

PYR/PYL/RCAR Abscisic Acid Receptors Regulate Root Cell hydraulic Conductivity through Activating Aquaporin expression

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Received: March 20, 2018

Accepted: April 9, 2018

Online Published: April 16, 2018

doi:10.5539/ijb.v10n3p7

URL: <https://doi.org/10.5539/ijb.v10n3p7>

Abstract

With a varied physical environment, plants have developed specific mechanisms that allow them to rapidly perceive and respond to stresses in the environment. As one of many pathways conserved in a long time evolution, the abscisic acid (ABA) signaling pathway has been identified as a central regulator to control gene expression and generate physiological adaptation to various stressful conditions in plant. As abscisic acid receptors, PYR/PYL/RCARs have been proved to regulate stomatal closure. Here we detected the root cell hydraulic conductivity and the aquaporin expression under treatment of exogenous ABA in wild-type and *pyr1/pyl1/pyl2/pyl4* mutant Arabidopsis using cell pressure probe and qRT-PCR technology. The results showed that PYR/PYL/RCAR receptors regulate root cell hydraulic conductivity through activating aquaporin expression. Lastly, we discussed how plants maintain water balance combined with the data obtained from published articles.

Keywords: PYR/PYL/RCAR Receptors, Root cell hydraulic conductivity, Aquaporin, Abscisic acid

1. Introduction

Plants are exposed to several stressful conditions, and water deficit is one of the most common abiotic stresses, which causes severe and even irreversible damage. The effects of water deficit are becoming more and more serious with global climate change and growing water scarcity. Water is an increasingly scarce resource given current and future human population and societal needs, putting an emphasis on sustainable water use (Harb, Krishnan, Ambavaram, & Pereira, 2010). Therefore, in-depth understanding of relation between plant water use and water deficit is necessary for the sustainable development of agriculture.

Plant growth in natural environment depends on an optimum balance between roots water uptake and water losses through the shoots (W. Wang, Yang, Zhang, & Sun, 2013). Water uptake by roots, which provides the original water source for whole-plant water balance, plays a vital role in maintaining the plant water balance especially in water deficit condition. According to Heinen (Heinen, Ye, & Chaumont, 2009), water moves across plant tissues through both apoplastic and cell-to-cell path-ways. The cell-to-cell pathway refers to water flow through the plasmodesmata and/or across membranes, substantially contributing to whole-plant hydraulic resistance. Root hydraulic conductivity represents the ability of plant absorbing water. Root hydraulic conductivity can be divided into three levels: root system ($L_{p_{rs}}$), individual root (L_{p_r}) and root cell ($L_{p_{rc}}$) hydraulic conductivity. Aquaporins located in the plasma membrane (plasma membrane intrinsic proteins, PIPs) affect the water trans-membrane movement significantly (Postaire et al., 2010; Qian, Song, Chaumont, & Ye, 2014).

A numerous of studies has showed ABA is involved plant responses to abiotic stresses such as cold, drought, and salinity as well as the regulation of plant growth and development, including embryogenesis, seed dormancy, shoot and root growth, and leaf transpiration (Acharya, Jeon, Zhang, & Assmann, 2013; Chen, Yang, Lur, Tsai, & Chang, 2006; Kempa, Krasensky, Dal Santo, Kopka, & Jonak, 2008; Pantin et al., 2013; Tardieu, Parent, & Simonneau, 2010; Xiong, Ishitani, Lee, & Zhu, 2001; Zhu, Schraut, Hartung, & Schäffner, 2005). Under water deficit stress, ABA content increases in leaves inducing stomatal closure that decreases the rate of transpiration and stomatal conductance. In this process, a basic core of ABA signaling that involves an ABA receptor complex, consisting of an ABA receptor family (PYR/PYL/RCAR), protein phosphatases 2C (PP2C) and Snf1-related protein kinase 2s (SnRK2s), induces a variety of molecular events in plant cells (Osakabe, Yamaguchi-Shinozaki, Shinozaki, & Tran, 2014). PYR/PYL/RCAR receptors constitute a 14-member family, almost all of which are able to activate ABA-responsive gene expression in protoplast transfection assays and six PYR/PYL receptors, namely

PYR1, PYL1, PYL2, PYL4, PYL5, and PYL8, is able to germinate and grow even on 100 μM ABA (Fujii et al., 2009; M. Gonzalez-Guzman et al., 2012). PYR/PYL/RCAR receptors play a major role in regulating stomatal aperture and transcriptional response to abscisic acid in Arabidopsis (M. Gonzalez-Guzman et al., 2012; Y. Wang, Chen, Zhang, Hills, & Blatt, 2013). However, whether PYR/PYL/RCAR receptors take part in roots water uptake, and if it have affected this process, how it works?

In this study, we examined the hypothesis that in plant PYR/PYL/RCAR receptors regulate root cell hydraulic conductivity through activating aquaporin expression. We detected the root cell hydraulic conductivity and the aquaporin expression under treatment of ABA in wild-type and *pyr1/pyl1/pyl2/pyl4* mutant Arabidopsis. We also analyzed the relationship between them. Lastly, based on our data and information obtained from published articles, a possible model PYR/PYL/RCAR receptors involved in maintaining whole plant water balance was written for a better understanding.

2. Materials and Methods

2.1 Plant Growth and Preparation

Wild-type Arabidopsis (*Arabidopsis thaliana* ecotype Columbia) and the *pyr1/pyl1/pyl2/pyl4* quadruple mutant Qm were sown in Murashige and Skoog medium (Murashige & Skoog, 1962) for 10 days and then transplanted to a quarter Hoagland nutrient solution grown under a 12-h/12-h day/night cycle ($300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) and 60% humidity in the growth chambers (AGC-D001P, Qiushi Corp., Hangzhou, China). After two weeks, third of the plants were transplanted to the 1/4 Hoagland solution containing ABA (final concentration = 1000 nm), third in containing ABA (final concentration=100nm), and the remaining plants, as controls, continued to grow in the 1/4 Hoagland solution without ABA. So this study had three treatments: controls and ABA stressed plants. After the 0, half and one hour of the treatment, three treatment plants were used to measure cell hydraulic parameters. Only the controls and 1000 nm treated plants were collected immediately immersed in liquid nitrogen and stored at $-80 \text{ }^\circ\text{C}$.

2.2 Quantitative Real-Time PCR

Total RNA was extracted from the samples using an RNAprep pure Plant Kit (TIANGEN, Beijing, China). The RNA extract was digested with DNase I and examined using a dissociation curve to ensure that DNA was eliminated. The cDNA was synthesized in vitro using a TIANScript RT Kit (TIANGEN, Beijing, China) according to the manufacturer's instructions. The quantitative real-time PCR was carried out according to Jang's Method (Jang, D. G. Kim, Y. O. Kim, J. S. Kim, & Kang, 2004). Based on Jang's result, we selected 5 *AtPIP* genes (*AtPIP1;1*, *AtPIP1;2*, *AtPIP1;4*, *AtPIP2;1* and *AtPIP2;6*) to detect.

2.3 Measurements of Cell Hydraulic Parameters

Cell pressure probe (CPP) was employed to meter cell hydraulic parameters. Method used in this procedure was referred to Javot (Javot et al., 2003) and Qian (Qian et al., 2014).

2.4 Statistical Analyses

Statistical analyses were performed with the SPSS version 13.0. The correlation and regression analyses were conducted using SigmaPlot version 12.01 (Systat Software; <http://www.sigmaplot.com>).

3. Results

3.1 Cell Hydraulic Parameters Measurements

For controls, the half time ($T_{1/2}$) of hydrostatic water flow across cell membrane ranged from 1.76 to 3.05 s (Figure 1A). Under ABA treatment in wild-type, both 100nm and 1000nm, $T_{1/2}$ significantly reduced (25%-78%), while in the Qm mutant it remains unchanged (Figure 1A). With the difference in $T_{1/2}$, the root cell hydraulic conductivity ($L_{p_{rc}}$) varied in those two treatments. With 1000nm ABA treatment 1h, the $L_{p_{rc}}$ increased to $5.51 \times 10^{-6} \text{ms}^{-1} \text{MPa}^{-1}$, which was 81% higher than controls. It was no surprises that under two different ABA concentrations treatments, the $L_{p_{rc}}$ of Qm had no statistical change compared to controls (Figure 1B).

3.2 Changes in *AtPIP* mRNA Levels in Response to ABA Treatment

PIPs have been identified and proved to influence the root hydraulic conductivity. To obtain evidence that some of these genes were regulated by PYR/PYL/RCAR receptors, we measured relative expression of 5 *AtPIP* genes in roots by quantitative real-time PCR. The qRT-PCR analyses with gene specific primers (Figure 2) revealed that these 5 *AtPIP* genes were expressed in roots of these two Arabidopsis. Of those genes, *AtPIP1;1*, *AtPIP1;2* and *AtPIP2;6* were significantly increased in wild-type after using 1000nm ABA treatment. Nevertheless, these 5 *AtPIPs* had no discernible influence in mutant Qm before or after the treatment with exogenous ABA.

To confirm whether it has correlation between $L_{p_{rc}}$ and the relative expression of *AtPIPs*, we make correlation analysis. The results showed significantly positive relationship between $L_{p_{rc}}$ and *AtPIP1;1* ($R^2=0.9502$; $P=0.0009$) and *AtPIP2;6* ($R^2=0.9592$; $P=0.0006$) (Figure 3).

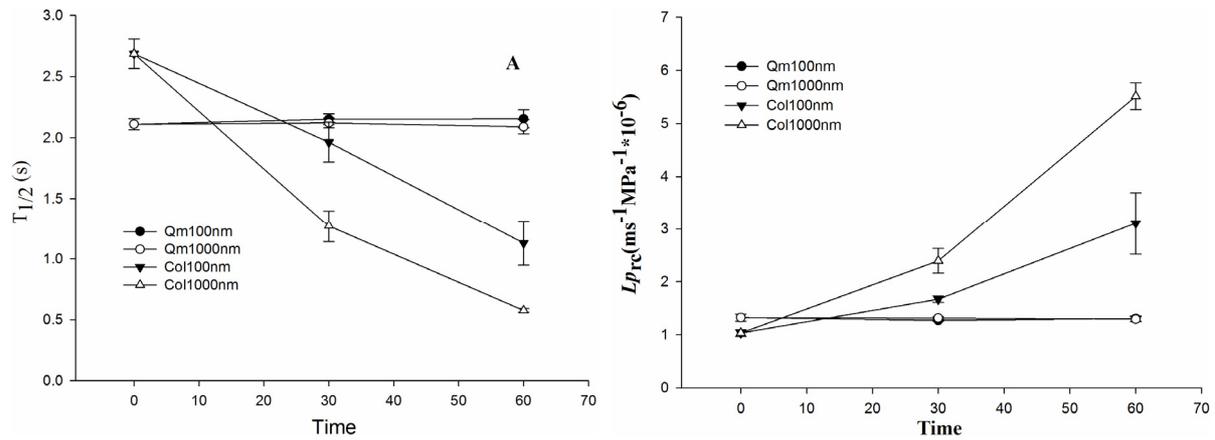


Figure 1. the half time ($T_{1/2}$) of hydrostatic water flow across cell membrane and root cell (A) and root cell hydraulic conductivities (B) in mutant Qm and wild type Col. X axis represents time duration of ABA treatment (0,30min and 60min). Data are mean \pm SD (n = 6 to 8 plants)

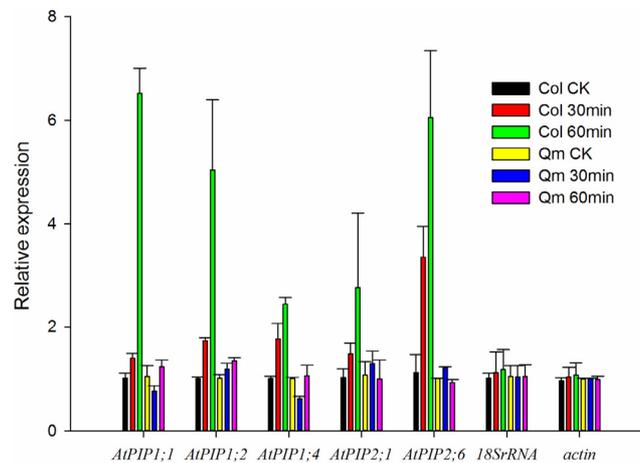


Figure 2. Relative expression of 5 *AtPIP* genes in roots from plants treated with exogenous ABA(Col-wild type;Qm-mutant). Gene expressions were determined by quantitative real-time PCR, and the geometric mean of the expression levels of three reference genes were used to normalize data. X axis represents 10 *AtPIP*s and three reference genes. Results are shown as relative changes of gene expression of ABA-treated plants to that of control plants. Different letters above columns represent a significant differences between stress-treated and control plants (mean \pm SD; $P < 0.05$)

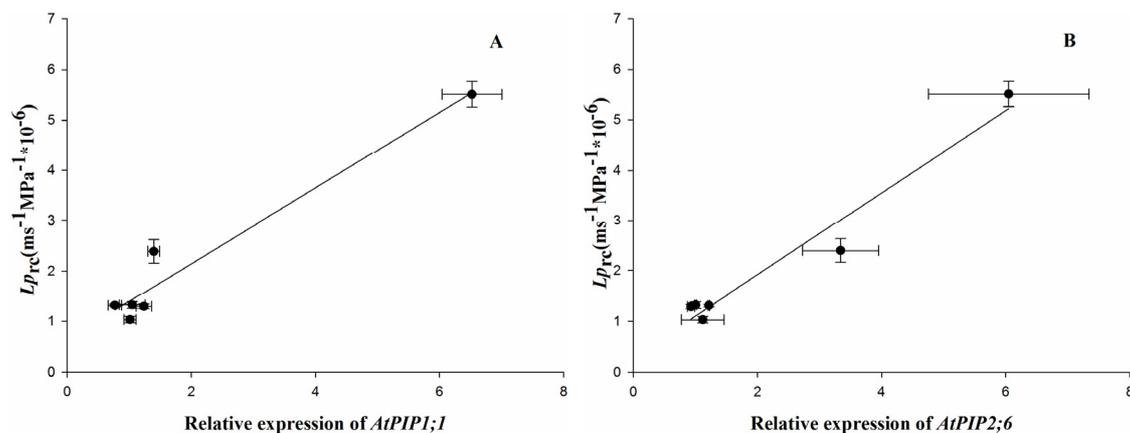


Figure 3. Root cell hydraulic conductivity (L_{prc}) is positively correlated with the relative expression of *AtPIP1;1*(A) and *AtPIP2;6*(B), respectively, in the roots. Points are the mean of parameters and error bars represent the S.D. (L_{prc} , n=11-15; relative expression, n= 3). The correlation analyses were performed using SigmaPlot version 12.01, and the relation coefficient (R2) and significant level (P) are shown

4. Discussion

Arabidopsis PYR/PYL/RCAR receptors have been extensively studied in regulation of stomatal aperture and the mechanism since it was identified (Fujii et al., 2009; M. Gonzalez-Guzman et al., 2012). We investigated PYR/PYL/RCAR receptors' effect on root water uptake and the expression of *AtPIPs*. Based on our data and some others obtained from previous studies, some questions or hypotheses that related to whole-plant water balance were discussed here.

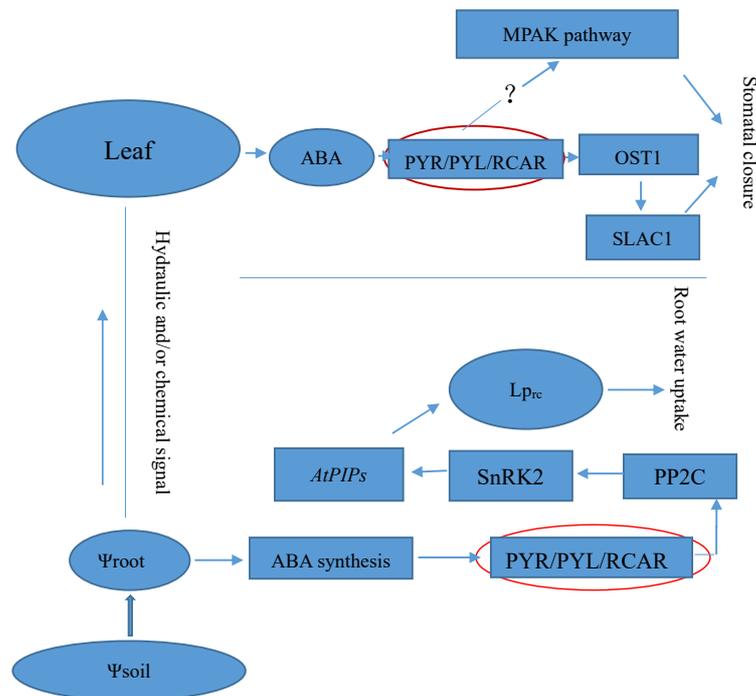


Figure 4. A possible model for PYR/PYL/RCAR receptors control whole-plant water balance. In water deficit status, root water potentials decrease. As a result, ABA content increase. Along the ABA signaling pathway, abundance of PIPs increases. Root cell hydraulic conductivity enhances. At the same time, root signaling transmits to leaf. In leaf, ABA accumulates. Lastly, stomata is closed and water loss by transpiration reduces

4.1 ABA Involved in Root Water Uptake

Root hydraulic conductivity is the most important part in water uptake from soil and loss into air by transpiration (Vandeleur et al., 2009). Mahdieh shows that ABA facilitates the root hydraulic conductivity by aquaporin expression in *Nicotiana tabacum* (Mahdieh & Mostajeran, 2009). And many other researches have demonstrated ABA facilitates the uptake of water by roots (Christmann, Weiler, Steudle, & Grill, 2007; Kudoyarova et al., 2011). Our data showed that exogenous ABA accelerated the root cell hydraulic conductivity. This result is consistent with Beaudette's study in *Pisum sativum* (Beaudette, Chlup, Yee, & Emery, 2007). And more in that study, they also found *PsPIP2-1* expression in lateral roots was strongly correlated with diurnal changes in L_{pr} , which is consistent to our results (Figure 3). So those results indicated that ABA was involved in regulating root water uptake.

4.2 PYR/PYL/RCAR Receptors Involved in ABA Regulated Root Cell Hydraulic Conductivity

PYR/PYL/RCAR receptors have the potential applications in enhancing plant drought resistance (Miguel Gonzalez-Guzman et al., 2014; Kim et al., 2014; Pizzio et al., 2013). Overexpression of PYL5 in rice modulates gene expression, most of which are associated with metabolic processes, cellular processes, and response to stress. And Overexpression of PYL5 in rice enhances drought tolerance (Kim et al., 2014). In our research, Qm mutant was insensitive to exogenous ABA both in L_{pr} and *AtPIPs* expression (Figure 1 and Figure 2). It indicates that ABA involved in root hydraulic conductivity maybe functions by PYR/PYL/RCAR signaling pathway. According to Jang's research, control the expression of *AtPIP1;2* was regulated by ABA-dependent signaling pathway under environmental stress. Combining with our data, we hold that ABA regulates *AtPIP1;2* expression via PYR/PYL/RCAR receptors.

4.3 A Possible Model for PYR/PYL/RCAR Receptors Control Plant Water Balance

Based on our results and information from the literatures, a possible model for PYR/PYL/RCAR receptors control whole-plant water balance was proposed here (Figure 4). Under drought stress, soil water potential (Ψ_{soil}) decreases, which induces Root or xylem water potentials decreases. With root water potentials decreasing, root ABA synthesis is started. Soon, PYR/PYL/RCAR receptors receipt ABA signal, then active PP2Cs to phosphorylate SnRK2 and lastly regulate *AtPIP*s expression in root. As a physiological response, root cell hydraulic conductivity increases and root water uptake is enhanced. At the same time, root hydraulic and/or chemical signal transmits to leaf (Christmann et al., 2007; Comstock, 2002). Later, ABA content in leaf increases. PYR/PYL/RCAR receptors regulates OST1 (Open stomata 1, protein kinase) and SLAC1 controlling ion in or out of guard cells (Acharya et al., 2013; Danquah, de Zelicourt, Colcombet, & Hirt, 2014; Mustilli, Merlot, Vavasour, Fenzi, & Giraudat, 2002). And another side, according to Gonzalez's data (M. Gonzalez-Guzman et al., 2012), the expressions of MAPK genes in PYR/PYL/RCAR mutant are lower than those in wild-type Col. So maybe MAPK pathways is partly regulated by PYR/PYL/RCAR receptors. And MAPK pathways take part in stomatal movement(Des Marais et al., 2014). All these responses induce stomatal closure. So water loss by transpiration decreases. All these data show that the PYR/PYL/RCAR receptors play a crucial role in controlling water in or out of plant.

Acknowledge

We thank Dr. Wu Biao from Yellow Sea Fishery Research Institute for his help in RT-PCR and Dr. Zhang Jingyuan from NWFU for her help in CPP. We also thank those authors of articles we cited for their excellent jobs in ABA pathway.

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