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SHORT COMMUNICATION



Impact of jasmonic acid on lignification in the hemp hypocotyl

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ABSTRACT

Phytohormones are crucial molecules regulating plant development and responses to environmental challenges, including abiotic stresses, microbial and insect attacks. Most notably, phytohormones play important roles in the biosynthesis of lignocellulosics. Jasmonates are involved in secondary growth and secondary metabolism, such as phenylpropanoids and lignin biosyntheses. At the physiological and molecular levels, the actions of phytohormones depend on subtle concentration changes, as well as antagonistic equilibria between two or more of these molecules. In this article, we investigate the consequences of jasmonic acid (JA) spraying on young hemp hypocotyls. First, we show that JA application results in changes in the monomeric composition of lignin. Second, we highlight that, five days after application, JA leads to an increase in salicylic acid (SA) content in hemp hypocotyls. These results are discussed in the light of the known antagonism between JA and SA at both the physiological and molecular levels.

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JA and related molecules, referred to collectively as jasmonates (JAs), are active in many developmental processes, including growth inhibition, mechanotransduction, secondary growth and male fertility.¹ JAs are also powerful elicitors of plant secondary metabolite synthesis, including alkaloids, glucosinolates, terpenoids and phenylpropanoids.² For example, the abundance of coniferyl alcohol and higher-order oligolignols and lignin is significantly higher in methyl jasmonate (MeJA)-treated *Arabidopsis* cells.³ This over-production of monolignols and lignin may result from a more global response to this hormone. Indeed, JA is a signal of herbivore attack. Mimicking this attack by applying JA was found to modify the shunt of photosynthates.⁴ In order to minimise the consequence of the attack, the plant stores the carbohydrates in tissues less prone to be targeted, *i.e.* roots and stems⁴, and induces the formation of lignin to increase its mechanical resistance.³ Accordingly, a JA-dependent cell wall thickening in fibre and xylem tissues has also been observed, as well as additional phloem fibres in *Arabidopsis*.⁵ The results published in our previous article⁶ confirm the positive role of JA on plant secondary growth,⁵ as well as monolignol biosynthesis/lignin deposition.³

To further characterize the impact of JA on lignification, we investigated, through pyrolysis coupled to GC-MS, the lignin monomeric composition of cell wall residues from hemp hypocotyls treated with 0.1 mM JA or a mock solution (3 days after application). We observed a slight but significant increase of the syringyl (S)/guaiacyl (G) ratio in the JA-treated hypocotyls (0.52 *vs* 0.47, *t*-test *p*-value = 2.10%), due to a higher molar area of S-related peaks. This result is consistent

with the histological changes induced by JA application: JA-treated hypocotyls have additional secondary bast fibres.⁶ Those cells of the sclerenchyma are characterized by an S/G ratio that is higher than that of xylem vessels.⁷

In order to better understand the global mechanism underlying JA application on the hypocotyls of textile hemp, a profiling of the phytohormone SA was additionally performed. The reason to focus on SA is because it antagonizes the JA signaling pathway through multiple mechanisms, ranging from sequestration of JA-responsive transcription factors to inhibition of MAPK cascades and redox signalling.⁸ Additionally, JA may enhance SA production by up-regulating the expression of those genes involved in SA biosynthesis, such as *PAL*, which is the committed entry enzyme for SA biosynthesis.⁹ Finally, SA has been shown to repress the expression of several genes involved in JA biosynthesis.¹⁰

In the light of the above-mentioned interplay between SA-JA, we have thus performed a time-course quantification of SA in mock- and JA-treated hypocotyls. The application of JA on 15-days-old hypocotyls (H15) first leads to a small decrease of SA content, followed by a progressive increase until the end of the measurement, 5 days after JA application, resulting in a significantly higher SA content in JA-treated hypocotyls (Figure 1). These data confirm that JA positively regulates the biosynthesis of SA.

These two phytohormones are key molecules of the plant defense *versus* biotic stresses. While SA has a key role in the response against microbial pathogens,¹¹ JA was shown to protect a plant from herbivore attack, for instance by promoting trichome formation¹² and promoting flavonoid

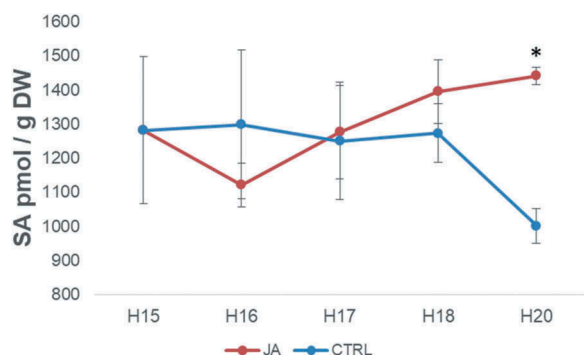


Figure 1. Salicylic acid (SA) content in the hemp hypocotyls aged between 15 and 20 days (H15 and H20, respectively) after jasmonic acid (JA) application (average \pm SEM, 3 biological replicates). A Student's *t*-test is performed for each time-point (*p*-value <0.05*), CTRL: control.

biosynthesis.¹³ The increase in SA content following JA spraying might thus be considered as an element of the plant trade-off between these various threats. The initial increase of JA content might be compensated by an enhanced SA accumulation to prevent a potential microbial attack.

In addition, SA and JA, as all phytohormones, play a crucial role in plant development. SA and JA antagonistically regulate several physiological processes.^{11,12} Root growth, flowering and leaf development are favored by SA while inhibited by JA; by contrast, JA promotes trichome formation while exogenous application of SA represses this process. However, both hormones positively regulate leaf senescence at different stages and induce stomatal closure. This SA-JA crosstalk is also particularly obvious at the transcriptional level. The impact of SA and MeJA application, alone or in combination, in 5-weeks old *Arabidopsis* seedlings was assessed by microarray profiling, revealing that 59 MeJA-inducible genes (including *NACs* and *GRAS* transcription factors, as well as *JAZs* genes) were suppressed by SA, while 15 MeJA-downregulated genes were upregulated by SA.¹⁴ This confirms previous results obtained on *Sorghum bicolor* showing an SA-dependent strong attenuation of the expression of JA-induced genes.¹⁵ Promoter and GUS reporter analyses strongly suggest that the GCC-box (AGCCGCC) is sufficient for SA-driven down-regulation of genes induced by MeJA, possibly through the repression of the accumulation of the ERF transcription factor ORA59.¹⁴ In addition, SA induces the gene expression of several families of transcription factors interfering with JA signalling.⁸ The TGA class of bZIP transcription factor is likely involved in the SA-mediated repression of the JA-inducible *PLANT DEFENSIN1.2* (*PDF1.2*). Some ERFs harboring the repressive EAR domain and several WRKYs can also suppress *PDF1.2* and other JA-responsive gene expression.

Altogether, our results show the important role of JA in plant development. JA strongly accumulates at the onset of hemp hypocotyl secondary growth¹⁶, has a positive role on this biological process, as well as on lignification⁶, and modifies the lignin monomeric content, possibly in relation with the increased number of phloem fibers. These physiological modifications increase the mechanical strength of the plantlets and are therefore in accordance with the role of JA in the response to herbivore attacks. In addition, JA favors SA biosynthesis through gene expression regulation⁹, resulting in an

equilibrium between these two phytohormones and their subsequent regulatory effects on plant physiology.

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Disclosure statement

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