Review

Not peer-reviewed version

The Impact of Post-Fire Smoke on Ecosystems All over the World

Mahboube Zahed * and Renata Baczek Kwinta *

Posted Date: 17 August 2023

doi: 10.20944/preprints202308.1207.v1

Keywords: plant butenolides; karrikins; seed germination; plant ecology; crop physiology; plant development; swailing; vegetation restoration

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 17 August 2023 doi:10.20944/preprints202308.1207.v1

Review

The Impact of Post-Fire Smoke on Ecosystems All over the World

Mahboube Zahed [1] and Renata Bączek-Kwinta [2]

[1] University of Agricultural Sciences and Natural Resources in Gorgon, Faculty of Agronomy, Department of Plant Production, Basij Square, Pardis No. 2 , 49189-43464, Gorgon, Iran
[2] University of Agriculture in Krakow, Faculty of Agriculture and Economics, Department of Plant Breeding, Physiology and Seed Science, ul. Podłuzna 3, 30-239 Kraków, Poland
* Correspondence: zahedmahboube1984@outlook.com, renata.baczek-kwinta@urk.edu.pl

Abstract: Fire-related cues could alter vegetation community composition by promoting or excluding different types of plants. Smoke-derived compounds have been a hot topic in plant and crop physiology. There are some fire-prone areas in Australia, both Americas, some Mediterranean countries and regions with extensive prescribed or illegal burning like central European, which are subjected to a direct impact of fire (heat, minerals accumulation from the burning matter) and/or the indirect one (smoke) and undergo compositional and structural changes. This review first updates information about the effect of the compounds on plants' kingdoms and focuses on the research advances in the field of smoke compounds and attempts to gather and summarize the recent state of research and opinions on the role of smoke-derived compounds in plants' lives. We finish our review by discussing major research gaps, which include: Why plants respond to smoke chemicals? Is the response of seeds to smoke and smoke compounds an evolutionary-driven trait allowing plants to adapt to local environment?

Keywords: plant butenolides; karrikins; seed germination; plant ecology; crop physiology; plant development; swailing; vegetation restoration

1. Introduction

It seems that fire can act as an ecological filter and selects plants with specific traits [1-3]. The response of plant taxa to fire depends on the fire itself (duration and frequency) and the functional traits. Resprouting ability and propagule persistence are identified on the basis fire-response traits [4,5]. These characteristics have shifted focus from studying the effects of fire on individual species to researching plant functional types related to fire in pyrogenic or fire-prone ecosystems. So fire is as an ecological factor plays a remarkable role in shaping and changing the plant communities structure [6,7]. Plant communities undergo the direct impact of fire (heat, minerals accumulation from the burning matter) and/or the indirect one (smoke). Fire-related cues affect various aspects of plant growth and development from germination to fruiting [8]. Heat shocks (dormancy breaking) and smoke (germination stimulation) are important complementary factors that affect species with different seed coat permeabilities [9-11]. The smoke produced from the burning of plants needs special attention as it affects plants through specific chemicals, which can affect plant metabolism [12]. Extensive efforts have been done to identify the active compounds responsible for smoke-stimulated seed germination. It is estimated that at least two groups of fire-related chemical (karrikins, KARs and nitriles), along with smoke products (aerosol smoke and smoke water) that promote germinationv [13,14]. The stimulatory effects of nitriles such as cyanohydrins glyceronitrile (2,3-dihydroxypropanenitrile) and mandelonitrile (MAN) on germination have also been determined in several studies [15-17]. There are also germination inhibitors like trimethylbutenolide (TMB) why some plant respond to smoke and pure smoke compounds in different ways [18].

Many studies provided evidences of smoke-stimulated germination in prone-fire and non-fire-prone ecosystems (prescribed burning and swailing) [11,16,19-22]. Investigating the effect of fire products, especially smoke on plant life makes it possible to obtain data associated with the response of different species, and the results can help to determine which species by which mechanism benefit from fire, and which species will be at a disadvantage? This serves as a starting point to answer the fundamental questions such as how smoke shapes and results in the evolution of plant communities? How smoke affects seed characteristics? How does the fire or its products stimulate seed dormancy and germination as key physiological processes in regions with wild or prescribed fires? How do plants receive smoke signals and react to them? And in general, what is the role of smoke in plants? This review aims to discuss the findings associated with smoke compounds, their mode of action, and the ecological implications.

2. The impact of post-fire smoke on plant communities

Studies conducted in Mediterranean-type climates (MTC) show that the life cycle of many plant species in this fire-prone ecosystem depends on fire. On the other hand, despite consisting only about two per cent of the world's area, these regions are important habitats for 1/6 of the world's vascular plants [4]. Thus, food and species conservation in these regions is highly regarded. In the Mediterranean ecosystem of Southeast Australia, the highest frequency of germination is related to obligate seeders (mostly annual species) and *Poaceae* species, whose germination is stimulated by smoke [23]. This phenomenon occurs when the species has a rich seed bank and can germinate after the fire [16]. In these regions, resprouter species can only survive in habitats which the interval between two fires is long enough for regrowth and seed production. However, the trees are suppressed if the fire is repeated frequently in these regions. Therefore, natural selection results in an ecosystem comprising African and grassland [23]. For example, Burkina Faso's natural vegetation mainly consists of savannas. In this biome, the high concentration of smoke decreases seed germination of some species. Also, the type of smoke can affect natural plant communities differently. For example, aqueous smoke solution did not affect the germination response of some species while their germination with aerosol smoke was delayed [8,24].

An experimental study on the role of fire in the germination of montane forest species in the southern portion of North America showed that the response of plants to fire products strongly depends on the type of dormancy and species of fire products. Hence, fire by-products may affect the composition and diversity of species in a post-fire environment [25]. Recently, the role of fire in the potential regeneration of peatland bryophytes from spores has been addressed in some studies and especially the promotive effect of smoke on spore germination has been demonstrated and proved that smoke–water can highly stimulate the germination of ten bryophyte spores in another part of the globe, Northeast China [26].

Annual, perennial and woody species are the dominant plant growth form in the Eastern Mediterranean basin. Çatav et al. [17] reported that annual species play an important role in the post-fire environment characterizing southwestern Turkey, Eastern Mediterranean Basin. Successful post-fire recruitment of annuals might be due to the enhanced germination by smoked-derived chemicals (KARs). In the biome, many woody plants (*Fabaceae*) were disable in germination due to dormancy and tend to withstand very high temperatures and their germination is stimulated by the heat. In these plants, the presence of various regenerative strategies, including the development of fire-resistant tissues and heat-isolated meristems, resprouting, fire-stimulated flowering, serotiny or fire-stimulated germination facilitates the post-fire recovery of vegetation [27,28]. For example, in Cabrera (characterized by mild temperatures and frequent precipitation), species with a high specific leaf area (SLA), resprouters, and obligate seeders with heat-stimulated germination respond better to burn severity. On the contrary, in Gátova (characterized by a drier and warmer climate), N_2-fixer species[1], facultatives, and heat-stimulated species present better regeneration at high burn severity [27].

Many species in boreal forest in North America area have physiological dormancy. Strategies such as scarification can be applied to alleviate seed dormancy of native forest species. Fire by-

---

[1] Nitrogen- fixer species

products such as smoke water extract is known to stimulate germination in seeds from this habitat in North America, but only for seeds treated previously with cold stratification [29].

On the other hand, an experimental study on the role of fire in the germination of the Florida scrub with a subtropical savanna and humid climate shows smoke-stimulated germination in some species. Also, some species were tolerant to heat shock (consequently to fire). Species' response to heat shock can relate to the specific post-fire regeneration strategy [6].

Heading to the south, Cerrado biomes in northeastern and southeastern Brazil are dominated by herbaceous and shrubby species. Some species of these regions germinate when exposed to smoke and heat shock during a fire. Smoke appears more effective than heat in savannas, especially in South America. The high temperatures produced by fire break the seed dormancy of some legumes. Contrary, temperature fluctuations due to fire in the Cerrado region, Brazil, had little influence on the dormancy elimination of most *Fabaceae* plants [10]. In fact, physical dormancy protects the seeds of these species against heat, and they emerge after the fire in vegetation gaps (due to reduced competition and more availability of light and water in these gaps) [30].

Continuing the review of the research performed in South America, Gómez-González et al. [19] evaluated the effect of smoke on the seed germination of 18 native woody species of the Mediterranean matorral of central Chile. They reported that although smoke and heat shock produced by fires generally inhibited the germination in native species of mature matorral communities, it stimulated the germination of several pioneer woody species such as *Acacia caven*, *Trevoa quinquenervia* and *Baccharis vernalis*. It seems seeds are intolerant to fire in Chilean matorral.

While taking into account Asia, a laboratory experiment investigated the effects of smoke on seed germination of 13 species in a monsoon climate region in China. The results showed that only one species, *Aristolochia debilis*, responded positively to smoke [31]. The lack of germination may be due to germination-inhibiting compounds in smoke. These compounds set the basis that why different plants respond to plant-derived smoke differently.

The investigation of native and exotic species in areas affected by anthropogenic fires in Sri Lanka (Patana grasslands, tropical dry forests) shows that plant-derived smoke generally stimulates seed germination, but the sensitivity of plants to smoke can vary. Plant-derived smoke generated from frequent wildfires could potentially increase weed and exotic species invasion [32]. Seed germination in response to fire-related cues has been widely studied in species from fire-prone ecosystems. In non-fire-prone parts of Europe, germination rates in *Brassicaceae* weeds have been reported to be fourfold to fivefold higher than control rates once exposed to smoke water. In fact, plant smoke contains karrikins (KARs), a family of compounds produced by wildfires known to stimulate the germination of dormant seeds of *Brassicaceae* weeds in the temperate region of Europe [33,34]. Investigating the effect of fire on rangelands by Wójcik and Janicka [35] and Wojcik et al. [36] showed that fire leads to a reduction in species richness in *Molinion* meadow. However, *Molinion* meadows are valuable types of meadows typical to Central Europe and protected under the European Natura 2000 network and fire produced rich and nutritious ash which was a suitable medium for the growth of rare and extinction-prone species. These observations for many years served as a pattern for farmers of the region to make use of prescribed burning to manage an ecosystem for agricultural purposes.

However, the germination characteristics of species from non-fire-prone ecosystems, such as the temperate regions and those of monsoon climate, where fire fires occur occasionally, and mostly because of swailing have been less studied [37]. Smoke-derived compounds emitted during accidental swailing, prescribed burning, or specifically formatted smoke can affect crops, trees, and natural plant communities differently. Considering an example of practical application outside the fire-prone habitats, Bączek-Kwinta [34] reported that germination of the seeds of *Myosotis arvensis*, a common plant in central European of moderate climate, was strongly suppressed by the application of smoke from burning local meadow plants. On the other hand, *Trifolium repens*, a native N_2-fixer species, responded positively to smoke. Germinability of seeds of one of the most invasive plants, Solidago gigantea (giant goldenrod) was also stimulated by smoke-generated volatiles. The plant response of Central European bio- and agricosystems varies within families, even species and cultivars. It is likely to be influenced by butenolide concentration. Therefore, research with different butenolide concentrations is needed. This study also stated that smoke generated by swailing can cause changes in habitat composition in Central Europe, especially in terms of suppression of invasive plants [34].

One year after the fire in a species-poor grassland community in the Czech Republic, also Central Europe, the results showed a decrease in the number of plant species. For instance, annual plants (dicots and grasses) were not found and perennial herbs were prevalent. Herbaceous species eliminated some endemic wind-dispersed species. Apparently, phytotoxicity in the soil is also responsible for the inhibition of germination and root growth [37]. The regeneration of plant species such as *Calluna vulgaris* common in British Islands led to increased productivity in grasslands [38]. The share of rare species possessing underground organs such as *Epipactis gentiana* increased due to the higher content of nutrients in ash in South of Poland [36]. Examples of species from several biomes that show germination stimulated by fire-cues mostly smoke are given in Table 1.

Table 1. Examples of species from several biomes that show germination stimulated by fire-cues mostly smoke.

plant ecosysytem	**Biomes**	**Plant Species**			**Reference**
Fire-prone ecosystem		**Smoke**	**Smoke water**	**Heat**	
South African and Australian	Fynbos		*Poaceae sp.*		[23]
The South America	Cerrado		*Mimosa somnians* *Cambessedesia hilariana* *Microlicia sp.*		[10]
The South America	Matorral		*Acacia caven,* *Baccharis vernalis* *Trevoa quinquenervia*		[19]
Asia, Sri Lanka habitats	Savanna-Woodland		*Flueggea leucopyrus* *Maesa indica* *Phyllanthus emblica L.* *Chromolaena odorata L.* *Hyptis suaveolens L.*		[32]
Africa, BurkinaFaso habitats	Sudanian Savanna-Woodland		*Pteleopsis suberosa* *Terminalia avicennioides* *Borreria scabra*		[8] [24]
Mediterranean Basin	Chaparral		*Annual herbaceous sp.*		[17]
Florida	Scrub		*Chrysopsis. highlandsensis* *Eryngium cuneifolium* *Lechea. cernua*		[6]
Mexico	Montane Forest		*Fuchsia encliandra* *Pinus douglasiana*	*Calliandra longirostrata* *Lupinus exaltatus* *Rhus schmidelioides* *Salvia iodantha*	[25]
non-fire prone ecosystem					
North Europe	Temperate Region		*Camelina microcarpa* *Descurainia sophia* *Plantago lanceolata*		[33]
North America	Boreal Forest		*Vaccinium myrtilloides*		[29]
China Plants	Monsoon Climate		*Aristolochia debilis*		[31]
Central Europe	Common Plants	*Matricaria chamomilla* *Solidago gigantea (alien, invasive)* *Trifolium repens*			[34]
Northeast China	Saline-Alkaline Grasslands		*Setaria viridis* *Kochia scoparia*	*Suaeda glauca* *Kochia scoparia*	[39]

Northeast China	Northern Peatland	*Sphagnum flexuosum* *Sphagnum subnitens* *Sphagnum imbricatum* *Sphagnum magellanicum* *Sphagnumfuscum* *Polytrichum strictum* *Sphagnum squarrosum* *Drepanocladus aduncus* *Physcomitrium sphaericum* *Hypnum callichroum*	[26]

3. Common physiological mechanisms of smoke compounds on plant physiology

Smoke and its active compounds affect cell metabolism by interacting with phytohormones such as ABA, GA, IAA and ethylene [40]. The smoke produced from the burning of plants consists of various complex chemical compounds, and this variation may be the reason behind the different responses of plants to smoke [12]. Many of these compounds belong to unsaturated lactones, i.e. butenolides. Karrikinolides (KAR1-KAR6) are butenolides compounds that were first discovered as post-fire germination stimulators in plants [14,41].

Detection of KARs by plants is done via the expression of a certain gene. In the plant cell exposed to smoke produced by fire, first, a receptor protein, karrikin insensitive 2 (KAI2) detects karrikin and its structure changes immediately after binding. Then, they form a complex with MAX2 and SMXL1 proteins which can degrade the repressor proteins in KAR signaling pathway. Thus, the activated transcription factor can regulate the expression of certain genes (genes responding to KAR) which eventually leads to specific growth characteristics such as germination, seedling growth [42] and adaptability to abiotic stress [43,44]. A recent study on *Arabidopsis* (a model plant) showed that morphological and growth changes will occur in plants if KAR signaling pathway is interrupted [45].

Phytohormones such as gibberellin, auxin, abscisic acid and ethylene can regulate plant growth and development either concurring with or against the function of SLs and KARs [44]. In recent years, various studies have been carried out regarding the response of plants to smoke at the molecular level and the role of smoke in physiological mechanisms in plants.

The response of model and arable plants to karrikin is not similar and varied in terms of growth and development and photosynthetic characteristics. Nonetheless, karrikin did not result in phytotoxicity or agronomic mutations [46-48]. In rice, smoke led to the expression of abscisic acid (ABA) and gibberellic acid (GA3) responsive cis-elements genes during imbibition. Probably, liquid smoke during imbibition makes it possible for the seed (by stimulating the enzymes required to translocate the seed reserves or by increased permeability of membranes to growth regulating hormones) to exploit its reserves to start the metabolic activities, which will lead to earlier radicle emergence [49].

The mechanism behind increased photosynthetic pigments due to smoke is not yet known, but due to semi-phytohormonal role of karrikin, it is probable that this bioactive compound stimulates the genes involved in chlorophyll biosynthesis pathway or inhibits chlorophyll-regrading genes and thus, increase chlorophyll concentration in which was indicated in basil (*Ocimum basilicum* L.) [50]. This increase in pigments enables the plant to intercept solar radiation better, which leads to improved photosynthetic productivity [12]. Concentrations of butenolides and other smoke-derived compounds can have adverse effects on germination. Hydroquinone is a strong bioactivator that is only active at low concentrations, and its high concentrations decrease KAR1 activity and inhibits seed germination [40]. Under various conditions like abiotic stresses, karrikin increased several abscisic acid signaling pathway genes including ABI5, ABI3, RELATED PROTEIN KINASE2.6,-SNF1 RELATED PROTEIN KINASE2.3,-NF1 without an increase in ABA. KAR1 significantly increases organic acid and amino acid contents. This shows that karrikins probably decrease abiotic stresses through redox homeostasis. Therefore, karrikins interact directly with ABA-regulating genes to regulate stress adaptability [51]. Improved drought tolerance in herbaceous weeds is associated with activation of genes responding to karrikin and transcription factors of genes related to increased expression capacity of antioxidants [52]. Karrikins decrease oxidative stresses resulted from drought, salinity and heavy metals by increasing the expression of different enzymes and genes involved in stress mitigation. In fact, karrikins provide a stress tolerance mechanism by controlling the cell antioxidant apparatus and activity of antioxidants such as SOD and CAT [53]. Aqueous smoke formulation (smoke water, SW) can affect crop productivity. For example, smoke water may emulate the mode of action of swailing-derived smoke on plants [34]. Tavşanoğlu et al. [16] studied both KAR1 and a cyanohydrin analogue, mandelonitrile (MAN), in the seeds of an annual plant, *Chaenorhinum rubrifolium*, that was characterized by strong physiological dormancy. KAR and MAN stimulated the germination of *Ch. rubrifolium*, used both individually and in combination, and the highest germination rate was achieved by a joint treatment with KAR1 and light. Therefore, not only the smoke-specific molecules but also environmental factors characteristic of the local environment must be considered. The active concentration of KAR differs in different species [54].

The active compounds in plant-derived smoke were separated from different plants, showing the diverse nature of smoke based on the plant used to produce smoke. These compounds set the base that why some plants respond to plant-derived smoke and pure smoke compounds differently. Plant-derived smoke contains a variety of stimulants and inhibitors (namely karrikins and TMB, trimethylbutenolide), that can have positive, negative, or neutral effects on plant growth, depending on their concentration and exposure period [18,42,55]. Compounds such as cyanide dinitrophenol, azide, fluoride, and hydroxylamine, have inhibited germination at concentrations approximating those which inhibit metabolic processes [18]. Some implications of using smoke formulations or individual smoke-derived compounds are presented in Table 2.

Table 2. The impact of various smoke compounds to seed germination and seedling vigour.

Plant Species	**Physiologically active smoke compound of smoke**	**Mode of Action**	**Reference**
Lactuca sativa cv.	KAR1	Stimulates seed germination	[56]
Chaenorhinum rubrifolium	Aqueous smoke, Nitrate	Breakdown of physiological dormancy	[16]
	KAR1, MAN	Stimulates seed germination	
Ansellia africana	TMB	Reduced the germination rate index and the development rate index	[57]
Heteropogon contortus	Benzaldehyde, Cyanide, Potassium cyanide	Stimulates seed germination	[58]
Lactuca sativa	MAN	Inhibit seed germination	[18]
Nicotiana attenuata	SAL	Stimulates seed germination	[59]
Artemisia absinthium L.	SGV	Stimulates seed germination	[34]
Plantago major L.		Stimulates seed germination	
Mediterranean plant species	Glyceronitrile and smoke/butanolide solution	Seed germination and seedling length were enhanced	[17]
Capsicum annuum L.	KAR1	Stimulate germination, seedling emergence	[60]
Daucus carota L.	KAR1	germination, plant height	[61]

Abbreviations: KAR1—karrikin 1; MAN—mandelonitrile; SAL—syringaldehyde; TMB—trimethylbutenolide; SGV—swailing-generated volatiles.

The plant response varies within the species, even cultivars, and is influenced by plant growth pattern and developmental stage, butenolide concentrations, soil composition and microbiota, and other environmental factors mostly light. Smoke-derived compounds emitted during accidental swailing, prescribed burning can affect crops, trees, and natural plant communities differently.

4. Conclusion

Plant metabolism is disrupted by various abiotic stresses and fire. Since plants are unable to avoid environmental challenges, they reconstruct metabolic networks and evolve mechanisms controlling their structural and functional traits. Then these stress-induced traits could be used as a selection criteria to combat stress which ensures their survival under adverse conditions. [62-64]

Fire and its byproducts (e.g. heat, smoke, charates), are now identified as a natural evolutionary force that has shaped and regulated organismal traits [7], provided a fitness benefit following fires and genetically fixed over time [28]. All Mediterranean-type climate (MTC), except Chile, show a remarkable degree of evolutionary convergence in response to fire in their floras [65,66]. This is reflected in evolutionary-driven traits allowing plants to adapt to local environment. Given that the majority of plant species positively respond to plant-derived smoke in the enhancement of seed germination and plant growth [12] and the germination of fire-adapted plants is stimulated by butenolide-related compounds (karrikins) present in smoke [28], it would appear that the most parsimonious adaptive solution was to take advantage of KAR to stimulate post-fire germination. This confirm that if a trait has evolved in response to selection by fire then the environment of the plant must have been fire-prone before the appearance of that trait [67]. Also, since flowering plants more clearly arose in a fire-prone environment, this means that the presence of KAR-sensitivity among flowering plants can be traced back to their fire-prone origins [68].

However, it is unclear whether these fire-related traits are the result of natural selection by fire because it is considered to lack supporting evidence. Therefore it is difficult to prove that these fire-related traits are adaptive responses [69]. Moreover, the above-mentioned metabolic interactions between KARs and different smoke compounds, and the spectrum of light as well, makes it complex.

References

1. Pausas, J.G.; Verdú, M. Fire reduces morphospace occupation in plant communities. *Ecol.* **2008**, *89*, 2181-2186.
2. Archibald, S.; Lehmann, C.E.; Belcher, C.M.; Bond, W.J.; Bradstock, R.A.; Daniau, A.-L.; Dexter, K.G.; Forrestel, E.J.; Greve, M.; He, T. Biological and geophysical feedbacks with fire in the Earth system. *Environ. Res. Lett.* **2018**, *13*, 033003.
3. Fox, S.; Sikes, B.A.; Brown, S.P.; Cripps, C.L.; Glassman, S.I.; Hughes, K.; Semenova-Nelsen, T.; Jumpponen, A. Fire as a driver of fungal diversity—A synthesis of current knowledge. *Mycol.* **2022**, *114*, 215-241.
4. Kelly, L.T.; Giljohann, K.M.; Duane, A.; Aquilué, N.; Archibald, S.; Batllori, E.; Bennett, A.F.; Buckland, S.T.; Canelles, Q.; Clarke, M.F. Fire and biodiversity in the Anthropocene. *Science* **2020**, *370*, eabb0355.
5. Pausas, J.G.; Keeley, J.E. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytol.* **2014**, *204*, 55-65.
6. King, R.A.; Menges, E.S. Effects of heat and smoke on the germination of six Florida scrub species. *S. Afr. J. Bot.* **2018**, *115*, 223-230.
7. He, T.; Lamont, B.B.; Pausas, J.G. Fire as a key driver of Earth's biodiversity. *Biol. Rev.* **2019**, *94*, 1983-2010.
8. Dayamba, S.D.; Tigabu, M.; Sawadogo, L.; Oden, P.C. Seed germination of herbaceous and woody species of the Sudanian savanna-woodland in response to heat shock and smoke. *For. Ecol. Manag.* **2008**, *256*, 462-470.
9. Penman, T.D.; Binns, D.; Allen, R.; Shiels, R.; Plummer, S. Germination responses of a dry sclerophyll forest soil-stored seedbank to fire related. cues. **2008**.
10. Zirondi, H.L.; Silveira, F.A.; Fidelis, A. Fire effects on seed germination: heat shock and smoke on permeable vs impermeable seed coats. *Flora* **2019**, *253*, 98-106.
11. Hodges, J.A.; Price, J.N.; Nicotra, A.B.; Neeman, T.; Guja, L.K. Smoke and heat accelerate and increase germination in fire-prone temperate grassy ecosystems. *Ecosphere* **2021**, *12*, e03851.
12. Khatoon, A.; Rehman, S.U.; Aslam, M.M.; Jamil, M.; Komatsu, S. Plant-derived smoke affects biochemical mechanism on plant growth and seed germination. *Int. J. Mol. Sci.* **2020**, *21*, 7760.
13. Chiwocha, S.D.; Dixon, K.W.; Flematti, G.R.; Ghisalberti, E.L.; Merritt, D.J.; Nelson, D.C.; Riseborough, J.-A.M.; Smith, S.M.; Stevens, J.C. Karrikins: a new family of plant growth regulators in smoke. *Plant sci.* **2009**, *177*, 252-256.
14. Waters, M.T.; Nelson, D.C. Karrikin perception and signalling. *New Phyto.* **2023**, *237*, 1525-1541.

15. Flematti, G.R.; Merritt, D.J.; Piggott, M.J.; Trengove, R.D.; Smith, S.M.; Dixon, K.W.; Ghisalberti, E.L. Burning vegetation produces cyanohydrins that liberate cyanide and stimulate seed germination. *Nat. Commun.* **2011**, *2*, 360.
16. Tavşanoğlu, Ç.; Ergan, G.; Çatav, Ş.S.; Zare, G.; Küçükakyüz, K.; Özüdoğru, B. Multiple fire-related cues stimulate germination in *Chaenorhinum rubrifolium* (Plantaginaceae), a rare annual in the Mediterranean Basin. *Seed Sci. Res.* **2017**, *27*, 26-38.
17. Çatav, Ş.S.; Küçükakyüz, K.; Tavşanoğlu, Ç.; Pausas, J.G. Effect of fire-derived chemicals on germination and seedling growth in Mediterranean plant species. *Basic Appl. Ecol.* **2018**, *30*, 65-75.
18. Pošta, M.; Papenfus, H.B.; Light, M.E.; Beier, P.; Van Staden, J. Structure–activity relationships of N-and S-analogs of the seed germination inhibitor (3, 4, 5-trimethylfuran-2 (5 H)-one) for mode of action elucidation. *Plant Growth Regu.* **2017**, *82*, 47-53.
19. Gómez-González, S.; Sierra-Almeida, A.; Cavieres, L. Does plant-derived smoke affect seed germination in dominant woody species of the Mediterranean matorral of central Chile? *For. Ecol. Manag.* **2008**, *255*, 1510-1515.
20. Bączek-Kwinta, R.; Markowicz, M. The impact of plant-derived smoke on seed germination in the context of swailing. *Grzesiak MT, Rzepka A., Hura T., Grzesiak S. Plant Functioning under Environmental Stress, The Franciszek Górski Institute of Plant Physiology, Polish Academy of Sciences, Cracow* **2013**, 233-239.
21. Moreira, B.; Pausas, J. Shedding light through the smoke on the germination of Mediterranean Basin flora. *S. Afr. J. Bot.* **2018**, *115*, 244-250.
22. Wilson, C.R.; Lusk, C.H.; Campbell, D.I. The role of the peat seed bank in plant community dynamics of a fire-prone New Zealand restiad bog. *Austral. Ecol.* **2022**, *47*, 1515-1527.
23. Carthey, A.J.; Tims, A.; Geedicke, I.; Leishman, M.R. Broad-scale patterns in smoke-responsive germination from the south-eastern Australian flora. *J. Veg. Sci.* **2018**, *29*, 737-745.
24. Dayamba, S.D.; Sawadogo, L.; Tigabu, M.; Savadogo, P.; Zida, D.; Tiveau, D.; Oden, P.C. Effects of aqueous smoke solutions and heat on seed germination of herbaceous species of the Sudanian savanna-woodland in Burkina Faso. *Flora-Morphol. Distrib. Func. Ecol. Plants* **2010**, *205*, 319-325.
25. Zuloaga-Aguilar, S.; Briones, O.; Orozco-Segovia, A. Seed germination of montane forest species in response to ash, smoke and heat shock in Mexico. *Acta Oecol.* **2011**, *37*, 256-262.
26. Yusup, S.; Sundberg, S.; Ooi, M.K.; Zhang, M.; Sun, Z.; Rydin, H.; Wang, M.; Feng, L.; Chen, X.; Bu, Z.-J. Smoke promotes germination of peatland bryophyte spores. *J. Exp. Bot.* **2023**, *74*, 251-264.
27. Huerta, S.; Fernández-García, V.; Marcos, E.; Suarez-Seoane, S.; Calvo, L. Physiological and regenerative plant traits explain vegetation regeneration under different severity levels in Mediterranean fire-prone ecosystems. *For.* **2021**, *12*, 149.
28. Lamont, B.B.; He, T.; Yan, Z. Evolutionary history of fire-stimulated resprouting, flowering, seed release and germination. *Biol. Rev.* **2019**, *94*, 903-928.
29. Mackenzie, D.D.; Naeth, M.A. Effect of plant-derived smoke water and potassium nitrate on germination of understory boreal forest plants. *Can. J. For. Res.* **2019**, *49*, 1540-1547.
30. Daibes, L.F.; Martins, A.R.; Silveira, F.A.; Fidelis, A. Seed tolerance to post-fire temperature fluctuation of Cerrado legume shrubs with micromorphological implications. *Flora* **2021**, *275*, 151761.
31. Zhou, J.; Teixeira da Silva, J.A.; Ma, G. Effects of smoke water and karrikin on seed germination of 13 species growing in China. *Cen. Euro. J. Bio.* **2014**, *9*, 1108-1116.
32. Alahakoon, A.; Perera, G.; Merritt, D.; Turner, S.R.; Gama-Arachchige, N. Species-specific smoke effects on seed germination of plants from different habitats from Sri Lanka. *Flora* **2020**, *263*, 151530.
33. Mojzes, A.; Kalapos, T. Plant-derived smoke stimulates germination of four herbaceous species common in temperate regions of Europe. *Plant Ecol.* **2014**, *215*, 411-415.
34. Bączek-Kwinta, R. Swailing affects seed germination of plants of European bio-and agricenosis in a different way. *Open Life Sci.* **2017**, *12*, 62-75.
35. Wójcik, T.; Janicka, M. Current state and changes in Molinion meadows from Kostrze environs in Kraków. *Ecol. Quest.* **2016**, *23*.
36. Wójcik, T.; Kostrakiewicz-Gierałt, K.; Makuch-Pietraś, I. The effect of accidental burning on habitat conditions and species composition of *Molinion caeruleae* meadows. *J. Nat. Conserv.* **2022**, *70*, 126294.
37. Li, T.; Jeřábek, J.; Winkler, J.; Vaverková, M.D.; Zumr, D. Effects of prescribed fire on topsoil properties: A small-scale straw burning experiment. *J. Hydrol. Hydromech.* **2022**, *70*, 450-461.
38. Harper, A.R.; Doerr, S.H.; Santin, C.; Froyd, C.A.; Sinnadurai, P. Prescribed fire and its impacts on ecosystem services in the UK. *Sci. Total Environ.* **2018**, *624*, 691-703.
39. Li, S.; Ma, H.; Ooi, M.K. Fire-related cues significantly promote seed germination of some salt-tolerant species from non-fire-prone saline-alkaline grasslands in Northeast China. *Plants* **2021**, *10*, 2675.

40. Singh, S.; Uddin, M.; Khan, M.M.A.; Chishti, A.S.; Singh, S.; Bhat, U.H. The role of plant-derived smoke and karrikinolide in abiotic stress mitigation: An Omic approach. *Plant Stress* **2023**, 100147.
41. De Lange, J.H.; Boucher, C. Autecological studies on *Audouinia capitata* (Bruniaceae). I. Plant-derived smoke as a seed germination cue. *S. Afr. J. Bot.* **1990**, *56*, 700-703.
42. Çatav, Ş.S.; Elgin, E.S.; Dağ, Ç.; Stark, J.L.; Küçükakyüz, K. NMR-based metabolomics reveals that plant-derived smoke stimulates root growth via affecting carbohydrate and energy metabolism in maize. *Metabolomics* **2018**, *14*, 1-11.
43. Meng, Y.; Shuai, H.; Luo, X.; Chen, F.; Zhou, W.; Yang, W.; Shu, K. Karrikins: regulators involved in phytohormone signaling networks during seed germination and seedling development. *Front. plant sci.* **2017**, *7*, 2021.
44. Yang, T.; Lian, Y.; Wang, C. Comparing and contrasting the multiple roles of butenolide plant growth regulators: strigolactones and karrikins in plant development and adaptation to abiotic stresses. *Int. j. mol. sci.* **2019**, *20*, 6270.
45. Stanga, J.P.; Smith, S.M.; Briggs, W.R.; Nelson, D.C. SUPPRESSOR OF MORE AXILLARY GROWTH2 1 controls seed germination and seedling development in *Arabidopsis*. *Plant physio.* **2013**, *163*, 318-330.
46. Ghebrehiwot, H.; Kulkarni, M.; Kirkman, K.; Van Staden, J. Smoke-water and a smoke-isolated butenolide improve germination and seedling vigour of *Eragrostis Tef* (Zucc.) Trotter under high temperature and low osmotic potential. *J. Agron. Crop Sci.* **2008**, *194*, 270-277.
47. Jain, N.; Kulkarni, M.G.; van Staden, J. A butenolide, isolated from smoke, can overcome the detrimental effects of extreme temperatures during tomato seed germination. *Plant Growth Regul.* **2006**, *49*, 263-267.
48. Wang, L.; Waters, M.T.; Smith, S.M. Karrikin-KAI2 signalling provides *Arabidopsis* seeds with tolerance to abiotic stress and inhibits germination under conditions unfavourable to seedling establishment. *New Phytol.* **2018**, *219*, 605-618.
49. Jamil, M.; Jahangir, M.; Rehman, S.U. Smoke induced physiological, biochemical and molecular changes in germinating rice seeds. *Pak. J. Bot* **2020**, *52*, 865-871.
50. Noroozi Shahri, F.; Jalali Honarmand, S.; Saeidi, M.; Mondani, F. Evaluation of some biochemical characteristics of medicinal plant basil (*Ocimum basilicum* L.) under the application of growth phytohormones and phytohormones-like. *J. Plant Proc. Func.* **2021**, *10*, 189-210.
51. Shah, F.A.; Wei, X.; Wang, Q.; Liu, W.; Wang, D.; Yao, Y.; Hu, H.; Chen, X.; Huang, S.; Hou, J. Karrikin improves osmotic and salt stress tolerance via the regulation of the redox homeostasis in the oil plant *Sapium sebiferum*. *Front. Plant Sci.* **2020**, *11*, 216.
52. Tan, Z.-Z.; Wang, Y.-T.; Zhang, X.-X.; Jiang, H.-Y.; Li, Y.; Zhuang, L.-L.; Yu, J.-J.; Yang, Z.-M. Karrikin1 Enhances Drought Tolerance in Creeping Bentgrass in Association with Antioxidative Protection and Regulation of Stress-Responsive Gene Expression. *Agron.* **2023**, *13*, 675.
53. Ahmad, B.; Qadir, S.U.; Dar, T.A.; Alam, P.; Yousuf, P.Y.; Ahmad, P. Karrikins: smoke-derived phytohormones from stress alleviation to signaling. *J. Plant Growth Regul.* **2022**, 1-13.
54. Bączek-Kwinta, R. An Interplay of Light and Smoke Compounds in Photoblastic Seeds. *Plants* **2022**, *11*, 1773.
55. Flematti, G.R.; Waters, M.T.; Scaffidi, A.; Merritt, D.J.; Ghisalberti, E.L.; Dixon, K.W.; Smith, S.M. Karrikin and cyanohydrin smoke signals provide clues to new endogenous plant signaling compounds. *Mol. Plant* **2013**, *6*, 29-37.
56. Pošta, M.; Light, M.E.; Papenfus, H.B.; Van Staden, J.; Kohout, L. Structure–activity relationships of analogs of 3, 4, 5-trimethylfuran-2 (5H)-one with germination inhibitory activities. *J. plant physio.* **2013**, *170*, 1235-1242.
57. Papenfus, H.B.; Naidoo, D.; Pošta, M.; Finnie, J.F.; Van Staden, J. The effects of smoke derivatives on in vitro seed germination and development of the leopard orchid *Ansellia africana*. *Plant Biol.* **2016**, *18*, 289-294.
58. Baldos, O.C.; DeFrank, J.; Sakamoto, G.S. Germination response of dormant tanglehead (*Heteropogon contortus*) seeds to smoke-infused water and the smoke-associated stimulatory compounds, karrikinolide and cyanide. *Hortic. Sci.* **2015**, *50*, 421-429.
59. Cao, D.; Schöttner, M.; Halitschke, R.; Li, D.; Baldwin, G.; Rocha, C.; Baldwin, I.T. Syringaldehyde is a novel smoke-derived germination cue for the native fire-chasing tobacco, *Nicotiana attenuata*. *Seed Sci. Res.* **2021**, *31*, 292-299.
60. Demir, I.; Ozden, E.; Yıldırım, K.; Sahin, O.; Van Staden, J. Priming with smoke-derived karrikinolide enhances germination and transplant quality of immature and mature pepper seed lots. *S. Afr. J. Bot.* **2018**, *115*, 264-268.

61. Akeel, A.; Khan, M.M.A.; Jaleel, H.; Uddin, M. Smoke-saturated water and karrikinolide modulate germination, growth, photosynthesis and nutritional values of carrot (*Daucus carota* L.). *J. Plant Growth Regul.* **2019**, *38*, 1387-1401.
62. Obata, T.; Fernie, A.R. The use of metabolomics to dissect plant responses to abiotic stresses. *Cell. Mol. Life Sci.* **2012**, *69*, 3225-3243.
63. Dolferus, R. To grow or not to grow: a stressful decision for plants. *Plant Sci.* **2014**, *229*, 247-261.
64. Leuendorf, J.E.; Frank, M.; Schmülling, T. Acclimation, priming and memory in the response of *Arabidopsis thaliana* seedlings to cold stress. *Sci Rep.* **2020**, *10*, 689.
65. Keeley, J.E. Fire in Mediterranean climate ecosystems—A comparative overview. *Isr. J. Ecol. Evol.* **2012**, *58*, 123-135.
66. Keeley, J.E.; Pausas, J.G.; Rundel, P.W.; Bond, W.J.; Bradstock, R.A. Fire as an evolutionary pressure shaping plant traits. *Trends plant sci.* **2011**, *16*, 406-411.
67. Lamont, B.B.; He, T. Fire-proneness as a prerequisite for the evolution of fire-adapted traits. *Trends Plant Sci.* **2017**, *22*, 278-288.
68. He, T.; Lamont, B.B. Baptism by fire: the pivotal role of ancient conflagrations in evolution of the Earth's flora. *Nat. Sci. Rev.* **2018**, *5*, 237-254.
69. Keeley, J.E.; Pausas, J.G. Evolutionary ecology of fire. *Annual Review of Ecology, Evol. Syst.* **2022**, *53*, 203-225.