Transcriptional interplay between gibberellic acid and jasmonic acid modulates root growth in *Arabidopsis thaliana*

Ernesto Vázquez-Chimalhua [1], Pedro Iván Huerta-Venegas[2], Tzvetanka D. Dinkova[1], León Francisco Ruíz-Herrera[2], Javier Raya-González[3], José López-Bucio[2]

[1] Departamento de Bioquímica, Facultad de Química, Universidad Nacional Autónoma de México, Ciudad de México, México.
[2] Instituto de Investigaciones Químico Biológicas, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México.
[3] Facultad de Químico-Farmacobiología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México.

Abstract

Phytohormones tune growth and development in response to environmental cues. Positive and negative feedbacks enable genetic responses from every signaling molecule and their transductional interactions. For example, xylem formation in roots of *Arabidopsis thaliana* is promoted by jasmonic acid and antagonized by cytokinin. In contrast, root meristem development is synergistically stimulated by auxins and cytokinins, which act as morphogens according to their local concentrations. Here, we report that gibberellic acid, a major regulator of stem elongation, cross-talks with jasmonic acid, the canonical defense sentinel, at the transcriptional level and leads to root growth inhibition. Gibberellic acid reduced root growth and exacerbated the induction of jasmonic acid-related genes upon supplementation of both phytohormones. On the other hand, jasmonic acid upregulates gibberellic acid response, indicating a positive feedback loop. These results open the possibility to manage plant growth and defense via the formulation of phytohormone mixtures that orchestrate fundamental cell processes.

***Keywords*:** jasmonic acid, gibberellic acid, root development, *Arabidopsis thaliana.*

Introduction

Phytohormones regulate morphological, physiological and genetic processes. Gibberellic acid (GA) and jasmonic acid (JA) play critical roles in stem elongation and plant protection against wounding and herbivory, respectively. The activation of JA signaling pathway and response stimulates the synthesis of defense compounds, which is costly and overall, reduces plant growth (Zrimec *et al.,* 2025). JA is synthesized by organisms belonging to phylogenetically diverse kingdoms such as bacteria, fungi and plants, and shares structural similarity with animal prostaglandins (Forchetti *et al*., 2007; Chini *et al*., 2018; Sá-Nakanishi *et al*., 2018). On the other hand, there are nearly 130 different types of GAs synthesized by microbes and plants (Zhang *et al.,* 2022).

GA compounds are based on a gibbane ring and some of these are composed by a tetracyclic diterpenoid C_{20} dicarboxylic acid or C_{19} monocarboxylic acid skeleton (Salazar-Cerezo *et al.,* 2018). The bioactive GA_1, GA_3 and GA_4 are perceived in the nucleus by the receptor GIBBERELLIN INSENSITIVE DWARF1 (GID1). GA-GID1 dimer binds to DELLA protein in a GA-dependent manner to build the GA-GID-DELLA complex. DELLA proteins are nuclear repressors including GIBBERELLIC ACID INSENSITIVE (GAI), REPRESSOR OF *GA1-3* (RGA), RGA-Like1 (RGL1), RGL2 and RGL3. Later on, DELLA is recruited by SLEEPY1 (SLY1), a specific F-box protein member of the SCF^{SLY1} complex for poly-ubiquitination and successive degradation by the 26S proteasome. Degradation of DELLA repressors releases MYELOBLASTOSIS (MYB) transcription factors, which trigger the GA response (Ueguchi-Tanaka *et al.,* 2005).

GA is involved in a wide variety of physiological process from seed germination to flowering (Hedden, 2020). Nonetheless, their roles in root development are not

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Corresponding author
Ernesto Vázquez Chimalhua
email: belengwer@yahoo.com
ORCID: 0000-0002-3118-4995

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well known. In *A. thaliana* roots, GA specifies xylem cell identity influencing auxin efflux carrier *PIN-FORMED1* (*PIN1*). Moreover, GA promotes early stages of secondary xylem formation and expansion of vessel cells (Mäkilä *et al.,* 2023).

GA is involved in longitudinal and radial root development. GA application or loss-of-function of the RGA repressor influences root meristems involving the transcription factor SCARECROW (SCR) (Moubayidin *et al.,* 2010; 2016). For radial axis pattering, GA plays a key role in the ground tissue, particularly, in middle cortex (MC). During early root development, GA is accumulated and the MC formation is inhibited through CYCLIN D6;1 (CYCD6;1), a cell cycle regulator that promotes cell division (Paquette and Benfey, 2005). Interestingly, GA acts as a negative regulator of lateral and adventitious root formation, under normal growth conditions or in response to nutrient deficiency (Hetherington *et al.,* 2021; Jing *et al.,* 2024).

JA is a biotic stress-related hormone that activates defensive reactions and controls root growth and branching (Staswick *et al.,* 1992; Ishimura *et al*., 2018; Major *et al.,* 2020). Within the cell nucleus, jasmonic acid-isoleucine (JA-Ile) is perceived by the F-box protein receptor CORONATINE INSENSITIVE1 (COI1), a specific moiety of the ubiquitin ligase complex SCF^{COI1}, or by the co-receptor complex SCF^{COI1}-InsP5-JAZ formed *a priori* (Mosblech *et al*., 2011). JASMONATE ZIM-domain (JAZ) proteins act as transcriptional repressors that bind to and inactivate MYELOCYTOMATOSIS (MYC) transcriptional activators, inhibiting expression of JA responsive genes. JA-Ile-COI1-JAZ interaction ubiquitinates JAZ repressors and promotes their degradation via the 26S proteasome, liberating MYC transcription factors and activating JA response (Li *et al.,* 2024). JA inhibits root development interfering with cell cycle progression and expression of stem cell niche maintenance genes (Chen *et al.,* 2011).

JA and GA may interact at different levels. In response to chewing herbivores, the transcription factor WRKY70 prioritizes defense rather than growth. In rice, WRKY70 upregulates JA-biosynthetic genes *hervibore-induced type2 13-lipoxygenase* (*OsHI-LOX*) or *OsAOS2* and downregulates GA-biosynthetic *gibberellin 20-oxidase7* (*GA20ox7*) gene (Li *et al.,* 2015). The JAZs repressors compete with the transcriptional activators of GA signaling PHYTOCHROME INTERACTING FACTORS (PIFs) for the binding to DELLAs. The complex JAZ-DELLA allows the PIFs bind to GA-responsive gene promoters. Perception of JA prompts degradation of JAZ proteins via ubiquitin-26S proteasome, antagonizing GA signaling by means of the PIF-DELLA dimerization (Yang *et al.,* 2012). Conversely, DELLAs bind to JAZs in competition with MYC2. GA perception promotes ubiquitin-26S proteasome degradation of DELLAs, releasing JAZs and subsequently dimerize with its cognate to form JAZ-MYC2 inhibitory complex (Hou *et al.,* 2010).

Here, we report a synergistic interaction of GA with JA, which leads to root growth inhibition in *Arabidopsis thaliana*. GA inhibits root growth from 100 µM onwards, whereas JA inhibits root growth at lower concentrations (i.e. 4 µM). Seedlings treated with a combination of GA plus JA (GA+JA) show an increased root growth inhibition. Analysis of *JAZ1/TIFY10A-GFP*, a JA-related gene marker, indicated that GA does not activate JA-responsive gene expression. However, the GA+JA condition triggered an enhanced reporter gene expression that the single JA treatment, suggesting a synergistic interaction. By using the JA insensitive mutant *coi1-1*, we observed that synergistic root growth inhibition induced by GA+JA operates in a COI1-dependent manner, since *coi1-1* mutant is more resistant to the combined treatment than Col-0 seedlings. Moreover, JA activates gibberellin responsive *RGL2::uidA* reporter gene, indicating that both phytohormones possibly interact at transcriptional level in *A. thaliana*. These data help to understand hormone interactions critical to protect plants against pathogens or to withstand environmental stress conditions.

Materials and methods

Plant materials and growth conditions

In this study, experiments were conducted seven days post germination in *Arabidopsis thaliana* seedlings, including the wild-type Columbia-0 (Col-0), the transgenic lines *JAZ1/TIFY10A-GFP* (Grunewald *et al.,* 2009) and *RGL2::uidA* (Lee *et al*., 2002), and the *coi1-1* mutant (Feys *et al.,* 1994). Seed preparation involved disinfection with 95% (v/v) ethanol for 5 minutes, followed by 20% (v/v) commercial bleach for 7 minutes, five rinses with sterile distilled water, and 2 days of stratification in darkness at 4 ºC to synchronize germination. Then, seeds were sown on axenic Petri plates containing agar solidified MS 0.2x medium adjusted to pH 7.0, 0.6% (g/L) sucrose, 1% (g/L) phytagar (Phytotechnology Laboratories), and 0.09% (g/L) Murashigue and Skoog Basal Salts Mixture (Sigma Aldrich). Plates were placed in a vertical position to allow root growth and shoot development into a plant growth chamber Percival AR-95L with a photoperiod of 16 h light and 8 h darkness, light intensity of 300 µmol/m^{2}s, and a temperature of 22 ºC.

Chemical compounds

The MS 0.2x medium was supplemented with increasing concentrations of gibberellic acid (GA), jasmonic acid (JA), and the combination of GA+JA to evaluate their effects on the *Arabidopsis thaliana* primary root growth. GA_3 (CAS number: 77-06-5) and JA (CAS number: 77026-92-7) were purchased from Sigma-Aldrich and dissolved in dimethyl sulfoxide (DMSO) or ethanol, correspondingly. For control conditions, the MS 0.2x medium was supplemented with the maximum volume of absolute ethanol employed in the experimental treatments.

Visualization of gene expression

The morphology of the root meristem and fluorescence signals from propidium iodide (PI) and green fluorescent protein (GFP) of the *JAZ1/TIFY10A-GFP* reporter gene were visualized and registered using a confocal microscope (Olympus FV1200). For sample preparation, roots were placed on a microscope slide with 90 µL of PI (0.5 mg/mL) and carefully covered with a coverslip. Fluorescence imaging was performed using the following parameters: PI was excited at 568 nm with emission detected at 585–610 nm, while GFP was excited at 458 nm with emission detected at 505–550 nm. Individual micrographs were acquired and subsequently merged to generate the final composite image.

To visualize the expression of the *RGL2::uidA* reporter gene, *Arabidopsis* seedlings were incubated overnight at 37 °C in an X-gluc staining solution (pH 7.0), and root apices were imaged using Nomarski optics (Leica DM5000B). The *uidA* gene encodes β-glucuronidase (GUS), which catalyzes the hydrolysis of X-gluc (5-bromo-4-chloro-3-indolyl-β-D-glucuronide), producing an insoluble blue color to indicate reporter gene expression (Jefferson *et al.,* 1987). The staining procedure was conducted according to Jefferson *et al.* (1987) with some modifications: the incubation X-gluc staining solution contained X-gluc 1 mg/mL, $NaHPO_4$ 50 mM, Na_2HPO_4 50 mM, EDTA 10 mM, Triton X-100 0.1% v/v, $K_3Fe[CN]_6$ 2 mM and $K_4Fe[CN]_6$ 2 mM. After incubation, the samples were clarified to enhance visualization. First, treatment with solution 1 (20% v/v methanol and 2% v/v HCl) for 40 minutes at 62 °C, followed by solution 2 (7% w/v NaOH and 60% v/v ethanol) for 30 minutes at room temperature (Malamy and Benfey, 1997). The clearing process was completed by sequential treatment with ethanol at decreasing concentrations (40%, 20%, and 10% v/v) for 30 minutes each. Finally, the cleared samples were mounted on microscope slides with 90 µL of 50% (v/v) glycerol.

Data analysis and software tools

The expression of the *RGL2::uidA* and *JAZ1/TIFY10A-GFP* reporter genes was quantified using the Fiji/ImageJ2 software (available at https://imagej.net/). For GUS activity quantification (Béziat *et al.,* 2017), images in JPG format color type RGB were converted to HSB stack. In saturation channel, expression area from meristem to columella were selected for grayscale values measurement within *RGL2::uidA* primary root. On the other hand, GFP fluorescence was quantified from confocal-microscopy-obtained composite images (.oib format). For this purpose, a defined region of interest (ROI) was selected using the polygon tool and green pixel intensity was measured within the expression area of *JAZ1/TIFY10A-GFP* in primary root. Total green pixel values were normalized by dividing them by the selected area and results were expressed as relative fluorescence units.

R statistical program (available at https://www.r-project.org/) was employed to stablish statistical difference among treatments applying an analysis of variance (ANOVA) followed by Tukey's post hoc test with a significance threshold of $p \leq 0.05$. Statistical differences among treatments are indicated with distinct letters in the graphs.

Results

Gibberellic acid has a mild growth repressing effect in *Arabidopsis* primary root growth at high micromolar concentrations

GA is a well know phytohormone promoting seed germination and stem elongation, but its role in post-embryonic root development has been scarcely investigated. To gain information on this process, the primary root growth in response to low and high GA concentrations was evaluated. GA showed a repressing effect on root growth inhibiting nearly 10% at 100 µM, while 300 µM reduced growth by 35%. This indicates that GA acts as a repressor of root elongation in *Arabidopsis thaliana* (**Figure 1**).

Jasmonic acid represses *Arabidopsis* primary root growth at low micromolar concentrations

To stablish the JA dose for analysis of GA-JA interaction, firstly, we evaluated several JA concentrations on *A. thaliana* root growth. As expected, and according to previous reports (Raya-González *et al*., 2012; Huang *et al*., 2021; Singh *et al*., 2025), JA had a 50% growth inhibition at 1 µM concentration, this effect was maintained at 2 µM and 4 µM (**Figure 2**). These results show the activity of JA in repressing root growth.

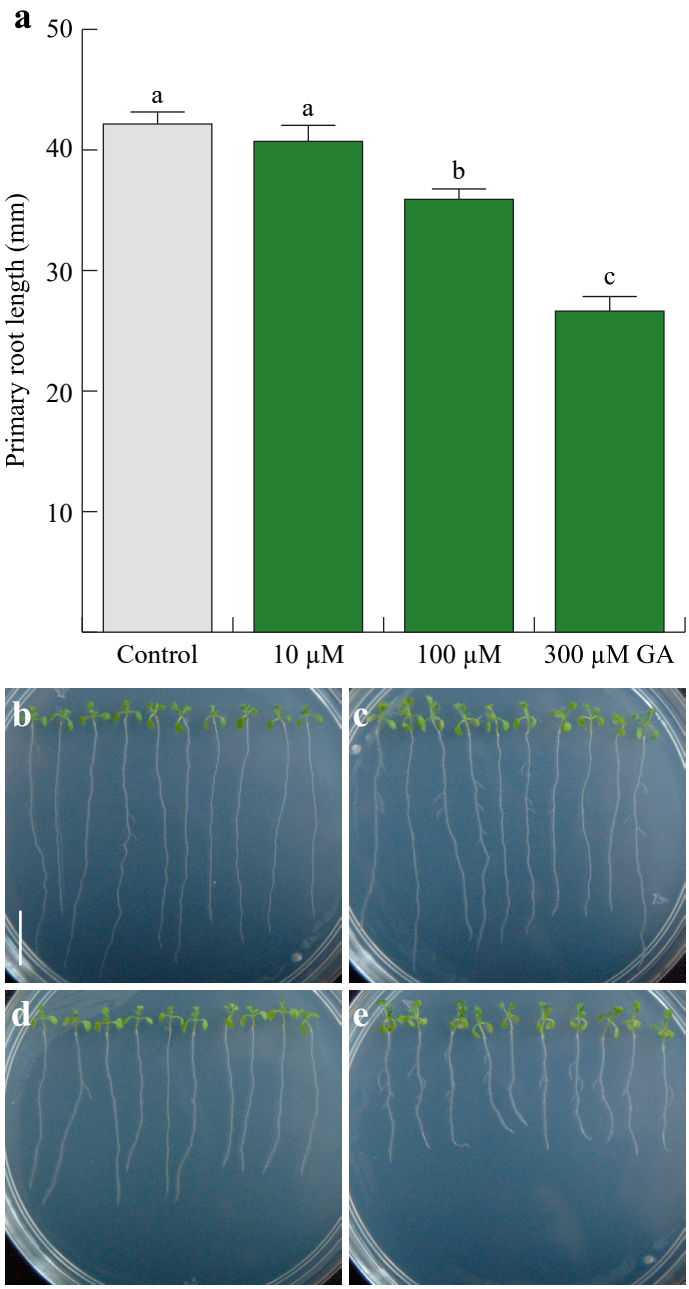

Figure 1. Gibberellic acid inhibits root growth of *Arabidopsis thaliana*. (**a**) Mean primary root length. Representative photos of *A. thaliana* seedlings in control condition (**b**), 10 µM (**c**), 100 µM (**d**), or 300 µM (**e**) GA. Scale bar = 1 cm. Different letters show statistically significant differences via ANOVA and Tukey´s HSD test ($p \leq 0.05$) from 50 seedlings. The experiment was repeated three times with comparable results.

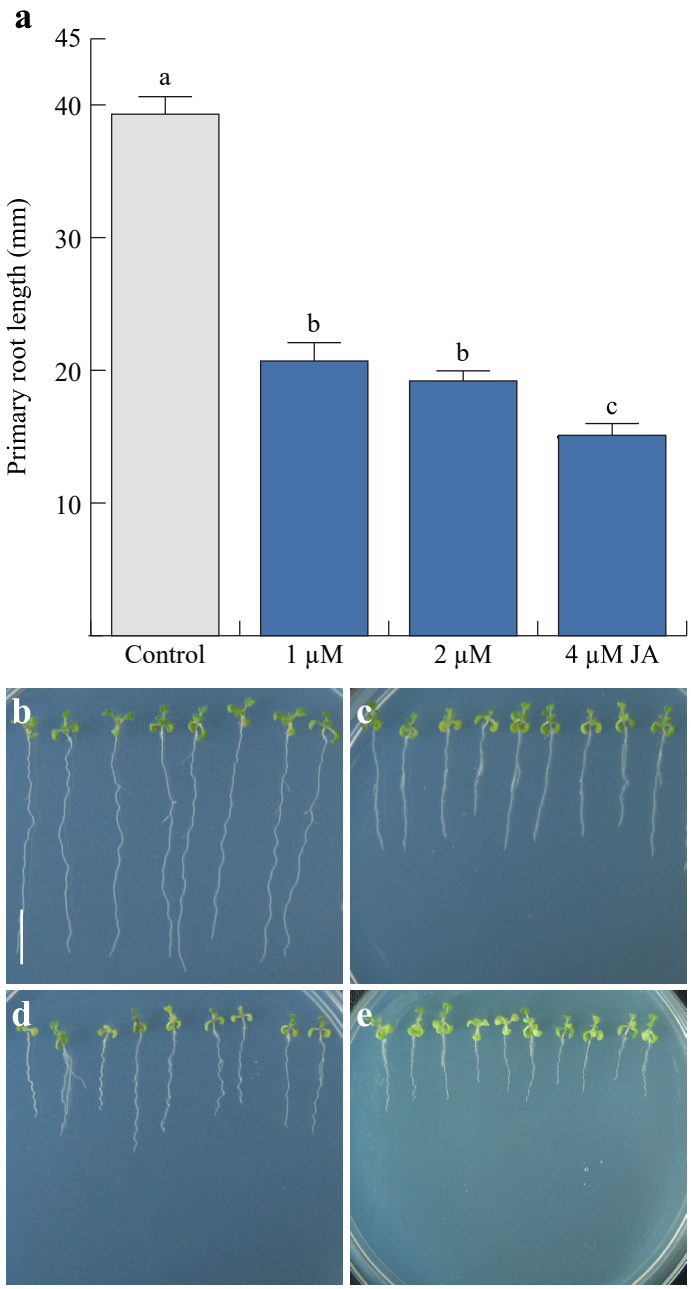

Figure 2. Jasmonic acid inhibits root growth of *Arabidopsis thaliana*. (**a**) Mean primary root length. Representative images of plants treated with the solvent only (**b**), 1 µM (**c**), 2 µM (**d**), or 4 µM (**e**) JA. Different letters indicate statistically significant differences via ANOVA and Tukey´s HSD test ($p \leq 0.05$) from 50 seedlings. Scale bar = 1 cm. The experiment was repeated three times with comparable results.

Gibberellic acid and jasmonic acid synergistically halt root growth

To study GA-JA interaction on root growth, 300 µM GA and 4 µM JA were applied together. Consistently with previous data, GA and JA inhibited primary root growth about 40% and 50%, respectively. However, when plants were grown in media supplemented with GA plus JA (GA+JA), the primary root inhibition was enhanced (about 80%) when compared to individual GA or JA treatments (**Figure 3**), suggesting a synergistic effect on root growth.

Gibberellic acid enhances jasmonic acid-responsive gene expression in *A. thaliana* root tips

The JA signaling pathway is activated upon perception

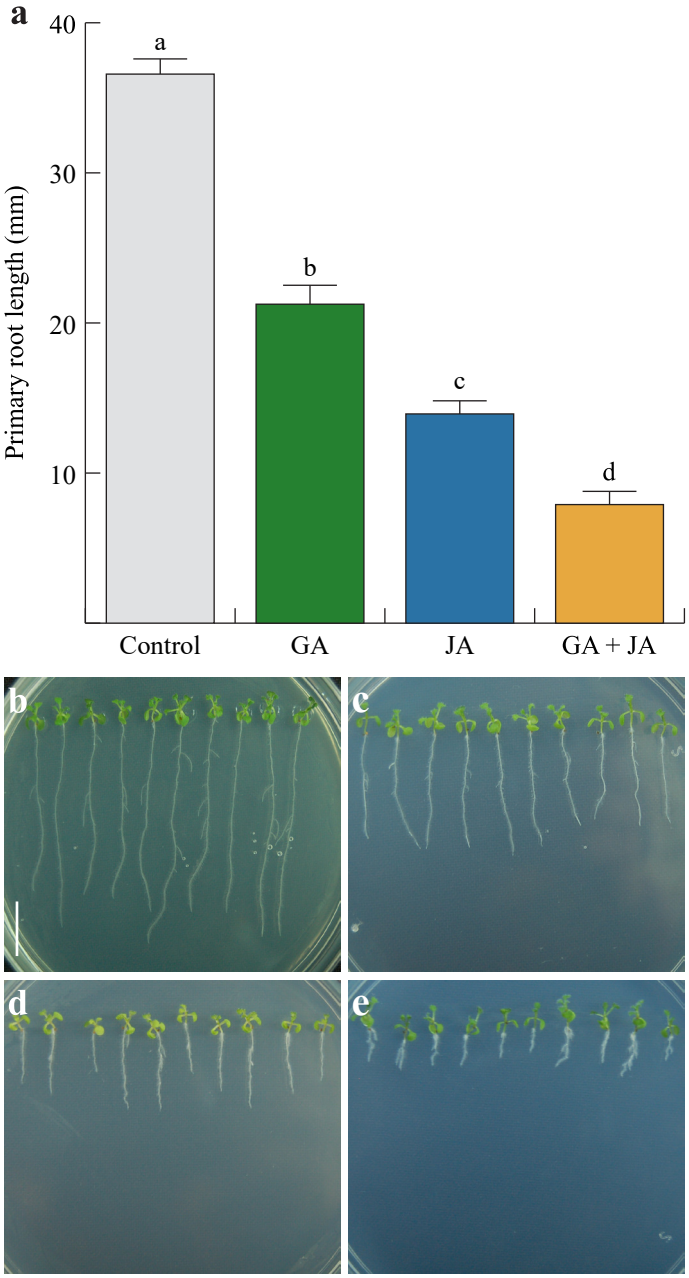

Figure 3. Root growth inhibition in *Arabidopsis thaliana* is exacerbated by GA-JA combination. (**a**) Mean primary root length. Representative images of plants treated with the solvent only (**b**), 300 µM GA (**c**), 4 µM JA (**d**) and 300 µM + 4 µM GA-JA, respectively (**e**). Different letters indicate statistically significant differences from ANOVA and Tukey´s HSD test ($p \leq 0.05$) from 50 seedlings. Scale bar = 1 cm. The experiment was repeated three times with comparable results.

of JA-Ile by its receptor COI1, a subunit of SCF^{COI1} complex, which leads to ubiquitination of JAZ transcriptional repressors and its posterior degradation by the 26S proteasome. The liberation of JAZ repressors allows transcriptional factor MYC2 to activate JA responsive genes. To explore whether GA is involved in JA response, we took advantage of the *A. thaliana* reporter line *JAZ1/TIFY10A-GFP*, a JA-inducible gene expression marker, to test the effects of the solvent only, 300 µM GA, 4 µM JA and combined treatments. Under control growth condition and GA treatment, *JAZ1/TIFY10A-GFP* reporter gene was not expressed in root tips (**Figure 4 a-c**). As expected, JA induced *JAZ1/TIFY10A-GFP* expression, preferentially in the external root tip cell layers, including epidermis, cortex and the root cap (**Figure 4 d)**. Interestingly, roots exposed to the GA+JA treatment, not only enhance *JAZ1/TIFY10A-GFP* expression, but also its expression domain, covered most root tissues (**Figure 4 e**). This indicates that GA acts synergistically, promoting JA response.

Synergistic interaction of gibberellic acid with jasmonic acid is dependent of COI1

To elucidate whether the GA+JA interaction for root growth inhibition involves the jasmonic acid receptor COI1, the growth of wild-type (Col-0) plants and *coi1-1* mutants was compared. Col-0 seedlings were germinated and grown under standard growth conditions, whereas those of *coi1/coi1* homozygous plants were germinated and selected in growth media supplemented with 4 µM JA. Four days post germination, Col-0 and *coi1-1* mutant seedlings were transferred to control medium or medium supplemented with GA (500 µM), JA (32 µM) or GA+JA (500 µM and 32 µM, respectively), and three days after transfer, primary root growth was recorded. GA did not affect root growth in Col-0 or *coi1-1* seedlings, compared with control condition. In contrast, JA inhibited root growth of Col-0 but not *coi1-1* seedlings. In GA+JA treatment, root growth inhibition of Col-0 was about 90%, while in *coi1-1* it was nearly 50% (**Figure 5**).

Gibberellic acid-jasmonic acid treatment causes the collapse of the root tip

Detailed analysis of the root tips in Col-0 and *coi1-1* seedlings shows that GA treatment did not affect the morphology and structure of the root tips of either genotype, whereas Col-0 seedlings exposed to JA developed thinner primary roots than control condition, but not the *coi1-1* mutant. GA+JA treatment drastically affected the root tip structure of Col-0 seedlings, showing primary roots thinner and root meristem shorter than control condition, whereas *coi1-1* mutant roots manifest a slightly affectation (**Figure 6**). Thus, the jasmonic acid receptor COI1 plays an important role in cellular and structural adjustments upon combined GA and JA treatment.

Jasmonic acid activates gibberellic acid-responsive gene expression in the *Arabidopsis* primary root

To determinate whether JA actives a GA response,

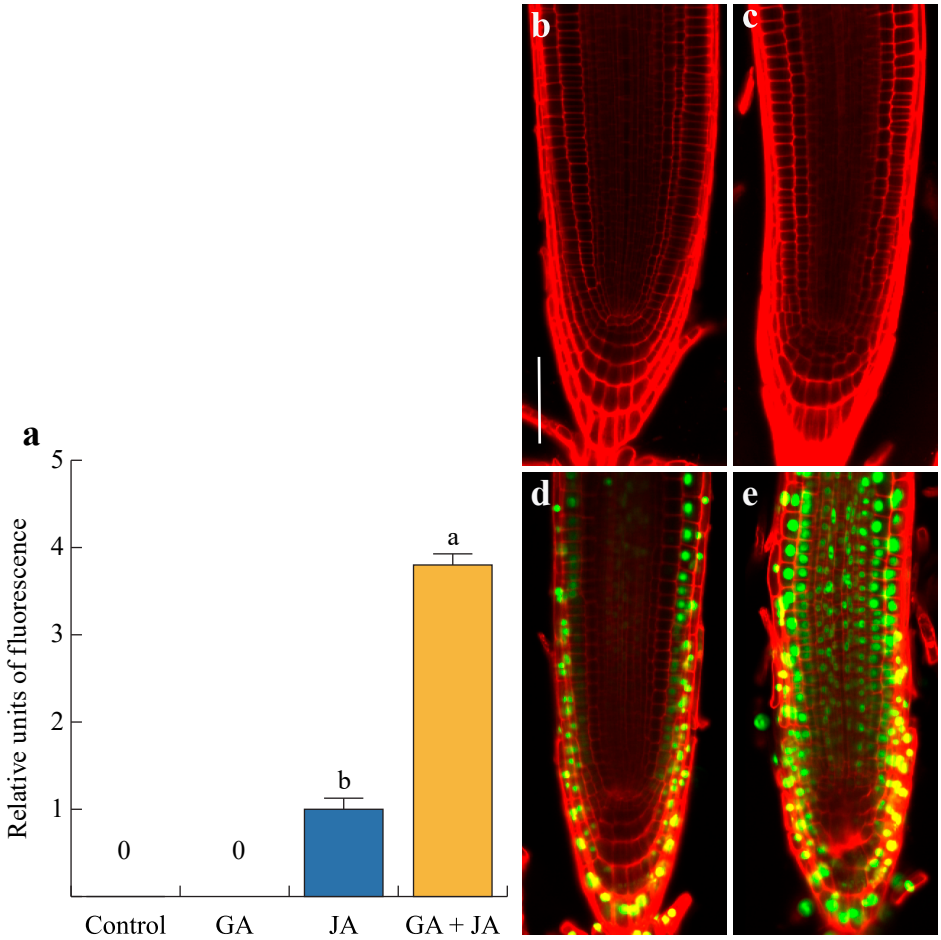

Figure 4. Gibberellic acid synergistically influences jasmonic acid-inducible gene expression. (**a**) Relative units of *GFP* fluorescence in *JAZ1/TIFY10A-GFP* expressing *Arabidopsis* seedlings. Representative confocal micrographs of *JAZ1/TIFY10A-GFP* roots in control condition (**b**), 300 µM GA (**c**), 4 µM JA (**d**) and GA+JA (**e**). Different letters indicate statistically significant differences by ANOVA and Tukey´s HSD test ($p \leq 0.05$) from 10 seedlings. Scale bar is 100 µm. The experiment was repeated three times with comparable results.

we evaluated the expression of GA-responsive gene expression by using seedlings harboring the *RGL2::uidA* gene construct. *RGL2* gene encodes a transcriptional regulator activated by GA. Under control conditions, *RGL2* is weakly expressed in the root cap. The JA negative effect on primary root growth and meristem were accompanied with a strong *RGL2* expression in the root tips showed in blue color (**Figure 7**).

Discussion

Phytohormones may interact at the biosynthesis, perception and genetic response levels. The concentration of gibberellic acid (GA) starts to decline after seed germination, and between 3- and 5-days post germination *RGA* accumulates and upregulates expression of type-B *ARABIDOPSIS RESPONSE REGULATOR1* (*ARR1*) from cytokinin response pathway that together with auxin signaling determine root meristem size and growth (Moubayidin *et al.,* 2010). Moreover, GA is synthetized and concentrated in cortex and endodermis to sustain cell expansion and division (Barker *et al.,* 2021). The fact that high concentrations of GA are required to inhibit growth suggests that modulating elements are required to amplify its effect. This could indeed be confirmed, as JA acts as a repressor of root elongation at low concentrations. The combined application of GA and JA exacerbated root growth inhibition in Col-0 seedlings, which correlated with upregulation of *JAZ1/TIFY10A-GFP* JA-responsive gene expression in comparison with JA treatment alone. Interestingly, the *coi1-1* mutant, defective on the JA receptor, had resistance to this hormonal combination suggesting its involvement in mediating the growth repressing effect.

Noteworthy, GA-responsive *RGL2::uidA* reporter gene was activated by JA treatment. This indicates a positive feedback loop among the transcriptional components that explains the reduction of root growth of Col-0

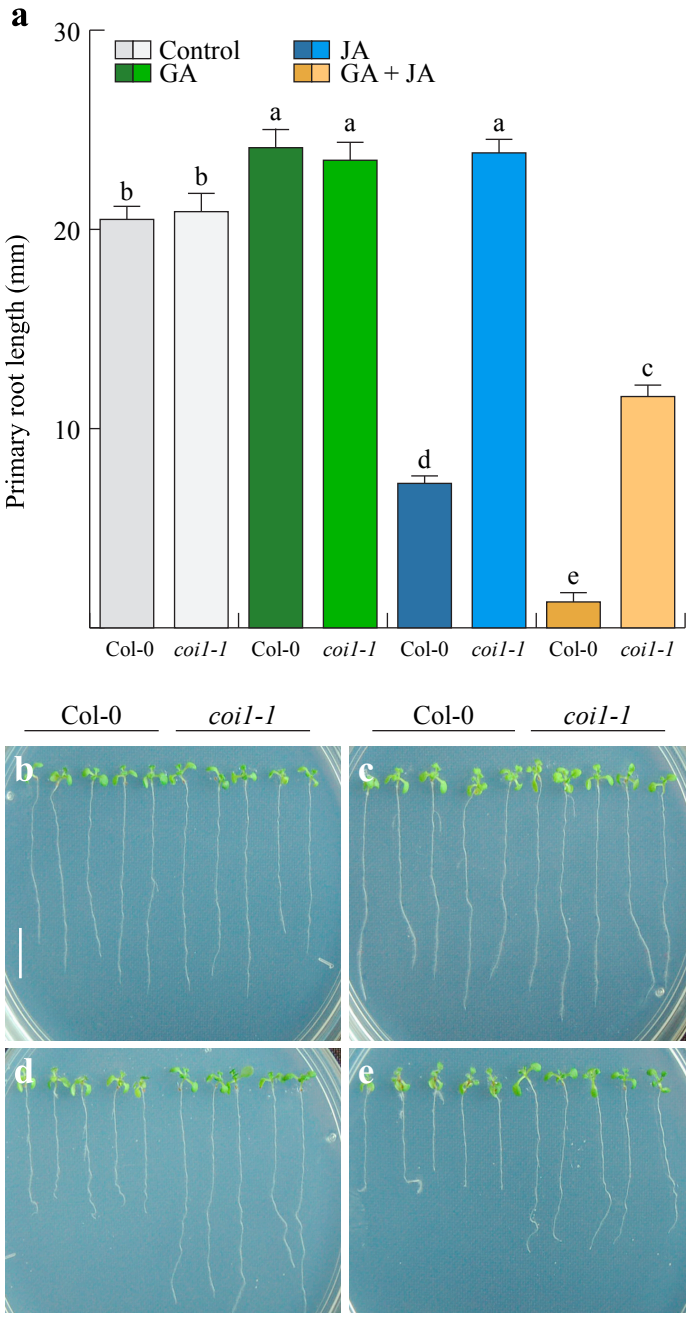

Figure 5. Root growth reduction in *coi1-1* mutant in combined application of gibberellic and jasmonic acid. (**a**) Primary root length. Representative photos of Col-0 and *coi1-1* seedlings grown side by side on the same plate three days after transfer to control condition (**b**), 500 µM GA (**c**), 32 µM JA (**d**) and 500 µM GA + 32 µM JA (**e**). Different letters indicate statistically significant differences by ANOVA and Tukey´s HSD test ($p \leq 0.05$) from 20 seedlings. Scale bar = 1 cm. The experiment was repeated three times with comparable results.

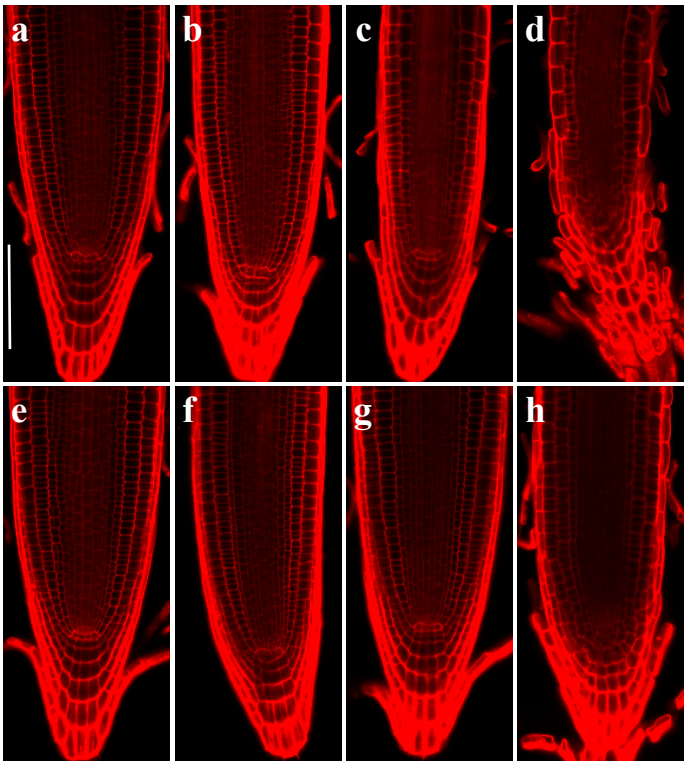

Figure 6. Combination of gibberellic acid and jasmonic acid disrupts root meristem structure in the WT but not in *coi1* mutants. Representative confocal micrographs of Col-0 (**a-d**) and *coi1-1* (**e-h**) mutant roots three days after transfer to solvent only or hormonal treatments. Control (**a**, **e**), 500 µM GA (**b**, **f**), 32 µM JA (**c**, **g**), and 500 µM GA + 32 µM JA (**d**, **h**). Scale bar = 100 µM. The experiment was repeated three times with comparable results.

and the partial resistance of *coi1-1* mutant to GA and JA combination. These results raise the question of how does JA interact with GA and the role of COI1 in the process. The precise mechanism by which GA and JA enhances JA response and the molecular components involved in this interaction remain to be investigated.

Recent studies on the development of the stamen in *A. thaliana* showed that the transcriptional regulators JAZ and DELLA bind to MYB21 and MYB24 promoters via R2R3 domains to attenuate its function and coordinately suppress filament elongation (Huang *et al.,* 2020). Additionally, JA-dependent MYC2, MYC3, MYC4 and MYC5 transcription factors interact with the GA-dependent transcription factors MYB21 and MYB25 to form a MYC-MYB complex. This complex unveils a fundamental mechanism by which GA and JA cooperate to regulate stamen development and seed production (Qi *et al.,* 2015).

The results suggest that JA controls root development involving GA signaling in *A. thaliana*. JA upregulation of GA responsive *RGL2::uidA* gene expression pointed out that both phytohormones probably interact at the transcriptional level since there was reduction of root growth in *coi1-1* mutant under combined GA and JA treatment. Several reports have described synergistic interactions between GA and JA at transcriptional level. For example, in *A. thaliana* DELLAs act as positive regulators of some transcription factors such as GAI-ASSOCIATED

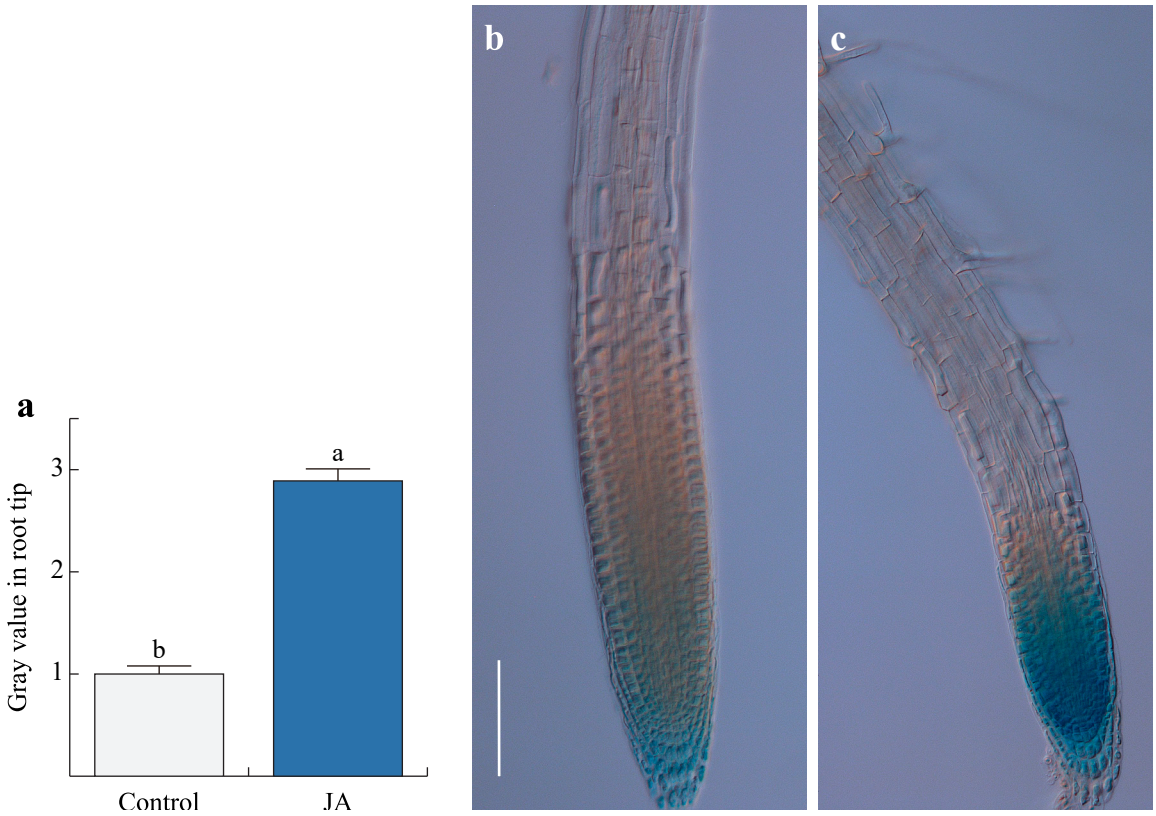

Figure 7. Jasmonic acid activates gibberellic acid related *RGL2::uidA* expression. (**a**) Quantitative units of GUS expression. Representative Nomarsky micrographs of root tips of *A. thaliana RGL2::uidA* transgenic seedlings under control condition (**b**) and JA treatment (**c**). Different letters indicate statistically significant differences by ANOVA and Tukey´s HSD test ($p \leq 0.05$) from 20 seedlings. Scale bar is 100 µm. The experiment was repeated three times with comparable results.

FACTOR1 (GAF1) and ARR1 (Fukazawa *et al.,* 2015). Besides, the normal development of the filament in stamen depends on the expression of JA-responsive *MYB21*, *MYB24* and *MYB57* genes and the production of JA is controlled by *DAD1* and *LOX1* genes that are regulated by GA (Cheng *et al.,* 2009). Here, we demonstrated that GA interacts synergistically with JA during root growth inhibition in a COI1 dependent-manner. However, the underlying molecular mechanism by which this positive interaction halts root growth remains to be clarified.

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