

A Novel Study on Physiological Importance and Biosynthesis of Strigolactone Hormone

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SUMMARY

Plant hormones known as strigolactones control a variety of developmental and environmental reactions. Additionally, it is recognised that these are chemical signals derived from the roots that control symbiotic and parasitic relationships with root parasite plants and arbuscular mycorrhizal fungi, respectively. The study of strigolactones has advanced significantly. Numerous advancements have been made, particularly in our comprehension of the production, transport, and perception of strigolactones. The revelation of a new classes of plant hormones as a result of the strigolactones' hormonal action was highly significant, as was the discovery of the long-sought strigolactones biosynthetic or response mutants. We were given the genetic resources to explore fundamental issues with strigolactones production thanks to these mutations in several plant species. Following additional analysis of these mutants, biochemical studies of these genetically discovered components have so far revealed the general framework of strigolactones manufacture. Reverse genetic investigations have also led to the discovery of additional strigolactones transport-related genes. With an emphasis on biosynthesis and its effects upon plant growth and development, we review recent strigolactones research developments.

INTRODUCTION

Strigolactones, a kind of terpenoid lactones produced from carotenoids, were first noted as germination accelerators for root parasitic species like witchweeds (*Striga* spp.). Strigolactones were eventually discovered to be arbuscular mycorrhizal fungi's symbiotic signalling molecules generated from roots. Over the past 40 years, strigolactones have primarily been investigated using a natural product chemistry method as allelochemicals inside the rhizosphere. On the other end, plant biologists have investigated the physiological and genetic factors that control shoot branching.

These investigations showed the existence of an undiscovered carotenoids-derived inhibitor of shoot branching. These hitherto distinct research areas were brought together by the identification of strigolactones being plant hormones, greatly advancing the study of these versatile plant signalling molecules.

Up until recently, the identification of the Strigolactones biosynthesis pathway had been a mystery. The identification of the SL precursor chemical carlactone was one important development. Carlactone was discovered to be an indigenous subject to natural for Strigolactones after being initially found as an enzymatic result of all-trans-carotene within an in vitro investigation. The subsequent pathway to carlactone has now also been thoroughly characterised, as is detailed below.

The finding of an ATP-binding circuit (ABC)-type transporter in the petunia (*Petunia hybrida*), that is in charge of strigolactone exudation from roots, was an important discovery regarding strigolactone transport. Its homologous genes have recently been involved in the transport of strigolactones. Uncertainty persists regarding the precise mechanisms of strigolactone exudation in roots and also in plant translocation.

In 2009, dwarf14 (d14), a strigolactones-insensitive rice (*Oryza sativa*) mutation, was identified, and it was discovered that the causative gene encodes a protein that belongs to the α -fold hydrolase superfamily. It is now commonly acknowledged that D14 is a strigolactones receptor based on genetic and biochemical evidence. However, because to D14's catalytic capacity to hydrolyze strigolactones, its signalling mechanism is still up for debate. We will sum up the most recent research on SL biosynthesis, transport, and perception in this review.

Chemical structures of strigolactones

Historically, strigol and strigol-related chemicals, which promote the germination of parasitic plants, were the source of the name for strigolactones. Naturally produced strigolactones have been extracted and identified from a variety of plant species ever since strigol was first isolated from cotton more than 50 years ago. Numerous reviews on strigolactones' chemistry, history, and distribution may be found elsewhere. According to their chemical structures, strigolactones were proposed to be divided into two groups: canonical and non-canonical SLs. Natural SLs that have been discovered so far have C-2' configurations that are (2'R). Three rings (ABC-

rings), which are part of the tricyclic lactone structure of canonical SLs, are joined to a butenolide unit (D-ring) by an enol-ether bridge. The enol-ether link and the D-ring components, particularly for plants, were at least demonstrated to be essential for their biological activity.

Relying here on stereochemistry of the C-ring, classical strigolactones are further divided into strigol- or orobancho kinds. In instance, non-canonical SLs have both basic enol-ether bridge with D-ring moieties but don't have the conventional ABC-rings. Recent research on the production of strigolactones in plants is presented in this section.

Core pathway of SL biosynthesis

Experiments with carotenoid-deficient mutants & carotenoid synthesis inhibitors have revealed that strigolactones were biosynthesized and through carotenoid route before SLs were discovered as a novel family of plant hormones controlling shoot branching. We were then considerably helped in our understanding of SL biosynthesis by a series of dominant mutants with enhanced shoot branching. These mutants, which include the *Arabidopsis* more apical growth (max) mutant, the *pisum sativum*, ramosus (rms), the *petunia* with decreased apical dominance (dad), and the rice cultivar dwarf (d/htd) mutant, were obtained through genetic research that sought to identify a novel shoot highly branched regulator other than the conventional hormones auxin and cytokinin (CK).

Regulation of SL Biosynthesis

Nutritional regulation

The biosynthesis of strigolactones is regulated in several ways, as has recently been discovered. The indicator of low phosphorus is one of the key regulators of SL biosynthesis. It has been noted that hyphal elongation or branching in AM fungus are stimulated by root exudates of phosphorus-deficient plants. These findings are in line with the hypothesis that AM fungus colonisation enhances the ability of host plants can efficiently absorb inorganic nutrients, notably phosphorus, from soil. Then, strigolactones were discovered to be symbiotic signals in AM fungus that can promote spore germination, increase hyphal branching, and encourage cell proliferation.

These results suggest that SLs are essential for AM fungus in the rhizosphere to absorb nutrients. The levels of SLs are dramatically raised in phosphorus-deficient circumstances in many plant species, according to later LC-MS/MS analysis of root exudates. Furthermore, it has been demonstrated that low nitrogen levels raise SL levels, albeit this form of regulation probably depends on the plant species. These findings imply a direct connection between plant nutrient acquisition strategies and low nutrition-dependent SL synthesis.

Additionally controlled by its own signals is SL biosynthesis. In order to maintain homeostasis, the indigenous levels of phytohormones are often precisely and carefully regulated by feedback control and feedback control. CCD7 and CCD8 are probably conserved targets of negative feedback control in SL biosynthesis. According to gene expression studies, strigolactones-deficient and SL-insensitive mutants of various plant species, including *Arabidopsis*, pea, *petunia*, and rice, had higher transcript levels of the CCD7 and CCD8 genes. In wild-type (WT) nor strigolactones deficient plants, the exogenous administration of GR24, an artificial strigolactones analogue, successfully reversed the overexpression of CCD7 and CCD8. Additionally, the fact that AtD27 was elevated in max mutants demonstrated that AtD27 was subject to feedback regulation in *Arabidopsis*.

Hormonal and other regulations

It has been suggested that strigolactones interact with the other plant hormones. Because auxin is essential for apical dominance and prevents axillary bud expansion, its impact on SL synthesis has received significant attention. CCD7 and CCD8 gene expression has been demonstrated to be induced by auxin in *Arabidopsis*, pea, and rice. Auxin has been shown to boost the transcription of CCD7/MAX3 & CCD8/MAX4 inside the bottom cauline internodes of *Arabidopsis*. The overexpressing *iaa12/bodenlos* mutation, which exhibits constitutive suppression of auxin signalling, had considerably lower MAX3 and MAX4 mRNA levels. Moreover, exogenous GR24 administration to rosette axils reversed the excitable phenotype of both the *iaa12* mutant. Similar to this, GR24 could lessen the enhanced branching of *Arabidopsis* auxin signalling mutants.

Identification of the SL signaling genes from SL-insensitive mutants

Some shoot branching mutants were determined toward being strigolactones biosynthetic mutants after the hormonal role of strigolactones was discovered; these mutants' characteristics could be recovered by exogenous SL treatment. The *Arabidopsis max2*, rice *d3*, and pea *rms4* mutants, on the other hand, were identified as being SL-insensitive. These three mutants are from distinct plant species, yet their causative genes all produce orthologous F-box proteins that belong to the same genetic lineage. As a result, it was proposed that SL signal transduction entails a process of ubiquitination-dependent targeted protein degradation, which is frequently observed in the signalling pathways of many other plant hormones, including such auxin, GA, and jasmonates (JAs).

CONCLUSION

The bioactive version of strigolactones that controls numerous aspects of the development of plants is still unknown, despite recent reports of several suggestions regarding strigolactones production. The branch-inhibiting hormones are produced in the later stages of SL biosynthesis, and it has been demonstrated that LBO is essential for this process. Due to the high conservation of LBO-like genes in seed plant species, additional biochemical and genetic studies are necessary to comprehend the production of bioactive strigolactones. In addition, although strigolactones are hydrolyzed, the deactivation pathway(s) has not yet been established. To fully comprehend the scenario of strigolactones synthesis and metabolism, further enzymes must be identified. The production, transport, and perception of strigolactones were briefly discussed in this review. Our comprehension of strigolactones biology has expanded quickly, particularly since it was discovered that it is an endogenous hormone. In the future, many significant questions will still need to be resolved.

REFERENCES

- Ablazov, A., Mi, J., Jamil, M., Jia, K.P., Wang, J.Y., Feng, Q. and Al-Babili, S. 2020. The Apocarotenoid zaxinone is a positive regulator of strigolactone and abscisic acid biosynthesis in *Arabidopsis* Roots. *Front. Plant Sci.* 11, 578.
- Alder, A., Jamil, M., Marzorati, M., Bruno, M., Vermathen, M., Bigler, P., Ghisla, S., Bouwmeester, H., Beyer, P. and Al-Babili, S. 2012. The path from beta-carotene to carlactone, a strigolactone-like plant hormone. *Science*, 335, 1348– 1351.
- Arite, T., Iwata, H., Ohshima, K., Maekawa, M., Nakajima, M., Kojima, M., Sakakibara, H. and Kyojuka, J. 2007. DWARF10, an RMS1/MAX4/DAD1 ortholog, controls lateral bud outgrowth in rice. *Plant J.* 51, 1019– 1029.
- Beveridge, C.A. and Kyojuka, J. 2010. New genes in the strigolactone-related shoot branching pathway. *Curr. Opin. Plant Biol.* 13, 34– 39.
- Brewer, P.B., Yoneyama, K., Filardo, 2016. LATERAL BRANCHING OXIDOREDUCTASE acts in the final stages of strigolactone biosynthesis in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA*, 113, 6301– 6306.
- Choi, J., Lee, T., Cho, J. 2020. The negative regulator SMAX1 controls mycorrhizal symbiosis and strigolactone biosynthesis in rice. *Nat. Commun.* 11, 2114.
- Hayward, A., Stirnberg, P., Beveridge, C. and Leyser, O. 2009. Interactions between auxin and strigolactone in shoot branching control. *Plant Physiol.* 151, 400– 412.
- Liu, W., Kohlen, W., Lillo, A. 2011. Strigolactone Biosynthesis in *Medicago truncatula* and Rice Requires the Symbiotic GRAS-Type Transcription Factors NSP1 and NSP2. *Plant Cell*, 23, 3853– 3865.
- Wang, J.Y., Haider, I., Jamil, M. 2019. The apocarotenoid metabolite zaxinone regulates growth and strigolactone biosynthesis in rice. *Nat. Commun.* 10, 810.