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Karrikins biosynthesis, signaling route, regulatory roles, and hormonal crosstalk in plant soil system

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Modern agriculture will face new obstacles, such as the increased frequency of forest and grassland fire outbreaks brought on by climate change, which will call for creative solutions. The chemicals known as karrikins are present in smoke produced by burning plant matter. Several additional known functions, including seed germination and other photo-morphogenetic processes, are linked to them. Nowadays, it is becoming clearer how KARs can improve plant performance in a variety of ecological limits. KARs not only regulate antioxidative metabolism (SOD, POX, GR, APX) but also up-regulate the expression of several stress-related genes in plants to reduce oxidative stress in plants brought on by biotic and abiotic factors. Plants have an intricate tolerance mechanism that includes stomatal pore management, systemic communication, redox equilibrium maintenance, and other functions to cope with abiotic stressors. In Arabidopsis thaliana, Karrikins signaling is mediated by the F-box protein MAX2, which also controls responses to the structurally related strigolactone family of phytohormones. This review paper goes into great detail about the discovery, biosynthesis, and signaling mechanism of karrikins as well as their interactions with other phytohormones and future prospects.

Keywords: Strigolactone, Plant hormones, Soil, Stress.

1. Introduction

Agriculture in today's world will encounter fresh challenges, such as the rising incidences of forest and grassland fire outbreaks caused by the effects of climate change, which must require novel solutions (Jolly et al., 2015; Soliman et al., 2024). Determining how these will affect ecosystems all across the planet, as well as the pathways generating these changes, is critical. Many researches on the nature of a germination signal provided by burning plant debris have been

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conducted since the first hint of its existence (Antala et al., 2019; Ziliang et al., 2023; Abd El-Kawy et al., 2024).

Karrikins are a chemically characterised class of plant growth regulators identified in plant-burning smoke. Karrikins are effective at breaking the dormancy of seeds from several species suited to regions with frequent fires and smoke (Chiwocha et al., 2009). Karrikins are an assortment of extremely small organic molecule that is formed when plant material burns. Some plants that sprout soon after bushfires or wildfires, in particular, have evolved so that their seeds remain latent in the soil until a fire creates karrikins that are attached to soil particulates. The karrikins then enhance seed germination after being washed into the soil by rainfall (Flematti et al., 2015). Karrikins are also recognised to boost seedling vigour in plants under abiotic stress situations (Shah et al., 2020). Smoke components were isolated by liquid fractionation and examined for their impacts on seed germination activity to discover the active chemicals that contribute to seed germination activity. Bioassays revealed numerous similar chemicals known as karrikins (Flematti et al., 2015). KARs are the most abundant germination-promoting substances found in smoke, and the KAR receptor is found in all phylogenetic taxa of vegetation. KARs represent promising novel plant growth regulators (Morffy *et al.*, 2016), and an unnoticed intrinsic molecule perceived through the identical signalling process is a potential intriguing hormone. However, smoke contains not only germination stimulators, but also inhibiting substances from butenolides (Scaffidi et al., 2012a). Using KARs instead of aerosol smoke or smoke-water is a better option for scientific study and farming, given the lower expense of aerosol smoke and smoke-water. A different way of applying KARs to cultivated soils is subsequently by means of biochar, where KARs were only recently discovered (Kochanek et al., 2016). Besides from the KARs information, biochar has various additional advantages. It increases the soil's mineral adsorption and water-holding efficiency. According to new investigations, karrikins imitate an undiscovered biological chemical that has a function in the germination of seeds as well as the initial development of plants. The innate signalling molecule is likely to be connected not just to karrikins, but also to strigolactone hormones (Antala et al., 2022). Many other plant products, including cellulose filter paper, and sugars, were discovered to produce karrikins when burnt. The pyran ring of karrikins, which is thought to be produced directly from pyranose sugars in plant material, is explained by their creation from carbohydrates. The specific chemical process is unclear, although it requires oxygen, and seed-germination operation may be generated by cooking/heating/roasting plant material at 180 °C for 30 minutes. Cigarette smoke promotes seed germination, most likely owing to the presence of karrikins. More study has revealed that karrikins are unstable at extremely elevated temperatures (Scaffidi et al., 2012b). As a result, it is believed that they are formed in the smaller severe portions of wildfires, vaporise and accumulate in the smoke, followed by condensation, and get attached to soil in the same manner that cooling smoke may be projected onto seeds to induce germination. Karrikins can be 'carried' in smoke by means of steam distillation, although they aren't transported to long distances and tend to stay nearby fire (Nelson et al., 2012).

Karrikin assessments in soil are physically complex, however seed-germination bioassays can be used to identify operations, with an investigation indicating that active compound(s) may continue to exist in the soil for a period of over seven years after a fire (Preston and Baldwin, 1999).Thus, they may be anticipated to expire fast in natural sunshine; nevertheless, smoke contains several volatile substances that can absorb UV light and potentially preserve karrikins by functioning as biological 'sunscreens' (Scaffidi *et al*., 2012b). On the contrary, may be swept away by rain and dissolve swiftly through sandy soils, thus their concentration will slowly reduce. Plant-derived smoke and smoke water (SW) have been shown to increase seed germination in a variety of plants from both fire-prone and fire-free locations, including cultivars and agricultural weeds (Kępczyński and Kępczyńska, 2023). It took several years to find the component responsible for accelerating smoke-driven germination among thousands of chemicals in smoke. In 2004, two independent researchers isolated butanolide, which is now known as karrikin 1 (Van staden et al., 2004). The first karrikin discovered, abbreviated as KAR_1, was initially named gavinone and then renamed as Karrikin. Karrikins are classified into six types: KAR1, KAR2, KAR3, KAR4, KAR5, and KAR6 (Flematti et al., 2015). The most active karrikins are KAR1, KAR2, KAR3, and KAR4. Because of its greater activity than KAR1, KAR2 is widely employed in Arabidopsis thaliana investigations (Nelson et al., 2009; Waters et al., 2023).

Karrikins only include the elements C, H, and O and have two ring configurations, one of which is a pyran and the other a lactones with a butenolide, a five-member ring. With a melting temperature of 118–119 °C, the pure compound is a crystalline material that readily dissolves in organic solvents but only sparingly in water. The structures of all karrikins are closely linked (Hrdlička et al., 2019). Smoke releases karrikins, release them in large numbers (Flematti et al., 2004). Karrikins are created when sugars and other polysaccharides, primarily cellulose, are heated or burned (Bursch et al., 2011). These sugars become karrikins when plant material burns. Karrikins may also be created by burning plant-based items including straw, filter paper, cigarettes, and certain sugars. After heating plant material to 180 °C for 30 minutes, seed germination activity may be produced. "Fire-followers" are plants that rely on karrikins to flourish (Flematti et al., 2015).

Karrikins are said to promote seedling vigour as well as seed germination (Antala *et al*., 2019). Karrikins have an impact on seedling photomorphogenesis in Arabidopsis, leading to shorter hypocotyls and bigger cotyledons (Bursch *et al*., 2011) .When seedlings erupt into the post-fire situation, such reactions could provide them a competitive advantage. Since the KAI2 protein is also necessary for the formation of leaves, karrikins may have an impact on several other aspects of plant development (Varshney *et al*., 2023). The recognition and confirmation of KAR1's enormous biological activity when isolated from plant-derived or synthesised smoke may enable application in farming and landscaping to reestablish natural plant life while implementing weed management methods (Kępczyński and Kępczyńska, 2023; Farooq *et al*., 2019). The current study aims to provide a comprehensive understanding of the various roles that karrikins play in plant growth and development, as well as a brief overview of their biosynthesis and signaling networks, as well as the metabolic changes that karrikins cause in plants, given their complex function in both normal and stressed environmental conditions. Furthermore discussed is the interplay between SLs, karrikins, and other phytohormones under adverse conditions.

2. History of Karrikins

For many years, it was believed that some fire-follower seeds were spurred to germinate not by the heat of fire but by the chemicals produced by themselves (Nelson et al., 2012). Smoke has the potential to have a similar outcome as fire, just as water that has been infused with char or has been exposed to smoke, resulting in the creation of a substance known as "smoke water" (De Lange and Boucher, 1990). Numerous international research teams embarked on a quest to identify the relevant chemical by employing a methodology that entailed the partitioning of the myriad compounds present in smoke water into distinct fractions by the utilization of liquid chromatography. Subsequently, each fraction was subjected to rigorous testing to ascertain its potential for stimulating seed germination. The fractions that were initially active were subjected to further fractionation and subsequent analysis. The utilization of bioassay-guided fractionation ultimately resulted in the identification and isolation of a bioactive molecule, afterward validated through chemical synthesis. The chemical under consideration consists of a distinct variety of lactone, specifically a butenolide, which is fused to a pyran ring. It is assigned the systematic name 3-methyl-2H-furo[2,3-c] pyran-2-one. Following this discovery, a number of similarly related compounds were subsequently identified in smoke and collectively designated as 'karrikins' (Flematti et al., 2004).

Karrikins, a group of chemical compounds, garnered attention in the early 2000s primarily for its notable function in facilitating seed germination. The phenomena of improved seed germination in plant species from fire-prone habitats after exposure to smoke or smoke-derived chemicals has attracted the attention of researchers. The observation incited interest and subsequently prompted a methodical investigation of these chemicals (Scaffidi et al., 2011). In a seminal study published in the renowned scientific magazine "Science" in 2004, a team of researchers from the University of Western Australia, led by Dr Kingsley Dixon and Dr Gavin Flematti, achieved notable advancements in their respective fields. The researchers successfully identified and characterized Karrikin-1 (KAR1), a highly effective stimulator for germination. This significant discovery yielded empirical evidence that substantiates the presence of these substances and their function in the process of seed germination, specifically in plants that have evolved to places prone to fires (Chiwocha et al., 2009). As of now, a total of six karrikins have been identified in smoke, each of which has been assigned the designations KAR1, KAR2, KAR3, KAR4, KAR5, and KAR6. The karrikins denoted as KAR1 to KAR4 exhibit the highest level of activity. KAR1, alternatively referred to as karrikinolode, represents the initial karrikin compound that was identified. The concentration of KAR1 in smoke is significantly higher, ranging from 5.5 to 38 times greater than that of other karrikins. The concentration of KAR1 was determined to be 6.7×10^{-7} M, which was observed to correlate to a dilution of 1:100 in SW (Van Staden et al., 2004; Nelson et al., 2012; Nair et al., 2014).

Karrikins are a class of chemical compounds that were first discovered in the smoke from wildfires. These chemicals have been shown to play an important part in the biology of plants and are also known as karrikin-like compounds or KARs (Chiwocha et al., 2009). These compounds are well-known for their exceptional capacity to increase seed germination, particularly in ecosystems that are prone to fire. They accomplish this remarkable feat by breaking seed dormancy and encouraging early growth in the seedling. Karrikins have an effect on a number of elements of plant development in addition to germination, including root growth, flowering period, and the plant's response to stress (You et al., 2020). Their activity is regulated by specific receptor proteins that go by the name KAI2, and these proteins start the signaling pathways that lead to a variety of different growth responses. Because of this discovery, researchers are looking at ways to harness the benefits of karrikin to improve crop yields, stress tolerance, and pest resistance (Fang et al., 2023). The consequences of this study are significant for the agricultural industry. In addition, karrikins have the potential to be used in environmental restoration, specifically in the process of assisting ecosystems in their recovery after being disrupted by natural disasters such as wildfires. In general, karrikins are a fascinating topic of study that holds a great deal of promise for the advancement of plant biology as well as human endeavours in the fields of agriculture and the management of ecosystems (Mukherjee et al., 2023). Karrikinolide, also known as butenolide or 3-methyl-2H-furo[2,3-c]pyran-2-one (KAR1), was initially discovered in 2003 as a highly effective germination stimulant found in smoke emitted from plants. The current literature has provided information regarding the isolation process of the compound (Flematti et al., 2007). Furthermore, the conclusive evidence supporting its structure was found through synthesis.

The synthetic compound KAR1 exhibited significant germination activity at concentrations lower than 1 ppb (10^-9 M) when tested on Grand Rapids lettuce seed (*Lactuca sativa* cv) and various smoke-responsive species from Australia (*Conostylis aculeata*, *Stylidium affine*), South Africa (*Syncarpha vestita*), and North America (*Nicotiana attenuata*, Emmenan thependuliflora). The structural arrangement of KAR1 was subsequently validated by an independent research team, who demonstrated that their isolated molecule, referred to as KAR1, also facilitated the germination process of Grand Rapids lettuce seed (Van staden et al., 2004). Several publications have been published recently that discuss the biological activity of the subject, as discussed in references (Light et al., 2009).

Karrikinolide has been found to induce seed germination in a diverse range of plant species, including both gymnosperms and angiosperms. This effect is observed across various plant life forms such as trees, shrubs, perennials, and herbs, as well as in different plant environments and seed dormancy classes. Additionally, karrikinolide's ability to stimulate seed germination is consistent with the response observed in species that are known to be responsive to smoke (Goddard-Borger et al., 2007). Thus far, our research has shown positive responses to KAR1 in seeds from over 60 species, which belong to 26 plant families with various evolutionary backgrounds. It is worth noting that all of these plants are known to be susceptible to smoke. The identification of KAR1 unveiled a previously unknown category of chemical compounds that exhibit activity in plants. These chemicals, referred to as karrikins, are distinct from other naturally occurring butenolides. Several synthetic karrikins have been synthesised and have demonstrated germination activity (Flematti et al., 2007). The response to karrikins, however, exhibits variation among different species. As an illustration, KAR2 (2) has been identified as the karrikin with the highest level of activity in Arabidopsis germination. However, it is noteworthy that its activity is significantly lower when compared to KAR1 in other species (Nelson et al, 2009). KAR3 (3) exhibits a similar capacity to increase germination as KAR1 (1), but KAR4 (4) does not demonstrate activity in Arabidopsis. However, it can stimulate germination at elevated concentrations in smoke-responsive species such as *Lactuca sativa* (lettuce), and *Solanum orbiculatum* (Waters et al., 2014). Moreover, it is probable that smoke comprises additional unidentified chemicals that possess the ability to induce seed germination. Hence, it is imperative to take caution when comparing research involving the utilisation of pure karrikins and purified smoke-water mixtures interaction with plant hormones.

3. Synthesis of Karrikins

The synthesis of karrikins in plants is a biological process that is both fascinating and complex, and it has been the focus of study that is now being conducted. Karrikins are not formed naturally by plants but are instead taken from external sources such as smoke, which is a typical occurrence in habitats that are prone to fire (Swaebreck et al., 2021). Karrikins are found in ecosystems that are prone to fire. The heat and the combustion of organic materials that occurs during wildfires as well as controlled burns cause the release of volatile compounds into the air (Nair et al., 2014). Some of these compounds are precursors to karrikin. A number of chemical reactions take place inside the plant tissues as a result of the deposition of these precursor compounds into the soil or the uptake of these compounds by plants. The metabolism of karrikin precursor chemicals is an important stage in the manufacture of karrikins in plants. This phase ultimately results in the creation of active karrikin molecules (Antala et al., 2019). This mechanism is not yet completely understood; however, research suggests that it most likely involves enzymes and metabolic pathways that are specific to plant responses to environmental stressors such as fire. The production of karrikins in plants is an integral part of the intricate signaling network that gives them the ability to respond to and recover from the effects of fire. Once formed, karrikin molecules link to certain receptor proteins (KAI2), which in turn sets off a signaling cascade that ultimately affects different aspects of plant growth and development. These features include seed germination, root growth, and responses to abiotic stress (De Cuyper et al., 2017). Understanding the complexity of karrikin synthesis and signaling pathways in plants has promise for uses in agriculture. Researchers are studying ways to utilize karrikin effects to boost crop growth and resistance, and this understanding holds potential for agricultural applications. In addition, this information helps to our broader understanding of the ways in which plants respond to environmental signals and the function that chemical signaling plays in determining the biology of plants in environments that are prone to fire (Flematti et al., 2015; Lili et al., 2023).

Here's an overview (Figure 1) of how karrikins are involved in the germination process and how plants respond to them:

Karrikin Production: Karrikins are not synthesized by plants themselves but are produced during the combustion of plant material, such as during wildfires or controlled burns. When plant material burns, it releases a complex mixture of volatile organic compounds, including karrikins.

Seed Germination: Karrikins play a crucial role in seed germination for many plant species. When smoke containing karrikins meets soil or seeds, it can break seed dormancy and stimulate the germination process. This adaptation is believed to be an evolutionary response to fire-prone environments, as it allows seeds to germinate and establish new plants after a fire has cleared the land (Maurya et al., 2014).

Karrikin Receptors: Plants have evolved specific receptors called KAI2 (Karrikin Insensitive 2) proteins that can detect and bind to karrikins. When a seed with KAI2 receptors is exposed to karrikin compounds, it triggers a signalling cascade that ultimately leads to changes in gene expression and the promotion of germination (Yao et al., 2021; Zejun et al., 2023; Farid et al., 2020).

Germination Promotion: The binding of karrikin compounds to KAI2 receptors leads to the activation of downstream genes associated with seed germination. This activation includes the expression of genes involved in breaking seed dormancy, increasing water uptake, and initiating root and shoot growth. While plants do not directly synthesize karrikins, they have evolved specific receptors to detect these compounds when they are present in the environment. This allows plants to take advantage of karrikins as a signal for the onset of favourable conditions for seed germination, such as after a fire. Karrikin perception and signaling are important adaptations that help plants thrive in fire-prone ecosystems.

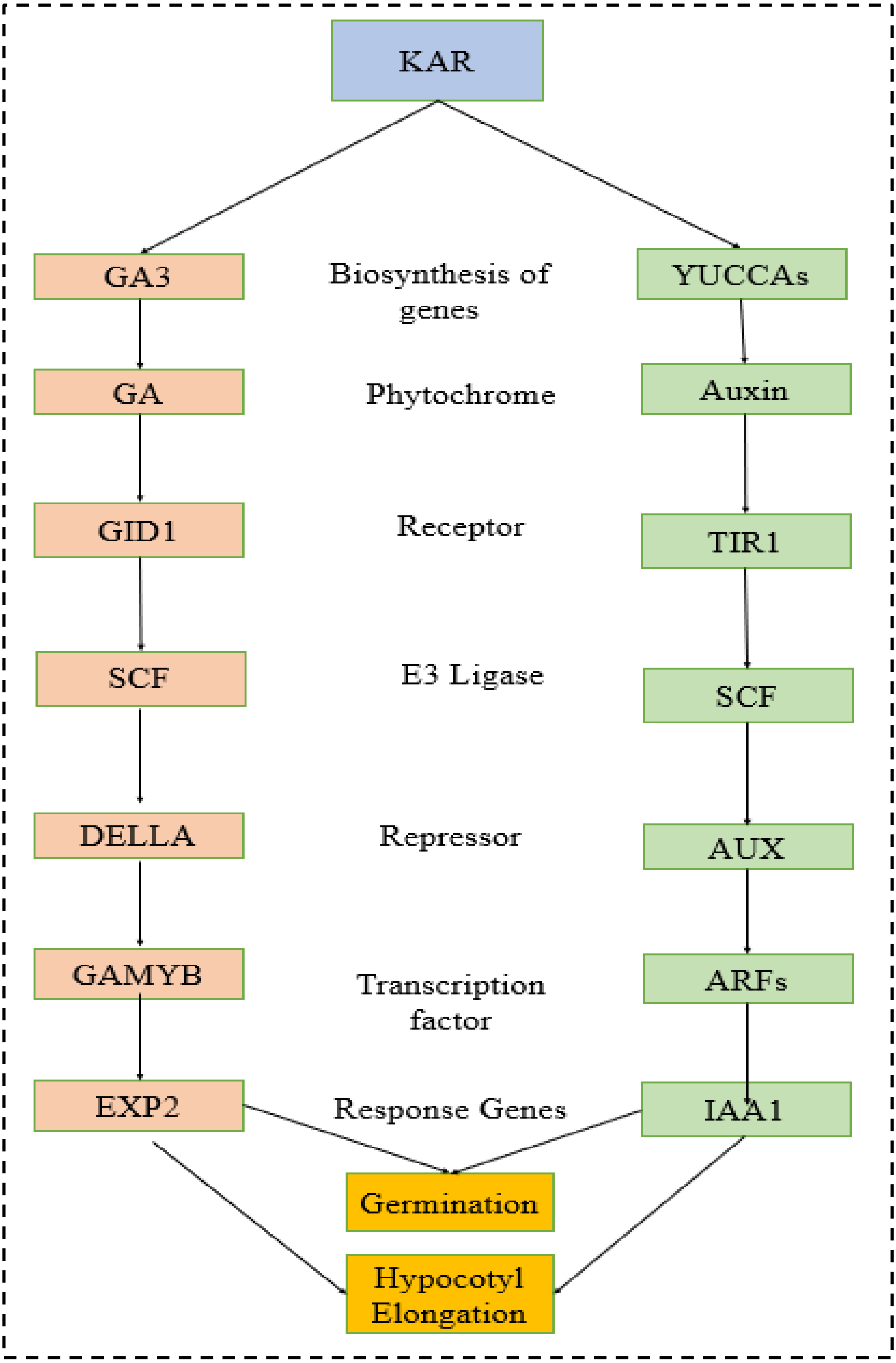

Fig. 1. Karrikins may control the crosstalk of endogenous phytohormones, which in turn controls seed germination and hypocotyl elongation.

4. Action Mechanism of Karrikins

The findings of Guo et al, (2013) offer fresh understanding of the mechanism behind how karrikins are seen by the brain. These researchers found that KAR1 was in a hydrophobic region within the active-site pocket of AtKAI2, but it was not close enough to the catalytic triad residues to be vulnerable to nucleophilic assault. A method for nucleophilic assault and esterase-type activity of KAI2 on karrikins had previously been proposed. Furthermore, molecular modelling predicted that the butenolide might sit near the active site serine catalytic triad. There is still a great deal to learn about these a/b-hydrolases, but a recurring idea is that they seem to lead a peculiar double life as both enzymes and receptors. This is an emerging theme in the field. Instead, Guo et al. (2013) hypothesised that the butenolide of KAR1 might be more functionally comparable to the C-ring lactone of SL than it would be to the structurally analogous D-ring butenolide. Modelling GR24 within the active site pocket of AtKAI2 required the authors to align the C-ring with the observed location of the butenolide ring of KAR1. This would place the D-ring of GR24 near the catalytic triad, which would then encourage nucleophilic assault upon the carbonyl group of the D-ring. Indeed, Zhao et al. (2013) demonstrated that nucleophilic assault takes place on the D-ring carbonyl by seeing the intermediate 2,4,4-trihydroxy-3-methyl-3-butenal which was covalently bonded through C1 to the serine in the active site of rice D14.

There is a lack of agreement regarding whether KAI2 is capable of processing GR24. On the one hand, both AtKAI2 and OsKAI2 have been reported to have no hydrolytic activity towards GR24, while another report suggests that GR24 does not interact with AtKAI2 in ITC assays (Kagiyama et al., 2013). However, there is a lack of agreement regarding whether KAI2 is capable of processing GR24. On the other hand, genetic studies show that Arabidopsis seeds and seedlings perceive GR24 through a process that is dependent on KAI2 (Wters and smith, 2013). Because of this, there is still a lack of clarity regarding the ligand specificity of KAI2, as well as its precise ligand–receptor interactions and natural substrates. It seems that karrikins can induce conformational change in KAI2 without the involvement of hydrolysis, in contrast to what happens to SL when they are seen by D14, which causes them to be hydrolysed and eliminated. Once an appropriate KAI2 binding partner has been found, it is possible that karrikins will be further pushed into the active site. This would result in the butenolide being positioned near the catalytic triad. There is still a lot that needs to be understood about these a/b-hydrolases, but one thing that is becoming clear is that they seem to have a peculiar double life as enzymes and catalysts.

5. Analysis of the karrikin response from a molecular and physiological perspective

The local ecosystem is altered in several different ways as a result of the fire. It gets rid of the leaves and the leaf litter, recycles the nutrients, enables the warming of the soil through the process of blackening, and produces a toxic mixture of chemicals, including karrikins. In order to take advantage of these events, what sorts of adjustments to the seed could be required? It is necessary for the seed to develop some kind of physiological dormancy in order to delay germination until conditions that are suitable for the post-fire period are satisfied (Table 1). This state of dormancy could be broken through a combination of different mechanisms, such as cold or warm stratification, wet–dry cycling, or exposure to chemical stimulants such nitrates, cyanohydrins, and karrikins (Footitt et al., 2013). In the case of a reaction to karrikins, we might be able to anticipate several alterations at the molecular and genetic levels. As part of the process of dormancy specialization, there is a possibility that the spatio-temporal expression pattern of the KAI2 and/or MAX2 genes will shift. It is presumed that KAI2 and MAX2 will need to be produced in a stable form before the arrival of the karrikin signal. It is also conceivable that there may be an increase in expression during the process of imbibition, though possibly only under specific light or temperature conditions. There is a possibility that the expression of KAI2 will reinforce itself:

Once a certain threshold concentration of karrikin is recognized, KAI2-dependent positive regulation of KAI2 transcripts or KAI2 translation would aid to commit the seed to germinate, which would be beneficial for the plant. Alterations in the main sequence of the KAI2 protein are also possible, possibly occurring in the active site to improve the affinity for a karrikin substrate and/or decrease the affinity for SL, or possibly occurring on the surface to attract specific protein binding partners (Villaécija-Aguilar et al., 2022). The fact that KAI2 naturally stimulates germination and probably interacts with an endogenous ligand or substrate while doing so adds an additional layer of complexity to the situation. For the seed to be able to detect exogenous karrikin at very low quantities, the abundance of this ligand or substrate and/or the affinity of KAI2 for it would need to decrease. Additional changes may take place in the seed of smoke-responsive species, including increased tolerance to the several inhibitory chemicals found in smoke. Table 2 contains karrikins responses to various abiotic stresses on different plants.

TABLE 1. Physiological role of karrikins in different plants.

Plant species	Specific role	References
C. monilifera ssp.	Promote germination of physiologically dormant seeds	Reynold et al., 2014
B. oleracea	Improvement of water absorption of seeds	Sami et al., 2021
A. fatua	An increase GSSG/GSH ratio indicates that the seeds have developed a tolerance to potential oxidative stress caused by reactive oxygen species.	Cembrowska et al., 2016
Triticum aestivum	Promotes germination and root length	Saglam et al., 2019
Brassica napus	Shortening of hypocotyl under continuous red light	Antala et al., 2019
Arabidopsis thaliana	The presence of germination-active karrikins intensified light-dependent cotyledon expansion and suppressed hypocotyl elongation.	Nelson et al., 2010
Brachypodium distachyon	Bdkai2 exhibits increased internode elongation and decreased leaf chlorophyll levels, with only a slight increase in water loss from detached leaves. An increased in number of lateral roots, reduced root hair growth, and an inability to support normal root colonization by arbuscular-mycorrhizal (AM) fungi was also observed	Meng et al., 2022
Sapium sebiferum KAI2	Plays a role in seed germination, hypocotyl growth, and the mitigation of salinity and osmotic stress.	Shah et al., 2021
Glycine max L.)	Cold plasma treatment notably enhances soybean seed germination, subsequently supporting seedling establishment and growth processes.	Meng et al., 2016
Brassica alboglabra	Enhances the defense response to temperature and cadmium-related environmental stresses by regulating plant physiological processes.	Ahmad et al., 2021

Table 2. Karrikins role in abiotic stress tolerance.

Abiotic Stress	Plant species	Role of Karrikins	References
Drought	*Trachyspermum copticum; Foeniculum vulgare; Cuminum cyminum*	Seed germination percentage, rate, index, radicle length seedling vigor and shoot length	MousaviNik, et al., 2016
Cold	*Solanum esculentum*	Improved Seed germination and vigor index of seedlings	Fang et al., 2023
Drought	*Lotus japonicas*,	Drought mitigation and growth enhancement	Ahmad et al., 2022
Drought and salt	*Sapium sebiferum*	Enhanced seedling biomass, extended taproot length, and increased the number of lateral roots under abiotic stress conditions.	Shah et al., 2020
Drought	*Agrostis stolonifera* cv. PennA4)	Leaf chlorophyll and proline content, membrane stability, and significantly elevated activities of antioxidant enzymes.	Tan et al., 2023
Salinity and heat	Arabidopsis	Preserve viability while preventing germination in unfavorable conditions.	Kamran et al., 2024; Zein et al., 2022
Fire-prone environments	Asteraceae	stimulate seed germination	Dawood et al., 2024
Cold	*Solanum lycopersicum*	Cold tolerance through the strigolactone and abscisic acid signaling network.	Liu et al., 2023
Salt stress	Arabidopsis	Signaling helps reduce water loss under salinity stress, maintaining relative water content.	Mostofa, et al., 2022

6. Signalling pathway of Karrikins

The signalling pathways of karrikins in plants involve a complex series of molecular interactions that play a crucial role in regulating various aspects of plant growth and development, particularly in response to environmental cues such as smoke from wildfires. These pathways are still a subject of ongoing research, but scientists have made significant progress in understanding how karrikins trigger these responses. Karrikins initiate their signalling pathway by binding to specific receptor proteins known as KAI2 (Karrikin Insensitive 2). KAI2 receptors are part of a larger family of proteins called α/β-hydrolases. When karrikins are present, they fit into the binding site of KAI2 receptors, triggering a conformational change in the receptor protein (Stanga et al., 2016). This conformational change in KAI2 is the key initiating event in the karrikin signalling pathway. It sets off a series of downstream molecular events, ultimately leading to changes in gene expression and cellular processes. While the exact details of this cascade are still being unravelled, some key components have been identified. One important downstream component in the pathway is MAX2 (More Axillary Growth 2), a protein that interacts with KAI2. MAX2 acts as an intermediary between KAI2 and other signalling proteins. When karrikins activate KAI2, MAX2 gets involved in transmitting the signal to other proteins, ultimately influencing various growth responses in the plant (Mizuno et al, 2021). The signalling pathway of karrikins is highly versatile and can affect different aspects of plant growth and development depending on the specific context. It can influence seed germination by breaking seed dormancy and promoting early growth. Additionally, it can stimulate root development, affect flowering time, and modulate stress responses, enabling plants to adapt to changing environmental conditions. Overall, while much has been discovered about the signaling pathways of karrikins, there is ongoing research to uncover the finer details of these intricate processes. Understanding these pathways not only sheds light on fundamental aspects of plant biology but also holds great potential for applications in agriculture, where researchers aim to harness the power of karrikins to improve crop yield, stress tolerance, and pest resistance, ultimately contributing to more sustainable and resilient agricultural systems.

Karrikins are signaling molecules that play a crucial role in promoting seed germination and other developmental processes in plants, especially in response to environmental cues such as smoke or charred plant material. The signaling of karrikins involves a series of molecular events that ultimately lead to changes in gene expression and the initiation of germination. Here's an overview of the signaling of karrikins:

- Detection of Karrikins: The process begins with the detection of karrikins by specific receptors in plants. These receptors are known as KAI2 (Karrikin Insensitive 2) proteins, and they are responsible for recognizing and binding to karrikin molecules (Sun et al., 2016).
- Binding to KAI2 Receptors: When karrikin molecules meet the KAI2 receptors on the plant's cell surface, they bind to these receptors. This binding event initiates a signalling cascade within the plant cell.
- Activation of Signalling Pathways: The binding of karrikin to KAI2 receptors triggers a series of intracellular events, including the activation of various signaling proteins and cascades. These signaling pathways often involve the release of secondary messengers, such as calcium ions (Ca2+), which transmit the signal from the cell membrane to the nucleus.
- Gene Expression Changes: The activated signaling pathways ultimately lead to changes in gene expression. Specific genes that are associated with seed germination and early seedling development are upregulated in response to the karrikin signal. These genes encode proteins involved in processes such as breaking seed dormancy, promoting root and shoot growth, and facilitating nutrient uptake (Weng et al., 2018).
- Germination and Seedling Development: The altered gene expression patterns result in the initiation of germination and the development of the seedling. This includes the degradation of inhibitory compounds that maintain seed dormancy, the emergence of the radicle (the embryonic root), and the elongation of the shoot (Meng et al., 2017).

Coordinated Growth: Karrikin signalling helps ensure that the timing of seed germination and early seedling growth is well-coordinated with favourable environmental conditions, such as the presence of moisture and nutrients in the soil. This adaptive response allows plants to take advantage of post-fire environments, where karrikins are often present. The signalling of karrikins in plants involves the recognition of these compounds by KAI2 receptors, which then initiate a series of molecular events that lead to changes in gene expression and the promotion of seed germination and early seedling development. This signaling pathway is an important adaptation that allows plants to respond to environmental cues associated with fire and smoke.

7. Interaction with plant hormones

Smoke chemicals derived from plants have been found to cause various effects on seeds. These effects include changes in the sensitivity of seeds to phytohormones and light needs, as well as variations in the morphology and permeability features of the seed coat (Egerton-Warburton, 1998). The idea suggests that KAR1's ability to induce germination in several species at doses lower than 1 ppb or 1 nM may be attributed to its influence on the generation or metabolism of other phytohormones. Gibberellic acid (GA) is known to have a significant impact on the release of dormancy and the facilitation of germination in several species. Conversely, abscisic acid (ABA) is responsible for inducing and prolonging seed dormancy (Kucera et al., 2005; Cheng et al., 2022).

The production of two important gibberellic acid (GA) biosynthetic enzymes, GA3ox1 and GA3ox2, was stimulated by the presence of KAR1 in initial dormant seeds of Arabidopsis thaliana. However, the levels of endogenous abscisic acid (ABA) and GA4 remained unchanged prior to the onset of germination. The lack of measurement for GA3-oxidase activity introduces the possibility that the observed increase in GA3-oxidase transcripts in samples treated with KAR1 does not accurately represent the quantity or functionality of the enzyme. The study found that KAR1 did not have a significant effect on increasing sensitivity to GA in an Arabidopsis mutant lacking GA, nor did it decrease sensitivity to ABA in an ABA-deficient mutant coat (Egerton-Warburton, 1998). The application of KAR1 has a significant impact on decreasing the quantities of exogenous GA3 and GA4 needed to stimulate the germination process in seeds of *Stylidium maritimum*. This plant species is representative of a smoke-responsive Australian genus, which was initially utilised to detect the effects of KAR1. Nevertheless, the levels of endogenous ABA, GA1, GA3, and GA4 were not found to be significantly modified throughout the pre-germination stage, as indicated by unpublished data from D. Merritt. On the other hand, previous research has examined the germination process of lettuce, a plant species that necessitates light for successful germination (Kucera et al., 2005). Additionally, studies have also been conducted on N. attenuate. In a study conducted by S.D.S. Chiwocha et al. (2009) in the field of plant science, it was demonstrated that extracts obtained from plants had the ability to elevate endogenous gibberellic acid (GA) levels while simultaneously reducing abscisic acid (ABA) levels. The findings from these investigations indicate that the role of KAR1 is not limited to altering the metabolism or perception of GA and ABA. However, additional experiments involving several species and a comparison between smoke extracts and pure karrikins are necessary.

8. Future Prospective of Karrikins

Karrikins are a class of growth regulators of plants that play an important part in a variety of areas of plant biology. They are also known as karrikin-like compounds (KARs). The investigation of karrikins has been going on for a number of years, and the prospects for their future hold promise for a number of different fields, including agriculture, environmental research, and even human health. The following is a list of possible future applications for karrikins:

- Karrikins have been demonstrated to accelerate the germination of seeds and enhance the development and proliferation of a variety of crops, which leads to an increase in crop yield as well as an improvement in crop quality. As research is carried on, there is the possibility that karrikins will be used in agricultural settings in creative ways in the future. Farmers may be able to boost yields of crops and improve the overall quality of agricultural goods by maximising the usage of these tools in their operations (Morffy et al., 2016).
- Karrikins could play a significant role in the movement towards more sustainable agricultural practises, which is an important consideration in light of the growing number of global concerns, such as the impact of climate change. These compounds have the potential to lessen the demand for artificial fertilisers and pesticides, which would pave the way for more sustainable agricultural practises.
- Resistance to Drought and Other Environmental Stressors: Research has shown that karrikins have the ability to increase a plant's tolerance to drought as well as other environmental stressors. This quality is particularly valuable in a world where climate change is leading to droughts that are both more frequent and more severe. It's possible that in the future, research will centre on generating crops that are more resistant to these obstacles (Salehi-Lisar et al., 2016).
- Biopesticides: Biopesticides based on karrikin have the potential to either replace or supplement conventional chemical pesticides. Not only would this lessen the toll that pesticide use takes on the natural world, but it would also lower the dangers posed to the health of both farmers and consumers.
- Karrikins have the potential to have an effect on both the biodiversity and the ecological restoration of plant groups. They can be put to use to assist in the restoration of degraded areas or in the promotion of the growth of particular plant species as part of restoration efforts.
- Human Health: Despite the fact that karrikin research has primarily been conducted on plants, there is the possibility that it could be applied to improving human health. Compounds with structural similarities to karrikin have been studied for their potential anti-inflammatory and anti-cancer effects. New medical applications for these chemicals might be discovered in the course of future study (Dell'Oste et al., 2021).
- Biotechnology and Genetic Engineering: Recent developments in biotechnology may one day make it possible to do precise manipulations of plant pathways connected to karrikin. This could pave the way for the creation of genetically engineered crops with improved growth characteristics or resilience to the effects of stress.
- Cleanup of Polluted Environments Another potential area of application for karrikins is in the field of environmental cleanup. They could be utilised to encourage the restoration of natural habitats or to boost the growth of plants that assist clean up contaminated soils.
- Commercialization: As our comprehension of karrikins grows, there may become potential for the industrial production of goods that are based on these chemicals. This may involve the

use of specialised fertilisers, growth promoters, or other agricultural inputs.

- Regulatory Considerations: It is highly likely that the usage of karrikins will be subject to regulatory examination. This is typical for the introduction of any new technology or agricultural practise. In order for products derived from karrikin to be successfully integrated into agriculture and other fields, it will be necessary to demonstrate that these products are both safe and effective (Yang et al., 2019).

9. Conclusion

The historical and current state of karrikins in the realm of plant biology elucidates an intriguing trajectory of exploration and prospective utilization. Karrikins were initially hypothesized to be chemical compounds synthesized by seeds that exhibit a propensity to thrive in areas affected by the fire. However, subsequent research efforts led to the identification of karrikins as bioactive molecules that play a crucial role in facilitating seed germination in fire-prone ecosystems. The chemical known as Karrikin-1 (KAR1) has been found to have a notable impact on the process of germination. This discovery has subsequently led to the identification of multiple karrikin compounds present in smoke. The existing knowledge on karrikins suggests that they play a crucial part in the process of seed germination and the overall development of plants. Plant growth is influenced by the activation of specialized receptors known as KAI2, which triggers complex signalling pathways. These pathways have a significant impact on numerous aspects of plant development, such as the release of dormancy, the formation of roots, and the plant's response to stress. The elucidation of these molecular mechanisms provides opportunities for leveraging the karrikin-induced effects in the field of agriculture, with the aim of augmenting crop productivity, fortifying plants against various stressors, and bolstering resistance against pests. The potential applications of karrikins extend beyond the realm of agriculture. They exhibit potential for the rehabilitation of the environment, study on human health, and breakthroughs in biotechnology. Additionally, the investigation of remediation strategies for contaminated settings and the exploration of potential applications of karrikins in commercial products are topics of significant interest. The integration of karrikin-based solutions into numerous industries is expected to be accompanied by regulatory considerations. As ongoing research progresses, karrikins are positioned to assume a substantial role in tackling the complexities associated with sustainable agriculture, ecosystem restoration, and human well-being. Consequently, they have become a subject of enduring intrigue and have the potential for significant advancements in the field of plant biology and beyond.

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