SCIENCE CHINA
Life Sciences

•COVER ARTICLE•

July 2020 Vol.63 No.7: 943–952
https://doi.org/10.1007/s11427-019-1584-4

Light promotes jasmonate biosynthesis to regulate photomorphogenesis in *Arabidopsis*

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Received September 24, 2019; accepted November 11, 2019; published online January 19, 2020

Light acts as the pivotal external environment cue to modulate plant growth and development. Seeds germinate in the soil without light to undergo skotomorphogenesis with rapidly elongating hypocotyls that facilitate emergence from the soil, while seedlings upon light exposure undergo photomorphogenesis with significantly inhibited hypocotyl elongation that benefits plants to stand up firmly and cope with the changing environment. In this study, we demonstrate that light promotes jasmonate (JA) biosynthesis to inhibit hypocotyl elongation and orchestrate seedling photomorphogenesis in *Arabidopsis*. We showed that JA-inhibition on hypocotyl elongation is dependent on JA receptor COI1 and signaling components such as repressor proteins JAZs and transcription activators MYC2/MYC3/MYC4. Furthermore, we found that MYC2/MYC3/MYC4 activate the expression of photomorphogenesis regulator *HY5* to repress cell elongation-related genes (such as *SAUR62* and *EXP2*) essential for seedling photomorphogenesis. Our findings provide a novel insight into molecular mechanisms underlying how plants integrate light signal with hormone pathway to establish seedling photomorphogenesis.

photomorphogenesis, jasmonate, COI1, MYC2, HY5, hypocotyl elongation

Citation: Yi, R., Yan, J., and Xie, D. (2020). Light promotes jasmonate biosynthesis to regulate photomorphogenesis in *Arabidopsis*. Sci China Life Sci 63, 943–952. https://doi.org/10.1007/s11427-019-1584-4

INTRODUCTION

Appropriate light responses are critical for plants to cope with the changing environment. Plants adopt completely different growth patterns depending on dark or light conditions. Seeds germinate in the soil without light to undergo skotomorphogenesis: cotyledons of seedlings are closed and hypocotyls grow rapidly to facilitate seedling emergence from the soil. When emerged from the soil and exposed to light for photoautotrophic growth, seedlings undergo photomorphogenesis: the elongation rate of hypocotyls will significantly slow down to benefit plants to survive in the changing environment against wind and collision/squeeze, cotyledons/leaves expand for photosynthesis, and anthocyanins accumulate in hypocotyls/leaves for photo-protection (Chen et al., 2004; Jiao et al., 2007).

Over the past several decades, accumulating research has uncovered how seedlings undergo the dramatic phase switches. Plants perceive different light wavelengths to modulate light responses via several photoreceptors, such as blue light receptors cryptochromes (such as CRY1 and CRY2) and red/far-red light receptors phytochromes (such as PhyA and PhyB). Upon light irradiation, cryptochromes and

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phytochromes act together to regulate a basic leucine zipper (bZIP) transcription factor ELONGATED HYPOCOTYL 5 (HY5) that acts as the photomorphogenesis-positive regulator (Chao and Lin, 2010; Chory, 1992; Liu et al., 2011; Paik and Huq, 2019; Quail, 2002; Su et al., 2017). It is well-known that light significantly induces the expression of HY5 and increases the biological activity of HY5, which promotes seedling photomorphogenesis by repressing the expression of cell expansion-related genes essential for hypocotyl elongation (Lee et al., 2007; Zhang et al., 2011).

Jasmonate (JA) is a lipid-derived plant hormone (Browse, 2009; Wasternack and Hause, 2013), which regulates various plant defense responses against pathogen infection and insect attack (Hu et al., 2013; Reymond et al., 2004; Rowe et al., 2010; Yan et al., 2018), and also modulates diverse plant developmental processes including root growth (Acosta et al., 2013; Chen et al., 2011; Staswick et al., 1992), plant pigmentation (Qi et al., 2011; Shan et al., 2009), trichome formation (Qi et al., 2011), flower development (Yuan and Zhang, 2015; Zhai et al., 2015), plant fertility (Dai et al., 2002; Huang et al., 2014; Song et al., 2013; Xie et al., 1998), and leaf senescence (Qi et al., 2015). In this study, we uncover a molecular mechanism underlying how light triggers JA signaling to promote photomorphogenesis in *Arabidopsis*. We demonstrate that light stimulates the biosynthesis of JA that triggers signaling transduction pathway to activate the expression of *HY5* essential for photomorphogenesis.

RESULTS

Light induces JA biosynthesis to suppress hypocotyl elongation

To investigate the correlations among light irradiation, hypocotyl length, and JA biosynthesis during seedling emergence, *Arabidopsis* wild-type (WT) seedlings were grown in different light intensity conditions to mimic the process from dark to normal light. As expected, with the increase of light fluence rate, the inhibitory effects of light on hypocotyl elongation were markedly enhanced (Figure 1A). Quantitative real-time PCR assay showed that the expression of JA biosynthesis genes *LOX2*, *AOC3*, and *AOS* was considerably elevated in response to the increase of light intensity (Figure 1B, Figure S1A and B in Supporting Information). Consistently, JA content was increased in *Arabidopsis* seedlings correlated with the intensity of light (Figure 1C). Compared to dark-grown seedlings, hypocotyl length of seedlings grown under light condition of 85 μmol m^{-2} s^{-1} was inhibited by about five-fold (from ~11 mm in dark to ~2 mm in light). These results demonstrate that light activates JA biosynthesis to repress hypocotyl elongation, indicating that over the course of seedling emergence, light promotes JA biosynthesis to achieve short hypocotyl that is a key characteristic of seedling photomorphogenesis.

Since light exerts its effects through various photoreceptors including blue light sensory receptors cryptochromes and red or far-red light sensory receptors phytochromes, we further analyzed the JA biosynthesis gene *LOX2* transcript and the hypocotyl length in WT and the light receptor mutants *cry1/2*, *phyB-9*, *phyA-211* under continuous monochromatic blue, red, and far-red light, respectively. We found that various monochromatic lights (blue, red, and far-red light) increased *LOX2* expression markedly in WT seedlings, but barely in the *cry1/2*, *phyB-9*, or *phyA-211* mutant, respectively. As expected, monochromatic light inhibited WT hypocotyl length, whereas hypocotyls of the corresponding photoreceptor mutants were fully elongated (Figure 1D–F). Correlated with the hypocotyl length, all the monochromatic lights increased *LOX2* expression markedly in WT seedlings with short hypocotyl, but barely in the *cry1/2*, *phyB-9*, or *phyA-211* mutant with long hypocotyl (Figure 1D–F).

To further validate JA inhibition on hypocotyl elongation, we measured the hypocotyl length of WT seedlings by exogenous application of various concentrations of MeJA. As shown in Figure 1G and H, an increase of JA concentration is correlated closely with the decrease of hypocotyl length. Compared to ~5.5 mm hypocotyl of seedlings grown in the light condition of 25 μmol m^{-2} s^{-1} without exogenous JA treatment, the hypocotyl length of seedlings treated with 100 μmol L^{-1} JA was significantly reduced to ~1 mm. The data shown in Figure 1 collectively demonstrate that light induces JA biosynthesis to inhibit hypocotyl elongation.

JA inhibits hypocotyl elongation in a COI1-JAZ-MYCs-dependent manner

To verify whether JA perception and signal transduction are required for JA inhibition on hypocotyl growth, we treated mutants deficient in JA perception and signaling with MeJA under white, blue, red, and far-red light. As shown in Figure 2, under all the examined light conditions, the hypocotyl length of JA receptor mutant *coi1-8* was largely unaffected by JA; similarly, the *JAZ1Δ3A* transgenic seedlings, which highly accumulate JAZ repressors due to over-expression of truncated JAZ1 lacking the C-terminal Jas domain (Thines et al., 2007), also abolished the JA inhibition on hypocotyl elongation. Furthermore, the *myc2-2* mutant exhibited a mild hypocotyl elongation inhibition phenotype compared with WT, the *myc2/3* double mutant exhibited a more obvious JA-insensitive response (Figure S2A and B in Supporting Information), while the *myc2/3/4* triple mutant almost abolished JA inhibition on hypocotyl growth and exhibited a long-hypocotyl phenotype under MeJA application in all the light treatments (Figure 2A and B). Even without MeJA

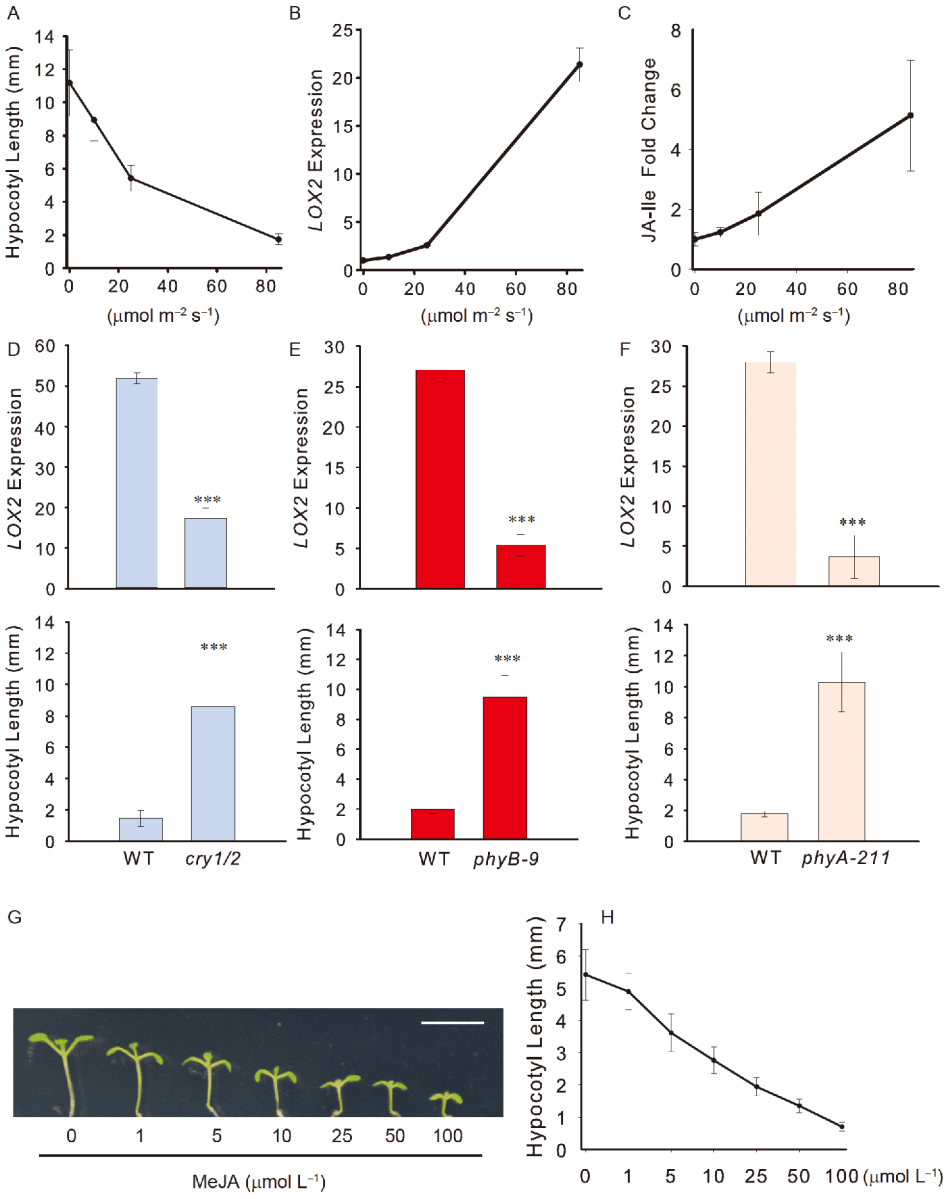

Figure 1 Light activates JA biosynthesis to inhibit hypocotyl elongation. A–C, The hypocotyl length (A), *LOX2* mRNA level (B), and JA content (C) of 6-day-old WT seedlings cultured with white light fluence rates of 0, 10, 25, 85 μmol m^{-2} s^{-1}. D–F, The *LOX2* mRNA level and hypocotyl length of 6-day-old WT and corresponding light receptor mutants *cry1/2* (D), *phyB-9* (E), *phyA-211* (F) cultured under 20 μmol m^{-2} s^{-1} blue light (BL), 30 μmol m^{-2} s^{-1} red light (RL), and 4 μmol m^{-2} s^{-1} far-red light (FRL), respectively. Data are expressed as mean±SD (n=3 for mRNA expression, n=30 for analysis of seedlings' hypocotyl length). Asterisks denote Student's t test significance between WT and *cry1/2*, *phyB-9*, or *phyA-211* samples (***P<0.001). G, The hypocotyl phenotype of WT seedlings grown on the MS medium containing indicated concentrations of MeJA in 25 μmol m^{-2} s^{-1} white light condition for 6 days. Scale bar, 5 mm. H, Quantitative analysis of hypocotyl length shown in (G). Data are expressed as mean±SD (n=30).

treatment, *coi1-8*, *JAZ1Δ3A*, and *myc2/3/4* seedlings also attenuated light inhibition on hypocotyl elongation to exhibit slightly longer hypocotyl under white, blue, red, and far-red light growth conditions (Figure 2C).

Having shown that deficiency in JA signaling attenuated inhibition on hypocotyl elongation (Figure 2), we further investigated whether overexpression of *MYC2*, *MYC3*, or *MYC4* enhances inhibition on hypocotyl elongation. Through analysis of our previously generated transgenic plants overexpressing *MYC2*, *MYC3*, or *MYC4* (Qi et al., 2015), we found that *MYC2*, *MYC3*, and *MYC4* overexpression lines showed hypersensitive responses to JA-mediated hypocotyl elongation inhibition under various light conditions (Figure S3A in Supporting Information). Furthermore, without MeJA treatment, these overexpression lines also exhibited shorter hypocotyl under all tested light conditions (Figure S3B in Supporting Information).

Taken together, our results demonstrate that JA inhibition on hypocotyl elongation requires the function of JA receptor COI1 and signaling components JAZs and MYCs.

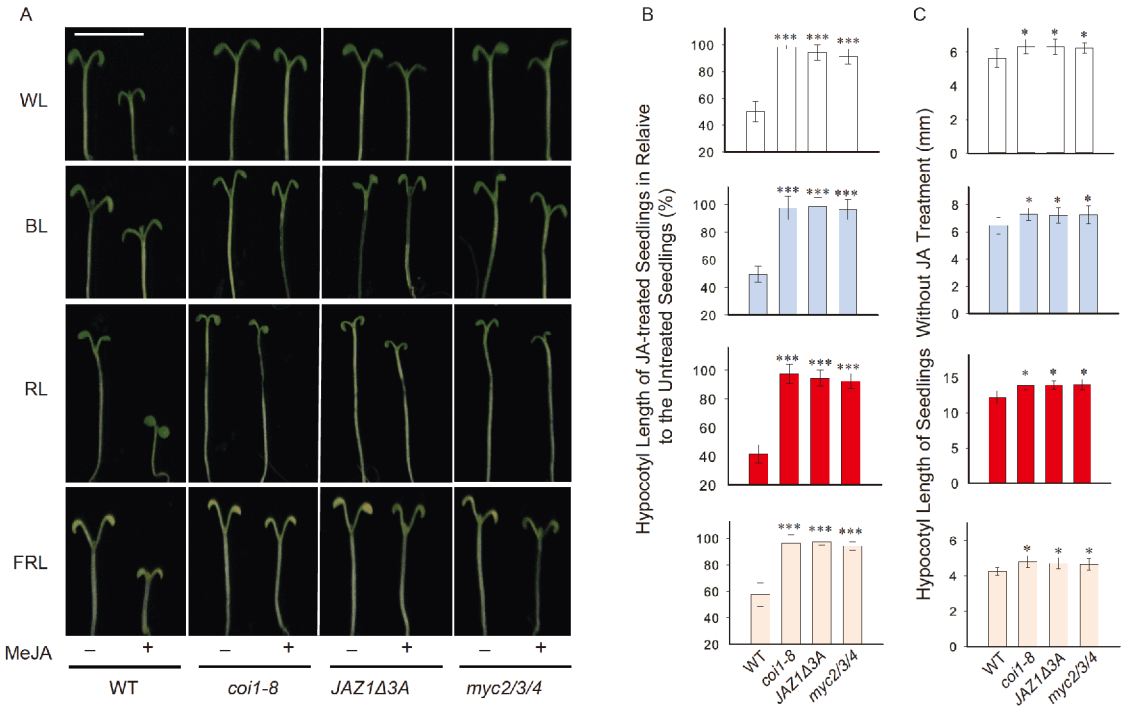

Figure 2 JA-repressed hypocotyl elongation is dependent on COI1, JAZ, and MYCs. A, The hypocotyl phenotype of 6-day-old WT, *coi1-8*, *JAZ1Δ3A*, *myc2/3/4* seedlings treated without (–) or with (+) 10 μmol L^{-1} MeJA under white light (WL), blue light (BL), red light (RL), and far-red light (FRL), respectively. Scale bar, 5 mm. B, Relative hypocotyl length of WT, *coi1-8*, *JAZ1Δ3A*, *myc2/3/4* seedlings treated with 10 μmol L^{-1} MeJA (+) compared with that of untreated (–) seedlings grown for 6 days under white light (WL), blue light (BL), red light (RL), and far-red light (FRL), respectively. Data are expressed as mean±SD (n=30). Asterisks denote Student's t test significance between WT and *coi1-8*, *JAZ1Δ3A,* or *myc2/3/4* samples (***P<0.001). C, The hypocotyl length of WT, *coi1-8*, *JAZ1Δ3A*, *myc2/3/4* seedlings without JA treatment grown for 6 days under white light (WL), blue light (BL), red light (RL), and far-red light (FRL), respectively. Data are expressed as mean±SD (n=30). Asterisks denote Student's t test significance between WT and *coi1-8*, *JAZ1Δ3A*, or *myc2/3/4* seedlings, respectively (*P<0.05).

HY5 is essential for JA-regulated photomorphogenesis

Since HY5 and PIFs are essential for photomorphogenesis and serve as key positive (for HY5) or negative (for PIFs) regulators of light-inhibited hypocotyl elongation (Osterlund et al., 2000; Xu et al., 2015), we investigated whether JA regulates hypocotyl elongation via HY5- or PIF-mediated photomorphogenesis through analysis of hypocotyl length of *hy5-205* or *pifq* (*pif1/3/4/5*) mutant treated with JA under various light conditions. Relative hypocotyl length analysis (hypocotyl length of the JA-treated seedlings in relative to the corresponding untreated seedlings) showed that the *hy5-205* mutant exhibited a reduced response to MeJA application in all the light conditions. However, the *pifq* (*pif1/3/4/5*) mutant exhibited a WT-like JA response (Figure 3A and B). These results showed that the mutation in *HY5* significantly attenuated the repression effect of JA on hypocotyl growth, suggesting that HY5 is critical for JA inhibition on hypocotyl elongation.

MYC2, MYC3, and MYC4 activate *HY5* expression

Using quantitative real-time PCR assay, we compared the JA effect on the expression level of *HY5* among WT, *coi1-1*, and *myc2/3/4* mutants. As shown in Figure 4A, JA treatment significantly triggered *HY5* expression in WT by about 5-fold, while JA-induced *HY5* expression was severely abolished in *coi1-1* and *myc2/3/4* mutants. Consistently, *HY5* expression was significantly enhanced in the JA-treated *MYC2-OE* line (Figure S4 in Supporting Information). In contrast, the expression of *PIF3* was not significantly affected by JA treatment in WT or *myc2/3/4* mutant (Figure S5 in Supporting Information). These data demonstrate that JA induces *HY5* expression and such JA-induced *HY5* expression requires the function of COI1 and MYCs.

As the promoter region of *HY5* is predicted to contain several G-box variants (Figure 4B), which is the characteristics of target sequences of bHLH transcription factors (MYC2, MYC3, and MYC4), we tested whether MYC2, MYC3, or MYC4 activates the promoter of *HY5* using the *Arabidopsis* protoplast dual-Luciferase assays (Qi et al., 2015). Two constructs, in which the *HY5* promoter drives the firefly *LUC* gene as a reporter (P_{HY5}-*LUC*) and the constitutive 35S promoter drives MYC transcription factor as the effector, were used in the assays (Figure 4C). Co-expression of MYC2 in the assays significantly increased P_{HY5}-

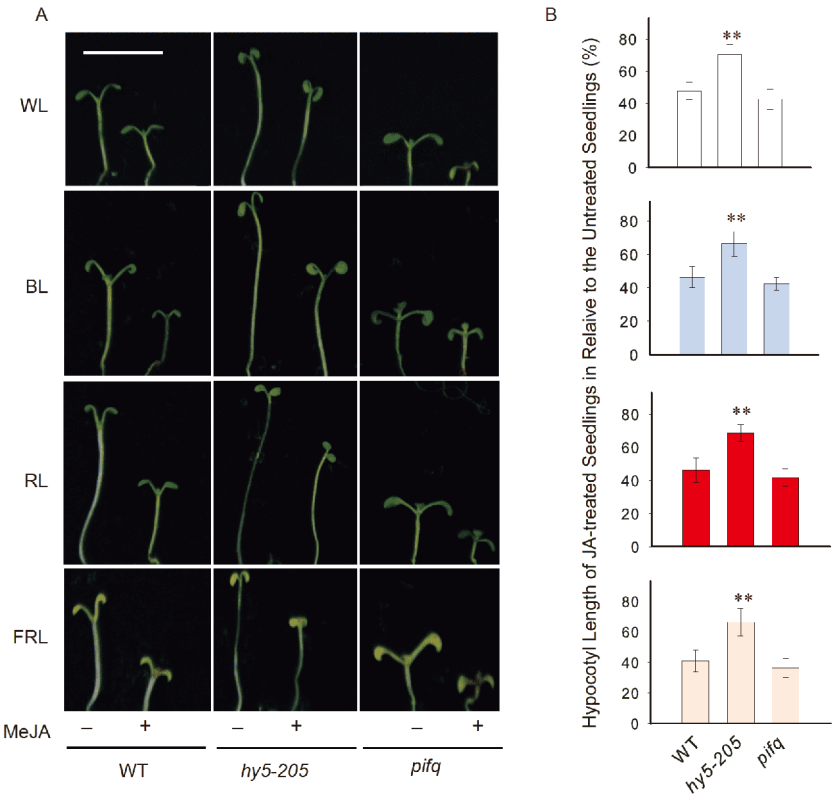

Figure 3 HY5 is essential for JA-repressed hypocotyl elongation. A, The hypocotyl phenotype of 6-day-old WT, *hy5-205*, *pifq* seedlings treated without (–) or with (+) 10 μmol L^{-1} MeJA under white light (WL), blue light (BL), red light (RL), and far-red light (FRL), respectively. Scale bar, 5 mm. B, Relative hypocotyl length of WT, *hy5-205*, *pifq* seedlings treated with10 μmol L^{-1} MeJA (+) compared with that of untreated (–) seedlings grown for 6 days under white light (WL), blue light (BL), red light (RL), and far-red light (FRL), respectively. Data are expressed as mean±SD (n=30). Asterisks denote Student's t test significance between WT and *hy5-205* or *pifq* samples (**P<0.01).

LUC expression compared with the control, suggesting that MYC2 activates the *HY5* promoter to positively regulate P_{HY5}-*LUC* expression. Similarly, MYC3 and MYC4 can also positively regulate P_{HY5}-*LUC* activity (though to a lesser extent than MYC2) (Figure 4D). The above-described results suggest that MYC2, MYC3, and MYC4 activate *HY5* promoter to induce *HY5* expression, in supportive to our above-mentioned observation that MYC2/MYC3/MYC4 are required for JA induction on *HY5* expression (Figure 4A).

JA regulates expression of HY5-targeted genes

It is known that HY5 promotes seedling photomorphogenesis via directly targeting a set of light-responsive genes including the cell expansion-related genes *Small Auxin Up RNA62* (*SAUR62*) and *Expasion2* (*EXP2*) (Cosgrove, 2000; Lee et al., 2007; Sun et al., 2016). Having shown that JA suppresses hypocotyl elongation by activating *HY5* expression (Figure 4A, Figure S4 in Supporting Information), we further investigate whether JA affects the expression of HY5-targeted genes.

As shown in Figure 5A, exogenous application of MeJA decreased the transcript levels of *SAUR62* and *EXP2* in WT, suggesting that JA represses the expression of *SAUR62* and *EXP2*. Furthermore, we found that such JA repression on the expression of *SAUR62* and *EXP2* was severely attenuated in *coi1-8*, *myc2/3/4* as well as *hy5-205* mutants. These results together demonstrate that JA represses the expression of HY5-targeted genes and that COI1 and MYCs are required for JA inhibition on the expression of HY5-targeted genes, suggesting that JA inhibits hypocotyl elongation through repression of the HY5-regulated cell elongation-related genes.

DISCUSSION

Light promotes photomorphogenesis, which is characterized by hypocotyl elongation inhibition, cotyledon expansion, apical hook opening, functional chloroplast development, and pigment accumulation (Chen et al., 2004). Previous reports revealed that JA promotes cotyledon expansion, apical hook opening, and flavonoids accumulation (Li et al., 2014; Shan et al., 2009; Song et al., 2014; Zheng et al., 2017). In this study, we uncover a molecular mechanism underlying how light promotes JA biosynthesis to inhibit hypocotyl elongation and orchestrate seedling photomorphogenesis in *Arabidopsis*. We speculate that plant seeds germinate in

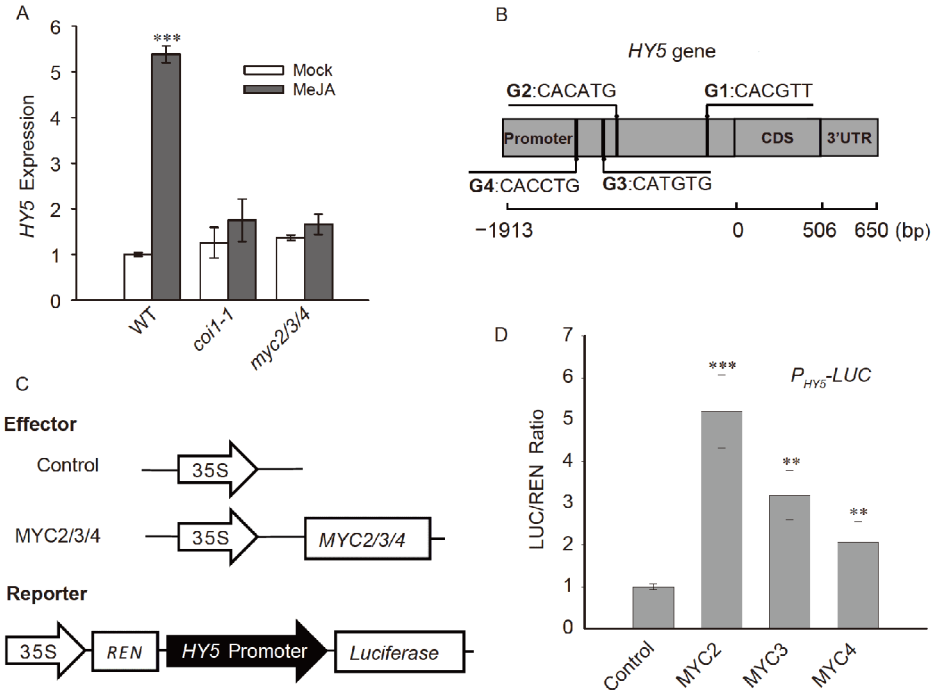

Figure 4 MYC2, MYC3, and MYC4 activate *HY5* expression. A, The *HY5* mRNA level of WT, *coi1-1*, *myc2/3/4* seedlings treated without (Mock) or with 100 μmol L^{-1} MeJA in white light for 8 h. Data are expressed as mean±SD (n=3). The *HY5* mRNA expression level of WT without MeJA treatment was set to 1. Asterisks denote Student's t test significance between the MeJA treated seedlings and untreated seedlings (Mock) (***P<0.001). B, The schematic diagram of the *HY5* gene. G1 to G4 represent the predicted G-box variants of the *HY5* promoter. Numbers indicate the nucleotide sites relative to the first nucleotide of the start code (ATG). C, The schematic diagram of the effector and reporter constructs used in the *Arabidopsis* protoplast transient expression assays. D, Transient expression assays show that P_{HY5}-*LUC* expression was activated by MYC2, MYC3, and MYC4. The LUC/REN ratio indicates P_{HY5}-*LUC* activity relative to the activity of REN driven by 35S promoter. Data are expressed as mean±SD (n=3). Asterisks denote Student's t test significance between the control and MYC2, MYC3, or MYC4, respectively (**P<0.01, ***P<0.001).

subterranean darkness, in which the etiolated seedlings retain JA at an extremely low level for rapid growth of hypocotyl to successfully emerge from the soil. While, after growing toward the soil surface, photoreceptors (such as Phys and CRYs) sense light to significantly induce the biosynthesis of JA, which is perceived by receptor COI1 that recruits repressor proteins JAZs for degradation and subsequently activates transcription factors MYC2/MYC3/MYC4, thereby activating *HY5* expression to regulate the expression of downstream target genes to undergo photomorphogenesis (such as cell elongation-related genes essential for hypocotyl elongation, and other unidentified target genes for cotyledon opening and flavonoids accumulation) (Figure 5B).

It is known that light induces the expression of *HY5* transcript (Osterlund et al., 2000), enhances the stability of HY5 protein via reducing COP1 protein accumulation in the nucleus (Ang et al., 1998; von Arnim and Deng, 1994), and increases biological activity of HY5 via dephosphorylating HY5 protein (Hardtke, 2000). This work reveals that light promotes JA biosynthesis to activate MYC2/MYC3/MYC4 transcription factors, which further activates the expression of *HY5* transcript. It would be of interest to explore whether JA affects the stability or activity of HY5 protein to promote photomorphogenesis.

A recent report concluded that MYC2 acts as a negative regulator of blue light response based on analysis of the single mutant *myc2-3* showing shorter hypocotyl under blue light (Chakraborty et al., 2019), which is inconsistent with our observation. We showed multiple lines of genetic and molecular evidence, through analysis of single, double, and triple mutants as well as overexpression lines of *MYC2/MYC3/MYC4*, to reveal that MYC2/MYC3/MYC4 are positive regulators to transcriptionally activate *HY5* expression and promote JA inhibition on hypocotyl elongation in the blue light, red and far-red light conditions. Moreover, we demonstrate that MYC2/MYC3/MYC4 activate the promoter of *HY5* to induce the expression of *HY5* that represses expression of *SAUR62* and *EXP2*, the HY5-targeted cell elongation-related genes, and mediates JA-inhibited hypocotyl elongation. It remains to be elucidated whether MYC2/MYC3/MYC4 also regulate other HY5-targeted genes essential for seedling photomorphogenesis.

MATERIALS AND METHODS

Plant materials and growth conditions

The *Arabidopsis thaliana* WT and mutants used in this re-

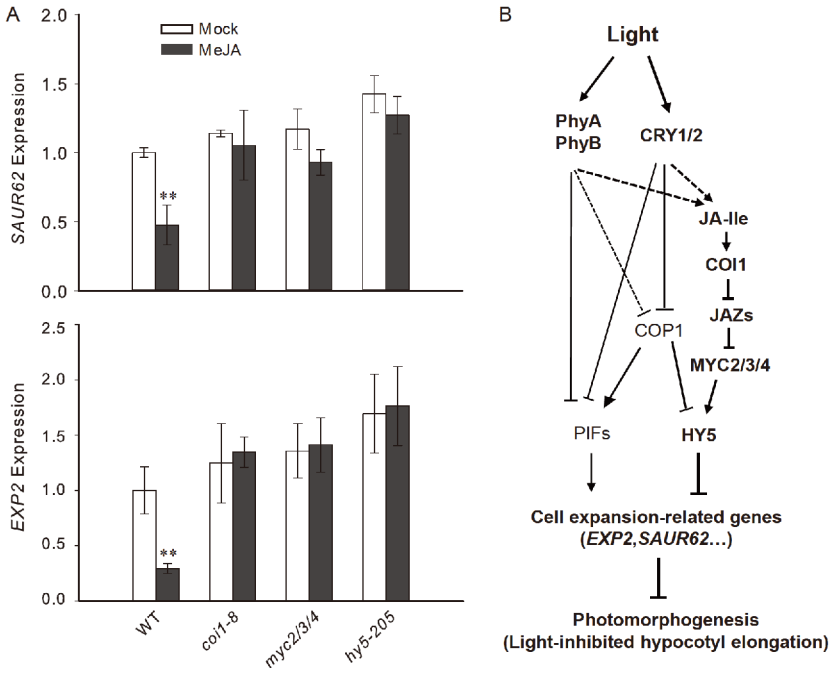

Figure 5 JA regulates HY5-targeted cell elongation-related genes. A, The mRNA level for *SAUR62* or *EXP2* of WT, *coi1-8*, *myc2/3/4*, *hy5-205* seedlings treated without (Mock) or with100 μmol L^{-1} MeJA in white light for 8 h. Data are expressed as mean±SD (n=3). The mRNA expression level of indicated genes in WT without MeJA treatment was set to 1. Asterisks denote Student's t test significance between the MeJA treated seedlings and untreated (Mock) seedlings (**P<0.01). B, Signaling pathways for photomorphogenesis. Previous studies have illustrated two major branches (COP1-HY5 and PIFs) modulating photomorphogenesis (Chen et al., 2011; Jiao et al., 2007; Kami et al., 2010; Su et al., 2017; Yang et al., 2017). Our work suggests that light, sensed by photoreceptors (such as PhyA, PhyB, and CRY1/2), promotes biosynthesis of JA, which is perceived by COI1 that recruits JAZs for degradation and activates transcription factors MYC2/MYC3/MYC4. These transcription factors further activate the expression of photomorphogenesis regulator *HY5* to repress cell elongation-related genes, thereby inhibiting hypocotyl elongation to undergo seedling photomorphogenesis. Solid lines, direct interactions or regulations; dashed lines, indirect interactions or regulations.

search were all in Columbia-0 (Col-0) background. Mutants *cry1/2* (Ahmad et al., 1998), *phyB-9* (Reed et al., 1993), *phyA-211* (Whitelam et al., 1993), *coi1-1* (Xie et al., 1998), *coi1-8* (Yan et al., 2009), *JAZ1Δ3A* (Thines et al., 2007), *myc2-2* (Boter et al., 2004), *myc2/3*, *myc2/3/4*, *MYC2-OE*, *MYC3-OE*, *MYC4-OE* (Qi et al., 2015), *hy5-205* (Osterlund et al., 2000), and *pifq* (Leivar et al., 2008) were described previously.

The *Arabidopsis* seeds were surface-sterilized with 20% bleach for 8 min, sown on Murashige and Skoog medium (Sigma-Aldrich, USA) containing 2% sucrose and 0.6% agar for germination and growth, placed at 4°C in the dark for 3 d, transferred to white light for 6 h to induce seed germination, then placed in the indicated light conditions for 6 d at 22°C. White, blue, red, or far-red light was supplied by LED light sources. For the experiment of MeJA-inhibited hypocotyl elongation, seedlings were cultured with white, blue, red, or far-red light fluence rates of 25, 8, 6, 1.5 μmol m^{-2} s^{-1}, respectively.

For the experiment of different light intensity conditions, WT seedlings were cultured with white light fluence rates of 0, 10, 25, 85 μmol m^{-2} s^{-1} for 6 d at 22°C, respectively. Light spectrum and intensity were measured with a Hand-held HR350 spectral radiometer (HiPoint).

Hypocotyl length measurement

After 6-day growth on MS medium with different treatments, the seedlings were photographed with a scanner. The hypocotyl length of seedlings was measured by the Digimizer software.

JA qualification and LC-MS/MS

The 6-day-old seedlings cultured in different white light intensity conditions (0, 10, 25, 85 μmol m^{-2} s^{-1}) were collected, weighed, and frozen in liquid nitrogen immediately. The metabolites extraction of samples, LC-MS/MS analysis, and data processing were previously described, with some modifications (Glauser et al., 2013). About 100 mg of freeze-dried powder was extracted with 99.5% isopropanol: 0.5% formic acid buffer containing internal reference d^5-JA. After centrifugation, supernatants were dried in a LABCONCO CentriVap vacuum centrifugal concentrator and resuspended with 85% methanol solvent. Then, a Waters C18 SPE tube was used for sample purification. The eluent was dried and resuspended with 50 μL 60% methanol solvent.

Positive/negative ionization mode data were acquired using an ACQUITY UPLC I-Class (Waters, USA) coupled

to a 4500 QTRAP triple quadrupole mass spectrometer (AB SCIEX) equipped with a 50×2.1 mm, 1.7 μm ACQUITY UPLC™ BEH C18 column (Waters, USA). 10 μL samples was loaded each time, and then eluted at a flow rate of 200 μL min^{-1} with initial conditions of 50% mobile phase A (0.1% formic acid in Acetonitrile) and 50% mobile phase B (0.1% formic acid in water) followed by a 10-min linear gradient to 100% mobile phase A. The quantitation mode was multiple reaction monitoring (MRM) mode using the mass transitions. The selected MRM transitions were 214.1494>62.0322 for d^5-JA, 322.202>130.0087 for JA-Ile. Four biological replicates were analyzed for each treatment.

RNA extraction and quantitative real-time PCR

The 6-day-old seedlings were treated with ethanol solvent or 100 μmol L^{-1} MeJA under 25 μmol m^{-2} s^{-1} white light for indicated time. Then the harvested materials were used for RNA extraction and reverse transcription (TRANSGEN, China). Quantitative real-time PCR analysis was performed using the Applied Biosystems QuantStudio 3 real-time PCR systems. The *ACTIN2* (At3g18780) was used as an internal reference. Primers used are presented in Table S1 in Supporting Information.

Arabidopsis protoplast transient expression assay

The pGreenII-62-MYC2/MYC3/MYC4 plasmids were previously described (Qi et al., 2015). The 1,913 bp *HY5* promoter region was amplified by primers ProHY5-KpnI-F and ProHY5-BamHI-R and ligated into the pGreenII-0800 to generate the P_{HY5}-*LUC* reporter construct. Primers used are presented in Table S1 in Supporting Information.

The *Arabidopsis* protoplast was prepared and transfected with the effector and reporter plasmids. The firefly LUC and renilla luciferase (REN) intensities were measured using the Dual-Luciferase Reporter Assay System (Promega, USA), and the LUC/REN ratio was measured and presented.

Accession numbers

Sequence data can be found in The Arabidopsis Information Resource (TAIR) under accession numbers: At3g45140 (*LOX2*), At3g25780 (*AOC3*), At5g42650 (*AOS*), At4g08920 (*CRY1*), At1g04400 (*CRY2*), At2g18790 (*phyB*), At1g09570 (*phyA*), At2g39940 (*COI1*), At1g19180 (*JAZ1*), At1g32640 (*MYC2*), At5g46760 (*MYC3*), At4g17880 (*MYC4*), At5g11260 (*HY5*), At1g09530 (*PIF3*), At5g05290 (*EXP2*), and At1g29430 (*SAUR62*).

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

Acknowledgements *We thank Dr. Deng X.W. (Peking University) for providing hy5-205, pifq mutant seeds; Dr. Yang H.Q. (Fudan University) for providing cry1/2, phyB-9, phyA-211 mutant seeds; and Lu Meng, Dr. Ran Du for their technical support. This work was supported by the National Key R&D Program of China (2016YFA0500501) and National Natural Science Foundation of China (31630085).*

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SUPPORTING INFORMATION

Figure S1 The expression of JA biosynthesis genes *AOC3 and AOS* is elevated upon light exposure.

Figure S2 MYC2, MYC3, and MYC4 function redundantly to regulate JA- repressed hypocotyl elongation.

Figure S3 Overexpression of *MYC2*, *MYC3*, and *MYC4* promote JA inhibition on hypocotyl elongation.

Figure S4 *HY5* is highly expressed in JA-treated *MYC2* overexpression line.

Figure S5 The *PIF3* expression is not significantly affected by JA.

Table S1 The primers used in this study

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