



Plant-derived Smoke: A Sustainable Technique for Seed Enhancement

Monika K.G. ^{a++*}, Dijee Bastian ^{a#},
Vidhu Francis Palathingal ^{a†}, Aparna A. Raj ^{a++},
S. Deepthy ^{a++} and Neeraja Rajan ^{a++}

^a Department of Seed Science and Technology, KAU, Thrissur, India.

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Smoke act as an important evolutionary factor involved in post fire germination cues. In South Africa, a study on the endangered fynbos species *Audouinia capitata* brought attention to the role smoke plays in promoting germination. Farmers of South Africa employ conventional method of exposing seeds to smoke as it provides protection against insects and pathogens. Additionally, this technique was shown to improve seedling vigor and germination in specific plant species. By directly exposing seeds to aerosol smoke, treating them with smoke water, or using dynamic compounds extracted from smoke at varying concentrations, the potential benefits of smoke in agriculture were realized. Among these, smoke water shows convenient and promising results. One well-known seed germination agent is butenolide (3-methyl-2H furo [2,3-c]pyran-2-one), which is

⁺⁺ Master Scholar;

[#] Professor and Head;

[†] Assistant Professor;

*Corresponding author: E-mail: gowdag000@gmail.com;

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produced from plant-derived smoke using bioactivity-guided fractionation. Following the initial isolation of KAR1, a whole new family of plant growth regulators, named 'karrikins' were isolated. Glyceronitrile or cyanohydrin is another compound isolated by using bioassay which stimulates germination in species which is insensitive to karrikins. Application of smoke had found to enhance germination by breaking dormancy, increasing seedling growth and mitigating abiotic stress conditions.

Keywords: Smoke treatment; karrikins; cyanohydrins; germination; plant derived smoke.

1. INTRODUCTION

“Fire act as a common disturbance element in many ecosystem and also provides opportunity for recreation of new species as a acquired response of plants to fire. Post fire events involves removing the upper foliage and plant detritus, which alters the amount and quality of light, adding more nourishment and water content to the soil, eliminating inhibitory allelochemicals” (Dixon et al., 2009; Nelson et al., 2012). “Smoke emitted during fire from plant materials is known to boost growth and development of many species” (Kamran et al., 2017) and has a favorable impact on plant species in different ecosystem (van Staden et al., 2007). The germination of some plant species, fully efficient after fire and subsequently rain, is a well-known phenomenon called “pyrophytism”, and these plants are referred to as “fire ephemeral” or “pyro endemic plants” that appears after many years of nonexistence, can emerge following a forest fire (Troumbis et al., 2021). Many aspects of fire have been studied for their effects on plant growth and/or seed germination. These include heat, the rapid release of nutrients from burned plant tissue, and compounds found in ash (Bernard & Ayeni, 2012). “Fire's stimulating mechanism could be from the removal of physical barriers by desiccating seed coat, overcoming physiological barriers of seed embryos, and/or the dormancy-breaking properties of chemicals such as ethylene, nitrogen dioxide and methane” (Keeley & Fotheringham, 2000). Majority of species in fire prone environment proven to trigger germination because of chemical germination cues found in smoke after burning vegetation but only few responds to heat stimulated germination (Keeley & Fotheringham, 2000). “The phytoactive nature of chemical compounds in smoke found to act as important environmental signals which either promote or inhibit the germination of many plant species following a fire” (Dixon et al., 2009; Marquita, 2004). Smoke-derived chemicals have been

recognized for their importance in promoting germination and breaking seed dormancy in specific species, with interest growing since 1990.

The potential of plant smoke compounds in accelerating seed germination was initially reported by De Lange & Boucher, (1990). “The significance of smoke in promoting germination was initially brought to light in a South African study focusing on the endangered fynbos species *Audouinia capitate*” (De Lange & Boucher, 1990). “Additional research on Australian species, Californian chaparral, and South African fynbos has demonstrated how smoke can generally encourage the emergence of numerous species from fire-prone regions” (Dixon et al., 1995; Keeley & Fotheringham, 1998; Brown, 1993). Smoke has also been found to elicit germination of many crop and weed species such as rice (*Oryza sativa*), wild oats (*Avena sativa*), and lettuce (*Lactuca sativa*) (Kulkarni et al., 2006; Light et al., 2009). As of now, smoke induced germination has been documented in over 1,200 species of 80 different genera across different ecosystem (Dixon et al., 2009).

“The research by Brown & Van Staden, (1998) confirmed the presence of certain water-soluble substances in smoke from burning plant tissues are crucial for thawing seed dormancy. From burned cellulose and smoke derived from plants, a biologically active butenolide compound (3-methyl-2H furo [2,3-c]pyran-2-one) was isolated” (Flematti et al., 2004). As per Merritt et al., (2007), this compound is known as karrikinolide (KAR1). It has the ability to stimulate seed germination in numerous plant species, even at incredibly low concentrations. Smoke water was shown to have effects akin to those of plant growth regulators by Kulkarni et al., (2006). Additionally, Karrikins, a novel group of plant growth regulators discovered in smoke, were reported by Chiwocha et al., (2009) to have the ability of breaking seed dormancy, and initiating seedling emergence in a variety of taxa. Smoke

may have a combined regulatory function during germination. It may stimulate germination but also inhibit it until there is enough water available (Light et al., 2002). In post-fire settings, this kind of dual signal system which includes both promotory and inhibitory compounds may be crucial. 2, 3, 4-trimethylbut-2-enolide, or 3, 4, 5-trimethylfuran-2(5H)-one, was the inhibitory compound that was isolated (Light et al., 2010; Momodu & Anyakora, 2010). Cyanohydrins is the another compound isolated from plant derived smoke known to release cyanide upon hydrolysis also reported to enhance seed germination and seedling growth by Nelson et al., (2012). This review article focuses on the chemical compounds in smoke responsible for stimulatory actions, method of application, factors affecting it, and also discusses about potential benefits of plant derived smoke such as promoter of germination, dormancy breaker, growth enhancer and reducer of negative impact of environmental stresses.

1.1 Bioactive Compounds in Smoke as a Trigger of Growth and Germination

“Chemically smoke contains many different compounds, and several attempts have been made to identify these active compounds” (Keeley & Fotheringham, 1998; Dixon et al., 2009). The two main active substances that have been identified and isolated with potential for use in agriculture are karrikins (KARs) and cyanohydrins. These are long-lasting, heat-stable, and water-soluble substances.

Karrikins (KARs): “A biologically active butenolide compound (3-methyl-2-H-furo [2,3-c]pyran-2- one) was isolated from burnt cellulose and plant-derived smoke” (Flematti et al., 2004) as a by product of pyrolysis. “This compound was termed as karrikinolide (KAR1)” (Flematti et al., 2009), is stable, “crystalline in nature having melting point of 118–119 °C and are easily soluble in organic solvent while sparingly soluble in water” (Antala et al., 2020) and even at very low concentrations it is effective in promoting seed germination in many different plant species. Following the initial isolation of KAR1, a whole new group of plant growth regulators, KAR2–KAR6 are collectively known as karrikins, were identified in smoke to separate germination stimulated butenolide compounds in smoke (Chiwocha et al., 2009), and several related compounds have been synthesized (Flematti et al., 2007). Of all the KARs the most abundant in smoke and active in seed germination is KAR1

(Nelson et al., 2012). KAR1 stimulates potent germination activity of seeds when used in nano molar concentrations (< 1 ppb or 1 nM) (Nelson et al., 2010). It is estimated that 2 - 5 g of KAR1 is sufficient for application of 1 ha land application which made the compound commercially viable (Dixon et al., 2009).

“Karrikins responses are not restricted to fire-prone species but also been effective in the germination, vigor, and stress tolerance of many crops” (Antala et al., 2019). Karrikins shares structural similarity with the phytohormones stringolactones (SLs) due to the related nature of their butenolide ring and lactone D ring of SLs (Waters et al., 2012). “The study of karrikin-insensitive (*kai*) mutant in *Arabidopsis thaliana* provided opportunity to understand the perception and signaling of KAR” (Nelson et al., 2011). The study conducted on *Arabidopsis thaliana*, revealed that KAR responses is due to the involvement of *MORE AXILLARY GROWTH (MAX2)* and *KARRIKIN INSENSITIVE 2 (KAI2)*. *MAX2*, which is responsible for encoding an F-box protein participate in KAR and SLs signaling (Nelson et al., 2011). KAR is perceived by α/β hydrolases superfamily member namely *KAI2*, a KAR receptor, further causing a configurational shift in *KAI2* at the active site entrance. “The activated *KAI2* enhances its interaction with *MAX2*, and both altogether lead to a complex degrading *SUPPRESSOR OF MAX2 (SMAX1)* and *SMAX1-LIKE2 (SMXL2)*. From this suppression, transcription factors are revealed, and a KAR response occurs” (Guo et al., 2013; Pandey et al., 2025). “As *KAI2* is essential for the response of KAR1 and has been well explained to bind with KAR1, it is generally called a KAR receptor” (Waters et al., 2012). “Karrikins boost seed germination by up-regulating the Gibberellic acid (GA) production genes, activating ROS-scavenging antioxidants, and mobilizing soluble carbohydrates in seeds” (Sunmonu et al., 2016; Banerjee et al., 2019; Shah et al., 2020).

Cyanohydrins: Several smoke-responsive plant species were found to be non-responsive to karrikinolide in studies conducted to isolate active compounds from smoke. It was discovered that fire ephemeral *Tersonia cyathiflora* (Gyrostemonaceae) germinated because of smoke, and failed to establish when treated with karrikinolide or smoke extracts made from burning cellulose (Downes et al., 2010). “A novel nitrogen-containing bioactive compound known as cyanohydrin glyconitrile was isolated by using a bioassay” (Flematti et al., 2011). “Afterwards, it was discovered that

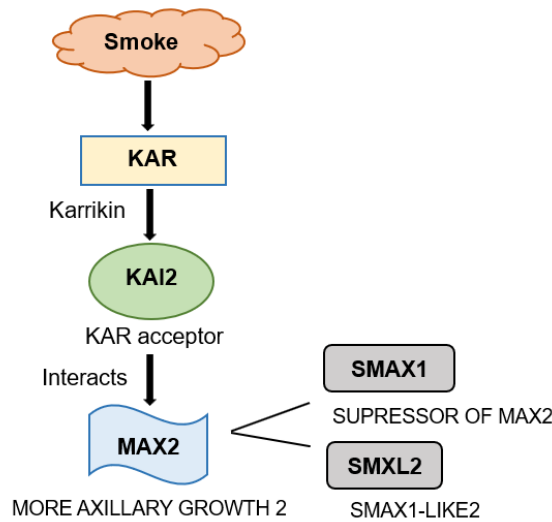


Fig. 1. Karrikin signaling pathway

Haemodoraceae species as well as other species from southern Africa and North America responded more actively towards glyconitrile” (Flematti et al., 2011). Mandelonitrile, glycolonitrile, and acetone cyanohydrin were among the other cyanohydrins that could induce germination. The activity of cyanohydrins was found to be due to hydrogen cyanide released upon hydrolysis. Cyanide has been widely reported to stimulate seed germination in many plant species (Major et al., 1968). There are a number of reports that have suggested cyanide as a regulator of seed germination and dormancy release, in rice (*Oryza sativa*), apple (*Malus domestica*), *Helianthus tuberosus*, and *Arabidopsis* (Cohn & Hughes, 1986; Bogatek et al., 1991; Bethke et al., 2006). “Treatment with cyanide breaks *Arabidopsis* seed dormancy, and the emission of hydrogen cyanide from many seeds has been detected during the pregermination period” (Bethke et al., 2006). “It was hypothesized that cyanide acts by creating

nitric oxide *in vivo*” (Bethke et al., 2006). “However, the mode of action of cyanide remains unclear but it is suggested that cyanide signaling interacts with reactive oxygen species (ROS)” (Oracz et al., 2007). The effect of cyanide on germination of dormant sunflower embryos shows increase in hydrogen peroxide and superoxide anion generation in the embryonic axes. This rise is caused by activation of NADPH oxidase as well as inhibition of the activities of catalase and superoxide dismutase. It was thought that ROS was likely to mediate the effect of cyanide on gene expression Oracz et al., (2009). Additionally, it was shown that transcription factor ERF1, a part of the ethylene signaling pathway, is activated by both cyanide and ROS. According to the theory (Oracz et al., 2009), ROS functions as a secondary messenger of cyanide and is crucial for sunflower seed germination.

1.2 Application of Plant-Derived Smoke

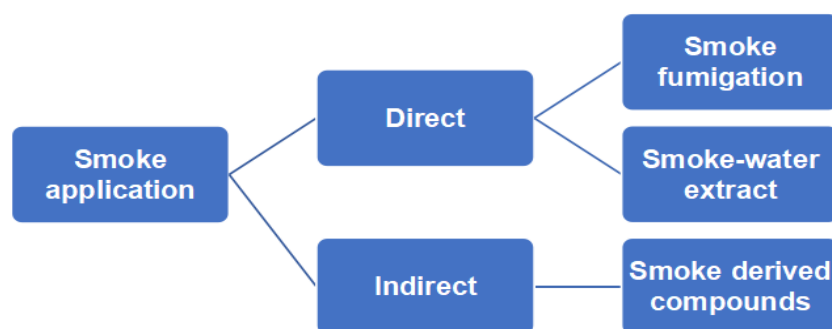


Fig. 2. Method of smoke application

Smoke fumigation: Applying aerosol smoke directly is one of the simplest way of treatment. This technique exposes seeds directly to smoke produced by burning plant matter (Sparg et al., 2006). Ghebrehiwot et al., (2013) reported on the aerosol treatment of tef [*Eragrostis tef* (Zucc.) Trotter] seeds, which were placed in sieves and exposed to cooled (~28 °C) aerosol smoke for 10 min. The sieves were placed inside a chimney (150 cm high) and smoldering smoke of semi-dry *Themeda triandra* Forssk (Poaceae) was generated at the bottom. This method was relatively simple and affordable technique for tef growers. The benefits of aerosol smoke can also be harnessed by treating planting media into which seeds could be placed (Abdollahi et al., 2011; Keeley & Fortheringham, 1998). This treatment offers an additional advantage of gradual release of active molecules over smoke water treatment (Dixon et al., 2009).

Smoke water extract: Water soluble property of active components in smoke was discovered (Nelson et al., 2012), this property was used to prepare smoke solution. To prepare plant-derived smoke solution most efficiently producers bubble smoke through water because this process allows the smoke's metabolites and active biological components to dissolve effectively into water. "The smoke can be generated in a drum/fask functioning as a combustion chamber and passed through a compressed air or vacuum pump channeled into the water, thus dissolving the smoke and its metabolites in water. Smoke generation takes place inside a closed drum/flask that works as a combustion chamber before the smoke passes through a compressed air or vacuum pump into water to dissolve both smoke and its metabolites" (Khaton et al., 2020; Pandey et al., 2025). In general, any type of plant can be used to make smoke water. A concentrated aqueous smoke extract subjected to different dilution ranges of which 1:250, 1:500, 1:1000, 1:1500, and 1:2000 (v/v) were proven safe to use. Dilutions within this range tend to be quite effective in enhancing germination, although the effectiveness may differ among species (Van Staden et al., 2004).

Smoke derived compounds: "Burnt cellulose and smoke derived from plants were used to isolate 3-methyl-2H furo [2, 3-c] pyran-2-one, a biologically active butenolide compound" (Flematti et al., 2004; Van Staden et al., 2004). "This compound referred to as 'karrikinolide' (KAR1)" (Commander et al., 2008). "It was

discovered that the compound facilitated the germination of specific seeds across a broad range of concentrations, with effective levels as low as 10^{-9} M for Grand Rapids lettuce seeds, and around 10^{-7} M for *Conostylis aculeata* and *Stylidium affine*" (Flematti et al., 2004). In a similar vein, Van Staden et al. (2004) demonstrated activity in Grand Rapids lettuce seeds from concentrations of 10^{-4} M down to 10^{-9} M. Mutagenic and genotoxic effects of butenolide compound was tested using the VITOTOX® test and the Ames assay. "The results confirmed that the compound is not toxic nor genotoxic at the levels tested (1×10^{-4} to 3×10^{-10} M), which indicating the possibility of wide-scale usage of the compound as both a germination stimulant and in a field setting" (Verschaeve et al., 2006).

Smoke stimulates germination positively, and it has been shown that high smoke-water concentrations have the opposite effect. The compounds in the smoke-water that are inhibitory, that is, different from the stimulatory karrikins, are most likely responsible for this effect. The inhibitory compound isolated was 3, 4, 5-trimethylfuran-2(5H)-one (2, 3, 4-trimethylbut-2-enolide TMB). But compared to karrikins, which encourage germination, a higher concentration of TMB compound is needed for inhibition action (Light et al., 2010).

1.3 Factors Affecting Seed Response to Smoke

Pretreatments: Certain plant seeds react to smoke when they are dry, while seeds from other plants require presoaking in water. "Conventional seed treatments like mechanical or acid scarification or soil storage can occasionally boost the effectiveness of smoke treatments" (Roche and others 1997).

Type of Plant Material: "Generally almost all the plants are suitable for preparation of smoke" (Jäger et al., 1996). "The material used for combustion has ranged from sawdust to both fresh and aged grass, and tree species tissue. Since their combustion would encourage the natural smokes produced by wild land fires, using the branches and foliage of native species is typically preferred. Smoke's chemical makeup, might differ amongst plant species and even between different tissue types within a species. However, commercial smoke flavoring products and tissue paper have proven to be effective" (Brown & Van Staden, 1997).

Combustion Temperature: “The chemical makeup of smoke changes with temperature, tests show that the most active compounds are generated between 160 and 200 °C (320 and 392 °F)” (Jager et al., 1996). It appears that at higher temperatures, volatilization causes the stimulatory chemicals to be lost. Therefore, a slow, smoldering fire will work best in practice (Brown & Van Staden, 1997).

Species Response: “The effect of smoke vary greatly on different species and ecotypes” (Dixon et al., 1995). Growers will need to experiment with different dilutions to get the best results, as highly concentrated solutions of smoke water may prevent the germination of certain species. “Researcher from China performed an experiment in which 13 plant species were studied and out of which one plant species named *A. debilis* showed positive response whereas other plant species such as *T. magnifica* and *A. auriculiformis* showed negative effects on seed germination this shows that not every plant species exhibits positive response” (Zhou et al., 2014).

Effects of smoke on seed germination : Light & van Staden, (2004) investigated the smoke and aqueous smoke extracts can potentially be used for a variety of applications. These include uses in horticulture, agriculture, ecological management and rehabilitation of disturbed areas. Baldwin et al., (1994) proposed that smoke interacts with the chemical inhibitors in the seed coat, endosperm or embryo to enhance seed germination and that stimulation of germination is due to smoke-specific signal molecule(s), possibly promotive hormones. “Plant-derived smoke solution significantly promoted seed germination in *Arabidopsis* and lettuce by increasing the activity of hydrolytic enzymes, which supports the mobilization of

stored food reserves” (Nelson et al., 2011; Khatoon et al., 2020) Daws et al., (2007) and Stevens et al., (2007) have shown that smoke extract promotes the germination of weed seed banks both in farming and restoration environment. As per the study, smoke aerosol treatment of wheat- *Triticum aestivum* seeds of different varieties for about 1 hr recorded 3-4% increase in germination compared to control and also recorded significant increase in germination index (Iqbal et al., 2016). Elsadek and Yousef, (2019) reported that seeds soaked in smoke water generated from different plant species for about 24 hr increases the germination and post-germination parameters in cucumber, tomato and marigold. Also, treated seeds under light conditions recorded high α -amylase activity and low abscisic acid which helps to establish relationships between α -amylase activity, ABA content, and germination parameters in the studied crops.

Effect of smoke on seed dormancy : Plant-derived smoke compounds were found to break dormancy present in seed of *Arabidopsis thaliana* after fire. “A study on molecular aspects of seed germination in lettuce by employing a transcriptomic technique reported that abscisic acid, seed maturation, and dormancy-related transcripts were up-regulated by trimethyl butenolide and suppressed by KAR1. This study clarified that increased seed germination by KAR1 might be due to suppression of abscisic acid and dormancy-related transcripts by KAR1 present in smoke” (Soos et al., 2012). Another investigation explaining the physiology of breaking seed dormancy in response to smoke water and KAR1 treatment was carried out by Gupta et al., 2019. It was demonstrated that smoke water and KAR1 significantly promoted the lettuce seed germination by reducing abscisic acid level and increasing the activity of hydrolytic

Table 1. Positive response of different crop plants towards application of smoke

Family name	Representative plants	Reference
Poaceae	<i>Triticum aestivum</i>	Iqbal et al., (2016)
Amaryllidaceae	<i>Allium cepa</i>	Kulkarni et al., (2011)
Malvaceae	<i>Abelmoschus esculentus</i>	Van Staden et al., (2005)
Apiaceae	<i>Dacuscarota</i>	Akeel et al., (2019)
Caricaceae	<i>Carica papaya</i>	Chumpookam et al., (2012)
Asteraceae	<i>Lactuca sativa</i>	Kamran et al., (2017)
Cucurbitaceae	<i>Cucumis sativus</i>	Elsadek and Yousef, (2019)
Iridaceae	<i>Gladiolus spp.</i>	Elsadek and Yousef, (2019)
Poaceae	<i>Zea mays</i>	Aslam et al., (2017)
Solanaceae	<i>Lycopersicon esculentum</i>	Indriati and Saparita, (2020)
Brassicaceae	<i>Raphanus sativus</i>	Gupta et al., (2024)

enzymes, which supports the mobilization of stored food reserves (Gupta et al., 2019). Elsadek and Yousef, (2019) provided evidence of smoke water actively breaking dormancy present in gladiolus.

Effect of smoke on seedling growth: “In addition to promoting germination, smoke treatment enhance seedling vigor as karrikin treated seeds are found to have more carbohydrate content, leading to stronger and more resilient plants” (Shah et al., 2020). Ibrahim et al., (2022) have found that smoke application increased shoot and root length, as well as fresh weight in wheat seedlings under heavy metal stress. “For vegetable growers, the most significant vectors of productivity is faster-growing seedlings, Meanwhile foliar application of smoke water and a butenolide in okra [*Abelmoschus esculentus* (L.) Moench] and tomato (*Lycopersicon esculentum* Mill.) seedlings imparted positive effects on shoot/root length, shoot fresh/dry weight, number of leaves, total leaf area and stem thickness and also remarkably increased absolute growth rate (AGR) per week” (Kulkarni et al., 2007). “This indicates that the foliar application of smoke-water or butenolide may be a feasible and inexpensive technique for enhancing seedling growth of vegetable crops” (Kulkarni et al., 2007). Sunmonu et al., (2016) have found that seedling growth improvement in smoke treated seeds are due to the increased activity of amylase enzyme in roots and above ground parts as well as breakdown of starch found in seed .

Effect of smoke on Antioxidant defense modulation system: “The study was conducted to demonstrates the role of plant-derived smoke on the morphological, physiological, and biochemical mechanisms of plant growth under stress conditions. Plant-derived smoke regulates the germination and growth of wheat by scavenging ROS directly, increasing antioxidant enzyme activity, and stimulating the expression of stress-responsive genes. Further recorded that there was an approximately fourfold increase in the positive effector of germination, increase in root and shoot length and a decrease in overall boron accumulation in the wheat seedling, leading to a reduction in B-triggered oxidative injury that takes place due to boron toxicity” (Khatoun et al., 2020) . “Plant-derived smoke can alleviate oxidative stress caused by heavy metals such as arsenic (As) and mercury (Hg) by modulating the cellular antioxidative defense system. Heavy metal stress can inhibit seed germination and seedling growth, reduce

photosynthetic pigments, and increase the levels of harmful compounds like H_2O_2 . Application of PDS can reverse these effects, enhancing seed germination rate, shoot/root length, and fresh weight while decreasing the levels of H_2O_2 and lipid peroxidation (Ibrahim et al., 2022). PDS can modulate the activity of antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and ascorbate peroxidase (APX) under heavy metal stress” (Ibrahim et al., 2022). In conclusion, smoke or aqueous smoke has been proven an effectively method to nullify the effect of abiotic stress like salinity, drought, or heavy metal toxicity, as it regulates the genes responsible for stress regulation and response.

2. CONCLUSION

Plant-derived smoke and its active components have significant potential in agriculture and horticulture, if this components combined with other priming methods such as osmopriming, biopriming resulting in establishment of plants tolerant to stress conditions, overcoming dormancy. Recent advancements have focused on understanding the mechanisms of action, optimizing application methods, and exploring the potential uses. While challenges remain, such as method of application-concentration, timing, and delivery method, Species response therefore continued research and development in this area promise to provide sustainable and effective solutions for improving crop production and promoting ecological diversity. At present, some information is known about regulation of phytohormones by KAR, if complete mechanism discovered would leads to better seed quality and opens door for new area of it's utilisation.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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