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Jasmonates in the model lycophyte *Selaginella moellendorffii*: biosynthesis, metabolism, and functions

(イヌカタヒバにおけるジャスモン酸類の同定および機能解析)

Plants began colonizing terrestrial area in the mid-Palaeozoic era (between 480 and 360 Mya) and have been adapting unique environmental stresses ever since. Jasmonic acid (JA) and its derivatives, called jasmonates, are known regulators of defense responses and plant development that are ubiquitously produced in seed plants. In contrast to seed plants, bryophytes produce only a JA intermediate; 12-oxo-phytodienoic acid (OPDA), but not JA, and JA is not substantial for the physiology of bryophytes. To get a better understanding about pivotal role of JA in plants for surviving in the land area, the evolutionary history of JA as a mediator to regulate the defense responses against wounding stress is investigated using *Selaginella moellendorffii*, a model of seedless vascular plant belonging to lycophytes group that is taxonomically positioned between bryophytes and euphyllophytes.

1. JA biosynthesis in *Selaginella moellendorffii*

JA plays important roles in stress adaptation. Wounding activates JA biosynthesis and subsequently accumulates JA, OPDA, and jasmonoyl-isoleucine (JA-Ile, a versatile JA signaling substance in seed plants). UPLC-MS/MS data showed that OPDA and JA are accumulated in wounded *S. moellendorffii*. Hence, this study suggests that JA biosynthesis occurred after bryophytes during plant evolution.

To further confirm the presence of JA, three key JA biosynthetic enzymes in *S. moellendorffii* were characterized: SmAOS2, SmAOC1, and SmOPR5 were actively involved in the octadecanoid pathway to produce JA. Furthermore, the expression of *SmAOC1* and *SmOPR5* were increased by wounding and JA treatment.

2. JA metabolism

JA can be metabolized into active and inactive JA derivatives. The conjugation of JA to isoleucine (JA-Ile) is the most biologically active form of JA and essential for JA signaling. *S. moellendorffii* synthesizes JA-Ile as a late response to mechanical wounding. This result was supported by the presence of functionally active SmJAR1 (a JA-Ile synthase).

The homeostasis of JA-Ile is substantial to suppress over-response of JA in plants. 12-hydroxyJA-Ile (12-OH-JA-Ile) and 12-carboxyJA-Ile (12-COOH-JA-Ile) are known as inactive forms of JA-Ile in *Arabidopsis*. This study provides the first evidence that *S. moellendorffii* is able to oxidize JA-Ile into 12-OH-JA-Ile, and 12-COOH-JA-Ile.

3. Physiological effects of jasmonates to *S. moellendorffii*

To understand the physiological effects of jasmonates towards *S. moellendorffii*, growth inhibitory activities of various jasmonates were examined. OPDA, JA, and JA-Ile significantly inhibited the growth of *S. moellendorffii* like those in seed plants. Since 12-OH-JA-Ile is an inactive form of JA-Ile, 12-OH-JA-Ile has relatively weak growth inhibitory activity to *S. moellendorffii*. Interestingly, 12-OH-JA-Ile promoted the emergence of double microphylls from a single bulbis *S. moellendorffii*.

4. Conclusions

This study provides the first evidence of the presence of JA and JA metabolites in the earliest vascular plant, *S. moellendorffii*. Furthermore, JA induces the expression of JA biosynthetic genes and retards the growth of *S. moellendorffii*. It is strongly suggested that JA functions as a defense signal molecule due to the acquisition of vascular system during plant evolution.