

Review

Unveiling the resilience mechanism: Strigolactones as master regulators of plant responses to abiotic stresses

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ABSTRACT

Strigolactones (SLs) are an emerging class of plant hormones that play important roles in plant growth, development, and response to environmental stresses. This review summarizes recent findings on the roles of SLs in mitigating heat, drought, and salinity stresses in plants. Under high temperatures, SLs help maintain photosynthesis, antioxidant activity, and expression of heat shock proteins to confer thermotolerance. During drought, SLs regulate stomatal closure and promote root growth and mycorrhizal associations to enhance water uptake and retention. SLs also modulate ion homeostasis and antioxidant systems under salinity stress. On the physiological level, exogenous SL can increase chlorophyll content, photosynthetic efficiency, proline accumulation, and activity of antioxidant enzymes like SOD, POD, and CAT across plant species. On the molecular level, SLs regulate genes involved in the cell cycle, heat shock proteins, hormone signaling (auxin, ABA, ethylene), and SL biosynthesis and signaling components like *MAX1-4*, *D14*, and *D53*. Overall, SLs are emerging as promising plant growth regulators that can potentially be applied exogenously to improve abiotic stress tolerance in crops through coordinated molecular, biochemical, and physiological responses. More studies are needed to fully elucidate SL signaling cascades in different plant species and environments.

1. Introduction

Metabolites are spatially distributed chemical signals that plants use to coordinate their physiological functions and react to environmental influences, such as nutrients in the soil and rhizospheric signals (Yoneyama and Bennett, 2024). A key mechanism facilitating interactions between neighboring plants, microbes, and parasites occurs when plants respond and adjust to rhizospheric stimuli by exuding specific metabolites, which contribute to their survival under biotic and abiotic stress (Massalha et al., 2017; Pang et al., 2021). It is common for plants to experience abiotic stress due to various unfavorable environmental conditions. Assisting plants in communicating with the external environment, phytohormones regulate several physiological processes

(Xin et al., 2019; Li et al., 2020). Scientists discovered Strigolactones (SLs) when they analyzed how cotton roots secreted a signaling substance designed to stimulate parasitic weed seed germination (Cook et al., 1966). It has been found that there are approximately 30 types of SLs in different plant species, and they can be divided into two groups according to their chemical structure, namely canonical and non-canonical types (Wang and Bouwmeester, 2018). Depending on the molecular structure of the SLs, two types can be classified, canonical or non-canonical SLs. Canonical SLs contain ABCD rings whereas non-canonical SLs lack B and C rings and contains A and D-ring, which are carlactonoate, carlactonoic acid (Zorrilla et al., 2022; Kun-Peng et al., 2018). Canonical SLs can form functional groups with numerous carbon atoms. Several canonical SLs have been identified with a few being

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strigol, orbanchol, medicol, and synthetic GR24 (Borghetti et al., 2021; Abe et al., 2014). While the non-canonical SL's and carlactonic acid have led to the formation of methyl phenlactonoate 3 (MP3), a promising SL in regulating plant activities (Jamil et al., 2018). The most common naturally occurring SLs are characterized by a butenolide ring (D-ring) and tricyclic ring (ABC-ring), which are coupled with an enol-ether bridge in canonical SLs or to less conserved construction in non-canonical SLs (Al-Babili and Bouwmeester, 2015). SLs serve dual functions, as both endogenous and exogenous signaling molecules. Many studies utilizing various SLs biosynthesis and signaling lines have demonstrated that SLs can positively modulate root hair (RH) elongation, primary root (PR) growth, and secondary shoot growth, but repress

adventitious roots (AR) development and axillary bud outgrowth. GR24 is the SL analog widely studied and has been used in the field of medicine and agriculture due to its bioactivities (Kurt et al. 2020). Zorrilla et al. (2022) reported numerous structures of synthetic GR24 due to its skeleton being the most common SL found in the literature with its applicability and potential for AMF branching and SL. Although GR24 is mainly recognized SL, however methyl phenlactonoate (MP's) is an emerging SL recognized for its growth retarding behavior and accelerated leaf senescence. This review provides an overview of the most recent information concerning the biological functions of SLs as well as expands and clarifies the functional role of SLs associated with hormonal networks that play a role in plant development and environmental

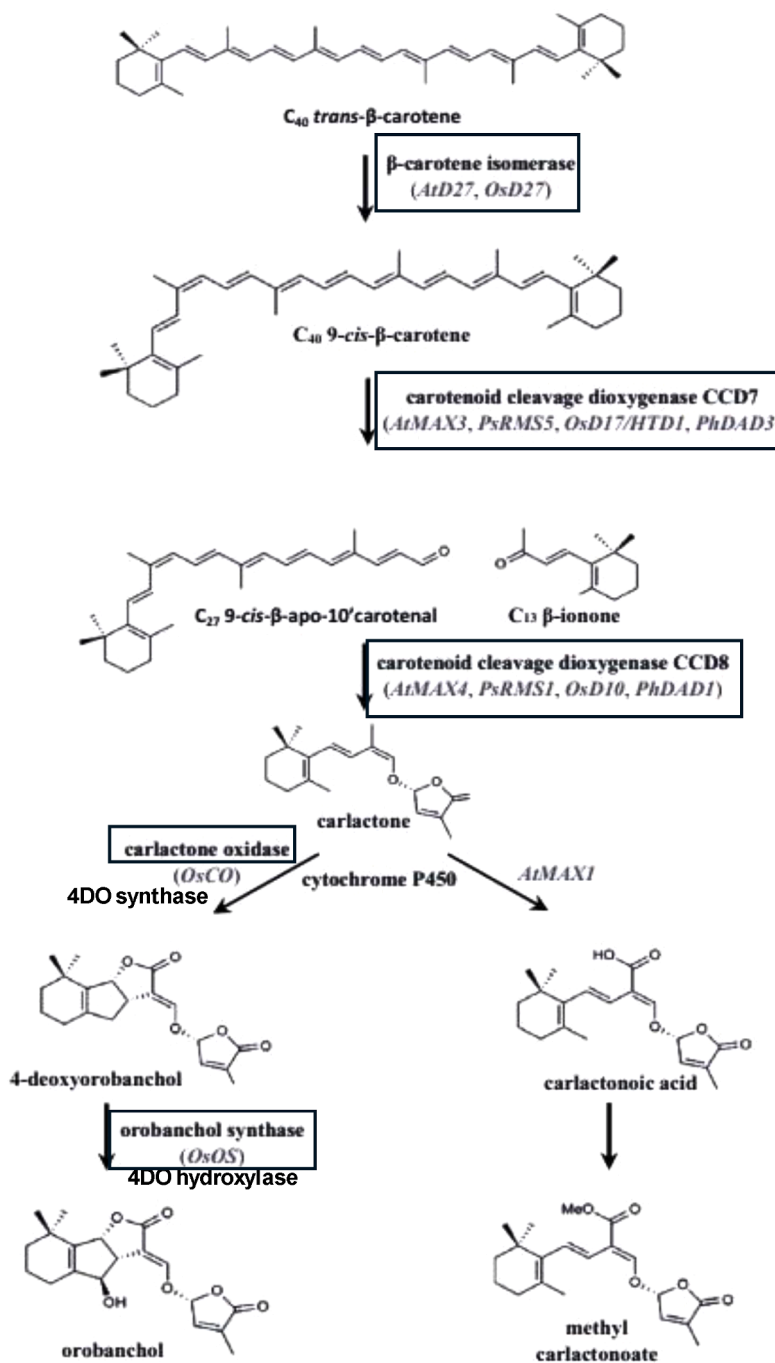


Fig. 1. Strigolactones biosynthesis pathway showing the substrates (in bold), proteins (in box), and genes (in italic) encoding the enzymes involved in Arabidopsis (At), rice (Os), pea (Ps), and petunia (Ph). Strigolactones biosynthesis for all-trans-β-carotene as substrate (Flematti et al., 2016; Aliche et al., 2020; Ito et al., 2022; Chen et al., 2023).

responses. SLs are derived from β -carotene. Partial elucidation of their biosynthesis in several plant species has been identified in Fig. 1 (Aliche et al., 2020).

2. Role of strigolactones under high temperature

SLs is being utilized to develop crops that can be tolerant to a variety of environmental stresses. The substantial significance of SLs has been characterized as a useful tool for stress-related occurrences, and its function in certain environmental issues has been observed (Tariq et al., 2023). One major environmental issue that has come to the fore in recent years is global warming and unintended heat waves. Temperatures above than optimum might be expected by severe climate change, which could threaten tree populations and seriously harm agriculture. (Shafqat et al., 2021). The plant needs a certain range of temperatures to execute its physiological (Khan et al., 2019) and biochemical function, whether long-term or short-term variations may put them under stress (Bermudez et al., 2021). The ability of SLs to stimulate the transcription of proteins and the activity of antioxidant enzymes positions them as beneficial regulators of the body's tolerance to heat stress (Chi et al., 2021). SLs signaling and biosynthesis are important for plants to adapt to temperature stresses (Pandey et al., 2016). Antioxidant induction in plants is linked with other mechanisms to prevent cellular damage in response to temperature stresses. SLs as signaling molecules function as endogenous hormones to regulate plant growth and as components of root exudates to encourage symbiotic relationships between plants and soil microorganisms.

2.1. Physiology and biochemical aspect

The heatwaves have a detrimental effect on the physiological and biochemical mechanism of plants *i.e.*, disruption of bio-membranes (Scafaro et al., 2021), misbalance of phytohormones (López et al., 2022), deterioration of main enzymes (Teskey et al., 2015), accumulation of reactive oxygen species (ROS), disturbance in plant gas exchanges (Zinta et al., 2014), dehydration ultimate affects plant growth and development (Marchin et al., 2022). Heatwaves disturb the normal

processes and stress response mechanism which in turn reduce the plant to tolerate heat, as well as the effectiveness of strategies used for thermotolerance improvements (Ali et al., 2020).

SLs are defined as new phytohormones that regulate plant functions as illustrated in Fig. 2. SLs also regulate plant metabolism, and, in turn, plant growth and development are utilized in plants against heat stresses (Faizan et al., 2020; EL Sabagh et al., 2022; Wang et al., 2022). SLs are plant hormones that operate as regulators in response to both internal and external signals (Faisal et al., 2023). In plants, photosynthesis is a crucial physiological and metabolic activity. SLs enhance photosynthesis and lessen oxidative stress to relieve plant stress (Ma et al., 2017). The pigment system (PS) II efficiency and quantum yield both decreased when the plant was subjected to heat stress. The accumulation of SL HSP70 results in improved heat tolerance responses in plant tissues. Light is the most important factor that determines whether photosynthesis occurs or not, and chlorophyll is the sensor that regulates the process. Synthetic SLs were applied to several plants to promote photosynthesis under low or normal light stress. This resulted in an increase in chlorophyll content, net photosynthetic rate, photochemical efficiency of the photosystem, and effective quantum yield of PSII (Alvi et al., 2022). Plants' reactions to nutrition (N and P) deficiencies, root and shoot architectural patterning, and leaf senescence are just a few of the apparent changes brought about by the application of SLs (Chen et al., 2023). The photosynthetic processes are improved by SL because it increases chlorophyll content. SLs were initially identified as a substance that promotes seed germination by reducing the abscisic acid (ABA) to gibberellins (GA) balance and further elevating the amounts of the chemical cytokinin (CK), which is a helpful step toward seed germination (Liu et al., 2022).

SL showed a positive response to biochemical changes if applied against heat stress (Sedaghat et al., 2017). SL improved the process of scavenging superoxide radicals during germination and seedling development despite the presence of heat stress. Under the influence of SL, both ascorbate peroxidase (APX) and peroxidase (POX) activity decreased, although seedlings were unaffected. SL promoted the activity of superoxide dismutase (SOD) and methylglyoxal (MG) detoxification, which helped to mitigate the potentially harmful consequences of heat



Fig. 2. Role of Strigolactone on plants growth, morphology, and physiology which promote or inhibit plant processes (Green arrows: increase; Red arrows: decrease).

stress. Malondialdehyde (MDA) is a biochemical marker of oxidative stress and an indicator of membrane structural integrity. It is an oxidation product of POX polyunsaturated fatty acids. Due to elevated membrane lipid oxidation brought on by oxidative stress, MDA levels rise. There is a possibility that GR24, a synthetic SL, was responsible for the increased SOD activity in seeds, which led to a reduction in the amount of lipid peroxidation. The effect of heat stress could not be completely mitigated by the presence of SOD activity. By applying SLs, the amount of proline, which is an osmolyte that accumulates to prevent cellular damage and maintain water balance under heat, was also enhanced (Sharma et al., 2019). The accumulation of phenolic chemicals in plants is both a response to and a coping mechanism for heat stress (Awasthi et al., 2015). Synthetic SL GR24 caused a considerable increase in phenolic compounds; nevertheless, this did not affect the seedlings' overall antioxidant capacity (Walton et al., 2016). Specific modifications are brought about by SLs, including improved proline content, lower lipid peroxidation, and increased germination indices. In tall fescue, GR24 promotes crown root extension in response to heat stress.

2.2. Molecular aspects

SL application by foliar and other application methods influences different pathways and functions by regulating the genes involved in developing the tolerance response of that specific genes pathways and functions (Table 1). The biosynthesis of SLs is regulated by several genes i.e., MORE AXILLARY GROWTH 1 (*MAX1*), CAROTENOID CLEAVAGE DIOXYGENASE 7 (*CCD7*) and CAROTENOID CLEAVAGE DIOXYGENASE 8 (*CCD8*) have been characterized (Bruno et al., 2014). Most plant processes have been demonstrated to be impacted by SL biosynthesis signaling gene deficits or transcriptional suppression. Under conditions of heat stress, SL was found to play a significant part in the process of repairing damage to cell cycle genes such as proliferating cell nuclear antigen (*PCNA*), Cyclin D (*CycD2*), and Cyclin-dependent kinase (*CDKB*). When compared to settings that are considered normal, the amount of expression of these genes is increased after being exposed to SL while they are under heat stress. In SLs-deficient mutants (*SL-ORT1*), treatment with GR24 (Synthetic SLs) increased the expression of genes involved in light harvesting. Arabidopsis heat stress stimulated *MAX3*,

the SLs-synthesis gene, further supporting the idea that SLs contribute to heat stress tolerance in plants.

Transcript analysis of biosynthetic genes was performed to measure the level of SL expression, and it was discovered that rice *OsCCD7* (*HTD1*) and *OsCCD8* (*D10*) expressed in the vascular parenchyma cells (Zhang et al., 2014). *AtCCD8* (*MAX4*) is expressed in the columella root cap of both primary and lateral roots (LRs), while *MAX1* (Arabidopsis) is primarily expressed in the root vasculature. The root elongation zone exhibits significant levels of expression for both *AtMAX2* and *OsD14* (Cheng et al., 2013). It has been demonstrated that significant quantities of the gene *SlCCD7* in tomatoes are expressed in immature green fruits, suggesting that SLs may have an extra function during fruit ripening and seed development (Vogel et al., 2010). The fact that SL biosynthesis genes are expressed in the roots lends credence to the theory that it acts as a germination stimulant. Branching is facilitated by SL at lower shoot levels. Increased transcription of the *CCD7* and *CCD8* genes in tomatoes in response to heat stress is consistent with the role of SLs in the positive regulation of tomato heat tolerance responses (Alvi et al., 2022). Gene silencing studies were conducted on *CCD7*, *CCD8*, *MAX1*, and *MAX2* to study their roles in SL signaling and regulation. Overcoming damage to cell cycle genes such as proliferating cell nuclear antigen (*PCNA*), *cyclin D* (*CycD2*), and *cyclin-dependent kinase* (*CDKB*) was a major focus of SL's function in the context of heat stress. After exposure to SL under conditions of heat stress, the expression level of these genes increases at a faster pace than it does under normal conditions. SL application lessens heat suppression at leaf elongation, which is connected to increased transcript levels of cell cycle-related genes and decreased transcript levels of auxin transport-related genes in tall fescue's elongating leaves.

3. Role of strigolactones under drought stress

In recent years, the intensity of water-related stresses has increased drastically such as drought and salinity, which significantly impacted the plant's growth and development. These problems are spreading worldwide due to global changes. Drought being chronic abiotic stress is responsible for approximately 70 % of the potential crop loss globally. With a significant change in moisture levels, drought hinders agriculture production worldwide. A major impact on moisture levels is mainly caused by the current trends of global warming which increases the

Table 1
Strigolactones influences different plants under varying temperature stresses.

Plant	Application	Concentration	Stress	Effects	References
<i>Festuca arundinacea</i>	Foliar spray	GR24 @0.01 μ M	Heat	Upregulation of genes in Cell cycle functions, cell number, crown root elongation, genetic expressions of D3 and D14, down regulate Auxin transport <i>PIN1</i> , <i>TIR1</i> , <i>PIN2</i> , and <i>PIN5</i> genes	(Zhang et al. 2018)
<i>Solanum lycopersicum</i>	Root tissues	–	Light	Improve tolerance against light and heat	(Koltai and Kapulnik, 2011)
<i>Festuca arundinacea</i>	Foliar spray	GR24@0.01 μ M	Heat	Expression of D3 and D14 genes functioning in leaf elongation, cell cycle, and cell division, Decreases <i>PIN1</i> , <i>PIN2</i> , and <i>PIN5</i> and <i>TIR1</i> Auxin transport-related genes	(Zhang et al., 2018)
<i>Brassica rapa</i>	Foliar spray	GR24@0.05, 0.1, 1.0, and 1.5 μ mol/L	Heat	GR24 pretreatment reduces damage to membranes and improves rape seedling cold resistance, GR24 + 4 °C boosted cell activity and lowered H2O2 and O2-concentration, leaf withering was minimized, and soluble protein and proline content rose considerably.	(Zhang et al. 2020)
<i>Arabidopsis thaliana</i>	Solution	GR24@20 and 0.1 μ M	Heat	Enhanced Germination of Seed, P level, Growth regulation accumulation of GA and CK, Decreased ratio of ABA/GA, and secondary dormancy	(Kamiya et al. 2012)
<i>Solanum lycopersicum</i>	Solution	1, 3 and 9 μ M GR24 (synthetic SL analogue)	Heat and cold	Increases <i>Hsp70</i> , ABA synthesis, transcription of <i>CBF1</i> , <i>CBF3</i> , SOD, APX, GR, MDAR, and DHAR activities, Reduces REL, MDA, H2O2, and heat sensitivity.	(Xu et al. 2021)
<i>Arabidopsis thaliana</i>	Root tissues	–	Heat and UV	Temperature tolerance to stresses	(Marzec and Muszynska 2015)
<i>Lupinus angustifolius</i>	Petri plate treatment	3 μ M rac-GR24	Heat stress	Increases seed heat resistance, SOD activity, proline content, glyoxalase I and II activity, Plabs, ROS scavenging mechanism, Reduces peroxidase, lipid peroxidation, ABS/RC ratio	(Kulkarni et al. 2020)
<i>Festuca arundinacea</i>	Foliar spray	0.01 μ M GR24	Heat	Decreases Auxin transport related genes (<i>TIR1</i> , <i>PIN1</i> , <i>PIN2</i> & <i>PIN5</i>) Increases Cell cycle-related genes, cell number, crown root elongation, expressions of D3 and D14	(Caixia Zhang et al. 2018)

intensity of drought. By the year 2050, productivity losses are expected to increase by 30 % due to drought stress. The condition where the transpiration of the plants exceeds the water absorbed by the roots due to insufficient precipitation or groundwater level drop is referred to as drought (Khalid et al., 2022). When subjected to drought stress the electron transport chain of the plants gets disturbed resulting in oxidative stress and ROS accumulation leading to the damage of essential organelles.

The main objective of the agriculture industry is to provide global food security using a sustainable approach. With the growing population, the challenging demand to feed the population requires high-intensity agriculture management (López-Ráez, 2015). Currently, the strategies used to cope with stresses to minimize crop losses are mainly focused on genetic engineering and traditional breeding crops to develop resistant cultivars, which are time-consuming and costly. To achieve the food demand, advancement in enhanced drought-tolerant plants, and finding cheaper and sustainable alternatives are urgently required (Khalid et al., 2022).

One alternative is the focus on plant symbiotic interactions taking place in the rhizosphere. The beneficial symbiotic relations between the microbes in the roots positively affect plant growth and alleviate stress symptoms (Mendes et al., 2013) (Fig. 3). Plants produce and provide carbohydrates and lipids to the fungus and in return, they get minerals (Kodama et al., 2022; Fiorilli et al., 2019). The arbuscular mycorrhiza (AM) symbiosis requires fungal metabolism which stimulates the hyphal branching in root-derived SLs (Lanfranco et al., 2018; Ho-Plágaro and García-Garrido, 2022). SLs (SL) are plant hormones recently discovered that are highly involved in multiple plant development processes (Prandi et al., 2021; Halouzka et al., 2020). In plants, SL plays a significant role in adapting to nitrogen and phosphorus deficiencies by modifying the root and shoot architecture and promoting leaf senescence by promoting symbiotic relations with nitrogen-fixing bacteria and arbuscular mycorrhizal fungi (AMF), increasing the response to

drought stress (Marzec, 2016; Yoneyama et al., 2018).

Drought stress common characteristic is the inhibition of growth. SLs were reported to enhance growth in roots and increase the activity of roots in apples under drought stress (Xu et al., 2022). Photosynthesis is essential in maintaining plant growth with photosynthetic pigments being a key factor. SL application significantly enhances photosynthetic pigment content under drought stress maintaining the chlorophyll content in leaves and promoting photosynthesis. The exogenous application of SL has been reported to act as a positive regulator in reducing abiotic stress in plants (Ha et al., 2013). The advancement in research based on SL implies hormonal interaction adapting to plant response to abiotic stresses, emphasizing the role of SL during unfavorable environmental conditions (Saeed et al., 2017). Plants increase their SL production under sub-optimal environmental conditions promoting symbiosis and coping mechanisms against drought stress.

3.1. Physiological and biochemical aspects

SL has been reported to have the potential to regulate drought inhibition in growth stages in multiple studies in various plants (Ito et al., 2022) (Table 2). Zhuang et al. (2017) reported the changes in SL production and inhibition of tiller production in perennial grass species during drought stress. The exogenous SL treatment significantly enhanced drought tolerance, resulting in more lateral branches compared to the control, doubling the SL content in crowns. Sedaghat et al. (2017) reported a reduction in electrolyte leakage, leaf stomatal limitation, and higher relative water content with the application of SL in wheat plants under drought stress, proposing SL to act as a signal mediator in response to stresses. Similar results were reported by Min et al., (2019) in Grapevine with the regulation in stomatal closure due to drought stress and activation of antioxidant defense mechanism in response to foliar application of SL. Moreover, the application of SL restored the chlorophyll content in drought stress. Haider et al. (2018)

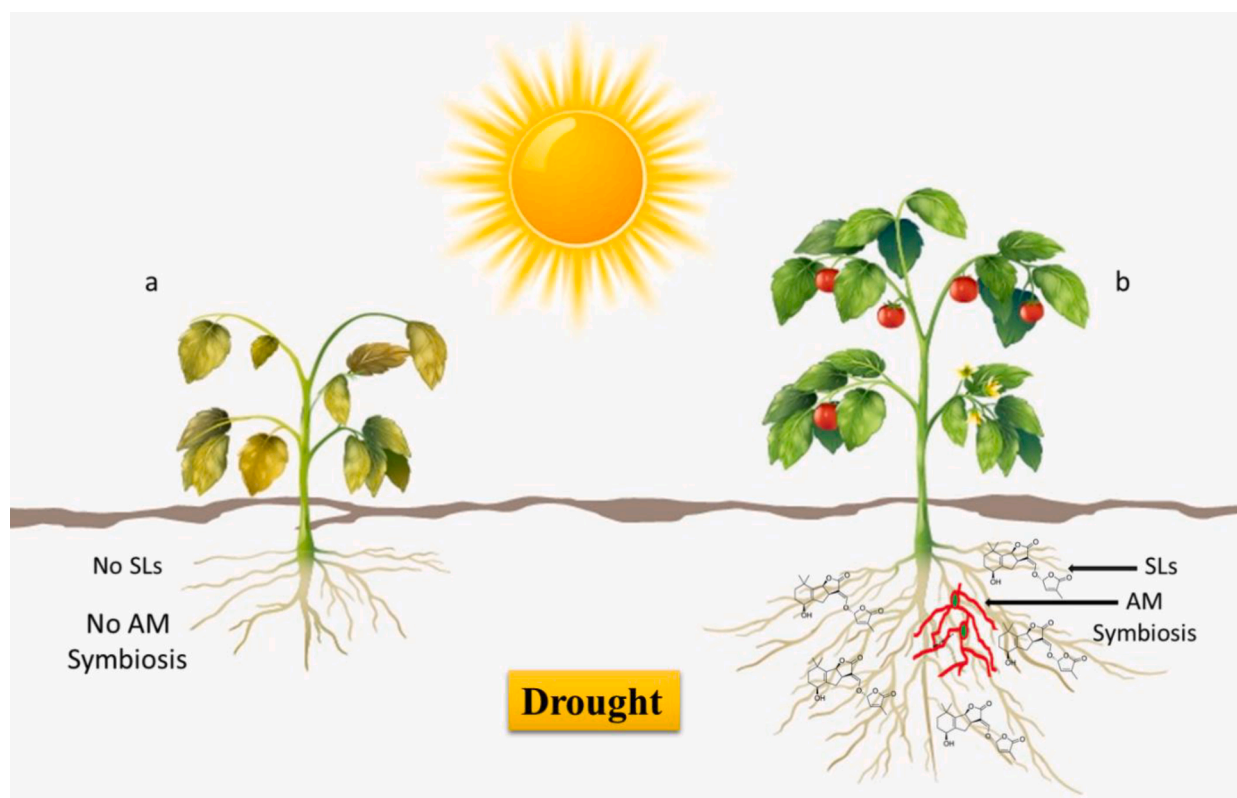


Fig. 3. Strigolactones production and arbuscular mycorrhizal fungi symbiosis relationship under drought stress. Drought stress negatively affects plant physiology in the absence of SLs (a). Conversely, elevated levels of SLs promote symbiosis with mycorrhizal fungi and enhance the performance of plants under stress (b).

Table 2
Application of Strigolactones in various plants species under drought stress.

Plant species	SL-detection site	Response	Reference
Tall fescue (<i>Festuca arundinacea</i>)	Buds	Higher lateral branches/ tiller growth in perennial grass species.	(Zhuang et al., 2017)
Winter wheat (<i>Triticum aestivum</i>)	Leaves	Lower electrolyte leakage, higher relative water content, leaf stomatal limitation (10 μM <i>rac</i> -GR24)	(Sedaghat et al., 2017)
Grapevine (<i>Vitis vinifera</i>)	Leaves	Regulating stomatal closure and activation of antioxidant enzymes mechanism (3 μM <i>rac</i> -GR24)	(Min et al., 2019)
Rice (<i>Oryza sativa</i>)	Root and Shoot	Stomata closure regulation and maintaining photosynthesis	(Haider et al., 2018)
Tomato (<i>Solanum lycopersicum</i>)	Shoot	Increased stomatal conductance and sensitivity (5 μM <i>rac</i> -GR24)	(Visentin et al., 2016)
Tomato (<i>Solanum lycopersicum</i>)		Higher enzymatic activity and membrane stability.	(Min et al., 2019)
Tomato (<i>Solanum lycopersicum</i>)		Higher proline and soluble sugar content and stomatal conductance (10 μM <i>rac</i> -GR24).	(Sedaghat et al., 2020)
Dracocephalum kotschy		Higher yield and increase in fresh and dry weights (10 μM <i>rac</i> -GR24).	(Bidabadi and Sharifi, 2020)
Tomato (<i>Solanum lycopersicum</i>)	Root extract	Increased root growth and higher photosynthesis rate	(Ruiz-Lozano et al., 2016)
Tomato (<i>Solanum lycopersicum</i>)	Shoot tissues	Drought responses Stomatal closure (5 μM <i>rac</i> -GR24)	(Visentin et al., 2016)
Tall fescue (<i>Festuca arundinacea</i>)	Crowns	Drought responses and axillary bud development (1 μM <i>rac</i> -GR24)	(Caixia Zhang et al., 2018)
Rice (<i>Oryza sativa</i>)	Stem base	Drought escape and tillering	(Du et al., 2018)

reported higher production of SL in roots and shoots in rice under mild drought stress increasing to 10-fold, whereas severe and prolonged drought conditions led to only a 2–3-fold increase in SL production resulting in stomata closure and water loss retention in plants. The SL production leads to higher root growth and increases the photosynthesis potential of the plant. Visentin et al. (2016) data supported that the depletion of SL in roots influences the physiological response in the shoot, with a high concentration of SL in shoots in drought conditions. High concentrations of SL in shoots are a necessity to increase stomatal sensitivity to ABA. Higher concentrations of SL in the root of AM-colonized plants effectively cover a larger area for the uptake of minerals and water, promoting photosynthesis and combatting adverse effects on the growth of the plants (Mostofa et al., 2018).

The application of SL was reported to decrease H_2O_2 and MDA content depicting the ROS scavenging and reducing lipid peroxidation in tomatoes (*Triticum aestivum*) under drought stress by accelerating the antioxidant enzyme activity (Sedaghat et al., 2020). Bhoi et al. (2021) also reported high proline content, soluble sugars, and photosynthetic rate leading to osmotic adjustment in tomatoes.

3.2. Molecular aspects

SLs are recently added to the plant's traditional growth promoters, ABA, cytokinin, and ethylene. A recent study of the characterization of the shoot branching mutants in plants established SL as a potential phytohormone by Pandey et al. (2016). SLs as ABA are apocarotenoids and collectively act as stress-induced phytohormones. ABA is considered a universal stress phytohormone in regulating abiotic stresses along with

SLs (Chen et al., 2022). López-Ráez et al., (2010) reported reduced levels of SLs in tomato plants that were treated with abamineSG and an inhibitor of 9-cis-epoxy carotenoid dioxygenase (*NCED*), which is an enzyme limiting the rate of ABA biosynthesis (Bruno et al., 2017). SL exhibits a pivotal role in drought response in *Arabidopsis* as *MAX3* and *MAX4* mutants, exhibiting stress sensitivity by delaying ABA-induced stomatal closure (Abuauf et al., 2018; Saeed et al., 2017; Liu et al., 2013). In the treatment of different plant species with ABA, higher stomatal conductance was observed in SL-depleted *LjCCD7* and *SICCD7*, supporting the SL's contribution to stomatal closure (Liu et al., 2015).

Mycorrhizal plants accumulate high levels of ABA and SLs when exposed to abiotic stress. With the increase in stress, the SL level increases in the roots and associates protection against hostile conditions and prevents fungal colonization in the rhizosphere. A negative correlation between ABA and SL has been reported by Ruiz-Lozano et al., (2015) in tomato and lettuce plants where the exogenous application of SL GR-24 down-regulated *LjNCED2* and prevented ABA accumulation. Similarly lowering the level of SL promotes the accumulation of ABA which helps in tackling abiotic stresses in the absence of mycorrhiza (Banerjee and Roychoudhury, 2018). Auxins reportedly promote growth by inducing SL-associated biosynthesis genes like *CCD7* and *CCD8* in rice and peas (López-Ráez, 2015). Auxin induces positive feedback regulation of SL triggers *MAX3* and *MAX4* expressions in *Arabidopsis d27* mutants, promoting primary roots and cortical tissues in the root zone with the treatment of synthetic auxin 1-naphthalene acetic acid (Rasmussen et al., 2012). SL has been reported to inhibit shoot growth in and promote root networks by indirectly inhibiting shoots through reducing auxin canalization (Waldie et al., 2014).

The exogenous application of GR24 is reported to significantly increase the growth of roots under drought stress by enhancing water absorption and improving drought tolerance (Xu et al., 2022). The expression of hormone-related genes *IAA* and *ETH* were upregulated with the treatment of GR24 on apple seedlings. Shim et al. (2018) have reported that *OsNAC14* overexpression improves drought tolerance in rice and Ju et al. 22 reported *VvNAC17* a NAC transcription factor in grapevine regulates drought resistance in transgenic *Arabidopsis*. Xu et al. (2022) studied the application of GR24 in crab apples in drought stress and numerous AP2/ethylene response elements transcription factors were unregulated indicating SL plays a role in ethylene signaling, suggesting the regulation of complex transcriptional networks by mediating TFs and increasing the resistance against drought stress. The D-group genes *D14* and *MAX2* have been reported to play an essential role in mitigating drought stress by SL in grape seedlings (Wang et al., 2009).

4. Role of strigolactones under salinity stress

Salinity, one of the primary abiotic stressors affecting crop production, poses a significant threat to global food security. An estimated 800 million to 1 billion hectares of land in at least 100 countries, spanning all continents, is saline or sodic (Duan et al., 2023). Approximately 23 % of cultivated lands and 25–30 % of irrigated land are affected by salt stress (Karaca et al., 2023). This detrimental condition in the soil leads to a substantial reduction in growth attributes, yield characteristics, and agricultural production worldwide (Daba and Qureshi, 2021). The issue is projected to worsen due to the utilization of high-salinity irrigation water resulting from insufficient rainfall and subpar agricultural techniques, particularly in arid and semi-arid regions where evapotranspiration surpasses precipitation (Amer, 2021). In response to salinity stress, cells actively exclude Na^+ ions while producing osmoprotectants, leading to alterations in the photosynthetic and antioxidant levels (Balasubramaniam et al., 2023).

Various crops and vegetables also experience diminishing effects under salinity stress, as demonstrated in *Triticum aestivum*, *Hordeum vulgare* (Akhter et al., 2021), and *Solanum lycopersicum* (Guo et al., 2023). Therefore, there is an urgent need to develop sustainable

solutions to combat salinity and to safeguard global food production.

SLs are among the various plant growth regulators (PGR) because of their relatively recent discovery, serving as crucial aids for plants to thrive under challenging conditions and enhance the signaling network (Lu et al., 2023). Moreover, they play a significant role in facilitating hyphal branching, promoting plant interactions with arbuscular mycorrhizal fungi, and fostering other symbiotic associations (Alvi et al., 2022; Omoarelojie et al., 2019). The involvement of SLs in plant development is multifaceted, influencing shoot enlargement, photomorphogenesis, root branching, and leaf senescence (Faizan et al., 2022). Notably, external application of the SL analog GR24 to salt-stressed ornamental sunflower seedlings (Ahsan et al., 2023) resulted in increased leaf chlorophyll content, heightened photosynthetic activity, improved antioxidant metabolism, and reduced production of ROS and MDA. The discoveries surrounding SLs hold promising implications for advancing our understanding of plant resilience and for developing innovative strategies for agricultural improvement (Table 3).

4.1. Physiology and biochemical aspects

Throughout their life cycle, plants encounter numerous environmental stressors, including both biotic and abiotic factors. These constraints are major contributors to crop losses and pose significant threats to sustainable agriculture and the ecological balance worldwide (Abdelrahman et al., 2017; Abu Qamar et al., 2017). To survive under adverse conditions, plants develop various responses that involve a series of morpho-physiological, biochemical, and molecular changes (Abdelrahman et al., 2018). These responses are perceived and controlled through signal transduction and reprogramming of genetic and metabolic pathways.

Phytohormones play a central role in this intricate process by orchestrating these changes to generate sophisticated responses that optimize plant growth and development under stressful conditions (Wani et al., 2016). These hormonal signals are crucial for enabling plants to adapt and thrive in challenging environments, contributing to their resilience, and ensuring the continuation of vital ecosystem services.

The SL signaling pathway involves several key enzymes, including the ubiquitin-related protein F-box leucine-rich repeat protein (*D3/MAX2*), SL receptor α/β hydrolase (*D14*), and transcriptional repressor Clp ATPase family protein (*D53/SMXL6/7/8*). When the synthesized SL,

Table 3
Application of strigolactones in various plant species under salt stress.

Crop	Strigolactones	Impact	Reference
Rice	GR24	Enhances SOD, POD, and CAT activities	Ling et al., 2020
Apple	GR24	Preserves chlorophyll levels, Maintains the photosynthetic rate, Enhances leaf fresh weight	Zheng et al., 2020
Rapeseed	GR24	Increased photosystem II quantum yield, Decreased non-photochemical quenching, Enhances SOD & POD activities	Ma et al., 2017
Cucumber	GR24	Alleviate salt-induced photodamage, Enhance efficiency of ascorbate-glutathione, Scavenge excessive ROS	Zhang et al., 2022
Tomato	GR24	Enhanced Plant growth, Higher level of protein & proline contents, Incremented stomatal conductance & chlorophyll index	Faisal et al., 2023
Lettuce	GR24	Altered hormonal profiles, Improves plant physiology	Aroca et al., 2013

GR24, is externally applied, it leads to significant increases in SOD and POD activity and reduces MDA levels, thereby maintaining the growth and development in salt-affected rice (Ling et al., 2020). Similarly, in apple seedlings subjected to KCl stress, the application of GR24 preserves chlorophyll levels and maintains the photosynthetic rate, with the most effective concentration being 100 μ M compared to 10 μ M and 1 mM, resulting in the lowest wilting rate and highest fresh weight (Zheng et al., 2020). This improvement was attributed to the increase in stomatal conductance and transpiration rate in apple seedlings due to exogenous GR24.

Reactive oxygen species (ROS) play a vital role as signaling molecules in regulating plant metabolism, growth, and stress response, but excessive ROS can cause oxidative damage (Zheng et al., 2020) (Fig. 4). However, GR24 application induces resistance to ROS damage by enhancing cell viability and inhibiting ROS production (Wang et al., 2021). This protective effect is also observed in wheat plants treated with GR24 under salinity stress, where the controlled production of O_2^- , H_2O_2 , and MDA reduces ROS damage (Sedaghat et al., 2017). These findings collectively suggest that SLs play a significant role in reducing lipid peroxidation in plants exposed to salinity-alkalinity stress.

In contrast, SOD, POD, and CAT are the three key enzymes responsible for plant defense mechanisms against abiotic stresses (Min et al., 2018). It is generally believed that salinity-alkalinity stress reduces the activities of these antioxidant enzymes. However, when GR24 was applied, the activities of SOD, POD, and CAT significantly increased. Salinity stress often leads to electrolyte leakage, but the application of SLs protects proline content by enhancing soluble sugar and protein levels (Wang et al., 2019). Exogenous application of SLs can also increase the concentration of proline and alleviate KCl stress in *M. hupehensis* (Ma et al., 2022).

4.2. Molecular aspect

Saline-alkaline conditions can cause ionic toxicity, high pH, oxidative damage, and osmotic stress in plants. This results in an excessive accumulation of Na^+ in the cytoplasm, which disrupts plant growth by disturbing the cytosolic Na^+/K^+ ratio (Xu et al., 2020; Dai et al., 2018).

Exogenous application of GR24 to apple leaves helps to decrease Na^+ content while increasing K^+ content, thereby lowering the leaf Na^+/K^+ ratio (Ma et al., 2022) (Table 3). Similar findings were observed in sunflowers, where GR24 treatment increased K^+ content and reduced the Na^+/K^+ ratio. Plants have evolved certain proteins, such as cation/ H^+ exchangers (SOS1) and cation exchangers, to protect against Na^+ toxicity by expelling Na^+ from the cells. The expressions of *MhCHX15*, *MhSOS1*, and *MhCAX5* were enhanced under exogenous GR24 application, contributing to the balance of Na^+ homeostasis in the cytoplasm under salinity-alkalinity stress. In contrast, genes such as *MhSKOR*, *MhNHX1*, and *MhNHX2*, responsible for K^+ efflux and influx, were inhibited after GR24 application, suggesting that GR24 helps retain K^+ within the cells to maintain Na^+/K^+ homeostasis under salinity-alkalinity stress (Xue et al., 2019; Xu et al., 2020).

Furthermore, Ca content was notably induced by exogenous GR24, possibly as a response to salinity-alkalinity stress in apple seedlings to balance Na^+/Ca^{2+} in the cytoplasm (Hu et al., 2016) (Table 3). Additionally, Fe content increased after GR24 treatment, as Fe plays a crucial role in enhancing plant resistance to oxidative stress caused by salinity-alkalinity conditions (Dai et al., 2018). These results highlight the beneficial effects of GR24 application on mitigating the negative impacts of salinity and alkalinity stress on plant physiology and growth.

Exogenous application of GR24 effectively regulated the expression levels of three AHA enzyme family genes (*MhAHA1*, *MhAHA3*, and *MhAHA9*) that play crucial roles in pH stress regulation by over-expressing H^+ -ATPase genes and inducing organic acid production. Additionally, six antioxidant enzyme genes were significantly affected by exogenous GR24. The expression patterns of *MhSOD*, *MhPOD*, and *MhCAT* genes were consistent with the activities of their corresponding

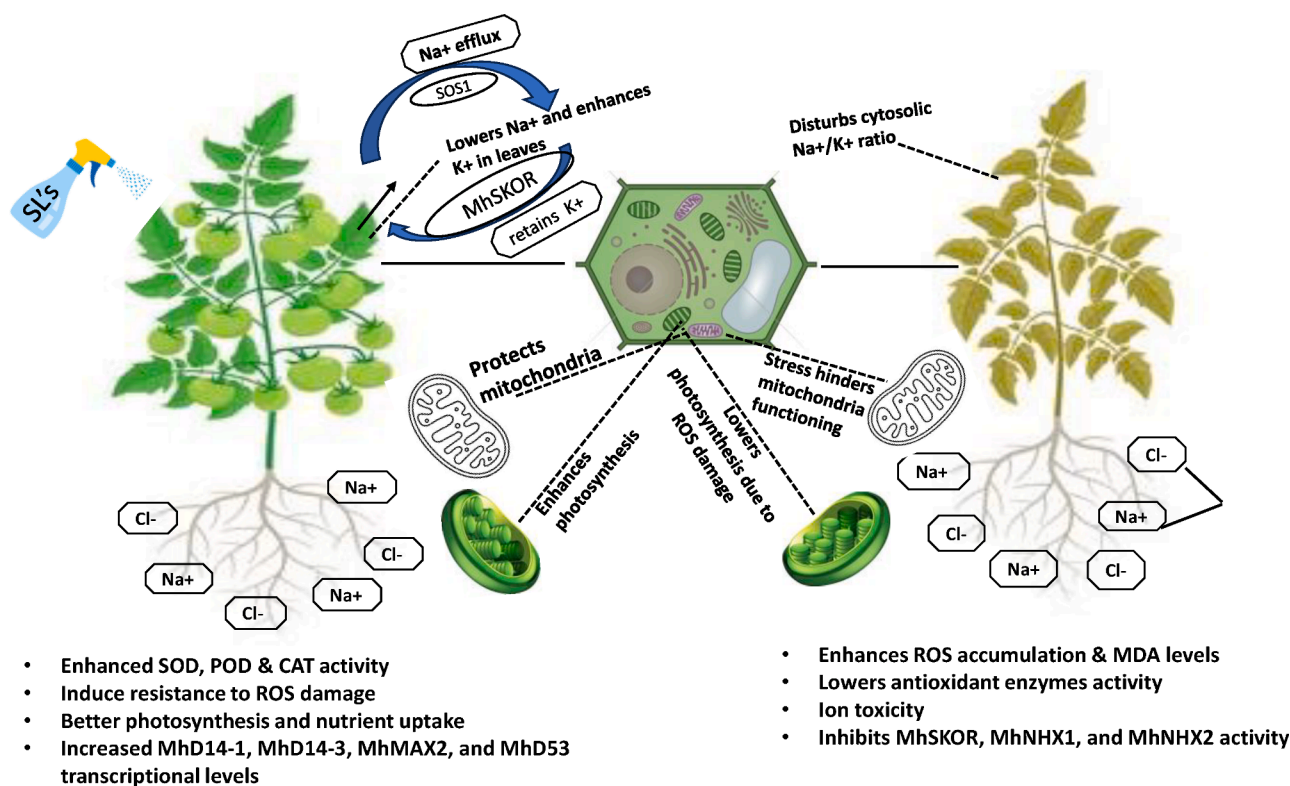


Fig. 4. The role of strigolactones on plants cellular level under salt stress.

enzymes, SOD, POD, and CAT, indicating that GR24 can alleviate oxidative damage by modulating the expression of antioxidant enzyme genes and enhancing the activities of SOD, POD, and CAT under salinity-alkalinity stress.

The pathway involved in Strigolactone (SL) signaling includes SL receptor D14, transcriptional repressor protein *D53/MXL6/7/8*, and F-box protein *D3/MAX2* (Shabek et al., 2018). Four SL signal transduction pathway genes (*MhD14-1*, *MhD14-3*, *MhMAX2*, and *MhD53*) experienced a substantial increase in transcript levels following treatment with exogenous GR24. Similarly, in apple seedlings, SL treatment induced the expression of *MdD14*, *MhMAX2*, and *MhD53* in apple leaves (Brewer et al., 2016). A decrease in SLs in tomatoes has been linked to drought stress signaling (Visentin et al., 2016). The expression of four SL biosynthetic enzyme genes (*MhCYP711*, *MhCCD7*, *MhCCD8*, and *MhD27*) decreased under salinity-alkalinity stress but was substantially increased by exogenous GR24 treatment. This suggests that the decrease in the expression of these four genes might be an energy-saving strategy for apples to cope with salinity-alkalinity stress.

5. Conclusion

SLs are emerging plant hormones that play important roles in plant responses to heat, drought, and salinity stresses. They regulate physiological processes like stomatal closure, root growth, and antioxidant activity as well as the expression of genes involved in the cell cycle, heat shock proteins, hormone signaling, and SL biosynthesis and signaling components. Exogenous application of SL analogs can increase abiotic stress tolerance in crops by coordinating molecular, biochemical, and physiological responses. More studies are needed to fully elucidate SL signaling cascades across plant species and environments.

6. Prospects

The SLs in plant research and agriculture are promising. As understanding of their roles in plant growth and stress responses continues to

evolve, several avenues of development and application can be anticipated. With increasing environmental challenges such as heat, drought, and salinity, the role of SLs in mitigating these stresses offers significant potential. Further research may uncover novel mechanisms by which SLs confer stress tolerance, leading to the development of crop varieties with improved resilience. Overall, the future of SLs in plant science and agriculture appears promising, with opportunities for continued research, innovation, and practical application to address global challenges in food security and environmental sustainability.

CRedit authorship contribution statement

Muhammad Fasih Khalid: Writing – original draft, Conceptualization. **Waqar Shafqat:** Methodology. **Rashid Iqbal Khan:** Investigation. **Muhammad Zaid Jawaid:** Visualization. **Sajjad Hussain:** Validation. **Muhammad Saqib:** Project administration. **Muhammad Rizwan:** Writing – review & editing. **Talaat Ahmed:** Writing – review & editing, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.stress.2024.100490](https://doi.org/10.1016/j.stress.2024.100490).

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