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SHORT COMMUNICATION

JA modulates phytochrome a signaling via repressing FHY3 activity by JAZ proteins

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ABSTRACT

Phytochrome A (phyA) is the primary photoreceptor mediating various plant responses to far-red (FR) light. The defense-related phytohorme jasmonic acid (JA) has been shown recently to play a role in regulating phyA-mediated FR signaling. However, the detailed molecular mechanisms governing phyA- and JA-mediated signaling cross talks are still not well understood. Here, we uncover a molecular cascade in which JAZ1 inactivates phyA signaling through repressing the transcriptional activity of FHY3 on *FHY1* and *FHL*. Furthermore, we demonstrate that the expression levels of *FHY1* and *FHL*, and some FR response genes are reduced in the *coi1* mutant. These findings unveil a previously unrecognized mechanism whereby JA modulates phyA signaling through repressing the activities of FHY3 by JAZs.

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Plant growth and development follows a highly plastic program, which is regulated by both internal cues (such as hormones) and external signals (such as light). Light and hormone coordinately control a set of plant growth and development processes, including seed germination, seedling de-etiolation, stomata and chloroplast movement, stem elongation, circadian rhythms and flowering.[1] Plants have evolved an array of photoreceptors to perceive the light information. Among them, phytochromes are responsible for detecting red and far-red light. Phytochromes exist in two photoreversible forms: the inactive red light-absorbing form (Pr) and the active far-red light-absorbing form (Pfr). Upon light irradiation, inactive Pr form is converted to the Pfr form which is translocated from the cytosol into the nucleus, triggering downstream signaling cascade.[2] There are five phytochromes exist in *Arabidopsis*, which are designated phyA–E. PhyA is the primary photoreceptor for perceiving FR light. Two small plant-specific proteins, FAR-RED ELONGATED HYPOCOTYL1 (FHY1) and its homolog FHY1-LIKE (FHL), are essential for the nuclear accumulation of light-activated phyA and subsequent FR light responses.[3–5] The activation and repression of FHY1/FHL-phyA signaling is energetically demanding. FHY3, a transposase-derived transcription factor, activate *FHY1/FHL* gene expression directly, which in turn facilitating phyA nuclear accumulation upon FR light irradiation.[6] Our prior work revealed that a group of JA signaling repressors, JAZ proteins can physically interact with FHY3 and repress its function in shade avoidance response.[7] As FHY3 is essential for *FHY1* and *FHL* genes expression, thus, we speculated that JAZ proteins might also affect FHY3-mediated *FHY1* and *FHL* transcription. To test this, we performed a transient gene expression assay in *N. benthamiana* leaf to examine the effect of JAZ1 on the ability of FHY3 to promote *FHY1* and *FHL* expression. As expected, our results showed that FHY3 could effectively induce the expression of the *FHY1p:LUC* and *FHLp:LUC* reporter genes, whereas co-expression of JAZ1 with FHY3 significantly repressed the expression of the *FHY1p:LUC* and *FHLp:LUC* reporter genes (Figure 1(a–d), indicating that JAZ1 can suppress the transcriptional activation activity of FHY3 on *FHY1* and *FHL in planta*. Consistent with the observation, JAZ1 overexpression and *coi1-2* mutant line (in which the JAZs protein are not degraded) exhibited an impaired phyA signaling phenotype: longer hypocotyl than wild type when seedlings were grown in continuous FR (FRc) conditions (Figure 2(a,b)). Furthermore, the *JAZ1D3A* transgenic plant, in which the overexpressed JAZ1 does not contain the JAS domain and dominantly represses JA responses probably by forming stable dimers with the native JAZ proteins,[8,9] also displayed a more pronounced long hypocotyl phenotype than wild-type seedlings when grew under FRc conditions (Figure 2(a,b)). These observations suggest that inactivation of JA signaling or over accumulation of JAZ proteins can attenuate phyA signaling, at least partially through inhibition of FHY3 activity.

Next, we investigated the effect of JAZ overexpression in regulating *FHY1* and *FHL* expression in vivo. Previous studies showed that the transcript levels of *FHY1* reduced

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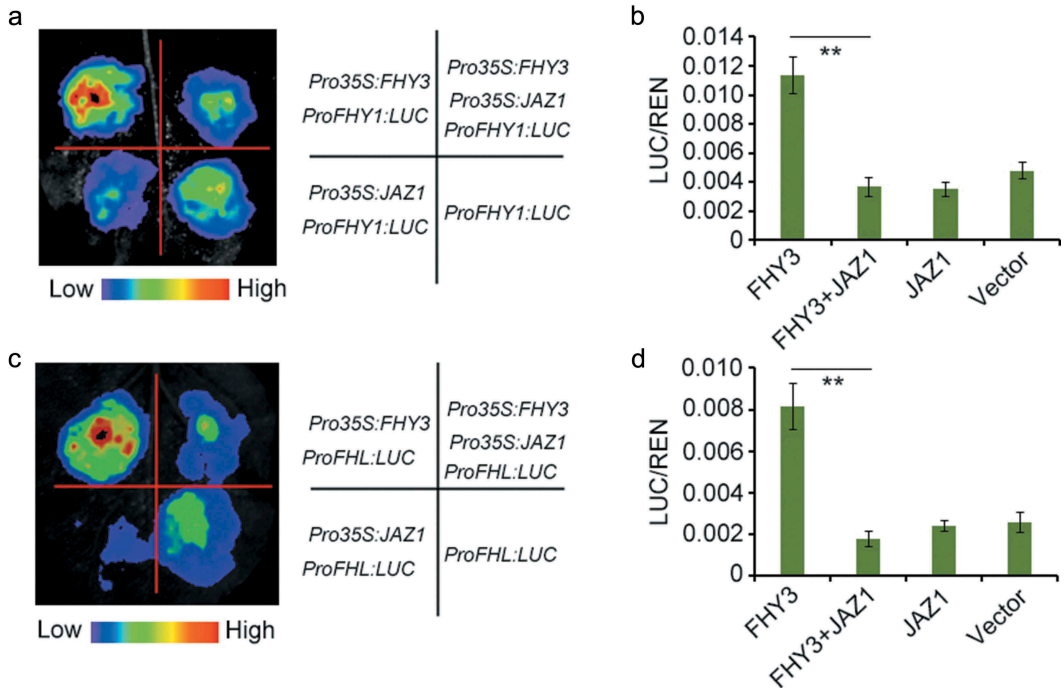

Figure 1. JAZ1 represses the transcriptional activation activity of FHY3 on *FHY1* and *FHL* expression.

(a) and (b) JAZ1 suppresses the activation activity of FHY3 on *FHY1* expression in *N. Benthamiana* leaves. (c) and (d) JAZ1 suppresses the activation activity of FHY3 on *FHL* expression in *N. Benthamiana* leaves. The relative LUC activities were normalized to the REN activity (LUC/REN). Significant differences are indicated: **, $P < .01$, Student's t-test. Values are mean ± SD; n = 3.

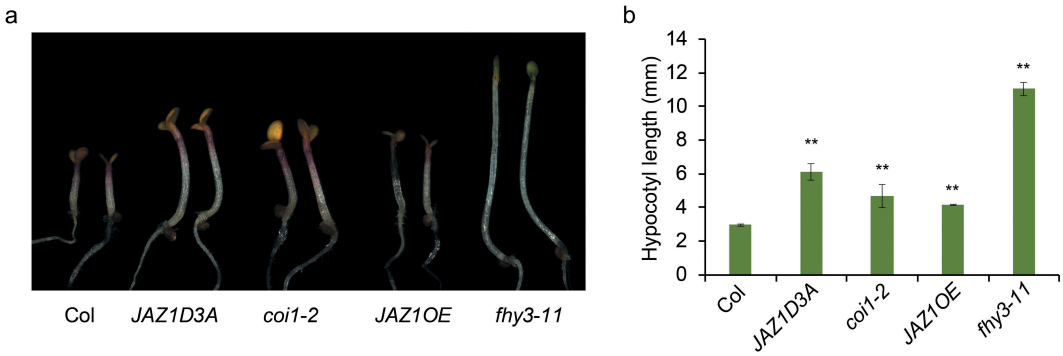

Figure 2. The *JAZ1D3A, coi1-2*, JAZ1OE and *fhy3-11* mutants exhibit exaggerated hypocotyl elongation under FRc conditions.

(a) Hypocotyl length of the wild type (Col) and *JAZ1D3A, coi1-2*, JAZ1OE, *fhy3-11* mutants grown under FRc conditions. (b) Quantification of hypocotyl length. Asterisks indicate significant differences compared with the wild type by Student's t-test ($p < .01$). Data are presented as means ±SD, n > 15.

when dark-grown seedling were transferred to FRc conditions.[6,10] Quantitative reverse transcriptase-PCR (qRT-PCR) analysis revealed that *FHY1* and *FHL* transcript levels were significantly reduced in the *coi1-2* plants (Figure 3(a,b)). Given that FHY1 and FHL are essential for phyA nuclear accumulation and subsequent FR signaling, we deduced that the expression of FR-responsive genes should be compromised in the *coi1-2* mutant. To test this, we examined the expression of several representative FR-responsive genes in wild-type and *coi1-2* seedlings grew under darkness and then transferred to FRc conditions. As shown in Figure 3(c–f), four FR-responsive genes *CAB2, CO, HY5* and *PIL1*, showed reduced expression levels in the *coi1-2* mutant relative to the wild-type. Together, these data suggest that JAZ proteins can antagonize FHY3-mediated activation of *FHY1/FHL* expression, thereby modulating the phyA signaling pathway. Thus, this work uncovers a previously unrecognized mechanism whereby JA modulates phyA signaling.

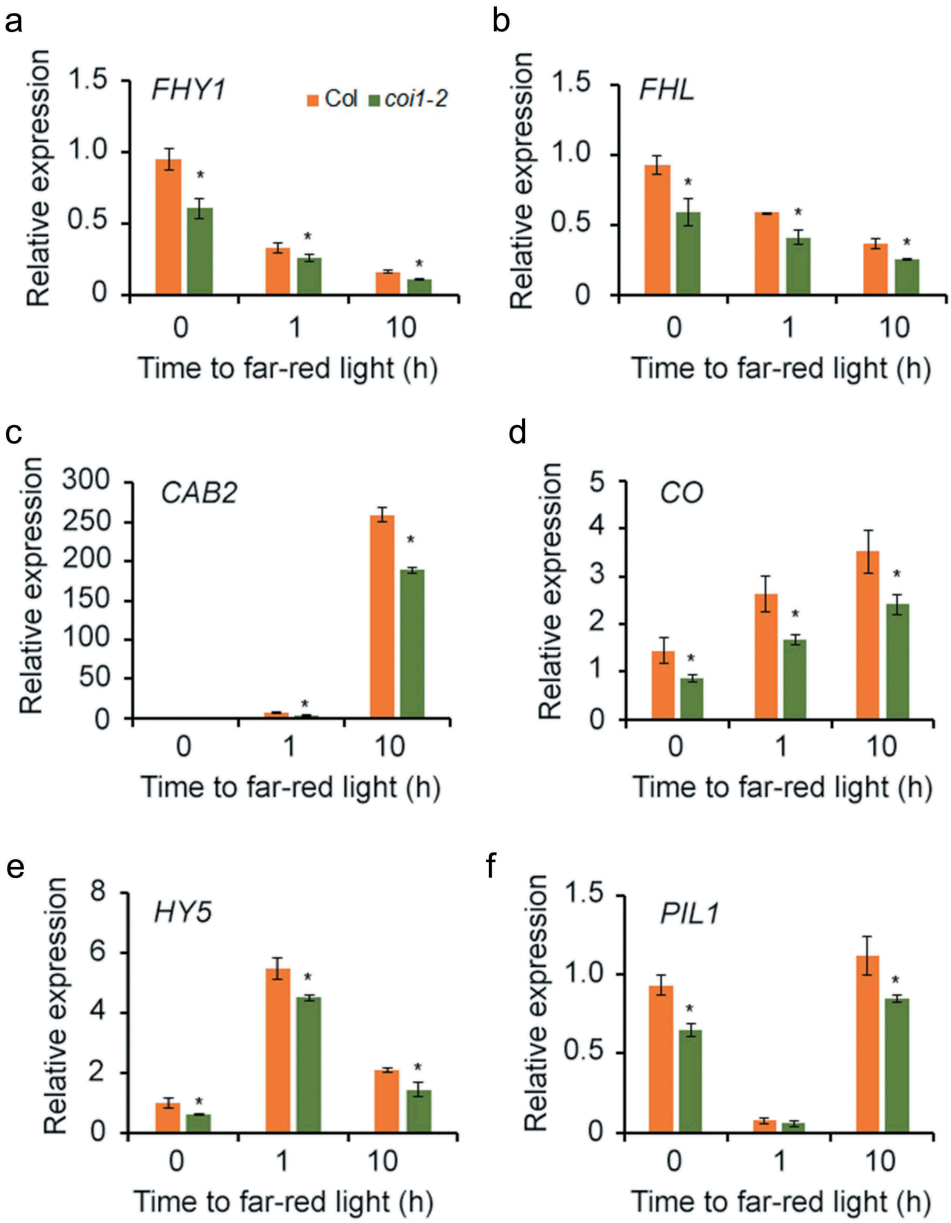

Figure 3. Expression of *FHY1*/*FHL* and FR-responsive genes is reduced in the *coi1-2* mutant.

(a) and (b) *FHY1* and *FHL* expression is significantly reduced in the *coi1-2* mutant compared with wild type. (C)–(F) qRT-PCR analysis of far-red responsive gene expression (*CAB2, CO, HY5* and *PIL1*) in wild-type and the *coi1-2* mutant. All the seedlings were grown in darkness for 4 d and then transferred to FRc for various time periods. The comparative CT method was used to determine the relative gene expression, with the expression of PP2A (At1g13320) used as the internal control. Asterisks indicate significant differences from the wild-type plants ($p < .05$, Student's t-test). Values are means ± SD; n = 3.

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