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Exploring strigolactones for inducing abiotic stress tolerance in plants

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Abstract: Strigolactones (SLs) are a comparatively novel class of phytohormones that are involved in the maintenance of plant architecture with key regulation of lateral branching. They are also reported to play an important role in regulating plant responses to various abiotic stresses. The potential of SLs to improve crop resilience and productivity needs to be effectively translated into agriculture. Therefore, both the endogenous biosynthesis of SLs and their exogenous application need to be thoroughly investigated to understand and exploit the mechanism underlying the alleviation of abiotic stress responses. Although several reviews have emphasised the biosynthesis of SLs in plants under abiotic stress, the mechanism underlying the alleviation of stress responses upon exogenous application has been less explored. Accordingly, in this review, although we have briefly discussed the beneficial effects of endogenous production of SLs in different sections, our main focus is to summarise the influence of exogenous SLs on the growth and development of different plant species grown under various abiotic stresses including drought, nutrient, heavy metal, and salinity stress. Apart from providing an overview of the transcriptomic studies conducted to observe the alleviating effects of SLs on abiotic stress responses, the research gaps in this field were briefly discussed. The review provides insight for researchers to conduct further research on SLs and fill the gap so that they can be effectively used for sustainable agriculture.

Keywords: climate change; drought; GR24; heavy metals; nutrients; phytohormones; salinity

Plants thrive in environmental conditions that are adverse and frequently present challenges that hinder their growth and productivity. The detrimental environmental circumstances comprise abiotic factors such as extreme temperatures, light stress, ozone stress, water deficit, deficiencies and toxicity of elements (Suzuki et al. 2014), and biotic factors induced by living organisms such as attack by herbi-

vore pests and infection by pathogens (Atkinson & Urwin 2012). Among these factors, abiotic stresses affect approximately 90% of cultivable areas, resulting in 70% yield reductions of significant food crops (Mantri et al. 2012). Integrating climate change with crop yield models has led to projections that major crops such as wheat, maize, and rice will experience further deterioration in productivity posing a signifi-

cant risk to food security (Tigchelaar et al. 2018). Consequently, extensive research is being conducted on the primary abiotic stresses such as drought, salt, and temperature stresses that impact plants and crops in their natural environment (Zhang et al. 2022a). To solve the problem of abiotic stress, it is important to understand how plants perceive stress indications and adjust themselves to unfavourable environments. Consequently, enhancing the ability of plants to withstand stress is not only important for boosting agricultural productivity but also for ensuring environmental sustainability because plants lacking in stress tolerance require excessive amounts of water and fertilizers, leading to an overwhelming impact on the environment. Plants have evolved well-developed mechanisms to deal with the complexities of abiotic stresses. Phytohormones provide a systematic mechanism at physiological, biochemical, and molecular levels to regulate abiotic stress responses (Ciura & Kruk 2018; Zheng et al. 2023). Strigolactones (SLs) are recently discovered carotenoid-derived phytohormones (Al-Babili & Bouwmeester 2015) that control plant development by positively affecting their photosynthetic rate, ion homeostasis, blooming, seedling growth, and leaf senescence (Banerjee & Roychoudhury 2018). Both exogenous application and endogenous production of SLs have been reported to effectively enhance the stress tolerance of plants towards abiotic stress conditions (Zheng et al. 2023). However, although over 30 SLs have been identified, their involvement in different stress-based pathways remains elusive. In this review article, we discuss SLs, their different forms, and the role of endogenous and exogenous SLs in alleviating the plant responses to different abiotic stresses including drought, nutrients, heavy metals, and salinity stress. The effects of SLs on gene expression of plants grown under abiotic stresses have also been discussed.

What are strigolactones?

SLs have been gradually characterized as germination stimulants for root parasitic plants (Cook et al. 1966), root-derived symbiotic signals (Akiyama et al. 2005) and shoot branching inhibitors (Gomez-Roldan et al. 2008). Depending on the chemical structures, SLs are categorized into two forms, canonical and non-canonicals. While canonical SLs possess the tricyclic ABC ring attached to a butenolide group (D-ring) through an enol-ether bridge, non-canonical

SLs do not have an ABC ring but have a D-ring and enol-ether bridge (Ueno et al. 2014; Charnikhova et al. 2017). The importance of D-ring and enol-ether bridges for the biological activities of SLs in plants has been demonstrated (Boyer et al. 2012; Umehara et al. 2015). Owing to the stereochemistry of the C-ring, canonical SLs can be classified into two types, orobanchol and strigol, with a-oriented and b-oriented C-ring respectively. While orobanchol (ORO) and 4-deoxyorobanchol (4DO) belong to the orobanchol type, strigol and 5-deoxystrigol (5DS) belong to the strigol type canonicals.

Among these, the first characterized SL, strigol was initially extracted from the root exudates of cotton, a deceptive host of *Striga* (Cook et al. 1966, 1972). Further, it was isolated from the root exudates of real hosts of *Striga*, prosomillet, maize, and sorghum (Siame et al. 1993). Aletrrol and sorgolactone that were respectively isolated from root exudates of cowpea and sorghum, are the two germination stimulants structurally related to strigol and thus were termed strigolactones (Müller et al. 1992; Butler 1995). On the other hand, orobanchol isolated from root exudates of red clover was the first germination stimulant recognized for *Orobanche* root parasites (Yokota et al. 1998). While tobacco produces both strigol and orobanchol, generally, only one form of SLs is produced by plant species (Xie et al. 2013). Non-canonical SLs with specific structures, lotuslactone, zealactone, heliolactone and avenaol were respectively isolated from *Lotus japonicum*, maize, sunflower, and wild oat (Yoneyama & Brewer 2021).

Initial experiments have suggested that the carotenoid pathway is involved in the biosynthesis of SLs (Matusova et al. 2005). Later, SL biosynthesis was deeply understood via enhanced shoot branching observed in the recessive mutants including rice dwarf/high tillering dwarf (d/htd), pea (*Pisum sativum*) ramosus (rms), and *Arabidopsis* more axillary growth (max) (Beveridge & Kyoizuka 2010). Primarily, it was discovered that rice d17 and d10, pea rms5 and rms1, and *Arabidopsis* max3 and max4 mutants with malfunctioned carotenoid cleavage dioxygenase 7 (CCD7) and CCD8 were deficient in SLs (Booker et al. 2004; Gomez-Roldan et al. 2008; Umehara et al. 2008, 2015). Further, it was determined that novel iron-binding proteins, AtD27 and D27 are involved in SL biosynthesis in rice and *Arabidopsis* respectively (Lin et al. 2009; Waters et al. 2012). Later, consecutive reactions of recombinant CCD8, CCD7, and D27 proteins from rice, pea, and *Arabidopsis*

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during *in vitro* analysis produced a non-canonical compound similar to SL called carlactone (CL) (Alder et al. 2012). *Arabidopsis* and rice produce carlactone as an endogenous compound that is converted to canonical ORO and deoxyorobanchol justifying its production during SL biosynthesis as an intermediate (Seto et al. 2014).

The conversion of CL into both canonical and noncanonical SLs in vascular plants is facilitated by a subfamily of cytochrome P450 oxygenases, CYP711A1 (cytochrome P450 MORE AXILLARY GROWTH (MAX1)). It was first demonstrated in *Arabidopsis* where CYP711A1 catalysed the oxidation of CL-producing carlactonoic acid (CLA) and consequently methyl carlactonoate (MeCLA) (Abe et al. 2014; Yoneyama et al. 2018). Moreover, it was reported that CYP711A18 of maize (*Zea mays*) and CYP711A17v1/v3 of *Selaginella moellendorffii* could catalyse the A3- and A2-type reactions, respectively (Yoneyama et al. 2018). The max1 mutant of *Arabidopsis* that is flawed in CYP711A1 showed the hyper-branching phenotype MAX3 and MAX4 and a major rise in the endogenous level of CL (Booker et al. 2005).

Similar to *Arabidopsis*, in rice, two of the five MAX1 homologs, CYP711A2 and CYP711A3 convert CL to CLA (Yoneyama et al. 2018). CYP711A2 additionally catalyses the termination of the B-C ring and promotes the conversion of CLA into rice SL, 4-deoxyorobanchol (4DO). It also catalyses the hydroxylation of 4DO to produce orobanchol. Several plants do not produce 4DO and directly produce orobanchol (Ueno et al. 2018; Wakabayashi et al. 2019). For example, the MAX1 homolog could not convert 4DO into orobanchol in tomato (Yoneyama et al. 2018). In cowpea and cotton, cytochrome CYP722C facilitates the direct conversion of CLA into orobanchol and 5-deoxystrigol (Wakabayashi et al. 2019, 2020). Similarly, in sorghum, 5DS is converted into sorgomol via another cytochrome P450, CYP728B35 (Wakabayashi et al. 2021). The genomic and transcriptomic sequences of plants can be compared to understand the association between these three cytochrome P450 clades involved in canonical SL production from CLA.

The non-canonical SLs such as lotuslactone, heliolactone, and zealactone possess the identical chemical substructure as non-canonical MeCLA leading to the hypothesis that MeCLA is involved in their synthesis (Charnikhova et al. 2017; Xie et al. 2019; Wakabayashi et al. 2020). However, this hypothesis

needs to be confirmed. It is difficult to understand the biological roles of non-canonical SLs as compared to canonical SLs due to their decreased stability. In SL biosynthesis, both enzymes upstream and downstream of non-canonical CL are involved in the biosynthesis of mechanistically diverse SLs. Zeaxanthin is involved in the conversion of all-trans- β -carotene into CL and 3-hydroxy-carlactone catalyzed by carotenoid isomerase, CCD7, and CCD8 (Baz et al. 2018). Despite being the predominant SLs in *Arabidopsis*, the functions of hydroxycarlactones have not been well explored yet (Yoneyama et al. 2020b). In *Arabidopsis*, shoot branching inhibitor MeCLA is metabolized by the LATERAL BRANCHING OXIDOREDUCTASE (LBO) enzyme (Brewer et al. 2016). The incubation of LBO with MeCLA produces CLA and hydroxymethyl-carlactonoate (1'-OHMeCLA), where 1'-OHMeCLA is considered the enzymatic product of LBO and is additionally dynamic in shoot branching inhibition (Brewer et al. 2016). However, due to its instability, 1'-OHMeCLA is quickly converted to CLA (Yoneyama et al. 2020a). *Arabidopsis* LBO homologs in tomato, sorghum, and maize act similarly to *Arabidopsis* LBO. MeCLA in *Lotus japonicus* produces 18-hydroxy-MeCLA that is converted to lotuslactone (Mori et al. 2020) suggesting that MeCLA is the precursor of non-canonical SLs. The biosynthesis of non-canonical SLs can be well understood by depicting the role of novel biosynthetic enzymes such as methyltransferase and the identification of unique metabolites involved in the conversion of CLA to MeCLA.

Transport of strigolactones

Plants regulate their growth and response to environmental changes by evolving the transport of endogenous hormones (Borghi et al. 2016). It has been determined that under nitrogen and phosphorus deficiency, SLs are released from the roots into the soil and act as symbiotic signals for arbuscular mycorrhizal (AM) fungi (Andreo-Jimenez et al. 2015). Moreover, in the shoot, root-derived signals are produced by combining the nutrient accessibility in the soil and shoot architecture (Kohlen et al. 2011; de Jong et al. 2014). Additionally, long-distance signaling of SLs in *Arabidopsis* from roots to shoots has been observed by the grafting approach (Turnbull et al. 2002). In an experiment, the max1 or max3 rootstocks inhibited branching even if these were grafted with wild type (WT) scions (grafted with

max1 or max3 mutants). Similarly, max1 and max3 scions showed inhibited branching even if these are grafted with WT rootstocks. This showed that the MAX1 and MAX3 genes are operative whether present in the root or shoot and prevent shoot branching. It directed that SLs are signalled from MAX1 and MAX3 in roots to shoots to inhibit branching (Turnbull et al. 2002).

The grafting of wild-type (grafted with max1 or max3 mutants) rootstocks in *Arabidopsis* rescue branching in max1 and max3 scions (Turnbull et al. 2002). Grafting of dad1 mutant of petunia and rms1, rms2, and rms5 mutants of pea showed similar results as max1 and max3 mutants (Beveridge et al. 1997; Morris et al. 2001). Although shoot-to-shoot signalling of branching does not involve MAX1, RMS, and DAD1 genes, these genes mediate root-to-shoot signalling via SLs. Although *Arabidopsis*, pea, and petunia show striking parallels and long-distance inhibition of branching seems to be a common occurrence in plants, it is still not possible to determine whether genes have orthologous links across species or not.

The movement of SL biosynthetic intermediates can be estimated via grafting experiments among SL-deficient mutants. CLA and MeCLA have been recognized as long-distance mobile signals through the recovery of the branching phenotype of max1 scions by LBO rootstocks (Brewer et al. 2016). LBO synthesizes 1'-OH-MeCLA from MeCLA that has been recognized as a long-distance mobile signal as rosette branches of the lbo mutant are decreased by grafting lbo scions onto WT rootstocks (Brewer et al. 2016). Shoot branching phenotype of max4 scions is rescued by max1 rootstocks confirming that CL is a movable signal as it is the merely recognized intermediate upstream of MAX1 and downstream of MAX4 (Booker et al. 2005). 9-cis-b-carotene and 9-cis-b-apo-10'-carotenal are not observed as mobile signals because max4 rootstocks could not rescue the shoot branching phenotype of Atd27 scions (Lin et al. 2009; Waters et al. 2012). Furthermore, it has been hypothesized that different SL and related compounds are transport signals that move from root to shoot via the xylem. Several SLs, including ORO, have been noticed in the xylem sap of tomato and *Arabidopsis* via LC-MS/MS analysis (Kohlen et al. 2011). However, in other studies, SLs and their biosynthetic intermediates were not noticed in xylem saps of *Arabidopsis* and tomato (Xie et al. 2015). Moreover, employing the stable isotope labelled ORO and 4DO, it was detected that these SLs reach

to shoots from roots via cell-to-cell transport and not through xylem saps (Xie et al. 2015). Owing to the differences obtained in the results of different experiments, the transport of SLs in plants and their followed paths should be thoroughly studied in different plant species. Moreover, it is required to identify which SLs act as endogenous signals and which SLs can be focused as external signals.

Strigolactones increase the plant tolerance toward abiotic stress conditions

In general, plants grown under normal laboratory conditions contain low amounts of strigolactone. This basic hormone level restricts root development while allowing certain branching for maximum light absorption to ensure adequate nutritional intake and structural integrity. However, strigolactone levels increase when the plant experiences certain environmental challenges, such as inadequate nutrient supply or abiotic stress, to optimize and adjust the development strategy of plants against the circumstances (Kohlen et al. 2011; Ling et al. 2020). SLs are involved in several morphological, physiological, and biochemical changes occurring in plants to sustain homeostasis under different abiotic stress conditions (Figure 1) some of which are described below.

Drought stress and SLs. Drought stress is one of the most drastic environmental stresses influencing plant development and growth (Hamurcu et al. 2020; Thingnam et al. 2023). Regional droughts are becoming more frequent and intense on an annual basis as a result of the impending global climate change (Banks et al. 2019). The stress damages the photosynthetic organs of the plants reducing their light absorption capacity and thus, decreasing their photosynthetic rate (Zhang et al. 2022b). Water deficit not only negatively affects the acquisition, transport, distribution, and storage of nutrients but also reduces root vigour and plant biomass (Bista et al. 2018). Different phytohormones including abscisic acid, auxin, brassinosteroids, ethylene, gibberellin, jasmonic acid, and salicylic acid are known to trigger drought tolerance in plants by getting involved in different physiological, biochemical, and molecular mechanisms (Iqbal et al. 2022). SLs are phytohormones that reportedly develop drought tolerance and act as positive regulators of plant responses to water deficit (Wang et al. 2021).

SLs are known to be regulating the response to drought both endogenously and exogenously.

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SLs interact with other phytohormones, especially abscisic acid (ABA), and develop drought tolerance in mycorrhizal and non-mycorrhizal plants (Ha et al. 2014). However, the effects of drought stress on the production of endogenous SLs are different in mycorrhizal and non-mycorrhizal plants. For example, while the enhanced level of drought stress decreased the production of SLs, DDH, and solanacol in nonmycorrhizal tomato plants, in mycorrhizal tomato plants their production increased under drought stress (Ruiz-Lozano et al. 2016). The down-regulation and upregulation of the tomato gene, *SICCD7* that is involved in the biosynthesis of SLs (Vogel et al. 2010; Kohlen et al. 2012) seems to be regulating the production level of SLs in non-AM and AM tomato plants, respectively (Ruiz-Lozano et al. 2016). Consequently, the concentration of SLs is related to the tolerance level of plants directing

towards their role in drought stress tolerance and their association with AM symbiosis (Ruiz-Lozano et al. 2016). In some plants, drought decreases SL synthesis in roots decreasing the movement of SL to shoots and providing a systemic signal of stress. This may or may not affect the levels of ABA in roots and ABA in roots is neither translocated nor required for shoot responses to stress. However, the externally applied or shoot-produced SL has a positive effect on the ABA sensitivity of stomata. SL signals towards shoots downregulate the expression of SL biosynthetic genes in roots that consequently enhance the transcripts of SL biosynthetic genes in shoots for developing drought stress tolerance (Visentin et al. 2016).

Several efforts are being made to understand the effects of the exogenous application of SLs on the mechanism of drought stress tolerance in plants (Figure 1). The role of exogenous SL has been established

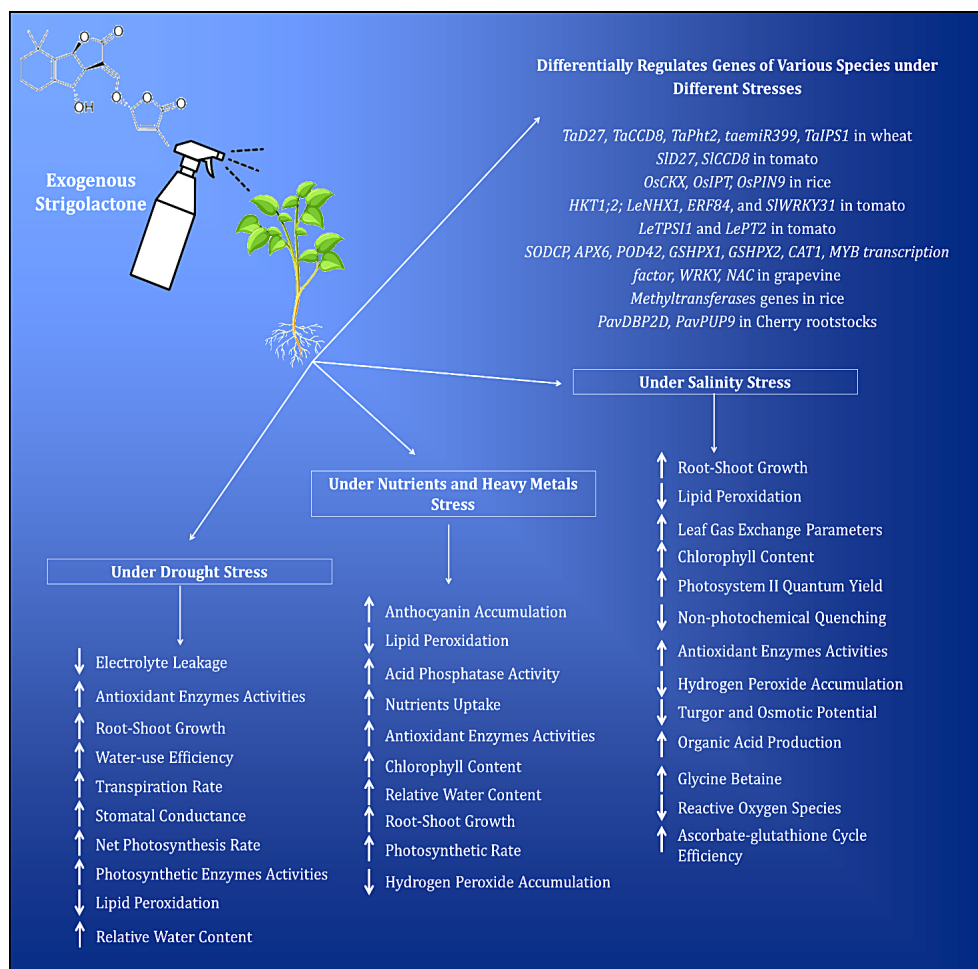


Figure 1. An overview of the effects of exogenous strigolactone on physiological, biochemical, and molecular aspects of different plant species

An upward (↑) arrow represents an increase in the given trait, while a downward (↓) arrow represents a decrease in the given trait

as a positive regulator when it increased the drought tolerance of both WT and SL-deficient max mutant *Arabidopsis* plants (Ha et al. 2014). Moreover, water deficit developed hypersensitivity in plants lacking in SL biosynthesis and signal transduction (Ha et al. 2014). SLs increase drought tolerance in wheat cultivars by reducing electrolyte leakage and increasing antioxidant enzyme activities. However, this increase is dependent on the tolerance level of the cultivars where drought-tolerant cultivars show greater improvement as compared to the drought-sensitive cultivars. SL has also been shown to work synergistically with salicylic acid to improve drought tolerance of wheat genotypes grown in water deficit (Sedaghat et al. 2017). The positive effect of external SL on the growth parameters of plants grown under drought stress has also been widely reported (Sattar et al. 2021). Exogenous SL treatment enhances water-use efficiency, transpiration rate, stomatal conductance, and net photosynthesis rate of plants grown under drought-stress conditions (Min et al. 2019; Li et al. 2022) (Figure 1). It also reduces the suppressive effects of drought on the performance index on the absorption basis and photosystem II maximum photochemical efficiency (Li et al. 2022). While SL application is reported to increase the activity of photosynthetic enzymes after 48 h, it decreases the ABA content of *Pennisetum purpureum* plants after 120 h (Li et al. 2022). External SLs control stomatal closure via reactive oxygen species (ROS) or ABA, manipulate chlorophyll components, and activate antioxidant capacity to lessen the negative impacts of drought and direct towards the crosstalk of SL and ABA. It reduces the level of malondialdehyde content, zeatin riboside (ZR), and indoleacetic acid (IAA) and increases the relative water content under drought stress. In maize, exogenous SL application enhanced leaf ascorbic acid, total phenolics, antioxidant activities, water use efficiency, stomatal conductance, chlorophyll content, gas exchange characteristics, net CO₂ assimilation rate, photosynthetic pigments and growth rate of plants grown under drought stress (Luqman et al. 2023). Although a number of experiments have been conducted to determine the effect of SLs on plants grown under drought stress, more optimization of application timing, dose and method of application is required to get better results.

Nutrients stress and SLs. Low or excessive mineral levels in a plant system can lead to nutrient deficiency or toxicity leading to reduced crop biomass and yield worldwide. The deficiency or toxicity of these ele-

ments including macro- and micronutrients change physiological and metabolic processes in plants. Nutrient stress has damaging effects on root-shoot growth parameters, reproductive organs, photosynthetic machinery, nutrient uptake, and carbohydrate and protein synthesis of plants. Despite the identification of the important role of SLs in several abiotic stresses in plants, its involvement in developing tolerance to nutrient deficiency and toxicity has been less explored. However, their contribution as a modulator of plant adaptation towards a few nutrient-deficient conditions particularly nitrogen and phosphorus deficit has been studied (Marzec et al. 2013).

One of the most crucial macronutrients needed for plant development and growth is phosphorus (P). Being a part of several crucial macromolecules including membrane lipids, adenosine triphosphate (ATP), and nucleic acid, it has a major participation in significant metabolic processes and governing pathways (Amtmann & Armengaud 2009). Another vital macronutrient for plants is nitrogen (N), which is present in many essential macromolecules including amino acids and nucleic acids. Even though N accounts for 78% of the atmosphere's volume, plants cannot absorb it because two N atoms are tightly bound together by a stable triple covalent bond (Beatty & Good 2011). This is why symbiotic bacteria that can transform atmospheric nitrogen into ammonium and subsequently transmit it to the host plant, interact with plants. A rapid reaction to the N/P deficit is necessary for a plant to survive since both macronutrients, N and P, are essential for plant growth.

Deficiency of these nutrients leads to a higher production of SLs in plants. For the first time, a 20 times higher production of orobanchol was reported in *Trifolium pratense* under P deficit. This orobanchol acted as a signal for mycorrhizal symbionts and a germination stimulant for root parasites (Yoneyama et al. 2007b). Low N and P exuded 30 times and 20 times higher 5-deoxystrigol in *Sorghum bicolor* as compared to control plants (Yoneyama et al. 2007a). Greater SLs led to a 100-fold increase in excitation of the seed germination of the parasitic plant *Striga hermonthica*. While N and P deficiency induces the production of SLs, K deficiency does not have such an effect. This not only directs toward the specific exudation mechanism of SLs in response to different nutrients but also suggests it depends on different mechanisms for nutrient uptake across plant species

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(Marzec et al. 2013). In an experiment on six different plant species including legumes and non-legumes, while P deficiency stimulated the production and exudation of SLs in all of them, N deficiency could not stimulate the production and exudation of SLs in two of them (Yoneyama et al. 2012; Foo et al. 2013). Interestingly, root exudates of rice plants grown under P and N deficiency conditions showed greater germination in *S. hermonthica* seeds as compared to the control plants along with an increase in five different SLs including 2'-epi-5-deoxystrigol and orobanchol (Jamil et al. 2011). However, SL production not only varies according to the stress condition but may also vary according to the genotypes within the species (López-Ráez et al. 2008; Jamil et al. 2011). It is necessary to explore whether the differential expression of gene-encoding proteins engaged in the biosynthesis of SLs is involved in the enhanced production of SLs in response to N and P deficit or not. Different gene-encoding proteins, D10, D17, and D27 involved in the biosynthesis of SLs in rice were highly expressed under P deficient growth environment. Similarly, ABC transporter protein-encoding genes *PRD1* of petunia that have a role in the movement of SLs are highly expressed under phosphorus deficit (Kretschmar et al. 2012). SLs under P-deficient growth conditions suppress primary root growth, encourage lateral root production, and increase the quantity and length of root hairs, which improves the capacity of the root system to explore the soil and acquire nutrients and/or water under stress (Kapulnik et al. 2011). Dissimilar to deficiency, high N and P content reduces the SL root exudates and thus, crop infestation of *Striga* and *Orobancha blanchi* (García-Garrido et al. 2009). Moreover, high P in the growing media decreases AM colonization of roots (García-Garrido et al. 2009).

The exogenous SLs have variable effects on plant species grown under N and P deficiency (Figure 1). External racGR24 supply stimulates accumulation of anthocyanin and activates acid phosphatases, under P deficiency in plants (Ito et al. 2015). The applied SL had an influence on the metabolic profile of the tomato roots where the levels of inorganic phosphate (Pi) deficiency-related metabolites were also increased (Gamir et al. 2020). Under Pi deficiency, a short exposure of the synthetic SL analogue 2'-epi-GR24 (a type of strigolactone) enhanced the accumulation of SL and the upregulation of Pi deficiency-related genes such as *TaD27* and *TaCCD8* in wheat and *SID27* and *SICCD8* in tomato (Gamir et al. 2020).

Similarly, racGR24 upregulates the expression of high affinity Pi transporter *Pht1;7* in *Arabidopsis* grown under P deficit (Prerostova et al. 2018). In rice, GR24 application increases the expression of *OsCKX* and *OsIPT* while decreasing the expression of *OsPIN9* under N stress. While several studies discussed the endogenous production and exudation of SLs under low P and N stress, very limited studies are available on the ameliorating effects of exogenous SL and need to be further explored. Moreover, there are other severe nutrient stress suppressing agricultural production worldwide such as boron toxicity (Khan et al. 2021), zinc and iron deficiency (Khan et al. 2022) magnesium deficiency, etc. Surprisingly, the influence of external SLs on the plant responses under these nutrient stress conditions has not been studied at all and must be focused.

Heavy metals stress and SLs. Along with nutrient stress, several nonessential and toxic heavy metals (HMs), as well as metalloids, such as aluminium (Al), arsenic (As), cadmium (Cd), chromium (Cr), lead (Pb), and mercury (Hg) have drastic effects on crops. Based on their level of toxicity and devastating effects on plants, heavy metals toxicity is regarded as the second most severe global environmental issue (Bhoi et al. 2021). With an accumulation in plant's organs, heavy metal toxicity manifests a delay in their growth and development (Syta et al. 2019). This accumulation of heavy metals in different plant tissues is regulated by different phytohormones (Syta et al. 2019). Heavy metal toxicity reduces antioxidant activities, chlorophyll (Chl) content, photosynthetic rate, and growth of the plants (Bhoi et al. 2021). Different phytohormones including SL reportedly alleviate the effects of stress caused by heavy metal toxicity both exogenously and endogenously.

The role of endogenous SLs in alleviating As stress symptoms have been studied in rice where mutants of SL biosynthetic genes, DWARF D10 and D17 revealed a greater suppressive response towards As stress as compared to wild-type plants (Mostofa et al. 2021). The absence of endogenous SLs in rice plants showed irregularities in their biomass, phenotype, and chlorophyll content (Mostofa et al. 2021). However, similar As content in both WT and SL-deficient d10 and d17 mutant plants directed that growth differences in both plants were not due to arsenic accumulation but due to the involvement of significant pathways and genetic mechanisms in the process. Endogenous SLs in As stressed rice plants seem to be increasing glutathione S-transferase, glutathione peroxidase,

ascorbate peroxidase, and superoxide dismutase activities, and lowering membrane damage, electrolyte leakage, water loss, and ROS to deal with the stress (Mostofa et al. 2021). SL production in rice plants also upregulates the expression of *OsABCC1*, *OsGSH1*, *OsGSH2*, and *OsPCS1* genes to sequester As into vacuoles (Mostofa et al. 2021).

Exogenous SL minimizes lipid peroxidation and Cd uptake and improves nutrient uptake including Cu, Fe, Mn, and Zn, activity of antioxidant enzymes, chlorophyll content, relative water content, and root-shoot development of Cd stressed switchgrass (Tai et al. 2017) (Figure 1). The effect of exogenous SL on Cd stress symptoms of plants may vary as per the tolerance level of the plants; however, it shows a positive effect in the case of both tolerant and sensitive genotypes. In Cd-tolerant and sensitive barley genotypes, external SL supply decreases the Cd accumulation, enhances chlorophyll and nutrient content, improves photosynthetic rate, and reduces malondialdehyde (MDA) and hydrogen peroxide accumulation (Qiu et al. 2021). With an increase in internal nitric oxide synthase (NOS) activity and thus, higher NO content and an increase in superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APOX), glutathione peroxidase (GPX), and glutathione reductase (GR) activity, exogenous SL could even alleviate the effect of Cd stress in Cd-sensitive barley genotype (Qiu et al. 2021). Similar effects were observed in melon plants, where exogenous SL have positive effects on antioxidant enzyme activities and root vigour of Cd-stressed roots (Chen et al. 2022). Based on the results of different studies, it is inferred that SLs may have a role in reducing the stress caused by heavy metals on plants. However, more research efforts are required to understand the detailed mechanism by which it mitigates heavy metal stress in plants.

Salinity stress and SLs. Salinity stress develops complex processes to hinder normal plant growth and development (Naeem et al. 2012). It has a negative effect on photosystem II (PSII) and reduces mesophyll and stomatal conductances to restrict CO₂ diffusion and photosynthesis (Flexas et al. 2004; Acosta-Motos et al. 2015). Lipid peroxidation accumulated greater MDA in tissues under salinity stress. Moreover, excess salt leads to oxidative damage in plants produced by ROS that in turn scavenged by antioxidant enzymes (Munns & Tester 2008).

It has been established that SLs can facilitate salinity tolerance in a MAX2-dependent way (Ha et al. 2014). SL-signaling max2 mutants as well as SL-deficient

max3 and max4 mutants of *Arabidopsis* showed salt-sensitive phenotypes when exposed to high salinity during germination and vegetative stages. However, there were no differences in root damage between the studied WT and max mutant plants (Ha et al. 2014). These findings suggest that salt stress tolerance of plants during developmental stages reduces if there is a decrement in endogenous SL levels or SL signalling. AM symbiosis also facilitates the involvement of SLs in developing salt tolerance (Aroca et al. 2013). In the presence of AMF, salt-stressed lettuce roots produce SL that increases stomatal conductance, Photosystem II efficiency, and growth of the plants (Aroca et al. 2013). Similarly, in *Sesbania cannabina* seedlings, salt stress is alleviated with an interaction of hydrogen peroxide with SLs in the presence of AMFs (Kong et al. 2017). Further, ABA treatment enhances SL production and consequently, induces the tolerance level of plants against salt stress due to a reported interaction between SL and ABA and an increase in the expression of SL biosynthesis genes (Ren et al. 2018). Moreover, altered expression of nine SL biosynthetic genes including two *CCD7*, two *CCD8*, two *D27*, and three *MAX1*, and seven SL signalling genes including two *D14*, three *D53*, and two *MAX2* was observed in soybeans grown under salt/alkaline stress (Qiao et al. 2020).

The external supply of SLs reportedly has ameliorative effects on plants' responses towards salinity stress. GR24, a synthesized strigolactone, improves the root-shoot growth of rapeseed plants under salinity stress by improving leaf gas exchange parameters, chlorophyll content, photosystem II quantum yield, and reducing non-photochemical quenching (Figure 1). Moreover, it reduces the MDA levels and increases the SOD and POX activities (Ma et al. 2017). In rice also, external SL increases the root-shoot length of the seedlings grown under salinity stress. Along with a decrease in MDA content, it enhances chlorophyll content, photosynthetic activities, and antioxidant enzyme concentrations in salt-stressed plants (Ling et al. 2020). The rice seedlings were tolerant to the suppressive effects of high salinity stress at 1 µM GR24 concentration (Ling et al. 2020). In contrast to rapeseed and rice, a decrease in antioxidant enzyme activity was supposed to have a role in alleviating salt stress symptoms on SL treatment in *Salvia nemorosa* plants (Sharifi & Bidabadi 2020). Foliar SL application reduces glutathione (GSH) and total phenol content and increases proline content and essential oil yield in *Salvia* plants grown in ex-

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cess saline conditions (Sharifi & Bidabadi 2020). Similar to the normal growth medium, in *in vitro* growth conditions as well, SL treatment decreases MDA, hydrogen peroxide, turgor potential, and osmotic potential, and enhances glycine betaine (GB), free proline, peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD) contents in sunflower plants grown under salt stress treatment (Zulfiqar et al. 2021). SL application also regulates the genes encoding stress enzymes including glutathione reductase, superoxide dismutase, and catalase, and the transcription factors *HKT1;2*, *LeNHX1*, *ERF84*, and *SlWRKY31* in tomato plants grown under high salinity (Hürkan 2022). External SL maintains Na/K ions homeostasis in apple seedlings by reducing the Na/K ions in the cytoplasm and controlling the expression of Na/K transporter genes to alleviate the symptoms of salinity-alkalinity stress (Ma et al. 2022). It enhances the antioxidant enzyme activity, induces organic acid production, and amplifies endogenous GA₃, zeatin riboside, abscisic acid, and acetic acid content to improve salinity-alkalinity tolerance of plants (Ma et al. 2022). Other than the positive effect on photosynthetic efficiency, stomatal conductance, and chlorophyll content, exogenous SLs reduce the production of ROS, decrease salt-induced photodamage, and enhance the efficiency of ascorbate-glutathione (AsA-GSH) cycle in cucumber under excessive saline growth conditions (Zhang et al. 2022c). It also regulates the expression of different genes including the ones involved in MAPK cascade pathways, photosynthesis, and antioxidant system to alleviate the symptoms of salinity stress (Zhang et al. 2022c). The exogenous SLs also interact with other molecules such as saccharides and nitric oxide (NO) to reduce the effects of salinity stress. Trehalose (Tre) is a disaccharide known to alleviate the symptoms of cold stress, drought stress, and salinity stress both exogenously and endogenously via enhancing flowering, seed germination and root growth in plants. Under salinity stress in tomato seedlings, external supply of GR24 is reported to regulate Tre metabolism via increasing the endogenous production of Tre and upregulating the genes involved in Tre biosynthesis. This consequently enhanced the salt resistance and promoted the growth of tomato seedlings (Lu et al. 2023). NO is a radical molecule that enhances the adaptability of plants towards abiotic stress conditions via reducing the negative effects of produced ROS (Pandey et al. 2023). Exogenous SL (15 µM GR24) increased the leaf area, stem

diameter, plant height, total root length, chlorophyll content, and activity of antioxidant enzymes in tomato plants when supplied with NO donor [10 µM S-nitrosoglutathione (GSNO)] under salinity stress. Moreover, the exogenous supply of SL increased the endogenous production of NO and thus, resulted in NO-enhanced salinity tolerance in tomato seedlings by enhancing the antioxidant capacity and photosynthetic pigment content in stressed plants (Liu et al. 2022). Both molecules together upregulated the expression of SLs synthesis genes (*SICC7*, *SICC8*, *SID27* and *SIMAX1*) and signal transduction genes (*SID14* and *SIMAX2*) under salinity stress (Liu et al. 2022). Functional characterization of differentially expressed genes on SL treatment in salt-stressed plants needs to be done to understand the association between these genes and SL activity in plants.

Transcriptomic changes in plants on strigolactone application under different abiotic stresses

Plants can regulate the expression of their genes to attain adaptability and tolerance towards different stress conditions, and thus, it is crucial to identify the differentially expressed genes (DEGs) under a particular stress (Pandey et al. 2022). An exogenous supply of SL may have variable effects on the differential expression of these genes influencing the stress symptoms. Thus, determining the association between SL supply and changes in the transcriptome of plants grown under stress conditions can be a crucial strategy for understanding stress tolerance developed on SL application. The external supply of strigolactone GR24 made significant changes to the transcriptome of salinity-stressed rapeseed plants with differential expression of more than 1 000 and 3 000 genes in shoots and roots respectively. SL treatment mitigated the salinity stress via differential expression of specific genes related to photosynthesis, plant hormone signalling, and tryptophan metabolism (Ma et al. 2017). Moreover, it stimulated P-associated signalling in tomato and increased the expression of the *LeTPSI1* and *LePT2* genes under P-limited conditions (Gamir et al. 2020). In wheat, 10 nM 2'-epi-GR24 application upregulated the expression of *TaPht2*, *taemiR399*, and *TaIPS1* genes (Gamir et al. 2020). Exogenous SLs alleviated the effects of drought stress in grapevine plants via upregulation of the key gene of strigolactone synthesis *D14* and antioxidant enzyme genes including *SODCP*,

APX6, *POD42*, *GSHPX1*, *GSHPX2*, and *CAT1*. Additionally, it downregulated four *MYB* transcription factors, three *WRKY*, and two *NAC* genes (Wang et al. 2021). The external supply of SL regulated the expression of genes related to flavonoid and jasmonic acid biosynthesis and *WRKY*, *bHLH*, *AP2/ERF*, and *MYB* transcription factor families in melon plants (Chen et al. 2022). Transcriptomic analysis of phosphorus-starved rice plants supplied with external synthetic SL GR24 revealed the upregulation of several genes involved in oxidoreductase, heme binding, and oxidation-reduction activity (Haider et al. 2023). Moreover, two methyl transferase encoding genes were also found to play a role in the alleviation of P deficiency stress via the involvement of SL biosynthesis (Haider et al. 2023). Pretreatment with 1 μ M rac-GR24, and 5 μ M rac-GR24 SL seemed to enhance drought resistance in cherry rootstocks via differential expression of 586 and 489 genes, respectively (Xu et al. 2023). SL application downregulated the expression of *PavDBP2D* which is a PAR leucine zipper transcription factor, and *PavPUP9* which is a CTK transporter gene in cherry rootstocks grown under drought stress conditions. Zhou et al. (2023) reported up- and down-regulation of respectively 2 325 and 1 826 DEGs in leaves, and respectively 765 and 622 DEGs in roots on SL foliar supply on drought-stressed elephant grass plants. Among all the genes, 44 DEGs were determined as crucial genes playing a main role in SL response to drought stress. These transcriptomics-based studies provided novel insights into the regulation of molecular mechanisms in plants by SLs for their adaptation to different stressed environments.

Conclusion and future prospects

Strigolactones are plant hormones that have been comprehensively studied during the last few decades due to their involvement in the growth and developmental processes of plants. However, more information is still required to understand their roles in plant adaptation towards different abiotic stresses. Although some of the candidate genes with significant differential expression on SL supply in stressed plants have been identified, there is a huge lack in their functional characterization. The candidate genes should be functionally characterized so that these can be further focused to increase the stress tolerance in plants along with the SL application. Moreover, in most of the physiological or molecular

studies, only single genotype was used for stress and SL application and their tolerance level towards that particular stress has not been considered. As the tolerance and susceptibility level of genotypes towards stress may change the alleviating effects of SL, it will be better to consider these levels to make a conclusive statement about the mechanism. In fact, comparisons should be made between tolerant and susceptible genotypes to observe the alleviating effects of SLs under different stresses. Moreover, morphological, physiological, and genetic variations of genotypes and species should be studied after exogenous SL supply on stressed plants. In the present scenario of continuous climate change where most of the agricultural land suffers from more than one stress at a time, not only under individual stresses, the effects of SLs should also be determined in plants grown under combined stresses. Most of the studies mentioned in the review are based on hydroponic and pot experiments. However, preference should be given to field experiments to avoid the unexpected changes in the results when SLs will be applied as abiotic stress reducing agents in the field growth conditions. Moreover, field experiments should be conducted to determine appropriate concentrations of SLs to be applied for the alleviation of different stresses in different plant species. Considering these points, more detailed research is required on the effects of SLs on plants grown under different abiotic stresses so that their direct application in agriculture can be increased.

REFERENCES

- Abe S., Sado A., Tanaka K., Kisugi T., Asami K., Ota S., Kim H.I., Yoneyama K., Xie X., Ohnishi T., Seto Y., Yamaguchi S., Akiyama K., Yoneyama K., Nomura T. (2014): Carlactone is converted to carlactonoic acid by MAX1 in *Arabidopsis* and its methyl ester can directly interact with AtD14 *in vitro*. *Proceedings of the National Academy of Sciences*, 111: 18084–18089.
- Acosta-Motos J.R., Diaz-Vivancos P., Álvarez S., Fernández-García N., Sánchez-Blanco M.J., Hernández J.A. (2015): NaCl-induced physiological and biochemical adaptive mechanisms in the ornamental *Myrtus communis* L. plants. *Journal of Plant Physiology*, 183: 41–51.
- Akiyama K., Matsuzaki K.-I., Hayashi H. (2005): Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature*, 435: 824–827.
- Al-Babili S., Bouwmeester H.J. (2015): Strigolactones, a novel carotenoid-derived plant hormone. *Annual Review of Plant Biology*, 66: 161–186.

<https://doi.org/10.17221/88/2023-CJGPB>

- Alder A., Jamil M., Marzorati M., Bruno M., Vermathen M., Bigler P., Ghisla S., Bouwmeester H., Beyer P., Al-Babili S. (2012): The path from β -carotene to carlactone, a strigolactone-like plant hormone. *Science*, 335: 1348–1351.
- Amtmann A., Armengaud P. (2009): Effects of N, P, K and S on metabolism: New knowledge gained from multi-level analysis. *Current Opinion in Plant Biology*, 12: 275–283.
- Andreo-Jimenez B., Ruyter-Spira C., Bouwmeester H.J., Lopez-Raez J.A. (2015): Ecological relevance of strigolactones in nutrient uptake and other abiotic stresses, and in plant-microbe interactions below-ground. *Plant and Soil*, 394: 1–19.
- Aroca R., Ruiz-Lozano J.M., Zamarreño Á.M., Paz J.A., García-Mina J.M., Pozo M.J., López-Raez J.A. (2013): Arbuscular mycorrhizal symbiosis influences strigolactone production under salinity and alleviates salt stress in lettuce plants. *Journal of Plant Physiology*, 170: 47–55.
- Atkinson N.J., Urwin P.E. (2012): The interaction of plant biotic and abiotic stresses: From genes to the field. *Journal of Experimental Botany*, 63: 3523–3543.
- Banerjee A., Roychoudhury A. (2018): Strigolactones: Multi-level regulation of biosynthesis and diverse responses in plant abiotic stresses. *Acta Physiologiae Plantarum*, 40: 86.
- Banks J.M., Percival G.C., Rose G. (2019): Variations in seasonal drought tolerance rankings. *Trees*, 33: 1063–1072.
- Baz L., Mori N., Mi J., Jamil M., Kountche B.A., Guo X., Balakrishna A., Jia K.-P., Vermathen M., Akiyama K. (2018): 3-Hydroxycarlactone, a novel product of the strigolactone biosynthesis core pathway. *Molecular Plant*, 11: 1312–1314.
- Beatty P.H., Good A.G. (2011): Future prospects for cereals that fix nitrogen. *Science*, 333: 416–417.
- Beveridge C.A., Kyozuka J. (2010): New genes in the strigolactone-related shoot branching pathway. *Current Opinion in Plant Biology*, 13: 34–39.
- Beveridge C.A., Symons G.M., Murfet I.C., Ross J.J., Rameau C. (1997): The rms1 mutant of pea has elevated indole-3-acetic acid levels and reduced root-sap zeatin riboside content but increased branching controlled by graft-transmissible signal(s). *Plant Physiology*, 115: 1251.
- Bhoi A., Yadu B., Chandra J., Keshavkant S. (2021): Contribution of strigolactone in plant physiology, hormonal interaction and abiotic stresses. *Planta*, 254: 1–21.
- Bista D.R., Heckathorn S.A., Jayawardena D.M., Mishra S., Boldt J.K. (2018): Effects of drought on nutrient uptake and the levels of nutrient-uptake proteins in roots of drought-sensitive and -tolerant grasses. *Plants*, 7: 28.
- Booker J., Auldrige M., Wills S., McCarty D., Klee H., Leyser O. (2004): MAX3/CCD7 is a carotenoid cleavage dioxygenase required for the synthesis of a novel plant signaling molecule. *Current Biology*, 14: 1232–1238.
- Booker J., Sieberer T., Wright W., Williamson L., Willett B., Stirnberg P., Turnbull C., Srinivasan M., Goddard P., Leyser O. (2005): MAX1 encodes a cytochrome P450 family member that acts downstream of MAX3/4 to produce a carotenoid-derived branch-inhibiting hormone. *Developmental Cell*, 8: 443–449.
- Borghi L., Liu G.-W., Emonet A., Kretzschmar T., Martinoia E. (2016): The importance of strigolactone transport regulation for symbiotic signaling and shoot branching. *Planta*, 243: 1351–1360.
- Boyer F.-D., de Saint Germain A., Pillot J.-P., Pouvreau J.-B., Chen V.X., Ramos S., Stévenin A., Simier P., Delavault P., Beau J.-M. (2012): Structure-activity relationship studies of strigolactone-related molecules for branching inhibition in garden pea: Molecule design for shoot branching. *Plant Physiology*, 159: 1524–1544.
- Brewer P.B., Yoneyama K., Filardo F., Meyers E., Scaffidi A., Frickey T., Akiyama K., Seto Y., Dun E.A., Cremer J.E. (2016): LATERAL BRANCHING OXIDOREDUCTASE acts in the final stages of strigolactone biosynthesis in *Arabidopsis*. *Proceedings of the National Academy of Sciences*, 113: 6301–6306.
- Butler L.G. (1995): Chemical communication between the parasitic weed *Striga* and its crop host: A new dimension in allelochemistry. In: *Allelopathy: Organisms, Processes, and Applications*. ACS Symposium Series, Vol. 582, Washington, D.C., ACS Publications: 158–168.
- Charnikhova T.V., Gaus K., Lumbroso A., Sanders M., Vincken J.-P., De Mesmaeker A., Ruyter-Spira C.P., Screpanti C., Bouwmeester H.J. (2017): Zealactones. Novel natural strigolactones from maize. *Phytochemistry*, 137: 123–131.
- Chen X., Shi X., Ai Q., Han J., Wang H., Fu Q. (2022): Transcriptomic and metabolomic analyses reveal that exogenous strigolactones alleviate the response of melon root to cadmium stress. *Horticultural Plant Journal*, 8: 637–649.
- Ciura J., Kruk J. (2018): Phytohormones as targets for improving plant productivity and stress tolerance. *Journal of Plant Physiology*, 229: 32–40.
- Cook C.E., Whichard L.P., Turner B., Wall M.E., Egley G.H. (1966): Germination of witchweed (*Striga lutea* Lour.): Isolation and properties of a potent stimulant. *Science*, 154: 1189–1190.
- Cook C., Whichard L.P., Wall M., Egley G.H., Coggon P., Luhan P.A., McPhail A. (1972): Germination stimulants. II. Structure of strigol, a potent seed germination stimulant for witchweed (*Striga lutea*). *Journal of the American Chemical Society*, 94: 6198–6199.

- de Jong M., George G., Ongaro V., Williamson L., Willetts B., Ljung K., McCulloch H., Leyser O. (2014): Auxin and strigolactone signaling are required for modulation of *Arabidopsis* shoot branching by nitrogen supply. *Plant Physiology*, 166: 384–395.
- Flexas J., Bota J., Loreto F., Cornic G., Sharkey T. (2004): Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. *Plant Biology*, 6: 269–279.
- Foo E., Yoneyama K., Hugill C.J., Quittenden L.J., Reid J.B. (2013): Strigolactones and the regulation of pea symbioses in response to nitrate and phosphate deficiency. *Molecular Plant*, 6: 76–87.
- Gamir J., Torres-Vera R., Rial C., Berrío E., de Souza Campos P.M., Varela R.M., Macías F.A., Pozo M.J., Flors V., López-Ráez J.A. (2020): Exogenous strigolactones impact metabolic profiles and phosphate starvation signalling in roots. *Plant, Cell & Environment*, 43: 1655–1668.
- García-Garrido J., Lendzemo V., Castellanos-Morales V., Steinkellner S., Vierheilig H. (2009): Strigolactones, signals for parasitic plants and arbuscular mycorrhizal fungi. *Mycorrhiza*, 19: 449–459.
- Gomez-Roldan V., Fermas S., Brewer P.B., Puech-Pagès V., Dun E.A., Pillot J.-P., Letisse F., Matusova R., Danoun S., Portais J.-C., Bouwmeester H., Bécard G., Beveridge C.A., Rameau C., Rochange S.F. (2008): Strigolactone inhibition of shoot branching. *Nature*, 455: 189–194.
- Ha C.V., Leyva-Gonzalez M.A., Osakabe Y., Tran U.T., Nishiyama R., Watanabe Y., Tanaka M., Seki M., Yamaguchi S., Dong N.V., Yamaguchi-Shinozaki K., Shinozaki K., Herrera-Estrella L., Tran L.S. (2014): Positive regulatory role of strigolactone in plant responses to drought and salt stress. *Proceedings of the National Academy of Sciences of the USA*, 111: 851–856.
- Haider I., Yunmeng Z., White F., Li C., Incitti R., Alam I., Gojobori T., Ruyter-Spira C., Al-Babili S., Bouwmeester H.J. (2023): Transcriptome analysis of the phosphate starvation response sheds light on strigolactone biosynthesis in rice. *The Plant Journal: For Cell and Molecular Biology*, 114: 355–370.
- Hamurcu M., Khan M.K., Pandey A., Ozdemir C., Avsaroglu Z.Z., Elbasan F., Omay A.H., Gezgin S. (2020): Nitric oxide regulates watermelon (*Citrullus lanatus*) responses to drought stress. *3 Biotech*, 10: 1–14.
- Hürkan K. (2022): Synthetic strigolactone regulates some stress related genes and transcription factors on tomato (*Lycopersium esculentum* L.). *Journal of Agriculture*, 5: 1–13.
- Iqbal S., Wang X., Mubeen I., Kamran M., Kanwal I., Díaz G.A., Abbas A., Parveen A., Atiq M.N., Alshaya H. (2022): Phytohormones trigger drought tolerance in crop plants: Outlook and future perspectives. *Frontiers in Plant Science*, 12: 3378.
- Ito S., Nozoye T., Sasaki E., Imai M., Shiwa Y., Shibata-Hatta M., Ishige T., Fukui K., Ito K., Nakanishi H. (2015): Strigolactone regulates anthocyanin accumulation, acid phosphatases production and plant growth under low phosphate condition in *Arabidopsis*. *PLoS ONE*, 10: e0119724.
- Jamil M., Charnikhova T., Cardoso C., Jamil T., Ueno K., Verstappen F., Asami T., Bouwmeester H. (2011): Quantification of the relationship between strigolactones and *Striga hermonthica* infection in rice under varying levels of nitrogen and phosphorus. *Weed Research*, 51: 373–385.
- Kapulnik Y., Resnick N., Mayzlish-Gati E., Kaplan Y., Winer S., Hershenhorn J., Koltai H. (2011): Strigolactones interact with ethylene and auxin in regulating root-hair elongation in *Arabidopsis*. *Journal of Experimental Botany*, 62: 2915–2924.
- Khan M.K., Pandey A., Hamurcu M., Avsaroglu Z.Z., Ozbek M., Omay A.H., Elbasan F., Omay M.R., Gokmen F., Topal A. (2021): Variability in physiological traits reveals boron toxicity tolerance in *Aegilops* species. *Frontiers in Plant Science*, 12: 736614.
- Khan M.K., Pandey A., Hamurcu M., Germ M., Yilmaz F.G., Ozbek M., Avsaroglu Z.Z., Topal A., Gezgin S. (2022): Nutrient homeostasis of *Aegilops* accessions differing in B tolerance level under boron toxic growth conditions. *Biology*, 11: 1094.
- Kohlen W., Charnikhova T., Liu Q., Bours R., Domagalska M.A., Beguerie S., Verstappen F., Leyser O., Bouwmeester H., Ruyter-Spira C. (2011): Strigolactones are transported through the xylem and play a key role in shoot architectural response to phosphate deficiency in nonarbuscular mycorrhizal host *Arabidopsis*. *Plant Physiology*, 155: 974–987.
- Kohlen W., Charnikhova T., Lammers M., Pollina T., Tóth P., Haider I., Pozo M.J., de Maagd R.A., Carolien Ruyter-Spira C., Bouwmeester H.J., López-Ráez J.A. (2012): The tomato CAROTENOID CLEAVAGE DIOXYGENASE 8 (SLCCD8) regulates rhizosphere signaling, plant architecture and affects reproductive development through strigolactone biosynthesis. *New Phytologist*, 196: 535–547.
- Kong C.-C., Ren C.-G., Li R.-Z., Xie Z.-H., Wang J.-P. (2017): Hydrogen peroxide and strigolactones signaling are involved in alleviation of salt stress induced by arbuscular mycorrhizal fungus in *Sesbania cannabina* seedlings. *Journal of Plant Growth Regulation*, 36: 734–742.
- Kretschmar T., Kohlen W., Sasse J., Borghi L., Schlegel M., Bachelier J.B., Reinhardt D., Bours R., Bouwmeester H.J., Martinoia E. (2012): A petunia ABC protein controls strigolactone-dependent symbiotic signalling and branching. *Nature*, 483: 341–344.

<https://doi.org/10.17221/88/2023-CJGPB>

- Li Y., Li S., Feng Q., Zhang J., Han X., Zhang L., Yang F., Zhou J. (2022): Effects of exogenous strigolactone on the physiological and ecological characteristics of *Pennisetum purpureum* Schum. seedlings under drought stress. *BMC Plant Biology*, 22: 578.
- Lin H., Wang R., Qian Q., Yan M., Meng X., Fu Z., Yan C., Jiang B., Su Z., Li J., Wang Y. (2009): DWARF27, an iron-containing protein required for the biosynthesis of strigolactones, regulates rice tiller bud outgrowth. *The Plant Cell*, 21: 1512–1525.
- Ling F., Su Q., Jiang H., Cui J., He X., Wu Z., Zhang Z., Liu J., Zhao Y. (2020): Effects of strigolactone on photosynthetic and physiological characteristics in salt-stressed rice seedlings. *Scientific Reports*, 10: 6183.
- Liu H., Li C., Yan M., Zhao Z., Huang P., Wei L., Wu X., Wang C., Liao W. (2022): Strigolactone is involved in nitric oxide-enhanced the salt resistance in tomato seedlings. *Journal of Plant Research*, 135: 337–350.
- López-Ráez J.A., Charnikhova T., Gómez-Roldán V., Matusova R., Kohlen W., De Vos R., Verstappen F., Puech-Pages V., Bécard G., Mulder P. (2008): Tomato strigolactones are derived from carotenoids and their biosynthesis is promoted by phosphate starvation. *New Phytologist*, 178: 863–874.
- Lu X., Liu X., Xu J., Liu Y., Chi Y., Yu W., Li C. (2023): Strigolactone-mediated trehalose enhances salt resistance in tomato seedlings. *Horticulturae*, 9: 770.
- Luqman M., Shahbaz M., Maqsood M.F., Farhat F., Zulfiqar U., Siddiqui M.H., Masood A., Aqeel M., Haider F.U. (2023): Effect of strigolactone on growth, photosynthetic efficiency, antioxidant activity, and osmolytes accumulation in different maize (*Zea mays* L.) hybrids grown under drought stress. *Plant Signaling & Behavior*, 18: 2262795.
- Ma C., Bian C., Liu W., Sun Z., Xi X., Guo D., Liu X., Tian Y., Wang C., Zheng X. (2022): Strigolactone alleviates the salinity-alkalinity stress of *Malus hupehensis* seedlings. *Frontiers in Plant Science*, 13: 901782.
- Ma N., Hu C., Wan L., Hu Q., Xiong J., Zhang C. (2017): Strigolactones improve plant growth, photosynthesis, and alleviate oxidative stress under salinity in rapeseed (*Brassica napus* L.) by regulating gene expression. *Frontiers in Plant Science*, 8: 1671.
- Mantri N., Patade V., Penna S., Ford R., Pang E. (2012): Abiotic stress responses in plants: Present and future. In: Ahmad P., Prasad M.N.V. (eds): *Abiotic Stress Responses in Plants: Metabolism, Productivity and Sustainability*. New York, Springer: 1–19.
- Marzec M., Muszynska A., Gruszka D. (2013): The role of strigolactones in nutrient-stress responses in plants. *International Journal of Molecular Sciences*, 14: 9286–9304.
- Matusova R., Rani K., Verstappen F.W., Franssen M.C., Beale M.H., Bouwmeester H.J. (2005): The strigolactone germination stimulants of the plant-parasitic *Striga* and *Orobanch* spp. are derived from the carotenoid pathway. *Plant Physiology*, 139: 920–934.
- Min Z., Li R., Chen L., Zhang Y., Li Z., Liu M., Ju Y., Fang Y. (2019): Alleviation of drought stress in grapevine by foliar-applied strigolactones. *Plant Physiology and Biochemistry*, 135: 99–110.
- Mori N., Sado A., Xie X., Yoneyama K., Asami K., Seto Y., Nomura T., Yamaguchi S., Yoneyama K., Akiyama K. (2020): Chemical identification of 18-hydroxycaractonoic acid as an LjMAX1 product and in planta conversion of its methyl ester to canonical and non-canonical strigolactones in *Lotus japonicus*. *Phytochemistry*, 174: 112349.
- Morris S.E., Turnbull C.G., Murfet I.C., Beveridge C.A. (2001): Mutational analysis of branching in pea. Evidence that Rms1 and Rms5 regulate the same novel signal. *Plant Physiology*, 126: 1205–1213.
- Mostofa M.G., Rahman M.M., Nguyen K.H., Li W., Watanabe Y., Tran C.D., Zhang M., Itouga M., Fujita M., Tran L.-S.P. (2021): Strigolactones regulate arsenate uptake, vacuolar-sequestration and antioxidant defense responses to resist arsenic toxicity in rice roots. *Journal of Hazardous Materials*, 415: 125589.
- Müller S., Hauck C., Schildknecht H. (1992): Germination stimulants produced by *Vigna unguiculata* Walp cv Saunders Upright. *Journal of Plant Growth Regulation*, 11: 77–84.
- Munns R., Tester M. (2008): Mechanisms of salinity tolerance. *Annual Review of Plant Biology*, 59: 651–681.
- Naeem M.S., Warusawitharana H., Liu H., Liu D., Ahmad R., Waraich E.A., Xu L., Zhou W. (2012): 5-Aminolevulinic acid alleviates the salinity-induced changes in *Brassica napus* as revealed by the ultrastructural study of chloroplast. *Plant Physiology and Biochemistry*, 57: 84–92.
- Pandey A., Khan M.K., Hamurcu M., Brestic M., Topal A., Gezgin S. (2022): Insight into the root transcriptome of a boron-tolerant *Triticum zhukovskyi* genotype grown under boron toxicity. *Agronomy*, 12: 2421.
- Pandey A., Khan M.K., Hamurcu M., Athar T., Yerlikaya B.A., Yerlikaya S., Kavas M., Rustagi A., Zargar S.M., Sofi P.A., Chaudhry B. (2023): Role of exogenous nitric oxide in protecting plants against abiotic stresses. *Agronomy*, 13: 1201.
- Prerostova S., Kramna B., Dobrev P.I., Gaudinova A., Marsik P., Fiala R., Knirsch V., Vanek T., Kuresova G., Vankova R. (2018): Organ-specific hormonal cross-talk in phosphate deficiency. *Environmental and Experimental Botany*, 153: 198–208.
- Qiao Y., Lu W., Wang R., Nisa Z.U., Yu Y., Jin X., Yu L., Chen C. (2020): Identification and expression analysis

- of strigolactone biosynthetic and signaling genes in response to salt and alkaline stresses in soybean (*Glycine max*). DNA and Cell Biology, 39: 1850–1861.
- Qiu C.-W., Zhang C., Wang N.-H., Mao W., Wu F. (2021): Strigolactone GR24 improves cadmium tolerance by regulating cadmium uptake, nitric oxide signaling and antioxidant metabolism in barley (*Hordeum vulgare* L.). Environmental Pollution, 273: 116486.
- Ren C.-G., Kong C.-C., Xie Z.-H. (2018): Role of abscisic acid in strigolactone-induced salt stress tolerance in arbuscular mycorrhizal *Sesbania cannabina* seedlings. BMC Plant Biology, 18: 274.
- Ruiz-Lozano J.M., Aroca R., Zamarreno A.M., Molina S., Andreo-Jimenez B., Porcel R., Garcia-Mina J.M., Ruyter-Spira C., Lopez-Raez J.A. (2016): Arbuscular mycorrhizal symbiosis induces strigolactone biosynthesis under drought and improves drought tolerance in lettuce and tomato. Plant, Cell & Environment, 39: 441–452.
- Sattar A., Ul-Allah S., Ijaz M., Sher A., Butt M., Abbas T., Irfan M., Fatima T., Alfarraj S., Alharbi S.A. (2021): Exogenous application of strigolactone alleviates drought stress in maize seedlings by regulating the physiological and antioxidants defense mechanisms. Cereal Research Communications, 50: 263–272.
- Sedaghat M., Tahmasebi-Sarvestani Z., Emam Y., Mokhtassi-Bidgoli A. (2017): Physiological and antioxidant responses of winter wheat cultivars to strigolactone and salicylic acid in drought. Plant Physiology and Biochemistry, 119: 59–69.
- Seto Y., Sado A., Asami K., Hanada A., Umehara M., Akiyama K., Yamaguchi S. (2014): Carlactone is an endogenous biosynthetic precursor for strigolactones. Proceedings of the National Academy of Sciences, 111: 1640–1645.
- Sharifi P., Bidabadi S.S. (2020): Strigolactone could enhances gas-exchange through augmented antioxidant defense system in *Salvia nemorosa* L. plants subjected to saline conditions stress. Industrial Crops and Products, 151: 112460.
- Siame B.A., Weerasuriya Y., Wood K., Ejeta G., Butler L.G. (1993): Isolation of strigol, a germination stimulant for *Striga asiatica*, from host plants. Journal of Agricultural and Food Chemistry, 41: 1486–1491.
- Suzuki N., Rivero R.M., Shulaev V., Blumwald E., Mittler R. (2014): Abiotic and biotic stress combinations. New Phytologist, 203: 32–43.
- Sytar O., Kumari P., Yadav S., Brestic M., Rastogi A. (2019): Phytohormone priming: Regulator for heavy metal stress in plants. Journal of Plant Growth Regulation, 38: 739–752.
- Tai Z., Yin X., Fang Z., Shi G., Lou L., Cai Q. (2017): Exogenous GR24 alleviates cadmium toxicity by reducing cadmium uptake in switchgrass (*Panicum virgatum*) seedlings. International Journal of Environmental Research and Public Health, 14: 852.
- Thingnam S.S., Lourembam D.S., Tongbram P.S., Lokya V., Tiwari S., Khan M.K., Pandey A., Hamurcu M., Thangjam R. (2023): A perspective review on understanding drought stress tolerance in wild banana genetic resources of Northeast India. Genes, 14: 370.
- Tigchelaar M., Battisti D.S., Naylor R.L., Ray D.K. (2018): Future warming increases probability of globally synchronized maize production shocks. Proceedings of the National Academy of Sciences, 115: 6644–6649.
- Turnbull C.G., Booker J.P., Leyser H.O. (2002): Micrografting techniques for testing long-distance signalling in *Arabidopsis*. The Plant Journal, 32: 255–262.
- Ueno K., Furumoto T., Umeda S., Mizutani M., Takikawa H., Batchvarova R., Sugimoto Y. (2014): Heliolactone, a non-sesquiterpene lactone germination stimulant for root parasitic weeds from sunflower. Phytochemistry, 108: 122–128.
- Ueno K., Nakashima H., Mizutani M., Takikawa H., Sugimoto Y. (2018): Bioconversion of 5-deoxystrigol stereoisomers to monohydroxylated strigolactones by plants. Journal of Pesticide Science, 43: 198–206.
- Umehara M., Hanada A., Yoshida S., Akiyama K., Arite T., Takeda-Kamiya N., Magome H., Kamiya Y., Shirasu K., Yoneyama K., Kyoizuka J., Yamaguchi S. (2008): Inhibition of shoot branching by new terpenoid plant hormones. Nature, 455: 195–200.
- Umehara M., Cao M., Akiyama K., Akatsu T., Seto Y., Hanada A., Li W., Takeda-Kamiya N., Morimoto Y., Yamaguchi S. (2015): Structural requirements of strigolactones for shoot branching inhibition in rice and *Arabidopsis*. Plant and Cell Physiology, 56: 1059–1072.
- Visentin I., Vitali M., Ferrero M., Zhang Y., Ruyter-Spira C., Novak O., Strnad M., Lovisolo C., Schubert A., Cardinale F. (2016): Low levels of strigolactones in roots as a component of the systemic signal of drought stress in tomato. The New Phytologist, 212: 954–963.
- Vogel J.T., Walter M.H., Giavalisco P., Lytovchenko A., Kohlen W., Charnikhova T., Simkin A.J., Goulet C., Strack D., Bouwmeester H.J., Fernie A.R., Klee H.J. (2010): SLCCD7 controls strigolactone biosynthesis, shoot branching and mycorrhiza-induced apocarotenoid formation in tomato. The Plant Journal, 61: 300–311.
- Wakabayashi T., Hamana M., Mori A., Akiyama R., Ueno K., Osakabe K., Osakabe Y., Suzuki H., Takikawa H., Mizutani M. (2019): Direct conversion of carlactonoic acid to orobanchol by cytochrome P450 CYP722C in strigolactone biosynthesis. Science Advances, 5: eaax9067.
- Wakabayashi T., Shida K., Kitano Y., Takikawa H., Mizutani M., Sugimoto Y. (2020): CYP722C from *Gossypium*

<https://doi.org/10.17221/88/2023-CJGPB>

- arboresum* catalyzes the conversion of carlactonoic acid to 5-deoxystrigol. *Planta*, 251: 1–6.
- Wakabayashi T., Ishiwa S., Shida K., Motonami N., Suzuki H., Takikawa H., Mizutani M., Sugimoto Y. (2021): Identification and characterization of sorgomol synthase in sorghum strigolactone biosynthesis. *Plant Physiology*, 185: 902–913.
- Wang W.N., Min Z., Wu J.R., Liu B.C., Xu X.L., Fang Y.L., Ju Y.L. (2021): Physiological and transcriptomic analysis of Cabernet Sauvignon (*Vitis vinifera* L.) reveals the alleviating effect of exogenous strigolactones on the response of grapevine to drought stress. *Plant Physiology and Biochemistry*, 167: 400–409.
- Waters M.T., Brewer P.B., Bussell J.D., Smith S.M., Beveridge C.A. (2012): The *Arabidopsis* ortholog of rice DWARF27 acts upstream of MAX1 in the control of plant development by strigolactones. *Plant Physiology*, 159: 1073–1085.
- Xie X., Yoneyama K., Kisugi T., Uchida K., Ito S., Akiyama K., Hayashi H., Yokota T., Nomura T., Yoneyama K. (2013): Confirming stereochemical structures of strigolactones produced by rice and tobacco. *Molecular Plant*, 6: 153–163.
- Xie X., Yoneyama K., Kisugi T., Nomura T., Akiyama K., Asami T., Yoneyama K. (2015): Strigolactones are transported from roots to shoots, although not through the xylem. *Journal of Pesticide Science*, 40: 214–216.
- Xie X., Mori N., Yoneyama K., Nomura T., Uchida K., Yoneyama K., Akiyama K. (2019): Lotuslactone, a non-canonical strigolactone from *Lotus japonicus*. *Phytochemistry*, 157: 200–205.
- Xu Y., Wang Y., Xu J., Lv Z., Manzoor M.A., Mao J., Zhang X., Liu R., Wang S., Whiting M.D., Jiu S., Zhang C. (2023): Strigolactone and salicylic acid regulate the expression of multiple stress-related genes and enhance the drought resistance of cherry rootstocks. *Scientia Horticulturae*, 313: 111827.
- Yokota T., Sakai H., Okuno K., Yoneyama K., Takeuchi Y. (1998): Alectrol and orobanchol, germination stimulants for *Orobancha minor*, from its host red clover. *Phytochemistry*, 49: 1967–1973.
- Yoneyama K., Brewer P.B. (2021): Strigolactones, how are they synthesized to regulate plant growth and development? *Current Opinion in Plant Biology*, 63: 102072.
- Yoneyama K., Xie X., Kusumoto D., Sekimoto H., Sugimoto Y., Takeuchi Y., Yoneyama K. (2007a): Nitrogen deficiency as well as phosphorus deficiency in sorghum promotes the production and exudation of 5-deoxystrigol, the host recognition signal for arbuscular mycorrhizal fungi and root parasites. *Planta*, 227: 125–132.
- Yoneyama K., Yoneyama K., Takeuchi Y., Sekimoto H. (2007b): Phosphorus deficiency in red clover promotes exudation of orobanchol, the signal for mycorrhizal symbionts and germination stimulant for root parasites. *Planta*, 225: 1031–1038.
- Yoneyama K., Xie X., Kim H.I., Kisugi T., Nomura T., Sekimoto H., Yokota T., Yoneyama K. (2012): How do nitrogen and phosphorus deficiencies affect strigolactone production and exudation? *Planta*, 235: 1197–1207.
- Yoneyama K., Mori N., Sato T., Yoda A., Xie X., Okamoto M., Iwanaga M., Ohnishi T., Nishiwaki H., Asami T., Yokota T., Akiyama K., Yoneyama K., Nomura T. (2018): Conversion of carlactone to carlactonoic acid is a conserved function of MAX1 homologs in strigolactone biosynthesis. *New Phytologist*, 218: 1522–1533.
- Yoneyama K., Akiyama K., Brewer P.B., Mori N., Kawano-Kawada M., Haruta S., Nishiwaki H., Yamauchi S., Xie X., Umehara M. (2020a): Hydroxyl carlactone derivatives are predominant strigolactones in *Arabidopsis*. *Plant Direct*, 4: e00219.
- Yoneyama K., Xie X., Nomura T., Yoneyama K. (2020b): Do phosphate and cytokinin interact to regulate strigolactone biosynthesis or act independently? *Frontiers in Plant Science*, 11: 438.
- Zhang H., Zhu J., Gong Z., Zhu J.-K. (2022a): Abiotic stress responses in plants. *Nature Reviews Genetics*, 23: 104–119.
- Zhang X., Hao Z., Singh V.P., Zhang Y., Feng S., Xu Y., Hao F. (2022b): Drought propagation under global warming: Characteristics, approaches, processes, and controlling factors. *Science of the Total Environment*, 838: 156021.
- Zhang X., Zhang L., Ma C., Su M., Wang J., Zheng S., Zhang T. (2022c): Exogenous strigolactones alleviate the photosynthetic inhibition and oxidative damage of cucumber seedlings under salt stress. *Scientia Horticulturae*, 297: 110962.
- Zheng Y., Wang X., Cui X., Wang K., Wang Y., He Y. (2023): Phytohormones regulate the abiotic stress: An overview of physiological, biochemical, and molecular responses in horticultural crops. *Frontiers in Plant Science*, 13: 1095363.
- Zhou J., Liu Y., Li Y., Ling W., Fan X., Feng Q., Ming R., Yang F. (2023): Combined analyses of transcriptome and metabolome reveal the mechanism of exogenous strigolactone regulating the response of elephant grass to drought stress. *Frontiers in Plant Science*, 14: 1186718.
- Zulfiqar H., Shahbaz M., Ahsan M., Nafees M., Nadeem H., Akram M., Maqsood A., Ahmar S., Kamran M., Alamri S., Siddiqui M.H., Saud S., Fahad S. (2021): Strigolactone (GR24) induced salinity tolerance in sunflower (*Helianthus annuus* L.) by ameliorating morpho-physiological and biochemical attributes under *in vitro* conditions. *Journal of Plant Growth Regulation*, 40: 2079–2091.

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