Strigolactones and their Role in Plant Stress Tolerance under Abiotic Conditions

Manju Jat, Madhurya Ray, Shreyashi Singh and Saurabh Bharti

Abstract

Strigolactones (SLs), carotenoid-derived molecules, play crucial roles in plant development and stress adaptation. Produced mainly in roots, SLs levels increase under nitrogen and phosphate deficiency, promoting primary root elongation while repressing lateral root formation. SLs also modulate adventitious root (AR) development, often in coordination with auxin signaling. These hormones play crucial roles in plant adaptation to abiotic stresses such as nutrient deprivation and canopy shade. They regulate processes like root development, shoot branching, and leaf senescence. SLs interact with phytohormones such as auxin, abscisic acid, cytokinin, and gibberellins, contributing to plant resilience under abiotic stresses, including salinity, drought, heat, cold, heavy metals, and nutrient deprivation. Their role in stress adaptation helps mitigate negative impacts on crop productivity.

Introduction

Strigolactones (SLs) are carotenoid-derived phytohormones synthesized within plastids and the cytosol. Known as non-traditional phytohormones or plant growth regulators, SLs are primarily produced in roots and secreted into the rhizosphere, with minor synthesis occurring in other plant tissues. Although over 1,000 SL types are predicted, only about 30 have been identified. SLs play a crucial role in various physiological processes, such as seed germination, root system architecture, shoot branching, tillering, and delaying leaf senescence, particularly under environmental stress. They help plants mitigate challenges like salinity, drought, extreme temperatures, nutrient deficiencies, and heavy metal toxicity. SLs achieve this by inducing oxidative responses and promoting the production of osmolytes, thereby maintaining cellular homeostasis during stress. First discovered in cotton root exudates in 1966, SLs initially gained attention for their role in host-parasite interactions, particularly with parasitic weeds such as Striga and Orobanche. Additionally, SLs act as key signaling molecules in establishing symbiotic relationships with arbuscular mycorrhizal fungi. Functioning at pico- to nanomolar concentrations, SLs demonstrate dual roles as endogenous regulators and exogenous signals. Their instability in soil, however, poses challenges in isolation and characterization. Through their multifaceted roles, SLs significantly enhance plant

Manju Jat, Madhurya Ray and Shreyashi Singh
Department of Plant Physiology, Institute of Agricultural Sciences, BHU, Varanasi, Uttar Pradesh
Saurabh Bharti
Department of Mycology and Plant Pathology, Institute of Agricultural Sciences, BHU, Varanasi, Uttar Pradesh

adaptability and resilience to various abiotic stresses, promoting survival and growth in hostile environments.

Chemical Variability and Structural Characteristics of Strigolactones

Strigolactones, a group of plant hormones, were first identified as strigol from cotton plant root exudates. Strigol shares the same molecular formula as gibberellic acid, and it is soluble in polar solvents but not in non-polar solvents like hexane. Strigol is classified as a sesquiterpene lactone. Other types of strigolactones include orobanchol, found in red clover, and alectrol, which is present in cowpea root exudates and contains a tertiary hydroxy group. Sorgolactone, another variant, is found in sorghum root exudates and has a unique structure compared to strigol. Despite their biological importance, these strigolactones are highly unstable and inactive even at high concentrations in plants, complicating their further characterization. The structures of these different strigolactones are illustrated in Figure 1.

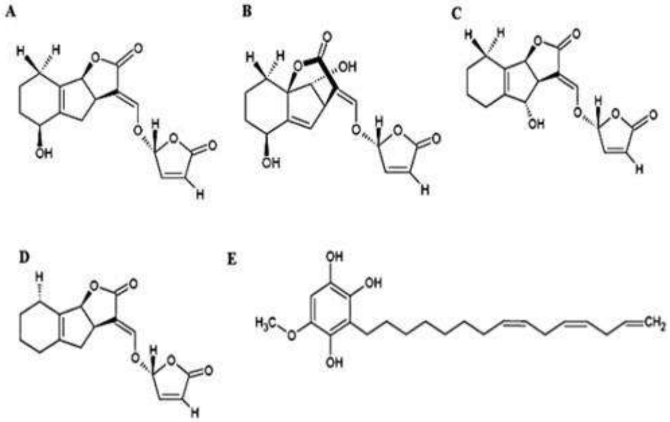

Fig. 1: Structure of different types of strigolactones present in plants. A: Strigol, B: Alectrol, C: Orobanchol, D: Sorgolactone, E: Sorgoleone.

Biosynthesis of Strigolactones

Strigolactones, a class of plant hormones, are synthesized from carotenoids via enzymatic reactions across diverse species. In rice, the D27 gene encodes an iron-dependent protein essential for the pathway. In Arabidopsis thaliana, strigolactone biosynthesis involves MAX3, MAX4, and MAX1, which act sequentially. Orthologs of these genes include RMS5 and RMS1 in Pisum sativum and D17/HTD1 and D10 in rice. MAX3 encodes CCD7, MAX4 encodes CCD8, and MAX1 encodes a cytochrome P450 enzyme responsible for modifying intermediates into bioactive strigolactones. The CCD7 enzyme, localized in plastids and present in low concentrations, initiates carotenoid cleavage, a critical early step. The MAX/RMS/D pathway is tightly coordinated, with MAX4 operating downstream of auxin. Mutations in MAX4 inactivate MAX3, confirming their interconnected function. These genes and their orthologs are conserved across plant genomes. Strigolactone biosynthesis interacts with other hormones like auxins and cytokinins. In P. sativum, RMS5 and RMS1 facilitate carotenoid cleavage, while Dad1 in Petunia hybrida performs polyene chain cleavage. The D10 gene in rice and SlCCD7 in tomato also encode carotenoid-cleaving enzymes. In rice, Os900 oxidizes carlactone (CL) into ent-2'-epi-5DS, which is hydroxylated by Os1400 to produce orobanchol. In Arabidopsis, additional enzymes for carlactone oxidation remain unidentified. The LBO gene mediates the final steps, producing strigolactone-related compounds. In parasitic plants like Striga, strigolactones are synthesized in specific tissues with unique gene expression patterns. In host plants like Orobanche, NCED catalyzes carotenoid cleavage. In rice and Medicago truncatula, NSP1 and NSP2 regulate the biosynthetic pathway, linking it to nodulation signaling. These findings highlight the conserved yet species-specific nature of strigolactone biosynthesis.

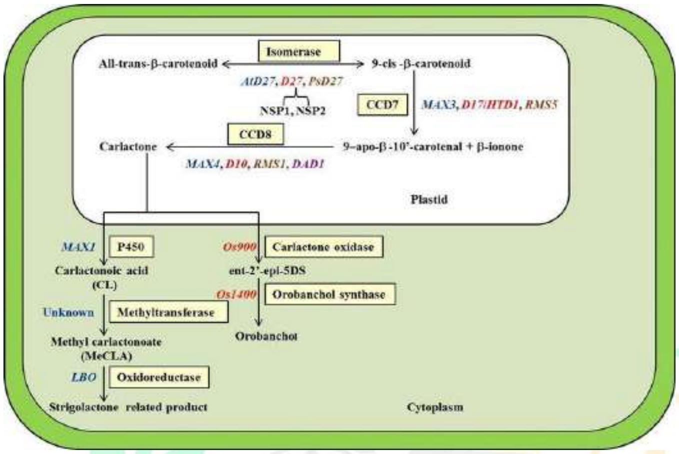

Fig. 2: The suggested biosynthesis pathway of strigolactones in plants. Genes involved in the strigolactone biosynthesis pathway of Arabidopsis, rice, pea, Petunia hybrida are shown in blue, red, brown and purple colors respectively. The respective encoded proteins are displayed in yellow color boxes.

Roles of SLs in abiotic stresses

Abiotic stresses such as salinity, drought, extreme temperatures, heavy metal toxicity, and nutrient deficiencies pose a significant threat to crop productivity and global food security. Strigolactones, a class of plant hormones, have been found to play a vital role in enhancing plant tolerance to these various abiotic challenges (refer to Fig. 3).

Role of Strigolactones in Enhancing Plant Resilience during Nutrient Starvation

Phosphorus (P), a vital macronutrient, is essential for the structural and metabolic functions of plants. Under P-starvation, plants adopt strategies such as altering root architecture and increasing root hair density to access localized P sources. Strigolactones (SLs) regulate lateral root (LR) formation in response to inorganic phosphate (Pi) levels, repressing LR development under sufficient Pi but promoting it under low Pi conditions. Under phosphorus-deficient conditions, strigolactone (SL) mutants of rice (d10 and d27, which are SL-deficient, and d3, which is SL-insensitive) exhibited reduced seminal root growth.

Strigolactones: Key Regulators of Plant Response and Adaptation to Drought Stress

Water deficiency is a common abiotic stress that disrupts plant development and productivity. Drought stress impairs the electron transport chain, leading to oxidative stress and organelle damage. Plants counter this through morphological adaptations, stomatal closure, osmotic adjustments, and enhanced antioxidant defenses. Reducation in strigolactone (SL) levels under drought stress, linked to downregulation of the SlCCD7 gene in tomato. In *Vitis vinifera*, GR24 application improved drought tolerance by enhancing chlorophyll content, photosynthesis, and antioxidant defense. Exogenous SL treatment restored drought tolerance in SL-deficient max3 and max4 mutants but showed no effect in max2 mutants.

Strigolactones: Enhancing Plant Resilience to Salinity Stress

Salinization is a growing global issue, with saline soils currently covering over 7% of land, potentially rising to 50% by mid-century. Exogenous GR24 treatment mitigates salinity stress, enhancing photosynthetic capacity in *Brassica napus*. SL-deficient (max3 and max4) and SL-signaling mutants of *Arabidopsis thaliana* were more sensitive to salinity during germination and vegetative stages compared to wild-type plants. In wheat, two cultivars, S-24 and PARI-73, showed reduced growth under salt stress, but GR24 treatment improved growth rates in the treated seedlings.

Strigolactones: Modulating Plant Response to Light Stress

Light is a crucial environmental factor influencing strigolactone (SLs) levels in plants, which play a role in photomorphogenesis. The pps (Pleiotropic Photosignaling) mutant of *Arabidopsis thaliana* showed hyposensitivity to blue, red, and far-red light. Strigolactones (SLs) inhibit hypocotyl growth in a light-dependent manner, requiring functional HY5. HY5 negatively regulates growth, and SLs enhance HY5 abundance. GR24 recovers elongated hypocotyls in hy1 and hy2 mutants, but not hy5. SLs also promote HY5 stability by inhibiting COP1, further reducing hypocotyl elongation, acting as a light supplement in the dark.

Strigolactones: Modulating Plant Tolerance to Heat Stress

Heat stress restricts root development in cold-season plants, which are sensitive to high temperatures. GR24 treatment in *Festuca arundinacea* improved crown root elongation and cell number by altering gene expression of PCNA, CycD2, and CDKB under heat stress. Exogenous GR24 treatment restored max1-1 mutant phenotypes but not max2-1. In *Lactuca sativa*, SLs enhanced seed germination under high temperature by reducing the ABA/GA ratio, indicating SL-GA interaction.

Strigolactones: Enhancing Plant Tolerance to Chilling Stress

Chilling temperatures reduced Photosynthesis and leaf area in *Arabidopsis thaliana* (max2-1, max4-1) and *Pisum sativum* (rms4) mutants compared to wild types. SL-related genes like max and rms4 suggest SLs play a key role in low-temperature tolerance. GR24 treatment in *Brassica rapa* under chilling stress improved photosynthesis, cell viability, and antioxidant enzymes, enhancing cold-related gene expression. Gene expression analysis in *Oryza sativa* showed upregulation of SL biosynthetic genes in mycorrhizal roots under chilling stress, suggesting SL involvement in chilling stress regulation, though further research is needed to confirm the mechanism.

SLs during heavy metal stress

Heavy metal toxicity, like Cadmium (Cd), reduces growth and photosynthesis in *Panicum virgatum*. However, GR24 treatment improved growth, chlorophyll content, and antioxidant activities while reducing Cd accumulation. Under Arsenic (As) stress, the antioxidant enzyme transcript levels (OsCuZnSOD1, OsCuZnSOD2, OsAPX1, OsAPX2, OsCATA) were higher in WT *Oryza sativa* roots compared to SL mutants (d10, d17). Conversely, transporter gene expression (OsPT1, OsPT2, OsPT4, OsPT8) was upregulated in mutant plants.

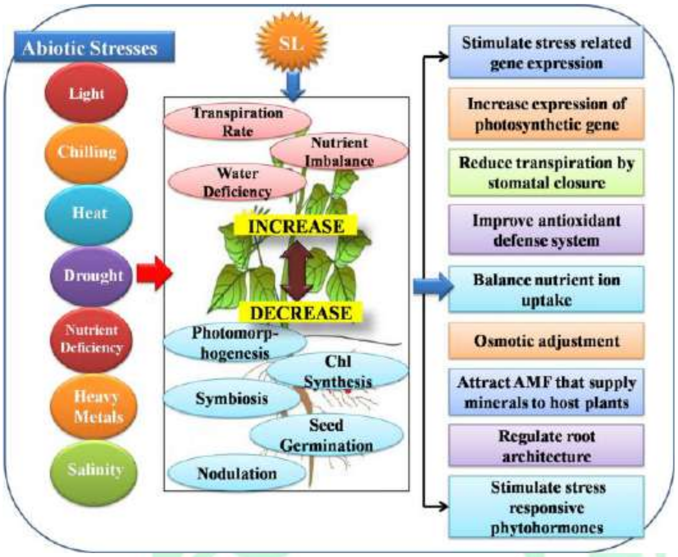

Fig. 3: A proposed model illustrating how strigolactones (SLs) help plants adapt to various abiotic stresses. Stresses such as salinity, heat, nutrient deficiencies, and heavy metals trigger different stress responses in plants. The exogenous application of SL analogs can mitigate these stress effects and improve plant resilience.

Conclusion

Strigolactones (SLs) are secondary metabolites derived from carotenoids, playing pivotal roles in regulating various plant growth and developmental processes such as seed germination, shoot branching, leaf senescence, and root architecture. Environmental stress can significantly influence the biosynthesis, signaling pathways, and interactions of SLs with other plant hormones. In recent years, SLs have garnered significant attention for their critical roles in helping plants adapt to various abiotic stresses, including drought, salinity, nutrient deficiencies, temperature extremes, and heavy metal toxicity. They are also involved in modulating key physiological and molecular processes in plants. The multifaceted functions of SLs underscore their potential in modern agriculture, particularly in addressing challenges posed by climate change and resource constraints. The application of SLs holds great promise for the development of innovative strategies and technologies aligned with the principles of sustainable agriculture, contributing to improved crop resilience and productivity.

References

Bhoi, A., Yadu, B., Chandra, J. and Keshavkant, S. (2021). Contribution of strigolactone in plant physiology, hormonal interaction and abiotic stresses. *Planta*, 254(2): 28.

Kapoor, R. T., Alam, P., Chen, Y. and Ahmad, P. (2024). Strigolactones in plants: from development to abiotic stress management. *Journal of Plant Growth Regulation*, 43(3): 903-919.

Nakandala, N. D. U. S., Ranaweera, L. T., Weeb-adde, C. K. and Sooriyapathirana, S. D. S. S. (2020). Strigolactone, a Novel Hormone with Essential Functions in Planta Possesses a Significant Value as a Cancer Therapeutic Agent: A.

Saeed, W., Naseem, S. and Ali, Z. (2017). Strigolactones biosynthesis and their role in abiotic stress resilience in plants: a critical review. *Frontiers in Plant Science*, 8: 1487.