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Mini Review

Current Understanding on the Roles of Ethylene in Plant Responses to Phosphate Deficiency

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Abstract

Phosphorus (P) is a macronutrient essential for plant growth and development. However, the solubility of inorganic phosphate (Pi), the available form for plant uptake, in soils is low. Plants have evolved various adaptive mechanisms to cope with Pi deficiency stress. Change of root system architecture (RSA) is a well-known adaption in response to Pi deficiency for exploration of available Pi at top soil layers. Although aux in has long been considered to be the key player controlling RSA under Pi deficiency, increasing evidences indicate ethylene also plays an important role in regulating these processes. In addition to RSA, it has been reported in recent years that ethylene is involved in the regulation of other Pi starvation responses (PSRs) including Pi transporter gene expression, acid phosphatase activity and anthocyan in accumulation. It reveals that ethylene may regulate a complex network for plant adaptive responses to Pi deficiency. Here, we review the current knowledge on the involvement of ethylene in plant PSRs.

ABBREVIATIONS

ACC: 1-Aminocyclopropane-1-Carboxylate; ACO: ACC Oxidase; ACS: ACC Synthase; AP2/ERF: APETALA2/Ethylene Responsive Factor; ATP: Adenosine Triphosphate; AVG: Aminoethoxy Vinyl Glycine; CTR1: CONSTITUTIVETRIPLERESPONSE1; EBF: EIN3-BINDINGF-BOX; EIL1: EIN3-LIKE1; EIN: ETHYLENE INSENSITIVE; ER: Endoplasmic Reticulum; ERS: ETHYLENERESPONSESENSOR; ETR: ETHYLENERESPONSE; hps: Hypersensitive to Phosphate Starvation; lpi: Low Phosphorus Insensitive; MCP: Methyl Cyclopro Pene; P: Phosphorus; PHL1: PHR1-LIKE1; PHR1: PHOSPHATE STARVATION RESPONSE1; PI: Inorganic Phosphate; PSR: Phosphate Starvation Response; RSA: Root System Architecture; RSL4: (ROOT HAIR DEFECTIVE 6 [RHD6]-LIKE4); SAM: S-adenosyl Methionine

INTRODUCTION

Phosphorus (P) is a fundamental component of major biomolecules including adenosine triphosphate (ATP), nucleic acids (DNA and RNA) and membrane phospholipids [1,2]. In addition, P is involved in various important metabolic reactions in plant, such as photosynthesis, glycolysis, respiration and enzyme activation/inactivation [3]. Inorganic phosphate (Pi) is the primary form of P taken up by plant root system [4,5]. However, its availability and mobility is low in soils due to slow diffusion in rhizospheres and formation of insoluble/immobile organic Pi or inorganic complex with cations. Under acid conditions, Pi easily reacts with aluminum and iron but it forms insoluble complex with calcium under alkaline conditions [1,5-6]. The available concentration of Pi in soil is often less than 10 μM [1]. Therefore, shortage of soluble Pi is one of the most important factors limiting plant growth and development [7]. To cope with Pi deficiency, plants have evolved an array of adaptive responses to increase Pi uptake/recycling and reduce Pi usage, such as inhibition of primary root growth, promotion of lateral root and root hair formation, upregulation of Pi transporter genes,

induction/secretion of acid phosphatase, ribonucleases and organic acids, replacement of membrane phospholipids by glycol lipids or sulfo lipids and enhancement of Pi remobilization [1,7-8]. Ethylene is a simple gaseous hormone involved in multiple aspects of plant growth and developmental processes including seed germination, root and shoot growths, fruit ripening, organ abscission and senescence. In addition, it also plays an important role in regulating plant responses to diverse environmental stresses [8-9]. Although ethylene have long been investigated in the regulation of developmental and stress responses in plants, its role in plant adaptions to nutrient deficiencies were mainly documented within these two decades [9-10]. The interactions between ethylene and macronutrients or micronutrients are still not clear; however, the current evidences indicate that several mineral nutrients significantly affect ethylene biosynthesis and perception [9]. Under nutrient starvation, the increased endogenous ethylene production may activate an array of genes to keep cellular homeostasis or induce nutrient transporter gene expression to acquire nutrients. In addition, ethylene may directly or through interaction with auxin to enhance root hair and adventitious root formation to increase nutrient uptake [9,11-12].

By application of ethylene precursors and antagonists or by analysis of different genotypes, mutants and transgenic plants with alterations of ethylene synthesis, signaling and perception, the role of ethylene in response to Pi starvation in plants has been investigated [8,9,13-14]. It is known that both ethylene synthesis and responsiveness are enhanced in plant roots under Pi deficiency. Remodeling of RSA (root system architecture) was demonstrated to be regulated by ethylene. Similar modifications in RSA can be observed when ethylene precursors are applied to Pi-sufficient medium. In contrast, treatment of ethylene inhibitors impedes these RSA changes [8,15-17]. Increasing evidences suggest that ethylene not only regulates RSA but also modulates other Pi starvation responses (PSRs), such as Pi transporter gene expression, activation of acid phosphatases and accumulation of anthocyanin [8,18,19]. In this mini-review, wesummarizedthe current understanding of the role of ethylene in PSRs in plants.

Pi deficiency activate ethylene biosynthesis and signaling pathway

Ethylene is biosynthesized from methionine through a three-step reaction. After conversion of methionine to S-adenosylmethionine (SAM) by SAM synthetase, in turn, 1-aminocyclopropane-1-carboxylatesynthase (ACCsynthase) and ACC oxidasecatalyze the synthesis of ACC and ethylene, respectively [20]. Ethylene responses are initiated by signal perception through a family of endoplasmicreticulum(ER) membrane-localized receptors. In Arabidopsis genome, there are five genes, *ETR1*, *ETR2*, *ERS1*, *ERS2* and *EIN4*, mediating ethylene perception and acting as negative regulators of ethylene responses. When binding to ethylene, the receptors are inactivated and the interaction between the receptors andCTR1, a Raf-like kinase, is disrupted. Subsequently, it leads to an activation of EIN2, a positive regulator of ethylene responses downstream of CTR1, and accumulation of EIN3 (ETHYLENE INSENSITIVE3) andEIL1 (EIN3-LIKE1) transcription factors. EIN3 and EIL1 regulate their target transcription factors, such as ERF1 (ETHYLENERESPONSEFACTOR1), and then initiate a transcriptional activation of various ethylene-responsive genes [21-23].

It is known that Pi deficiency enhance ethylene biosynthesis in plants although some reports show different conclusions, such as the researches done in maize and tomato [14,24]. The involvement of ethylene biosynthesis in root responses of common bean (*Phaseolus vulgaris*) to Pi deficiency was investigated by using amino ethoxyvinyl glycine (AVG), an inhibitor of ethylene biosynthesis. The increase of root-to-shoot ratio induced by Pi deficiency was repressed by AVG treatment but partially restored by exogenous application of ethylene. The enhancement of endogenous ethylene production was further demonstrated in Pi-deficient roots comparing to Pi-sufficient roots [25]. An increase in ethylene production was also detected in proteoid root development of white lupin (*Lupinusalbus*) under Pi deficiency [26]. In legume plants of *Medicagofalcata* L, ethylene production was enhanced when the seedlings were transferred from Pi-sufficient to Pi-deficient condition. This Pi deficiency-induced ethylene production could be blocked by the antagonists of ethylene biosynthesis, $CoCl_2$ and AVG [27]. A possible link between Pi deficiency and ethylene production was also found in the model plant, *Arabidopsis thaliana*, through expression analysis of ethylene biosynthetic genes in that the transcript levels of *ACC synthase* 2 (*ACS2*), *ACS4* and *ACS6* were increased under Pi deficient condition [28]. In addition, the expression of the genes encoding ACC synthases (*ACS6* and *ACS9*) and ACC oxidases (*ACO1*, *ACO2* and *ACO4*) was enhanced in an Arabidopsis mutant, *hps7* (*hypersensitive to Pi starvation7*) [29]. Other supporting evidences are from transcript to mic studies in different plant species that Pi deficiency up regulated several genes involved in the ethylene biosynthetic pathway [30-33]. More recently, ethylene production induced by low Pi was examined in a japonica rice variety, Nippon bare, and an indica variety, Kasalath. Interestingly, Nippon bare, with higher Pi utilization efficiency, showed a greater level of ethylene in roots comparing to the less efficient variety, Kasalath [34]. Al together, these results indicate ethylene biosynthesis plays some roles in plant responses to Pi deficiency. However, it should be noted that up regulation of ethylene biosynthetic genes under Pi starvation seems to be very tissue- or stage-dependent [19]. It may explain the inconsistent findings among researches examined in different species, tissues or stages.

In addition to ethylene biosynthesis, alteration of ethylene sensitivity is also induced by Pi deficiency and in turn involved in the regulation of PSRs. The genes related to ethylene perception, signal transduction and responsiveness have been reported to be regulated under Pi deficiency or the mutation of these genes causes phenotypes in response to Pi deficiency. EIN3-BINDING F-BOX (EBF2) is involved in degradation ofEIN3and EIL1which regulate downstream ERF transcription factors subsequently leading to activation of ethylene-responsive genes. *EBF2* has been shown to be induced in Arabidopsis roots and shoots under Pi deficiency [18]. Transcrip to mic analysis of differentially expressed genes in the *lpi4* (*low phosphorus insensitive4*) mutant

Table 1: Overview of Arabidopsis mutants related to phosphate deficiency-induced ethylene biosynthesis and signaling.

Arabidopsis gene identifier (AGI)	Mutant/transgenic plant	Function or phenotype	References
AT5G03730	*hps2* (*ctr1*)	CTR1 interacts with ETR1 and ERS and acts as a negative regulator in the ethylene signaling pathway; Inhibition of primary root growth; Enhancement of root hair formation; Increase of PSI gene expression (*AtPT1*, *ACP5*, *AT4*, *IPS1*, *RNS1*) and Apaseactivity; Reduction of anthocyanin accumulation.	28
AT3G51770	*hps3* (*eto1*)	Mutated in *ETO1* (*ETHYLENE OVERPRODUCTION 1*); Overproduction of root surface-associated Apases; Inhibition of primary root growth; Enhancement of root hair formation; Increase of PSI gene expression (*AtPT1*, *ACP5*, *RNS1*, *PAP10*); Reduction of anthocyanin accumulation.	38
AT1G58250	*hps4* (*SABRE*)	Antagonistically interacts with ethylene signaling; Enhancement of root surface-associated Apases; Inhibition of primary root growth; Earlier lateral root formation; Increase of PSI gene expression (*PHT1;1*, *PHT1;4*, *ACP5*, *RNS1*, *PAP10*, *AT4*, *IPS1*); Reduction of anthocyanin accumulation; Induction of auxin-responsive and biosynthetic genes and IAA accumulation in the root tips.	39
AT2G40940	*hps5* (*ERS1*)	Constitutive ethylene response; High expression of EIN3 protein; Inhibition of primary root growth; Enhancement of root hair formation; Increase of PSI gene expression (*ACP5*, *RNS1*, *PAP10*, *AT4*, *IPS1*); Reduction of anthocyanin accumulation; Induction of RHS (Root Hair-Specific) genes.	40
AT1G08030	*hps7* (*TPST*)	Encodes a tyrosylprotein sulfotransferase; Inhibition of primary root growth; Earlier lateral root formation; Enhancement ofApaseactivity; Increase of ethylene biosynthetic gene expression.	29
AT5G09860	*hps8* (*AtTHO1*)	Enhancement ofApaseactivity and root hair formation; Induction of *miR399a*, *miR399b* and *miR399f*; Ethylene perception inhibitor, Ag^{+}, eliminates the induced activity of Apase in the mutant.	41
AT1G66340	*etr1-1*	A gain-of-function mutant with ethylene insensitivity. Reduction of *AtPT2* gene expression.	28
	eto1-1	An ethylene over-producing mutant. Increase of *AtPT2* gene expression.	28
AT5G03280	*ein2-5*	*EIN2*, downstream of *CTR1*, is involved in ethylene signal transduction. Decrease of PSI gene expression (*AtPT1*, *ACP5*, *AT4*, *IPS1*, *RNS1*); Enhancement of anthocyanin accumulation.	28
AT1G71130	*ERF070RNAi*	Enhancement of primary and lateral root growth and root hair formation; Increase of shoot and root Pi content.	36
	lpi4	Defective in the low-Pi responses; Long primary roots and few lateral roots under Pi deficiency; Downregulation of *ERF2* and *ERF5* in the *lpi4* mutant.	32

Abbreviations: Apase: Acid Phosphatase; AtPT1: ARABIDOPSIS THALIANA PHOSPHATE TRANSPORTER 1; CTR1: CONSTITUTIVE TRIPLE RESPONSE 1; EIN3: ETHYLENE INSENSITIVE 3; ERS: ETHYLENERESPONSESENSOR; ETO1: ETHYLENEOVERPRODUCTION1; ETR1: ETHYLENERESPONSE1; HPS: Hypersensitive To Phosphate Starvation; IPS1: INDUCED BY PHOSPHATE STARVATION1; lpi: Low Phosphorus Insensitive; PAP10: PURPLEACIDPHOSPHATASE10; PHT1;1: PHOSPHATE TRANSPORTER 1;1; PSI: Phosphate Starvation Induced; RHS: RootHair-Specific; RNS1: RIBONUCLEASE 1; TPST: TYROSYLPROTEIN SULFOTRANSFERASE

(Table 1), with a defect in response to low Pi, indicates ethylene signaling could be involved in the Pi starvation response [32]. The transcript levels of several Arabidopsis ERF transcription factor genes, such as *ERF1*, *ERF2*, *ERF5* and *ERF070*, were also altered by low Pi treatment [31,35,36]. In addition, at least eight *AP2/ERF* (*APETALA2/Ethylene Responsive Factor*) genes were down regulated in the double mutant of Arabidopsis *PHR1* and *PHL1* (*PHR1-LIKE 1*) transcription factor genes which regulate a subset of PSRs [18,37]. A series of Arabidopsis *hps* (*hypersensitive to Pi starvation*) mutants, *hps2*, *hps3*, *hps4*, *hps5*, *hps8*, were identified (Table 1) with the mutated alleles related to ethylene signaling [28,38-41]. Alterations of PSI (Pi starvation-induced) gene abundance, acid phosphatase activity and anthocyanin accumulation in the mutants indicate ethylene signaling and responsiveness are involved in the regulation of PSRs triggered by Pi deficiency.

The involvement of Pi deficiency-induced ethylene in PSRs

The role of ethylene in plant responses to Pi deficiency have long been focused on investigating changes of root morphology. Several review articles have summarized in detail [8,10,18,19]. The Pi deficiency-induced changes of ethylene production or responsiveness promote modification of RSA including inhibition of primary root growth as well as enhancement of lateral root or root hair growth to explore available Pi at top soil layers. In earlier studies, using ethylene precursor, ACC, ethylene biosynthesis inhibitors, AVG or Co^{2+}, and ethylene perception

inhibitors, Ag^+ or MCP, ethylene was demonstrated to be involved in regulation of RSA modification in different plant species [15-16,25,32,42]. Similarly, a number of Arabidopsis mutants with different sensitivity to ethylene including *ein2* to *ein7*, *etr1*, *eto1* and *ctr1* were also employed to investigate the role of ethylene in later root and root hair growth under low Pi condition [16,42]. In addition, Pi deficiency-induced formation of adventitious root was found to be impeded in the ethylene-insensitive tomato cultivar, Never-ripe [14]. More recently, an Arabidopsis *ERF* gene, *AtERF070*, was examined to be related to low Pi-induced lateral root development by RNA interference and over expression approaches. *AtERF070* was specifically induced in Pi-deficient roots and shoots. RNAi-mediated silencing of *AtERF070* enhanced lateral root development and increase Pi accumulation in both roots and shoots. However, the phenotype was reversed in the over expression lines. The results indicate a negative role of *AtERF070* in Pi homeostasis [36].

From a large-scale screening for Arabidopsis mutants with altered PSRs, 10 *hps* mutants have been identified and characterized although *hps9* and *hps10* have not been published [41]. Among these mutants, *hps2*, *hps3*, *hps4*, *hps5*, hps7 and *hps8* have been demonstrated to be related to ethylene biosynthesis or signaling [28-29,38-41]. In addition to *hps8*, the other 5 *hps* mutants showed much shorter primary root lengths comparing to the wild-types, indicating their hypersensitivities to Pi starvation. Different to previous studies, these mutants not only showed changes of root morphology but also displayed other PSRs under Pi deficiency. *hps2* is mutated in *CTR1*, the key negative regulator of the ethylene signaling pathway, and showed an enhanced PSI gene expression and acid phosphatase activity. However, the low Pi-induced anthocyanin accumulation was lower in the mutant than the wild-type [28]. When the same experiments were done in the ethylene-insensitive mutant *ein2-5*, the opposite results were observed. Furthermore, the expression of *AtPT2*, a low Pi-inducible Pi transporter gene, was increase in the ethylene over-producing mutant, *eto1-1*, as in *hps2*, but reduced in the ethylene insensitive mutant, *etr1-1*. It is the first demonstration that ethylene play a broad role in plant responses to Pi deficiency. The similar phenotypes were found in *hps3* and *hps4*. Molecular cloning indicated that *ETO1* and *SABRE* are mutated in *hps3* and *hps4*, respectively [38-39]. The results in *hps3* are consistent with the previous study in *eto1-1* [28]. SABRE is an important regulator of cell expansion and known to antagonistically interact with ethylene signaling. A higher accumulation of auxin in the root tips of Pi-deficient *hps4* may explain the inhibited primary root growth and provide an evidence for the interaction between ethylene and auxin in response to Pi deficiency [39]. Recently, *hps5* was characterized to possess constitutive ethylene responses due to a mutation in ERS1, an ethylene receptor [40]. In the *hps5* mutant, a high level of EIN3 protein, a key transcription factor regulating ethylene response, was detected. A group of low Pi-inducible genes involved in root hair development were up regulated in the *EIN3* over expression lines but suppressed in the *ein3* mutant. A direct binding of EIN3 to the promoters of those genes was demonstrated. Because some of the genes are also the direct targets of the RSL4 transcription factor, a key regulator of root hair development, the authors thus propose RSL4 as well as its homologues may regulate root hair development through activation of those genes under normal condition. However, for further enhancement of root hair formation in response to Pi deficiency, EIN3 may be required. Although the phenotype of *hps8*, cause by mutation of *AtTHO1*, is different to those of the other *hps* mutants, the acid phosphatase activity was also higher than the wild-type [41]. *AtTHO1* encodes a subunit of the THO/TREX protein complex which functions in mRNA export and mi RNA biogenesis. The enhanced acid phosphatase activity in the mutant was eliminated by the ethylene perception inhibitor, Ag^+. This reduction was also found in the double mutant of *AtTHO1* and *EIN2*, indicating the THO/TREX complex may negatively regulate low Pi-induced acid phosphatase activity through inhibiting ethylene signaling. Future studies are required to better understand the ethylene-mediated regulatory network controlling these PSRs.

CONCLUSION AND PERSPECTIVES

Ethylene plays an important role in modulating plant PSRs (Figure 1). Both biosynthesis and responsiveness of ethylene are involved in this complex regulatory network. The induction of Pi transporter and acid phosphatase by ethylene in response to Pi deficiency reveal the involvement of ethylene in external Pi acquisition, internal Pirecycling or Pi releasing from external organophosphates. It is known that ethylene interacts with auxin to regulate remodeling of RSA under Pi deficiency. Further studies are required to understand whether this interaction is also involved in the responses other than RSA as well as whether or how ethylene interacts with other plant hormones to regulate these processes. An increased expression of several ERF genes in response to Pi deficiency was observed, it is intriguing to investigate whether these ERFs participate in the regulation

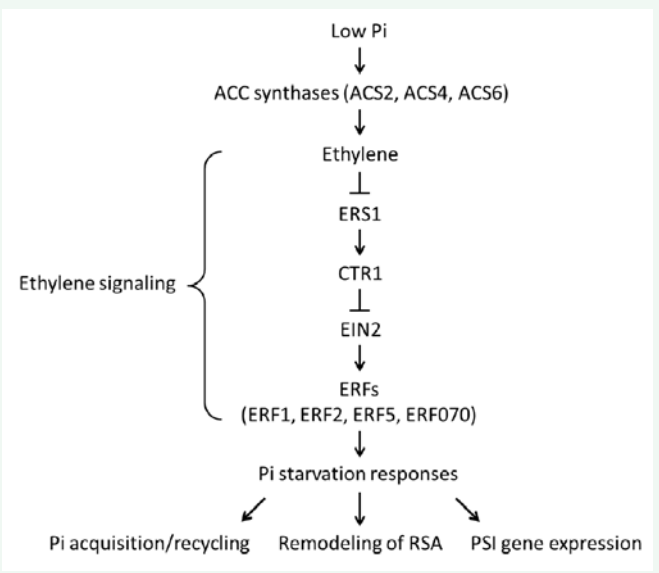

Figure 1 A schematic model of the role of ethylene in phosphate starvation responses. The ethylene biosynthesis and signal transduction are activated under Pi deficiency and subsequently mediate Pi starvation responses to maintain Pi homeostasis. The ethylene biosynthetic and signaling genes presented in this figure have been demonstrated to be induced by Pi starvation or involved in Pi starvation responses [28,31,35,36,40].

of different PSRs and whether these ERFs are also involved in other nutrient starvation responses. A better understanding of the mechanisms will contribute to the future breeding of crops tolerant to nutrient deficiency.

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