



## Review article

## Strigolactones can be a potential tool to fight environmental stresses in arid lands

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## ABSTRACT

**Background:** Environmental stresses pose a significant threat to plant growth and ecosystem productivity, particularly in arid lands that are more susceptible to climate change. Strigolactones (SLs), carotenoid-derived plant hormones, have emerged as a potential tool for mitigating environmental stresses.

**Methods:** This review aimed to gather information on SLs' role in enhancing plant tolerance to ecological stresses and their possible use in improving the resistance mechanisms of arid land plant species to intense aridity in the face of climate change.

**Results:** Roots exude SLs under different environmental stresses, including macronutrient deficiency, especially phosphorus (P), which facilitates a symbiotic association with arbuscular mycorrhiza fungi (AMF). SLs, in association with AMF, improve root system architecture, nutrient acquisition, water uptake, stomatal conductance, antioxidant mechanisms, morphological traits, and overall stress tolerance in plants. Transcriptomic analysis revealed that SL-mediated acclimatization to abiotic stresses involves multiple hormonal pathways, including abscisic acid (ABA), cytokinins (CK), gibberellic acid (GA), and auxin. However, most of the experiments have been conducted on crops, and little attention has been paid to the dominant vegetation in arid lands that plays a crucial role in reducing soil erosion, desertification, and land degradation. All the environmental gradients (nutrient starvation, drought, salinity, and temperature) that trigger SL biosynthesis/exudation prevail in arid regions. The above-mentioned functions of SLs can potentially be used to improve vegetation restoration and sustainable agriculture.

**Conclusions:** Present review concluded that knowledge on SL-mediated tolerance in plants is developed, but still in-depth research is needed on downstream signaling components in plants, SL molecular mechanisms and physiological interactions, efficient methods of synthetic SLs production, and their effective application in field conditions. This review also invites researchers to explore the possible application of SLs in improving the

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survival rate of indigenous vegetation in arid lands, which can potentially help combat land degradation problems.

## 1. Introduction

Environmental stresses such as drought, temperature, salinity, and nutrient deficiency are affecting plant growth and agronomic yield worldwide by disrupting cellular structures and vital physiological functions (Krasensky and Jonak, 2012). Climatic changes and global warming-associated drought fluctuations and salinity are putting enormous pressure on agricultural and non-agricultural plants (Ullah et al., 2021). The world's population is already eight billion in the next decade, making food production a critical challenge for the growing population (Negacz et al., 2022). Environmental stresses are collectively affecting crops production and plant growth, especially in arid and semi-arid parts of the world (hereafter described as arid lands) (Zhang et al., 2022). Arid lands cover 25.8% of the global land surface and are home to 18.5% of the world's population (Maestre et al., 2021). Arid regions face drought and salinity problems that considerably affect plant growth by reducing nutrient and water uptake and ultimately plant metabolism and growth (Perri et al., 2020) (Tariq et al., 2022a). In arid lands, evapotranspiration is increasing (higher surface air temperature) and precipitation is decreasing due to climate change. Anthropogenic activities such as agriculture expansion and unsustainable land use management practices due to high pressure of population and income growth, especially in developing countries further increase water scarcity (Stafford-Smith et al., 2017; Berdugo et al., 2022). In recent decades, the arid lands have already been expanded and climate change forecasted further expansion of arid lands in coming future making drought and salinity a global challenge (Butcher et al., 2016; Stavi et al., 2021). In the current scenario of increased warming and drought events (further intensifying salinity), arid lands face serious threats due to low survival rate of seedlings, successive establishment of seedlings, biodiversity loss, vegetation restoration, desertification, and land degradation problems, resulting in further expansions of arid lands worldwide and demanding serious attention of researchers and policymakers (Tariq et al., 2022a).

Plants exhibit dynamic responses to environmental stresses involving complex crosstalk between metabolic adjustments and gene expression for morphological and physio-biochemical adaptations. Plant acclimation to the new environmental conditions is crucial to ensure the continuity of ecosystem functions. There are many hormones that are known to protect plants from abiotic stresses (Wani et al., 2016). Phytohormones play a crucial role as signaling molecules in plants and trigger coordinate mechanisms for acclimation to the stress. In addition to other hormones such as auxins, gibberellins, ethylene, brassinosteroids, cytokinins (CKs), jasmonic acid, plant peptide hormones, abscisic acid (ABA), nitric oxide (NO), salicylic acid (SA), and polyamines (PA), few recently emerged strigolactones (SLs) have attracted plant biologists attention due to their role in regulation and signal transduction in plants (Bhatt and Bhatt, 2020). SLs were first distinguished as stimulators for seed germination in the roots of *Striga* and *Orobanche* (parasitic plants), more than 45 years ago (Ruyter-Spira et al., 2013; Xie et al., 2017). Later it was suggested that SLs act as root-derived signals that enhance the symbiotic relationship between plant roots and arbuscular mycorrhiza (AM) fungi due to their ability to increase the branching of AM fungi (Akiyama et al., 2005). SLs are carotenoids-derived signaling molecules that have diverse functions in improving plant capacity and resistance to intermingle with diverse growing environments (Wang et al., 2020; Al-Babili and Bouwmeester, 2015). Hence, SLs can significantly influence the development/growth of plants due to their active functions at the synthesis and transportation sites. In this review, our aim is to provide the best information on the potential role of SLs to counteract major environmental stresses in plants and to identify scientific gaps for future

studies that would have a positive impact on vegetation restoration, land rehabilitation, and combating desertification problems in arid lands.

## 2. Biosynthesis of strigolactones

SLs are carotenoid-derived sesquiterpene lactones (Fig. 1) comprising a four-ring system structure that is ABC tricyclic core linked to the D-ring (fourth ring) by an enol-ether bridge (Bürger and Chory, 2020; Dell'Oste et al., 2021). Structurally, SLs are divided into two classes: canonical and non-canonical SLs. Canonical strigolactones (SLs) consist of the ABC fused tricyclic-rings, with a butenolide D-ring bonded to the C-ring through an enol ether bond. The AB-rings can vary in the number of carbon (C) atoms, double bonds, and functional groups, but the C and D rings must be lactone and methyl furanone, respectively (Mashiguchi et al., 2021). Based on the stereochemistry of the C-ring, canonical SLs are divided into two classes: strigol-type ( $\beta$ -oriented C-ring) and orobanchol-type ( $\alpha$ -oriented C-ring). Non-canonical SLs lack AB or C rings but contain the enol ether-D ring moiety, which is biologically essential (Zorrilla et al., 2022). Non-canonical SLs have no defined classes or common precursor or core enzyme, resulting in a diversity of molecules due to biosynthesis enzymes in different species (Guercio et al., 2022). However, the stability of non-canonical SLs is lower than that of canonical SLs due to their gradual decomposition during purification and storage (Yoneyama et al., 2018). Moreover, while canonical SLs are widely distributed in different plant species, non-canonical SLs are species-specific and exhibit greater structural diversity than the former (Ito et al., 2022). Through bioassay-guided purification research, more than 30 SLs (canonical and noncanonical) have been identified as stimulators for germinating parasitic root weeds (Yoneyama and Brewer, 2021). Non-canonical SLs were characterized recently, such as zealactone from maize (Xie et al., 2017; Charnikhova et al., 2017), avenaol from wild oat (Kim et al., 2014), heliolactone from sunflower (Ueno et al., 2014), and lotuslactone from *Lotus japonicum*30. However, it's likely that more non-canonical SLs will be discovered in future because of their higher structural diversity than canonical SLs. But, this would not be possible without discovering effective methods of their purification and storage.

Genes involved in SLs biosynthesis and perception are named MAX (MORE AXILLARY GROWTH) in *Arabidopsis*, DAD (DECREASED APICAL DOMINANCE) in *petunia*, D (DWARF) in rice, and RMS (RAMOSUS) in pea (Yoneyama and Brewer, 2021) (Fig. 2). Genetic screening of shoot branching mutants explored that SLs biosynthesis is regulated by several enzymes such as carotenoids isomerase D27, carotenoids cleavage dioxygenases CCD7, cytochrome P450 monooxygenases, and carotenoids cleavage dioxygenases CCD8. SLs biosynthesis starts from all-*trans*- $\beta$ -carotene, which then converts to 9-*cis*- $\beta$ -carotene with the help of the D27 isomerase enzyme, and then 9-*cis*- $\beta$ -carotene converts to carlactone (CL) through sequential reactions with the use of CCD7 and CCD8 enzymes (Fig. 2). First time discovery of CL was reported in *Escherichia coli* with the functions of inhibiting tillering (in rice plants) and inducing germination (in parasitic root plants) (Alder et al., 2012).

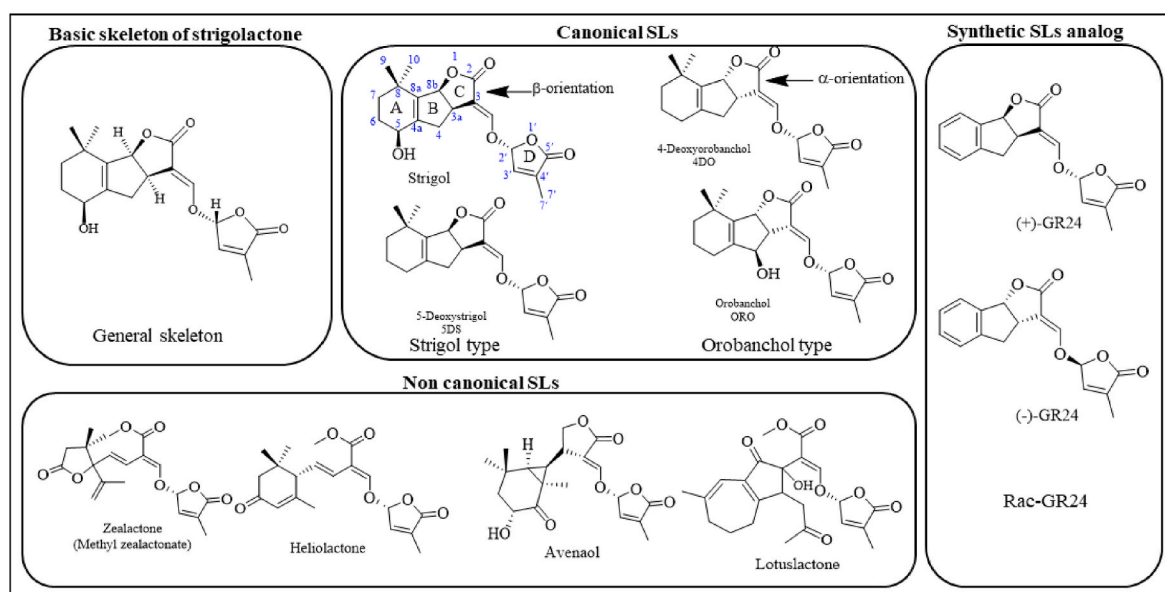
Seto et al. (2014) later discovered that in *Arabidopsis thaliana* and *Oryza sativa*, CL is an indispensable precursor for both types of SLs in *A. thaliana* and rice plants. In *Arabidopsis*, cytochrome P450 more auxiliary growth (MAX) 1 (*CYP711A1*) oxidizes CL to produce carlactonic acid (CLA), an important signaling molecule in the rhizosphere, which is then converted to methyl carlactonoate (MeCLA) by an unknown methyltransferase (Abe et al., 2014). Brewer et al. (2016) further identified and characterized lateral branching oxidoreductase (LBO) that encodes a 2-oxoglutarate and Fe (II)-dependent dioxygenase using transcriptomics and reverse genetics. It was further suggested that SLs

biosynthesis genes and LBO highly co-expressed, indicating that the LBO enzyme might convert MeCLA into hydroxymethyl carlactonate ( $1'-OH-MeCLA$ ) (recombinant LBO in-vitro) (Yoneyama et al., 2020). This is a general mechanism of SLs synthesis, but it varies among different plants. For example, compared to *Arabidopsis*, rice comprises five homologous MAX1. Among them, Os900 (*CYP711A2*) and Os1400 (*CYP711A3*) convert CL to CLA (Yoneyama et al., 2018), but Os900 has an additional role in catalyzing B–C ring closure and stereo-selectively converts CLA into a major rice SL named 4-deoxyorobanchol (4DO) (Zhang et al., 2014). Then, Os1400 catalyzes the hydroxylation of 4DO into orobanchol. However, in tomato plants MAX1 homologous (*CYP711A21*) is unable to convert 4DO into orobanchol and thus cannot produce 4DO (Yoneyama et al., 2018). In comparison, in cowpea, *CYP722C* converts CLA directly into orobanchol without forming a 4DO intermediate, and *CYP722C* is from a completely different cytochrome P450 clade to MAX1, while in cotton *CYP722C* converts CLA to 5-deoxystrigol (5DS) (Wakabayashi et al., 2020). In sorghum, an additional P450 (*CYP728B35*) belonging to another clade converts 5DS to sorgomol (Wakabayashi et al., 2021). Three P450 clades are involved in producing canonical SLs, while MeCLA is considered the precursor for non-canonical SLs production. For example, MeCLA can be converted into heliolactone in sunflower plants (Wakabayashi et al., 2020). However, it is hard to study their biological functions due to the less stability of non-canonical SLs than canonical SLs (Yoneyama et al., 2020). Overall, this suggests that MAX1 serves three enzymatic functions: conversion of CL to CLA, release of an important signal in the rhizosphere as CLA, and conversion of CLA to MeCLA, a precursor of non-canonical SLs. Therefore, MAX1 is a crucial biosynthesis enzyme involved in both endogenous and rhizosphere signaling. However, it remains intriguing why this enzyme has evolved multiple functions.

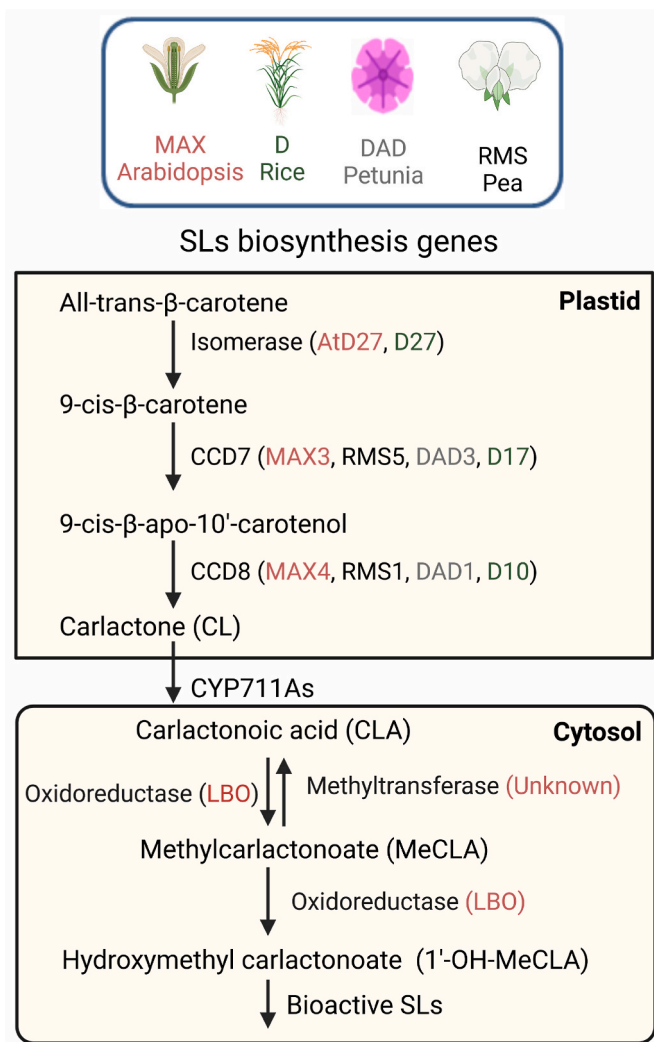
### 3. Transport of strigolactones

Plants have evolved a sophisticated transport system for internal hormones to maintain their growth under changing environmental circumstances (Borghi et al., 2015; Park et al., 2017). SLs act as symbiotic signals for AM fungi and are excreted into the soil from roots, particularly under low nitrogen or phosphorus conditions (Andreo-Jimenez et al., 2015). Grafting experiments with mutants (DAD, MAX, and RMS) revealed that SLs production in shoots is sufficient to restrain elongation

of axillary bud because wild type scions grafted on SLs-deficient mutant rootstocks exhibited the normal phenotypes (Domagalska and Leyser, 2011). However, Wild-type rootstocks could rescue the hyperbranching phenotype of the scion of SLs-deficient mutants, indicating that long-distance SLs transportation from the root to the shoot may occur. This means that regulation of shoot growth could be integrated with the nutrient availability perceived by the root. There are some possible candidates to be the mobile form of SLs; however, research is still ongoing to identify the exact molecules acting as endogenous signals in plants. Grafting experiments between mutants suggested the movement of intermediates involved in SLs biosynthesis. Booker et al. (2005) indicated that MAX1 rootstocks could retrieve the shoot branching phenotype (sbp) of MAX4 scions, indicating that CL can be a functional signal because it is the only known intermediate upstream of MAX1 and downstream of MAX4. Only MAX1 (but not MAX4 rootstocks) could rescue the sbp of *A. thaliana* Dwarf (At27) scions, indicating that 9-cis- $\beta$ -carotene and 9-cis- $\beta$ -apo-10'-carotenal are not mobile signals (Lin et al., 2009; Waters et al., 2012). Several researchers supported these findings because SL biosynthesis (from all-trans- $\beta$ -carotene to CL) is performed in the plastid (Lin et al., 2009; Aldridge et al., 2006; Arite et al., 2007). LBO rootstocks have also been reported to recover the sbp of MAX1 scions, indicating the possibility that CLA, MeCLA, and their uncharacterized metabolites can be a long-distance functional signal (Brewer et al., 2016). As previously noted, oxidized metabolites of CL and CLA have been identified in the roots of various species, suggesting their involvement in chemical signaling communication within the rhizosphere (Yoneyama et al., 2018). This suggests that CL and CLA play a role not only in long-distance endogenous signaling transport, but also in rhizospheric communication. Moreover, LC-MS/MS examination of the xylem sap also suggests considering the movement of SLs as several SLs, including ORO, were found in the xylem sap of tomato and *Arabidopsis*47. In contrast, the research by (Xie et al., 2015) found no ORO, CL, CLA, and MeCLA in *Arabidopsis* xylem sap, and even in other plants, but they did detect isotopic-labeled ORO and 4DO labeled isotopically (applied to rice roots) in the shoot within 20 h, but not in the xylem sap. These results divert attention from xylem-mediated transport to cell-to-cell-mediated transport of SLs in rice (Xie et al., 2015), but this also suggests the possibility that there might be some other unknown intermediates or compounds related to SLs that move through the xylem in long-distance transport from root to shoot. Together, grafting and



**Fig. 1.** Structural classification of SLs and related compounds. Structurally, SLs are divided into two classes: canonical and non-canonical SLs. The main difference between the two classes is that canonical SLs contain the ABCD rings while non-canonical ones lack ABC and contain enol ether–D ring. Based on the stereochemistry of B/C-ring junction, canonical SLs are divided into strigol and ORO types. GR24 is a widely used synthetic analog of SLs. Blue color shows carbon atoms position.



**Fig. 2.** Proposed pathway of SLs biosynthesis. The genes of SL biosynthesis are named MAX (MORE AXILLARY GROWTH) in *Arabidopsis* (red), D (DWARF) in rice (dark green), DAD (DECREASED APICAL DOMINANCE) in petunia (dark grey), and RMS (RAMOSUS) in pea (black). SLs biosynthesis starts from all-*trans*- $\beta$ -carotene, which then converts to 9-*cis*- $\beta$ -carotene with the help of the D27 isomerase enzyme, and then 9-*cis*- $\beta$ -carotene converts to CL through sequential reactions with the use of CCD7 and CCD8 enzymes. In *Arabidopsis thaliana* and *Oryza sativa*, CL is an indispensable precursor for both types of SLs. In *Arabidopsis*, cytochrome P450 MAX1 (CYP711A1) oxidizes CL to generate CLA, which is further converted to MeCLA via an unknown methyltransferase. LBO that encodes a 2-oxoglutarate and Fe (II)-dependent dioxygenase was further identified and characterized and suggested that SLs biosynthesis genes and LBO highly co-expressed, indicating that the LBO enzyme might convert MeCLA into 1'-OH-MeCLA. This is a general mechanism of SLs synthesis but varies among different plants.

LC-MS/MS findings indicate that there could be several mobile molecules of SLs and their intermediate that have not been identified. Identifying molecules that act as endogenous signals in long-distance transport is crucial for a better understanding of SL mechanisms. It should also be noted that CL and its oxidized molecules are present in a wide range of plant species, and it is possible that non-canonical SLs are involved in regulating shoot branching and other biological mechanisms. Therefore, it is important to determine which specific molecules are involved in endogenous signaling from root to shoot in order to unravel the mystery of long-distance transport.

#### 4. Strigolactones and salinity stress

According to the Food and Agriculture Organization (FAO), the salinity-affected topsoil (0–30 cm) covers 424 million hectares, while the subsoil (30–100 cm) covers 833 million hectares globally, and most of these affected areas are in arid lands (Huang et al., 2019). Salinity affects plant growth and metabolism in different ways (Negrão et al., 2017) and to counteract salinity stress, there are a variety of tolerance mechanisms in plants such as osmotic adjustment, accumulation of osmolytes, antioxidant defense system, and regulation of hormones and stress-related genes (Munns and Tester, 2008)– (Flowers et al., 2015; Miransari, 2014). Current approaches (traditional breeding and genetic engineering) to tackle salinity problems and improve food production are costly and require extensive scientific knowledge (Sanan-Mishra et al., 2005; Cuartero et al., 2006). Therefore, it is imperative to find cost-effective, eco-friendly and sustainable approaches to combating salinity problems in arid lands. Phytohormones are involved in improving stress-related responses of plants. However, very limited studies have reported the role of SLs in salinity tolerance (Yu et al., 2022), including effects on root and shoot growth, photosynthesis, pigments, antioxidants, and osmolytes, among others (Table 1).

Besides morphological and physiological acclimations in response to salinity, plants interact with microorganisms and, as a result, can develop a mutualistic association relevant to tolerating abiotic stresses (Raaijmakers et al., 2009; López-Ráez et al., 2011). The most intensively studied and well-known mutualistic associations are with soil AM fungi arbuscular mycorrhiza (Smith and Read, 2010). This symbiotic union system is more efficient than the roots alone in improving tolerance against various stresses including salinity (Ruiz-Sánchez et al., 2010). For example, the host plant produces and releases exudates as signaling molecules, including SLs, under stress conditions (under nutrient starvation). These signals are recognized by AM fungi, helped by an uncharacterized receptor, and increase its hyphal growth and branching, which improves the probability of developing this symbiotic union (Andreo-Jimenez et al., 2015). SLs are one of these signals and have recently emerged as essential cues that act as a 'cry for help' alarm during environmental stress conditions (López-Ráez et al., 2011; Ruiz-Lozano et al., 2016). Once mutualism is established, AM fungi enhance and alter SL levels of host plants and help alleviate saline stress by improving nutrient acquisition, water uptake, and cellular osmotic potential by accumulating osmoregulators (Kong et al., 2017).

Based on current research, the molecular mechanism triggered by SLs interaction occurs when salinity stress initiates the production of nitric oxide, reactive oxygen species (ROS), and  $\text{Ca}^{2+}$  signaling, instigating efficient signaling to reduce cellular oxidative damage (Seifkhalhor et al., 2019). The biosynthesis and downstream signaling pathways of phytohormone, and abscisic acid (ABA), are changed, generating controlled stress responses. Phosphorylation of ABA-responsive element (ABRE)-binding protein/ABRE-binding factor (AREB/ABF) transcription factors is caused by SNF1-related protein kinase 2 (SnRK2s). It is noteworthy that MAX4 (CCD8), MAX3 (CCD7), MAX2, and MAX1 have ABRE cis-regulatory sequences in their promoter (Yu et al., 2022; Qiao et al., 2020). Research suggests that the SLs-biosynthesis genes (MAX1, MAX3, and MAX4) displayed a greater affinity to be induced in response to ABA treatment for a longer time. MAX3 and MAX4 were stimulated four- and eight-fold with ABA treatment (after 10 h) (Ha et al., 2014). This research indicates that the ABFs directly bind to the promoters of MAX1, MAX2, MAX3, and MAX4 and activates the SLs biosynthesis pathway. In turn, SLs elevate the production of SOD, POD and intercellular  $\text{CO}_2$  and limit MDA production, helping mitigate the salt stress (Fig. 3). Aroca et al. (2013) found a positive correlation between SL production and AM symbiosis that alleviated saline stress by altering growth and physiological traits (biomass, stomatal conductance, and photosystem II) of lettuce plants. However, salinity negatively affects SL production in non-mycorrhizal plants. Enhanced stomatal conductance and photosystem II efficiency

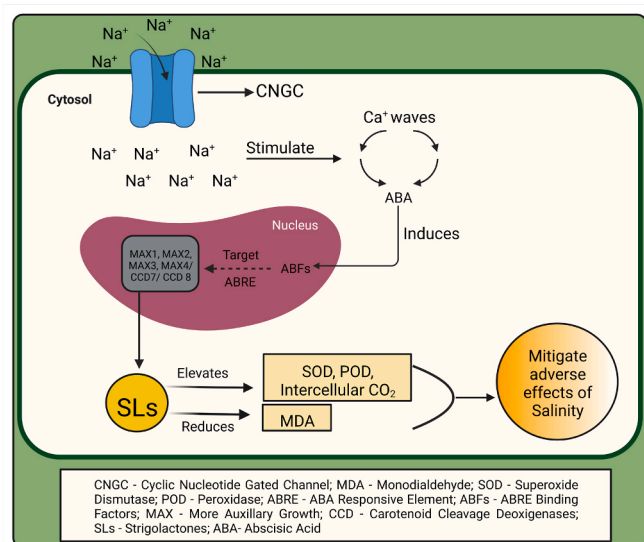
**Table 1**  
Production and role of SLs in improving plants tolerance against abiotic stresses.

Plant system	Type of stress	Site of SLs detection	SLs compound name	SLs effects	References
<b>Salinity stress</b>					
<i>Arabidopsis thaliana</i>		Leaf tissues	NA	SLs positively regulated plant responses to stress.	(Ha et al., 2014)
<i>Arabidopsis thaliana</i>		Leaf tissues	NA	Osmotic stress responses	Lv et al. (2018)
<i>Brassica napus</i>		Root and leaf tissues	NA	Osmotic stress on stomata closure	Ma et al. (2017)
<i>Helianthus annuus</i>		Foliar application	GR24	GR24 improves the shoots and root's growth under salt stress	
<i>Helianthus annuus</i>		Callus induction	GR24	Ameliorated the inhibiting effects of salinity, improved biomass, enhanced the transpiration rate, sub-stomatal CO <sub>2</sub> concentration, Ci/Ca ratio, increased the osmotic potential and relative water contents	Sarwar and Shahbaz (2020)
<i>Oryza sativa</i>		Solution	GR24	Fresh and dry weight, different enzymes, and proteins	(Zulfiqar et al., 2021)
Phelipancheramos		AM symbiosis	SLS production	Photosynthesis and physiological characteristics improved growth, stomatal conductance, and efficiency of photosystem II	(Ling et al., 2020) (Aroca et al., 2013)
<i>Salvia nemorosa</i>		Foliar treatment	GR24	Plant growth rate, chlorophyll content, gas exchange parameters, electrolyte leakage, lipid peroxidation, H <sub>2</sub> O <sub>2</sub> content, proline content, antioxidant enzymes, total phenol content, glutathione pool estimation and essential oil yield	Sharifi and Bidabadi (2020)
<i>Sesbania cannabina</i>		Root extracts	AMF (†) total SLs (by crosstalk with H <sub>2</sub> O <sub>2</sub> and salt tolerance)	SLs enhances salt stress tolerance, and the H <sub>2</sub> O <sub>2</sub> -induced SLS accumulation was accompanied by increased salt tolerance	Kong et al. (2017)
<i>Triticum aestivum</i>		Foliar spray and seed treatment	GR24	Net CO <sub>2</sub> assimilation rate increased; growth improves	Kausar and Shahbaz (2017)
<b>Drought stress</b>					
<i>Festuca arundinacea</i>	Drought	Crowns	(†) Total SLs	SLs accumulation and signaling. Drought responses and Axillary bud development	(Zhuang et al., 2017)
<i>Lotus japonicus</i>	Low P		NA	SLs contribute to drought resistance	(Liu et al., 2015)
<i>Oryza sativa</i>	Drought	Stem base	NA	Drought escape and tillering	Du et al. (2018)
<i>Oryza sativa</i>	Drought		NA	SLs biosynthesis interferes with ABA formation	Haider et al., (2018)
<i>Solanum lycopersicum</i>	Drought responses	Root extracts	(†) Solanacol and didehydro-orobanchol isomers 1 and 2	Low levels of SLs act as components of the systemic signal of drought response and AMF symbiosis	(Ruiz-Lozano et al., 2016), (Visentin et al., 2016)
<b>Temperature stress</b>					
<i>Arabidopsis thaliana</i>	Heat, UV, and wound	Root tissues	NA	Abiotic stresses responses	(Marzec and Muszynska, 2015)
<i>Glycine max</i>	Dark chilling	Root tissues	NA	Chilling tolerance	Cooper et al. (2018)
<i>Solanum lycopersicum</i>	Light	Root tissues	(†) Solanacol, orobanchol, and didehydro-orobanchol isomer	SLs produce tolerance to light	Koltai and Kapulnik (2011)
<b>Nutrient stress</b>					
<i>Arabidopsis thaliana</i>	Low P	Root and xylem sap	(†) Orobanchol	SLs regulate the response of plants to low Pi. Axillary shoot branching	Kohlen et al. (2011)
<i>Arabidopsis thaliana</i>	Low N	Root tissues	NA	Leaf senescence and plant growth	Ito et al. (2016)
<i>Astragalus sinicus</i>	Low P and N	Root exudates	(†) Sorgomol and 5-deoxystrigol	Plant growth	(Yoneyama et al., 2012)
<i>Dendranthema grandiflorum</i>	Low P	Root exudates and whole plant	Chrysanthemum SLs analogues	Shoot branching under P Starvation	Xie et al. (2010)
<i>Lactuca sativa</i>	Low P and N	Root exudates	(†) Orobanchol and orobanchyl acetate	Plant growth	(Yoneyama et al., 2012)
<i>Medicago sativa</i>	Low P	Root exudates	(†) Orobanchol and orobanchyl acetate	Plant growth	Yoneyama et al. (2012)
<i>Medicago sativa</i>	Low P and High N with rhizobium	Root extracts	(†) Orobanchol and orobanchyl acetate	Rhizobium-legume symbiosis under nutrient shortage	(Peláez-Vico et al., 2016)
<i>Oryza sativa</i>	Low P	Roots	(†) 2'-epi-5-deoxystrigol	Inhibition of tiller bud outgrowth	Umehara et al. (2010)
<i>Oryza sativa</i>	Low P and N	Root exudates	(†) Orobanchol, 2'-epi-5-deoxystrigol	SLs produce root growth in rice under P and N limitation by decreasing auxin transport from shoots to roots and helps in germination	(Jamil et al., 2011)
<i>Oryza sativa</i>	Low N and Low P	Roots	NA	SLs involve in NO-activated elongation of seminal root under low N and P	(Sun et al., 2016)
<i>Pisum sativum</i>	High P	Root exudates	(↓) Fabacyl acetate and orobanchyl acetate	Regulation of AMF symbiosis	Balergue et al. (2011)
<i>Solanum lycopersicum</i>	Low P		(†) Orobanchol, solanacol, and didehydro-orobanchol isomers	NA	(López-Ráez, 2016)
<i>Solanum lycopersicum</i>	Low P	Root exudates	(†) Orobanchol	Plant growth	(Yoneyama et al., 2012)
<i>Sorghum bicolor</i>	Low P, Low N	Roots	(†) 5-deoxystrigol	Germination	Yoneyama et al. (2007)
<i>Tagetes patula</i>	Low P and N	Root exudates	(†) Orobanchol and orobanchyl acetate	Plant growth	Yoneyama et al. (2012)

(continued on next page)

Table 1 (continued)

Plant system	Type of stress	Site of SLs detection	SLs compound name	SLs effects	References
<i>Trifolium pretense</i>	Low P	Roots	(†) Orobanchol	Germination	Yoneyama et al. (2012)
<i>Triticum aestivum</i>	Low P and N	Root exudates	(†) Orobanchol	Plant growth	Yoneyama et al. (2012)



**Fig. 3.** An overview of signal transduction and signal cascade between SLs and ABA in plants during salt stress. The Na<sup>+</sup> ion uptake by plant roots stimulates Ca<sup>2+</sup> ion waves in vacuole and through a cascade of signaling, it stimulates the biosynthesis of ABA. The accumulation of ABA in plant roots induces ABF transcription factors that target the promoters containing ABRE cis regulatory elements. Since the SLs biosynthesis pathway genes (MAX1, MAX2, MAX3, MAX4, CCD7, CCD8) contain ABRE cis regulatory elements in their promoters, we propose that ABFs trigger the biosynthesis of SLs by targeting its biosynthesis pathway genes. The accumulation of SLs in roots elevates SOD, POD and intercellular CO<sub>2</sub> and reduces MDA that in turn mitigate the adverse effects of salinity by scavenging the ROS and other probable mechanisms.

in mycorrhizal plants resulted in lower photorespiration and production of ROS, leading to improved salinity tolerance and growth (Ruiz-Sánchez et al., 2010). ABA levels also increased in roots colonized with non-colonized and AMF due to augmented salinity, suggesting a strong connection between both phytohormones (Parvez et al., 2022). The role of ABA in the synthesis of SLs was confirmed as ABA-deficient tomato mutants, and plants treated with specific ABA inhibitors showed low efficiency in the production of SLs (López-Ráez et al., 2010). These findings suggest a potential role for AMF in protecting plants against salinity stress, and indicate that AMF symbiosis could be applied to promote sustainable agriculture in various ecosystems, including arid regions. Interestingly, the biosynthesis of SLs was enhanced under salinity stress, which suggests that in addition to nutrient deficiencies, other environmental stresses may also affect SLs production. Furthermore, AMF development was further stimulated in response to SLs production in mycorrhizal plants under salt stress. Although the fundamental mechanisms regulating SLs production under salinity stress and the mycorrhization process require further exploration, the involvement of ABA is evident from the aforementioned findings.

Furthermore, Ren et al. (2018) revealed the H<sub>2</sub>O<sub>2</sub>-mediated salinity tolerance in mycorrhized seedlings of *Sesbania cannabina*, where the production of H<sub>2</sub>O<sub>2</sub> increased in response to the perception of ABA signaling and increased the SLs biosynthesis. However, more research is required to reveal the genetic evidence on the role of ABA in

H<sub>2</sub>O<sub>2</sub>-mediated SL production and to characterize the main signaling components responsible for SLs production and improvement in salinity tolerance in mycorrhized *S. cannabina*. Ha Van et al. (Ha et al., 2014) highlighted the positive role of SLs in regulating high salinity responses in *Arabidopsis*. These results show that SLs positively tackles the stress responses in *Arabidopsis* via ABA-dependent and ABA-independent pathways. The complex biological adaptive phenomenon, including multiple hormone regulatory pathways, has also been observed using transcriptomics analysis. SLs, cytokinins (CK), and ABA were involved in regulating the stomatal closure and leaf senescence, and these attributes are closely linked with stress responses and adaptation. Furthermore, AtMAX2, AtMAX3, and AtMAX4 gene expression have been identified to play a positive role against salt stress by (Ha et al., 2014). This underlines a greater understanding of the interaction between SLs and ABA is needed to support future research.

The participation of SLs in the tolerance to saline can be analyzed through the exogenous application of hormones or regulators. GR24, a synthesized SL applied to *Brassica napus* seedlings as aqueous at a concentration of 0.18 μM, improved the growth of shoots and roots under salt stress. The application of GR24 on *B. napus* reversed salinity-induced effects on gas exchange and chlorophyll fluorescence traits (Ma et al., 2017). Under salt stress conditions, the application of GR24 increased the quantum productivity of photosystem II and decreased non-photochemical quenching. The application of GR24 improved the peroxidase and superoxide dismutase, but reduced the lipid peroxidation rate. Transcriptomics analysis of the shoot and root showed 166 specifically differentially expressed genes (DEGs) after treatment with GR24 under salinity stress. The expression of genes related to tryptophan metabolism, photosynthesis, and auxin signal transduction are all linked to stress reduction. The research shows that the beneficial effects of GR24 on alleviating saline stress in rapeseed have also been associated with crosstalk with auxin. GR24 has also been tested to investigate its impact on helping induced salt stress in rice. Rice growth traits, such as plant height and root length, decreased by 14% and 40%, respectively, under saline stress, and the application of GR24 improved plant height, root length, leaf photosynthesis, and physio-biochemical indices in salt-affected rice seedlings compared to control (Ling et al., 2020). Kausar and Shahbaz (2017) demonstrated that salt stress adversely affected growth, gas exchange, chlorophyll fluorescence, non-photochemical quenching (NPQ), and the coefficient of non-photochemical quenching (qN) in wheat plants. However, wheat seeds of wheat showed a slight increase in net carbon dioxide (CO<sub>2</sub>) assimilation rate, NPQ, qN and reduced stomatal conductance. More recently, Sarwar and Shahbaz (2020) suggested that pre-sowing achene treatment with GR24 significantly enhanced sunflower biomass and shoot length (*Helianthus annuus*) plants and increased K<sup>+</sup> and Ca<sup>2+</sup> concentrations in shoots and roots under saline stress. Similarly, Zulfiqar et al. (2021) reported that 0.01 mg L<sup>-1</sup> level of GR24 revealed significantly higher callus biomass, antioxidant enzymatic activities, K<sup>+</sup> and Ca<sup>2+</sup> ions and stress-related metabolites. These findings suggest the potential for synthetic SLs (such as GR24) to improve salinity tolerance in various plant species. The research highlights the possibility of using SLs through direct application or, more importantly, using breeding or genetic engineering to enhance salinity tolerance by manipulating SL biosynthesis or signaling pathways. This is evidenced by the improved salinity tolerance of plants treated with GR24.

## 5. Strigolactones and drought stress

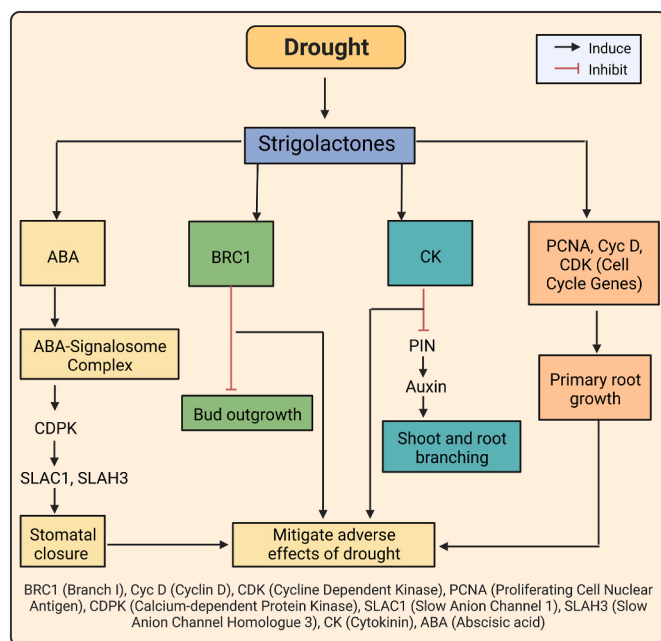
SLs' role under water stress conditions has been observed to exhibit interplay with other plant hormones. For example, SLs act as a positive regulator in the drought response through ABA signaling, as evidenced by all *Arabidopsis* max mutants that showed lower sensitivity to ABA under drought stress (Mostofa et al., 2018). SLs and ABA crosstalk are critical in integrating stress signals to control stomata growth and function. The SLs application improved drought tolerance in wild type plants and recovered the drought-sensitive phenotype of SLs-deficient mutants but not of SLs-response mutants, verifying the SLs role in the stress response (Ha et al., 2014).

Literature review showed that SLs improve hydrogen peroxide ( $H_2O_2$ ) and NO synthesis and activate the Slow Anion Channel-Associated1 (SLAC1) anion channel, which results in stomatal closure and thus helps plants adaptation to environmental stresses (Zhang et al., 2018). SLAC1 is a plasma membrane protein and plays crucial role in stomatal closure in response to changes in humidity, light/dark transition,  $CO_2$ , ABA, calcium ions, ozone, NO, and  $H_2O_2$  (Vahisalu et al., 2008). Lv et al. (2018) suggested that guard cells require  $H_2O_2$  and NO for an enhanced SL response. It was discovered that SLs-induced stomatal closure was disrupted in the SLAC1 mutant, indicating that SLAC1 is vital for SLs-induced stomatal closure. Thus, SLAC1 anion channels were destroyed, resulting in ABA and SL insensitivity in stomata. It indicates that the two signaling pathways might overlay the SLAC1 anion channel by adjusting the internal turgor pressure. Besides this, jasmonic acid (JA) interrelates with stomatal closure (ABA-regulated) by elevating  $Ca^{2+}$  influx, stimulating production of calcium-dependent protein kinase (CDPK), and the resulting signaling pathways. The interaction between SLs and ABA is essential during stress conditions for regulating stomatal responses and development (Ha et al., 2014) (Fig. 4) Furthermore, SLs-biosynthetic (MAX1-1, MAX3-9, and MAX4-1) and

SLs-signaling (Atd14-5 and MAX2-1) *A. thaliana* mutants showed greater stomatal opening than wild types, indicating that SLs positively regulates stomatal closure (Lv et al., 2018). Higher stomatal conductance and broadly opened stomata were observed in *Lotus japonicus* SL mutants (Liu et al., 2015). Dun et al. (2012) suggested that BRC1 is expressed in auxiliary buds during shoot branching inhibition and acts downstream in *Arabidopsis* and pea plants. Furthermore, the expression of BRC1 upregulated in response to the SL application, while opposite to the CK application. Additionally, the ratio of ABA to GA was reduced with GR24 application but increased CK levels. CK, in turn, inhibits PIN auxin transport proteins and thus inhibits the production of auxin and retard shoot and root branching under drought stress. Cell division, elongation, and differentiation in the root apical meristem (RAM) have been shown to be regulated by SL, CK, and auxins. The length of primary root (PR) in SLs mutants MAX1, MAX3, MAX4 (biosynthetic) and MAX2 (perception) is shorter compared to wild type plants. GR24 application can rescue this phenotypic trait in the biosynthetic mutants of SLs but not in the perception mutant. Kapulnik et al. (2011) suggested that SLs promote root hair elongation and repress the formation of lateral root (LR) formation. SLs may influence lateral root formation by regulating PIN-formed auxin transporter proteins, which determine the lateral position, initiation, and elongation via changes in auxin efflux (Koltai, 2014). Positive effects of GR24 on root cell number and crown root elongation were observed by investigating changes in the expression patterns of cell division and cell cycle-associated gene expression patterns (Cyclin-D2, proliferating cell nuclear antigen, and cyclin-dependent kinase B) in root tips of *Festuca arundinacea* (Hu et al., 2018). Based on the information presented, it can be concluded that the role of SLs in inducing drought tolerance in plants is a complex interplay among different hormones that regulate stomatal conductance through different signaling pathways. However, further investigation is needed to understand how different hormones behave under SL application and whether changes in hormone levels resulting from SL application can impact the potential ability of SLs to induce drought tolerance through various endogenous signaling pathways. As SLs are common regulators of stomatal closure in different plant species, genetic modification of SL content and signaling could be effectively used for stress tolerance. This highlights the need to uncover the molecular mechanisms underlying SL-mediated stomatal closure, including downstream components that regulate SL signaling in guard cells. Future experiments should explore these areas in more depth.

## 6. Strigolactones and temperature stress

Temperature is one of the critical environmental stresses impacting plant species' morphological and physio-biochemical behavior, especially in arid ecosystems. SLs have been found to improve seed germination in the parasitic plants and other plant species. The application of SLs was found to reverse dormancy (temperature-induced) in *Pastureia ramosa* seeds. Lechat et al. (2015) discovered that GR24 application enhanced ABA catabolic gene (CYP707A1) expression, resulting in ABA breakdown and seed germination even under the conditions of heat stress. The SLs-mediated regulation of germination has been demonstrated in SLs-defective *A. thaliana* mutants under heat stress (Tsuchiya et al., 2010). Gene silencing experiments with CCD7, CCD8, MAX1, and MAX2 revealed that silent lines were more susceptible to water loss (under dehydration) and higher stomatal conductance. Omoarelojie et al. (2020) stated that the GR24 treatment decreased the inhibitory effects of heat stress on *Lupinus polyphyllus* seed germination. GR24 increases antioxidant activity, which scavenges ROS during the germination phase. Toh et al. (2012) reported that the response to the germination of *A. thaliana* MAX mutant seeds was highly sensitive to the heat stress compared to wild type. Exogenous treatment with GR24 restored MAX1-1 mutant phenotypes but not those of MAX2-1. The seed germination rate of *Lactuca sativa* was reduced at high temperatures, further stimulated by the application of SLs, and decreased the ABA/GA



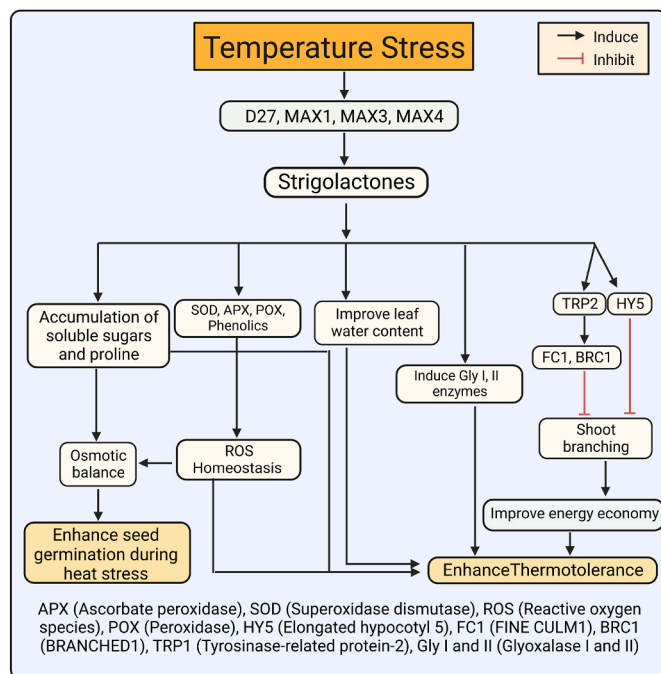
**Fig. 4.** An overview of SLs, ABA, auxin and CK and their interplay within the plant during drought stress. Drought induces strigolactones in plant, which in turn produce a cascade of signals to mitigate the adverse effect caused by drought stress. SLs induce ABA that form ABA Signalosome Complex and induce CDPK. CDPK in turn induce SLAC1/SLAH3 that causes stomatal closure. SLs also induce BRC1 and inhibit bud outgrowth. It induces CK in roots that inhibit PIN auxin transporter proteins (the auxin inducing factors) and thus inhibit shoot and root branching. In roots, the SLs activate the cell cycle genes (PCNA, CycD and CDK) and promote the primary root growth.

ratio (Gonai et al., 2004). Unlike CK and gibberellic acid (GA), ABA negatively affects the seed germination process in plants. It assumes that seed with lowering SL levels enhances the ABA/GA ratio, increasing the response to thermo-inhibition, while SLs application decreases the ABA/GA ratio and increases CK levels, which results in alleviating the thermo-inhibition of seeds. SLs are involved in improving the dark-cold tolerance of photosynthesis in *Pisum sativa* and *A. thaliana*. Dark chilling decreased the fresh shoot weights of both species, and in RMS5-3, RMS3-1, and MAX4-1 mutants, dry biomass was also drastically reduced. Cooper et al. (2018) suggested that SL protect shoots by improving dry biomass. The GR24 application significantly increased the expression of genes that are thought to be involved in light harvesting. It has been hypothesized that SLs could be positive regulators of other light-related mechanisms (Fig. 5) that contribute to root and shoot growth (Koltai and Kapulnik, 2011). SLs have also been shown to regulate the expression of CRX genes, which encode CK oxidase/dehydrogenase needed for CK catabolism (Fig. 5). In MAX2 plants, the CRX genes such as CKX1, CKX2, CKX3, and CKX5 were down-regulated (Ha et al., 2014; Reguera et al., 2013). Previous research has shown that GR24 can induce heat stress tolerance in lupine seedlings by mitigating heat-induced disruption of ROS homeostasis (Omoarelojie et al., 2020). through the induction of enzymatic (SOD, APX, and POX) and non-enzymatic (phenolics) ROS scavenging mechanisms. The study also found that glyoxalase enzymes were involved in GR24-mediated thermo-tolerance, as both Glyoxalase I and II activities were significantly enhanced by GR24 treatment. Interestingly, inhibition of SL signal perception did not limit PSII thermo-tolerance, indicating that GR24 may work through a different signaling pathway. The accumulation of

soluble sugars and proline, as well as the improvement of leaf water content, suggest that GR24 can also mitigate abiotic stress via osmotic adjustment. Overall, the literature suggests that SLs may positively alleviate temperature stress in plants by forming a coordinated network with CK, GA, and perhaps other hormones. While some studies have demonstrated the innate ability of plants to biosynthesize SLs, other studies have shown the potential of exogenous application of GR24 to alleviate thermal stress in plants, supporting the possible application of synthetic SLs in agriculture. However, more research is needed to fully understand the molecular mechanisms underlying GR24-mediated thermo-tolerance and its potential use in agriculture.

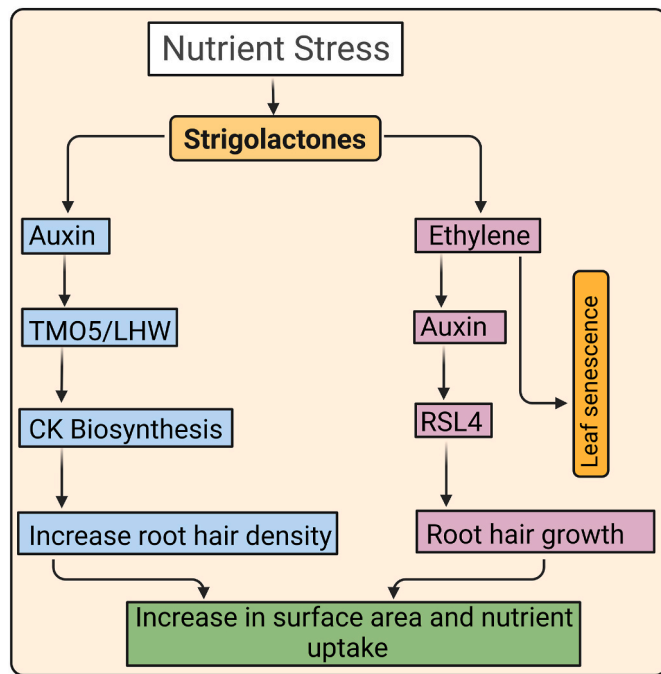
## 7. Strigolactones and nutrient stress

Soil solution is the primary reservoir for a plant to gain nutrients for optimal growth. Water stress, temperature, and salinity all lead to nutritional stress. SLs play a vital role in shoot and root architecture based on nutritional conditions and regulate plant interactions with microorganisms (Wani et al., 2016). Plants are responsive to nutrient availability in soil, particularly phosphorus (P), and exude SLs significantly under P starvation, while P sufficiency suppresses SLs production (Kapulnik et al., 2011; Yoneyama, 2019). Plant SLs exudation promotes AMF symbiosis under P deficit conditions. AMF symbiosis plays a vital role in P acquisition by the host plants and improves tolerance in nutrient-stress conditions (Yoneyama, 2019; Koltai, 2011). This indicates that SLs serve as modulators of plant responses against P deficiency, as the application of SLs reduced P starvation in tomato and Arabidopsis plants by activating acid phosphatase enzymes, the expression of the P starvation marker gene and anthocyanins accumulation (Gamir et al., 2020; Ito et al., 2016). These findings suggest an effective interaction between P starvation signaling pathways and SL signaling in plants. Furthermore, SLs stimulate root growth in *Oryza sativa* under nutrient deficiency, especially phosphate and nitrate limitation (Sun et al., 2014). It was further suggested that the shoot-to-root movement of auxin was vital for determining the effect of SLs on mediating lateral and seminal root development under P starvation. Previous studies suggested a positive association between primary root length and the production under wheat, rice, and tomato in P-deficit conditions (Jamil et al., 2011; Yoneyama et al., 2012). Moreover, Arite et al. (2012) and Sun et al. (2014) reported that SLs were involved in elongating rice's crown and seminal roots under nutrient deficit conditions. SLs play a crucial role in root architecture regulation. Despite adequate Pi, strigolactones inhibit the development of lateral roots. However, when Pi is constrained, they switch from negative to positive regulation, expressing their positive role in nutrient-deficient stress as observed in Arabidopsis15. Under P-deficit conditions, SLs were found to inhibit the growth of tiller buds and shoot branching in rice and Arabidopsis. However, such effects were not observed in their SL biosynthetic mutants, indicating their role in shaping the aboveground architecture in response to nutrient stress conditions (Kohlen et al., 2011; Umehara et al., 2008, 2010). The Pi deficit significantly elevates the synthesis and half-life (Datta et al., 2015) giving a clue that RSL4 might serve as a connection for SLs-auxin crosstalk in influencing root hair development (Fig. 6). Moreover, in vascular cells the TMO5/LHW heterodimer activates CK biosynthesis. It improves the density of root hairs density during low Pi conditions by altering epidermal cells' length and cell fate. Furthermore, root hair responses under Pi-deprived conditions are TMO5 and CK-dependent (Wendrich et al., 2020). In addition to starvation with P, the deficiency of other inorganic nutrients such as nitrogen (N) and sulfur (S) also triggers SLs production in different plants. For example, N deficiency improved SL exudation in some plants such as lettuce, maize, and sorghum, while in rice, S deficiency triggered SL production, indicating the dependency of these plants on AMF for N and S acquisition (Yoneyama, 2019; Shindo et al., 2018). Under S starvation, only one SL biosynthesis gene (D27) was expressed. In contrast, in P starvation, all the SLs biosynthesis genes were expressed,



**Fig. 5.** An Overview of Strigolactones (SLs) and the Signaling Pathways Involved in Heat Stress Response. Heat stress induces the expression of SL pathway genes (D27, MAX1, MAX3, and MAX4) that produce SLs. SLs trigger TRP2 (which further induces FC1, BRC1) and HY5, inhibiting shoot branching during heat stress to conserve plant energy for coping with heat stress. Moreover, SLs induce the expression of Glyoxalase-I and II, which enhance thermo-tolerance in plants. Through a cascade of signaling, SLs induce ROS scavenging enzymes (SOD, APX, and POX) and phenolics, helping plants maintain ROS homeostasis and delaying senescence. Additionally, SLs improve leaf water content, keeping plants cooler in hot summers. They also accumulate soluble sugars and proline, aiding in osmotic adjustment and ensuring membrane stability.





**Fig. 6.** An overview of SLs, auxin, ethylene, and CK and the cascade of signaling among these hormones during nutrient stress. Nutrient stress induces SLs which in turn promote the biosynthesis of auxin and ethylene. Auxin promotes the biosynthesis of CK through TMO5/LHW and thus increases the root hair density in plant roots. On the other side, ethylene cause leaf senescence and well as induces the biosynthesis of auxin that promote root hair growth through RSL4. The increase in root hair density and growth increases surface area of the roots and hence improve nutrient uptake. TMO5/LHW = Target of Monopteros/Lonesome Highway. RSL = RHD Six-Like.

indicating that D27 plays a crucial role in S acquisition through AMF symbiosis (Yoneyama et al., 2020; Yoneyama, 2019; Umehara et al., 2010). SLs are also crucial in nodulation with bacteria in soybean symbiosis and are highly relevant in the in plants of N nutrition (Rehman et al., 2018), In addition to inorganic nutrients, phytohormones, particularly ABA and auxin, also act as positive regulators of SL biosynthesis (Ito et al., 2016; Yoneyama et al., 2015), although antagonism can occur (Parwez et al., 2022; Rehman et al., 2018). The interplay between biosynthesis pathways of SLs, other phytohormones, and mineral nutrients in plants is complex and still not fully understood. Further research is needed to uncover the molecular mechanisms of how these factors regulate the production and exudation of SLs in plants. SLs are known to regulate phosphate transporters, but their impact on heavy metals transport remains unclear. Therefore, it is important to investigate whether SLs have any interaction with heavy metals uptake process in plants. SLs may have potential applications in phytoremediation strategies, as they can help establish AM or rhizobial symbiosis, which can enhance the plants' ability to remove excessive metals from polluted soil. However, more research is needed to determine the efficacy and safety of using SLs in such applications.

## 8. Arid lands and strigolactones

Arid lands are home to unique biological diversity, including wild relatives of important crop plants (Tariq et al., 2022a). However, geochemical cycles of these ecosystems are slow, and the availability and mobility of nutrients are low, while extended periods of drought and intense temperature due to climate change further affect biogeochemical cycles, soil fertility, and species composition (Zhang et al., 2022; Zhang et al., 2021; Griffis-Kyle et al., 2018; Yao et al., 2020). Nutrient cycling significantly affects the composition and survival of endemic

plant species in arid regions (Sardans et al., 2021). Field experiments have shown that water-deficit conditions can greatly impact P and N in the plant-soil system (Berdugo et al., 2022; Luo et al., 2018; Jiao et al., 2016), highlighting the need for novel approaches to alleviate the far-reaching consequences of harsh environmental conditions.

In desert ecosystems, plant ecology is heavily influenced by environmental stresses such as drought, salinity, high temperature, and nutrient deficiency in the soil. The main challenge for desert plant species is germination and establishing seedlings (Lai et al., 2019)–(Zhang et al., 2020). For example, in the Taklamakan desert (Northwest China), where the annual precipitation is less than 40 mm, germination occurs mainly at sites where the soil has been thoroughly wetted through flooding or inundation by rivers and lack of competing vegetation (Zeng et al., 2013; Gao et al., 2021; Tariq et al., 2022b). After germination, the seedlings are still threatened by desiccation and suffer a high mortality rate, so they must strive to grow their roots into the water-saturated zone of the soil as rapidly as possible to survive. Therefore, any practices that can help desert plant species in germination, nutrient uptake, and root architecture growth would have a positive impact on vegetation restoration, reducing soil erosion and land degradation.

However, most research on SL-mediated tolerance in plants has focused on agricultural plants, with little attention given to the indigenous vegetation of arid regions that play a crucial role in combating land degradation problems and improving the livelihoods of dependent communities. For example, *Alhagi sparsifolia* is an important ecological engineer plant species that combats desertification and land degradation in Central and Eastern Asia (Ullah et al., 2022b)–(Tariq et al., 2022c). It is also an essential source of forage for livestock and used as ethnomedicines. However, *A. sparsifolia* is facing a variety of environmental stresses that affect its germination, growth, and metabolism, resulting in low seedling densities and survival (Tariq et al., 2022b; Ullah et al., 2022a; Yin et al., 2021; Gao et al., 2022). Previous analyses suggest that suitable habitats, distribution, and abundance of *A. sparsifolia* will tend to decrease in coming decades, making it even more important to pay attention to indigenous vegetation of arid lands and find possible ways to improve vegetation survival and tolerance.

Based on the above discussion, it is clear that strigolactones (SLs) play an essential role in regulating plant development against unfavorable environmental conditions such as nutrient limitation, particularly phosphorus (P), drought, salinity, and temperature, prevalent in arid regions. Plants use SLs to adapt their shoot and root architecture to limited P availability while enhancing arbuscular mycorrhizal fungi (AMF) association to improve P and other nutrient uptake. Given that salinity is one of the major environmental stresses in arid regions, disrupting plants' metabolism and survival rate, it would be interesting to investigate whether SLs application can improve vegetation responses to salinity and promote vegetation restoration in arid ecosystems. Additionally, SLs application could help improve root hair formation and elongation, aiding the initial growth stages of indigenous vegetation in arid regions where moisture content is low in the upper soil surfaces. As germination rates of seeds are typically low in desert ecosystems due to intense temperature, treating seeds with SL formulations before planting in nutrient-deficient soil can significantly enhance root development at the seedling stage before the onset of drought. A significant proportion of arid land communities are reliant on agriculture, and unsustainable agricultural practices are resulting in further degradation of these ecosystems (Zhang et al., 2022; Kang et al., 2020; Lian et al., 2021). As our understanding of hormone application in enhancing crop productivity improves, it is plausible that GR24 or other synthetic SLs formulations can be optimized and used in the fields to improve nutrient uptake and use efficiency, stress tolerance, and yield of major crops in arid lands to promote sustainable agriculture. It is worth noting that P is scarce in arid lands, and the low moisture content further decreases its uptake in indigenous plant species (Luo et al., 2018; Gao et al., 2022; He and Dijkstra, 2014). Therefore, studying the types of SLs being exuded from

the roots of plants adapted to the nutrient-deficient environment is worthwhile, potentially leading to the identification of novel SLs from arid land plant species.

## 9. Conclusions and future perspectives

This review provides detailed information on the regulatory role of strigolactones (SLs) in enhancing plant tolerance to various environmental stresses through changes in plant development and soil microbes, such as arbuscular mycorrhizal fungi (AMF). The interesting functions of SLs make them a potential target for designing plant tolerance enhancer chemicals for sustainable and modern agriculture. However, there is still a dire need for in-depth research on downstream signaling components in plants, SL molecular mechanisms, and physiological interactions. Additionally, environmental gradients driving SL biosynthesis and exudation are predominant in arid regions, but most experiments have been conducted on crop species under in vitro and in vivo conditions, with less attention paid to arid lands' indigenous vegetation responsible for combating desertification and land degradation. SLs improve seed germination rate, root system development, and stomatal conductance, which can effectively help arid land vegetation with low seed germination and seedling survival rates, nutrient and water deficient soil, and high temperature. These plants have adapted to harsh environmental conditions and must have well-established tolerance mechanisms mediated by SLs. Therefore, focusing on arid land plants in future research studies can lead to identifying and characterizing novel SLs, responsible genes and enzymes, and unknown SL biosynthesis and exudation mechanisms.

Despite our improved understanding of SLs in the past decade, very little information is available on the field-scale application of SLs, mainly due to their expensive synthesis. Moreover, our understanding of the side effects and environmental risks associated with SL application in the field needs improvement. Therefore, future research should address essential unresolved questions, such as the appropriate time of application, specificity of different SLs, dose-dependent above or below-ground environmental risks, and microbiota responses to SL application, particularly at the community level rather than effects on a single species or genus. In addition, studies providing concrete evidence of SLs' effects in improving plant tolerance should be adequately acknowledged and emphasized. Furthermore, there must be a healthy collaboration among all stakeholders regarding the ultimate large-scale application of synthetic SLs. Regulatory support and capacity building of the general public is necessary to provide factual information about SLs to policymakers, farmers, and local people, enabling them to formulate their opinions and judgments.

## Author contributions

**Akash Tariq, Sakina Mussarat, Fanjiang Zeng, Jordi Sardans, Corina Graciano, Josep Peñuelas:** Conceptualization.; **Akash Tariq, Sakina Mussarat:** Methodology.; **Akash Tariq:** Software.; **Akash Tariq, Abd Ullah, Zeeshan Ahmed, Sikandar Ali, Zhihao Zhang:** Data curation.; **Akash Tariq, Jordi Sardans, Sakina Mussarat, Corina Graciano:** Writing- Original draft preparation.; **Akash Tariq, Visualization:** **Akash Tariq, Investigation.:** **Fanjiang Zeng, Josep Peñuelas, and Jordi Sardans,** Supervision.; **Akash Tariq, Aftab Yaseen, Zeeshan Ahmed, Zhihao Zhang, Sikandar Ali,** Software, Validation.; **Akash Tariq, Jordi Sardans, Ihteram Ullah, Weiqi Wang, Dhafer A. Al-Bakre, Josep Peñuelas, Fanjiang Zeng, Corina Graciano:** Writing-Reviewing and Editing.

## 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.

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