

Strigolactones in Plant Stress Adaptation: Mechanisms and Agricultural Potential

Humayra Ferdus, Mahabuba Mostafa, Md. Motaher Hossain*

Department of Plant Pathology, Gazipur Agricultural University, Gazipur, Bangladesh

*Corresponding Author: hossainmm@gau.edu.bd

Abstract: Abiotic stresses have significant negative effects on the growth, development, and productivity of crop plants, which are critical to global agricultural production and ecosystem stability. Strigolactones (SLs), a family of carotenoid-derived plant phytohormones, have been identified as playing key roles in plant development and adaptive responses to environmental stimuli. Initially recognized as signaling molecules in host-parasite interactions and as symbiotic signals for arbuscular mycorrhizal fungi, SLs are now understood to have broader physiological and molecular functions related to plant stress tolerance. SLs are crucial in regulating key developmental processes, including shoot branching, root system architecture, and flowering. Their biosynthesis is highly regulated under abiotic stress conditions, including drought, salinity, temperature extremes, and nutrient deficiency. To fully understand the mediating roles of SLs, it is necessary to investigate their biosynthetic pathways, structural diversity, and classification in plants. Given their multifunctional characteristics, SLs represent potential targets for enhancing crop performance in unfavorable environmental conditions. This review uniquely integrates recent molecular advances and practical implications of SL signaling in multi-stress environments, distinguishing it from earlier reviews.

Keywords: Phytohormones, Signaling Molecule, Structural Diversity, Biosynthetic Pathways

Received: 23-07-2025 | **Revised:** 22-08-2026 | **Accepted:** 30-07-2026 | **DOI:** 10.3844/ojbsci.2026.26.04.084

Introduction

Plants are continuously exposed to numerous environmental challenges. These biotic and abiotic stresses pose serious threats to sustainable agriculture and global ecosystems, representing among the main contributors to the reduction of crop yield [1, 2]. As a survival strategy in response to adverse conditions, plants have developed several responses based on providing a series of signals in order to metabolize and genetically reprogram [3]. Phytohormones are natural signal molecules that align with other stresses and enhance growth, as well as the development of plants, through the generation of intricate responses to such conditions in the environment [4].

Strigolactones (SLs) are a class of carotenoids that are derived from phytohormones and play a key role in signaling and in the growth and development of plants, as well as how they interact with their surroundings [5]. First of all, it was found to be a germination stimulant of root parasitic plants: Striga and Orobanche [6]. In addition to parasitism, SLs have been shown

to contribute to positive plant-fungal associations. As an example, SLs are signalling molecules that induce hyphal branching in Arbuscular Mycorrhizal Fungi (AMF) (Fig. 1) to facilitate symbiosis between these organisms, which has been found to increase nutrient and mineral uptake in more than 80 percent of terrestrial plant species and especially in soils with limited nutrients [7, 8].

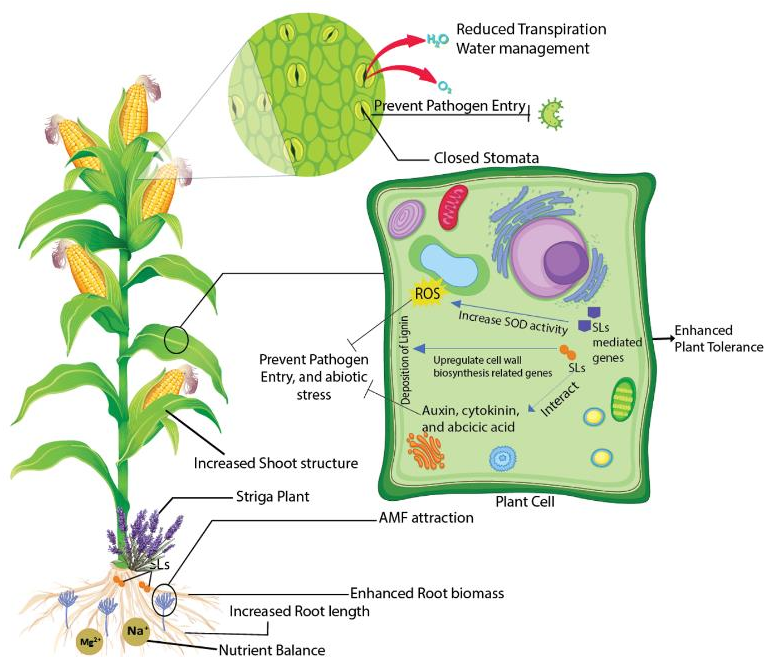


Fig. 1: Strigolactone-mediated regulation of plant growth and stress responses

Strigolactones coordinate plant development and environmental adaptation by regulating multiple physiological and cellular processes. SLs promote the establishment of beneficial symbiosis with Arbuscular Mycorrhizal Fungi (AMF) through stimulation of fungal hyphal branching, thereby enhancing nutrient acquisition, root biomass, and root system architecture under nutrient-deficient conditions. Under abiotic stress conditions, including drought, salinity, and nutrient deficiency, SL signaling enhances stress tolerance by inducing stomatal closure to reduce transpiration and water loss, limiting pathogen entry, maintaining Reactive Oxygen Species (ROS) homeostasis through activation of antioxidant enzymes such as Superoxide Dismutase (SOD), and stimulating the expression of stress-responsive and cell wall biosynthesis-related genes. Furthermore, SLs interact with other phytohormones, including Absciscic Acid (ABA), auxin, and cytokinins, to coordinate adaptive responses that improve water-use efficiency, ion and nutrient balance, root system plasticity, and overall plant resilience.

SL biosynthesis and signaling mutants such as MAX in Arabidopsis, DWARF (D) in rice, and RAMOSUS (RMS) in pea have provided valuable insights into the regulatory roles of SLs in plant development. These studies underscore SLs as multifunctional phytohormones that govern a wide range of physiological processes, including shoot branching, root architecture modulation, and the establishment of symbiotic relationships with AMF (Fig. 1) [5, 9-11]. Furthermore, SL biosynthesis is regulated by various abiotic stresses such as nutrient stress, drought, and salinity [2, 12-14]. Beyond their established roles in shaping plant architecture and mediating symbiotic relationships, increasing evidence demonstrates that SLs act as pivotal regulatory molecules that coordinate a broad range of physiological and molecular processes involved in plant adaptation to adverse environmental conditions [11, 15]. During exposure to abiotic stresses such as drought, salinity, and nutrient limitation, SLs improve water-use efficiency by facilitating stomatal closure through coordinated interactions with Absciscic Acid (ABA)-mediated signaling networks and signaling molecules, including hydrogen peroxide (H_2O_2) and Nitric Oxide (NO) [13]. Furthermore, SLs play an essential role in maintaining Reactive Oxygen Species (ROS) balance by enhancing the activity of antioxidant enzymes such as Superoxide Dismutase (SOD), Catalase (CAT), and Ascorbate

Peroxidase (APX), thereby reducing oxidative injury and protecting cellular membrane stability [15-17]. In addition to these physiological functions, SL-mediated signaling modulates the transcription of numerous stress-responsive genes involved in antioxidant defense, ion transport, and cell wall formation. Extensive interactions between SLs and other phytohormones, particularly auxin and cytokinin, further regulate root architectural plasticity, optimize nutrient uptake, and promote adaptive growth responses under challenging environmental conditions [15, 18]. Taken together, these integrated regulatory networks highlight the central role of SLs in linking plant developmental programs with abiotic stress signaling, ultimately strengthening plant resilience, sustaining growth, and enhancing productivity under fluctuating environmental conditions [11].

Although the biosynthesis pathways of Strigolactone (SL) have been extensively studied in prior literature [2, 11, 19, 20], these are briefly described here as part of the important context. However, this review summarizes existing knowledge on the structural diversity and classification of SLs, alongside their various functions in plant growth, nutrient uptake, and environmental adaptation, with a specific focus on the mechanistic foundations of SL-mediated responses to significant abiotic stresses. This study also includes a comprehensive synthesis of recent mechanistic advancements regarding SLs' role in abiotic stress tolerance, incorporating hormonal interactions with abscisic acid, auxin, and cytokinin across various and combined stress conditions, in contrast to previous reviews that primarily focused on individual stress types or model organisms [21, 22]. The article encompasses species-specific responses, current advancements in synthetic SL analogs, and their prospective uses in climate-resilient and sustainable agriculture, providing a thorough and progressive approach.

Structural Diversity and Classification of Strigolactones

SLs represent one of the groups of terpenoid lactones that are carotenoids, a special chemical structure of the molecules occupying a critical position in the biological activities of SLs. Their core structure is a tricyclic lactone (the ABC ring system) with a bridge across it to a butenolide (D ring) in the form of an enol ether. This characteristic structure is essential in the engagement of SLs in plant-microbe relationships and regulation of plant architecture [11]. The carotenoid pathway produces the ABC ring system. In particular, the A ring is a gamma-lactone coupled with the B and C rings, comprising a tricyclic structure. The B ring is a six-membered hexane ring, and the C ring is a 5-membered cyclic ether. The C ring is connected to the D ring by a methyl butenolide bond, which is an important biological activity characteristic of SLs because the D ring binds to receptor proteins in the target organisms, such as plants or fungi [23]. The structural variability of SLs is due to changes in the ABC tricyclic ring system and the butenolide D-ring. Diversity in these areas leads to hydroxylation, methylation, and glycosylation, producing other analogs of SLs, each with different levels of biological activity. Specifically, the enol ether bonding between the C and D rings is biologically important to the bioactivity of SLs because this bond is hydrolyzed in water, liberating the D ring, thought to be the active species that induces biological effects [24].

SLs display a considerable level of structural variation, which encouraged the grouping of these molecules into two categories: canonical and non-canonical SLs (Fig. 2A-B) [25]. The canonical SLs have a characteristic ABC tricyclic lactone ring system to which the D ring is connected through an enol ether bridge [11]. 23 canonical SLs have been recognized, mostly discovered by bioassay-guided purification of root exudates from plants [23, 26]. Major canonical SLs were identified as root parasitic weed germination factors as well as hyphal branching factors for Arbuscular Mycorrhizal (AM) fungi, with 5-deoxystrigol being the first to be discovered [7]. Popular canonical SLs include strigol, orobanchol, and sorgomol. Depending on the orientation of the C ring, canonical SLs are further classified into two subtypes: the strigol-type and the orobanchol-type. Strigol-type SLs have a β -oriented C ring derived from 5-deoxystrigol (5DS), and orobanchol-type SLs have an α -oriented C ring derived from 4-Deoxyorobanchol (4DO) [27, 28]. Another structural characteristic determining the variability of canonical SLs is the modification of the AB rings, including hydroxylation, methylation, acetylation, ketolation, and epoxidation [11]. The A ring may also be replaced by a benzene group, increasing the variety of SL molecules [29]. Some plant species, such as tomato, petunia, and pea, synthesize exclusively orobanchol-type SLs, while others, such as tobacco and sorghum, can synthesize both orobanchol- and strigol-type SLs [29-31].

Non-canonical SLs, however, do not have the traditional ABC tricyclic scaffold, yet still contain the more fundamental enol ether spacer and D ring [32]. Non-canonical SLs are represented by, among others, carlactone, carlactonic acid, helilactone, methylcarlactone, and avenaol. Non-canonical SLs also display a wider structural diversity, since they lack a shared core precursor or enzyme pathway. For example, the non-canonical SL precursor, methyl-carlactonate (MeCLA), derived from carlactone, is produced by the enzyme Lateral Branching Oxidoreductase (*LBO*) in *Arabidopsis* and is related to maize, sorghum, and tomato [33]. According to [34], *CYP722C* catalyzes a crucial step in the latter stages of SL production. By modifying carlactone, *CYP722C* enables the formation of bioactive SLs, which are crucial for plant responses to environmental factors, such as nutrient availability and interactions with symbiotic organisms like arbuscular mycorrhizal fungi. *CYP722C*, a

cytochrome *P450* enzyme, plays an important role in the biosynthesis of SLs by converting carlactone, a precursor in the SL biosynthetic pathway, to a bioactive SL compound. This enzyme is part of the biosynthetic network that regulates SL production in plants, influencing processes like shoot branching and root architecture. Bioactive non-canonical SLs, including *MeCLA* and hydroxymethylCLA, can undergo further transformations via *LBO* to synthesize secondary products, such as helicolactone found in sunflower, lotuslactone found in lotus, and methyl zealactone found in maize [35-37]. These molecules, such as lotuslactone, are also derived with the participation of the 2-oxoglutarate-dependent dioxygenase enzyme [38]. Moreover, synthetic SLs such as GR24 [39], Nijmegen-1 [40], Strigolactams [41], and the fluorescent *EGO-15* and *ST-23b* have been synthesized (Fig. 2C). This study emphasizes how the multivariate structural differences and functional importance of SLs in plant biology relate to their role as hormones in plant architecture and their role in the ecology of symbiosis and parasitism.

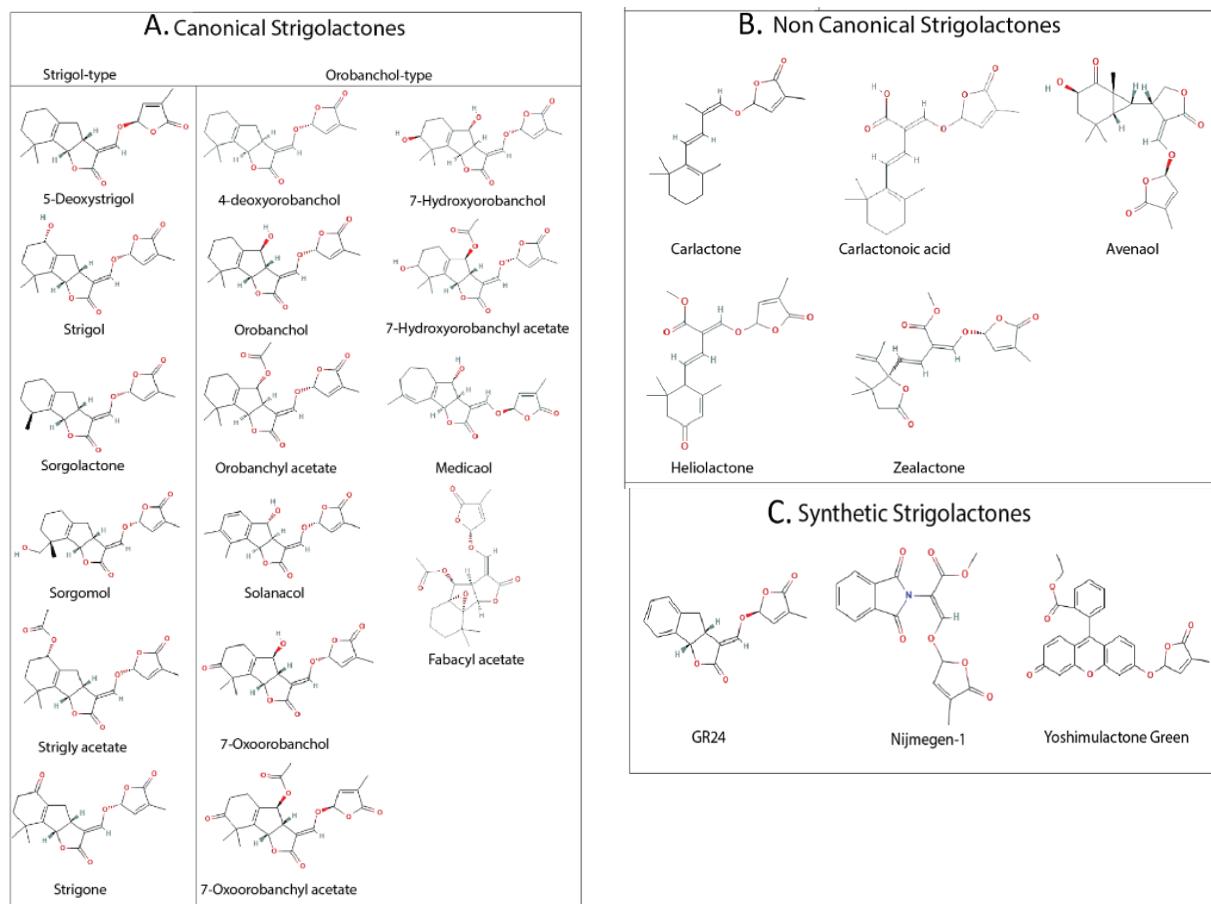


Fig. 2: Structure of different strigolactones: (A) canonical strigolactones; (B) Non-canonical strigolactones; (C) Synthetic strigolactones

All types of SLs have the bioactive butenolide D-ring with the 2'R configuration. The canonical SLs possess a conserved ABC-ring system which is connected to the D-ring by an enol ether bridge. The non-canonical SLs take a different form, as they do not usually have all three rings (ABC-rings), where the D-ring is only bound to various moieties. Synthetic SL analogs resemble SL in structure and activity, retaining (usually) the D-ring but substituting other groups, either to improve stability or specificity.

Biosynthesis and Evolutionary Conservation of Strigolactones in Plants

SLs are synthesized from carotenoids, which are generated by isoprenoid intermediates such as terpenes or isoprenes. Those carotenoids and, subsequently, also SLs fall into the category of terpenoid or isoprenoid compounds. Carotenoids can be used in various ways: the pigments help fruits, such as bananas, carrots, and tomatoes, be colored in their distinctive colors, and are important in photosynthesis, where they convert light into chemical energy and protect the photosynthetic

machinery against oxidative injury. Absciscic acid is another hormone whose precursors are carotenoids; it is a regulator in the response of plants to environmental stress. It has also been identified that biosynthesis of SLs occurs under the action of the enzymes in the chloroplasts, which take β -carotene and convert it to an intermediate called Carlactone (CL) [42].

Plastids and the cytosol are the two primary locations in plant roots where SL is synthesized [43]. SL synthesis necessitates three essential enzymes: DWARF 27 (D27) and two carotenoid cleavage dioxygenases (CCD7 and CCD8) [42]. These enzymes are conserved among species. However, they are known by different names in various plants, including MAX in *Arabidopsis*, D in rice, and RMS in peas [44]. The mechanism initiates in the plastid, where D27 converts all-trans- β -carotene into 9-cis- β -carotene (Fig. 4). CCD7 converts 9-cis- β -carotene into 9-cis- β -apo-10'-carotenal, which is then transformed by CCD8 into (Z)-(R)-carlactone, the biosynthetic precursor of SLs [42]. Alongside carlactone, the route results in 3-hydroxycarlactone (Fig. 4) [45].

The essential SL biosynthesis route is present in most plant species. However, the biochemical mechanisms that convert carotenoid-derived compounds into various strigolactones exhibit species-specific differences that remain inadequately elucidated. In *Arabidopsis*, MAX1, a member of the CYP711A family of cytochrome P450s, was identified as the initial downstream enzyme of carlactone [28]. The CYP711A enzymes are considered to be situated in the endoplasmic reticulum and catalyze the oxidation of carlactone at the C19 methyl group, resulting in the formation of carlactonic acid (CLA) [32]. The CYP711A enzymes are categorized into three subtypes: A1, which transforms CL into CLA; A2, which subsequently changes CLA into 4-Deoxyorobanchol (4-DO); and A3, which executes both transformations [32]. In *Arabidopsis*, tomato, poplar, rice, and maize, A1-type CYP711A enzymes are primarily found, whereas rice additionally possesses A2- and A3-type enzymes, facilitating the conversion of CL to orobanchol (Fig. 3). Conversely, upstream of CLA, the CYP722C family of cytochromes P450 has recently been recognized as essential for SL production. The disruption of CYP722C in species such as *Lotus japonicus* and tomato led to the complete absence of detectable SLs, highlighting its significance [38]. In vitro studies have demonstrated that CYP722C from tomato and cowpea can convert CLA into orobanchol and its stereoisomer, ent-2'-epi-orobanchol, although the latter is rarely seen in either species. This indicates that supplementary regulatory systems may be involved in several plant species [46].

The figure illustrates the core Strigolactone (SL) biosynthetic pathway, showing the conversion of all-trans- β -carotene to carlactone in the plastid via the sequential action of DWARF27 (D27), CAROTENOID CLEAVAGE DIOXYGENASE 7 (CCD7/D17/MAX3), and CCD8 (D10/MAX4). Carlactone is then transported to the cytosol, where it is oxidized by the cytochrome P450 enzyme MAX1 to form carlactonic acid. Subsequent methylation produces methyl carlactonic acid, which is further modified by LATERAL BRANCHING OXIDOREDUCTASE (LBO) to generate an as-yet-unidentified strigolactone-like bioactive compound.

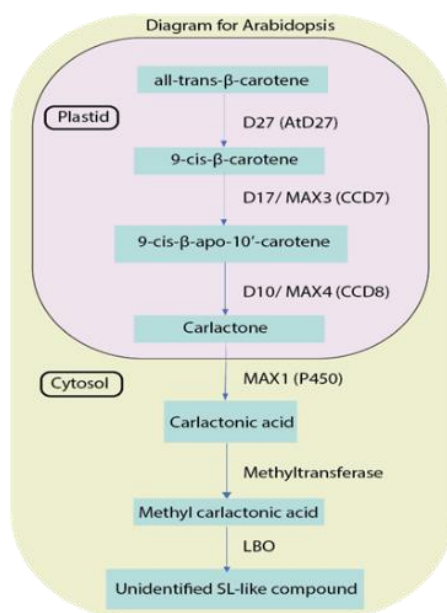


Fig. 3: Biosynthesis pathway of strigolactone in *Arabidopsis*

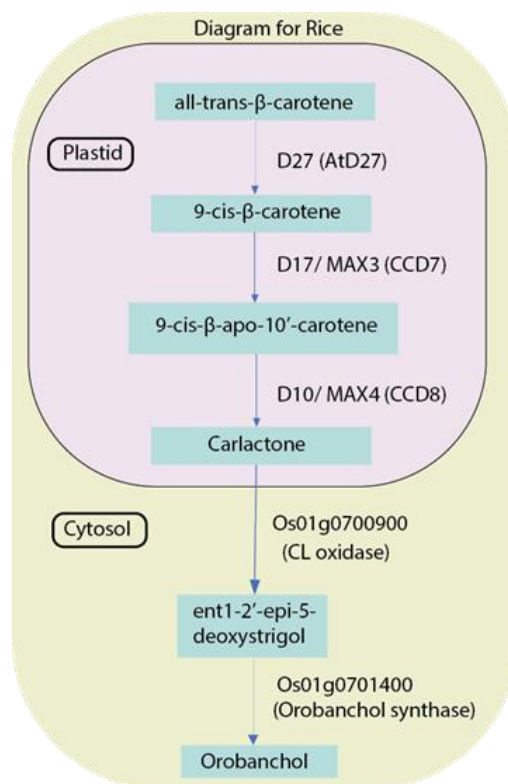


Fig. 4: Biosynthesis pathway of strigolactone in rice

The figure illustrates the strigolactone (SL) biosynthesis route in rice, initiating in the plastid with the transformation of all-trans-β-carotene into carlactone via the successive activities of *DWARF27* (*D27*), *CAROTENOID CLEAVAGE DIOXYGENASE 7* (*CCD7/D17/MAX3*), and *CCD8* (*D10/MAX4*). Carlactone is then translocated to the cytosol, where it undergoes oxidation by carlactone oxidase (*Os01g0700900*) to yield ent-1,2'-epi-5-deoxystrigol. This intermediate is subsequently transformed by orobanchol synthase (*Os01g0701400*) into orobanchol, a major bioactive strigolactone in rice.

In addition to cytochromes P450, 2-oxoglutarate-dependent dioxygenases also contribute to SL diversification. *LBO* acts downstream of methyl carlactonoate (MeCLA) in *Arabidopsis*. *LBO* reduces MeCLA to produce hydroxymethyl carlactonoate [47], and phylogenetic studies suggest that *LBO*-like proteins are present across all land plants [48]. Although detailed functional studies on *LBO* in other species remain limited, it is known that 2-oxoglutarate-dependent dioxygenases from related families play a role in noncanonical SL production in *Lotus japonicus*, where mutants lack the noncanonical SL lotuslactone [38].

Once synthesized, canonical SLs serve as substrates for decorated SL production. Experimental studies have demonstrated that 5-deoxystrigol and 4-DO can be hydroxylated into more complex SLs in plants [49]. It is suspected that cytochrome P450s, likely involved in this decoration process, are inhibited by compounds such as uniconazole-P, as shown in sorghum, where the conversion of 5-deoxystrigol to sorgomol was blocked [27]. However, the specific P450s responsible for these steps are still unidentified.

The last step of biosynthesis of SL is the distribution of (Z)-(R)-carlactone from the plastid into the cytosol and additional oxidation in the presence of enzymes, such as Cytochrome P450 monooxygenase (*MAX1*) and others, to produce numerous SLs [50]. After the synthesis, SLs are released from the cell either to be transported within the plant or leaked out of the roots [51]. It has also been shown that an ATP-dependent transporting protein is essential to active export of SLs [51].

The enzymes involved in SL biosynthesis are highly conserved in a broad diversity of plants, covering both liverworts and mosses to gymnosperms and angiosperms [15, 48]. A study about algae proposes that charophytes might possess precursors to biosynthesize SLs, but they do not possess SL-specific enzymes such as *SMXL*, in favor of the hypothesis that SL biosynthesis is characteristic of land plants and has evolved early in the evolution of plants [15, 52].

Multiple Roles of SLs in Plant Development, Nutrient Acquisition and Environmental Interaction

SLs are multifunctional plant hormones that considerably affect plant growth and response to the environment. SLs are known to govern shoot architecture in various intricate ways, involving many characteristics including the number of branches, angle, height of the plant, and the thickness of the stem. Mutants of different species lacking SL have traits such as elevated branching rates, lower branch angles, smaller stem thickness, and semi-dwarfism. They have phenotypes resulting from SL regulation of axillary bud avoidance, gravitropic responses, secondary growth, and induction of internode elongation. The increase in stem and root thickness due to proliferation of the cambium has been found to be reduced in SL mutants, as evidenced in *Arabidopsis* and pea [53]. Also, GR24, an SL analogue, induces cambium proliferation in species such as *Eucalyptus globulus* and *Arabidopsis*, indicating that a conserved role of SLs in stimulating secondary growth can be downstream of the auxin signalling pathway [53].

SLs also regulate root system architecture (Fig. 5), although their impacts within different species are different. Under normal circumstances, SLs stimulate elongation of the primary roots, especially in times of stress like lack of carbohydrates or nutrient limitation. In *Arabidopsis*, application of GR24 increased the primary root length, which did not occur in the SL mutants [54]. The same effect was observed with barley and rice, whereby GR24 did promote seminal root growth in the wild-type plant but not in SL mutants [14, 55]. This is, however, species-specific since there is no major root response to SLs in other plant species such as tomato and *Medicago truncatula* [56]. The importance of SLs in the development of primary roots provides the possibility of increasing water uptake in plants, particularly in stress-prone environments.

As far as the lateral roots are concerned, SLs usually suppress their development in normal growth conditions, whereas SL mutants exhibit an accelerated expansion in the lateral roots [57]. Interestingly, proper lateral root formation conditions provoke the necessity of SLs under phosphate-limiting conditions, and this fact correlates with the greater expression level of SLs in conditions of nutrient deprivation [54]. This suggests that SLs function as adaptive regulators, enhancing the plant's ability to cope with nutrient shortages.

SLs also influence root hair development, where GR24 has been shown to enhance root hair elongation in *Arabidopsis* [10], potentially by acting upstream of ethylene signaling. This ability to promote root hair growth, demonstrated in species like maize, could be utilized to increase nutrient uptake efficiency. Additionally, SLs negatively regulate adventitious rooting, a crucial process for clonal propagation. In SL mutants, adventitious rooting is increased, suggesting that targeting SL pathways could improve propagation success, which remains a challenge in several economically important crops [58, 59].

SLs also enhance plant tolerance to drought and osmotic stress by promoting stomatal closure, reducing water loss. SL mutants show accelerated water loss and reduced survival under water deprivation, which can be mitigated by exogenous GR24 in biosynthesis mutants [13]. The modulating mechanism of SLs on stomatal behavior is mediated by the second messengers H_2O_2 and NO , which are crucial to the process of stomatal closure in response to stress [60]. Whereas drought has a uniform upregulation of Absciscic Acid (ABA), the regulation of SL is more complex, as both upregulation and downregulation occur at the species and plant organ level [61]. Specifically, it is mentioned that roots and shoots have been reported to accumulate high concentrations of SL under osmotic stress in plants such as rice and tall fescue [62, 63].

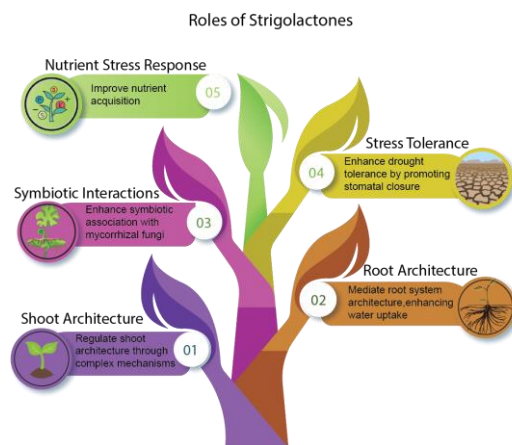


Fig. 5: Multifaceted Roles of Strigolactones in Plant Development, Nutrition, and Stress Adaptation

The symbiotic interactions also depend on SLs, and they stimulate associations of Arbuscular Mycorrhizal (AM) fungi with improved nutrient uptake and resistance of plants to stress. Because they excel as signaling molecules in the rhizosphere, SLs provoke the development of hyphal branching, germination, and even mycorrhizal colonization [7, 64]. Plants with impairments in SL or defects in SL transport exhibit low AM colonization rates, and once again this observation shows that SLs play an essential role in promoting favorable plant-mycorrhizal associations [51]. Besides the effects on mycorrhization, SLs are also involved in nodulation, which is essential in nitrogen fixation in legumes. GR24 improves nodulation in alfalfa, pea, and soybean, and this underlines the potential of SLs in boosting nutrient absorption and productivity of crops grown in nitrogen-depleted soils [65, 66].

Incorporation of SLs in plant nutrient stress response strengthens their importance in plant growth. Low phosphate is the primary nutrient treatment that causes SL accumulation in plants of a variety of species [67]. The critical changes that SLs mediate include suppression of branching, extension of root hairs, and promotion of primary root growth under nutrient limitation, rendering SLs a potential target to enhance self-sufficiency in fertilizers and crop productivity in low-fertility soils. There can be no doubt that SLs are significant modulators of plant architecture/root system development, drought tolerance, and symbionts, and hence their diverse roles in enhancing crop adaptation to climatic and environmental stresses, achieving optimum strategies in nutrient uptake. Their complex crosstalk with other hormones and environmental signals makes them crucial players in plant adaptation and offers numerous opportunities for agricultural advancements.

Strigolactones (SLs) in Plant Adaptation to Abiotic Stresses

Plants frequently encounter various adverse abiotic stresses, including nutrient deficiencies, drought, extreme temperatures (both high and low), salinity, and heavy metal toxicity. In major crops, these stresses particularly drought and high soil salinity are responsible for reducing average yields by 20% to 50% compared to their potential, and these issues are expected to intensify with ongoing climate change [68]. Global warming is contributing to the expansion of arid regions, affecting over 10% of arable land and leading to crop yield reductions exceeding 50% in Middle Eastern countries [69]. As immobile organisms, plants have developed highly sophisticated signaling networks where they perceive, respond, and adapt to challenges in the environment. In these networks, phytohormones are important players in the signaling of stress. SLs are a group of phytohormones of special importance in mediating plant response to abiotic stress. They coordinate plant structure, strengthen nutrient acquisition, and adjust stress response, thus increasing the survival rate of plants even under adverse conditions. It is worth noting that SLs are both endogenous and exogenous signaling molecules, which indicates just how crucial this plant-environment interaction is. SLs are very promising in terms of agricultural innovation given that they are involved in the process of adapting to stress. Selective modification of SL routes may possibly result in the creation of crop varieties that are more resistant to drought, salinity, and nutrient-deficient soils.

Strigolactones in the Management of Drought

Drought has become a critical threat to the whole world that interferes with various aspects of the economy, including agriculture, water resources, and economic well-being. It does not have geographical boundaries and affects arid, semi-arid, as well as temperate areas. Drought effects are not simple, as they lead to a decrease in crop yield, food insecurity, and financial loss [70]. Drought stress is the main trigger of serious changes in plant physiology, morphology, and biochemical processes, so a mitigation strategy is a crucial approach.

SLs have been identified to improve plant resilience in drought conditions. These hormones stimulate adaptive mechanisms and contribute to water savings and drought tolerance (Table 1). As an example, SLs enhance water relations, photosynthetic pigment content, and gas exchange qualities of maize seedlings and stimulate the activity of antioxidant enzymes, thus promoting the drought tolerance of plants. These are the common effects in SL-mediated responses to drought stress across different species [71]. The lateral roots in *Pennisetum purpureum* also extend their total length with exogenous SL by up to 7-fold when compared to the control group [72]. Equally, in wheat, SLs have been observed to increase yield, relative water content, membrane stability index, Catalase (CAT) and Ascorbate Peroxidase (APX) activity, proline, and sugar content too. On the other hand, SLs decrease electrolyte leakage, malondialdehyde (MDA) and hydrogen peroxide content, the rate of transpiration, and water potential [16, 73-76]. In *Vitis vinifera*, foliar application of SLs increases relative water and chlorophyll content, photosynthetic rate, and antioxidant activity, while reducing Reactive Oxygen Species (ROS), MDA, electrolyte leakage, and stomatal opening [77]. In *Dracocephalum kotschyi*, SL treatment enhances both biomass and essential oil content under drought stress [78]. In *Capsicum chinense*, SLs improve pigment concentrations, modify root architecture, and increase relative chlorophyll content as measured by SPAD values [79].

Table 1: Role of strigolactones in drought management and their effects on plants

Plant species	SL-mediated responses under drought stress	Reference
<i>Arabidopsis thaliana</i>	Restored drought tolerance in SL-deficient mutants; improved wild-type survival	[13]
<i>Brassica rapa</i>	Enhanced photosynthetic performance	[80]
<i>Capsicum chinense</i>	Increased RWC; reduced oxidative stress	[79]
<i>Dracocephalum kotschy</i>	Increased biomass and essential oil content; reduced MDA, H ₂ O ₂ , and electrolyte leakage	[78]
<i>Malus hupehensis</i>	Improved chlorophyll content, photosynthetic efficiency, and antioxidant capacity	[82]
<i>Pennisetum purpureum</i>	Improved photosynthetic efficiency and gas exchange parameters	[81]
<i>Pennisetum purpureum</i>	Increased root length, WUE, and photosynthetic traits	[72]
<i>Triticum aestivum</i>	Enhanced RWC, membrane stability, antioxidant enzyme activity, osmolytes, photosynthesis, and yield	[16, 73-76]
<i>Vitis vinifera</i>	Increased RWC, chlorophyll content, photosynthesis, and antioxidant activity; reduced ROS and stomatal aperture	[77]
<i>Zea mays</i>	Improved water relations, pigment content, and gas exchange	[71]

Exogenous SL treatment also rescues drought sensitivity in SL-deficient *Arabidopsis* mutants and enhances drought tolerance in Wild-Type (WT) plants [13]. In *Brassica rapa*, SL application under water-deficit conditions significantly increases root fresh and dry weights by 34% and 37%, respectively, and improves photosynthetic traits, though it has minimal effect on shoot biomass [80]. Foliar spraying of SLs on *Pennisetum purpureum* enhances photosynthetic efficiency, as evidenced by elevated Photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), Water Use Efficiency (WUE), and performance index (Plabs), surpassing improvements seen with rehydration alone [81]. Moreover, in apple seedlings, SLs improve chlorophyll content, photosynthetic parameters, and antioxidant capacity, while suppressing ROS and MDA accumulation under drought conditions [82].

Strigolactones in the Management of Salinity Stress

Soil salinity is a major global concern due to its detrimental impact on crop productivity. Primary salinization typically arises from natural sources such as rock weathering and seawater intrusion or spray in coastal regions, whereas secondary salinization results from anthropogenic activities like excessive fertilizer use, irrigation with poor-quality water, waterlogging, and industrial brine discharge or spillage [83]. Globally, over 50% of irrigated agricultural lands are affected by salinization, which impairs plant growth, development, and survival [84].

In recent years, phytohormones have gained attention for their role in mitigating the harmful effects of salt stress. Among them, SLs are known to enhance plant growth, stabilize cellular pH, and activate Na⁺/H⁺ antiporters under salinity stress (Table 2). A pot experiment demonstrated that seed treatment with the synthetic strigolactone analog GR24 improved Na⁺, K⁺, and Ca²⁺ uptake in both roots and shoots of wheat. Although shoot fresh and dry weight and root length were not significantly affected, GR24 treatment increased the net CO₂ assimilation rate in both wheat genotypes [85].

In bread wheat, a 10 µM application of strigolactone significantly improved several physiological and biochemical traits under salt stress, including reduced electrolyte leakage, H₂O₂, and MDA levels, while enhancing grain yield, total protein, proline, glycine betaine, and antioxidant enzyme activities (APX and POX) [96]. Similarly, rice seedlings treated with 1 µM GR24 exhibited increased resistance to salt stress, characterized by greater plant height, root length, Superoxide Dismutase (SOD) activity, and photosynthetic rate [92]. In *Salvia nemorosa*, the protective role of GR24 against NaCl toxicity was associated with increased proline accumulation and decreased antioxidant enzyme activity, contributing to enhanced salt tolerance [93]. In rapeseed, GR24 application under salinity stress significantly enhanced photosystem II quantum yield while reducing non-photochemical quenching [86]. In sunflower, 0.01 mg L⁻¹ GR24 treatment improved callus fresh weight (30.59%), dry weight (45.26%), free protein content (55.87%), and uptake of Ca²⁺ (13.04%) and K⁺ (11.76%) [89]. Moreover, pre sowing treatment of sunflower achenes with GR24 significantly increased plant biomass, shoot length, and carotenoid content, along with enhanced Na⁺, K⁺, and Ca²⁺ accumulation in roots and shoots [90], indicating its potential to alleviate salinity stress in sunflower cultivation. In maize, strigolactone application promoted plant growth, yield, root length, leaf area, photosynthetic pigments, gas exchange traits, cob diameter, grain number per cob, and K⁺ concentration in shoots and roots, while reducing Na⁺ levels in roots [97, 98]. Foliar application of SLs in cucumber under salt stress improved chlorophyll content, stomatal conductance, photosynthesis, and the efficiency of the ascorbate-glutathione cycle [88]. In chili, 20 µM

strigolactone treatment significantly enhanced plant height (21.07%), dry weight (33.60%), fruit length (19.24%), girth (35.37%), and yield (60.74%). Chlorophyll a, b, and total chlorophyll contents also increased by 18.65%, 43.52%, and 25.09%, respectively, under salinity stress, validating its efficacy [87]. Similarly, in *Trachyspermum ammi*, strigolactone application increased shoot fresh weight, enzymatic antioxidants (SOD, POD, CAT), and non-enzymatic antioxidants (total phenolics) under salt stress [95]. In *Solanum lycopersicum* seedlings, GR24 (2 μ M) enhanced antioxidant enzyme activity, proline (8%), protein content (14%), and improved photosynthetic (33%) and transpiration (34%) rates. Notably, growth parameters such as shoot length (29%), root length (21%), shoot fresh weight (31%), root fresh weight (23%), shoot dry weight (26%), and root dry weight (19%) were significantly increased. Furthermore, treated plants showed higher chlorophyll index (14%) and stomatal conductance (16%) under salinity stress [94]. Additionally, GR24 application in *Malus hupehensis* under saline-alkaline stress led to elevated levels of endogenous hormones such as acetic acid, abscisic acid, zeatin riboside, and gibberellic acid (GA_3), which may contribute to enhanced stress tolerance [91].

Table 2: Involvement of the role of Strigolactones in salinity stress management and their effects on plants

Plant species	SL-mediated responses under salinity stress	Reference
<i>Brassica napus</i>	Improved PSII efficiency; reduced non-photochemical quenching	[86]
<i>Capsicum annuum</i>	Increased chlorophyll content and yield	[87]
<i>Cucumis sativus</i>	Enhanced chlorophyll content, photosynthesis, stomatal conductance, and AsA–GSH cycle	[88]
<i>Helianthus annuus</i>	Increased callus biomass, protein, glycine betaine, and antioxidant activity	[89]
<i>Helianthus annuus</i>	Enhanced plant biomass, shoot length, carotenoid content, and ion uptake	[90]
<i>Malus hupehensis</i>	Elevated endogenous ABA, IAA, GA_3 , and zeatin riboside	[91]
<i>Oryza sativa</i>	Increased plant height, root length, SOD activity, and photosynthetic rate	[92]
<i>Salvia nemorosa</i>	Improved pigment content, photosynthesis, stomatal conductance, and essential oil production	[93]
<i>Solanum lycopersicum</i>	Enhanced antioxidant enzymes, proline, protein, photosynthesis, and growth	[94]
<i>Trachyspermum ammi</i>	Increased shoot biomass and antioxidant enzyme activity	[95]
<i>Triticum aestivum</i>	Improved CO_2 assimilation, grain yield, osmolytes, and antioxidant defense	[85, 96, 97]
<i>Zea mays</i>	Increased root length, leaf area, yield, and K^+ content; reduced Na^+ accumulation	[98]

Strigolactones in the Management of Heavy Metal Stress

Heavy Metal (HM) toxicity represents a serious abiotic stress that adversely affects plant growth and breeding, thereby posing a significant challenge to sustainable agriculture. While certain heavy metals serve as essential micronutrients involved in various physiological and biochemical processes in plants, their excessive accumulation becomes detrimental disrupting growth, metabolism, physiological functions, and accelerating senescence. HM-induced phytotoxicity, along with the excessive generation of Reactive Oxygen Species (ROS) and Methylglyoxal (MG), can lead to lipid peroxidation, protein oxidation, enzyme inhibition, DNA damage, and impairment of other critical cellular components [99].

To counteract these negative effects, plant hormones play a crucial regulatory role. Among them, SLs, a class of natural phytohormones, have shown potential in alleviating Cadmium (Cd) toxicity and mitigating the associated damage (Table 3). In tomato plants, SL application has proven effective in reducing stress caused by Cd, Arsenic (As), and Chromium (Cr). A synergistic treatment involving zinc oxide nanoparticles (ZnO NPs) and SLs enhanced plant growth, pigment content, photosynthetic efficiency, and antioxidant defense, along with increased osmolyte accumulation to help maintain water balance under stress conditions [100]. Under As stress, the combined application of SLs and Nitric Oxide (NO) significantly improved growth parameters, chlorophyll biosynthesis, and proline content, while reducing oxidative damage by inhibiting malondialdehyde (MDA) production and ROS accumulation in both roots and leaves of tomato plants [101]. To the same extent, melatonin (ML) and SLs were shown to be effective in the nature of the reduction of Cr plant uptake and related phytotoxic impacts in tomato plants that grew under Cr-polluted soils [102]. On M26 apple rootstock, $AlCl_3$ -induced stress was only partially alleviated by applying 1 μ M GR24 (synthetic SL analogue) because it restricted the movement of aluminum in the cell wall and thus enhanced its sequestration to vacuoles [103]. Also, robust plant growth occurred on Cd-contaminated soils due to the add-on effect of SLs and acidified biochar on radish [104]. The SLs enhanced membrane stability, decreased

Cd content, and optimally regulated the stomatal aperture to facilitate gas exchange in *Artemisia annua* under Cd stress [105]. Exogenous use of SLs in soybean decreased yield losses (12%), maintained chlorophyll amount (3%), and considerably reduced Cd-related oxidative pressure biomarker buildup [106]. The co-application of NO and SLs in lentils protected plants from mercury (Hg) induced oxidative stress by enhancing antioxidant enzymes and the glyoxalase system [107]. In Cd-stressed melon seedlings, SLs increased antioxidant activity, enhanced root vigor, and reduced MDA accumulation [108]. A combination of Silicon (Si) and SLs improved Cd tolerance in maize seedlings by modulating morphological, physiological, and biochemical traits, including photosynthetic pigments and osmolyte levels [109]. In barley, exogenous application of 1 μ M GR24 alleviated growth inhibition caused by 10 μ M Cd, lowered Cd accumulation in plant tissues, enhanced uptake of essential nutrients, protected chlorophyll content, sustained photosynthesis, and markedly reduced H₂O₂ and MDA levels [110].

Table 3: Function of Strigolactones in heavy metal stress management, highlighting their effects on plants

Metal stress	Plant species	SL-mediated responses	Reference
Cd	<i>Raphanus sativus</i>	Improved growth, chlorophyll content, and biomass	[104]
Cd	<i>Solanum lycopersicum</i>	Enhanced growth, pigment accumulation, and photosynthesis	[100]
As	<i>Solanum lycopersicum</i>	Improved growth, chlorophyll biosynthesis, NO and proline accumulation	[101]
Al	<i>Malus domestica</i>	Restricted Al translocation and enhanced vacuolar sequestration	[103]
Cr	<i>Solanum lycopersicum</i>	Activated antioxidant defense system	[102]
Cd	<i>Artemisia annua</i>	Maintained redox balance and PSII efficiency	[105]
Cd	<i>Glycine max</i>	Reduced yield loss and oxidative stress	[106]
Hg	<i>Lens culinaris</i>	Strengthened antioxidant and glyoxalase systems	[107]
Cd	<i>Zea mays</i>	Improved morpho-physiological traits and pigment content	[109]
Cd	<i>Cucumis melo</i>	Increased antioxidant activity and root vigor	[108]
Cd	<i>Hordeum vulgare</i>	Reduced Cd accumulation; improved nutrient uptake and photosynthesis	[110]

Strigolactones in the Management of Extreme Temperatures

Extreme temperatures pose a significant threat to global food security by adversely affecting plant growth and productivity. Plants require a specific temperature range to maintain their physiological and biochemical processes, and deviations whether short-term or prolonged can trigger stress responses [111]. These temperature extremes can interfere with plant genetics, leading to substantial growth impairments and resulting in abnormal phenotypes. SLs play a pivotal role in enhancing plant tolerance to heat stress by promoting the transcription of stress-responsive proteins and activating antioxidant enzymes [112]. Both SL biosynthesis and signaling pathways are crucial for plants to cope with temperature-related stress during preharvest and postharvest stages [44] (Table 4).

Table 4: Overview of the purpose of Strigolactones in extreme temperature management and their effects on pre-harvest and post-harvest conditions

Stress type	Plant species	SL-mediated responses	Reference
Cold	<i>Brassica rapa</i>	Enhanced antioxidant activity, protein and proline accumulation, photosynthesis	[113]
Cold	<i>Cucurbita pepo</i>	Reduced chilling injury, MDA content, and electrolyte leakage	[114]
Heat	<i>Festuca arundinacea</i>	Upregulated cell-cycle-related genes	[115]
Cold	<i>Litchi chinensis</i>	Suppressed PPO and POD activities; reduced oxidative damage	[116]
Heat	<i>Lupinus perennis</i>	Improved germination, proline accumulation, antioxidant defense	[117]
Cold	<i>Malus domestica</i>	Improved cold tolerance via growth regulation	[118]
Cold	<i>Vigna radiata</i>	Maintained PSII efficiency under chilling stress	[119]

The synthetic SL analog GR24 has been shown to counteract chilling-induced damage by preserving photosystem II efficiency and reducing the accumulation of superoxide anions and hydrogen peroxide in mung bean seedlings [119]. In apple

plants, SLs have been found to enhance cold stress resistance by supporting structural adaptations [118]. Similarly, exogenous application of GR24 at low temperatures (4°C) in rape (*Brassica rapa* L.) suppressed seedling growth inhibition and mitigated the effects of cold stress [113].

The efficacy of postharvest application of SLs in reducing cold-induced damage in litchi and zucchini has also been established. A 0.1 µM dip of GR24 (GR24- 0.1) provided delayed browning and color loss of pericarp litchi fruit in refrigerated storage. It was also used to reduce oxidative stress and avert membrane decline, as evidenced by the drop in levels of Reactive Oxygen Species (ROS), Relative Electrolyte Leakage (REL), and malondialdehyde (MDA). Moreover, GR24-0.1 also suppressed the functions of Polyphenol Oxidase (PPO) and Peroxidase (POD), and the number of total phenolic compounds, flavonoids, and anthocyanins increased [116]. On the same note, the fruits of zucchini treated with SL recorded much more resistance against chilling injury than the control ones. Treatment with postharvest SL decreased fresh weight loss and MDA content as well as ion leakage [114]. GR24 seed priming enhanced germination parameters, proline accumulation, and reduced lipid peroxidation in lupine seedlings under heat stress. It also increased the antioxidant defense enzymes as well as glyoxalase system activities [117]. In *Festuca arundinacea*, cell cycle-related genes were upregulated under the SL treatment in heat stress, which promotes root and cell number [115].

Strigolactones in the Management of Nutrient Stress

The association between soil macronutrients and the production of SLs in plant root systems has been documented across several plant species. The SLs are very important in regulating nutrient distribution and are also important in regulating plant response to nutrient starvation [120]. It is established that when Phosphorus (P) and/or Nitrogen (N) are deprived, plants greatly increase SL biosynthesis and release through their roots [26]. SLs are some of the most important modifying and regulatory agents of N and P dynamics in the rhizosphere. The complex interplay between N and P, along with SLs, has been focused on by multiple studies, especially when nutrient signaling and nutrient deficiencies are at stake [121, 122]. However, further analyses demonstrated that low levels of other nutrients, such as potassium (K), did not influence the production or exudation of 5-deoxystrigol in sorghum. Additionally, root exudates from plants grown under K deficiency failed to induce germination in parasitic seeds [123]. These findings indicate that potassium deficiency neither enhances the biosynthesis nor the exudation of 5-deoxystrigol, as determined by liquid chromatography coupled with tandem mass spectrometry (LC-MS/MS). Moreover, it does not affect the release of other SLs that could trigger the germination of *Striga hermonthica* seeds. Comparative studies in sorghum and red clover suggest that the exudation response of SLs to nutrient availability varies among plant species. One proposed explanation is that these differences arise from distinct macronutrient uptake strategies between legumes (e.g., red clover) and non-legumes (e.g., sorghum) [123, 124].

Another way through which SLs influence the nutrient-associated microorganisms is through interaction with arbuscular mycorrhizal (AM) fungi and other microbes involved in nodulation, which are essential to the processes of preventing N and P loss in plants [121, 125]. Symbiotic interactions of *Arabidopsis thaliana* and AM fungi result in a higher rate of SL biosynthesis and exudation in a low phosphate environment. On the other hand, SL levels decline at a high rate upon the availability of phosphate, which further supports the importance of SL in the regulation of phosphate starvation responses [126].

Additionally, SLs have been reported to regulate the expression of regulatory genes entailing signaling operation linked to N and P shortage [122]. They also influence the activity of NIGT/HHO transcription factors, which are integral to the phosphate deficiency signaling cascade [122]. For instance, the OsPIN1b gene responds to low N and P levels by regulating root apical meristem activity, thereby promoting seminal root elongation in rice [127]. Expression studies of SL biosynthetic genes under such conditions have shown the upregulation of DWARF27.

Interestingly, some findings suggest that Sulfur (S) deficiency is sensed in the shoot, which then triggers an increase in SL production in the roots of rice plants [128]. This supports the hypothesis that enhanced SL biosynthesis under S-deficient conditions represents a conserved stress-response mechanism aimed at facilitating AMF symbiosis, akin to responses observed under P or N deficiencies particularly since AMF can also aid in sulfur uptake [129]. However, the relationship between SLs and other essential nutrients such as potassium, magnesium, and boron remains largely unexplored. Comparative research on how SLs mediate responses to various nutrient deficiencies is still significantly underdeveloped.

Mechanism of Strigolactones in Maintaining Environmental Stress

SLs mediate plant adaptation to abiotic stresses through a coordinated network of physiological, biochemical, and molecular mechanisms rather than through stress-specific linear pathways. Increasing evidence indicates that SLs function as integrative modulators that fine-tune plant architecture, redox balance, water relations, nutrient homeostasis, and

hormonal signaling under adverse environmental conditions [11, 15, 130]. To avoid redundancy, the mechanistic basis of SL-mediated stress tolerance is synthesized below into core functional modules that collectively underpin plant responses to diverse abiotic stresses.

Root System Architecture and Resource Acquisition

Regulation of root system architecture is a central mechanism by which SLs enhance plant stress adaptation. SLs modulate primary root elongation, lateral root density, root hair development, and adventitious rooting, thereby optimizing water and nutrient acquisition under limiting conditions [24, 54, 59]. Under nutrient deprivation and drought stress, increased SL biosynthesis promotes deeper and more efficient root systems, improving access to soil resources [14, 55]. Importantly, SLs act as fine-tuners of root plasticity rather than universal growth stimulators, integrating environmental cues with auxin transport and distribution to balance growth and stress tolerance [24, 59].

Stomatal Regulation and Water Use Efficiency

SLs contribute to drought and osmotic stress tolerance primarily through regulation of stomatal behavior and transpiration. SL-deficient mutants often exhibit accelerated water loss and impaired drought survival, whereas exogenous SL application restores stomatal responsiveness and improves water-use efficiency [13]. This regulation is largely mediated through crosstalk with abscisic acid (ABA) signaling and involves secondary messengers such as hydrogen peroxide (H₂O₂) and Nitric Oxide (NO), which are essential for stress-induced stomatal closure [60, 62]. These findings indicate that SLs modulate drought responses indirectly by enhancing ABA sensitivity rather than acting as primary stomatal regulators.

Antioxidant Defense and Redox Homeostasis

Maintenance of redox balance represents one of the most consistent mechanisms underlying SL-mediated stress tolerance. SLs enhance both enzymatic (superoxide dismutase, catalase, ascorbate peroxidase, peroxidase) and non-enzymatic antioxidant systems, thereby limiting oxidative damage under drought, salinity, temperature, and heavy metal stress [16, 73, 131]. Exogenous application of the synthetic SL analog GR24 has been shown to reduce Reactive Oxygen Species (ROS) accumulation and malondialdehyde (MDA) content while preserving membrane integrity and photosynthetic efficiency [13, 17]. Although the precise molecular targets remain unresolved, evidence suggests that SLs regulate upstream ROS-producing pathways rather than directly activating antioxidant enzymes [132].

Ion Homeostasis and Osmotic Adjustment

SLs play an important role in maintaining ionic balance and osmotic stability under salinity and heavy metal stress. SL signaling has been associated with improved Na⁺/K⁺ ratios, enhanced Ca²⁺ uptake, and restricted translocation of toxic ions such as Cd²⁺ and Al³⁺ [103, 110, 133]. In addition, SLs promote osmotic adjustment by increasing the accumulation of compatible solutes, including proline, soluble sugars, and glycine betaine, which protect cellular structures and maintain turgor pressure under stress [17, 134]. These mechanisms collectively enhance cellular stability and metabolic resilience during ionic and osmotic stress.

Hormonal Crosstalk and Signal Integration

SLs operate within complex phytohormonal networks and exert their stress-adaptive functions largely through hormonal crosstalk. Interactions between SLs and auxin regulate shoot branching and root architecture by modulating auxin transport rather than biosynthesis [24, 59]. Crosstalk with ABA is particularly important during drought and salinity stress, where SLs enhance ABA sensitivity and signaling efficiency [18, 62]. SL interactions with ethylene and gibberellins further influence growth stress trade-offs, enabling plants to prioritize survival over biomass accumulation under adverse conditions [130].

Stress-Responsive Gene Expression and Photosynthetic Stability

At the molecular level, SLs influence the expression of stress-responsive genes involved in antioxidant defense, hormone signaling, and ion transport. Upregulation of SL biosynthetic genes such as CCD7, CCD8, and MAX1 under abiotic stress conditions supports a feedback mechanism reinforcing stress adaptation [15, 135]. SLs have also been linked to improved photosystem II efficiency, chlorophyll retention, and stabilization of photosynthetic machinery under heat and salinity stress, effects that are largely mediated through enhanced antioxidant protection rather than direct regulation of photosynthetic complexes [15, 86].

Indirect Stress Mitigation Via Symbiotic Interactions

Under nutrient-limited conditions, increased SL biosynthesis and exudation promote Arbuscular Mycorrhizal Fungal (AMF) colonization, enhancing phosphorus and nitrogen uptake and indirectly improving drought tolerance [7, 32, 125]. While this symbiosis confers clear stress-adaptive benefits, excessive SL release may increase susceptibility to parasitic weeds, highlighting a trade-off that must be carefully managed in agricultural applications [11].

Conclusion and Future Perspectives

SLs have emerged as phytohormones that play a variety of roles in plant growth and stress tolerance. Their importance in plant resilience is highlighted by their dynamic regulation under abiotic stress conditions, as well as their role in regulating root architecture, shoot branching, and symbiotic relationships. The potential of SLs as important modulators of plant responses to drought, salinity, nutrient deprivation, and temperature extremes has been demonstrated by recent developments in our understanding of their biosynthesis, signaling, and structural diversity.

There are encouraging opportunities to improve stress tolerance, nutrient efficiency, and overall agricultural sustainability by incorporating SL-based techniques into crop improvement initiatives. Understanding SL biosynthesis and signaling allows the possibility of creating crops with streamlined root architecture, enhanced stress tolerance levels, as well as enhanced resistance against parasitic weeds. This can be done through either genetic manipulation of SL pathways or use of synthetic analogs, which would result in enhancement of sustainable agriculture that trains efficiency in the utilization of nutrients and productivity of crops under adverse environmental factors.

Acknowledgment

The authors express sincere gratitude to the lab members for helping to conduct this study.

Funding Information

The author(s) disclosed receipt of no funding for conducting this article.

Author's Contributions

Humayra Ferdus: Drafting, research implementation, data collection, and data analysis.

Mahabuba Mostofa: Drafting, data collection, and data analysis.

Md Motaher Hossain: Conception, Research design, and draft review.

Ethics

This manuscript is original and has not been previously submitted to any other publication. The corresponding author confirms that all authors have reviewed and approved the final version of the manuscript and that there are no ethical issues to disclose.

References

1. AbuQamar, S., Moustafa, K., & Tran, L. S. (2017). Mechanisms and strategies of plant defense against *Botrytis cinerea*. *Critical Reviews in Biotechnology*, 37(2), 262–274. <https://doi.org/10.1080/07388551.2016.1271767>
2. Mostofa, M. G., Li, W., Nguyen, K. H., Fujita, M., & Tran, L. P. (2018). Strigolactones in plant adaptation to abiotic stresses: An emerging avenue of plant research. *Plant, Cell & Environment*, 41(10), 2227–2243. <https://doi.org/10.1111/pce.13364>
3. Banerjee, A., Wani, S. H., & Roychoudhury, A. (2017). Epigenetic Control of Plant Cold Responses. *Frontiers in Plant Science*, 8, 1643. <https://doi.org/10.3389/fpls.2017.01643>
4. Choudhary, S. P., Yu, J.-Q., Yamaguchi-Shinozaki, K., Shinozaki, K., & Tran, L.-S. P. (2012). Benefits of brassinosteroid crosstalk. *Trends in Plant Science*, 17(10), 594–605. <https://doi.org/10.1016/j.tplants.2012.05.012>
5. 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(7210), 195–200. <https://doi.org/10.1038/nature07272>

6. Yoneyama, K., Awad, A. A., Xie, X., Yoneyama, K., & Takeuchi, Y. (2010). Strigolactones as Germination Stimulants for Root Parasitic Plants. *Plant and Cell Physiology*, 51(7), 1095–1103. <https://doi.org/10.1093/pcp/pcq055>
7. Akiyama, K., Matsuzaki, K., & Hayashi, H. (2005). Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature*, 435(7043), 824–827. <https://doi.org/10.1038/nature03608>
8. Smith, S. E., & Read, D. J. (2010). *Mycorrhizal symbiosis*. Academic press.
9. Brewer, P. B., Koltai, H., & Beveridge, C. A. (2013). Diverse Roles of Strigolactones in Plant Development. *Molecular Plant*, 6(1), 18–28. <https://doi.org/10.1093/mp/sss130>
10. Kapulnik, Y., Delaux, P.-M., Resnick, N., Mayzlish-Gati, E., Winer, S., Bhattacharya, C., Séjalon-Delmas, N., Combier, J.-P., Bécard, G., Belausov, E., Beeckman, T., Dor, E., Hershenhorn, J., & Koltai, H. (2011). Strigolactones affect lateral root formation and root-hair elongation in *Arabidopsis*. *Planta*, 233(1), 209–216. <https://doi.org/10.1007/s00425-010-1310-y>
11. Al-Babili, S., & Bouwmeester, H. J. (2015). Strigolactones, a Novel Carotenoid-Derived Plant Hormone. *Annual Review of Plant Biology*, 66(1), 161–186. <https://doi.org/10.1146/annurev-arplant-043014-114759>
12. Du, H., Huang, F., Wu, N., Li, X., Hu, H., & Xiong, L. (2018). Integrative Regulation of Drought Escape through ABA-Dependent and -Independent Pathways in Rice. *Molecular Plant*, 11(4), 584–597. <https://doi.org/10.1016/j.molp.2018.01.004>
13. Ha, C. V., Leyva-González, 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. P. (2014). Positive regulatory role of strigolactone in plant responses to drought and salt stress. *Proceedings of the National Academy of Sciences*, 111(2), 851–856. <https://doi.org/10.1073/pnas.1322135111>
14. Sun, H., Tao, J., Liu, S., Huang, S., Chen, S., Xie, X., Yoneyama, K., Zhang, Y., & Xu, G. (2014). Strigolactones are involved in phosphate-and nitrate-deficiency-induced root development and auxin transport in rice. *Journal of Experimental Botany*, 65(22), 6735–6746. <https://doi.org/10.1093/jxb/eru029>
15. Alvi, A. F., Sehar, Z., Fatma, M., Masood, A., & Khan, N. A. (2022). Strigolactone: An Emerging Growth Regulator for Developing Resilience in Plants. *Plants*, 11(19), 2604. <https://doi.org/10.3390/plants11192604>
16. 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. <https://doi.org/10.1016/j.plaphy.2017.08.015>
17. Wang, X., Lv, S., Han, X., Guan, X., Shi, X., Kang, J., Zhang, L., Cao, B., Li, C., Zhang, W., Wang, G., & Zhang, Y. (2019). The Calcium-Dependent Protein Kinase CPK33 Mediates Strigolactone-Induced Stomatal Closure in *Arabidopsis thaliana*. *Frontiers in Plant Science*, 10, 1630. <https://doi.org/10.3389/fpls.2019.01630>
18. Abuauf, H., Haider, I., Jia, K.-P., Ablazov, A., Mi, J., Bilou, I., & Al-Babili, S. (2018). The *Arabidopsis* DWARF27 gene encodes an all-trans-9-cis-β-carotene isomerase and is induced by auxin, abscisic acid and phosphate deficiency. *Plant Science*, 277, 33–42. <https://doi.org/10.1016/j.plantsci.2018.06.024>
19. Lumba, S., Holbrook-Smith, D., & McCourt, P. (2017). The perception of strigolactones in vascular plants. *Nature Chemical Biology*, 13(6), 599–606. <https://doi.org/10.1038/nchembio.2340>
20. Waters, M. T., Gutjahr, C., Bennett, T., & Nelson, D. C. (2017). Strigolactone Signaling and Evolution. *Annual Review of Plant Biology*, 68(1), 291–322. <https://doi.org/10.1146/annurev-arplant-042916-040925>
21. Saeed, W., Naseem, S., & Ali, Z. (2017). Strigolactones Biosynthesis and Their Role in Abiotic Stress Resilience in Plants: A Critical Review. *Frontiers in Plant Science*, 8, 01487. <https://doi.org/10.3389/fpls.2017.01487>
22. Khalid, M. F., Shafqat, W., Khan, R. I., Jawaid, M. Z., Hussain, S., Saqib, M., Rizwan, M., & Ahmed, T. (2024). Unveiling the resilience mechanism: Strigolactones as master regulators of plant responses to abiotic stresses. *Plant Stress*, 12, 100490. <https://doi.org/10.1016/j.stress.2024.100490>
23. Xie, X., Yoneyama, K., & Yoneyama, K. (2010). The Strigolactone Story. *Annual Review of Phytopathology*, 48(1), 93–117. <https://doi.org/10.1146/annurev-phyto-073009-114453>
24. Waldie, T., McCulloch, H., & Leyser, O. (2014). Strigolactones and the control of plant development: lessons from shoot branching. *The Plant Journal*, 79(4), 607–622. <https://doi.org/10.1111/tpj.12488>
25. Wang, Y., & Bouwmeester, H. J. (2018). Structural diversity in the strigolactones. *Journal of Experimental Botany*, 69(9), 2219–2230. <https://doi.org/10.1093/jxb/ery091>
26. Xie, X. (2016). Structural diversity of strigolactones and their distribution in the plant kingdom. *Journal of Pesticide Science*, 41(4), 175–180. <https://doi.org/10.1584/jpestics.J16-02>
27. Motonami, N., Ueno, K., Nakashima, H., Nomura, S., Mizutani, M., Takikawa, H., & Sugimoto, Y. (2013). The bioconversion of 5-deoxystrigol to sorgomol by the sorgomol, *Sorghum bicolor* (L.) Moench. *Phytochemistry*, 93, 41–48. <https://doi.org/10.1016/j.phytochem.2013.02.017>
28. Zhang, Y., Dijk, A. D. J. van, Scaffidi, A., Flematti, G. R., Hofmann, M., Charnikhova, T., Verstappen, F., Hepworth, J., Krol, S., van der Leyser, O., Smith, S. M., Zwanenburg, B., Al-Babili, S., Ruyter-Spira, C., & Bouwmeester, H. J. (2014). Rice cytochrome P450 MAX1 homologs catalyze distinct steps in strigolactone biosynthesis. *Nature Chemical Biology*, 10(12), 1028–1033. <https://doi.org/10.1038/nchembio.1660>
29. Xie, X., Kusumoto, D., Takeuchi, Y., Yoneyama, K., Yamada, Y., & Yoneyama, K. (2007). 2'-Epi-orobanchol and Solanacol, Two Unique Strigolactones, Germination Stimulants for Root Parasitic Weeds, Produced by Tobacco. *Journal of Agricultural and Food Chemistry*, 55(20), 8067–8072. <https://doi.org/10.1021/jf0715121>
30. Mohamed, N., Charnikhova, T., Bakker, E. J., van Ast, A., Babiker, A. G., & Bouwmeester, H. J. (2016). Evaluation of field resistance to *Striga hermonthica* (Del.) Benth in *Sorghum bicolor* (L.) Moench. The relationship with strigolactones. *Pest Management Science*, 72(11), 2082–2090. <https://doi.org/10.1002/ps.4426>
31. Gobena, D., Shimels, M., Rich, P. J., Ruyter-Spira, C., Bouwmeester, H., Kanuganti, S., Mengiste, T., & Ejeta, G. (2017). Mutation in sorghum LOW GERMINATION STIMULANT 1 alters strigolactones and causes *Striga* resistance. *Proceedings of the National Academy of Sciences*, 114(17), 4471–4476. <https://doi.org/10.1073/pnas.1618965114>
32. Yoneyama, K., Xie, X., Yoneyama, K., Kisugi, T., Nomura, T., Nakatani, Y., Akiyama, K., & McElean, C. S. P. (2018). Which are the major players, canonical or non-canonical strigolactones? *Journal of Experimental Botany*, 69(9), 2231–2239. <https://doi.org/10.1093/jxb/ery090>

33. Yoneyama, K., Xie, X., Nomura, T., & Yoneyama, K. (2020). Do Phosphate and Cytokinin Interact to Regulate Strigolactone Biosynthesis or Act Independently? *Frontiers in Plant Science*, 11, 00438. <https://doi.org/10.3389/fpls.2020.00438>
34. Wakabayashi, T., Hamana, M., Mori, A., Akiyama, R., Ueno, K., Osakabe, K., Osakabe, Y., Suzuki, H., Takikawa, H., Mizutani, M., & Sugimoto, Y. (2019). Direct conversion of carlactonoic acid to orobanchol by cytochrome P450 CYP722C in strigolactone biosynthesis. *Science Advances*, 5(12), eaax9067. <https://doi.org/10.1126/sciadv.aax9067>
35. 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. <https://doi.org/10.1016/j.phytochem.2014.09.018>
36. Charnikhova, T. V., Gaus, K., Lumbroso, A., Sanders, M., Vincken, J.-P., Mesmaeker, A. D., Ruyter-Spira, C. P., Screpanti, C., & Bouwmeester, H. J. (2017). Zealactones. Novel natural strigolactones from maize. *Phytochemistry*, 137, 123–131. <https://doi.org/10.1016/j.phytochem.2017.02.010>
37. 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. <https://doi.org/10.1016/j.phytochem.2018.10.034>
38. Mori, N., Nomura, T., & Akiyama, K. (2020). Identification of two oxygenase genes involved in the respective biosynthetic pathways of canonical and non-canonical strigolactones in *Lotus japonicus*. *Planta*, 251(2), 40. <https://doi.org/10.1007/s00425-019-03332-x>
39. Besserer, A., Bécard, G., Jauneau, A., Roux, C., & Séjalon-Delmas, N. (2008). GR24, a synthetic analog of strigolactones, stimulates the mitosis and growth of the arbuscular mycorrhizal fungus *Gigaspora rosea* by boosting its energy metabolism. *Plant Physiology*, 148(1), 402–413. <https://doi.org/10.1104/pp.108.121400>
40. Nefkens, G. H. L., Thuring, J. W. J. F., Beenackers, M. F. M., & Zwanenburg, B. (1997). Synthesis of a phthaloylglycine-derived strigol analogue and its germination stimulatory activity toward seeds of the parasitic weeds *Striga hermonthica* and *Orobancha crenata*. *Journal of Agricultural and Food Chemistry*, 45(6), 2273–2277. <https://doi.org/10.1021/jf9604504>
41. Mesmaeker, A. D., Screpanti, C., Fonné-Pfister, R., Lachia, M., Lumbroso, A., & Bouwmeester, H. (2019). Design, Synthesis and Biological Evaluation of Strigolactone and Strigolactam Derivatives for Potential Crop Enhancement Applications in Modern Agriculture. *CHIMIA*, 73(7–8), 549. <https://doi.org/10.2533/chimia.2019.549>
42. 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(6074), 1348–1351. <https://doi.org/10.1126/science.1218094>
43. Mashiguchi, K., Seto, Y., & Yamaguchi, S. (2021). Strigolactone biosynthesis, transport and perception. *The Plant Journal*, 105(2), 335–350. <https://doi.org/10.1111/tpj.15059>
44. Pandey, A., Sharma, M., & Pandey, G. K. (2016). Emerging Roles of Strigolactones in Plant Responses to Stress and Development. *Frontiers in Plant Science*, 7, 00434. <https://doi.org/10.3389/fpls.2016.00434>
45. Baz, L., Mori, N., Mi, J., Jamil, M., Kountche, B. A., Guo, X., Balakrishna, A., Jia, K.-P., Vermathen, M., Akiyama, K., & Al-Babili, S. (2018). 3-Hydroxycarlactone, a Novel Product of the Strigolactone Biosynthesis Core Pathway. *Molecular Plant*, 11(10), 1312–1314. <https://doi.org/10.1016/j.molp.2018.06.008>
46. Wakabayashi, T., Hamana, M., Mori, A., Akiyama, R., Ueno, K., Osakabe, K., Osakabe, Y., Suzuki, H., Takikawa, H., Mizutani, M., & Sugimoto, Y. (2019b). Direct conversion of carlactonoic acid to orobanchol by cytochrome P450 CYP722C in strigolactone biosynthesis. *Science Advances*, 5(12), eaax9067. <https://doi.org/10.1126/sciadv.aax9067>
47. Brewer, P. B., Yoneyama, K., Filardo, F., Meyers, E., Scaffidi, A., Frickey, T., Akiyama, K., Seto, Y., Dun, E. A., Cremer, J. E., Kerr, S. C., Waters, M. T., Flematti, G. R., Mason, M. G., Weiller, G., Yamaguchi, S., Nomura, T., Smith, S. M., Yoneyama, K., & Beveridge, C. A. (2016). LATERAL BRANCHING OXIDOREDUCTASE acts in the final stages of strigolactone biosynthesis in *Arabidopsis*. *Proceedings of the National Academy of Sciences*, 113(22), 6301–6306. <https://doi.org/10.1073/pnas.1601729113>
48. Walker, C. H., Siu-Ting, K., Taylor, A., O'Connell, M. J., & Bennett, T. (2019). Strigolactone synthesis is ancestral in land plants, but canonical strigolactone signalling is a flowering plant innovation. *BMC Biology*, 17(1), 70. <https://doi.org/10.1186/s12915-019-0689-6>
49. 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(3), 198–206. <https://doi.org/10.1584/jpestics.d18-021>
50. Wang, D., Pang, Z., Yu, H., Thiombiano, B., Walmsley, A., Yu, S., Zhang, Y., Wei, T., Liang, L., Wang, J., Wen, X., Bouwmeester, H. J., Yao, R., & Xi, Z. (2022). Probing strigolactone perception mechanisms with rationally designed small-molecule agonists stimulating germination of root parasitic weeds. *Nature Communications*, 13(1), 3987. <https://doi.org/10.1038/s41467-022-31710-9>
51. 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(7389), 341–344. <https://doi.org/10.1038/nature10873>
52. Nishiyama, T., Sakayama, H., Vries, J. de, Buschmann, H., Saint-Marcoux, D., Ullrich, K. K., Haas, F. B., Vanderstraeten, L., Becker, D., Lang, D., Vosolsobé, S., Rombauts, S., Wilhelmsson, P. K. I., Janitza, P., Kern, R., Heyl, A., Rümpler, F., Villalobos, L. I. A. C., Clay, J. M., ... Rensing, A. C. (2018). The Chara Genome: Secondary Complexity and Implications for Plant Terrestrialization. *Cell*, 174(2), 448–464.e24. <https://doi.org/10.1016/j.cell.2018.06.033>
53. Agustí, J., Herold, S., Schwarz, M., Sanchez, P., Ljung, K., Dun, E. A., Brewer, P. B., Beveridge, C. A., Sieberer, T., Sehr, E. M., & Greb, T. (2011). Strigolactone signaling is required for auxin-dependent stimulation of secondary growth in plants. *Proceedings of the National Academy of Sciences*, 108(50), 20242–20247. <https://doi.org/10.1073/pnas.1111902108>
54. Ruyter-Spira, C., Kohlen, W., Charnikhova, T., Zeijl, A. van, Bezouwen, L. van, Ruijter, N. de, Cardoso, C., Lopez-Raez, J. A., Matusova, R., Bours, R., Verstappen, F., & Bouwmeester, H. (2011). Physiological Effects of the Synthetic Strigolactone Analog GR24 on Root System Architecture in *Arabidopsis*: Another Belowground Role for Strigolactones? *Plant Physiology*, 155(2), 721–734. <https://doi.org/10.1104/pp.110.166645>
55. Marzec, M., Gruszka, D., Tylec, P., & Szarejko, I. (2016). Identification and functional analysis of the HvD14 gene involved in strigolactone signaling in *Hordeum vulgare*. *Physiologia Plantarum*, 158(3), 341–355. <https://doi.org/10.1111/ppl.12460>

56. Cuyper, C. D., Fromentin, J., Yocgo, R. E., De Keyser, A., Guillotin, B., Kunert, K., Boyer, F.-D., & Goormachtig, S. (2015). From lateral root density to nodule number, the strigolactone analogue GR24 shapes the root architecture of *Medicago truncatula*. *Journal of Experimental Botany*, 66(1), 137–146. <https://doi.org/10.1093/jxb/eru404>
57. Rameau, C., Goormachtig, S., Cardinale, F., Bennett, T., & Cubas, P. (2019). Strigolactones as Plant Hormones. *Strigolactones - Biology and Applications*, 47–87. https://doi.org/10.1007/978-3-030-12153-2_2
58. Muhr, M., Prüfer, N., Paulat, M., & Teichmann, T. (2016). Knockdown of strigolactone biosynthesis genes in *Populus* affects BRANCHED1 expression and shoot architecture. *New Phytologist*, 212(3), 613–626. <https://doi.org/10.1111/nph.14076>
59. Rasmussen, A., Mason, M. G., Cuyper, C. D., Brewer, P. B., Herold, S., Agusti, J., Geelen, D., Greb, T., Goormachtig, S., Beeckman, T., & Beveridge, C. A. (2012). Strigolactones Suppress Adventitious Rooting in *Arabidopsis* and *Pea*. *Plant Physiology*, 158(4), 1976–1987. <https://doi.org/10.1104/pp.111.187104>
60. Lv, S., Zhang, Y., Li, C., Liu, Z., Yang, N., Pan, L., Wu, J., Wang, J., Yang, J., Lv, Y., Zhang, Y., Jiang, W., She, X., & Wang, G. (2018). Strigolactone-triggered stomatal closure requires hydrogen peroxide synthesis and nitric oxide production in an abscisic acid-independent manner. *New Phytologist*, 217(1), 290–304. <https://doi.org/10.1111/nph.14813>
61. Seki, M., Umezawa, T., Urano, K., & Shinozaki, K. (2007). Regulatory metabolic networks in drought stress responses. *Current Opinion in Plant Biology*, 10(3), 296–302. <https://doi.org/10.1016/j.pbi.2007.04.014>
62. Haider, I., Andreo-Jimenez, B., Bruno, M., Bimbo, A., Floková, K., Abuau, H., Ntui, V. O., Guo, X., Charnikhova, T., Al-Babili, S., Bouwmeester, H. J., & Ruyter-Spira, C. (2018). The interaction of strigolactones with abscisic acid during the drought response in rice. *Journal of Experimental Botany*, 69(9), 2403–2414. <https://doi.org/10.1093/jxb/ery089>
63. Zhuang, L., Wang, J., & Huang, B. (2017). Drought inhibition of tillering in *Festuca arundinacea* associated with axillary bud development and strigolactone signaling. *Environmental and Experimental Botany*, 142, 15–23. <https://doi.org/10.1016/j.envexpbot.2017.07.017>
64. Besserer, A., Puech-Pagès, V., Kiefer, P., Gomez-Roldan, V., Jauneau, A., Roy, S., Portais, J.-C., Roux, C., Bécard, G., & Séjalon-Delmas, N. (2006). Strigolactones Stimulate Arbuscular Mycorrhizal Fungi by Activating Mitochondria. *PLoS Biology*, 4(7), e226. <https://doi.org/10.1371/journal.pbio.0040226>
65. Foo, E., & Davies, N. W. (2011). Strigolactones promote nodulation in pea. *Planta*, 234(5), 1073–1081. <https://doi.org/10.1007/s00425-011-1516-7>
66. Rehman, N. ur, Ali, M., Ahmad, M. Z., Liang, G., & Zhao, J. (2018). Strigolactones promote rhizobia interaction and increase nodulation in soybean (*Glycine max*). *Microbial Pathogenesis*, 114, 420–430. <https://doi.org/10.1016/j.micpath.2017.11.049>
67. 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(6), 1197–1207. <https://doi.org/10.1007/s00425-011-1568-8>
68. Shrivastava, P., & Kumar, R. (2015). Soil salinity: A serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. *Saudi Journal of Biological Sciences*, 22(2), 123–131. <https://doi.org/10.1016/j.sjbs.2014.12.001>
69. Bistgani, Z. E., Barker, A. V., & Hashemi, M. (2024). Physiology of medicinal and aromatic plants under drought stress. *The Crop Journal*, 12(2), 330–339. <https://doi.org/10.1016/j.cj.2023.12.003>
70. Şimşek, Ö., Isak, M. A., Dönmez, D., Dalda Şekerci, A., İzgü, T., & Kaçar, Y. A. (2024). Advanced Biotechnological Interventions in Mitigating Drought Stress in Plants. *Plants*, 13(5), 717. <https://doi.org/10.3390/plants13050717>
71. Sattar, A., Ul-Allah, S., Ijaz, M., Sher, A., Butt, M., Abbas, T., Irfan, M., Fatima, T., Alfarraj, S., & Alharbi, S. A. (2022). Exogenous application of strigolactone alleviates drought stress in maize seedlings by regulating the physiological and antioxidants defense mechanisms. *Cereal Research Communications*, 50(2), 263–272. <https://doi.org/10.1007/s42976-021-00171-z>
72. 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(1), 578. <https://doi.org/10.1186/s12870-022-03978-y>
73. Sedaghat, M., Sarvestani, Z. T., Emam, Y., Bidgoli, A. M., & Sorooshzadeh, A. (2020). Foliar-Applied GR24 and Salicylic Acid Enhanced Wheat Drought Tolerance. *Russian Journal of Plant Physiology*, 67(4), 733–739. <https://doi.org/10.1134/s1021443720040159>
74. Sedaghat, M., Emam, Y., Mokhtassi-Bidgoli, A., Hazrati, S., Lovisolo, C., Visentin, I., Cardinale, F., & Tahmasebi-Sarvestani, Z. (2021). The Potential of the Synthetic Strigolactone Analogue GR24 for the Maintenance of Photosynthesis and Yield in Winter Wheat under Drought: Investigations on the Mechanisms of Action and Delivery Modes. *Plants*, 10(6), 1223. <https://doi.org/10.3390/plants10061223>
75. Song, M., Hu, N., Zhou, S., Xie, S., Yang, J., Ma, W., Teng, Z., Liang, W., Wang, C., Bu, M., Zhang, S., Yang, X., & He, D. (2023). Physiological and RNA-Seq analyses on exogenous strigolactones alleviating drought by improving antioxidation and photosynthesis in wheat (*Triticum aestivum* L. *Antioxidants*, 12(10), 1884. <https://doi.org/10.3390/antiox12101884>
76. Fang, B., Li, X., Wang, H., Yue, J., Shao, Y., Zhang, D., Yang, C., & Qin, F. (2021). Effects of spraying strigolactone on photosynthetic characteristics, antioxidant capacity and yield of wheat under drought condition. *Journal of Henan Agricultural Sciences*, 50(6), 37.
77. Min, Z., Li, R., Chen, L., Zhang, Y., Li, Z., Liu, M., Ju, Y., & Fang, Y. (2018). Alleviation of drought stress in grapevine by foliar-applied strigolactones. *Plant Physiology and Biochemistry*, 135, 99–110. <https://doi.org/10.1016/j.plaphy.2018.11.037>
78. Bidabadi, S. S., & Sharifi, P. (2021). Strigolactone and Methyl Jasmonate-Induced Antioxidant Defense and the Composition Alterations of Different Active Compounds in *Dracocephalum kotschy* Boiss Under Drought Stress. *Journal of Plant Growth Regulation*, 40(2), 878–889. <https://doi.org/10.1007/s00344-020-10157-6>
79. Shu, H., Xu, K., Li, X., Liu, J., Altaf, M. A., Fu, H., Lu, X., Cheng, S., & Wang, Z. (2024). Exogenous strigolactone enhanced the drought tolerance of pepper (*Capsicum chinense*) by mitigating oxidative damage and altering the antioxidant mechanism. *Plant Cell Reports*, 43(4), 106. <https://doi.org/10.1007/s00299-024-03196-w>
80. Ali, A., Shah, T., Haider, G., Awan, M. I., Gohar, M., Munsif, F., & Ahmad, I. (2023). Strigolactone-Mediated Oxidative Stress Alleviation in *Brassica rapa* Through Upregulating Antioxidant System Under Water Deficit Conditions. *Journal of Plant Growth Regulation*, 42(8), 4675–4687. <https://doi.org/10.1007/s00344-023-10925-0>

81. 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. <https://doi.org/10.3389/fpls.2023.1186718>
82. Xu, J., Li, L., Liu, Y., Yu, Y., Li, H., Wang, X., Pang, Y., Cao, H., & Sun, Q. (2023). Molecular and physiological mechanisms of strigolactones-mediated drought stress in crab apple (*Malus hupehensis* Rehd.) seedlings. *Scientia Horticulturae*, 311, 111800. <https://doi.org/10.1016/j.scienta.2022.111800>
83. Sahab, S., Suhani, I., Srivastava, V., Chauhan, P. S., Singh, R. P., & Prasad, V. (2021). Potential risk assessment of soil salinity to agroecosystem sustainability: Current status and management strategies. *Science of The Total Environment*, 764, 144164. <https://doi.org/10.1016/j.scitotenv.2020.144164>
84. Guo, J., Shan, C., Zhang, Y., Wang, X., Tian, H., Han, G., Zhang, Y., & Wang, B. (2022). Mechanisms of Salt Tolerance and Molecular Breeding of Salt-Tolerant Ornamental Plants. *Frontiers in Plant Science*, 13, 854116. <https://doi.org/10.3389/fpls.2022.854116>
85. Kausar, F., & Shahbaz, M. (2017). Influence of Strigolactone (GR24) as a Seed Treatment on Growth, Gas Exchange and Chlorophyll Fluorescence of Wheat under Saline Conditions. *International Journal of Agriculture and Biology*, 19(02), 321–327. <https://doi.org/10.17957/ijab/15.0283>
86. 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, 01671. <https://doi.org/10.3389/fpls.2017.01671>
87. Danish, S., Hareem, M., Dawar, K., Naz, T., Iqbal, M. M., Ansari, M. J., Salmen, S. H., & Datta, R. (2024). The role of strigolactone in alleviating salinity stress in chili pepper. *BMC Plant Biology*, 24(1), 209. <https://doi.org/10.1186/s12870-024-04900-4>
88. Zhang, X., Zhang, L., Ma, C., Su, M., Wang, J., Zheng, S., & Zhang, T. (2022). Exogenous strigolactones alleviate the photosynthetic inhibition and oxidative damage of cucumber seedlings under salt stress. *Scientia Horticulturae*, 297, 110962. <https://doi.org/10.1016/j.scienta.2022.110962>
89. 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(5), 2079–2091. <https://doi.org/10.1007/s00344-020-10256-4>
90. Sarwar, Y., & Shahbaz, M. (2020). Modulation in growth, photosynthetic pigments, gas exchange attributes and inorganic ions in sunflower (*Helianthus annuus* L.) by strigolactones (GR24) achene priming under saline conditions. *Pakistan Journal of Botany*, 52(1), 23–31. [https://doi.org/10.30848/pjb2020-1\(4\)](https://doi.org/10.30848/pjb2020-1(4))
91. 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(7), 770. <https://doi.org/10.3390/horticulturae9070770>
92. 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(1), 6183. <https://doi.org/10.1038/s41598-020-63352-6>
93. Sharifi, P., & Bidabadi, S. S. (2020). Strigolactone could enhance gas-exchange through augmented antioxidant defense system in *Salvia nemorosa* L. plants subjected to saline conditions stress. *Industrial Crops and Products*, 151, 112460.
94. Faisal, M., Faizan, M., Tonny, S. H., Rajput, V. D., Minkina, T., Alatar, A. A., & Pathirana, R. (2023). Strigolactone-Mediated Mitigation of Negative Effects of Salinity Stress in *Solanum lycopersicum* through Reducing the Oxidative Damage. *Sustainability*, 15(7), 5805. <https://doi.org/10.3390/su15075805>
95. Mujahid, N., Shahbaz, M., Kiran, A., & Wahid, M. A. (2023). Modulations Induced by Seed Priming of Strigolactone (GR24) in Morpho-Physiological and Biochemical Attributes of Ajwain (*Trachyspermum ammi* L.) Under Salt Stress. *Journal of Plant Growth Regulation*, 42(5), 2893–2906. <https://doi.org/10.1007/s00344-022-10755-6>
96. Mehrabi, S. S., Sabokdast, M., Bihanta, M. R., Soorni, J., & Mirmazloum, I. (2024). Strigolactone-mediated amelioration of salinity stress in bread wheat: Insights from phytochemical and ion channels related genes expression analyses. *Plant Stress*, 11, 100324. <https://doi.org/10.1016/j.stress.2023.100324>
97. Iftikhar, I., Shahbaz, M., Maqsood, M. F., Zulfiqar, U., Rana, S., Farhat, F., Farooq, H., Ahmad, K., Jamil, M., Haider, F. U., & Aghayeva, S. (2024). Resilient mechanism of strigolactone (GR24) in regulating morphological and biochemical status of maize under salt stress. *Biocatalysis and Agricultural Biotechnology*, 60, 103340. <https://doi.org/10.1016/j.bcab.2024.103340>
98. Iftikhar, I., Shahbaz, M., & Wahid, M. A. (2023). Potential Role of Foliage Applied Strigolactone (GR24) on Photosynthetic Pigments, Gas Exchange Attributes, Mineral Nutrients and Yield Components of *Zea mays* (L.) Under Saline Regimes. *Gesunde Pflanzen*, 75(3), 577–591. <https://doi.org/10.1007/s10343-022-00720-4>
99. Jorjani, S., & Karakas, F. P. (2024). Physiological and Biochemical Responses to Heavy Metals Stress in Plants. *International Journal of Secondary Metabolite*, 11(1), 169–190. <https://doi.org/10.21448/ijsm.1323494>
100. Raja, V., Singh, K., Qadir, S. U., Singh, J., & Kim, K.-H. (2024). Alleviation of cadmium-induced oxidative damage through application of zinc oxide nanoparticles and strigolactones in *Solanum lycopersicum* L. *Environmental Science: Nano*, 11(6), 2633–2654. <https://doi.org/10.1039/d3en00796k>
101. Alsubaie, Q. D., Al-Amri, A. A., Siddiqui, M. H., & Alamri, S. (2024). Strigolactone and nitric oxide collaborate synergistically to boost tomato seedling resilience to arsenic toxicity via modulating physiology and antioxidant system. *Plant Physiology and Biochemistry*, 207, 108412. <https://doi.org/10.1016/j.plaphy.2024.108412>
102. Raja, V., Qadir, S. U., Kumar, N., Alsahli, A. A., Rinklebe, J., & Ahmad, P. (2023). RETRACTED: Melatonin and strigolactone mitigate chromium toxicity through modulation of ascorbate-glutathione pathway and gene expression in tomato. *Plant Physiology and Biochemistry*, 201, 107872. <https://doi.org/10.1016/j.plaphy.2023.107872>
103. Zhang, Y., Li, J., Guo, K., Wang, T., Gao, L., Sun, Z., Ma, C., Wang, C., Tian, Y., & Zheng, X. (2024). Strigolactones alleviate $AlCl_3$ stress by vacuolar compartmentalization and cell wall blocking in apple. *The Plant Journal*, 119(1), 197–217.
104. Shahzad, K., Danish, S., Mubeen, S., Dawar, K., Fahad, S., Hasnain, Z., Ansari, M. J., & Almoallim, H. S. (2024). Minimization of heavy metal toxicity in radish (*Raphanus sativus*) by strigolactone and biochar. *Scientific Reports*, 14(1), 13616. <https://doi.org/10.1038/s41598-024-64596-2>

105. Wani, K. I., Naeem, M., Khan, M. M. A., & Aftab, T. (2023). Insights into strigolactone (GR24) mediated regulation of cadmium-induced changes and ROS metabolism in *Artemisia annua*. *Journal of Hazardous Materials*, 448, 130899. <https://doi.org/10.1016/j.jhazmat.2023.130899>
106. Shah, T., Asad, M., Khan, Z., Amjad, K., Alsahli, A. A., & D'amato, R. (2023). RETRACTED: Strigolactone decreases cadmium concentrations by regulating cadmium localization and glyoxalase defense system: Effects on nodules organic acids and soybean yield. *Chemosphere*, 335, 139028. <https://doi.org/10.1016/j.chemosphere.2023.139028>
107. Kapoor, R. T., Ahmad, A., Shakoor, A., Paray, B. A., & Ahmad, P. (2023). Nitric Oxide and Strigolactone Alleviate Mercury-Induced Oxidative Stress in *Lens culinaris* L. by Modulating Glyoxalase and Antioxidant Defense System. *Plants*, 12(9), 1894. <https://doi.org/10.3390/plants12091894>
108. 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(5), 637–649. <https://doi.org/10.1016/j.hpj.2022.07.001>
109. Sattar, A., Sher, A., Ijaz, M., Ul-Allah, S., Abbas, T., Hussain, S., Hussain, J., Khalil, H. B., Alharbi, B. M., El-Yazied, A. A., Mahmoud, S. F., & Ibrahim, M. F. M. (2023). Silicon and Strigolactone Application Alleviates the Adversities of Cadmium Toxicity in Maize by Modulating Morpho-Physiological and Antioxidants Defense Mechanisms. *Agronomy*, 13(9), 2352. <https://doi.org/10.3390/agronomy13092352>
110. 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. <https://doi.org/10.1016/j.envpol.2021.116486>
111. Bermudez, R., Stefanski, A., Montgomery, R. A., & Reich, P. B. (2021). Short- and long-term responses of photosynthetic capacity to temperature in four boreal tree species in a free-air warming and rainfall manipulation experiment. *Tree Physiology*, 41(1), 89–102. <https://doi.org/10.1093/treephys/tpaa115>
112. Chi, C., Xu, X., Wang, M., Zhang, H., Fang, P., Zhou, J., Xia, X., Shi, K., Zhou, Y., & Yu, J. (2021). Strigolactones positively regulate abscisic acid-dependent heat and cold tolerance in tomato. *Horticulture Research*, 8(1), 237. <https://doi.org/10.1038/s41438-021-00668-y>
113. Zhang, X., Zhang, L., Sun, Y., Zheng, S., Wang, J., & Zhang, T. (2020). Hydrogen peroxide is involved in strigolactone induced low temperature stress tolerance in rape seedlings (*Brassica rapa* L.). *Plant Physiology and Biochemistry*, 157, 402–415. <https://doi.org/10.1016/j.plaphy.2020.11.006>
114. Wang, L., Liu, L., Huang, A., Zhang, H., & Zheng, Y. (2024). The metabolism of amino acids, AsA and abscisic acid induced by strigolactone participates in chilling tolerance in postharvest zucchini fruit. *Frontiers in Plant Science*, 15, 1402521. <https://doi.org/10.3389/fpls.2024.1402521>
115. Hu, Q., Zhang, S., & Huang, B. (2018). Strigolactones and interaction with auxin regulating root elongation in tall fescue under different temperature regimes. *Plant Science*, 271, 34–39. <https://doi.org/10.1016/j.plantsci.2018.03.008>
116. Liu, Z., Zhang, S., Zhu, S., & Huang, D. (2024). Strigolactone Preserves Fresh-Cut Apple Quality during Shelf Life. *Agriculture*, 14(9), 1588. <https://doi.org/10.3390/agriculture14091588>
117. Omoarelojie, L. O., Kulkarni, M. G., Finnie, J. F., Pospíšil, T., Strnad, M., & Staden, J. V. (2020). Synthetic strigolactone (rac-GR24) alleviates the adverse effects of heat stress on seed germination and photosystem II function in lupine seedlings. *Plant Physiology and Biochemistry*, 155, 965–979. <https://doi.org/10.1016/j.plaphy.2020.07.043>
118. Yang, Y.-Y., Ren, Y.-R., Zheng, P.-F., Zhao, L.-L., You, C.-X., Wang, X.-F., & Hao, Y.-J. (2020). Cloning and functional identification of a strigolactone receptor gene MdD14 in apple. *Plant Cell, Tissue and Organ Culture (PCTOC)*, 140(1), 197–208. <https://doi.org/10.1007/s11240-019-01722-3>
119. Omoarelojie, L. O., Kulkarni, M. G., Finnie, J. F., & Van Staden, J. (2021). Strigolactone analog (rac-GR24) enhances chilling tolerance in mung bean seedlings. *South African Journal of Botany*, 140, 173–181. <https://doi.org/10.1016/j.sajb.2021.03.044>
120. Park, S.-Y., Yu, J.-W., Park, J.-S., Li, J., Yoo, S.-C., Lee, N.-Y., Lee, S.-K., Jeong, S.-W., Seo, H. S., Koh, H.-J., Jeon, J.-S., Park, Y.-L., & Paek, N.-C. (2007). The Senescence-Induced Staygreen Protein Regulates Chlorophyll Degradation. *The Plant Cell*, 19(5), 1649–1664. <https://doi.org/10.1105/tpc.106.044891>
121. 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(1), 76–87. <https://doi.org/10.1093/mp/sss115>
122. Marro, N., Lidoy, J., Chico, M. A., Rial, C., García, J., Varela, R. M., Macías, F. A., Pozo, M. J., Janoušková, M., & López-Ráez, J. A. (2022). Strigolactones: New players in the nitrogen–phosphorus signalling interplay. *Plant, Cell & Environment*, 45(2), 512–527. <https://doi.org/10.1111/pce.14212>
123. Yoneyama, K., Yoneyama, K., Takeuchi, Y., & Sekimoto, H. (2007a). Phosphorus deficiency in red clover promotes exudation of orobanchol, the signal for mycorrhizal symbionts and germination stimulant for root parasites. *Planta*, 225(4), 1031–1038. <https://doi.org/10.1007/s00425-006-0410-1>
124. Yoneyama, K., Xie, X., Kusumoto, D., Sekimoto, H., Sugimoto, Y., Takeuchi, Y., & Yoneyama, K. (2007b). 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(1), 125–132. <https://doi.org/10.1007/s00425-007-0600-5>
125. Marzec, M., Muszynska, A., & Gruszka, D. (2013). The Role of Strigolactones in Nutrient-Stress Responses in Plants. *International Journal of Molecular Sciences*, 14(5), 9286–9304. <https://doi.org/10.3390/ijms14059286>
126. 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(2), 974–987. <https://doi.org/10.1104/pp.110.164640>
127. Sun, H., Tao, J., Bi, Y., Hou, M., Lou, J., Chen, X., Zhang, X., Luo, L., Xie, X., Yoneyama, K., Zhao, Q., Xu, G., & Zhang, Y. (2018). OsPIN1b is Involved in Rice Seminal Root Elongation by Regulating Root Apical Meristem Activity in Response to Low Nitrogen and Phosphate. *Scientific Reports*, 8(1), 13014. <https://doi.org/10.1038/s41598-018-29784-x>

128. Shindo, M., Nagasaka, S., Kashiwada, S., Shimomura, K., & Umehara, M. (2021). Shoot has important roles in strigolactone production of rice roots under sulfur deficiency. *Plant Signaling & Behavior*, 16(4), 1880738. <https://doi.org/10.1080/15592324.2021.1880738>
129. Shindo, M., Shimomura, K., Yamaguchi, S., & Umehara, M. (2018). Upregulation of DWARF27 is associated with increased strigolactone levels under sulfur deficiency in rice. *Plant Direct*, 2(4), e00050. <https://doi.org/10.1002/pld3.50>
130. Visentin, I., Pagliarani, C., Deva, E., Caracci, A., Turečková, V., Novák, O., Lovisolo, C., Schubert, A., & Cardinale, F. (2020). A novel strigolactone-miR156 module controls stomatal behaviour during drought recovery. *Plant, Cell & Environment*, 43(7), 1613–1624. <https://doi.org/10.1111/pce.13758>
131. Sharma, V., Goel, P., Kumar, S., & Singh, A. K. (2019). An apple transcription factor, MdDREB76, confers salt and drought tolerance in transgenic tobacco by activating the expression of stress-responsive genes. *Plant Cell Reports*, 38(2), 221–241. <https://doi.org/10.1007/s00299-018-2364-8>
132. Wang, Y., Yao, R., Du, X., Guo, L., Chen, L., Xie, D., & Smith, S. M. (2021). Molecular basis for high ligand sensitivity and selectivity of strigolactone receptors in *Striga*. *Plant Physiology*, 185(4), 1411–1428. <https://doi.org/10.1093/plphys/kiaa048>
133. Xu, L., Yuan, K., Yuan, M., Meng, X., Chen, M., Wu, J., Li, J., & Qi, Y. (2020). Regulation of Rice Tillering by RNA-Directed DNA Methylation at Miniature Inverted-Repeat Transposable Elements. *Molecular Plant*, 13(6), 851–863. <https://doi.org/10.1016/j.molp.2020.02.009>
134. Bhoi, A., Yadu, B., Chandra, J., & Keshavkant, S. (2021). Contribution of strigolactone in plant physiology, hormonal interaction and abiotic stresses. *Planta*, 254(2), 28. <https://doi.org/10.1007/s00425-021-03678-1>
135. Bruno, M., Vermathen, M., Alder, A., Wüst, F., Schaub, P., Steen, R. van der, Beyer, P., Ghisla, S., & Al-Babili, S. (2017). Insights into the formation of carlactone from in-depth analysis of the CCD8-catalyzed reactions. *FEBS Letters*, 591(5), 792–800. <https://doi.org/10.1002/1873-3468.12593>