auxin and ABA in Arabidopsis development and stress response.^{20,24-30} For instance, defection of gibberellin metabolism or signaling partially repressed photomorphogenesis, which is attributed to the fact that gibberellins reduced the abundance of HY5 via COP1-mediated pathway.^{25,29,30} In addition, the interaction of LIP1 and LONG1, the pea ortholog of *Arabidopsis thaliana* COP1 and HY5, respectively, regulated the expression of gibberellin catabolism gene *GA2ox2* and gibberellin levels.²⁶ Distinctive to gibberellins, cytokinin induced HY5 protein accumulation likely mediating COP1 under light conditions.²⁷ And HY5 and its homolog HYH (HY5 HOMOLOG) negatively regulate AUXIN RESISTANT2 (AXR2) and SOLITARY ROOT (SLR) genes,

possibly directly targeting the potential AUX/IAAs and AUXIN RESPONSE FACTOR genes in auxin signaling.^{24,28} And the fact that HY5 directly transcriptionally regulated the expression of ABA responsive *ABI5* reveals that the HY5 integrates ABA and light signal transduction pathways.²⁰ More importantly, we found that HY5 was a novel negative regulator of ethylene biosynthesis, and this regulation was through ABA-dependent activation of *AtERF11* expression, evidencing that HY5 was a key factor in the regulation of ethylene synthesis. However, differences were observed between *eto1*, *eto2* and *eto3* in terms of the growth phenotypes and ABA responsiveness, and the observation of ACS different expression pattern in *hy5* suggests that HY5-regulated ethylene biosynthesis may be occurred in numerous pathways. Actually, a genome survey of the *in vivo* targets of HY5 using chromatin-immunoprecipitation identified the potential ethylene biosynthesis and ERF genes,³¹ which probably occurred in three pathways: (1) HY5 directly transcriptionally regulates the expression of ACS genes; (2) ERF proteins, such as *AtERF4*, *AtERF7*, *Sub1A* and *LeERF2/TERF2* downstream of ethylene signaling pathway, regulate ethylene biosynthesis,³²⁻³⁸ but the possibility that HY5 transcriptionally activates the expression of other ERF genes that mediate the ABA response remains to be effectively approved; (3) HY5 is a key factor in normal development under light conditions to integrate hormone balance, other regulators conceivable transcriptionally regulated by HY5 might participate in ethylene biosynthesis. Further investigation of HY5 regulation in the expression of ACS genes would be important for revealing the mechanism of integration in ethylene biosynthesis and light signaling pathway.

Perspective

Considering that both light and ethylene stimulate seed germination in normal or stress conditions, it is of great importance

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to note the components involved in the two signaling pathways. For example, light promotes ethylene biosynthesis through the action of PIF5 (PHYTOCHROME INTERACTING FACTOR 5);³⁹ and our recent report also evidenced that HY5 regulates this process.¹⁴ The low extend of red to far-red light ratio regulated the emission of ethylene,⁴⁰ indicating that light modulates ethylene biosynthesis. More than that, ethylene and light are critical regulators of plant responses to salt stress. In *Arabidopsis*, STO interacted with COP1 to enhance root growth in high salinity stress;^{41,42} in rice, overexpression of *OsHAL3* increased seedling growth under normal light/dark cycles and enhanced salt tolerance and Na⁺/K⁺ homeostasis.⁴³ These studies, combined with the regulation of ethylene in salt response,⁴⁴ indicate that ethylene and components of the light signaling pathway are key regulators of salt stress. Furthermore, the EIN2 interacted with a putative COP9 signalosome (CSN) component EER5 (Ethylene Enhanced Response 5),⁴⁵ implying a role of EIN2 in the regulation of SCF activity through the modulation of the CSN. In addition, the evidence that EIN3/EIL1 downstream of COP1 activates the ethylene-induced seedling greening reveals that compounds of ethylene signal pathway participate in photomorphogenic development,⁴⁶ implying a complex mode of interactions between ethylene and light signaling pathways in *Arabidopsis*. Further investigations that excavate the cross-talk of the two signal pathways would be significantly important.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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