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Alisha Goyal
Department of Basic Science,
Maharana Pratap Horticultural
University, Karnal, Haryana,
India

Preeti
Department of Botany, NIILM
University, Kaithal, Haryana,
India

Anita Kumari
Department of Botany and Plant
Physiology, CCS HAU, Hisar,
Haryana, India

Karrikins: A novel plant growth regulator with emerging agronomic applications

Alisha Goyal, Preeti and Anita Kumari

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Abstract

Karrikins (KARs) are a group of small butenolide organic compounds produced during the combustion of plant material, particularly cellulose, in wildfires. Unlike classical plant hormones that are endogenously synthesized, karrikins are exogenous fire-derived signals that profoundly influence seed germination, seedling development, and plant adaptation to abiotic stresses. The first active compound, KAR1 (3-methyl-2H-furo[2,3-c]pyran-2-one) was identified in 2004 and after that other six karrikin molecules (KAR1–KAR6) have also been characterized. KARs are perceived through the α/β -hydrolase receptor KAI2 (KARRIKIN INSENSITIVE 2) and transduce their signal through MAX2 and SMXL proteins, a pathway strikingly parallel to that of strigolactones (SLs). Despite their structural similarity to SLs, KARs originate from pyrolysis rather than plant biosynthesis and signal ecological contexts in which plant competition is absent. Research across multiple crop species — including tomato, maize, rice, and okra — demonstrates that KARs and smoke water significantly enhance shoot growth, root development, seedling vigor, and tolerance to temperature extremes. KAR signaling modulates interactions with gibberellic acid, abscisic acid, and indole-3-acetic acid to regulate dormancy and germination. Under abiotic stress conditions such as drought, KARs enhance antioxidant defense, stomatal regulation, cuticle formation, and anthocyanin biosynthesis. The ecological role of KARs in post-fire revegetation further underscores their relevance to sustainable agriculture and stress-resilient crop management. This review consolidates current knowledge on karrikin chemistry, signaling mechanisms, hormonal interactions, and agronomic significance, with a focus on future research directions.

Keywords: Karrikins, phytohormones, germination, strigolactones, abiotic stresses, smoke water, seedling vigor

Introduction

Plant growth regulators (PGRs), commonly referred to as plant hormones or phytohormones, are organic molecules that govern fundamental aspects of plant growth and development. These include the regulation of branching, shoot elongation, return bloom, fruit thinning, and maturity modification. Phytohormones are typically produced in small amounts at a specific site within the plant (the source) and then transported to a other site (the target) where they exert their effects. All plant groups, including algae, produce phytohormones, and these molecules serve roles analogous to those found in higher plants (Tarakhovskaya *et al.*, 2007) [25]. Some phytohormones are also found in microorganisms such as unicellular fungi and bacteria, though they don't have a hormonal activity so it is better to classified as secondary metabolites (Rademacher, 1994) [22].

The classical group of phytohormones including auxins, gibberellins, cytokinins, abscisic acid, and ethylene. In recent decades, novel hormones including brassinosteroids, salicylic acid, strigolactones, and polyamines have also been added to this repertoire. Among the most recently discovered is karrikins — butenolide compounds that are not endogenously produced within plants but are generated externally during the combustion of plant material (Flematti *et al.*, 2013) [6]. Unlike conventional PGRs, karrikins are fire-derived exogenous signals that exhibit remarkable biological activity across a wide range of plant species, including important agricultural crops.

The present review comprehensively summarizes the discovery, chemistry, mechanism of action, comparison with strigolactones, smoke water preparation, interaction with other

Corresponding Author:
Alisha Goyal
Department of Basic Science,
Maharana Pratap Horticultural
University, Karnal, Haryana,
India

hormones, role under abiotic stress, and effects of karrikins on crop growth and development, with perspectives on future

research.

Table 1: Classification and functions of major plant hormones.

Hormone	Auxin	Gibberellic acid	Cytokinin	Abscisic acid	Ethylene
Where produced or found in plant	The embryo of seed, meristem of apical buds & young leaves	Meristem of apical buds and roots, young leaves, and embryo	Synthesized in roots and transported to other organs	Leaves, stem, roots, green fruit	Tissues of ripening fruit, nodes of stem, aging leaves, and flowers
Functions	Stimulate cell elongation; Root formation; Xylem differentiation; Involved in tropisms and apical dominance	Break dormancy of seeds and buds; Stem elongation; Stimulate flowering & development of fruit	Stimulate cell division & growth; Shoot formation; Delays senescence	Promote Bud and seed dormancy; Inhibit growth; Closes stomata during water stress; Leaf senescence	Stimulates fruit ripening & Abscission; Opposes some auxin effects

Karrikins: Overview and Ecological Significance

Karrikins are a group of small organic compounds produced when plant material is burned (Nelson *et al.*, 2012) [19]. They are notable for their ability to stimulate seed germination across a wide spectrum of plant species. Wildfires, often known as bushfires, are a natural occurrence globally — from Australia and California to South Africa. During these events, the combustion of vegetation generates smoke and ash laden with karrikins (KARs). After the fire subsides, KARs accumulate on the soil surface in a dormant state until rainfall occurs. Upon the arrival of rain, karrikins are leached into the soil and stimulate the germination of seeds that had remained dormant in the seed bank (Fig. 1).

Certain plant species have evolved to exploit this phenomenon, growing rapidly, flowering, producing seed, and completing their lifecycle within one to two years after a fire. These are referred to as 'fire-followers' or 'fire-ephemerals.' This ecological strategy is highly adaptive: wildfires liberate nutrients that were bound in plant biomass, reduce competition from established vegetation, and create an open environment where seedlings can successfully establish. Importantly, rainfall without a preceding fire does not induce germination in fire-ephemeral species, indicating that these seeds can undergo repeated cycles of imbibition (Wet) and dehydration (dry) while remaining dormant and karrikin-sensitive. Such seeds may persist viably in the soil seed bank for decades between fire events. KARs thus play a significant role in the ecological regeneration of fire-devastated landscapes.

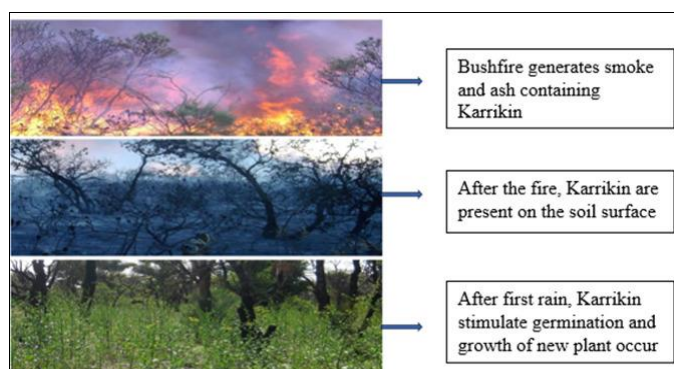


Fig 1: The role of karrikins in revegetation after a fire (Flematti *et al.*, 2015) [4]

Discovery of Karrikins:

The first instance of seed germination induced by the combustion of plant material was made by Wicklow in 1997, who demonstrated that charred stem segments placed on damp filter paper could stimulate the germination of dormant seeds.

However, the identification of the active chemical compound responsible for this effect did not occur until 2004. In that year, two scientific groups simultaneously identified the first active chemical in smoke — KAR1 (3-methyl-2H-furo[2,3-c]pyran-2-one) — using bioassay-guided fractionation of smoke water, gas chromatography–mass spectrometry (GC-MS), and nuclear magnetic resonance (NMR) spectroscopy. Flematti *et al.* (2004) [5] used burnt cellulose as the smoke source, while Van Staden *et al.* (2004) [27] employed smoke-saturated water generated from burned plant material.

The butenolide compounds identified from plant-derived smoke were subsequently named 'Karrikins' (KARs), derived from the Noongar Aboriginal word 'karrik' meaning smoke. KAR1 was recognized as the most potent germination stimulator among the karrikins. Structurally, karrikin is a bicyclic molecule with a molecular mass of 150 Da produced during partial combustion of cellulose. It promotes cotyledon expansion and chlorophyll accumulation while inhibiting hypocotyl elongation. KARs improve seedling vigor and photomorphogenesis and play a crucial role in plant abiotic stress tolerance. Biological activity has been observed not only in fire-follower species but also in non-fire followers, including *Arabidopsis thaliana*, tomato, maize, rice, and lettuce. To date, six karrikin molecules (KAR1 to KAR6) have been identified from plant-derived smoke, each differing in the presence and position of methyl group(s) (Fig. 2).

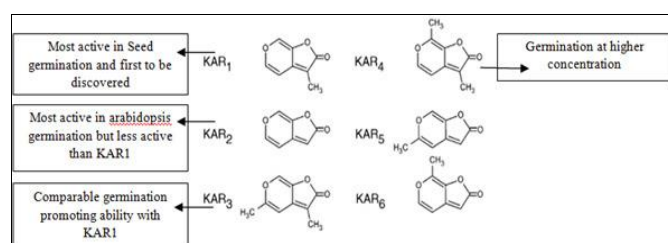


Fig 2: Chemical structures of karrikin compounds (KAR1–KAR6).

4. Preparation of Smoke Water

The water solubility of active smoke compounds was first demonstrated by De Lange and Boucher (1990) [3], which led to the development of smoke water (SW) as a practical formulation for horticultural and agricultural use. Smoke water is prepared by bubbling smoke generated from the controlled burning of plant material through water (Fig. 3), a process in which the biologically active components rapidly dissolve. This technique, described by Brown and Van Staden (1997) [1] and refined by subsequent researchers (Van Staden *et al.*, 2004; Kulkarni *et al.*, 2011) [27, 12], is valued for being low-cost, simple to execute, and requiring minimal material.

KARs sustain seed germination-promoting activity at concentrations as low as 10^{-9} mol/L (Light *et al.*, 2009). Smoke water exhibits a 'dual regulatory' effect on germination: stimulating germination at lower concentrations while inhibiting it at higher concentrations (Light *et al.*, 2002) [15]. The germination-inhibiting compound has been identified as 3,4,5-trimethylfuran-2(5H)-one (Light *et al.*, 2010) [13]. Depending on the plant species, smoke water should be diluted at ratios of 1:250, 1:500, 1:1000, 1:1500, or 1:2000 (v/v) before application. Once autoclaved, smoke water can be stored for extended periods (Van Staden *et al.*, 2004; Light *et al.*, 2004) [27, 16].



Fig 3: Apparatus designed for the preparation of smoke water (Gupta *et al.*, 2020) [9].

Comparison of Karrikins and Strigolactones

Karrikins are structurally and functionally analogous to strigolactones (SLs). The first strigolactone, strigol, was isolated from cotton root exudates and named for its ability to stimulate germination in the parasitic plant *Striga lutea*. Strigolactones promote the growth and branching of symbiotic arbuscular mycorrhizal fungi and regulate shoot branching in plants. Both KARs and SLs are butenolide molecules, yet they differ significantly in their origin, biological context, and molecular targets. Table 2 presents a comparative summary of these two classes of plant regulators.

Table 2: Comparative overview of strigolactones and karrikins.

Strigolactones	Karrikins
SLs are butenolide molecules but have different sources and effects on growth	KARs are also butenolide molecules but have different sources and effects on growth
SLs are synthesized from carotenoids via an intermediate by a carotene isomerase	KARs are produced by pyrolysis of cellulose or sugars and are therefore generated by all wildfires
SLs found in soil are exuded by roots, therefore signaling 'plants are present'	As fire-derived compounds, KARs indicate a low-competition environment in which 'plants are absent'
Most abundant SL is GR 24	Most abundant KAR is KAR 1
20 different naturally occurring strigolactones have been characterized	6 KARs have been identified
Mode of action is fully explained	Very little is known about mode of action

Molecular Signaling Mechanisms of Karrikins

The molecular pathway for karrikin perception and response in plants closely parallels that of strigolactones (De Cuyper *et al.*, 2017; Morffy *et al.*, 2016; Waters, 2017) [2, 18, 29]. Two key genes govern the karrikin response: KAI2 (KARRIKIN INSENSITIVE 2) and MAX2 (MORE AXILLARY GROWTH 2). Figure 4 presents a model of KAR and SL signaling pathways.

KAI2 belongs to the α/β -hydrolase superfamily and serves as the karrikin receptor. Upon karrikin binding, KAI2 forms a

receptor-ligand complex, analogous to the role of DWARF14 (D14) in strigolactone signaling (Guo *et al.*, 2013) [8]. The F-box protein MAX2, a member of the leucine-rich-repeat (LRR) family, forms part of an SKP1–Cullin–F-box (SCF) E3 ubiquitin ligase complex. This complex facilitates substrate-specific polyubiquitination via the 26S proteasome pathway, leading to the targeted degradation of repressor proteins (Waters, 2017) [29]. The downstream repressors in karrikin signaling are SMAX1-LIKE (SMXL) proteins, which function as transcriptional co-repressors related to ATP-dependent heat shock proteins (Yao and Waters, 2019) [32]. The SMXL family comprises eight members: SMAX1 and SMXL2 are engaged in KAR signaling; SMXL3–SMXL5 govern phloem development independently of both KAR and SL; and SMXL6–SMXL8 are involved in SL signaling (Stanga *et al.*, 2013; Soundappan *et al.*, 2015; Wallner *et al.*, 2017) [24, 23, 28].

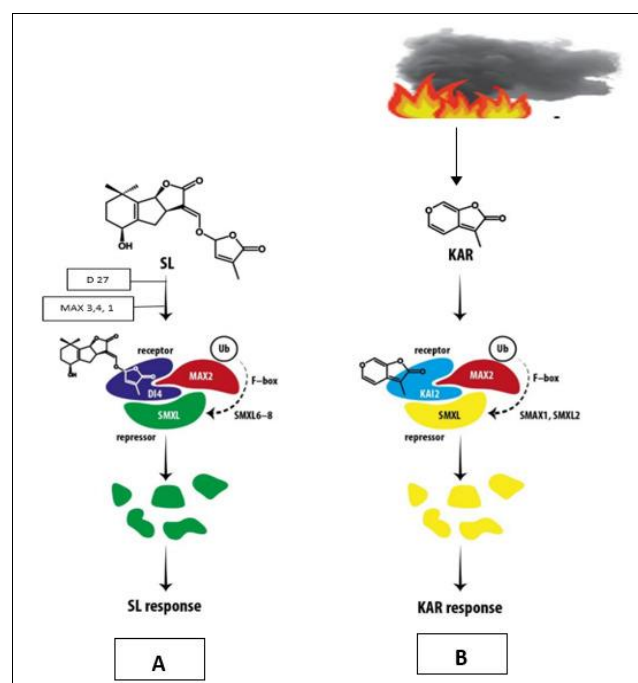


Fig 4: Molecular model of strigolactone (A) and karrikin (B) signaling pathways.

Interaction of Karrikins with other Plant Hormones

Plant growth and development involve complex hormonal crosstalk. Understanding how karrikins interact with other plant hormones is essential for elucidating their role in seed germination and plant development.

1. ABA inhibits the action of KARs on seed germination.
2. KARs promote seed germination by stimulating GA biosynthesis, whereas ABA counteracts this effect by promoting seed dormancy (Nelson *et al.*, 2009) [20].
3. KARs suppress the expression of IAA (auxin) response genes (Nelson *et al.*, 2011; Gilkerson *et al.*, 2015) [21, 7], potentially accelerating germination by attenuating auxin signaling.
4. KARs inhibit hypocotyl elongation and lateral root development through mechanisms yet to be fully characterized, while simultaneously promoting root hair elongation, nodule development, and arbuscular mycorrhizal colonization (Yang *et al.*, 2019) [31].
5. The interactions between KARs and gibberellins, abscisic acid, and auxins collectively orchestrate transitions between dormancy and active germination under varying environmental conditions.

A. Role of Karrikins under Abiotic Stress

1. In *Arabidopsis*, KARs protect seeds from abiotic stress during germination and promote drought resistance by enhancing antioxidant defense, cuticle formation, stomatal closure, and anthocyanin biosynthesis (Yang *et al.*, 2019) ^[31].
2. KAR–KAI2 signaling maintains seed dormancy under unfavorable abiotic conditions while promoting germination under favorable conditions (Fig. 5) (Yang *et al.*, 2019) ^[31].
3. KARs improve seedling sensitivity to light and enhance seedling establishment under low-light conditions (Waters and Smith, 2013) ^[30].
4. Meng *et al.* (2016) ^[17] demonstrated that KARs delay soybean seed germination specifically under shaded conditions by promoting ABA biosynthesis and inhibiting GA production. This effect was not observed under white light or darkness, indicating a light-dependent modulation of karrikin activity distinct from its role in *Arabidopsis*.

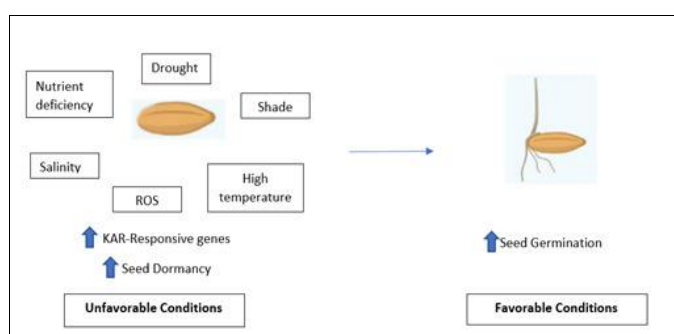


Fig 5: Karrikin response under abiotic stresses.

B. Effects of Karrikins on Crop Growth and Development

1. In tomato, okra, maize, and rice, both smoke water (1:500 dilution) and KAR1 (100 nM) significantly increased shoot and root growth (Kulkarni *et al.*, 2006; Van Staden *et al.*, 2006) ^[11, 26].
2. In maize, soaking kernels in 100 nM KAR1 for 1 hour enhanced post-germination seedling growth compared to untreated controls (Van Staden *et al.*, 2006) ^[26].
3. KAR1 has been demonstrated to promote tomato seed germination and subsequent seedling vigor even when grown at sub-optimal (10°C) or supra-optimal (40°C) temperatures. KAR1 also increased plant height, fresh and dry weight, stem thickness, and leaf number (Jain *et al.*, 2006) ^[10].
4. KAR2 promotes *Arabidopsis* seed germination under favourable environmental conditions.

Conclusion and Future Perspectives

Karrikins are a new and intriguing class of plant growth regulators that have important ramifications for both applied agronomy and basic plant biology. The KAI2 receptor, the MAX2 F-box protein, and the SMXL repressor proteins are among the fundamental elements of KAR signaling that have seen significant advancements. Nevertheless, there is still much to learn about the exact molecular role of this route under both normal and stress conditions. The next logical stages in determining the whole mode of action of karrikins are genomic and transcriptome techniques. Furthermore, comprehensive research utilizing integrated physiological, biochemical, and molecular methods is necessary to understand how KARs interact with other plant hormones under various abiotic stress

conditions. The practical use of smoke water and pure karrikin formulations in crop production—especially for enhancing seedling establishment, stress tolerance, and germination under severe temperatures—offers significant agricultural potential. A fascinating new area in the fields of molecular plant physiology, plant evolutionary biology, and fire ecology has been made possible by the discovery of karrikins. As our understanding grows, karrikins have the potential to be valuable tools in the establishment of sustainable, stress-resilient cropping systems.

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