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PERCEPTION OF KARRIKINS IN SEED GERMINATION: A CONTINUING ENIGMA

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Introduction

Smoke from burning plant material stimulates seed germination in more than 1200 species of 80 genera from various plant groups and ecosystems (Dixon *et al*., 2009). The effect is independent of species type, geography and seed dormancy. Smoke from various biotic sources including wood, straw and mixed plant materials have an insignificant stimulatory effect on germination. Nitrogen compounds like NO_2 (nitrogen dioxide) and NO (nitric oxide), as well as other compounds such as karrikins, char/tar, CN^- (cyanide), NO_3^- (nitrate) and NO_2^- (nitrite), contribute to this germination response (Fig. 1).

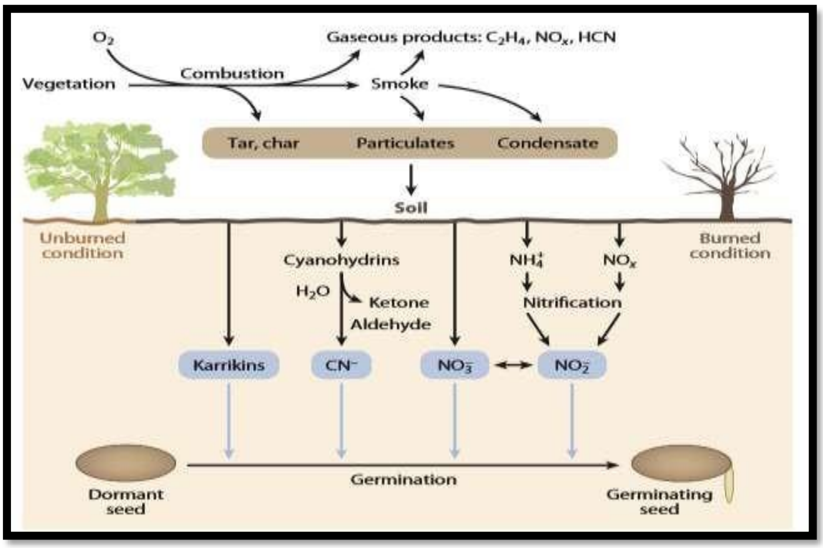

Fig.1: Known germination stimulants derived from combustion of plant material.

These compounds, derived from both smoke and soil microbiota, infiltrate the soil and promote germination, that nitrogenous compounds may not be necessary for this effect (Preston *et al*., 2004).

The butenolide classes of plant growth regulators known as karrikins/ karrikinolides/ KARs were initially discovered as plant smoke derived seed germination stimulants (Flematti *et al.*, 2004). These are quite basic compounds that have an impact on several physiological and morphological traits in many plant species. These can be as little as one nano molar (nM) to be active in some plant species and resemble strigolactone plant hormones in terms of structure and signaling pathway. The regeneration of yellow tail flowers (*Anthocercis littorea*) in Australia's King's Park after 20 years of fire and subsequent rain is one of the better examples.

Discovery

- Various research efforts have aimed to identify the active compounds responsible for smoke-stimulated seed germination. Initial research on the chemistry of smoke made from plants and its impact on germination dates back to the early 1990s. Following researches, with a focus on *Nicotiana attenuata* seeds, used methods like gas chromatography mass spectrophotometry (GC-MS) and atomic absorption spectrometry to discover various chemicals in smoke.
- In 2004, it was discovered that butenolides, particularly 3-methyl-2H-furo [2,3-c] pyran-2-one, played a crucial role in promoting germination in smoke exposed seeds.

Etymology

The first karrikin discovered was initially called gavinone after its discoverer Gavin Flematti and later renamed karrikin due to its complex formal name and the need for a recognizable common name. This name change was inspired by the aboriginal term "karrik" referring to smoke from the Western Australian Noongar people. Adding the "-in" suffix is a common biological practice to denote related molecules, such as "cytokinins" in plants or "endorphins" in animals. The original compound is often referred to as "karrikinolide" with the "-olide" suffix denoting its lactone nature. Karrikins are abbreviated as KAR and numbered based on their order of discovery in smoke (KAR_1, KAR_2, KAR_3, KAR_4, KAR_5 and KAR_6).

Structure and properties of KARS

Karrikins only include the elements C, H and O, and have two ring configurations, one of which is a pyran and the other a lactone with a butenolide, a five membered ring. The pure substance has a melting point of 118 - 119 °C and is crystalline in nature. It rapidly dissolves in organic solvents but only sparingly soluble in water. The first substance (KAR_1) discovered is typically most prevalent in smoke and effective at promoting seed germination.

Reception and signal transduction of karrikins

Karrikin signal molecules require a single LRR (leucine-rich repeats) type F-box gene (*MAX2*) and α/β hydrolase fold protein (KAI2 or DAD2/D14) for signal transduction. The KARs are perceived by the KAI2 receptor, which by interaction with F-box protein MAX2 (MORE AXILLARY GROWTH) causes degradation of SMAX1 (SUPPRESSOR OF MAX 2) and SMXL2 (SUPPRESSOR OF MAX LIKE). The SMAX1 represses seed germination, SMAX1 and/or SMXL2 represses cotyledon expansion, root straightness, root width and root hair development and promote lateral root development and root skewness and hypocotyl elongation by reduction of seedling light sensitivity, SMAX1 promotes expansion of rosette leaves blade under long day conditions. The ubiquitination of protein complex (KAI2 + MAX2 + KAR) degrades the SMAX1 which releases the transcription factors responsible for seed germination, whereas strigolactones are perceived by receptor protein D14, which interacts with MAX2 and causes degradation of SMXL6, 7, 8. This promotes cotyledon expansion, branching and lateral root development; represses petiole and leaf blade elongation under long day conditions.

Roles of KAR under variable environmental factors

Karrikinolides is deployed by the plant system to confer protection against different combinations of abiotic factors like oxidative stress, drought and low light intensities. The KARs balances the excess production of reactive oxygen species (ROS) by inducing the activities of crucial antioxidative enzymes like superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), glutathione S-transferase (GST) and ascorbate peroxidase. As a result, the ascorbate-glutathione (AsA-GSH) cycle exhibits increased efficiency in ROS scavenging. The KARs promotes the biosynthesis of GA and inhibits ABA production, thereby stimulating seed germination. ABA is the universal stress phytohormone which plays major role in abiotic stress tolerance. However, its reduced production does not affect stress tolerance, as KARs probably stimulates the ABA-responsive pathways to promote physiologically significant events like stomatal closure during drought. In some species, the KARs is known to increase ABA biosynthesis as well. Strigolactones are close analogs of KARs which generate multiple stress tolerance by inducing ABA anabolism *via* ABA-responsive pathways. Auxins (IAA) potentially inhibit germination. Thus, IAA transport *via* PINFORMED1 (PIN1) transporters is suppressed by KARs to promote GA induced germination under sub-optimal conditions.

Conclusion

Karrikins are a new family of naturally occurring plant growth regulators of widespread importance. Genomic approaches are the obvious next step forward to uncovering the karrikin mode of action. However, germination based screens using *Arabidopsis* will require further criteria to distinguish karrikin insensitivity from non specific alterations in dormancy or hormone signaling pathways (such as GA and ABA). Karrikin specific reporter genes or additional karrikin induced phenotypes will be valuable in this respect. As components of the karrikin response pathway emerge, it will also be able to address the potential relationship between karrikins and strigolactones. This may in turn reveal aspects of strigolactone mode of action. The discovery of karrikins establishes an exciting new nexus between fire ecology, plant evolution and molecular plant physiology.

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