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REVIEW PAPER

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KARRIKINS – EFFECT ON PLANTS, INTERACTION WITH OTHER GROWTH REGULATORS, AND POTENTIAL USE IN HORTICULTURE

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ABSTRACT

Karrikins are a group of chemicals found in plant-derived smoke from burning plant material. To date, scientists have concentrated on their effect on seed germination in plants sensitive to smoke. However, there are reports on the effect of karrikins on the physiology and morphology of plants that do not occur in fire areas and are not naturally treated by smoke. These chemicals positively affect the biometric parameters of *in vitro* cultured plants. Their effect on pollen germination rate in several species has been recently confirmed. They interact with plant growth regulators, enhancing their effects, for example, using them together with auxins, cytokinins, gibberellins, abscisic acid, or ethylene. This paper reviews the present research on karrikins and proposes perspectives for further investigations and applying these chemicals in horticultural production as a new group of plant growth regulators.

Key words: plant growth regulators, butenolide, karrikinolide, KAR1

INTRODUCTION

Fires have accompanied humankind since the beginning of its existence. They were caused by atmospheric conditions or provoked artificially. They occur on nearly all continents except Antarctica. People have observed fire effects on a given biotope (in which fires are a natural phenomenon and an integral part of the proper functioning of the ecosystem, for example, Australia) and its gradual return to the original stage due to ecological succession. As they found that fire plays a vital role in ecological processes, they started to use it to improve the regeneration ability of the soil seed bank, to preserve plant species, and to protect specific habitats [Modi 2002, Rokich et al. 2002, Crisp et al. 2011, Twidwell et al. 2013]. In horticulture, fire destroys certain weeds and stimulates the germination of valuable plant species [Light and van Staden 2004, Kulkarni et al. 2011].

During the fire, vegetation burns produce chemicals that stimulate the germination of seeds hidden in the soil. Numerous investigations have focused on the identification of compounds present in smoke that are responsible for releasing seeds from dormancy [Light et al. 2009]. The first reports on potential new growth regulators appeared in 1990 [De Lange and Boucher 1990)], and in 2003/2004 [Chiwocha et al. 2009, van Staden et al. 2004], butenolide, 3-metylo-2H-furo[2,3-c]piran-2-on, was described as karrikin 1 (KAR1). The name comes from “karrik”, which in the language of Australian aborigines means the fire in Nyanguar. It was given to the plant-derived smoke ingredient to distinguish butenolides of plant origin from those produced by fungi in no way affecting plants. Until now, karrikins (KARs) have remained a poorly recognized group of chemicals studied

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mainly regarding their effect on seed germination. Reports have confirmed that KAR1 stimulates germination in 60 species belonging to 29 families [Brown and van Staden 1997, Flematti et al. 2004, Dixon et al. 2009, Flematti et al. 2009].

Reports on the effects of these chemicals on biometric parameters and biochemical changes occurring in plants have appeared in the literature. The examples presented in this review confirm that KARs are very promising for growth regulation in different plant species [Morffy et al. 2016, Kępczyński 2020].

Karrikins – their structure and impact on plants

The structure of the butenolide derivative (3-methyl-2H-furo[2,3-c]pyran-2-one) has been identified and named KAR1. Later, its derivatives were synthesized and described as 'karrikins' KAR2 to KAR6 (Fig. 1) [Flematti et al. 2009]. Each produces different effects depending on the plant species or the concentration used to stimulate germination; for example, KAR2 is the most active in *Arabidopsis* and shows less activity toward other genera than KAR1 [van Staden et al. 2004, Nelson et al. 2009, Waters 2017]. The structure of KARs resembles that of other phytohormones, namely, strigolactones (SLs) [Antala et al. 2020, Carbonnel et al. 2021, Oláh et al. 2021]. KARs are small molecules with a simple structure, often composed of butenolide and pyran rings [Flematti et al. 2005, Khatoon et al. 2020, Guercio et al. 2021, Hrdlička et al. 2021]. They have crystal characteristics, and their melting temperatures range between 118 and 119°C. Only gentle stirring is needed to dissolve them in water, and organic solvents can also be used [Flematti et al. 2015].

The application of growth regulators affects metabolic processes occurring in plants, which can better accumulate nutrients necessary for the growth of vegetative organs and later for generative development [Shakirova et al. 2010]. Additionally, KARs may affect different aspects of plant growth. Differences in plant morphology have been reported, for example, a change in the shape and size of cucumber leaf blades and a reduction in petioles in *Arabidopsis thaliana* [Guo et al. 2013], stimulation of new roots in *A. thaliana* [Yang et al. 2019], an increase in the size and number of stomata in *Daucus carrota* [Akeel

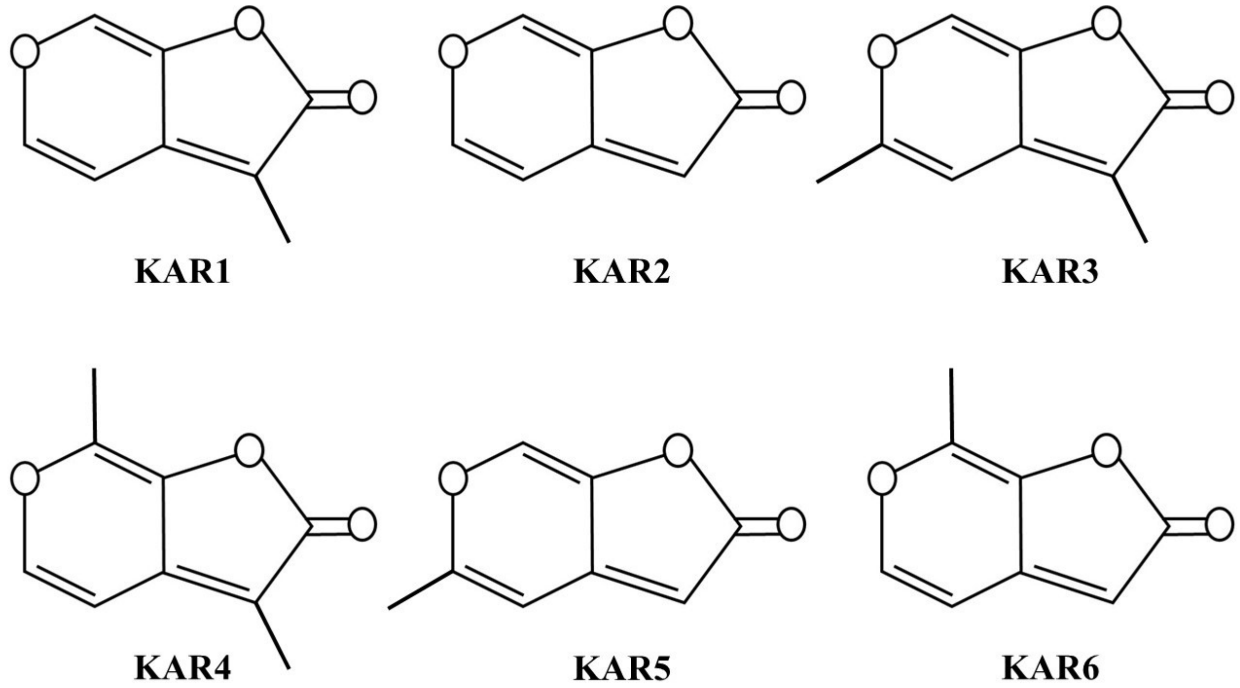

Fig. 1. Chemical structure of karrikins (KAR1 – KAR6)

et al. 2019] and stimulation of pollen tube elongation in several ornamental plants: *Aechmea kertesziae*, *Kniphofia uvaria* and *Paeonia lactiflora* [Kumari et al. 2014]. *Arabidopsis* hypocotyl elongation was inhibited after KAR application [Smith and Li 2014]. In onions in which seeds were sown into the soil and watered with KAR solution, the fresh weight of leaves and bulbs increased compared to the water-irrigated plants [Kulkarni et al. 2010]. Stomata of plants treated with KAR1 was considerably more prominent and exposed than those untreated with KAR1 [Akeel et al. 2019].

For biochemical changes produced due to KAR1 application, increased contents of chlorophylls, carotenoids, and vitamin C were observed in *Daucus carrota*. The latter authors found that the increase in the contents of assimilation pigments in plants depended on the KAR1 concentration [Akeel et al. 2019]. Studies confirmed the long-term effect of KARs on beta-carotene concentration in *D. carrota*, which was higher in treated than nontreated plants.

Interactions with other growth regulators. The positive effects of KARs are enhanced by their joint action with other growth regulators, i.e., auxins, cytokinins (CK), gibberellins (GA), abscisic acid (ABA), or ethylene. Such interactions have been reported in publications on hormonal effects in plants. They all underline the importance of hormonal balance [Chiwocha et al. 2009, Janas et al. 2010, Yang et al. 2019]. It was confirmed, for example, in *Eucomis autumnalis*, where naphthalene acetic acid (NAA) was combined with KAR1, and in *Avena fatua*, where synergism between GA_3 and KAR occurred [Aremu et al. 2016, Meng et al. 2017, Kępczyński 2018]. Additionally, antagonistic action can appear relative to individual growth regulators. In *Arabidopsis thaliana*, the effects of KARs were opposite to those of endogenous indole-3-acetic acid (IAA). KARs stimulate seed germination; thus, they act differentially to ABA [Ramaih et al. 2003, Banerjee et al. 2019, Yang et al. 2019].

The application of KARs in plants

For example, *Arabidopsis thaliana* regulates the contents of specific plant hormones, e.g., inhibiting gibberellic acid (GA) production while increasing ABA production [Waters et al. 2014, Shah et al. 2020]. In a study by Meng et al. [2017], treating *Arabidopsis* seeds with KAR1 increased the expression of the gene responsible for GA_3 oxidase. Additionally, KAR1 and GA_3 regulators activate seeds to germinate due to the inhibition of ABA activity [de Saint Germain et al. 2013]. Kępczyński et al. [2018] performed a study on seed dormancy breaking in *Avena fatua* and confirmed the interaction of GA with KARs and GA. Furthermore, it was observed in *Glycine max* plants that application of KARs before seed harvest inhibited seed germination. It was due to an increased amount of endogenous ABA compared to a decreasing amount of GA, thus causing a hormonal imbalance, particularly the correlation of ABA with GA_4 [Meng et al. 2016].

The hormones that play a crucial role in plant growth and development are auxins, which are also involved in seed germination to a small extent [Wang and Estelle 2014]. Studies on preharvest germination of *Triticum aestivum* seeds show that application of indole-3-butyric acid (IBA) inhibited this process [Ramaih et al. 2003]. KARs act in opposition to auxins. Therefore, it can be speculated that using KAR growth regulators would decrease the expression of genes that respond to auxin group hormones, particularly IAA [Yang et al. 2019]. A study was conducted on the survival of *Eucomis autumnalis* subsp. *autumnalis* explants on medium supplemented with growth regulators (KAR, NAA, BA) and showed that combining KAR with NAA resulted in the highest percentage of explant survival. Additionally, the experiments have shed some light on the correlation of KARs with CKs. Applying KAR1 in the media of *Eucomis autumnalis* leaf explants resulted in increased levels of endogenous cytokinins in the tissues, which resulted in improved growth and normal development of the plants under *ex vitro* conditions. Plants evaluated after four months had higher fresh weight, bulb circumference, and leaf blade area than control plants. Additionally, they produced longer roots [Aremu et al. 2016].

Ethylene is indisputable in plant development as an essential signal substance and growth inhibitor. It causes both elongations of hypocotyl and root hairs and can lead to inhibition of lateral root development [Wang et al. 2020a, 2020b]. The effect of ethylene on seed germination and pollen tube growth is also essential [Hong et al. 2020]. Ethylene also regulates plant aging and fruit ripening [Jibran et al. 2013, Hong et al. 2020], stimulates root hair growth, and inhibits cell elongation in the root meristem [Ruzicka et al. 2007].

Studies indicate the involvement of a small molecule signaling pathway called the "karrikin pathway" in ethylene synthesis, affecting, among other things, seed germination and root system architecture, as we discuss further. Sami et al. [2021] noted that KAR1 might not respond similarly to gene expression and ethylene biosynthesis in different plant species, so more species studies are needed.

Karrikins in plant response to abiotic stresses

KARs can impact several abiotic stressors, such as drought, salinity, low and high temperature, heavy metals, or nutrition deficiency [Antala 2022].

In *A. thaliana,* two genes are responsible for plant reactions to KARs, i.e., MAX2 and KARRIKIN INSENSITIVE 2 (KAI2) [Stirnberg et al. 2002, Yamada et al. 2014, Hull et al. 2021]. Because of their structural resemblance to SLs, both genes participate in strigolactone signaling [Waters et al. 2012, Waters et al. 2013, Waters 2017, Hrdlička et al. 2019]. MAX2 is the primary regulator of SL signaling and is also necessary for the plant response to KARs [Waters et al. 2012, Li and Tran 2015].

Due to structural and operational mode similarities, KARs and SLs may participate in plant responses to different abiotic stresses [Dixon et al. 2009, Kim et al. 2017, Banerjee et al. 2019]. For example, KAI2 stimulates the biosynthesis of anthocyanins, which protect plants against reactive forms of oxygen appearing under stress conditions [Li et al. 2017]. Smoke water containing KAR increases seedlings' vigor and survival rate growing under high temperatures or low osmotic potential [Ghebrehiwot et al. 2008].

Water deficit is the main factor responsible for crop losses worldwide. Breeding plant cultivars more resistant to periodical water deficit has been very intense. Using substances that decrease water stress and increase the survival rate under drought may be an alternative to creating new cultivars [Jogaiah et al. 2013]. Investigations on *Arabidopsis* indicate that KAI2 signalization improves plant adaptation to drought. Such plants were less sensitive to water deficit, had a more considerable fresh weight and relative water content (RWC), and their stomata closed sooner, while electrolyte leakage through membranes was reduced under stress [Li et al. 2017]. A positive synthetic KAR (GR24) effect during water deficit was also shown in seeds whose germination ability was increased due to KAR application. In 3 herbs, *Trachyspermum copticum*, *Foeniculum vulgare*, and *Cuminum cyminum* vigor of young plants and their root and shoot length were increased due to KARs [MousaviNik et al. 2016].

KARs also have the potential to protect plants during salinity stress. Black cumin (*Nigella sativa* L.) seeds were treated with or without 10 µmol KAR, and then seedlings were treated foliar with calcium at three concentrations (0, 50, or 100 mmol). The combination of KAR treatment of seeds with calcium chloride spraying of seedlings proved to be the most effective in mitigating the harmful effects of substrate salinity, which reduced plant oxidative stress and improved the yield of seeds harvested after 15-week cultivation and their oil content. It also increased proline content, reduced H_2O_2 production and malondialdehyde (MDA) accumulation, and increased antioxidant enzyme activity. Worse results were obtained for untreated KAR seeds and their treated and untreated seedlings with calcium chloride [Sharifi and Shirani Bidabadi 2020]. Several studies, including those on black cumin or wheat (*Triticum*), have shown an increase in antioxidant enzyme activity and reversal of some of the changes in the plant under salinity stress [Sharifi and Shirani Bidabadi 2020, Shah et al. 2021a]. A similar effect was observed for cucumber seedlings treated with KAR smoke water. The positive effect of KAR was more pronounced with an increase in salinity (NaCl concentration). Additionally, during these studies, the effect of KAR on increasing endogenous phytohormones (IAA, GA, CKs) during salinity stress was demonstrated [Mathnoom and Al-Timmen 2020]. Thomas and van Staden [1995] found long ago that substances in smoke extract stimulate GA biosynthesis during salt stress. Recent studies have shown that KAR1 application in wheat seedlings under salinity stress reduces Na^+ concentrations and induces K^+ concentrations. These results suggest that KAR1 maintains redox and K^+/Na^+ homeostasis in wheat seedlings under saline conditions. It may be a key component of plant defense mechanisms at the physiological level in KAR1-induced salt stress tolerance [Shah et al. 2021a] (Fig. 2).

The scheme shows potential plant responses to different types of abiotic stresses from the environment after applying exogenous KAR. The interaction

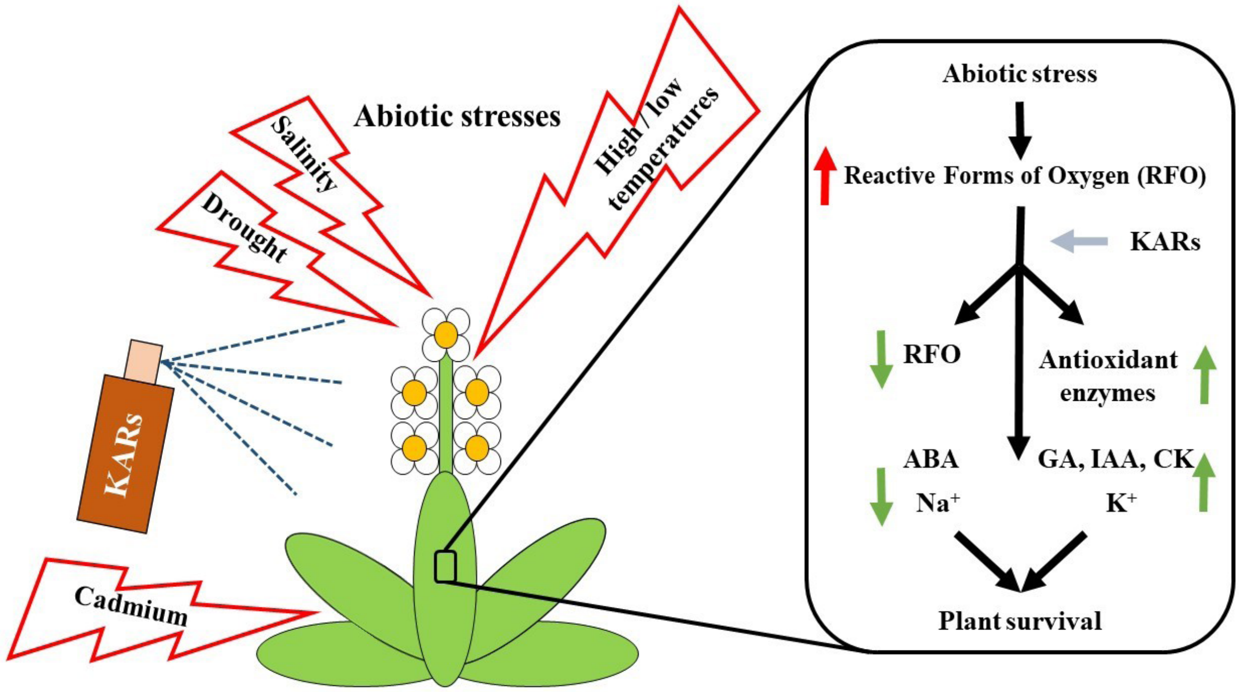

Fig. 2. Scheme of likely karrikin-mediated plant responses to various abiotic stresses

between plants and KAR causes inhibition of reactive forms of oxygen (RFO) production due to the increased activity of antioxidant enzymes. In addition, the biosynthesis of some phytohormones (GA, IAA, CKs) and the inhibition of ABA, which is a stress hormone, are induced, and cationic Na+/K+ homeostasis is maintained to protect cells from damage.

Noticeable changes under different stress factors (high temperature, elevated cadmium content) were also reported in studies conducted on *Brassica alboglabra*. Plants treated with KAR1 showed increased activity of antioxidant enzymes, resulting in improved growth and development [Ahmad et al. 2021]. KARs counteract the effects of both high and low temperatures (0°C to as low as –20°C) by regulating redox homeostasis, increasing ABA sensitivity, and inducing the expression of genes responsible for the plant response to temperature reduction stress [Shah et al. 2021b]. In a study conducted by Sardar et al. [2021] on seed germination of *Coriandrum sativum* under conditions of increased cadmium content, it was observed that KAR application inhibited the action of the stressor, as a result of which seedlings developed usually and the content of essential compounds in the plant – chlorophyll a and b, carotenoids and total sugars – was not reduced (Fig. 2).

Effect on seed germination

Due to the observations of the action of KARs in the environment related to the presence of these substances in the smoke accompanying fires, most studies concern their use in seed germination [Alahakoon et al. 2020, Bursch et al. 2021, Isoda et al. 2021]. In experiments conducted on *Brassica oleracea*, a positive effect of this group of regulators on seed germination was demonstrated. Under the influence of exogenous KAR1, ACS synthase activity increased, and ethylene release was released enhanced, leading to the breaking of seed dormancy [Sami et al. 2019]. In an experiment by Monthony et al. [2020], three different KARs – KAR1, KAR2, and KAR11 – were applied to seeds of *Balsamorhiza deltoidea* and *Balsamorhiza sagittata* (*Asteraceae*) at two concentrations – 5 or 10 μM. Each of them affected the percentage of germinated seeds to a different extent. The application of KAR1, irrespective of the concentration, did not stimulate germination in *B. sagittata*, while the application of the other two KARs significantly improved germination compared to seeds not treated with any KAR. In *B. deltoidea*, applying KAR1 and KAR11 at a concentration of 5 μM reduced the percentage of germinated seeds, while at a concentration of 10 μM, it maintained the percentage of germinated seeds at the same level as in the control treatment.

Studies by Papenfus et al. [2016] on *in vitro* seed germination of the orchid *Ansellia africana* and Chiwocha et al. [2009] on lettuce (*Lactuca sativa*) 'Grand Rapids' showed that the effect of KARs is dependent mainly on their concentration. Pošta et al. [2013] showed that applying KAR1 at concentrations ranging from 0.001–0.1 μM stimulated the germination process of *Lactuca sativa* 'Grand Rapids' seeds. Flematti et al. [2007] observed that the percentage of germinated *Lactuca sativa* 'Grand Rapids' seeds at the lowest concentration of 1 μg/L increased compared to the control not treated with KARs, and as the concentration of KARs increased, the ratio further increased and reached 100% at a KAR concentration of 1000 μg/L.

Many experiments using KARs have also been conducted on vegetable and cereal plants such as tomato (*Lycopersicon esculentum*), onion (*Allium cepa*), rice (*Oryza sativa)*, sweat pepper (*Capsicum annuum*) and carrot (*Daucus carrota*) [Antala et al. 2020]. According to van Staden et al. [2005], the use of butenolide, a compound belonging to the carrikinolide group, to promote seed germination of tomato (*L. esculentum*), okra (*Abelmoschus esculentus*), beans (*Phaseolus vulgaris*) and maize (*Zea mays*) has beneficial ef-

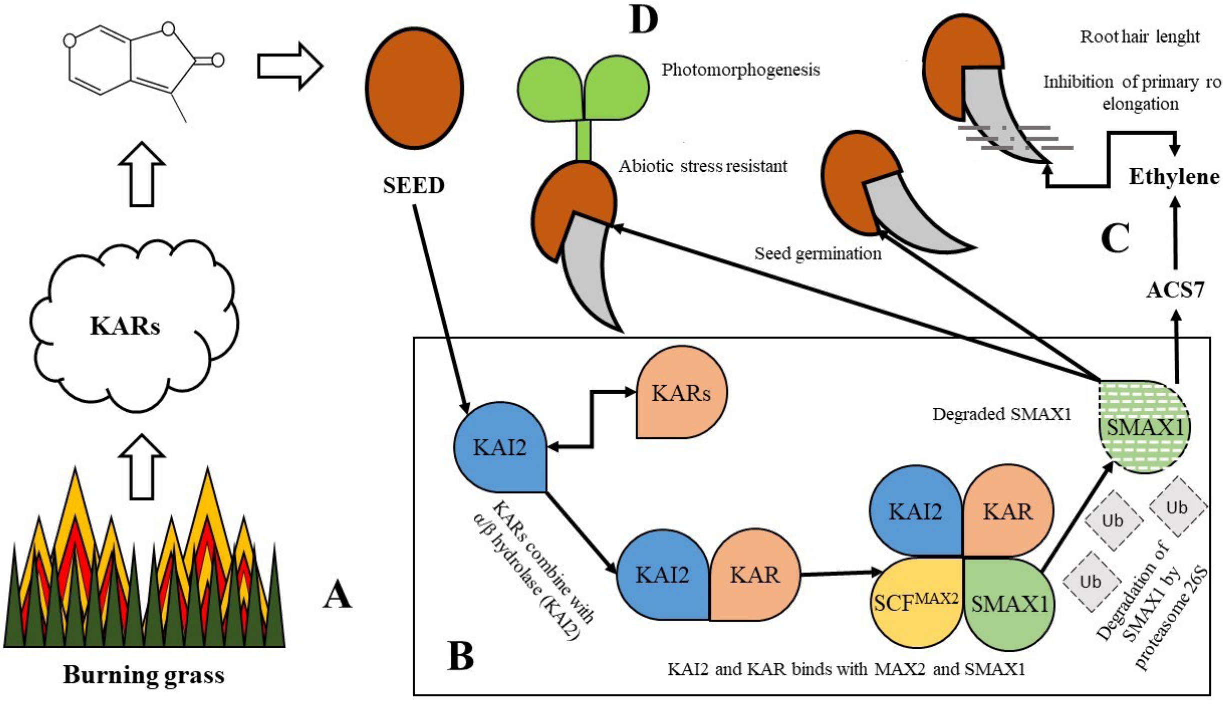

Fig. 3. Scheme of karrikin signaling pathways in seed germination, rhisogenesis, and root system architecture. A – The burning of plant matter produces smoke containing KARs, which interact with seed banks in the soil. B – KARs interact with the KAI2 protein, which is an α/β hydrolase receptor. A conformational change in KAI2 allows interaction with the MAX2 protein, which is part of the ubiquitin ligase complex (E3) Skp1-Cullin-F-box (SCF) and a suppressor protein of KAR signaling SMAX1. The SMAX1 protein undergoes ubiquitination (ubiquitin attachment – Ub) and is then degraded by the 26S proteasome. C – Degradation of SMAX1 leads to the accumulation of transcripts of the *ACS7* gene encoding ACC synthase, which leads to ethylene biosynthesis. As a result, the elongation growth of primary root cells is inhibited, and the growth of root hairs occurs. D – Degradation of SMAX1 allows KAR to affect seed germination, photomorphogenesis, and abiotic stress reduction

fects on a shoot and root length. Moreover, the seedling vigor index (the quotient of the average length of a seedling in mm and the percentage of germination) increased significantly in all the studied species compared to the index of control seedlings, and in the case of tomato, even up to six times. The survival rate of *Zea mays* plants was up to 89% compared to control plants, which survived at 63%. Another study on tomato seeds showed that for the genus *Balsamorhiza*, butenolide concentration strongly influenced the percentage of germinated seeds. At a concentration of 10^{-10} M butenolide, shoot and root formation was best, while a concentration of 10^{-9} M inhibited this process [Jain and van Staden 2006]. Applying karrikinolides by spraying germinated seedlings under greenhouse conditions with an aqueous solution of 0.1 μM butenolide [Kulkarni et al. 2007] improved the growth and development of tomato plants.

Effect on pollen grains germination

A new insight into the effect of KARs was provided by an experiment conducted by Papenfus et al. [2013] on three species of the family *Amaryllidaceae*, i.e., *Clivia gardenii*, *Cyrtanthus mackenii,* and *Scadoxus multiflorus*. They applied KAR1 at three concentrations to test its effect on pollen grain germination and tube length. It was observed that there were significant improvements in both parameters in each species. The most surprising result was the effect of KAR1 at a concentration of 10^{-6} M on obtaining 8 times longer pollen tubes of *Clivia gardenia* compared to the length of tubes not treated with KAR.

Other studies carried out on plants from different genera – *Aloe maculata*, *Kniphofia uvaria*, *Lachenalia aloides* var. *aloides*, *Tulbaghia simmleri*, *Aechmea kertesziae*, *Nematanthus crassifolius*, and *Paeonia lactiflora* have shown that the application of KARs effectively affects the germination of pollen grains and significantly improves the elongation growth of pollen tubes. These experiments proved the species' importance and taxonomic origin in the beneficial effects of these growth regulators [Kumari et al. 2014].

Effect on rhisogenesis and root system architecture

SLs and KARs represent new classes of phytohormones whose many aspects of action in plants are still unexplored. All indications are that they have much in common. However, despite their high structural similarity, KARs and SLs are not recognized by the same signaling pathways [Oláh et al. 2021]. Since the KAR and SL signaling pathways converge on the MORE AXILLARY GROWTH2 (MAX2) complex but elicit different growth effects, it can be speculated that KARs and SLs are distinguishable, in addition, may initiate different signaling responses [Morffy et al. 2016]. The results of the available studies indicate differentiation of the effects of SLs and KARs on rooting, defining a clear area for KAR signaling only. KAR-insensitive mutants of *A. thaliana* display a range of developmental phenotypes (longer hypocotyls, increased lateral root density, increased number of adventitious roots, increased rightward root skew, and longer root hairs). However, some of these phenotypes are also shared with SL-insensitive mutants (increased lateral root density, increased number of adventitious roots, and shorter root epidermal cells) [Conn and Nelson 2016, Swarbreck 2021].

KARs may interact with other phytohormones that affect root system architecture [Swarbreck et al. 2021]. As an example, SLs regulate shoot branching, secondary growth, and leaf senescence and, as indicated by many studies, control many aspects of root development, such as root initiation, length, lateral root formation, and root hair development [Kapulnik et al. 2011, Rasmussen et al. 2012, Oláh et al. 2021]. Recent studies on root development in *Arabidopsis* support the hypothesis of an interaction between nitric oxide, SLs, and KARs, the bioactive signaling molecules controlling root morphology [Oláh et al. 2021].

One pathway for the influence of KARs on rooting is the joint interaction of this group of regulators and ethylene. "Karrikin signaling" regulates ethylene biosynthesis, resulting in altered root architecture; additionally, this biosynthesis does not affect the elongational growth of the hypocotyl [Carbonnel et al. 2020]. KARs link to a hydrolase called KAI2 (KAI2α/β), changing conformation so that KAI2 can interact with MAX2 to form a complex with the suppressor protein SMAX1. SMAX1 undergoes ubiquitination and is then degraded by the 26S proteasome. This results in the synthesis of ACS7 (encoding the ethylene precursor ACC), which leads to increased ethylene synthesis (Fig. 3) [Morffy et al. 2016, Banerjee et al. 2019, Antala et al. 2020, Swarbreck 2021].

Such a relationship was demonstrated in studies on *Lotus japonicus*, where it inhibited the primary root's growth and stimulated the root hair's elongation. Seedlings of mutants of this protein (SMAX1) have up to 50% shorter primary roots and up to 300% longer root hairs than the control, with significantly increased ethylene biosynthesis. Thus, karrikin signaling regulates ethylene biosynthesis and thus affects the development and appearance of the root system of seedlings [Carbonnel et al. 2020]. For *Arabidopsis*, KAI2 was shown to control root bending (angle to vertical), root hair density, and length, thereby influencing root system architecture [Swarbreck et al. 2019]. Recent studies on *Pisum sativum* [Guercio et al. 2022] have uncovered the diversity of KAI2 receptors and revealed stereoselective catalysis during signal perception.

A second significant effect of KARs on the root system is their ability to interact with beneficial soil microorganisms. Studies have reported the potential influence of the KAR signaling pathway on the establishment of plant-arbuscular mycorrhizal symbiosis [Nasir et al. 2020]. It was demonstrated in rice, whose root cells lost the ability to detect and establish symbiosis with *Rhizophagus irregularis* when mutations disrupted KAR responses [Gutjahr et al. 2015]. However, the mechanism is still not fully understood.

Summary and prospects for the use of karrikins in horticulture

The scientific literature reports extensively on the applicability and effect of KARs on the seed germination processes of many horticultural and agricultural plants. However, many examples exist of using these compounds in *in vitro* cultures. Studies have confirmed that compounds from this group greatly influence the course of *in vitro* organogenesis, vital processes of plant *in vitro* cultures, and anatomical changes in tissues [Aremu et al. 2016, Kępczyński 2020]. This is mainly due to the spontaneous action of KARs and their interaction with other growth regulators added to the media. Research into the use of this group of regulators could result in the development of many plant propagation protocols. It contributes to faster production of commercial crop material, as well as for species conservation purposes. Contemporary research on this group of growth regulators should focus on a more detailed analysis of their relationship and individual phytohormones. Studies should cover the effects of KARs on many levels – genetic, physiological, and morphological.

It is crucial to conduct studies on KARs in as many plant species as possible, as the mechanisms of action and pathways of karrikin signaling are plant genotype dependent. This review article shows only a small part of the possibilities of using KARs in plant production. Very little data in the scientific literature concern the effect of KARs on the *in vitro* propagation of geophytic plants. According to Aremu et al. [2016], research on this group of plants should focus on the interaction between KARs, auxins, and CKs.

In breeding practice, a common problem in the pollination and fertilization process is the presence of cross-breeding barriers. Problems with pollen grain germination or pollen tube elongation are examples of prezygotic barriers that prevent successful fertilization and, thus, zygote formation [Zenkteler 2007]. In a cited study on horticultural crops [Papenfus et al. 2013, Kumari et al. 2014], the use of KAR in contact with pollen grains of the plants to be tested contributed to an increase in the number of germinating grains and elongation of the pollen tube, which in the future can be used in breeding many plant species with problems in pollen tube penetration or germination of pollen grains on the stigma.

We can conjecture that KARs mimic the action of some hormones with a similar structure, butenolide. The genes responsible for the plant response to KARs are essential signaling molecules of the SL pathway, as confirmed by studies by Hrdlička et al. [2019] and Waters [2017]. These studies further uncover similarities between the two groups and link them to signaling mechanisms in economically essential plants subjected to stress factors such as drought, salinity, or excessive temperature. Considering the positive effect of KARs in mitigating plant responses to stress factors, it is conceivable that they would be necessary during the critical stage of micropropagation, which is an adaptation to *ex vitro* conditions. Due to their action, it would probably be possible to obtain higher plant survival rates and thus higher efficiency of this propagation method for many species important in horticultural production.

It is also worth noting the possibility of using these regulators in urban gardening. Stress conditions caused by fog and leading to loss of plant attractiveness severely limit species selection. According to Cirillo et al. [2016] and Setayesh et al. [2017], the response of plants to stress factors can be to stunt plant growth, reducing photosynthetic area by reducing leaf blade size and root number. The size and number of leaves is the most common determinant of water deficiency, as the defense mechanism reduces the area from which water evaporation occurs [Toscano et al. 2019]. Long-term salinization of the substrate can result in plants reducing the surface area of the root system through partial plant death. In the case of the aboveground part, a shortening of shoots and a reduction in leaf blade area can be observed in particular, while flowering plants additionally experience a reduction in the size of inflorescences/flowers in favor of their number [Nandal and Hooda 2013, Li and Li 2017]. What is visible to the eyes has its answer in plant tissues, as it is in them that many processes take place that cause some biochemical changes. First and foremost, there is a reduction in the amount of the primary plant pigment chlorophyll, leading to a disruption in the proper functioning of the photosynthetic process [Feng et al. 2014, Kibria and Hoque 2019]. The studies cited in this review indicate the great potential of KARs in protecting plants from abiotic stresses by mitigating their effects at the morphological and biochemical levels.

Currently, as Kępczyński [2020] pointed out, there are only a few examples of KAR1 use as elicitors increasing the biosynthesis of some secondary metabolites. Research in this aspect could contribute to the general knowledge of this little-known group of phytohormones and increase the bioreactor extraction of valuable substances used in the pharmaceutical industry.

The research review presented in this paper demonstrates the high potential of this group of growth regulators and sheds new light on the possibilities of using these compounds, not only in seed science and plant cultivation but also in tissue culture of plants from different groups.

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