Strigolactones and karrikins: Butenolide signals shaping plant development and stress adaptation

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Abstract

Strigolactones (SLs) and karrikins (KARs) are small butenolides but originate from distinct sources and serve different roles. Strigolactones, derived from carotenoids, are synthesized endogenously and regulate shoot branching, root growth, leaf senescence and reproductive development. Karrikins, on the other hand, are exogenous smoke-derived molecules that trigger seed germination and post-fire seedling vigour. Despite this diversity of origin, SLs operate through the DWARF14 (D14) receptor, while KARRIKIN INSENSITIVE 2 (KAI2) is assumed to be the karrikin receptor, both working through many overlapping pathways. These signalling receptors work as complexes with the F-box protein MORE AXILLARY GROWTH 2 (MAX2) which assists pathway activation via repressor degradation mediated by SMXL/D53 proteins. Beyond developmental modulation, SLs have recently been uncovered as pivotal mediators in plant abiotic stress-responsive pathways. The plant thus becomes tolerant to drought and salinity, as well as nutrient limitation, through stomatal modulation by SLs, root system architecture and antioxidant defence adjustments. KAR/KAI2 signalling influences a wide range of developmental responses, including cuticle formation, antioxidant defence and seedling establishment under stress. It helps to regulate osmotic adjustment and seed germination in response to stress conditions. This crosstalk involves interactions with abscisic acid (ABA), auxin, gibberellins, cytokinins (CKs), ethylene and other redox molecules such as reactive oxygen species (ROS) and nitrous oxide (NO) to regulate adaptive responses under stress conditions. This review covers recent breakthroughs in SL and KAR biology, with a particular focus on their developmental functions, roles in stress and potential applications for engineering crop resilience.

Keywords: abiotic stress; hormonal crosstalk; karrikins; osmotic adjustment; plant development; strigolactones

Introduction

Plants face several challenges, both living (biotic) and non-living (abiotic), that impact their development, survival and productivity (1, 2). Furthermore, the ongoing global climate crisis exacerbates these challenges and threatens the future of agriculture. Plants have developed a range of survival mechanisms, including physical changes, rearrangements of internal functioning and other biochemical and molecular responses that involve considerable changes in gene expression (3). The survival mechanisms of a plant are primarily the result of the action of the phytohormones abscisic acid (ABA) and others-brassinosteroids (BRs), jasmonic acid (JA), salicylic acid (SA), ethylene and cytokinins (CKs). These hormones operate in intricate networks to maintain equilibrium between growth and stress response (4, 5). Recent advances have highlighted a unique class of plant signaling molecules known as butenolides, including strigolactones (SLs) and karrikins (KARs). Although structurally similar, SLs and KARs differ in origin and function: SLs are endogenous and involved in developmental regulation, whereas KARs are exogenous cues linked to seed germination and stress priming (6, 7). These molecules are of considerable importance in the plant response integration network.

Strigolactones were initially discovered in the 1960s and are now recognised as root exudates that induce germination in parasitic weeds, including *Striga* and *Orobanche* (8, 9). Later studies have shown that these metabolites act as phytohormones derived from carotenoids, rather than as straightforward chemical clues (8). Strigolactones regulate various aspects of plant development, including shoot branching, root architecture, leaf senescence and mutualistic relationships with arbuscular mycorrhizal fungi (10, 11). In this regard, they are the key to imparting resilience to environmental stresses. Many abiotic conditions, such as nutrient deprivation, drought, high salinity, low temperature and heat, significantly impact SL biosynthesis and signal transduction. Strigolactones can help plants become more tolerant to adverse environments by regulating stomatal behaviour, improving antioxidant responses, remodelling root systems and interacting with hormonal circuits (12).

A recently discovered type of pyrogenic phytomorphogenic compounds known as KARs has been reported as one of the key factors in seed germination, especially in ecosystems prone to wildfire regimes (13). While plants do not naturally produce these substances, they have a structure similar to SLs and utilise a

comparable signalling process (14). Karrikins are detected by a specific receptor known as KARRIKIN INSENSITIVE 2 (KAI2). This receptor interacts with the F-box protein MAX2 similarly to the SL receptor D14 and therefore, promotes the degradation of SMAX1/SMXL repressors (15). Although it was initially assumed that the role of KAR signalling is mainly playing a leading role in seed germination and seedling growth during illuminated conditions, current data has shown that it plays a vital role in plant resilience to drought and osmotic stress by maintaining cuticular integrity, suppressing the formation of reactive oxygen species (ROS) and regulating inter-hormonal communication (16–18). Despite their structural resemblance and convergence through the shared MORE AXILLARY GROWTH 2 (MAX2)-dependent signalling pathway, SLs and KARs exhibit distinct physiological functions, particularly in their roles in regulating plant development and environmental stress responses (19). Strigolactones are natural plant hormones that play crucial roles in growth and in how plants adapt to stress (20, 21).

In contrast, KARs are external signals that plants have evolved to use in improving their ability to germinate and respond to stress. Understanding both the shared functions and unique effects is essential, not only for comprehending plant biology but also for advancing agricultural practices. This review delves into the processes involved in the biosynthesis and signalling of SLs and KARs. Additionally, we evaluate the roles of these substances in promoting plant growth and their regulatory activities under abiotic stress conditions. Moreover, we examine the interaction between SLs, KARs and other plant hormones, highlighting recent advances that could help develop new strategies to improve crop performance.

Classical structure and biosynthesis of SLs and KARs

Strigolactones are a subclass of natural plant hormones that are derived from carotenoids. Carotenoids are natural pigments that produce the orange and yellow colours in carrots and other fruits. The synthesis of SLs begins with the enzymatic modification of all-trans-β-carotene by the enzyme encoded by DWARF27 (D27). As shown in Fig. 1, following this initial step, two other enzymes, carotenoid cleavage dioxygenases encoded by CCD7 and CCD8, progressively break down the carotenoid molecule (22, 23). Different plants have their own specific names for these enzymes. For instance, in *Arabidopsis*, they are referred to as *MAX3* and *MAX4*; in

peas, they are known as *RMS5* and *RMS1* and in rice, they are labelled as *HTD1/D17* and *D10* (23–25). All these processes work together to create a vital intermediate called carlactone (CL), which is essential for SLs formation (26). At this stage, the molecule undergoes further changes. A specific enzyme, a cytochrome P450 enzyme encoded by *MAX1*, transforms CL into various downstream SL molecules. For example, certain MAX1 enzymes in rice function as either CL oxidase or orobanchol synthase, producing different strigolactone varieties (27, 28). In *Arabidopsis*, another enzyme, lateral branching oxidoreductase encoded by *LATERAL BRANCHING OXIDOREDUCTASE (LBO)*, plays a role in the final steps of synthesising compounds similar to SLs (29). These sequential modifications result in a broad spectrum of SLs, which include well-known forms such as orobanchol and strigol as well as lesser-known variations. This process contributes to rich diversity in structure and a wide range of functional capabilities (29). The diversity in SL structures resulting from these biosynthetic modifications plays a critical role in modulating plant architecture, particularly shoot branching inhibition and enhances tolerance to abiotic stresses such as drought and salinity.

Karrikins originate from a different source than SLs. Rather than being produced within plants, these are tiny compounds derived from smoke, formed when plant materials such as cellulose, glucose, or other simple sugars are burned. During pyrolysis, a chain of butenolide-containing molecules is produced as shown in Fig. 2 (30). To date, scientists have characterised six different types of KARs referred to as KAR1–KAR6, with slight differences in their chemical structures. Karrikin 2 has been the most extensively studied of these variants due to its bioactivity, which is of great significance in *A. thaliana* (31). Another significant property of KARs is that they are thermostable; they do not degrade their structure at room temperature and can be readily dissolved in aqueous solutions, making it easy to experiment with them in the laboratory and deploy them in the field (32). In short, SLs are a group of phytohormones synthesised from carotenoid precursors in angiosperms and KARs are a group of smoke-volatile compounds synthesised by the pyrolysis of plant biomass. Even though they have different origins, both families of compounds share a common conserved butenolide core, which allows them to act on similar signalling cascades in plant systems.
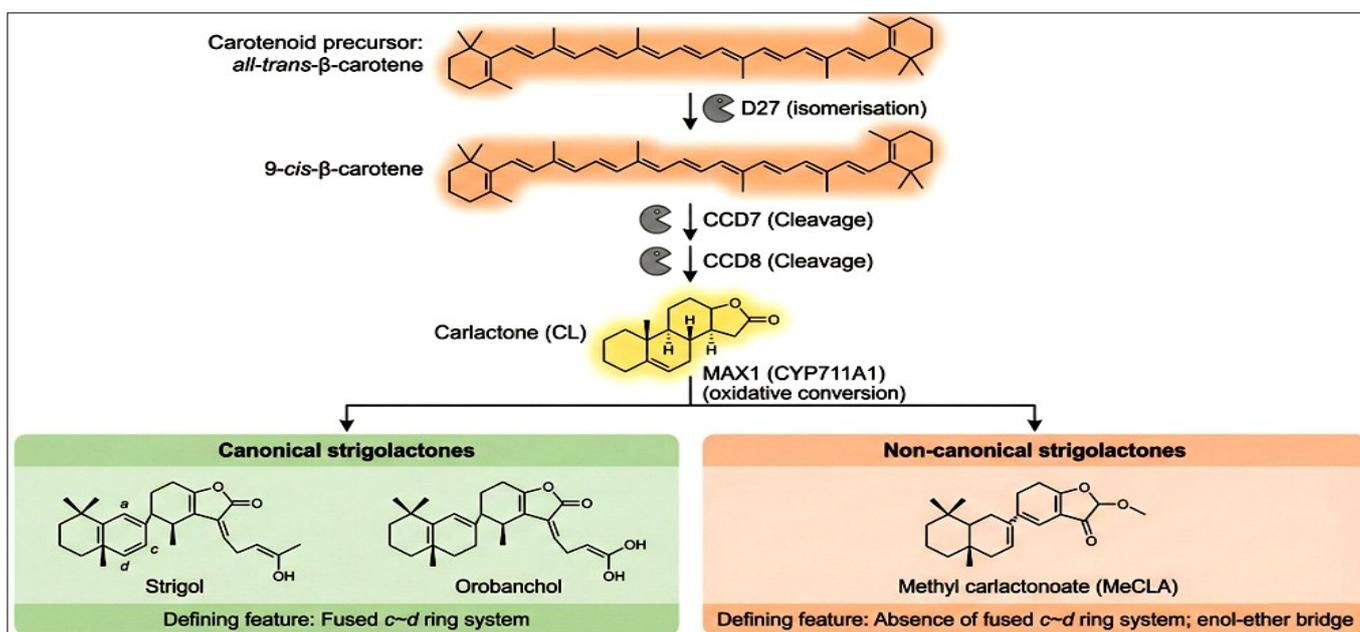

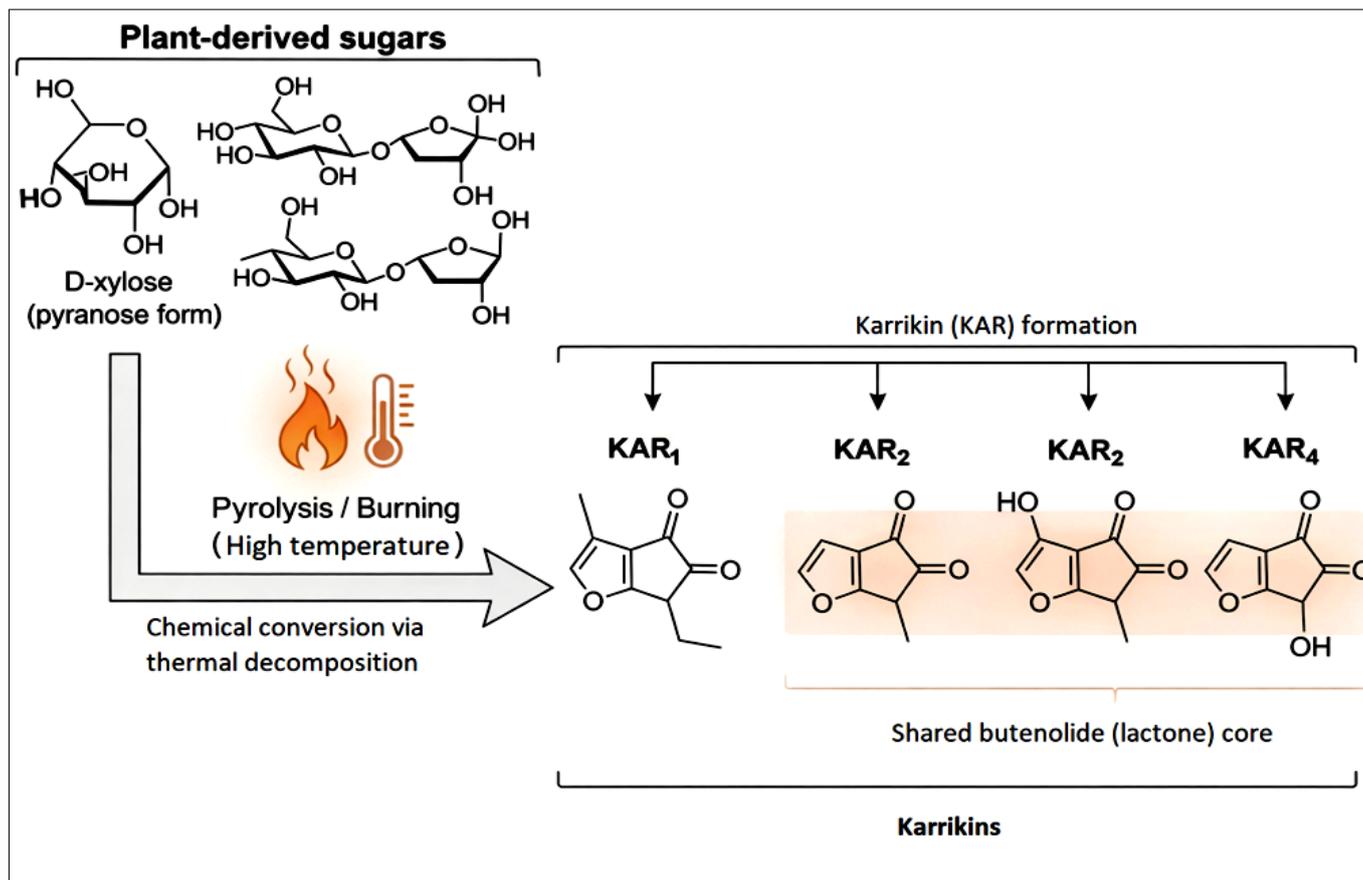**Fig. 1.** Biosynthesis and chemical diversity of SLs.

Fig. 2. Formation of KARs from sugar pyrolysis.

Signal transduction of SLs and KARs

Strigolactones and KARs, both of which are butenolides, represent the former and the latter respectively. Although they exhibit some structural similarities, they induce different responses in plants because they operate through different signalling pathways, as shown in Fig. 3. Recent advancements in structural biology have focused on how plants recognise these small molecules and how their signals are relayed. Perception of SLs involves a receptor D14, a non-canonical α/β hydrolase. Crystallographic studies reveal that when SLs bind to the D14 receptor, the ligands occupy the catalytic site in an open conformation. Following ligand association, D14 hydrolyses the SL, resulting in a D-ring-derived product that is permanently trapped within the catalytic cavity. This conformational change, which involves a transition from an open to a closed state, enables the interaction between D14 and the F-box protein encoded by MAX2, a leucine-rich repeat protein containing an F-box and the active incorporation of the complex into an SCF ubiquitin ligase complex. This activates the SCF^MAX2 complex, which then ubiquitinates a group of transcriptional repressors, including *D53* in rice or *SMXL6, SMXL7, SMXL8* in *Arabidopsis*, ultimately leading to their degradation via the 26S proteasome (33–35). Removal of these repressors triggers a cascade of downstream transcriptional events, which ultimately fine-tune phenotypic processes such as shoot branching, root growth and stress responses.

The mediator of KAR perception is a protein encoded by *KAI2,* which is mainly homologous to D14. Genetic and biochemical studies have revealed that the KAR1 directly interacts with KAI2, triggering a signalling cascade similar to the SL signalling pathway (36). In line with the actions of D14, KAI2 interacts with MAX2 to form an SCF^MAX2 ubiquitin ligase complex, which, in turn, promotes the degradation of particular transcriptional repressors, the principal one being the protein encoded by SMXL1 (37, 38). It is a postulated proteolytic event

that releases downstream transcriptional responses, which are part of KAR signalling, including physiological processes such as seed germination and light-dependent seedling development (39). Despite strong genetic evidence supporting this signal axis, the biochemical specificities of this pathway are still not fully understood and additional elements may be required to fully elucidate the mechanistic complexity of KAI2 signalling. Recent research shows that KAI2 protein stability may also be regulated through an alternative mechanism involving the Ser95 residue, independent of MAX2 and the 26S proteasome; however, the core KAR1 signalling pathway still relies on MAX2-mediated degradation via the 26S proteasome. MAX2, a shared hub linking D14 and KAI2-mediated signalling, is the central connection point between these two pathways. Although both pathways rely on this common factor, the outcomes associated with SL and KAR signalling differ significantly (40, 41). Strigolactones primarily act as natural hormones that influence plant structure and help plants adapt to stress.

In contrast, KARs are external signals derived from smoke that encourage germination and support the early growth of seedlings. This difference likely stems from specific interactions between receptors and ligands, as well as from the distinct SMXL repressors targeted in each pathway. These insights reveal both the evolutionary connection and the specialised roles of SL and KAR signalling (42). Research aimed at understanding how D14 and KAI2 uniquely recognise various butenolide ligands and how MAX2 differentiates their effects will enhance our comprehension of how plants develop and adapt to their environments.

The D14 receptor perceives SL signalling. Upon perception, D14 becomes activated and interacts with MAX2 to form an SCF^MAX2 complex. This complex initiates the ubiquitination of specific protein repressors, SMXL6, SMXL7 and SMXL8, leading to their degradation via the proteasome. De-repression of target genes induces morphological
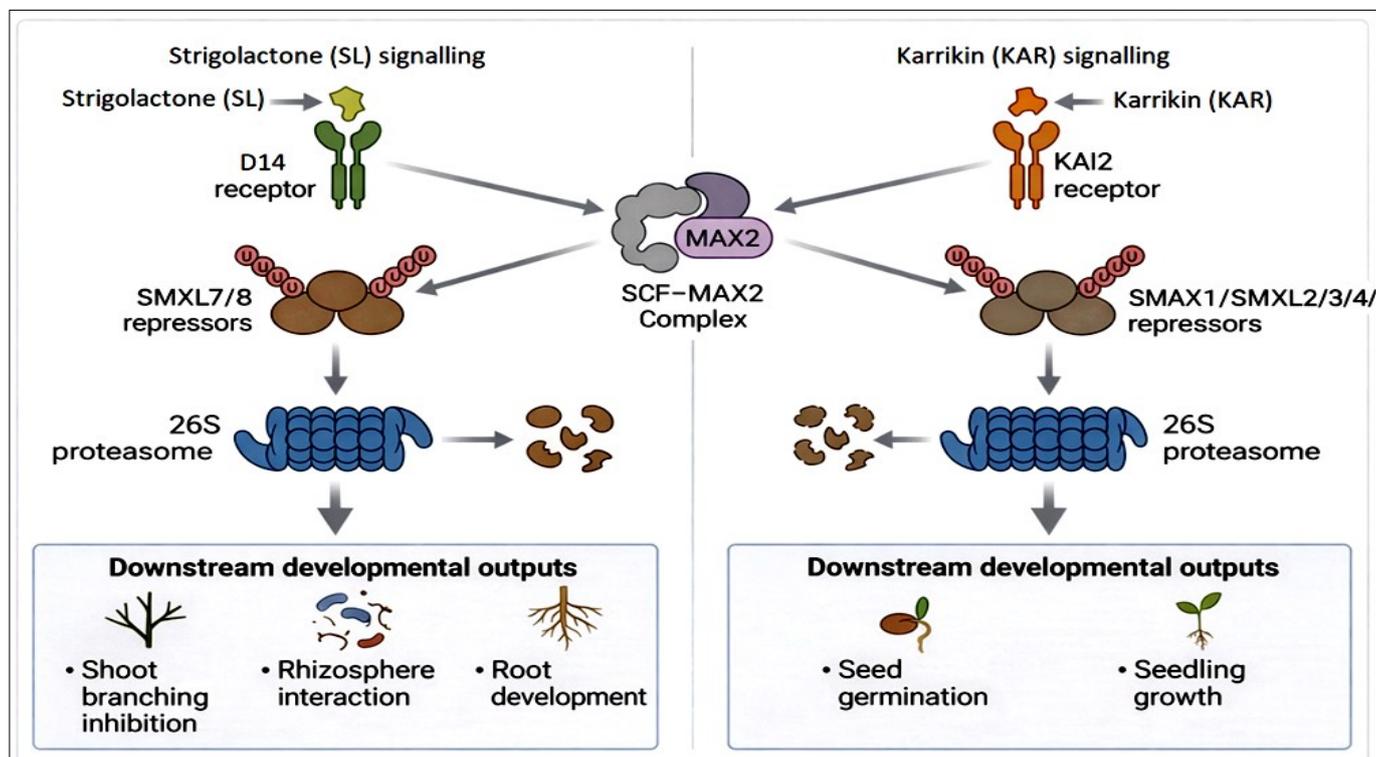
Fig. 3. Parallel signal transduction of SLs and KARs.

changes such as shoot branching and alterations in root architecture. KARRIKIN INSENSITIVE 2 perceives KAR signalling and similarly interacts with MAX2 to form an SCF^MAX2 complex. This complex also initiates the degradation of the repressor SMXL1 via ubiquitination and subsequent proteasomal processing, thereby de-repressing genes related to seed germination and seedling vigour. Although both pathways share the common component MAX2, they require different receptors and repressors, resulting in distinct downstream biological outputs in plants.

Role of SLs and KARs in plant development

Strigolactones and KARs play critical roles in various plant growth processes. Although the two molecules belong to the same group, the butenolides and share some functional similarities in their signalling cascades, the degree of functional overlap between them is minimal. The significant functions of each compound are outlined in the paragraphs below and current research from 2020 onwards is highlighted to demonstrate how these roles are being refined or expanded within contemporary conceptual perspectives on these newly described signalling agents.

Seed dormancy and germination

Karrikins were identified due to their remarkable ability to break seed dormancy in ecosystems affected by smoke, which remains their most evident physiological function. Karrikins especially KAR1 and KAR2, stimulate germination through various processes. Karrikins, particularly KAR1 and KAR2, directly promote seed germination by enhancing gibberellin (GA) biosynthesis and reducing ABA sensitivity. This effect has been well documented in *Arabidopsis* and lettuce, where KARs act through the KAI2 receptor, independent of SL biosynthesis (43). Recent reviews have highlighted that these plants may also detect an internal ligand known as KAI2, often referred to as KAI2 ligand (KL). This discovery sheds light on why KAI2 mutants exhibit defects in germination and early seedling growth, even in the absence of smoke.

In summary, the KAR/KAI2 signalling pathway enables seeds to detect favourable conditions after a fire and helps regulate their release from dormancy (44). Strigolactones also play a significant role in germination, but within a unique ecological background. Plant roots secrete natural SLs, which act as powerful stimulants that induce the germination of parasitic weed species, such as *Striga* and *Orobanche* (45). Strigolactones influence seed germination more indirectly by regulating the host plant's responses under stress conditions and affecting hormonal balance, particularly the ABA:GA ratio. Strigolactones are also exuded by plant roots to stimulate the germination of parasitic weed seeds such as *Striga* and *Orobanche* (46).

Seedling photomorphogenesis and early growth

The influence of KAR signalling on early photomorphogenic traits is quite significant. Using KARs on the seedlings induces a decrease in hypocotyl growth and a stimulation of cotyledon growth and in general, an enhancement in vigour in the presence of light. These phenotypic changes are mediated by the KAI2–MAX2–SMAX1/ SMXL1 signalling cascade, which regulates classical light-signalling networks, including transcription factors such as HY5 and PIFs (43, 47). Transcriptional profiling and genetic screens have demonstrated the pivotal role of KAI2-dependent signalling in balancing photic and hormonal cues during seedling development, thereby improving early vegetative growth and enhancing stress tolerance (48). By comparison, SLs also affect hypocotyl elongation and photomorphogenic progression, although their effects are more pronounced during later developmental stages. GR24 and similar exogenous SL analogues can restructure seedling architecture under specific conditions and simultaneously recalibrate light responsiveness through interactions with phytochrome- and cryptochrome-mediated signalling pathways (49).

Shoot branching, tillering and plant architecture

The role of SLs in regulating shoot branching is definite and well documented (50, 51). Mutants affecting SL biosynthesis and signalling, including *ccd*, *max*, *d* and *rms* mutants, among others, display

increased branching or tillering. Application of SLs or synthetic analogues has been found to inhibit bud growth in a wide range of plant species (52).

Recent studies have illuminated the mechanisms within the last five years. In particular, SL signalling regulates polar auxin transport, alters the activity and localisation of PIN transporters and affects the expression of branching regulators, including *BRC1*, *FC1* and *IPA1* (53). Recent discoveries in cereals and perennial plants suggest that SLs also contribute to determining grain size, the number of tillers and reproductive allocation; therefore, this pathway is important for enhancing crop yields (54). Moreover, recent reviews and experimental studies emphasise that the response of SLs is context-dependent and this process co-purifies with sugar signalling, trehalose-6-phosphate to control bud fate (55). It is worth noting that KARs are not typically linked to shoot branching. However, emerging evidence suggests that despite the primary role of SLs in regulating shoot branching, KAR–KAI2 signalling may indirectly influence plant architecture under specific environmental cues or developmental stages. These effects, though less characterized, could involve shared downstream targets or hormonal crosstalk, warranting further investigation into their integration within the broader butenolide signalling network (56).

Root system architecture and root hairs

Strigolactones play diverse roles in regulating different components of the root system. They mainly promote the elongation of primary roots and support root hair development, while inhibiting lateral root formation. This results in a root architecture that enables deeper rooting under specific conditions and in particular plant species (57, 58). When phosphate or nitrogen levels are low, SL production and signalling enable adaptive changes in roots that enhance the plant's ability to locate nutrients (59). Furthermore, in some species, SLs facilitate the development of hypodermal passage cells, which play a crucial role in exchanging water and nutrients (60). Recent studies employing advanced techniques and mutant analysis have revealed that the influence of SLs on roots is linked to their interactions with auxin transport and the formation of local auxin gradients.

KAI2/KAR signalling is important for root hair density and overall root structure (61). Several recent findings highlight those mutations in *KAI2* lead to changes in root hair density, causing unusual behaviours in root development, such as skewing and waving. While SLs predominantly influence primary root elongation and lateral root suppression through auxin redistribution, KAR/KAI2 signalling appears to exert a subtler but distinct impact by modifying root hair density and root directional growth (61). Comparative studies are still limited, but current data suggest that SLs have more pronounced effects on overall root architecture, whereas KAR/KAI2 influences are more evident in fine-scale traits such as epidermal cell patterning and gravitropic sensitivity (62). Moreover, KAI2-driven signalling appears to regulate how roots respond to stress caused by osmotic changes and salt levels. These understandings suggest that the perception of KAR/KAI2 ligand (KL) is crucial for determining root system organisation in both young seedlings and mature plants.

Mycorrhizal symbiosis and rhizosphere signalling

Strigolactones are important signals in the rhizosphere that initiate hyphal branching and establish symbiotic associations with arbuscular mycorrhizal fungi (63). This function is essential for ecological equilibrium and farming activities, as enhanced mycorrhization improves phosphate uptake and increases drought resistance. Variation in SL structures contributes to the specificity of these host interactions. Recent research has shown how different homologues of MAX1 activities correspond to various SL structures in rice and other crops, highlighting how biosynthetic differences shape communication in the rhizosphere. In contrast, KARs do not serve as rhizosphere signals in the same manner. However, proteins from the KAI2 family, including D14 like variants, can still affect symbiosis in specific species. Although KARs do not directly mediate rhizosphere signalling like SLs, emerging evidence suggests that receptor KAI2 can influence microbial associations indirectly by altering root architecture and exudate profiles. These changes can modify the rhizosphere environment and microbial recruitment patterns under stress conditions. For example, *KAI2/D14*-like genes have been linked to mycorrhizal interactions in rice, suggesting that KAI2-based recognition of KL-like ligands may also contribute to communication between roots and microbes (64, 65).

Leaf development, senescence and secondary growth

Strigolactones play a significant role in shaping leaves and influencing their ageing process. When SL signalling is disrupted, it often results in changes to the leaf's shape and a delay in the ageing process. On the other hand, application of SLs can speed up the movement of nutrients out of the leaves, which is linked to the processes that cause leaves to age through ethylene (66, 67).

Furthermore, SLs contribute to the growth of secondary structures by affecting the activity of vascular cambial tissues. When the *MAX2* gene is expressed in these cambial tissues, it can restore some secondary growth features typically lost in SL mutants. This connection between SLs and the overall distribution of resources in the plant is vital during stressful conditions, where the movement of nutrients becomes critical. Regarding KAR signalling, its impact on leaf morphology appears more subtle and is not evidently defined in well-characterised plant taxa. However, recent studies in smaller-scale species suggest that KAR can regulate leaf growth and influence the intensity of stress-related pigment accumulation, often in coordination with phytohormones such as CKs and BRs (68).

Reproduction, flowering and yield components

Strigolactones influence reproductive traits indirectly by affecting branching, number of tillers and resource allocation. Recent studies in cereals indicate that manipulating SL levels can shift assimilate allocation, ultimately altering grain size and quantity, making SLs an appealing target for breeding efforts (68). Research shows that slight adjustments to SL signalling can enhance plant architecture without causing significant drawbacks, primarily through field-relevant knockdowns and allele mining in crops. On the other hand, no direct correlation has been established between KARs and flowering phenology or yield. However, KARs can also positively impact reproductive success, as seedling establishment and physiological stress tolerance can be improved. Recent studies indicate that KAR treatments may reduce the toxicity of certain heavy metals and stabilise photosynthetic activity, potentially increasing yields under stressful conditions.

Integration with hormone networks and regulatory hubs

Since 2019, significant breakthroughs have been made in understanding the role of SMXL/D53 family proteins. These proteins are now recognised as key regulators that link butenolide signalling with various hormonal pathways and transcriptional processes. Remarkably, SMXL proteins, which function primarily as

transcriptional repressors, serve dual roles: they act as targets for MAX2-mediated proteolysis and as modulators of other hormone-related transcriptional complexes (69). This unique ability allows them to guide tissue-specific responses to SLs or KARs. Such versatility explains how the MAX2-dependent ubiquitination process can lead to different physiological outcomes depending on the receptor and SMXL family member involved (70).

Hormonal crosstalk and new players: ROS, nitric oxide and melatonin

The relationship between SL and KAR signalling is an interesting aspect of the complexity of these pathways, particularly in terms of their roles within larger hormonal and stress-responsive systems. Strigolactones and KARs do not act alone but instead synergise with traditional plant hormones and novel regulatory organs, including ROS, nitric oxide (NO) and melatonin, to optimise developmental pathways and adaptive responses, particularly under stressful conditions.

Crosstalk with classical phytohormones

Strigolactones play a crucial role in plant responses to auxin, particularly in regulating shoot branching and root system development. They inhibit bud growth by regulating directional auxin transport, which is linked to the action of PIN proteins.

Moreover, SLs regulate the development of root hairs and lateral root density by altering the distribution of auxin in the root tips (71). The interaction between SLs and CKs is well established: CKs tend to enhance branching, whereas SLs suppress this activity (72). This bidirectional signalling interaction plays a decisive role in shaping plant architecture. In addition, the SLs are known to interact with ABA, particularly under drought and high-salinity stress conditions. Under such adverse conditions SL signalling promotes the ability of ABA to trigger stomatal closure and augment drought tolerance. In cereals, the combined action of SL and ABA plays a crucial role in regulating tillering in response to stress and maintaining grain yield stability.

Moreover, evidence suggests a considerable interaction between SLs and other phytohormones, including ethylene and gibberellins (GAs). Such crosstalk is critical for processes such as leaf senescence, stem elongation and seed germination (73). Karrikins play a crucial role in regulating the interaction between light perception and GA signalling pathways, thereby influencing seed germination and photomorphogenesis (74). Empirical evidence has proven that KAR/KAI2 signalling regulates GA and ABA metabolism, shifting the balance towards germination under favourable conditions. In addition, KARs interact with BRs and ethylene signalling pathways during seedling development and cuticle formation; thus, smoke-derived cues are incorporated into broader hormonal interaction networks.

Reactive oxygen species (ROS)

Reactive oxygen species have traditionally been regarded as dangerous products of plant stress. However, they also play a significant role as secondary messengers in different signalling pathways (75). According to recent studies, SLs contribute to the regulation of ROS balance by increasing the activity of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) and by influencing components of the ascorbate-glutathione cycle (76). This regulation is essential for plants, as it helps them adapt to drought, salinity and heavy metal stress.

It is also noteworthy that exogenous treatment with SL analogues, including GR24, typically results in a reduction in ROS formation and a decrease in lipid peroxidation, especially under stressful conditions (77). Similarly, KARs are involved in ROS signalling pathways, particularly during seed germination and early seedling development. Application of KARs to seedlings improves ROS-scavenging capacity, thereby enhancing resistance to oxidative damage during emergence. Recent transcriptome studies have shown that NADPH oxidase- and antioxidant-related genes are regulated by KAI2-dependent signalling (78). However, the exact molecular mechanisms underlying these processes are not yet fully understood.

Nitric oxide (NO)

Nitric oxide is a highly versatile signalling molecule that plays a central role in seed germination, root growth and plant responses to environmental stress. Recent studies have shed light on intriguing interactions between NO and SLs, expanding our understanding of plant regulatory processes (79). For instance, in rice and tomato plants, application of SLs leads to increased levels of natural NO, which then fosters the development of lateral roots and enhances the plants' ability to withstand stress. When NO synthesis is inhibited, the beneficial effects of SLs are often diminished or completely lost, highlighting the dependence of SL action on NO signalling pathways (80). During seed germination, NO is recognised for its ability to counteract the inhibitory effects of ABA (81). Interestingly, KAR treatments may work, in part, through NO-related mechanisms. Early findings suggest that KAR–KAI2 signalling may initiate NO bursts, thereby activating subsequent defence and growth processes (82, 83).

Melatonin

Conventionally recognised in animal systems as an indoleamine, melatonin has recently been recognised as a versatile regulator of plant stress tolerance, circadian rhythms and reproduction (84). Recent studies have revealed interactions between SLs and melatonin. Exogenous melatonin application under drought and salinity stress enhances the biosynthesis of SLs and the transcription of SL-responsive genes in a synergistic manner (85). Both SLs and melatonin influence stomatal control, strengthen antioxidant defences and improve osmotic adjustment, thereby increasing stress resilience. There is some initial evidence to indicate that melatonin can promote seed germination and seedling growth through KAR-mediated pathways by stabilising antioxidant systems. The potential use of a melatonin-KAI2 signalling nexus is a new and promising research direction, with implications for significantly improving seed vigour and plant stress responsiveness.

Strigolactones and KARs during abiotic stress: Responses and adaptation

Dynamic regulation of SLs under stress

Table 1 summarises key mutations and genetic evidence linking strigolactones and karrikins to abiotic stress responses. Over the past decade, a growing body of literature has accumulated, indicating that SLs and KARs play crucial roles in plant adaptive responses to various environmental stresses, including drought, salinity, chilling and nutrient deficiency. It is essential to note that SLs exhibit a high level of variability and their biosynthesis and signalling are highly sensitive to stress intensity and the specific plant organs exposed to adverse conditions. For example, when tomato roots experience drought stress, SL production is reduced, potentially serving as a

warning signal that influences SL levels in above-ground tissues. On the other hand, drought leads to a notable increase in the expression of SL biosynthetic genes in shoots, such as *SlCCD7* and *SlCCD8* in tomatoes, as well as *D27* and *MAX1* gene relatives in rice. Similar signs in *Arabidopsis* suggest that foliage may upregulate the transcription of *MAX3* and *MAX4* genes in response to drought and salinity stress (86). These findings highlight distinct patterns of SL biosynthesis in root and shoot tissues under stress conditions. For instance, inhibition of SL accumulation in roots can serve as an anticipatory response to drought. However, the enhancement of SL production in shoots can trigger downstream signalling pathways that increase osmotic stress tolerance in the plant.

Strigolactones and KAR-mediated plant adaptation to abiotic stress

Drought and salinity stress

Loss-of-function mutants of the SL biosynthetic genes *MAX3* and *MAX4*, as well as the signalling receptor MAX2 are characterised by increased sensitivity to drought and salinity stress in *Arabidopsis* (87). Transcriptomic analysis of the *MAX2* loss-of-function mutants revealed that the downregulated genes were those involved in response to drought and ABA. On the other hand, photosynthetic genes (which are usually suppressed in dehydration) were upregulated. These results indicate that MAX2 is critical in coordinating both ABA-dependent and ABA-independent responses to drought (88). Supporting this conclusion, the exogenous application of SLs shows beneficial effects.

For instance, in grapevine, GR24 application to leaves improves drought resistance by enhancing stomatal closure, boosting photosynthesis and strengthening antioxidant defences (89). Similar supportive roles of SLs have been observed in tomato mutants, which exhibit increased sensitivity to osmotic stress (90). Additionally, SLs interact with ABA and redox signalling by stimulating the production of H_2O_2 and NO, thereby linking SL pathways to the regulation of stomata under drought stress.

Role of KAR/KAI2 signalling in drought responses

Plants exhibiting drought resilience have demonstrated significant involvement of the KAI2-mediated KAR signalling pathway. KARRIKIN INSENSITIVE 2 plays a vital role in enhancing cuticle formation, promoting stomatal closure, improving cell membrane stabilisation and increasing anthocyanin production in *Arabidopsis*, thereby reducing water loss and improving drought tolerance (91). All these processes contribute to minimising water loss under conditions of water scarcity. Mutants of *MAX2* and *KAI2* exhibit thinner cuticles and greater water permeability, whereas *D14* mutants, which are impaired in SL signalling, do not show these traits. This suggests that KAR/KAI2 signalling has a distinct function in helping plants adapt to drought (92). What is fascinating is that the *D14* and *KAI2* double mutants are even more susceptible to drought than the respective single mutants, indicating that the SL (D14) and the KAR (KAI2) pathways function in a complementary manner to enhance drought resistance.

Table 1. Mutations and genetic evidence linking SLs and KARs to abiotic stress responses

Plant species	Stress type	Mutants / transgenic lines	Observed effects	Summary	Interaction with other hormones	References
Arabidopsis	Drought, salinity	*max2-3, max2-4, max3-11, max3-12, max4-7, max4-8*	Loss of SL signalling increases stress sensitivity	SL-deficient mutants wilt rapidly and show poor tolerance to drought and salinity	ABA, cytokinins	(7, 86, 87)
Arabidopsis	Drought	*max2-1, max2-2, max1, max3, max4*	Impaired stomatal regulation under drought	Lack of *MAX2* disrupts stomatal closure, causing excessive water loss	ABA	(36, 48)
Tomato (*Solanum lycopersicum*)	Drought	*SlCCD7*-silenced lines	Reduced SL levels weaken root–shoot drought signalling	Roots fail to transmit drought signals efficiently to shoots	ABA	(4, 79, 89)
Tomato + AMF symbiosis	Drought	Wild type	AMF colonisation enhances SL biosynthesis	Mycorrhizal association increases SLs and improves drought tolerance	ABA	(9, 63, 85, 88)
Rapeseed (*Brassica napus*)	Salinity	Wild type + GR24	Exogenous SL analogue alleviates salt stress	GR24 application improves shoot and root growth under salinity	–	(18, 37)
Rice (*Oryza sativa*)	Drought	*d10, d17, d27, d3* mutants; *D27* overexpression	Altered SL biosynthesis affects ABA accumulation	SL-deficient rice is drought-sensitive, while enhanced *D27* improves tolerance	ABA	(23, 61, 87)
Rice (*Oryza sativa*)	P and N deficiency	*d3, d10, d27* mutants	Reduced auxin transport limits root elongation	Mutants fail to develop deep roots under nutrient limitation	Auxin	(44, 45)
Rice (*Oryza sativa*)	N and P deficiency	*d3, d10, d53* mutants	SLs promote NO-mediated seminal root elongation	SL signalling supports root growth under nutrient stress	Nitric oxide	(57, 79)
Arabidopsis, *Pisum sativum*	Chilling (dark stress)	*max2-1, max3-9, max4-1*; pea *rms5-3, rms4-1, rms3-1*	SL pathway enhances chilling tolerance	SL-deficient plants show reduced photosynthesis and biomass under cold stress	–	(34)
Arabidopsis	Drought	*kai2-2, kai2-4, d14-2*	KAR signalling improves drought resistance	*KAI2*-mediated signalling promotes cuticle formation and water conservation	ABA	(90)
Arabidopsis	Osmotic stress, salinity	*kai2-2, d14-1, max2-1, max2-7*	KAR–KAI2–MAX2 pathway mitigates osmotic damage	KAR signalling balances germination control and stress protection	GA, ABA	(35, 60)

Seed germination and osmotic stress

KARRIKIN INSENSITIVE 2 is crucial for seed germination, especially under harsh environmental conditions. Seeds of *KAI2* mutants show increased sensitivity to osmotic stress, high salt levels and elevated temperatures. On the other hand, signalling triggered by KAR facilitates germination when conditions are ideal, but KAR signalling inhibits germination during stressful periods. This helps maintain the seeds' viability even when the environment is harsh (93). This process, known as the "germination checkpoint," enables seeds to adapt to various environmental stresses in a flexible manner.

Nutrient deficiency stress (N and P)

Deficiency of nutrients, particularly phosphate (P) and nitrogen (N), represents a major challenge that explains the importance of SLs. SL -deficient mutants of rice, such as *d10*, *d27* and *d3*, generally have reduced seminal root development, although lateral root proliferation can compensate under P or N shortage. Notably, the application of GR24 in an exogenous way can restore the development of seminal root development in these mutants (94). Similarly, mutations in the *MAX4* and *MAX2* genes in *Arabidopsis* result in phenotypes characterised by reduced root hair length in plants subjected to phosphate limitation; this effect can be reversed by applying GR24 (95). These observations reveal that SLs can orchestrate root system development under nutrient stress to promote deeper rooting and enhance a plant's capacity for efficient nutrient acquisition.

Chilling stress

The strigolactone (SL) signalling pathway plays a significant role in the acclimation of plants to low temperatures. In *Pisum sativum*, lines lacking SLs, especially *RMS5* and *RMS3* mutants, exhibit reduced biomass accumulation and lower photosynthetic activity following chilling stress (96). Similar effects have been observed in *Arabidopsis* mutants such as *MAX3*, *MAX4* and MAX2, all of which struggled with carbon uptake under cold stress (97). Interestingly, when GR24, a synthetic SL, was applied externally, it helped to reduce the adverse effects of chilling by limiting leaf growth. This suggests that SL signalling modulates growth as a defence mechanism against cold stress.

Secondary metabolite regulation (flavonoids and anthocyanins)

Strigolactone and KAR signalling pathways regulate the production of secondary metabolites that help plants cope with stress. In *Arabidopsis*, when faced with dehydration stress, flavonoid production is hindered in the *MAX2* and *KAI2* mutants, leading to lower levels of anthocyanins. However, when treated with GR24, flavonol accumulation is restored, but this response depends on MAX2 (98). Considering flavonoids and anthocyanins as effective antioxidants that protect plant tissues against oxidative stress, these results highlight the role of SL and KAR signalling pathways in enhancing metabolic resistance to abiotic stress in plants.

Future prospects and applications in agriculture

Recent studies have increasingly shown the central functions of SLs and KARs in plant development and stress tolerance. This knowledge has led to the generation of synthetic analogues of SLs, including GR24 and KAR derivatives, which can be used as foliar sprays or seed-priming agents. These interventions are expected to enhance seedling establishment and improve crop drought tolerance, salinity tolerance and nutrient acquisition efficiency. The application of CRISPR/Cas-based genome editing to target genes that regulate SL/

KAR biosynthesis and signalling is a promising strategy to improve plant architecture, enhance stress tolerance and improve resource use without causing harmful impacts on yield in breeding programmes. Another promising direction is to clarify the endogenous interactions between SLs and KARs, which are mediated by phytohormones such as ABA, auxin and melatonin. Crops can be supported in dealing with several stressors simultaneously by designing combinatorial treatments that combine these hormonal signals.

Conclusion

Strigolactones and KARs are central butenolide-derived signals that shape plant development and modulate stress responses. Genetic and physiological studies show that these signals regulate root architecture, axillary branching, stomatal behaviour, reproductive traits and symbiotic interactions. These effects largely arise through crosstalk with classical hormones such as ABA and auxin. Both pathways intersect with redox networks involving ROS, nitric oxide and melatonin, linking development to stress adaptation under drought, salinity and nutrient limitation. Key gaps remain in our understanding of KAR signalling in crops, particularly with respect to tissue-specific expression, crop-relevant downstream targets and the reprogramming of SL–KAR crosstalk under combined stresses. Addressing these questions will require comparative transcriptomic, metabolomic and targeted genetic studies across diverse crops to identify tractable regulatory nodes for improving stress resilience without compromising yield.

Authors' contributions

UK designed the review structure, collected literature and drafted the manuscript. PM and MC contributed to literature collection and critical revision. SG and SN assisted with data organization and formatting. VBK and ISR provided guidance, critical comments and supervised the overall work. All authors read and approved the final manuscript.

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During the preparation of this work, the authors used Grammarly to improve language clarity, structure and editing. After using this tool, the authors carefully reviewed and edited the content and take full responsibility for the final version.

References

1. Omoarelojie LO, Kulkarni MG, Finnie JF, Van Staden J. Strigolactones and their crosstalk with other phytohormones. Ann Bot. 2019;124(5):749–60. https://doi.org/10.1093/aob/mcz100

2. Yao R, Ming Z, Yan L, Li S, Wang F, Ma S, et al. DWARF14 is a non-canonical hormone receptor for strigolactone. Nature. 2016;536 (7617):469–73. https://doi.org/10.1038/nature19073

3. Pandey P, Irulappan V, Bagavathiannan MV, Senthil-Kumar M. Impact of combined abiotic and biotic stresses on plant growth and

avenues for crop improvement by exploiting physio-morphological traits. Front Plant Sci. 2017;8:537. https://doi.org/10.3389/fpls.2017.00537

4. Chi C, Xu X, Wang M, Zhang H, Fang P, Zhou J, et al. Strigolactones positively regulate abscisic acid-dependent heat and cold tolerance in tomato. Hortic Res. 2021;8(1):237. https://doi.org/10.1038/s41438-021-00668-y

5. Khalid MF, Shafqat W, Khan RI, Jawaid MZ, Hussain S, Saqib M, et al. Unveiling the resilience mechanism: Strigolactones as master regulators of plant responses to abiotic stresses. Plant Stress. 2024;12:100490. https://doi.org/10.1016/j.stress.2024.100490

6. Xie X, Yoneyama K, Yoneyama K. The strigolactone story. Annu Rev Phytopathol. 2010;48:93–117. https://doi.org/10.1146/annurev-phyto-073009-114453

7. Germain S, Ligerot Y, Dun EA, Pillot P, Ross JJ, Beveridge CA, et al. Strigolactones stimulate internode elongation independently of gibberellins. Plant Physiol. 2013;163(2):1012–22. https://doi.org/10.1104/pp.113.220541

8. Xie F, Liu Y, Zhao Q, Liu X, Wang C, Wang Q, et al. Exogenous application of melatonin and strigolactone improves drought resistance in fodder soybean seedlings. Agronomy. 2024;14(8):1803. https://doi.org/10.3390/agronomy14081803

9. Soliman S, Wang Y, Han Z, Pervaiz T, El-Kereamy A. Strigolactones in plants and their interaction with the ecological microbiome in response to abiotic stress. Plants. 2022;11(24):3499. https://doi.org/10.3390/plants11243499

10. Dvořák P, Krasylenko Y, Zeiner A, Šamaj J, Takáč T. Signaling toward reactive oxygen species-scavenging enzymes in plants. Front Plant Sci. 2021;11:618835. https://doi.org/10.3389/fpls.2020.618835

11. Machin DC, Hamon-Josse M, Bennett T. Fellowship of the rings: A saga of strigolactones and other small signals. New Phytol. 2019;225(2):621–36. https://doi.org/10.1111/nph.16095

12. Kępczyński J, Kępczyńska E. Plant-derived smoke and karrikin 1 in seed priming and seed biotechnology. Plants. 2023;12(12):2378. https://doi.org/10.3390/plants12122378

13. Kelly JH, Gilmore AJ, Situmorang A, Porker KD, Marzec M, Tucker MR, et al. Strigolactones coordinate barley tillering and grain size. J Exp Bot. 2025. https://doi.org/10.1093/jxb/eraf229

14. Snowden KC, Simkin AJ, Janssen BJ, Templeton KR, Loucas HM, Simons JL, et al. The decreased apical dominance1/*Petunia hybrida* carotenoid cleavage dioxygenase8 gene affects branch production and development. Plant Cell. 2005;17(3):746–59. https://doi.org/10.1105/tpc.104.027714

15. Das D, Kashtoh H, Panda J, Rustagi S, Mohanta YK, Singh N, et al. From hormones to harvests: Strengthening plant resilience for sustainable development goals. Plants. 2025;14(15):2322. https://doi.org/10.3390/plants14152322

16. Seto Y, Yasui R, Kameoka H, Tamiru M, Cao M, Terauchi R, et al. Strigolactone perception and deactivation by DWARF14. Nat Commun. 2019;10(1):191. https://doi.org/10.1038/s41467-018-08124-7

17. Faizan M, Faraz A, Sami F, Siddiqui H, Yusuf M, Gruszka D, et al. Role of strigolactones: Signalling and crosstalk with other phytohormones. Open Life Sci. 2020;15(1):217–28. https://doi.org/10.1515/biol-2020-0022

18. Shah FA, Wei X, Wang Q, Liu W, Wang D, Yao Y, et al. Karrikin improves salt tolerance in *Sapium sebiferum*. Front Plant Sci. 2020;11:216. https://doi.org/10.3389/fpls.2020.00216

19. Wang P, Zhu K, Lang Z. Nitric oxide suppresses ABA inhibition of seed germination. Plant Signal Behav. 2015;10(6):e1031939. https://doi.org/10.1080/15592324.2015.1031939

20. Alvi AF, Sehar Z, Fatma M, Masood A, Khan NA. Strigolactone: An emerging growth regulator. Plants. 2022;11(19):2604. https://doi.org/10.3390/plants11192604

21. Al-Babili S, Bouwmeester HJ. Strigolactones are a novel carotenoid-derived hormone. Annu Rev Plant Biol. 2015;66:161–86. https://doi.org/10.1146/annurev-arplant-043014-114759

22. Deng Q, Wang H, Qiu Y, Wang D, Xia Y, Zhang Y, et al. Multifaceted impact of karrikin signaling. Int J Mol Sci. 2025;26(6):2775. https://doi.org/10.3390/ijms26062775

23. Arite T, Iwata H, Ohshima K, Maekawa M, Nakajima M, Kojima M, et al. DWARF10 controls lateral bud outgrowth in rice. Plant J. 2007;51(6):1019–29. https://doi.org/10.1111/j.1365-313X.2007.03210.x

24. Booker J, Auldridge M, Wills S, McCarty D, Klee H, Leyser O. MAX3/CCD7 required for synthesis of a novel plant signal. Curr Biol. 2004;14(14):1232–38. https://doi.org/10.1016/j.cub.2004.06.061

25. Singh S, Uddin M, Khan MMA, Chishti AS, Singh S, Bhat UH. Plant-derived smoke and karrikinolide in abiotic stress mitigation. Plant Stress. 2023;7:100147. https://doi.org/10.1016/j.stress.2023.100147

26. Alder A, Jamil M, Marzorati M, Bruno M, Vermathen M, Bigler P, et al. From β-carotene to carlactone. Science. 2012;335(6074):1348–51. https://doi.org/10.1126/science.1218094

27. Zha M, Zhao Y, Wang Y, Chen B, Tan Z. Strigolactone–cytokinin interaction in rice tillering. Front Plant Sci. 2022;13:837136. https://doi.org/10.3389/fpls.2022.837136

28. Wu F, Gao Y, Yang W, Sui N, Zhu J. Biological functions of strigolactones. Front Plant Sci. 2022;13:821563. https://doi.org/10.3389/fpls.2022.821563

29. Brewer PB, Yoneyama K, Filardo F, Meyers E, Scaffidi A, Frickey T, et al. Lateral branching oxidoreductase in *Arabidopsis*. Proc Natl Acad Sci U S A. 2016;113(22):6301–306. https://doi.org/10.1073/pnas.1601729113

30. Fichtner F, Humphreys J, Barbier F, Feil R, Westhoff P, Moseler A, et al. Strigolactone signalling inhibits trehalose 6-phosphate signalling. New Phytol. 2024;244(3):900–13. https://doi.org/10.1111/nph.20072

31. Nelson DC, Flematti GR, Riseborough JA, Ghisalberti EL, Dixon KW, Smith SM. Karrikins enhance light responses in *Arabidopsis thaliana*. Proc Natl Acad Sci U S A. 2010;107(15):7095–100. https://doi.org/10.1073/pnas.0911635107

32. Waters MT, Nelson DC. Karrikin perception and signalling. New Phytol. 2023;237(5):1525–41. https://doi.org/10.1111/nph.18598

33. Sepulveda C, Guzmán MA, Li Q, Villaécija-Aguilar JA, Martinez SE, Kamran M, et al. KUF1 regulates karrikin metabolism in *Arabidopsis thaliana*. Proc Natl Acad Sci U S A. 2022;119(11):e2112820119. https://doi.org/10.1073/pnas.2112820119

34. Yang T, Lian Y, Wang C. Roles of strigolactones and karrikins. Int J Mol Sci. 2019;20(24):6270. https://doi.org/10.3390/ijms20246270

35. Mostofa MG, Abdelrahman M, Rahman M, Cuong TM, Nguyen KA, Watanabe Y, et al. KAI2 coordinates salt tolerance in *Arabidopsis thaliana*. Plant Cell Physiol. 2022;63(8):1146–60. https://doi.org/10.1093/pcp/pcac121

36. Wang Q, Smith SM, Huang J. Origins of strigolactone and karrikin signaling. Trends Plant Sci. 2022;27(5):450–59. https://doi.org/10.1016/j.tplants.2021.11.009

37. Li C, Lu X, Liu Y, Xu J, Yu W. Strigolactone alleviates salt stress in cucumber. Antioxidants. 2023;12(5):1043. https://doi.org/10.3390/antiox12051043

38. Varshney K, Gutjahr C. KAI2 function in plant development. Plant Cell Physiol. 2023;64(9):1077–87. https://doi.org/10.1093/pcp/pcad077

39. Bürger M, Chory J. Models of strigolactone signaling. Trends Plant Sci. 2020;25(4):395–405. https://doi.org/10.1016/j.tplants.2019.12.009

40. Ma B, Zhu J, Huang X. Diversification of SMAX1-like genes in cotton. BMC Plant Biol. 2023;23:419. https://doi.org/10.1186/s12870-023-04421-6

41. Guan Y, Li L, Wang D, Zhou J, Qi W, Cheng Y, et al. Multifaceted functions of strigolactones. Plant Stress. 2025;16:100895. https://doi.org/10.1016/j.stress.2025.100895

42. Mitra D, Rad KV, Chaudhary P, Ruparelia J, Sagarika MS, Boutaj H, et al. Strigolactone in root development and mycorrhiza. Curr Res Microbiol Sci. 2021;2:100026. https://doi.org/10.1016/j.crmicr.2021.100026

43. Nakamura H, Xue Y, Miyakawa T, Hou F, Qin HM, Fukui K, et al. Mechanism of strigolactone perception by DWARF14. Nat Commun. 2013;4:2613. https://doi.org/10.1038/ncomms3613

44. Kumar M, Pandya-Kumar N, Kapulnik Y, Koltai H. Strigolactone signaling in phosphate starvation. Plant Signal Behav. 2015;10 (7):e1045174. https://doi.org/10.1080/15592324.2015.1045174

45. Yoneyama K. Strigolactones and nutrient deficiencies. Cold Spring Harb Perspect Biol. 2019;11(8):a034686. https://doi.org/10.1101/cshperspect.a034686

46. Cheng X, Ruyter-Spira C, Bouwmeester H. Interaction between strigolactones and other hormones. Front Plant Sci. 2013;4:199. https://doi.org/10.3389/fpls.2013.00199

47. Jia KP, Luo Q, He SB, Lu XD, Yang HQ. Strigolactone-regulated hypocotyl elongation. Mol Plant. 2014;7(3):528–40. https://doi.org/10.1093/mp/sst093

48. Wang H, Chen W, Eggert K, Charnikhova T, Bouwmeester H, Schweizer P, et al. ABA modulates strigolactones in barley. J Exp Bot. 2018;69(16):3883–98. https://doi.org/10.1093/jxb/ery200

49. Gupta S, Plackova L, Kulkarni MG, Dolezal K, Van Staden J. Smoke biomolecules regulate seed germination of *Lactuca sativa*. Plant Physiol. 2019;181(2):458–70. https://doi.org/10.1104/pp.19.00644

50. Drummond RSM, Martinez-Sanchez NM, Janssen BJ, Templeton KR, Simons JL, Quinn BD, et al. *Petunia hybrida* CCD7 and branching. Plant Physiol. 2009;151(4):1867–77. https://doi.org/10.1104/pp.109.146720

51. Dun EA, Brewer PB, Gillam EMJ, Beveridge CA. Strigolactones and shoot branching. Plant Cell Physiol. 2023;64(9):967–83. https://doi.org/10.1093/pcp/pcad088

52. Waters MT, Gutjahr C, Bennett T, Nelson DC. Strigolactone signaling and evolution. Annu Rev Plant Biol. 2017;68:291–322. https://doi.org/10.1146/annurev-arplant-042916-040925

53. Brewer PB, Dun EA, Gui R, Mason MG, Beveridge CA. Strigolactone inhibition of branching. Plant Physiol. 2015;168(4):1820–9. https://doi.org/10.1104/pp.15.00014

54. Kamran M, Melville KT, Waters MT. Karrikin signalling and stress tolerance. J Exp Bot. 2024;75(4):1174–86. https://doi.org/10.1093/jxb/erad476

55. Fang P, Hu Y, Guo Q, Li L, Xu P. Karrikins and redox regulation. Plant Stress. 2023;9:100185. https://doi.org/10.1016/j.stress.2023.100185

56. Sami A, Ur Rehman S, Tanvir M, Zhou X, Zhu Z, Zhou K. Germination of *Brassica oleracea* seeds treated with karrikin 1. J Plant Growth Regul. 2021;40:1922–32. https://doi.org/10.1007/s00344-020-10186-1

57. Sun H, Li W, Burritt DJ, Tian H, Zhang H, Liang X, et al. Strigolactones modulate root growth. Crop J. 2022;10(6):1517–27. https://doi.org/10.1016/j.cj.2022.07.014

58. Kodama K, Xie X, Kyozuka J. D14 and KAI2 orthologs in gymnosperms. Plant Cell Physiol. 2023;64(9):1057–65. https://doi.org/10.1093/pcp/pcad072

59. Yasmin H, Chakraborty T. Impact of abiotic stresses on plant growth. Int J Adv Res. 2023;11(1):249–57. https://doi.org/10.21474/IJAR01/16875

60. Li Q, Martín-Fontecha ES, Khosla A, White ARF, Chang S, Cubas P, et al. D14 targets SMAX1 under osmotic stress. Plant Commun. 2022;3 (2):100303. https://doi.org/10.1016/j.xplc.2022.100303

61. Chen Y, Dan Z, Li S. Rice GRF7 regulates strigolactone synthesis. Plant Signal Behav. 2020;15(10):1804685. https://doi.org/10.1080/15592324.2020.1804685

62. Villaécija-Aguilar JA, Hamon-Josse M, Carbonnel S, Kretschmar A, Schmidt C, Dawid C, et al. SMAX1/SMXL2 regulate root development. PLoS Genet. 2019;15(8):e1008327. https://doi.org/10.1371/journal.pgen.1008327

63. Akiyama K, Ogasawara S, Ito S, Hayashi H. Structural requirements of strigolactones in AM fungi. Plant Cell Physiol. 2010;51(7):1104–11. https://doi.org/10.1093/pcp/pcq058

64. Khan N. Decoding phytohormone signaling in plant stress physiology. Environ Exp Bot. 2025;231:106099. https://doi.org/10.1016/j.envexpbot.2025.106099

65. Ueda H, Kusaba M. Strigolactone regulates leaf senescence in *Arabidopsis*. Plant Physiol. 2015;169(1):138–47. https://doi.org/10.1104/pp.15.00325

66. Tariq A, Ullah I, Sardans J, Graciano C, Mussarat S, Ullah A, et al. Strigolactones in arid land stress tolerance. Environ Res. 2023;229:115966. https://doi.org/10.1016/j.envres.2023.115966

67. Agusti J, Herold S, Schwarz M, Sanchez P, Ljung K, Dun EA, et al. Strigolactone signaling in secondary growth. Proc Natl Acad Sci U S A. 2011;108(50):20242–7. https://doi.org/10.1073/pnas.1111902108

68. Chang SH, George WJ, Nelson DC. SMAX1-like transcriptional regulators in *Arabidopsis thaliana*. Proc Natl Acad Sci U S A. 2025;122(24):e2412793122. https://doi.org/10.1073/pnas.2412793122

69. Cao S, Li X, Wang L. Karrikin signaling and phytohormone interactions. Innov Life. 2025;3:100148. https://doi.org/10.59717/j.xinn-life.2025.100148

70. Liu G, Stirnemann M, Gübeli C, Egloff S, Courty PE, Aubry S, et al. Strigolactones shape exodermal morphology. Science. 2019;17:144–54. https://doi.org/10.1016/j.isci.2019.06.024

71. Sun H, Tao J, Gu P, Xu G, Zhang Y. Role of strigolactones in root development. Plant Signal Behav. 2016;11(1):e1110662. https://doi.org/10.1080/15592324.2015.1110662

72. Zeng W, Mostafa S, Lu Z, Jin B. Melatonin-mediated abiotic stress tolerance. Front Plant Sci. 2022;13:847175. https://doi.org/10.3389/fpls.2022.847175

73. Nelson DC, Riseborough JA, Flematti GR, Stevens J, Ghisalberti EL, Dixon KW, et al. Karrikins trigger seed germination. Plant Physiol. 2009;149(2):863–73. https://doi.org/10.1104/pp.108.131516

74. Flematti GR, Dixon KW, Smith SM. What are karrikins? BMC Biol. 2015;13(1):108. https://doi.org/10.1186/s12915-015-0219-0

75. Dun EA, de Saint Germain A, Rameau C, Beveridge CA. Strigolactone dynamics in *Pisum sativum*. Mol Plant. 2013;6(1):128–40. https://doi.org/10.1093/mp/sss131

76. Ahmad S, Zulfiqar T, Yang H, Farooq M. Strigolactones mitigate drought stress in maize. Ann Agric Sci. 2025;70(1):100389. https://doi.org/10.1016/j.aoas.2025.100389

77. Lee I, Choi S, Lee S, Soh MS. KAI2-KL signaling and photomorphogenesis. Plant Signal Behav. 2019;14(4):e1588660. https://doi.org/10.1080/15592324.2019.1588660

78. Morffy N, Faure L, Nelson DC. Evolution of karrikin and strigolactone signaling. Trends Genet. 2016;32(3):176–88. https://doi.org/10.1016/j.tig.2016.01.002

79. Alsubaie QD, Al-Amri AA, Siddiqui MH, Alamri S. Strigolactone and nitric oxide synergy in tomato. Plant Physiol Biochem. 2024;207:108412. https://doi.org/10.1016/j.plaphy.2024.108412

80. Spallek T, Mutuku M, Shirasu K. The genus *Striga*. Mol Plant Pathol. 2013;14(9):861–69. https://doi.org/10.1111/mpp.12058

81. Wang L, Waters MT, Smith SM. Karrikin-KAI2 signaling in *Arabidopsis*. New Phytol. 2018;219(2):605–18. https://doi.org/10.1111/nph.15192

82. Sami A, Riaz M, Zhou X, Zhu Z, Zhou K. Dormancy alleviation in *Brassica oleracea*. BMC Plant Biol. 2019;19:211. https://doi.org/10.1186/s12870-019-2118-y

83. Raza A, Razzaq A, Mehmood SS, Zou X, Zhang X, Lv Y, et al. Climate change and crop adaptation. Plants. 2019;8(2):34. https://doi.org/10.3390/plants8020034

84. Zhang YX, van Dijk ADJ, Scaffidi A, Flematti GR, Hofmann M, Charnikhova T, et al. MAX1 homologs in rice. Nat Chem Biol. 2014;10(12):1028–33. https://doi.org/10.1038/nchembio.1660

85. Yoneyama K, Awad AA, Xie X, Yoneyama K, Takeuchi Y. Strigolactones as germination stimulants. Plant Cell Physiol. 2010;51(7):1095–103. https://doi.org/10.1093/pcp/pcq055

86. Wu S, Li Y. Sulfotransferase-involving strigolactone biosynthesis in sorghum. Front Plant Sci. 2021;12:793459. https://doi.org/10.3389/fpls.2021.793459

87. Ha CV, Antonio M, Osakabe Y, Tran UT, Nishiyama R, Watanabe Y, et al. Strigolactone positively regulates drought and salt stress responses. Proc Natl Acad Sci U S A. 2014;111(2):851–56. https://doi.org/10.1073/pnas.1322135111

88. Dong J, Fu H, Wang Z, Zhang L, Liu Z, Hu Y, et al. Strigolactone-regulated abiotic stress responses in plants. Plants. 2025;14(16):2582. https://doi.org/10.3390/plants14162582

89. Min Z, Li R, Chen L, Zhang Y, Li Z, Liu M, et al. Strigolactones alleviate drought stress in grapevine. Plant Physiol Biochem. 2019;135:99–110. https://doi.org/10.1016/j.plaphy.2018.11.037

90. Agliassa C, Morabito C, Prati M, Secchi F, Said-Pullicino D, Sahin N, et al. Strigolactones enhance salinity stress tolerance in tomato. Environ Exp Bot. 2025;237:106181. https://doi.org/10.1016/j.envexpbot.2025.106181

91. Li W, Nguyen KH, Chu HD, Ha CV, Watanabe Y, Osakabe Y, et al. KAI2 promotes drought resistance in *Arabidopsis thaliana*. PLoS Genet. 2017;13(11):e1007076. https://doi.org/10.1371/journal.pgen.1007076

92. Li W, Nguyen KH, Chu HD, Watanabe Y, Osakabe Y, Sato M, et al. Functional comparison of DWARF14 and KAI2 in drought adaptation. Plant J. 2020;103(1):111–27. https://doi.org/10.1111/tpj.14712

93. Wang L, Xu Q, Yu H, Ma H, Li X, Yang J, et al. Strigolactone and karrikin signaling regulate SMXL2 proteolysis. Plant Cell. 2020;32(7):2251–70. https://doi.org/10.1105/tpc.20.00140

94. Sun H, Tao J, Liu S, Huang S, Chen S, Xie X, et al. Strigolactones regulate nutrient-deficiency-induced root development in rice. J Exp Bot. 2014;65(22):6735–46. https://doi.org/10.1093/jxb/eru029

95. Kohlen W, Charnikhova T, Van Zeijl A, Van Bezouwen L, De Ruijter N, Cardoso C, et al. GR24 effects on root system architecture in *Arabidopsis*. Plant Physiol. 2011;155(2):721–34. https://doi.org/10.1104/pp.110.166645

96. Cooper JW, Hu Y, Beyyoudh L, Yildiz Dasgan H, Kunert K, Beveridge CA, et al. Strigolactones regulate chilling tolerance in pea and *Arabidopsis*. Plant Cell Environ. 2018;41(6):1298–310. https://doi.org/10.1111/pce.13147

97. Deslous P, Bournonville C, Decros G, Okabe Y, Mauxion JP, Jorly J, et al. Ascorbic acid overproduction impairs pollen fertility in tomato. J Exp Bot. 2021;72(8):3091–107. https://doi.org/10.1093/jxb/erab040

98. Soundappan I, Bennett T, Morffy N, Liang Y, Stanga JP, Abbas A, et al. SMAX1-like proteins mediate MAX2-dependent SL and KL responses. Plant Cell. 2015;27(11):3143–59. https://doi.org/10.1105/tpc.15.00562