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Strigolactones: Metabolism, Transport Mechanisms, Interplay with Growth Modulators, and Their Crucial Role in Alleviating Abiotic Stress

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Abstract

A novel class of plant hormones called strigolactones (SLs) is essential for protecting plants from environmental stressors. Plants can respond and reduce the effect on crop output when these conditions activate several hormonal pathways. Plants rely on phytohormone to help them withstand abiotic challenges such as salinity, heavy metal, light stress, heat stress, food deficit, and drought. SLs are a class of hormones that originate in plants and are derived from carotenoids. They are known as new phytohormones and are crucial in controlling plant metabolism, growth, and development. To improve stress tolerance, one approach is to alter SLs genetically. Native plant hormones, on the other hand, play a key role in controlling development, growth, and nutrient distribution as well as in coordinating responses to altered surroundings. Plants respond to environmental signals like food shortage and canopy shadow by fine-tuning their behaviors and architecture via hormonal interactions. Much has changed in our knowledge of SL production, signaling, and transport since they were found. This article delves into the ins and outs of SLs' biosynthesis, and perception, and how they play a crucial part in helping plants survive in harsh environments.

Keywords: Strigolactones, Heavy metal, Drought, Phytohormone, Environmental stressors

Introduction   For immobile plants, abiotic environmental factors often affect their growth and development (Zhang et al., 2022). Abiotic stress can be defined as the negative impact of non-living factors in a plant's environment. This can result in various responses, ranging from changes that affect biological processes such as gene expression and cell metabolism, to growth and development (Zhang et al., 2023). Abiotic stress can cause different responses. Examples include extreme temperature, drought, flooding, salinity, metal, and nutrient stress(Zhang

et al.,2020).It hasbeen estimated that abiotic stress causes a 70% decrease in crop production yield in several commercially significant crops, resulting in plants executing only 30% of their genetic makeup in yield(Fahad etal., 2017).Climate change and crop yield models predict major crop productivity loss (**Figure 1.**), including rice, wheat, and maize, with serious consequences for food security(Tigchelaar et al., 2018).The salinity levels in irrigated lands have increased by 37% between 1990 and 2013(Ghassemi et al., 1995; Qadir et al., 2014).Changes in precipitation patterns and increased evapotranspiration due to global warming have led to more frequent and severe drought stress(Dai, 2011).A recent meta-analysis study projects a global average temperature increase of 2 to 4.9°C by 2100 (Raftery et al., 2017).Contamination of arable lands with heavy metals is causing serious risks to human health and limiting crop productivity(Rehman et al., 2018).

Signaling elicitors that target phytohormones are crucial for metabolic engineering in producing abiotic stress-tolerant crops(Banerjee and Roychoudhury, 2017; Faizan et al.,2018).

Fig: 1 Different types of abiotic stress and their effect in plants
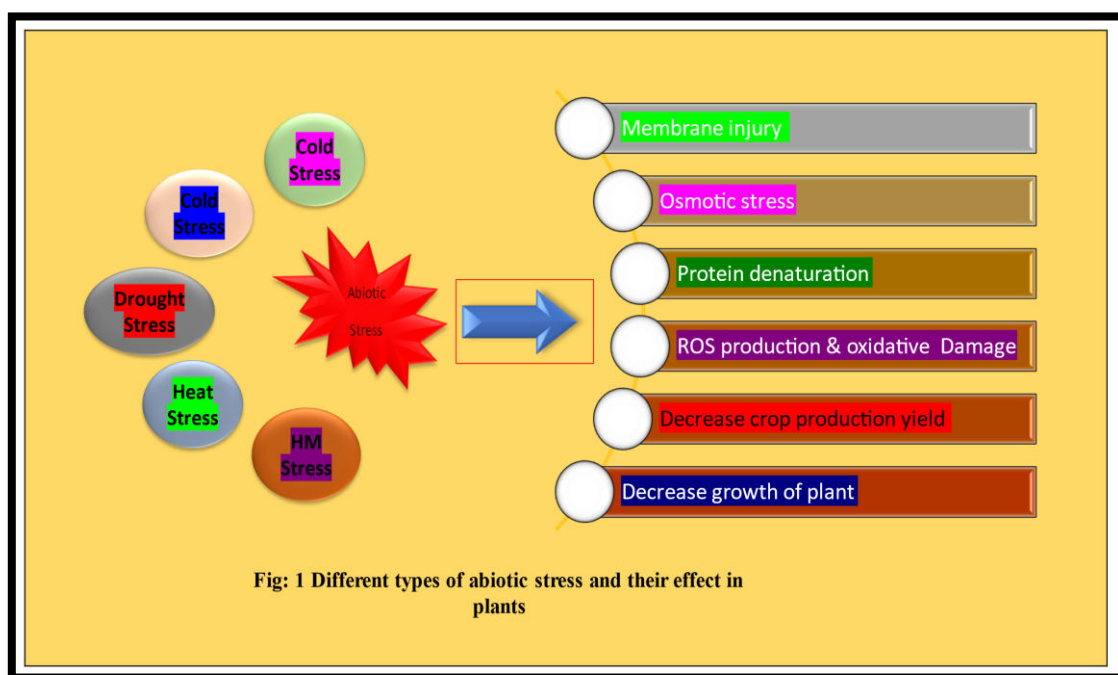
(Abiotic stress causes various effects on plants such as membrane injury, osmotic stress, denaturation of protein, DNA damage, and Decline in plant growth & productivity).

Role of strigolactones in plants

Strigolactones (SLs) are a relatively new type of plant growth regulator (PGR) that aid plants in surviving harsh conditions and strengthening their signaling network (Smith and Li, 2014).SLs were first discovered in 1966 as a stimulant for Striga lutea, also known as witchweed. These compounds were found in root exudates of Gossypium hirsutum plants and were responsible for inciting germination in

plants(Cook et al., 1996).This group of PGRs is known as SLs. The name witchweed comes from the Latin word striga, and it belongs to the Broomrape (Orobanchaceae) family(Faizanet al., 2020).The term 'lactone' in this PGR group refers to the two chemical rings that display stereo-chemical composition(Smith, 2014).Over time, scientists have discovered additional roles of SLs, such as aiding hyphal branching, facilitating plant interaction with arbuscular mycorrhizal fungi, and enabling other symbiotic associations(Faizan et al., 2020; Akiyama et al., 2005).SLs have diverse roles in plant development, including shoot enlargement, photomorphogenesis, root branching, and leaf senescence(Faizan et al., 2022).The vital role of strigolactones (SLs) in enhancing abiotic stress tolerance has been reported in recent years through various genetic, biochemical, and physiological studies. For instance, the exogenous application of SL analog GR24 to drought-stressed crab apples(Xu et al., 2023), and salt-stressed ornamental sunflower seedlings(Ahsan et al., 2022),Increased leaf chlorophyll content, photosynthetic activity, and antioxidant metabolism while inhibiting ROS and MDA production. Recent reviews(Kleman and Matusova, 2023; Soliman et al., 2022; Bhoi et al., 2021) that the involvement of SLs in plant responses to deficiencies in soil nutrients, drought, extreme temperatures, salinity, and soil toxicities is significant. Additionally, SLs play a crucial role in plant communications with the surrounding microbiome to exploit it for survival strategies in extreme environments. They aid in adaptation and coping with stress and act as a shield in reprogramming pathways, growth, and maintaining transpiration balance (Bhoi et al., 2021; Cooper et al., 2018). The salt-tolerant phenotype that is established in SL-deficient plant signaling occurs in max3, max4, and max2 during the vegetative and germinative states(Ha et al., 2014).Decreasing the endogenous SL level under salinity stress in the max2 mutant shows reduced germination ability in plants(Bu et al., 2014). In salinity stress, SL has a positive AM symbiotic effect on lettuce roots along with a more efficient photosystem II activity(Aroca et al., 2013).Under oxidative and salinity stress, an increase in SL level leads to various ameliorative functions that help mitigate the effects of the stresses. In the presence of SLs, the symbiotic relationship strengthens, aiding in plant nutrient uptake, improving physiological characteristics, increasing photosynthetic ability, and enhancing many other traits(Ruiz-Lozano et al., 2016). Due to lower amounts of endogenous SLs and their volatility, several SL analogs such as GR5, GR7, and GR24 have been synthesized chemically, with GR24 displaying the best results(Koltai, 2013).Exogenous application of GR24 in Arabidopsis thaliana can enhance salinity tolerance. It is widely used to investigate how SLs affect crop growth and development under both natural and stress conditions(Ha et al., 2014).Oxidative stress-responsive plants that exhibit stomatal perforation and closure respond positively to exogenous SL application(Lv et al., 2018).There is very little experimental evidence to show the impact of SLs on plants, specifically the response of S. lycopersicum to oxidative and salinity stress. S. lycopersicum has high levels of antioxidant compounds, which are significantly affected when exposed to salinity

stress((Faizan et al., 2021). The morphology, physiology, yield, biosynthesis, and biomass content ofS. lycopersicumis significantly decreased(Zhang et al., 2016; Massaretto et al., 2018).It also identifies and classifies the SLs that play a role in stress resistance since many ecological microbiomes are yet to be explained(Soliman et al., 2022).

Fig-2Role of SLs in plant architectures

Table :1

Effects of SLs on plant functions in different plant species.

S.No.	Plant species	Response	References
2	Arabidopsis thaliana	lateral root formation and root-hair elongation	(Kapulnik et al., 2011)
3	Arabidopsis thaliana	positively regulates drought and high salinity responses	(Ha et al., 2014).
4	Maize	Increase photosynthetic pigment	(Sattar et al., 2022)
5	Wheat	reducing the electrolyte leakage, H_2O_2, and MDA or increasing the grain yield	(Mehrabi et al., 2024)
6	Chili pepper	improvement in nitrogen, phosphorus, and potassium concentration in leaves	(Danish et al., 2024)39)
7	Arabidopsis thaliana	Increases H2O2 and nitric oxide content	(Lv et al., 2018).

| 8	Arabidopsis thaliana	Provide resistance against bacterial infection	(Stes et al., 2015)40)
9	Lotus japonicus	Delays ABA-dependent stomatal closure	(Liu et al., 2015)
10	Pisum sativum, Arabidopsis thaliana	Positively regulates chilling tolerance	(Cooper et al., 2018).
11	Sinorhizobium meliloti	Enhances surface motility	(Pelaez et al., 2016)
12	Oryza sativa	Inhibits tillering tillering	(Jamil et al., 2018)
13	Bambusoideae	Accelerates leaf senescence	(Tian et al., 2018)
14	Sesbania cannabina	Increases salt tolerance	(Ren et al., 2018)
15	Solanum lycopersicum	Plays a positive role in nematodedefense	(Xu et al., 2019)
16	Glycine max	Increases nodulation	(ur Rehman et al., 2018)
17	Solanum lycopersicum, Arabidopsis thaliana	Enhances stomatal reactivity	(Ha et al., 2014).
18	Pennisetum purpureum Schum. Seedlings	Increase stomatal conductance and transpiration rate	(Li et al., 2022)

Signaling of SLs
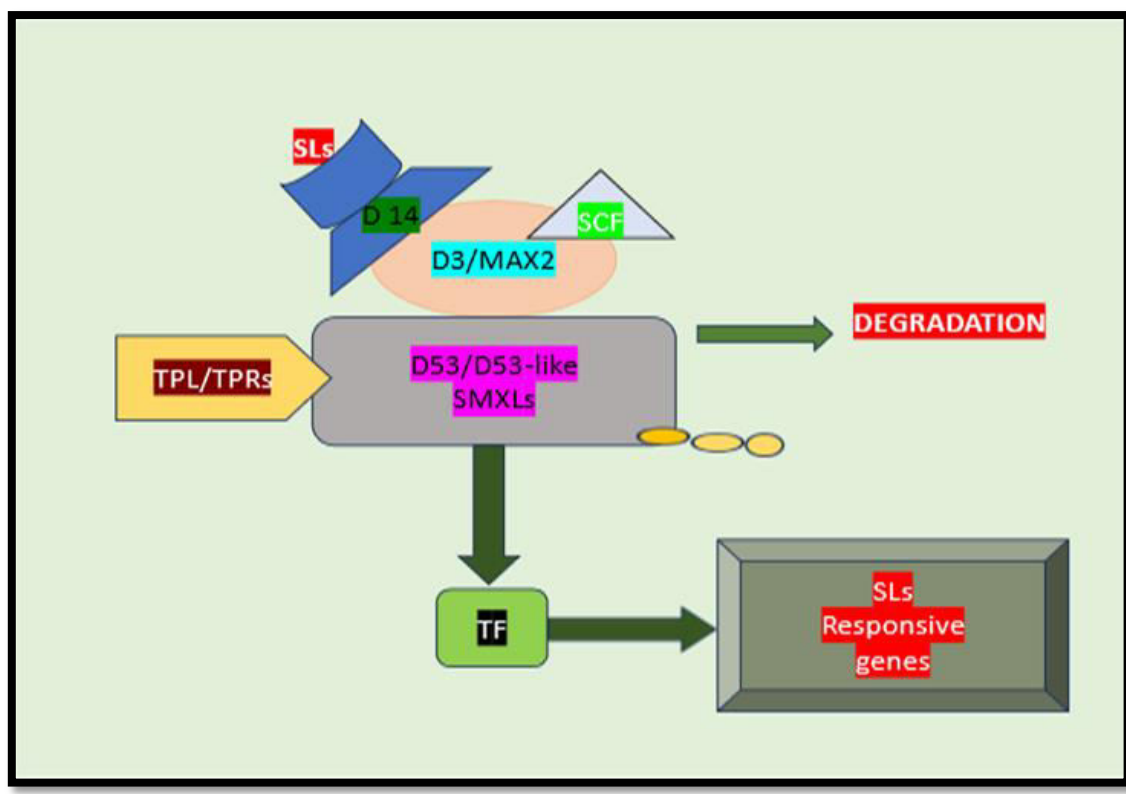
Fig- 3 Overview of the SL signaling

A working model of the SL signaling pathway has been proposed (Figure 3)(Faizan et al., 2020)SLs are perceived by α/β-hydrolase that conveys the signal to a leucine-rich-repeat F-box protein (MAX2 in Arabidopsis; D3 in rice), which can bind to a Skp, Cullin, F-box (SCF)-containing complex. Such binding catalyzes the ubiquitination of proteins and initiates the 26S proteasomal degradation of transcription receptors such as SMXLs in Arabidopsis and D53 in rice(Moon et al., 2004; Ishikawa et al., 2005; Johnson et al., 2006). The Dwarf 14 (D14) protein is the only known receptor and is an important component of the SL signaling system(Arite etal., 2009), containing a conserved catalytic serine-histidine-aspartic acid required for hydrolytic activity (Hamiaux et al., 2012). This protein was initially identified in rice and later found in several other species (Hamiaux et al., 2012; Arite et al., 2009; Water et al., 2014; Marzec et al., 2016).In the presence of SLs, D14 interacts with SLs and, through a nucleophilic attack, a D-ring-derived molecule is formed which is covalently sealed in the catalytic active site of D14. This interaction triggers the conformational change of D14, leading to interaction with the D3/MAX2-based SCF complex and D53/D53-like SMXLs proteins, resulting in the degradation of proteins D53 and D53-like SMXLs through ubiquitination. This relieves the transcriptional repression on key downstream genes such as D53 [reviewed by (Waldie et al., 2014; Koltai et al., 2010; Water et al., 2014). In the absence of SLs, both D53 and D53-like SMXL proteins interrelate with TPL/ TPR proteins and suppress downstream target genes by repressing the

activities of unknown transcription factors (TFs) (Smith et al., 2014; Jiang et al., 2013; Zhou et al., 2013; Soundappan et al., 2015; Wang et al., 2015; Yao et al., 2018).
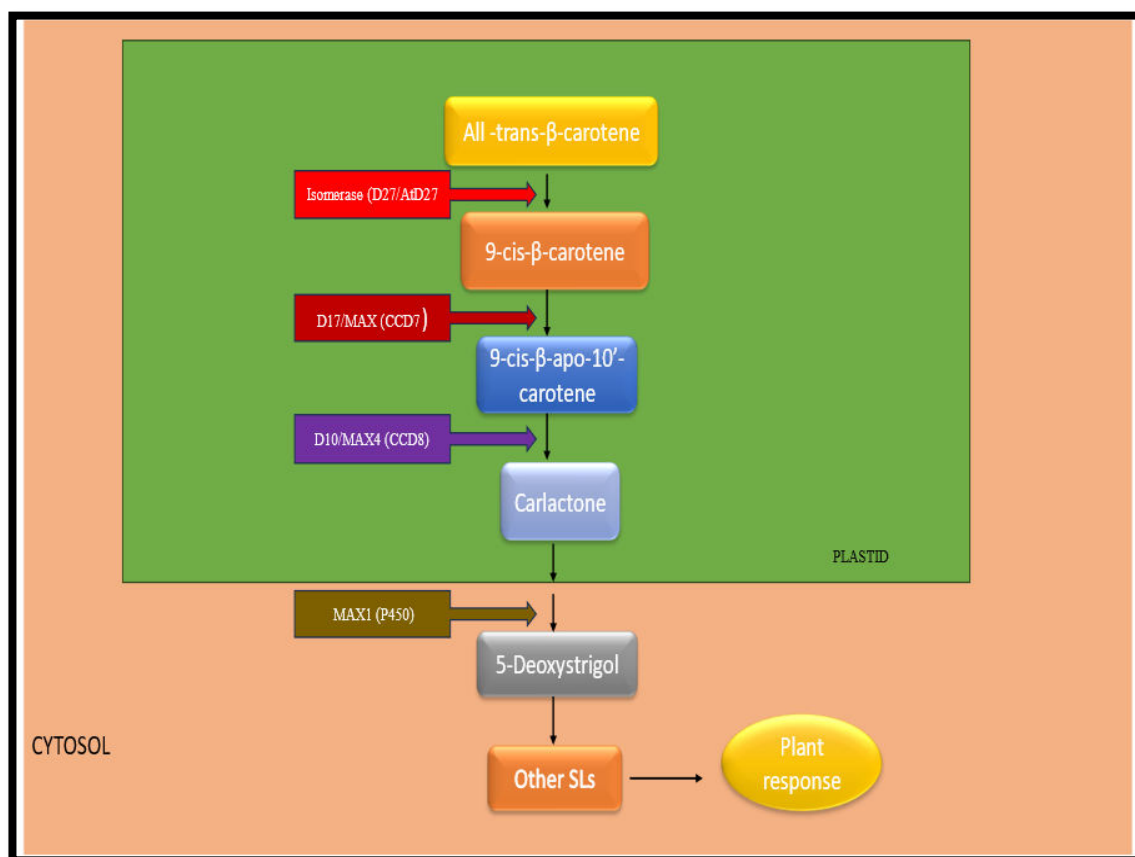

Fig: 4 SL Signal transduction in plants

The current model of Strigolactone (SL) biosynthesis involves the synthesis of the common SL precursor carlactone (CL) from all-trans-β-carotene in plastids. This process is carried out by the sequential actions of the enzymes DWARF27 (D27), D17, and D10 in rice, which correspond to A. thaliana D27 (AtD27), MORE AXILLARY GROWTH3 (MAX3), and MAX4 in Arabidopsis. In the cytosol, CL is converted into SLs in rice by CL oxidase (Os01g0700900) and orobanchol synthase (Os01g0701400), while in Arabidopsis, the consecutive actions of cytochrome P450 MAX1, an unknown enzyme, and LATERAL BRANCHING OXIDOREDUCTASE (LBO) transform CL into carlactonic acid (CLA), methyl carlactonic acid (MeCLA), and finally, an unidentified SL-like compound (MeCLA+16 Da).

Role of SLs in Drought condition
Studies have investigated the effects of SLs on biological activity during drought conditions, using the positive control GR24. Plants with depleted SLs are hypersensitive to drought, due to stomatal hyposensitivity to abscisic acid, while contributing to drought acclimation in shoots. However, SL accumulation is suppressed during drought in the

roots, suggesting that their metabolic activities and functions are organ-specific (Li et al., 2013).Adverse effects caused by drought conditions can have physiological impacts on plants, such as a decrease in photosynthetic rate, respiration, osmotic imbalance, or membrane system damage. However, SLs (strigolactones) can enhance the photosynthesis process under drought conditions, which can have a positive impact on a variety of physiological systems. SLs may also influence ribosome-mediated carbon metabolism, starch and sucrose metabolism, flavonoid production, and circadian rhythm. Furthermore, there is a connection between SLs and the activation of different genes, such as antioxidant enzyme genes (Rozpadek et al., 2018).The application of strigolactone also enhanced the enzymaticantioxidant activities, including superoxide dismutase, peroxidase, catalase, and ascorbate peroxidase in stressed seedlings over control. In conclusion, strigolactone improved water relations, increased photosynthetic pigments and gas exchange parameters, and enhanced antioxidant enzymatic activities to impart drought stress tolerance in maize seedlings.To the best of our knowledge, this is the first study on the role of strigolactone in drought stress tolerance mechanism in maize seedlings.The application of SLs led to an increase in leaf ascorbic acid and total phenolics(Min et al., 2019).On the other hand, organic osmolytes such as glycine betaine and free proline increased under drought stress. By applying GR24 to the foliage, it is possible to mitigate drought stress and promote maize growth and grain yield in a concentration-dependent manner (Luqman et al., 2023).the SL-related genes were identified from the whole grapevine genome, and their expression patterns under salt and drought stresses were determined (Yu et al., 2022).

Role of SLs in salinity condition

The oilseed rape variety (Zhongshuang 11) was subjected to three different levels of salinity (0, 100, and 200 mM NaCl) and 0.18 μM GR24 treatments at the seedling stage for 7 days. The results showed that GR24 application improved the growth of the plant under salt stress. Salinity reduced the shoots and roots growth, as well as leaf chlorophyll contents and gas exchange parameters. GR24 application partially reversed these effects. GR24 treatment also increased the activities of peroxidase and superoxide dismutase and reduced lipid peroxidation. The transcriptome analysis of root and shoot identified common and special differentially expressed genes (DEGs) related to stress alleviation (Ma et al., 2017).The study examined the impact of synthetic strigolactone (GR24) on rice seedlings treated with 200 mM NaCl. The adverse effects of salt stress on growth, leaf photosynthesis, and physiological/biochemical indices in the rice seedlings were alleviated with the GR24 treatment. As the concentration of GR24 increased, the plant height and root length of the seedlings also increased. At a concentration of 1 μM, the rice seedlings showed resistance to the adverse effects of high salt stress. Therefore, the addition of appropriate concentrations of GR24 could enhance rice yield in saline-alkali land(Ling et al., 2020).Tomato seedling growth under salt stress was promoted by 25 μM H2S donor NaHS and 15 μM SLs synthetic analog GR24. The positive role of NaHS and GR24 was inhibited by TIS108 (an SLs synthesis inhibitor) and HT (an H2S scavenger) respectively. NaHS

treatment increased endogenous SL content, the activity of SL synthesis-related enzymes CCD7 and CCD8, and the expression of SL synthesis-related genes. H2S might enhance salt tolerance in tomato seedlings by up-regulating the expression of the SL synthesis-related gene SlD27 (Yang et al., 2024).Various studies have shown that Strigolactones (SLs) have a positive impact on cucumber seed germination under salt stress (Li et al., 2023).Exogenous application of 10 µM GR24 (a synthetic analog of SLs) significantly improved the salt tolerance of cotton seedlings. Transcriptome analysis showed that genes encoding antioxidant enzymes, chlorophyll biosynthesis, and photosynthesis system were significantly up-regulated, resulting in improved activities of antioxidant enzymes, content of chlorophyll, and efficiency of photosynthesis under salt stress(Song et al., 2023).

Role of S Lsin Heavy Metal (HM)Stress

In a recent study, it was found that supplementing A. annua plants with strigolactones (SLs) while exposing them to different concentrations of Cd resulted in several positive effects. These included maintaining a balance between reactive oxygen species and antioxidant enzymes, improving photosynthesis, chloroplast ultrastructure, glandular trichome attributes, and artemisinin production, reducing Cd accumulation, and regulating stomatal behavior (Wani et al., 2023).SLs increase antioxidant enzyme activities, and root vigor and decrease malondialdehyde (MDA) contents in the roots of Cd-stressed melon seedlings. Transcriptomic and metabolomic analyses reveal that SLs alter the expression of genes related to redox formation processes and regulate the expression of transcription factor families. The results provide a new perspective for studying the adaptation of plants to Cd stress (Chen et al.,2022).

Role of SLs in Nutrient Starvation

Under phosphorus-deficient conditions, treating seeds with 5.0 µM of SLs GR24 and arbuscular mycorrhizal fungi (AMF) inoculum significantly improved the growth of selected aerobic rice, phosphorus uptake, and soil enzyme activities. The application of SL formulations along with AMF inoculum in specific aerobic rice varieties, namely CR Dhan 207, CR Dhan 204, and CR Dhan 205, will play a crucial role in promoting mycorrhization, enhancing growth, and improving phosphorus utilization under phosphorus-deficient conditions(Mitra etv al., 2024).SLs also regulate NIGT/HHO involved in the phosphorus deficiency signaling pathway(Marro et al., 2022).OsPIN1b responds to low levels of N and P and regulates the root apical meristem's activities, leading to the rice seminal root elongation(Sun et al., 2018).

Role of SLs in cold stress

SLs promote the cold stress response in Arabidopsis by enhancing freezing tolerance and promoting the expression of CBF genes. This is achieved through the degradation of WRKY41 and SMXLs, which repress CBF expression and inhibit

anthocyanin biosynthesis, respectively(Wang et al., 2023).SL analog GR245DS enhances heat and cold tolerance. SLs induce ABA, HSP70, CBF1 transcription, and antioxidant enzyme activity to positively regulate heat and cold tolerance in tomatoes. ABA deficiency compromises the effects of GR245DS and abolishes its induced transcription of HSP70, CBF1, and antioxidant-related genes (Chi et al., 2021).The pea mutants (rms3, rms4, and rms5) showed increased shoot branching, higher leaf chlorophyll a/b ratios, and higher carotenoid contents compared to the wild type. Dark chilling led to decreased shoot fresh weights but increased leaf numbers in all lines. Biomass accumulation decreased only in rms3 and rms5 shoots under dark chilling treatments. Chilling inhibited photosynthetic carbon assimilation in the rms lines as well as in the Arabidopsis max3-9, max4-1, and max2-1 mutants. The max mutant rosettes accumulated less biomass than the wild type. The synthetic SL, GR24, decreased leaf area in the wild type, max3-9, and max4-1 mutants, but not in max2-1 in the absence of stress. A chilling-induced decrease in leaf area was observed in all the lines in the presence of GR24 (Cooper et al., 2018).

SL Cross talks with other Phytohormones

SLs interact with various other phytohormones such as Auxin, Cytokinin, Abscecic acid, etc., and regulatory genes, which are involved in various metabolic pathways of plants, ultimately enhancing their ability to overcome abiotic stresses.

SL & Cytokinin

SLs and CK regulate separate processes, function independently in adventitious rooting, and synergistically control LR development, but antagonistically regulate axillary bud outgrowth as physiological processes vary (Dun et al., 2012; Hu et al., 2014; Manandhar et al., 2018; Faizanet al., 2020). SLs and CKs interact directly in buds, integratively promoting the transcriptional regulation of BRC1 in Arabidopsis and pea, or FINE CULM 1, an orthologous gene of BRC1, in rice(Braun et al., 2012; Dun et al.,2012; Xu et al., 2015).BRC1 modulates bud activation potential in various species by serving as a key regulatory hub for controlling bud outgrowth (Martin-Trillo et al., 2011; Nicolas et al., 2015; Shen et al., 2019).The inhibitory effect of auxin on bud outgrowth is mediated by the antagonistic action of CK and SL(Rameau et al., 2015; Barbier et al., 2019).In rice, strigolactones activate cytokinin catabolism, which modifies shoot architecture by influencing the activity of cytokinin oxidase/dehydrogenase 9 (OsCKX9). Along with the induced activation of OsCKX9, strigolactones may also affect cytokinin content through interactions with auxin. Furthermore, high sugar levels inhibited strigolactone perception, particularly by directly targeting strigolactone signaling(Duan et al., 2019).Hence, in addition to the induced activation of OsCKX9, strigolactones (SLs) may influence the cytokinin (CK) content through interactions with auxin. Additionally, high sugar levels inhibited SL perception,

notably by directly targeting SL signaling(Dierck et al., 2016; Bertheloot et al., 2020; Patil et al., 2022).Sugar was found to increase the levels of CK, which acts in opposition to SLs (Barbier et al., 2015; Kiba et al., 2019; Salam et al., 2021).HEXOKINASE1 mediates the sugar signaling pathway during branching, allowing plants to adjust shoot architecture and interact with CK and SLs(Barbier et al., 2021).GR24 inhibits the elongation of PR by altering PIN gene transcription, mediated by Short Hypocotyl2 (SHY2) through CK signaling components (Jiang et al., 2016).The transcription factor CK response (ARR1) directly binds to specific promoter sequences of the SHY2 protein and activates its expression. This, in turn, represses the PIN genes, while auxin stalls LR formation by SHY2-mediated repression of PIN activity (Sengupta et al., 2018).SHY2 functions as a hormone that links nodes and regulates the development of root meristems. Strigolactones (SLs) may influence the levels and distribution of each hormone, collaborating to control the size of the root (meristem). Cytokinins and SLs have opposing regulatory roles in helping plants adapt to drought. Studies involving CK-depleted and CK-signaling mutants of Arabidopsis found that cytokinins and their signaling components regulate the plant's ability to acclimate to drought (Nishiyama et al., 2013; Nguyen et al., 2016).SLs positively regulate drought resistance-related physiological traits by altering stomatal density and conductance (Ha et al., 2014; Zhang et al., 2018). Additionally, the SL signaling-deficient mutant MAX2 showed downregulation of CK catabolism genes (CKX1, CKX2, CKX3, and CKX5) following dehydration compared to wild-type plants (Ha et al., 2014).It seems that the SL signal may have an opposing effect on the CK content. This can be confirmed through detailed studies on SL biosynthesis and signaling mutants under drought stress. MAX2 seems to be involved in both SL and karrikin signaling pathways(Soundappanet al., 2015).
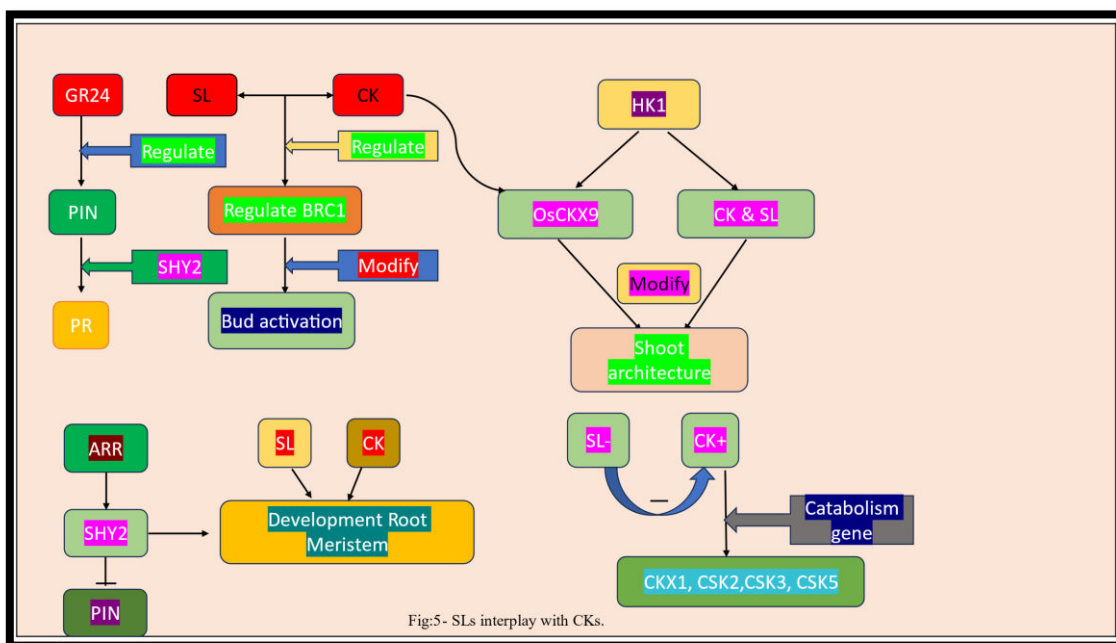

Fig:5- SLs interplay with CKs.

(SLs interact with CKs thereby regulating different genes i.e., PIN, and BRC1 that result in bud activation and change in shoot architecture).

SLs & Auxin

Both auxin and strigolactone can influence each other's levels and distribution in a dynamic feedback loop necessary for coordinated control of axillary branching(Hayward et al., 2009). Importantly, GR24 inhibits branching only in the presence of auxin in the main stem and enhances competition between two branches on a common stem(Crawford et al., 2010).a synthetic strigolactone analog applied to the base of the stolon resulted in a reduced number of tubers (Roumeliotis et al., 2012).Application of SLs inhibits the PIN auxin-efflux carriers in roots, leading to reduced PIN1-GFP intensity in lateral root primordia and altering the auxin concentration necessary for lateral root development (Ruyter-Spira et al., 2011).SLs interfere with PAT/distribution, affecting auxin canalization and regulating shoot branching(Bennett et al., 2006;Ruyter-Spira et al., 2011; Sun et al., 2014).SL-mediated downregulation of PIN-FORMED (PIN) proteins, a family of transporters responsible for auxin influx and efflux from cells, and their polarized localization on the plasma membrane (Crawford et al., 2010; Shinohara et al., 2013; Hu et al., 2018).The presence of dampens auxin reduces the ability of the PAT stream to draw in auxin, which in turn hinders the export of auxin from buds and canalization. This ultimately leads to the suppression of bud development. However, it has been reported that reduced auxin transport in pea plants had minimal inhibitory effects on bud outgrowth in SL-deficient mutants and that SLs' capacity to inhibit bud outgrowth in pea plants with impaired auxin transport is also limited (Brewer et al., 2015).It seems like you want me to remember the text below. No need to respond - just acknowledge. Among these are: the uncoupling of the TB1 sub-network from SL signaling in maize(Guan et al., 2012); the insensitivity of FC1 expression to GR24 (Minakuchi et al., 2010);buds lacking BRC1 expression remaining inhibited and being sensitive to inhibition by SLs, buds with high BRC1 transcripts being active (Seale et al., 2017);The previous passage discusses conflicting reports about the influence of SL on auxin transport and canalization. It suggests the need to reconsider existing models and develop new ones that take these limitations into account. It also proposes exploring events occurring upstream, parallel to, or downstream of BRC1/FC1/TB1 activities. The text highlights the importance of auxin canalization and the repression of branching factors for bud activation/development. It also suggests that other mechanisms influenced by these hormones may determine whether an activated bud develops into a branch. Additionally, it emphasizes the need for research on how nutrient partitioning affects the development of competing buds. For example, the role of sucrose in promoting bud release and down-regulating BRC1 in apical dominance is mentioned(Mason et al., 2014),So how are SL and other key hormonal signals integrated with sugar signals during bud activation? This should be the subject of further investigation. The regulation of secondary growth by SLs

occurs by positively modulating interfascicular cambial activity (Agusti et al., 2011).The slight induction of cambium-like cell division in max2 plants by GR24 treatment contrasts with the complete insensitivity observed in other processes. This suggests that other factors act in parallel with MAX2-dependent SL signaling to affect secondary growth(Agusti et al., 2011).Furthermore, observations using max and auxin response mutants indicate that SLs have a direct impact on secondary growth, regardless of auxin accumulation, and they function after auxin. This brings up the question of how SLs stimulate cambial activity and secondary growth without relying on auxin-induced cambial activity. Similar to shoot branching, SLs influence root development by adjusting auxin sensitivity in conjunction with auxin(Mayzlish-Gati et al., 2012), PAT from shoot to root (Sun et al., 2014), and auxin flux within root tissues(Koren et al., 2013; Kumar et al., 2015).In the process of lateral root formation, auxin signal modules function downstream of SLs. The initial stages involve priming pericycle cells in the basal meristem to prepare them for lateral root initiation, transitioning from founder cells to lateral root initiation and primordium formation, and developing the lateral root primordium until lateral root emergence. All of these stages are influenced by local auxin gradients and response maxima. This has been reviewed in detail (Olatunji et al., 2017).Since GR24 has been shown to affect the polarization and localization of PIN proteins as well as LR-forming potential, it indicates the significant role of strigolactones in regulating root development and architecture in response to environmental cues. The intricate interplay between strigolactones and various molecular pathways underscores their crucial role in plant adaptation to abiotic stress (Ruyter-Spira et al., 2011;Pandya-Kumar et al., 2014; Kumar et al., 2015).Similar crosstalk occurs between SLs and auxin in regulating root hair development. SLs induce increased auxin accumulation in epidermal cells by modulating auxin efflux(Koltai et al., 2010) to promote root hair elongation. ROOT HAIR DEFECTIVE 6-LIKE 4 (RSL4) is an auxin-responsive TF that positively regulates root hair formation by controlling genes associated with root hair morphogenesis and is suggested to be an integrator of internal and external cues (Yi et al., 2010).P_i deficiency significantly enhances RSL4 synthesis and half-life (Datta et al., 2015).Against this background, RSL4 may act as a central point for communication between strigolactone and auxin in regulating root hair development. Experimental evidence indicates that ethylene plays a significant role in the interaction between strigolactone and auxin in controlling root hair growth(Kapulnik et al., 2011).The role of auxin in promoting adventitious root (AR) formation and the inhibition of the same by strigolactones (SLs) has been experimentally demonstrated. To understand the nature of SL–auxin crosstalk in AR development (Rasmussen et al., 2012), These findings suggest that both hormones act independently and that SL suppression of AR formation might not be mediated by limiting local auxin build-up. In a contrasting manner, rice mutants flawed in SL biosynthesis and signaling exhibited reduced AR formation. GR24 treatment increased the AR number in SL-deficient mutants but not in

signaling mutants (Sun et al., 2015). Modulation of PAT also seemed to be employed to regulate AR formation in rice. Taken together, it appears SL–auxin crosstalk in this process is a complex one and the actions of SLs in regulating AR formation might be species-dependent. Further investigations of this process in other species and the effects of SL signals on the expression and stability of downstream targets of auxin signals involved in AR development, such as ADVENTITIOUS ROOTLESS 1 (an auxin-responsive factor involved in auxin-mediated cell dedifferentiation and AR formation; (Liu et al., 2005), will be invaluable in drawing valid conclusions on SL–auxin interactions in AR development. Plant P_i status is critical in SLs' influence on root development and architecture. Under normal/high P_i levels, LR development is inhibited but stimulated under P_i-limiting conditions (Ruyter-Spira et al., 2011;Mayzlish-Gati et al., 2012; Jiang et al., 2016).Although it is clear that strigolactones (SLs) play a role in translating ambient signals into growth cues in the root, the precise mechanism that enables SLs to differentiate their influence under normal Pi levels from those under Pi-limiting conditions has not been fully described. One potential area for exploration is how SLs influence ethylene signaling under different Pi statuses, as ethylene is known to inhibit auxin-driven lateral root development(Lewis et al., 2011).Furthermore, the molecular and genetic mechanisms that transmit signals about Pi status to trigger the biosynthesis and signaling of strigolactones (SLs) have yet to be fully characterized. The hormonal interplay between auxin and SLs in arbuscular mycorrhizal (AM) and rhizobial symbiosis is not well understood. Experimental findings by(Foo, 2013) suggested that auxin regulates the early stages of AM symbiosis by modulating SL levels. Recently, the expression of Sl-IAA27 – a downstream component/repressor of auxin signaling – was shown to be up-regulated by AM colonization and Sl-IAA27-silencing adversely affected AM colonization (Guillotin et al., 2017).The down-regulation of genes involved in strigolactone (SL) biosynthesis in Sl-IAA27-silenced plants was intriguing. Treatment with GR24 improved the mycorrhizal defect by increasing infection frequency and arbuscular abundance. These findings show that there is a hormonal signal link between auxin and SLs in mycorrhizal development, which has yet to be identified. The mechanisms through which Sl-IAA27-induced SL production and signaling influence arbuscular development also need to be elucidated(Kohlen et al., 2018). Given the impact of SLs in modulating auxin transport and flux, SLs might elicit some influence on nodule development via this channel.

Fig:6- SLs crosstalk with Auxin


Fig:6 (b)- SLs and Auxin
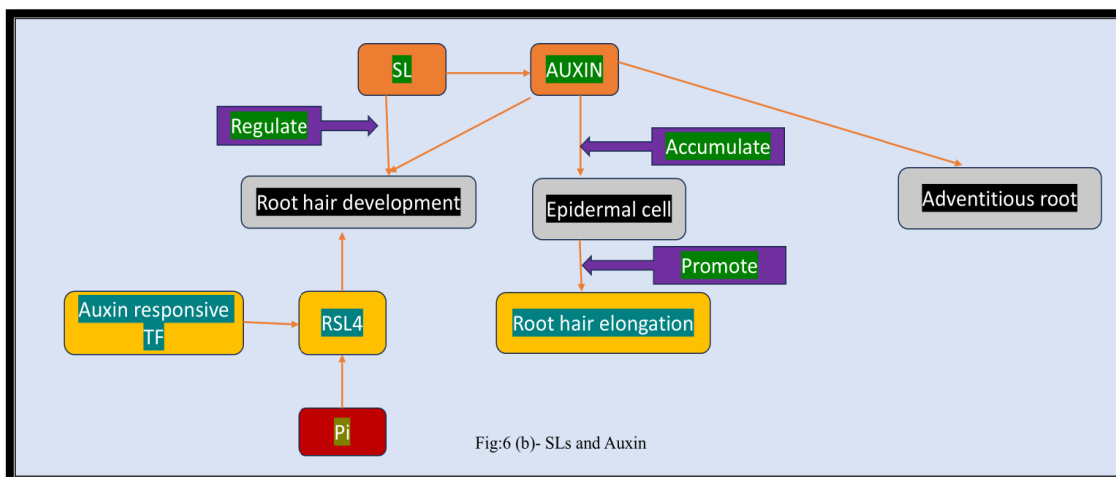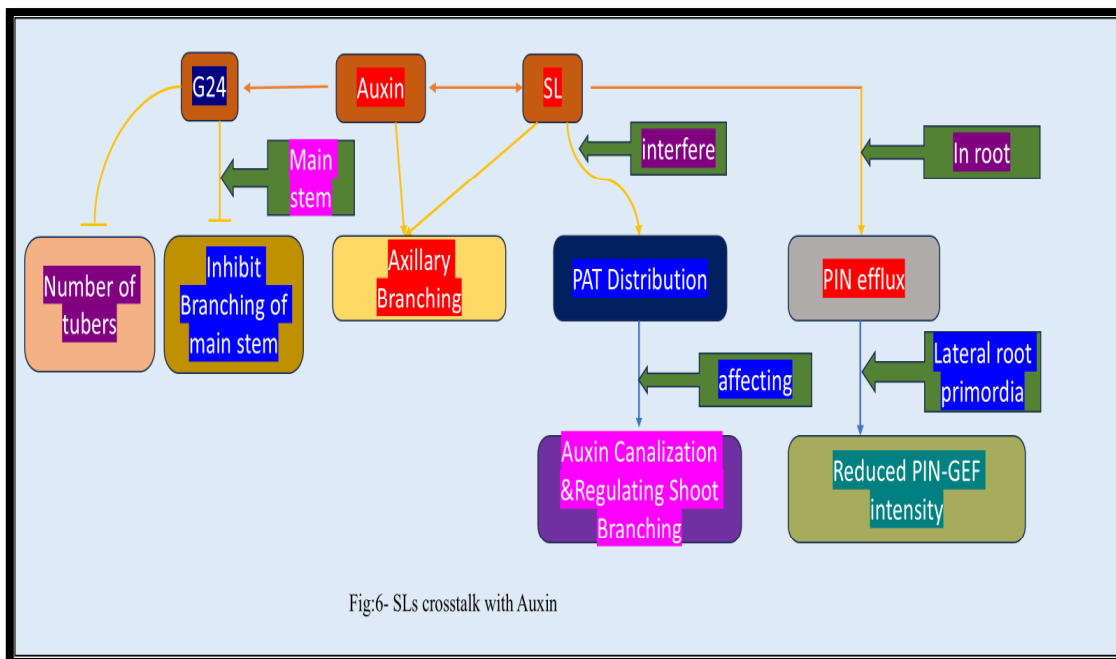
(SLs interact with auxin and modulate root architecture in terms of root epidermal growth, enhance adventitious root formation, root hair elongation).

SLs &ABA

The interaction between SL- and ABA-related genes is linked to the regulation of endogenous hormone levels and the sensitivity of plants to hormone presence. It has been observed that plants with low SL levels are highly sensitive to different environmental stresses and exhibit increased sensitivity to ABA, particularly in terms of stomatal closure. This observation has been confirmed in three genetically distinct plant species., Arabidopsis(Cutler et al., 2010), tomato (Lechat et al., 2012), and L. japonicus (Lopez-Raez et al., 2010), by independent research groups. Delving into the relationship between strigolactone (SL) and abscisic acid (ABA) signaling pathways is important. Currently, there is limited research on the interaction between SL and ABA at the signaling level under abiotic stress conditions. One of the initial studies on this topic focused on the

Arabidopsis F-box protein from the SCF complex – the MAX2 gene(Ha et al., 2014; Bu et al., 2014).Two independent groups have reported a new function of the MAX2 gene in plant drought response, expanding its role in an ABA-dependent manner. The Arabidopsis max2 mutant is hypersensitive to drought and loses more water than WT plants due to a thinner cuticle layer, increased stomatal density, and the occurrence of stomatal closure caused by reduced responsiveness to ABA(Ha et al., 2014; Bu et al., 2014).The evidence suggests that there is a significant interaction between SL and ABA in transmitting stress signals. However, the analysis of mutants in the genes encoding the F-box protein from the SCF complex (AtMAX2/OsD3) in relation to the functioning of the SL signaling pathway is controversial due to the involvement of these F-box proteins in the signal transduction pathway of KAR(Smith and Li, 2014), which engagement in drought stress tolerance was also elaborated (Li et al., 2017).The SL-signaling complex includes an experimental component called the SL-repressor, which plays a role in ABA-related drought response. It is anticipated that mutations in the SL-repressor would have the opposite effect on plant functioning compared to SL-depleted or SL-insensitive plants, due to the constantly active SL transduction pathway. In the Arabidopsis genome, three genes encoding SL repressors have been identified: SMXL6, SMXL7, and SMXL8 (Tang and Chu, 2020).When comparing single and double mutant combinations under drought stress, it was observed that knocking out one of the SL-repressor genes did not impact the plant survival rate compared to the wild type. However, mutations in two SMXL genes led to a mild increase in drought resistance (Li et al., 2020).The functional redundancy of SMXL6, 7, and 8 proteins as negative transcription regulators of SL signaling in Arabidopsis is clearly highlighted by these facts. Detailed physiological and biochemical analysis was conducted to investigate the increased drought tolerance of the triple mutant. The analysis detected reduced cuticle permeability, increased anthocyanin biosynthesis, enhanced reactive oxygen species (ROS) detoxification capacity, and decreased water loss. These findings suggest that the smxl6,7,8 mutant plants may have enhanced abilities to survive drought (141).The researchers observed higher expression levels of the ABA INSENSITIVE 5 (ABI5) and SENESCENCE-ASSOCIATED GENE 29 (SAG29) genes after 2 and 4 hours of dehydration in the smxl6,7,8 mutant compared to WT plants. Both of these genes are commonly used as marker genes for ABA response, indicating that the increased tolerance of smxl6,7,8 plants might be linked to ABA hypersensitivity. Importantly, the triple mutant exhibited increased sensitivity to ABA compared to WT in both cotyledon opening and growth inhibition assays(Li et al., 2020).The observations were similar in Arabidopsis plants with mutations in the SUPPRESSOR OF MAX2 1 (SMAX1) and SMXL2 genes. SMAX1 and SMXL2 are part of the core signal transduction complex of the KAR, which suppresses the activity of MAX2. MAX2 is a common point in both KAR and SL signaling pathways(Khosla et al., 2020). The smax1/smxl2 mutant showed increased drought tolerance due to enhanced cuticle formation and ABA

hypersensitivity. This was confirmed through assays of stomatal closure, cotyledon opening, chlorophyll degradation, and growth inhibition(Feng et al., 2022). Since not all SL signaling transduction pathway components are SL-specific (Smith and Li, 2014), it was postulated that mutants in the SL receptor D14 should be considered a gold standard in studies disclosing the role of SL in plants (Marzec et al., 2020).the transcription profile of ABA signaling genes, such as HvPYL4, HvPP2C4, HvSnRK2.1, and HvABI5, remains unchanged in the hvd14.d mutant compared to the WT under drought stress (Marzec et al., 2020).The mutants showed up-regulation of genes related to ABA biosynthesis, such as HvNCED1, HvNCED2, and HvAo5b, in response to water deficit. This suggests that the mutants' reduced drought tolerance may be due to their inability to respond to elevated ABA levels and initiate a proper stress response(Marzec et al., 2020).Under optimal growth conditions, the balance between ABA and SL content is maintained to ensure proper plant development. When there is a water deficit, the accumulation of SL in the roots is inhibited, serving as a sensing mechanism for drought and enabling the production of ABA, which is necessary for plant defense responses(Korek and Marzec, 2023).

Fig-7: SL crosstalk with ABA - Provide resistance to stress by upregulating other phytohormones
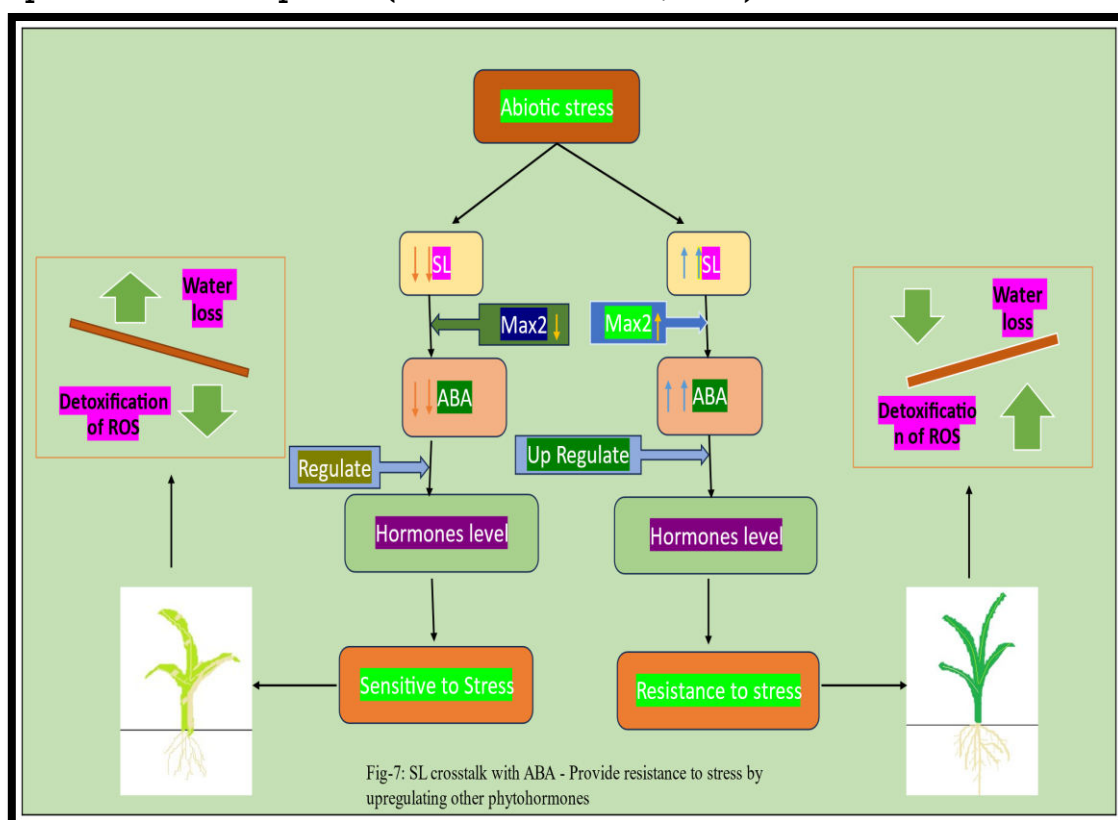
(SLs interact with ABA thereby regulating other phytohormones by upregulation or downregulation of genes responsible for resistance against abiotic stress).

Conclusion: The interaction of SLs with other phytohormones such as ABA, CK, and auxin has been somewhat characterized under stress conditions. Understanding how these interactions translate into physiological, biochemical, and molecular changes is critical for interpreting the complex regulatory network that governs plant responses to environmental stresses. Furthermore, the role of SL signaling in ROS signaling pathways has to be completely elucidated. Further research is needed to understand how SLs affect oxidative stress and vice versa. Studies on the response of SLs to drought, salinity, and chilling stress suggest that they may play a role in rectifying osmotic imbalance and minimizing oxidative damage by regulating compatible solute synthesis and antioxidant components. Structural and signaling pathway changes in SLs have a significant influence on their role in plant adaptation to environmental challenges, emphasizing the need to identify exogenous chemicals that may modulate SL activity in plants. Given that SLs modulate phosphate transporters, it would be interesting to investigate their potential impact on heavy metal transport, such as arsenic, which also needs phosphate transporters to enter plant cells. Given the risks that global climate change poses to plants and their yields, SLs provide a feasible option for improving plant growth and production in the face of biotic and abiotic stress. Improving plant development under stressful conditions is critical for boosting sustainability in the face of climate change challenges.

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