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## Unravelling diverse roles of strigolactones in stimulating plant growth and alleviating various stress conditions: A review

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### Abstract

Strigolactones (SLs) are carotenoid derived root exudates, recently classified as phytohormones, play important role in plant growth and development *via* complex signalling pathways, involving other phytohormones too. Based on relevant literature, this review evinces on role of SLs in stimulating the hyphal branching of AM fungi and various other plant development stages *like* seed germination, shoot branching, tillering, nodulation, root architecture, and highlights various researches carried out to support the role of SLs in regulating the plant growth under nutrient deficient conditions, drought and salt stress, ROS, temperature variations and, to some extent, biotic stresses for future agriculture. Versatile nature of SLs un-wraps various possibilities for their enactment in future agriculture, however, a more comprehensive knowledge on signalling and regulation mechanisms is required to exploit the full potential.

**Keywords:** Nutrient deprivation, AM fungi, abiotic stress, plant hormones and development, strigolactones

### Introduction

Plants are sessile in nature and have evolved an intricate signalling mechanism (by participation of various Hormones) to sense, respond, and adapt to the continuously changing environmental conditions such as light, temperature, water, pathogens, and nutrient availability (Wang and Irving, 2011; Smith and Li, 2014) [103, 91]. Phytohormones play central roles in boosting plant tolerance to environmental stresses, which negatively affect plant productivity and threaten future food security. Plants have evolved sophisticated mechanisms to flexibly adapt themselves against various a/biotic stresses. To attain such adaptations, plants needs to coordinate and control defence responses, which are regulated through a complex network of myriad signalling pathways, in which hormones play a key role (Andreo-Jimenez *et al.*, 2015) [4]. Recent identification and characterization of shoot branching mutants from various plant species such as *more axillary growth1-4 (max1-4)* in *Arabidopsis*, *dwarf* and *high tillering dwarf (d/htd)* in rice, *decreased apical dominance 1 (dad1)* in *Petunia hybrida*, *ramosus1-5 (rms1 to 5)* in *Pisum sativum* has established SLs as a phytohormone (Leyser, 2009; Beveridge and Kyozyuka, 2010) [56, 12]. SLs, a class of carotenoid-derived phytohormones, were initially discovered as an 'ecological signal' for parasitic seed germination and establishment of symbiotic relationship between plants and beneficial microbes (Mostofa *et al.*, 2018) [70], plant growth, development, signalling and delay of senescence (Banerjee and Roychoudhury, 2018) [103]. In addition, SLs are also involved in signalling pathways in promoting seed germination in crop plants (Pepperman and Bradow, 1988) [78] and rhizobium-legume interaction (Foo and Davies, 2011) [31]. Detailed analysis of the mutants revealed additional roles of SLs in regulating root architecture, leaf shape and senescence, internode elongation, secondary growth, and drought stress responses (Brewer *et al.*, 2013; de Saint Germain *et al.*, 2013; Ha *et al.*, 2014) [14, 22, 38]. Besides all these functions, SL also acts as a molecular cue, helps plants to communicate with their environment (Andreo-Jimenez *et al.*, 2015) [4]. Recent studies reported that SLs play essential roles in the regulation of various physiological and molecular processes during the adaptation of plants to abiotic stresses (Mostofa *et al.*, 2018) [70] and biotic stresses. Moreover, SLs play a positive role in plant responses to drought and salt stress through MAX2 (Li *et al.*, 2015) [58].

SLs are exuded primarily from the roots in a wide variety of plant species including dicots, monocots, and primitive plants such as mosses, liverworts, charophyte green algae, and stoneworts (Delaux *et al.*, 2012) [24]. SLs possibly accumulate in plant tissues in response to stress conditions like drought, salinity, nutrient deprivation, oxidative stress (ROS) and light

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stress and induce the expression of downstream osmolytes to maintain metabolic homeostasis in the stressed cells (Banerjee and Roychoudhury, 2018) [10]. SLs actively participate within regulatory networks of plant stress adaptation that are governed by other phytohormones (Mostofa *et al.*, 2018) [70]. Moreover, reports suggest that the production of SLs in plants is strictly regulated and dependent on the type of stresses that plants confront at various stages of development.

Various analytical tools have been used to determine that roots have relatively high level of SLs as compared to other plant tissues such as hypocotyl, stem, and leaves. In *Arabidopsis* *MAX1* is primarily expressed in the root vasculature and *AtCCD8 (MAX4)* is expressed in the columella root cap of both primary and lateral roots. *AtMAX2* show high level of expression in the root elongation zone (Cheng *et al.*, 2013) [17]. Expression of SL biosynthetic genes in the roots corroborates with its role as a germination stimulant. Moreover, lower SL levels in shoots promote shoot branching (Pandey *et al.*, 2016) [76].

### Regulatory Mechanisms of SLs Signalling:

Microarray analysis revealed that exogenously applied SL (example GR24, a synthetic analog of SL), regulated the expression of several genes, including light signaling-related genes and auxin-inducible genes (Mashiguchi *et al.*, 2009) [65]. Biochemical approaches have suggested two classes of TFs as down-stream targets of *MAX2*, including *bri1*-EMS-suppressor 1 (*BESI*) and *DELLA* (Nakamura *et al.*, 2013; Wang *et al.*, 2013) [72, 104]. SLs have been shown to regulate auxin localization and transport via trafficking and cytoskeleton rearrangements (Pandya-Kumar *et al.*, 2014) [77]. One of the regulatory mechanism of SL signalling requires the Leucine-rich repeat F-box protein (*ORE9/MAX2/RMS4/D3*) which acts as a substrate recruiting subunit of SCF-type ubiquitin E3ligase and an  $\alpha/\beta$ -fold hydrolase (*D14/D88/HTD2* of rice and *DAD2* of *Petunia*), which might act as the probable SL receptor (Wang *et al.*, 2013; Chevalier *et al.*, 2014) [103, 18]. *D14* and *MAX2/D3* can function in SL signalling in a manner similar to that of *GID1* and *SLY1/GID2* in GA signalling. Interestingly, *SLENDER RICE1 (SLR1)*, a rice *DELLA* protein, has been proposed as potential target of the SL signalling (Zheng *et al.*, 2014) [115]. *D14*-mediated hydrolysis of SLs results in activation of downstream targets such as *SLR1*, a rice *DELLA* protein (Nakamura *et al.*, 2013) [72]. *D53* is rapidly degraded in the presence of GR24 (Zhou *et al.*, 2013) [116]. *D53* is a target of SL signaling in shoot branching and acts as a negative regulator of the SL response (Pandey *et al.*, 2016) [76].

Kolbert, 2019 [48] detected NO levels in different organs of *max1-1* and *max2-1* *Arabidopsis* and compared to the WT, these mutants showed enhanced NO levels in their root tips indicating the negative effect of endogenous SLs on NO metabolism. NO can be an upstream negative regulator of SL biosynthesis or an upstream positive regulator of SL signaling depending on the nutrient supply.

### Regulation under Nutrient Deficiency

SLs might be factors that have an influence on the plant response to a deficiency of macronutrients. In LC-MS/MS analysis, an elevated level of SLs in root and root exudates under phosphate and nitrate deficient conditions is detected, for instance, leguminous plants show increase in SL levels in response to both Pi and N -deficient conditions (Foo *et al.*, 2013; Marzec *et al.*, 2013; Sun *et al.*, 2014) [33, 65, 95]. Moreover, biosynthesis of SLs is regulated by auxins

(Hayward *et al.*, 2009) [44]. SLs have been shown to regulate Auxin transport via AP-2 and PIN1 protein (Trevisan *et al.*, 2015) [98] and SL mediated regulation of root architecture requires Auxins by controlling the localization of PIN proteins (Shinohara *et al.*, 2013) [89]. These results indicate that down-regulation of SLs in the Roots Transition Zone could be the early response to nutrient insufficient conditions (Pandey *et al.*, 2016) [76].

**Under Pi-deficient conditions**, WT *Arabidopsis* plants show inhibition of lateral bud outgrowth and increase in orobanchol levels in the root and xylem sap, respectively. Because *Arabidopsis* is a non-host for AMF, therefore, SLs probably primarily increase the efficiency of Pi usage by modulating plant architecture (Kohlen *et al.*, 2011; Mayzlish-Gati *et al.*, 2012) [48, 67]. Under Pi-deficiency, *max2* and *max4* show altered expression of Pi-deficiency hallmark genes including type 5 acid phosphatase (*ACP5*), phosphate transporter1;5 (*PHT1;5*), and *PHT1;4*. Auxin transporter gene (*TIR*) was shown to be involved in the SL-mediated response to low Pi, suggesting SLs and auxins coordinate the response to low Pi (Mayzlish-Gati *et al.*, 2012) [67]. Whereas, under sufficient P conditions, SLs have suppressive effect on lateral root formation. Accordingly, SL-deficient mutants have a higher lateral root density (Kapulnik *et al.* 2011) [45] and have a shorter primary root, not only in *Arabidopsis*, but also in rice and maize (Arite *et al.*, 2012; Guan *et al.*, 2012; Ruyter-Spira *et al.* 2011) [5, 36, 85]. Therefore, the effect of SLs on the regulation of root system architecture was shown to depend on the plant's P status (Kapulnik *et al.*, 2011; Ruyter-Spira *et al.*, 2011) [46, 85].

**Under N-deficient conditions** an increase in SL production has been shown to occur in pea (Foo *et al.*, 2013) [33], and also in some non-legume plant species such as rice, sorghum, wheat and lettuce (Jamil *et al.*, 2011; Yoneyama *et al.*, 2007, 2012) [41, 113, 114].

### SLs and Arbuscular Mycorrhizal Fungi (AMF):

Another beneficial role of SLs to plants was discovered in mycorrhizal symbiosis between plants and fungi (example Glomeromycota). SLs regulate hyphal branching in AMF symbiosis and is credited for the evolution of land plants and rendering them more tolerant to abiotic and biotic stresses (Harrison, 1999; Liu *et al.*, 2007) [40, 61]. The root exudates from plants are able to induce hyphal branching in AMF and were characterized as SLs. GR24 showed induction of hyphal branching in AMF, *Gigaspora margarita*, confirming the role of SLs in hyphal branching (Akiyama and Hayashi, 2006) [1]. In lower plants SLs promote rhizoid elongation in moss, liverworts, and stoneworts of which only liverworts show mycorrhizal symbiosis (Delaux *et al.*, 2012) [24]. Alternatively to the 'direct pathway' of obtaining P by root hairs and lateral roots, another plant strategy to improve P acquisition is by establishing symbiosis with certain soil microorganisms such as AM fungi (Smith and Read 2008; Smith and Smith 2011) [91, 92]. Fungal hyphae, acting as 'helper roots' that can search for P beyond the P depletion zone. It is well known that phytohormone homeostasis is altered during AM symbiosis establishment and functioning (Bucher *et al.*, 2014; Foo *et al.*, 2013; Gutjahr 2014; Pozo *et al.*, 2015) [16, 32, 37, 81]. Plants themselves are able to actively influence the level of AM colonisation by controlling the production of SLs depending on the P status (Foo *et al.*, 2013; López-Ráez *et al.* 2008; Yoneyama *et al.* 2007, 2012) [33, 64, 114, 113]. SLs also promote

lateral root formation (Ruyter-Spira *et al.*, 2011) <sup>[85]</sup>, therefore, this initial fungal-mediated induction of SLs may serve to increase the number of colonisation sites.

Besides a better nutrient supply, AM symbiosis provides also increased tolerance against other abiotic stresses such as heavy metals, drought and salinity (Aroca *et al.*, 2013; Evelin and Kapoor 2014; Li *et al.*, 2014; Ruiz-Lozano *et al.*, 2012; Singh *et al.*, 2011) <sup>[7, 28, 57, 84, 90]</sup>. Mycorrhizal plants show a higher WUE and root turgor, alleviating the negative effects of water shortage on plant physiology (Al-Karaki *et al.*, 2004; Augé *et al.*, 2015; Bárzana *et al.*, 2014; Li *et al.*, 2014; Wu and Xia 2006) <sup>[3, 9, 11, 57, 107]</sup>. A negative effect on SL production in the absence of mycorrhizal colonization has also been observed in *Lotus japonicus* plants subjected to osmotic stress (Liu *et al.*, 2015) <sup>[60]</sup>. These results might suggest that plants sense the presence of the AM fungus and that they respond by producing SLs under unfavourable conditions to improve colonization (Andreo-Jimenez *et al.*, 2015) <sup>[4]</sup>. As plants in nature are simultaneously affected by biotic and abiotic stresses, it would not be surprising if the production of compounds that favour beneficial plant-microbe symbioses are further enhanced when perceiving both biotic and abiotic stresses (Pineda *et al.*, 2013) <sup>[80]</sup>. Under salt stress, mycorrhizal plants increase the production of SLs (Aroca *et al.*, 2013) <sup>[7]</sup>.

### SLs Role in Growth and Plant Physiology

Roots serve as the primary site for SL biosynthesis, from where SLs are either exuded out into the rhizosphere or transported via xylem to different plant parts, also confirmed by early grafting experiments in *Arabidopsis* and tomato, which provided insight into SL signaling regulation via localization and transport (Kohlen *et al.*, 2011) <sup>[48]</sup>. SLs act as positive regulator of PIN protein localization, transcription, translation, and trafficking by reorganizing actin cytoskeleton, modulating its distribution.

**Germination:** *ccd7* and *ccd8* mutants from different plant species showed a reduced production of SLs (Drummond *et al.*, 2009; Gomez-Roldan *et al.*, 2008; Kohlen *et al.*, 2012; Ledger *et al.*, 2010; Umehara *et al.*, 2008; Vogel *et al.*, 2010) <sup>[26, 35, 47, 55, 100, 102]</sup>. Genetic engineering using RNAi technology on the tomato *CCD7* and *CCD8* genes resulted in a significant reduction in SLs, which correlated with a lower germination of *P. ramosa* seeds (Kohlen *et al.*, 2012; Vogel *et al.*, 2010) <sup>[47, 102]</sup> and decreased *P. ramosa* infection of the transgenic tomato lines in pot experiments (Kohlen *et al.*, 2012) <sup>[47]</sup>. Epigenetic regulation (DNA methylation) plays role in SL signalling specifically during germination process studied in *P. ramosa*. GR24 activates *PrCYP707A1*, an ABA catabolic gene, during germination process, reducing the level of ABA, a seed dormancy hormone. Treatment with 5-azacytidine (hypo-methylation reagent) shortens the conditioning period (Lechat *et al.*, 2015) <sup>[54]</sup>, indicates GR24 causes hypo-methylation of *PrCYP707A1* thereby reducing ABA levels and inducing seed germination.

**Shoot Branching and Tillering:** SLs function in shoot branching was unveiled by increased shoot branching mutants from various plant species such as *dad1*, *rms1* to 5 in *P. sativum*, *max1-4* and *d1htd* (Leyser, 2009; Beveridge and Kyozuka, 2010) <sup>[56, 12]</sup>. *ccd8* mutants (pea *rms1* and rice *d10*) are deficient in SLs and the branching phenotype is rescued by treatment with GR24 and natural SLs. On the other hand, when GR24 is applied to signal perception mutant *rms3* of

pea and *d3* of rice, the branching phenotype is not rescued (Gomez-Roldan *et al.*, 2008; Umehara *et al.*, 2015) <sup>[35, 101]</sup>. Tomato plants expressing *SICCD7* antisense constructs show excessive shoot branching phenotype and reduced levels of SLs. These plants showed higher expression levels of SL biosynthesis genes in unripe fruits, suggesting additional SL function in fruit ripening or seed development (Vogel *et al.*, 2010) <sup>[102]</sup>. SLs accelerate PIN1 removal from the plasma membrane causing the shoot branching phenotype. Additionally, PIN1 levels are also depleted in the plasma membrane of xylem parenchyma cells in the stem and this process is clathrin mediated (Shinohara *et al.*, 2013) <sup>[89]</sup>. All these studies established SLs as a negative regulator of branching. SL deficient mutants are semi-dwarf and show increased outgrowth of tillers from axillary meristems, giving the mutants a bushy appearance. KK094 (1,2,3-triazole ureas, irreversible inhibitor of SL signalling), was able to reduce plant height at 10mM and promote outgrowth of second tillers at 5 mM (Nakamura *et al.*, 2019) <sup>[71]</sup>.

**Nodulation:** SLs regulate nodule number in dosage dependent manner. The pea SL-deficient mutant *rms1* established about 40% less nodules than the corresponding WT, and the phenotype was partially rescued by exogenous GR24 application, probably by down-regulation on NOD1. Further, GR24 application also increased the nodule number in WT plants (Foo and Davies 2011) <sup>[31]</sup>.

**Root Length:** SLs have several demonstrated functions in the rhizosphere, all favoured by the steep SL gradient around the root, which makes the presence of SLs in soil a reliable indicator of proximity to a living plant root. (Al-Babili and Bouwmeester, 2015) <sup>[2]</sup>. The primary root length in SL mutants *max1-4* is shorter than in WT plants, a phenotype rescued by GR24 application in the SL biosynthetic mutants (*max1*, *max3*, and *max4*) but not in the SL perception mutant (*max2*). Studies have also shown that SLs repress Lateral root formation and promote Root hair elongation (Kapulnik *et al.*, 2011; Ruyter-Spira *et al.*, 2011) <sup>[45, 46, 85]</sup>. SL signalling affects auxin flux by regulating PIN proteins in the root tip thereby affecting lateral root formation, primary root meristem size, and root hair elongation (de Smet, 2012; Koltai, 2014) <sup>[23, 51]</sup>.

**Senescence:** Plant hormones like ABA, Ethylene and jasmonic acid are known to enhance the process of senescence, whereas cytokinins delays the process (Jibrán *et al.*, 2013) <sup>[43]</sup>. During senescence, reallocation of nutrients takes place from older to younger tissues. *Arabidopsis oesara9 (ore9)/max2* and rice *d3* mutants, exhibit delayed senescence, suggest a role for SLs during senescence. Similarly, transgenic *L. japonicus*, silenced for *LjCCD7/MAX3* show delayed leaf senescence and increased branching (Yan *et al.*, 2007; Czarnecki *et al.*, 2013; Yamada *et al.*, 2014) <sup>[109, 21, 108]</sup>. In rice, GR24 restores normal leaf senescence in SL-deficient mutants (*d10*, *d27*, and *d17*), whereas it has no effect on SL response mutants (*d3* and *d14*). Additionally, it was found that SLs regulate leaf senescence in response to Pi-deficient conditions (Yamada *et al.*, 2014) <sup>[108]</sup>.

### SLs role in alleviating and tolerating Stress

**Drought & Salinity:** SLs regulate drought stress response partially through ABA signaling. López-Ráez *et al.*, 2010 <sup>[64]</sup>, reported that the tomato ABA-deficient mutants *notabilis*, *sitiens* and *flacca*, blocked at different steps of the ABA

biosynthetic pathway, and WT plants treated with specific ABA inhibitors produced less SLs. *max-2* mutant show down-regulation of ABA import genes (*ABCG22* and *ABCG40*), CK catabolism genes (*CKX1*, *CKX2*, *CKX3*, and *CKX5*), positive regulators of ABA and osmotic stress (*CIPKI*), and abiotic stress responsive genes (*AtNAC2*) (Ha *et al.*, 2014) [38]. *At max* mutants are hypersensitive to salt stress at the germination and vegetative stages of growth, and a reduction in endogenous SL content or impairment in SL signaling compromises the plant's ability to tolerate drought and salt stress. By using this dehydration assay, it was observed that SL-deficient and SL-signaling *max* mutant plants lost water faster than WT plants suggesting that an altered transpiration rate might be responsible for the lower tolerance of *max* plants to water deficit stress. Exogenous application of SL (GR24) rescues the these phenotype of SL-deficient Mutants and enhances the drought tolerance of WT Plants. (Ha *et al.*, 2014) [38]. Interestingly, a reduction in ABA content has been reported in mycorrhizal roots (Aroca *et al.*, 2008, 2013; Fernández *et al.*, 2014) [7, 7, 8, 29], suggesting that AM plants are less stressed than non-mycorrhizal ones.

Cytokinins are known to enhance drought tolerance and SLs have been shown to regulate expression of *CRX* genes, encoding CK oxidase/ dehydrogenase, required for CK catabolism. The *CRX* genes are down-regulated in *max2* plants (Reguera *et al.*, 2013; Ha *et al.*, 2014) [81, 38]. Additionally, *max2* mutant plants under drought stress have thinner cuticle and larger stomata aperture. qRT-PCR assays indicated that drought stress led to reduced expression of ABA-inducible marker genes. This expression profile is *max2* specific and not observed in other SL signalling pathway genes, suggesting that *MAX2* might act as a common component of different signalling pathways. *MAX2* expression is induced by *ABI3* and *ABI5*, suggesting that *MAX-2* acts down-stream of ABA signalling (Bu *et al.*, 2014) [15].

Moreover, a correlation between ABA and SL levels was reported in mycorrhizal lettuce plants subjected to salt stress (Aroca *et al.*, 2013) [7]. *max2* plants also show reduced expression of *ABCG22* and *ABCG40* (ABA import genes) lead to reduced stomata closure and increased transpiration, supporting the positive regulatory role of ABA in drought signalling responses (Osakabe *et al.*, 2014) [73]. In Lotus (*L. japonicus*), osmotic stress decreases SL levels in tissues and root exudates, primarily by altering transcription of SL biosynthetic and transporter encoding genes. Pre-treatment of plants with SLs inhibited the osmotic stress- induced ABA increase in roots by down-regulating the ABA biosynthetic gene *NCED2*. During osmotic stress, SL levels decrease to allow an increase in ABA in the roots of lotus plant. Evidently, the SL metabolism and effects on ABA levels are opposite in roots and shoots under stress conditions (Liu *et al.*, 2015) [59].

**Light:** The R: FR light ratio perceived by phytochromes controls plastic traits of plant architecture, including branching. Phytochrome effects on the degree of correlative inhibition required functional BRANCHED1 (BRC1 and BRC2) and MORE AXILLARY GROWTH (MAX2 and MAX4) proteins (Finlayson *et al.*, 2010) [30]. The changes in light quality (decrease in the R:FR ratio) trigger the shade avoidance syndrome by which stems elongate at the expense of leaf and storage organ expansion, branching is inhibited, and flowering is accelerated (Tao *et al.*, 2009) [95]. GR24 application markedly induced expression of genes putatively

involved in light harvesting. GR24 treatment interferes with the root's response to IAA treatment and SLs are potentially positive regulators of light harvesting in plants (Mayzlish-Gati *et al.*, 2009) [68]. It is intriguing that enhanced SLs levels resemble light-induced effects on roots. Exposure of plants to SL inhibits the COP1 activity, suggesting that SL can mimic light perception in plants (Tsuchiya *et al.*, 2010) [99] and *max2* mutant is hypersensitive to Red, FR and Blue light (Shen *et al.*, 2007) [87]. The key transcription factor of light signalling HY5 requires SLs in order to stimulate *Arabidopsis* seed germination during thermo-inhibition (Toh *et al.*, 2012) [97]. It was shown that light impacts on the actin cytoskeleton, also increased abundance and recycling of PIN2 auxin transporter (Laxmi *et al.*, 2008; Dyachok *et al.*, 2011; Wan *et al.*, 2012; Pandya-Kumar *et al.*, 2014) [52, 27, 103, 77].

**Reactive Oxygen Species (ROS):** Plants produce ROS in various cell compartments, during photosynthesis, photorespiration, electron transport in mitochondria, and biotic and abiotic stresses (Foyer and Noctor, 2005) [34] and production enhanced in response to the nutrient deprivation (Shin and Schachtman, 2004) [88]. ROS have emerged as major second messenger molecules acting as signals to modulate gene expression, which in turn helps in adaptation to various stresses (Sagi and Fluhr, 2006) [86]. ROS generated in the illuminated cells are likely to modulate cellular signaling resulting in the regulation of light-induced root escape growth (Yokawa *et al.*, 2014) [111]. The link between SLs and ROS comes from the finding that *FAR-REDELONGATED HYPOCOTYL3* (*FHY3*, a key component of phytochrome A signalling and the circadian clock) acts as a negative regulator of *RBOH* genes (Lin *et al.*, 2007). *FHY3* suppresses both root and shoot branching in *Arabidopsis fhy3max2* double mutant plants, suggesting *FHY3* acts as a suppressor of *MAX2* (Ouyang *et al.*, 2011) [75]. Moreover, *RBOH* has been shown to regulate shoot branching in tomato, where antisense *RBOH* expression causes increased shoot branching (Koltai *et al.*, 2011) [49]. ROS is a known second messenger during ABA signalling and it is quite likely that *RBOH* is involved in SL-dependent shoot and root branching regulation and other stress responses (Xia *et al.*, 2015) [108]. Moreover, transcriptome analysis in *M. truncatula* roots has shown that activation of NADPH oxidases under P- and N-limiting conditions results in expression of SL biosynthesis genes (Bonneau *et al.*, 2013) [13]. Inhibition of NADPH oxidase activity and chemical scavenging of H<sub>2</sub>O<sub>2</sub> significantly reduced SL induced salt tolerance and decreased SL levels. The H<sub>2</sub>O<sub>2</sub> induced SL accumulation was accompanied by increased tolerance to salt stress. This indicates that elevated H<sub>2</sub>O<sub>2</sub> concentration resulting from enhanced NADPH oxidase activity regulated SL induced salt stress tolerance in AM (Kong, 2017) [51].

**Temperature:** Germination in SL-defective *Arabidopsis* mutants under high temperature conditions is stimulated by GR24 application. Moreover, GR24 reduces the ABA to GA ratio and increases CK levels. RT-PCR analysis revealed that GR24 represses transcription of *NCED9*, an enzyme required for ABA biosynthesis (Tsuchiya *et al.*, 2010) [99]. Similarly, SLs release *P. ramosa* (broomrape) seed dormancy by reducing ABA levels during warm stratification (Lechat *et al.*, 2015) [53]. SL plays an important role in the control of dark chilling tolerance. Pea mutants (*rms3*, *rms4*, and *rms5*) had significantly greater shoot branching with higher leaf

chlorophyll a/b ratios and carotenoid contents than the WT. Exposure to dark chilling significantly decreased shoot fresh weight, but increased leaf numbers in all lines. Unlike the WT plants, chilling-induced inhibition of photosynthetic carbon assimilation was observed in the *rms* lines and also in the *Arabidopsis max3-9*, *max4-1*, and *max2-1* mutants that are defective in SL synthesis or signalling. GR24 application, cause decrease in leaf area in WT, *max3-9*, and *max4-1* mutants but not in *max2-1* in the absence of stress. In addition, a chilling-induced decrease in leaf area was observed in all the lines in the presence of GR24 (Cooper *et al.*, 2018) <sup>[19]</sup>.

**Fire:** Karrikins are formed from burnt vegetation and function as an abiotic cue for germination in post fire habitat. A genetic screen for *karrikin-insensitive (kai)* mutants revealed that karrikin signaling requires *MAX2* function. *KAR1* and *KAR2* are known germination stimulants of *Arabidopsis*, promoting germination of dormant *Landsberg erecta* seeds in addition to GR24. Both karrikin and GR24 inhibit hypocotyl elongation in WT and *max1*, *max3*, and *max4* plants during photomorphogenesis (Nelson *et al.*, 2011) <sup>[72]</sup>.

**Biotic Stress:** Salicylic acid, Jasmonic Acid, and ABA play major roles in plant defence responses (Robert-Seilaniantz *et al.*, 2011) <sup>[82]</sup>. *MAX2* was identified as a component of plant defence response during disease resistance. *max2* mutant plants showed increased stomata conductance probably promoting pathogen entry into the apoplast. Moreover, these plants show decreased tolerance to pathogen-triggered ROS and hormonal signalling (Piisilä *et al.*, 2015) <sup>[78]</sup>. In *Arabidopsis*, GR24 application reduced the auxin level in young developing rosette leaves, resulting in a decreased leaf area (Ruyter-Spira *et al.*, 2011) <sup>[84]</sup>. GR24 has an inhibitory effect on the auxin transport capacity of the polar auxin transport stream in the stem (Crawford *et al.* 2010) <sup>[84]</sup>, auxin levels initially accumulate, which negatively feeds back on auxin biosynthesis. With respect to the interaction with ethylene, it was proposed that SLs promote its biosynthesis, which in turn induces auxin biosynthesis, transport and signalling in the roots (Stepanova and Alonso 2009) <sup>[93]</sup>. Indeed, it was shown that the low SL producing tomato mutants *Sl-ORT1* and *high pigment-2 (hp-2<sup>dg</sup>)* are more resistant to infection by different *Orobanche* and *Phelipanche* species than the corresponding wild-types (Dor *et al.*, 2011; López-Ráez *et al.*, 2008) <sup>[25, 63]</sup>. In rice, cultivars with lower SL production also displayed reduced infection by *Striga hermonthica* (Jamil *et al.*, 2011) <sup>[42]</sup>. Similarly, root exudates from faba bean lines resistant against *Orobanche* and *Phelipanche spp.* showed low levels of SLs (Fernández-Aparicio *et al.*, 2014) <sup>[29]</sup>.

## Discussion

There are myriad of SLs produced by different plants, which directly or indirectly participate in plant growth & developmental processes, and very less is known about their specificity. There is vast scope for improvisation by exploring less non-classical chemicals stimulants like SLs and investigate cross talk between SL and other Phytohormones for betterment of agricultural crop productivity. Genetic modulation of SL content/response could be applied as a potential approach to reduce the negative impact of abiotic stress on crop productivity (Ha, 2014) <sup>[38]</sup>. Plant biotechnology and breeding approaches could be suggested to obtain resistant plant by targeting biosynthesis of SLs. Root

parasite plants are difficult to manage because most of their life cycle occurs belowground and exert the greatest damage prior to their emergence of main crop. Breeding for cultivars with reduced SL production and/or exudation could be a suitable strategy to combat these pests (Andreo-Jimenez *et al.*, 2015) <sup>[4]</sup>. Exogenous treatments or transgenic approaches for higher SL bioaccumulation can be potential strategies for developing multiple abiotic stress tolerance in crops and plants (Banerjee and Roychoudhury, 2018) <sup>[10]</sup>. However, careful evaluation is needed before application in agro ecosystems to avoid possible undesired side-effect (Andreo-Jimenez *et al.*, 2015) <sup>[4]</sup>. Future research should focus on the action of individual SL and/ or their specific receptors to further explore their targeted uses in agriculture (López-Ráez *et al.*, 2017) <sup>[62]</sup>. The plant receptor for endogenous SLs—DWARF14 (D14)—is a functional enzyme that hydrolyzes and destroys the ligand as part of the signal transduction mechanism (Yao *et al.*, 2018) <sup>[110]</sup>, this provides important insights to target SL signaling to benefit agriculture (Waters, 2017) <sup>[105]</sup>.

## Conclusion

Research update tells that importance and involvement of SLs in biology and ecology of rhizosphere. Multi-facet nature of this root released chemical, opens a range of possibilities for its role in plant morphology and interaction with other Phytohormones and secondary metabolites. Further exploiting the mode of action, signalling mechanism and application in plant biotechnology, SLs could be effective for application in sustainable agriculture and combating various biotic and abiotic threats.

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