

Review

Smoke and Hormone Mirrors:
Action and Evolution of
Karrikin and Strigolactone
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Karrikins and strigolactones are two classes of butenolide molecules that have diverse effects on plant growth. Karrikins are found in smoke and strigolactones are plant hormones, yet both molecules are likely recognized through highly similar signaling mechanisms. Here we review the most recent discoveries of karrikin and strigolactone perception and signal transduction. Two paralogous α/β hydrolases, KAI2 and D14, are respectively karrikin and strigolactone receptors. D14 acts with an F-box protein, MAX2, to target SMXL/D53 family proteins for proteasomal degradation, and genetic data suggest that KAI2 acts similarly. There are striking parallels in the signaling mechanisms of karrikins, strigolactones, and other plant hormones, including auxins, jasmonates, and gibberellins. Recent investigations of host perception in parasitic plants have demonstrated that strigolactone recognition can evolve following gene duplication of KAI2.

Diverse Roles for Karrikins and Strigolactones in Plant Growth

Karrikins (KARs) and strigolactones (SLs) have been studied intensively over the past decade as two new classes of plant growth regulators. KARs and SLs are both butenolide molecules (Box 1), but they have very different sources and effects on growth. KARs, which are found in smoke, activate germination of many species after fire [1–3]. KAR effects are not limited to plants from fire-prone environments, however. KARs enhance *Arabidopsis thaliana* germination and seedling responses to light [4,5]. KARs also increase seedling vigor and stress tolerance of several crop species [6–8]. SLs were first discovered in cotton root exudates nearly 50 years ago as germination stimulants of parasitic weeds [9]. SLs have since been found to act as rhizosphere signals that promote symbiotic interactions between roots and arbuscular mycorrhizal fungi [10–12], and as hormones that influence shoot branching [11,13], root architecture [14–16], leaf shape [17–19], leaf senescence [20,21], and cambial growth [22].

Substantial progress has been made toward understanding how SLs are synthesized [23–28] and transported [29–31], how KARs and SLs are sensed, and how these signals control different aspects of plant growth. Strikingly, KAR and SL signaling mechanisms involve homologous genetic components. Therefore, this system can provide broader insights into how new signaling mechanisms arise and how signaling specificity is achieved. In this review, we focus on recent breakthroughs in the mechanisms and evolution of KAR and SL signaling.

Genetic Screens Link KAR and SL Signaling

Despite a basic structural similarity, KARs and SLs are not interchangeable signals (Box 1). KARs do not restore branching suppression to SL-deficient mutants, implying that KARs and SLs are

Trends

Compelling evidence that KAI2 and D14 are karrikin (KAR) and strigolactone (SL) receptors with hydrolytic activity has been provided through recent genetic, biochemical, and structural studies in several plant species. Ligand hydrolysis promotes protein-protein interactions.

The elusive targets of KAR and SL signaling have been discovered. Two clades within the SMXL/D53 family regulate growth processes that are associated with either KAR or SL responses.

SL receptors in parasitic weeds, which enable host-triggered germination, evolved from KAI2 paralogs. Other KAI2 paralogs in parasites detect KARs specifically or an unidentified endogenous ligand, KL.

KAR and SL signaling mechanisms share features of other plant hormone pathways, including hormone-activated proteolysis of EAR motif-containing proteins that likely interact with transcriptional corepressors.

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Box 1. Comparing Karrikins and Strigolactones

KARs are produced by pyrolysis of cellulose or sugars, and are therefore generated by all wildfires [75] (Figure 1A). KARs in smoke are thought to be deposited on the soil surface during a fire, and then absorbed by seeds buried in the soil in the following months after being dissolved by rain [3]. KAR₁ is the most abundant KAR in smoke–water solutions, and is usually the most bioactive. Five additional KARs with methyl group substitutions have been identified [1].

SLs are synthesized from carotenoids via a carlactone intermediate by a carotene isomerase (D27), two carotenoid cleavage dioxygenases (CCD7/MAX3 and CCD8/MAX4), and a cytochrome P450 (MAX1) [23–28]. Carlactone is converted to carlactonoic acid by MAX1 in three-step oxidative reactions. Carlactonoic acid is a precursor of SLs as well as methyl carlactonoate, a D14 substrate with SL-like activities [25]. Approximately 20 SLs have been found in plants. All feature a tricyclic lactone (ABC-ring) connected to a butenolide (D-ring) in a 2′*R* configuration [76]. MAX1 paralogs in rice contribute to SL diversity [23,77]. SLs fall into two classes based upon stereochemistry at the B–C-ring junction that are typified by 5-deoxystrigol (5DS) and 4-deoxyorobanchol (Figure 1B). The D-ring and a cleavable ether linkage are essential elements of active SLs. However, stereochemistry at the 2′ carbon atom is also critical for signaling specificity [37,39]. GR24 is a commonly used synthetic SL analog that is typically a racemic mixture of two enantiomers (Figure 1C). GR24^{5DS} mimics 5DS stereochemistry; however, its enantiomer GR24^{ent-5DS} has an unnatural 2′*S* configuration. The Arabidopsis SL receptor D14 preferentially recognizes 2′*R* SLs (blue) versus 2′*S* SLs, while its paralog KAI2 is responsive to KARs and GR24^{ent-5DS} (red) [37]. True SL responses are thus best verified by testing SL-deficient mutants and optically pure SL enantiomers.

Although KARs and SLs are both butenolide molecules that trigger germination, from the perspective of a seed these signals convey opposite messages. As fire-derived compounds, KARs indicate a low-competition environment in which ‘plants are absent’, whereas SLs found in soil are exuded by roots, therefore signaling ‘plants are present’. Selective germination responses to KARs and SLs are important ecological adaptations for some plants. For example, the fire-following species *Brassica tournefortii* germinates in response to KARs, but is much less responsive to *rac*-GR24 [5]. By contrast, root parasitic weeds in the Orobanchaceae family that require a host plant for survival are highly sensitive to SLs and unresponsive to KARs [50].

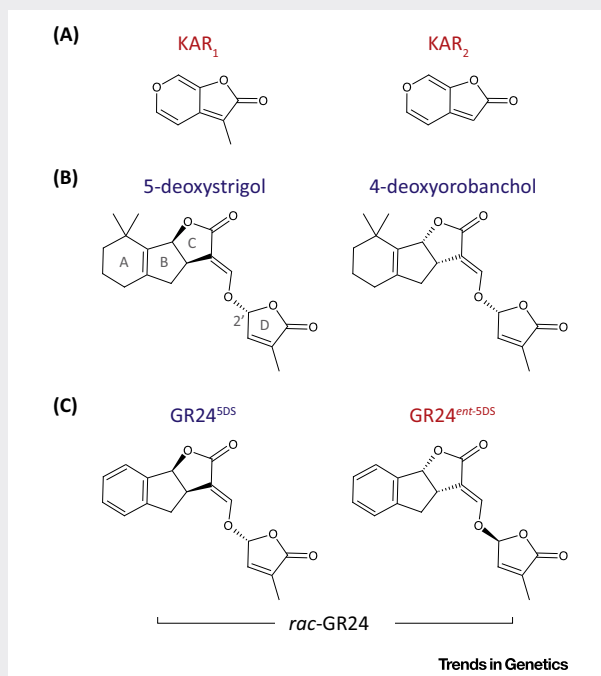


Figure 1. Structures of Karrikins (KARs) and Strigolactones (SLs). Molecular structures of KARs (A), representatives of the two major classes of natural SLs (B), and a commonly used synthetic SL analog GR24 (C). KAR₂ is commonly used in *Arabidopsis thaliana* experiments because of its higher activity than KAR₁ [5]. Note the stereochemistry at the 2′ carbon of the butenolide D-ring in SL structures. *rac*-GR24 is a mixture of GR24^{5DS} and its enantiomer. Compounds that signal primarily or exclusively through KAI2 are labeled in red; those that signal through D14 are labeled in blue. Abbreviations: KAI2, KARRIKIN-INSENSITIVE2; D14, DWARF14.

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