火烧信号对种子萌发影响的研究进展

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摘要 火作为一个基础的生态因子, 对森林、草地等陆地生态系统的结构和功能有着重要的影响。种子萌发是种子植物的重要生活史阶段, 也是火后植被更新和恢复的主要途径。植被燃烧产生了烟、热以及与烟相关的一系列火烧信号, 在打破种子休眠, 促进种子萌发方面发挥重要作用。该文将火烧信号分为物理信号和化学信号, 物理信号主要是伴随火烧产生的高温, 化学信号主要包括气态烟以及近年来从烟水中提取的影响种子萌发的关键化学物质karrikins和glyceronitrile。该文围绕火烧的基本信息, 火烧信号对种子萌发的影响, 火烧信号在实践中的应用3个方面进行系统综述, 重点探讨了不同类别的火烧信号及其交互作用对种子萌发的影响。在系统总结火烧信号对种子萌发影响的研究进展的基础上, 提出未来的研究应与烟信号作用机理的探究以及全球变化等方面相结合, 旨在充分发挥火的生态服务功能, 为火的科学管理应用和退化生态系统恢复提供理论支撑。

关键词 种子萌发; 火烧; 物理信号; 化学信号; 交互作用

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Research progress on the effects of fire-related cues on seed germination

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Abstract

Fire is a fundamental ecological factor profoundly affecting many terrestrial ecosystems including forest and grassland ecosystems. Seed germination is an important life-history stage of plants, and it is also the main strategy for the regeneration and restoration of vegetation after fire events. Vegetation combustion produces smoke, heat and a series of fire cues associated with smoke, and plays critical roles in breaking seed dormancy and seedling establishment. In this study, we clustered the fire cues into two categories, i.e., physical cues (heat) and chemical cues (aerial smoke, karrikins, glyceronitrile) and focused on the basic information of fire, the effects of fire cues on seed germination, and the application of fire cues. In addition, we focused on the effects of different types of fire cues and their interactions on seed germination. Based on a systematic review of the research progress on the effects of fire cues on seed germination, this study also provided suggestions for the future research, such as mechanism of smoke cues on seed germination and seedling growth via molecular technologies, and interaction of smoke cues with climate changes. In summary, based on the review of the ecological functions of fire-related cues on seed germination, this study aims to provide theoretical support for the scientific management of grassland and forest ecosystems and also provide basis for the applications of fire and the restoration of degraded ecosystems.

Key words seed germination; fire; physical cues; chemical cues; interaction

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火烧作为一个基础的生态过程, 深刻影响着森林、草原等陆地生态系统(Bond *et al.*, 2005; 王谢等, 2013; 杨健等, 2013; Pausas & Keeley, 2019; McLau-

chlan *et al.*, 2020)。火在参与塑造全球生物群系的分布, 维持群落结构和功能的同时, 也作为一种自然选择力量, 驱动了物种的进化(Bond & Keeley, 2005;

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He *et al.*, 2011; Keeley *et al.*, 2011)。

火烧可以影响植物的开花、种子传播、萌发、幼苗建植和死亡等生长发育的各个方面(Todorović *et al.*, 2010)。种子萌发是火烧后植被更新和恢复的主要方式。土壤种子库及植冠种子库作为退化植被动态变化的重要组成部分, 直接影响着生态系统的恢复能力(Qiu *et al.*, 2010; Lü *et al.*, 2017)。火烧可以降低物种间的竞争和提高资源的可利用性, 从而为种子萌发和幼苗建植提供有利环境, 进而实现种群的延续(Purdie, 1977; Kemp *et al.*, 2019)。植被燃烧产生了烟、热、karrikins (KARs)、glyceronitrile (SP₁)等火烧信号。这些信号在打破种子休眠, 促进种子萌发方面发挥了重要作用。例如, 火烧显著增加了 *Molinia caerulea* 的生物量、结实率和萌发率(Brys *et al.*, 2005)。Cuello等(2020)探究了乌拉圭温带草原土壤种子库对于火烧的响应情况, 结果表明火烧处理显著增加了种子萌发的密度和丰富度, 提前了萌发高峰。火烧信号可以促进澳大利亚西南地区将近900种植物种子的萌发(Auld & Denham, 2006)。火烧信号对种子萌发的影响在农业、园艺生产, 提高种子抗逆性和植被恢复等方面具有广泛的应用(He *et al.*, 2019; Pausas & Keeley, 2019)。

本文分别从火烧信号的基本信息, 火烧信号对种子萌发的影响, 火烧信号在实践中的应用3个方面进行系统地综述, 重点探讨了不同类别的火烧信号及其交互作用对种子萌发的影响, 并对未来的重点研究方向进行了展望, 旨在充分发挥火的生态服务功能, 为火的科学管理应用和退化生态系统恢复提供理论支撑。

1 火烧概况

1.1 火在陆地生态系统中的发生

陆地生态系统中约90%的火烧事件是由人类活动导致, 10%是由闪电和火山爆发等自然原因引起(Shikwambana & Kganyago, 2021)。火烧主要发生在地中海沿岸、美国加利福尼亚沿岸、澳大利亚西南部等地中海气候区(Moreira & Pausas, 2018; Stevens-Rumann & Morgan, 2019)。温带干旱半干旱气候区、热带干旱半干旱气候区的森林和草原也属于易发生火灾的生态系统(Hodges *et al.*, 2019; Ramos *et al.*, 2019)。丰富的可燃物储量, 干热的天气和气候为这些地区的火灾频发创造了条件(Bowman *et al.*,

2009)。在易发生火烧的生态系统中, 植物已经进化出一些适应性特征用于保证物种在火烧环境中存活和火烧后植被的恢复和更新(Keeley *et al.*, 2011)。在不易发生火烧的生态系统中, 系统内部缺乏足够的燃料和合适的气候条件来支持火烧现象的发生。然而全球气候和土地利用方式的变化改变了火烧发生地区的气候、地形、燃料等条件, 加剧了火烧情势的时空变化(Morgan *et al.*, 2001; 吕爱锋和田汉勤, 2007; Kelly *et al.*, 2020; 岳超等, 2020)。Silveira等(2020)探究了2019年巴西热带雨林大火发生的原因, 结果表明森林砍伐程度高的地区其月度火烧发生的频率显著高于砍伐程度低的地区。

1.2 火烧信号

根据火烧产物的理化性质将其分为物理和化学信号两个类别(图1)。植物燃烧产生的含氮化合物、烟、KARs和SP₁等萌发刺激物质被称为化学信号。燃烧过程中产生的高温和燃烧后光照条件的变化属于物理信号。火烧对于土壤的增温效果受燃料的生物量、组成成分和含水量, 土壤的湿度、深度等因素影响会呈现时空上的差异(Liyanage & Ooi, 2015; Veenendaal *et al.*, 2018)。表层土壤(0–3 cm)是土壤种子库集中分布的区域, 火烧可以使该区域的温度增至60–120 °C (Bradstock & Auld, 1995)。然而不同的生态系统如森林、草地等, 其火烧情势差异很大, 需要深入调查不同生态系统的热激温度和持续时间, 从而更好地模拟热激这一物理信号对种子萌发的影响。此外, 火烧对地表植被的破坏改变了到达地表的光强和光质, 对需光或者嫌光种子的萌发具有重要影响(López-Mársico *et al.*, 2019)。

火烧后, 植物源烟中促进种子萌发的化学物质会沉积在土壤表面。这些萌发刺激物质具有挥发性和水溶性(Staden *et al.*, 2000)。萌发刺激物质溶于水形成烟水, 既可以避免挥发, 实现长久保存, 又可以在地表转移到地下, 透过种皮, 刺激土壤种子库中的种子萌发(Brown & van Staden, 1997)。因此火烧后一场降雨对于火烧生境中的植被恢复和种子萌发具有重要意义(Quintana *et al.*, 2004)。在实验室中, 将植物燃烧产生的烟雾经抽气装置抽取通过去离子水制得实验所需的烟水(Coons *et al.*, 2014)。烟水在制备过程中的水量和燃料量决定了烟水的浓度。此外, 火烧后产生的灰烬中含有大量的无机离子如K⁺、NO₃⁻、NO₂⁻等, 同样会影响火烧生境下种子的

图1 影响种子萌发的火烧信号, 修改自Nelson等(2012)和Kamran等(2014)。红色和蓝色箭头分别表示植被燃烧产生的物理和化学信号。两种信号单独或者交互作用于种子萌发。热激的温度会随着土壤深度的增加而降低。化学信号可以借助雨水进入到土壤中。 NO_x 代表NO或者 NO_2 , 通过硝化作用, NO_2 或者 NO_3 氧化变成 NO_2 或者 NO_3 。

Fig. 1 Fire cues of affecting seed germination, modified from Nelson *et al.* (2012) and Kamran *et al.* (2014). The red and blue arrows represent the physical and chemical cues produced by vegetation combustion, respectively. Two cues individually or interactively affect seed germination. The heat shock temperature decreases with increasing soil depth. Chemical cues would normally be eluted into the soil by rain. NO_x represents NO or NO_2 . Oxidation of NH_4^+ or NO_x to NO_2 or NO_3 can occur by nitrification.

萌发(Downes *et al.*, 2014; Mackenzie & Naeth, 2019)。但是这些物质并非是火烧所特有的产物, 当前关于化学信号对种子萌发影响的研究多集中在烟信号以及从中提取的萌发刺激物质等方面。

KARs是由植被燃烧产生的存在于烟和烟水中一系列小的丁烯酸内酯分子的总称(Yao & Waters, 2020)。植物源烟中成分复杂, 含有上千种化合物, Flematti等(2004)将烟水中化合物进行分离、测定, 最终发现了对种子萌发具有刺激作用的生物活性化学物质karrikinolide (KAR₁)(图2A)。目前已经从植物源烟中发现了6种KAR (KAR₁₋₆), 其中KAR₁₋₄比较活跃(Nelson *et al.*, 2012)。KARs在紫外线下不稳定, 自然光可导致其含量减少(Scaffidi *et al.*, 2012)。KARs是烟中的主要萌发刺激物质, 但以*Anigozanthos manglesii*为代表的部分植物其萌发对烟水响应而对KARs不响应, 促使了新的萌发刺激化合物glyceronitrile的发现(图2B)。Glyceronitrile是氰醇类物质, 可以通过缓慢地释放氰化物刺激部分植物种子萌发(Flematti *et al.*, 2011)。Preston和Baldwin (1999)

图2 植物源烟中关键生物活性物质的化学结构。参考自Flematti等(2011)。

Fig. 2 Chemical structure of key bioactive compounds in plant-derived smoke. Redrawn from Flematti *et al.* (2011).

研究发现火烧发生后萌发刺激物质可以在土壤中存在超过7年时间, 对种子萌发的影响具有持久性。

2 火烧信号及其互作对于种子萌发的影响

在陆地生态系统中诸多一年生草本、多年生草本、灌木和乔木等不同生活史特征的植物种子萌发皆会对火烧信号产生响应(Nelson *et al.*, 2012; Ferraz *et al.*, 2013; Ramos *et al.*, 2019)。目前对影响种子萌发的火烧信号的研究主要集中在物理信号(热激效应), 化学信号(烟、烟水、KARs、SP₁), 以及物理和化学信号的交互作用。

2.1 物理信号

热激效应刺激种子萌发的现象已经在豆科、菊科、半日花科等多种植物类群中得到验证(表1)。热激通过破坏种皮/果皮厚实的不透水层,打破种子的物理休眠,促进种子萌发(Baskin *et al.*, 2000)。物理休眠是控制种子库动态变化的主导机制,持久种

子库对于火烧后植被恢复具有重要意义(Baskin & Baskin, 2014; Ooi *et al.*, 2014)。Auld和O'connell (1991)发现,热激促进了澳大利亚东部地区35种豆科植物种子的萌发,并且可以根据物种间打破休眠所需温度阈值(40、60、80 °C)的差异,将其分为不同的类别。Moreira等(2010)探究了地中海沿岸豆科、

表1 热激效应对种子萌发的影响
Table 1 Effects of heat shock on seed germination

科 Family	物种 Species	实验设计 Experiment design	主要发现 Main findings
豆科 Fabaceae	鹰爪豆 <i>Spartium junceum</i>	$T(80, 110, 150\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率最大值在110 °C-5 min处理下达到80% (Reyes & Traubad, 2009)。The maximum germination percentage reached 80% at the 110 °C-5 min treatment (Reyes & Traubad, 2009).
豆科 Fabaceae	<i>Bituminaria bituminosa</i>	$T(80, 110, 150\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率在110 °C-5 min处理下达到最大值, 110/150 °C-10 min处理完全抑制了萌发(Reyes & Traubad, 2009)。The germination percentage reached the maximum at the 110 °C-5 min treatment, and the germination was completely inhibited at 110/150 °C-10 min treatments (Reyes & Traubad, 2009).
豆科 Fabaceae	阿拉伯胶树 <i>Senegalia senegal</i>	$T(60, 90, 120, 150\text{ }^{\circ}\text{C}) \times t(1, 5, 10\text{ min})$	在90 °C-5 min处理下萌发率最大值达到82%, 比对照提高了23% (Herrero <i>et al.</i> , 2019)。The maximum germination percentage reached 82% at the 90 °C-5 min treatment, which was 23% higher than the control (Herrero <i>et al.</i> , 2019).
豆科 Fabaceae	金雀儿 <i>Cytisus scoparius</i>	$T(80, 110, 150\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率最大值在80 °C-10 min处理下达到36%, 同对照相比提高了30% (Rivas <i>et al.</i> , 2006)。The maximum germination percentage reached 36% at the 80 °C-10 min treatment, which was 30% higher than the control (Rivas <i>et al.</i> , 2006).
豆科 Fabaceae	<i>Genista tridentata</i>	$T(80, 110, 150\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率最大值在110 °C-5 min处理下达到65%, 同对照相比提高了50% (Rivas <i>et al.</i> , 2006)。The maximum germination percentage reached 65% at the 110 °C-5 min treatment, which was 50% higher than the control (Rivas <i>et al.</i> , 2006).
豆科 Fabaceae	<i>Cytisus striatus</i>	$T(80, 110, 150\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率最大值在110 °C-10 min处理下达到58%, 同对照相比提高了46% (Rivas <i>et al.</i> , 2006)。The maximum germination percentage reached 58% at the 110 °C-10 min treatment, which was 46% higher than the control (Rivas <i>et al.</i> , 2006).
豆科 Fabaceae	<i>Genista triacanthos</i>	$T(80, 100, 120\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率最大值在100 °C-5 min, 120 °C-10 min处理下达到91%, 比对照提高了87% (Moreira <i>et al.</i> , 2010)。The maximum germination percentage reached 91% at 100 °C-5 min and 120 °C-10 min treatments, which was 87% higher than the control (Moreira <i>et al.</i> , 2010).
豆科 Fabaceae	<i>Viminaria juncea</i>	$T(40, 60, 80, 100, 120\text{ }^{\circ}\text{C}) \times t(10\text{ min})$	萌发率在100 °C-10 min处理下达到最大值, 在120 °C下不萌发(Liyanage & Ooi, 2015)。The germination percentage reached the maximum at the 100 °C-10 min treatment, and the germination was completely inhibited at 120 °C treatments (Liyanage & Ooi, 2015).
杨柳科 Salicaceae	大青杨 <i>Populus ussuriensis</i>	$T(70, 90, 110\text{ }^{\circ}\text{C}) \times t(5, 10, 15\text{ min})$	萌发率最大值在70 °C-15 min处理下达到46% (巴丽娜等, 2018)。The maximum germination percentage reached 46% at the 70 °C-15 min treatment (Ba <i>et al.</i> , 2018).
番杏科 Aizoaceae	<i>Mesembryanthemum crystallinum</i>	$T(103\text{ }^{\circ}\text{C}) \times t(17\text{ h})$	热激处理的萌发率比对照提高了56% (Visscher <i>et al.</i> , 2018)。The germination percentage of the heat shock treatments increased by 56% compared with the control (Visscher <i>et al.</i> , 2018).
锦葵科 Malvaceae	<i>Guazuma ulmifolia</i>	$T(60\text{ }^{\circ}\text{C}) \times t(10, 20, 40\text{ min})$, $T(80\text{ }^{\circ}\text{C}) \times t(5, 10, 20\text{ min})$, $T(100\text{ }^{\circ}\text{C}) \times t(2.5, 5, 10\text{ min})$	萌发率最大值在100 °C-5 min处理下达到18%, 对照处理不萌发(Ribeiro <i>et al.</i> , 2013)。The maximum germination percentage reached 18% at the 100 °C-5 min treatment, and no germination was observed in the control treatment (Ribeiro <i>et al.</i> , 2013).
锦葵科 Malvaceae	<i>Fremontodendron californicum</i>	$T(100, 110, 130, 140, 150\text{ }^{\circ}\text{C}) \times t(5\text{ min})$, $T(80\text{ }^{\circ}\text{C}) \times t(1\text{ h})$	新鲜采集种子的萌发率最大值在100 °C-5 min处理下超过了60%, 对照处理不萌发(Keeley <i>et al.</i> , 2005)。The maximum germination percentage of fresh seeds was more than 60% at the 100 °C-5 min treatment, while the control treatment did not germinate (Keeley <i>et al.</i> , 2005).

表 1 (续) Table 1 (Continued)

科 Family	物种 Species	实验设计 Experiment design	主要发现 Main findings
半日花科 Cistaceae	<i>Cistus albidus</i>	$T(80, 100, 120\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率最大值在120 $^{\circ}\text{C}$ -5 min处理下达到61%, 同对照相比提高了50% (Moreira <i>et al.</i> , 2010)。 The maximum germination percentage reached 61% at the 120 $^{\circ}\text{C}$ -5 min treatment, which was 50% higher than the control (Moreira <i>et al.</i> , 2010).
半日花科 Cistaceae	<i>Cistus monspeliensis</i>	$T(80, 100, 120\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率最大值在120 $^{\circ}\text{C}$ -5 min处理下达到73%, 同对照相比提高了62% (Moreira <i>et al.</i> , 2010)。 The maximum germination percentage reached 73% at the 120 $^{\circ}\text{C}$ -5 min treatment, which was 62% higher than the control (Moreira <i>et al.</i> , 2010).
半日花科 Cistaceae	<i>Cistus creticus</i>	$T(80, 100, 120, 150\text{ }^{\circ}\text{C}) \times t(5\text{ min})$	萌发率在100、120、150 $^{\circ}\text{C}$ 处理下显著高于对照处理(Tavsanoglu, 2011)。 The germination percentage at 100, 120 and 150 $^{\circ}\text{C}$ treatments was significantly higher than the control (Tavsanoglu, 2011).
半日花科 Cistaceae	<i>Helianthemum apenninum</i>	$T(80, 100, 120\text{ }^{\circ}\text{C}) \times t(10\text{ min})$	萌发率最大值在80 $^{\circ}\text{C}$ -10 min处理下达到39%, 同对照相比提高了19% (Luna <i>et al.</i> , 2007)。 The maximum germination percentage reached 39% at the 80 $^{\circ}\text{C}$ -10 min treatment, which was 19% higher than the control (Luna <i>et al.</i> , 2007).
唇形科 Labiatae	宽叶薰衣草 <i>Lavandula latifolia</i>	$T(80, 100, 120\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率最大值在100 $^{\circ}\text{C}$ -5 min处理下达到32%, 同对照相比提高了19% (Moreira <i>et al.</i> , 2010)。 The maximum germination percentage reached 32% at the 100 $^{\circ}\text{C}$ -5 min treatment, which was 19% higher than the control (Moreira <i>et al.</i> , 2010).
唇形科 Labiatae	<i>Lavandula stoechas</i>	$T(80, 100, 120\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率最大值在120 $^{\circ}\text{C}$ -5 min处理下达到72%, 同对照相比提高了62% (Moreira <i>et al.</i> , 2010)。 The maximum germination percentage reached 72% at the 120 $^{\circ}\text{C}$ -5 min treatment, which was 62% higher than the control (Moreira <i>et al.</i> , 2010).
菊科 Asteraceae	<i>Catananche caerulea</i>	$T(80, 100, 120\text{ }^{\circ}\text{C}) \times t(10\text{ min})$	萌发率最大值在80 $^{\circ}\text{C}$ -10 min处理下达到55%, 同对照相比提高了44% (Luna <i>et al.</i> , 2007)。 The maximum germination percentage reached 55% at the 80 $^{\circ}\text{C}$ -10 min treatment, which was 44% higher than the control (Luna <i>et al.</i> , 2007).
禾本科 Poaceae	小穗臭草 <i>Melica ciliata</i>	$T(80, 110, 150\text{ }^{\circ}\text{C}) \times t(5, 10\text{ min})$	萌发率在110 $^{\circ}\text{C}$ -5 min处理下达到最大值, 150 $^{\circ}\text{C}$ -10 min热激处理完全抑制了萌发(Reyes & Trabaud, 2009)。 The germination percentage reached the maximum at the 110 $^{\circ}\text{C}$ -5 min treatment, and the germination was completely inhibited at the 150 $^{\circ}\text{C}$ -10 min treatment (Reyes & Trabaud, 2009).

T , 温度; t , 时间。
 T , temperature; t , time.

半日花科、唇形科等7个科共30个物种种子萌发对于热激的响应情况, 结果表明有21个物种在热激下萌发率显著增加。热激的温度和持续时间是探讨热信号对于种子萌发影响的两个重要变量, 高温长时间的热激会使种子失去活性(Ooi *et al.*, 2014)。例如, 小穗臭草(*Melica ciliata*)的萌发率在110 $^{\circ}\text{C}$ -5 min处理下达到最大值, 但在150 $^{\circ}\text{C}$ -10 min热激处理下则完全抑制了萌发(Reyes & Trabaud, 2009)。

相近类群的植物种子萌发对于热激效应的响应并不完全一致。同属于相思树属(*Acacia*)的两个物种的种子萌发对于热激的响应存在差异。在90 $^{\circ}\text{C}$ 热激时, 只有阿拉伯胶树(*Senegalia senegal*)的萌发率显著增加(Herrero *et al.*, 2019)。Liyanage和Ooi (2015)研究了澳大利亚东南部具有物理休眠的5种灌木种子打破休眠所需的温度阈值在种群内的变化规律, 结果表明同一种群内部, 不同个体之间打破休眠所需的温度阈值存在显著差异, 有的个体在较低温度热激时便可以萌发, 有的则需要高温热激。

并不是所有物理休眠的物种种子萌发都会对热激响应, 同样热激也不是物理休眠种子的专属信号。Ma等(2020)对形态生理休眠的*Anigozanthos flavidus*种子进行了100 $^{\circ}\text{C}$ -30 min的热激处理, 结果显示12个种群中有6个种群的种子萌发率显著提高。一些生理休眠的物种也可以对热激产生萌发响应。无论是储存的还是新鲜采集的*Drosophyllum lusitanicum*种子, 经80 $^{\circ}\text{C}$ 或者100 $^{\circ}\text{C}$ 热激后萌发率显著增加(Cross *et al.*, 2017)。澳大利亚西南部*Darwinia*的5个物种的种子皆具有透水性, 经过热激处理后, 5个物种的萌发率均显著增加(Auld & Ooi, 2009)。

光是某些植物种子萌发所必需的环境条件(Moreira & Pausas, 2018)。火烧通过移除地表植被改变了到达地表的光强和光质, 进而对部分植物的种子萌发产生影响。同大种子植物相比, 小种子植物的萌发对于光照有着更强的依赖性。Milberg等(2000)探究了54种植物种子萌发对于光照的响应情

况,并且在分析过程中考虑了系统发育因素,结果表明种子萌发对于光照的需求与种子大小出现了共同进化。Roeder等(2019)发现火烧后开阔的生境可以为小种子植物虾子花(*Woodfordia fruticosa*)的萌发提供必需的光照条件。植被冠层的存在使到达地表的红光和远红光的比例维持在一个较低的水平,抑制了种子萌发(López-Mársico *et al.*, 2019)。Baeza和Roy (2008)研究发现,火烧通过破坏冠层的完整性改变了红光和远红光的比例,显著提高了豆科植物*Ulex parviflorus*种子的萌发率。目前对光信号的研究主要集中在单一光因子对种子萌发的影响,而

光信号与其他火烧信号的交互作用对种子萌发的影响研究较少(Tavşanoğlu *et al.*, 2017; López-Mársico *et al.*, 2019)。

2.2 化学信号

火烧产生的一系列烟信号刺激种子萌发的现象已经在菊科、十字花科、鸢尾科等多个植物类群得到验证(表2)。van de Venter和Esterhuizen (1988)率先指出高温不是火烧信号中唯一影响种子萌发的因素,种子萌发与多种火烧信号密切相关。Keeley和Fotheringham (1998)发现植物源烟可以促进美国加利福尼亚地区11个科中25种灌木种子的萌发,而这

表2 烟信号对于种子萌发的影响
Table 2 Effects of smoke cues on seed germination

科 Family	物种 Species	实验设计 Experiment design	主要发现 Main findings
菊科 Asteraceae	<i>Gutierrezia sarothrae</i>	SW (1:5, 1:10, 1:100)	萌发率最大值在1:5浓度下达到46%, 同对照相比增加了14% (Chou <i>et al.</i> , 2012)。 The maximum germination percentage reached 46% at the concentration of 1:5, which was 14% higher than the control (Chou <i>et al.</i> , 2012).
豆科 Fabaceae	<i>Astragalus crassicaarpus</i>	SW (1:5, 1:10, 1:100)	萌发率最大值在1:100浓度下达到28%, 同对照相比增加了8% (Chou <i>et al.</i> , 2012)。 The maximum germination percentage reached 28% at the concentration of 1:100, which was 8% higher than the control (Chou <i>et al.</i> , 2012).
芸香科 Rutaceae	<i>Boronia floribunda</i>	SW (1:10, 1:100)	同对照相比, 所有个体的萌发率经烟水处理后均显著增加(Ma <i>et al.</i> , 2018)。 Compared with the control, the germination percentage of all individuals were significantly increased after smoke water treatments (Ma <i>et al.</i> , 2018).
十字花科 Brassicaceae	小果亚麻荠 <i>Camelina microcarpa</i>	SW (1:2)	萌发率在烟水处理下比对照提高了2.24倍(Mojzes & Kalapos, 2014)。 The germination percentage of the smoke water treatment increased by 2.24 times compared with the control (Mojzes & Kalapos, 2014).
十字花科 Brassicaceae	荠 <i>Capsella bursa-pastoris</i>	SW (1:2)	萌发率在烟水处理下比对照提高了3.20倍(Mojzes & Kalapos, 2014)。 The germination percentage of the smoke water treatment increased by 3.20 times compared with the control (Mojzes & Kalapos, 2014).
十字花科 Brassicaceae	播娘蒿 <i>Descurainia sophia</i>	SW (1:2)	萌发率在烟水处理下比对照提高了4.21倍(Mojzes & Kalapos, 2014)。 The germination percentage of the smoke water treatment increased by 4.21 compared with the control (Mojzes & Kalapos, 2014).
十字花科 Brassicaceae	<i>Brassica tournefortii</i>	KAR ₁ (0.67, 6.70, 67.00 nmol·L ⁻¹ ; 0.67, 6.70 μmol·L ⁻¹)	萌发率最大值在6.70 μmol·L ⁻¹ 浓度梯度下达到93%, 比对照增加了89% (Stevens <i>et al.</i> , 2007)。 The maximum germination percentage reached 93% at the concentration of 6.70 μmol·L ⁻¹ which was 89% higher than the control (Stevens <i>et al.</i> , 2007).
十字花科 Brassicaceae	野萝卜 <i>Raphanus raphanistrum</i>	KAR ₁ (0.67, 6.70, 67.00 nmol·L ⁻¹ ; 0.67, 6.70 μmol·L ⁻¹)	萌发率最大值在6.70 μmol·L ⁻¹ 浓度梯度下达到91%, 比对照增加了40% (Stevens <i>et al.</i> , 2007)。 The maximum germination percentage reached 91% at the concentration of 6.70 μmol·L ⁻¹ , which was 40% higher than the control (Stevens <i>et al.</i> , 2007).
车前科 Plantaginaceae	长叶车前 <i>Plantago lanceolata</i>	SW (1:2)	同对照相比, 经烟水处理后萌发率提高了41% (Mojzes & Kalapos, 2014)。 The germination percentage of the smoke water treatment increased by 41% compared with the control (Mojzes & Kalapos, 2014).
马兜铃科 Aristolochiaceae	马兜铃 <i>Aristolochia debilis</i>	SW (1:10)	同对照相比, 经烟水处理后萌发率提高了27% (Zhou <i>et al.</i> , 2014)。 The germination percentage of the smoke water treatment increased by 27% compared with the control (Zhou <i>et al.</i> , 2014).
葫芦科 Cucurbitaceae	黄瓜 <i>Cucumis sativus</i>	SW (100%)	同对照相比, 经烟水处理后萌发率提高11% (Elsadek & Yousef, 2019)。 The germination percentage of the smoke water treatment increased by 11% compared with the control (Elsadek & Yousef, 2019).
鸢尾科 Iridaceae	<i>Gladiolus hybridus</i>	SW (100%)	同对照相比, 经烟水处理后萌发率提高了10% (Elsadek & Yousef, 2019)。 The germination percentage of the smoke water treatment increased by 10% compared with the control (Elsadek & Yousef, 2019).
唇形科 Lamiaceae	<i>Lavandula stoechas</i>	SW (1:1, 1:10, 1:100)	萌发率最大值在1:100浓度下达到95%, 同对照相比提高了26% (Çatav <i>et al.</i> , 2014)。 The maximum germination percentage reached 95% at the concentration of 1:100, which was 26% higher than the control (Çatav <i>et al.</i> , 2014).

表2 (续) Table 2 (Continued)

科 Family	物种 Species	实验设计 Experiment design	主要发现 Main findings
唇形科 Lamiaceae	<i>Origanum onites</i>	SW (1:1, 1:10, 1:100)	萌发率最大值在1:100浓度下达到97%, 同对照相比提高了14% (Çatav <i>et al.</i> , 2014). The maximum germination percentage reached 97% at the concentration of 1:100, which was 14% higher than the control (Çatav <i>et al.</i> , 2014).
唇形科 Lamiaceae	<i>Satureja thymbra</i>	SW (1:1, 1:10, 1:100)	萌发率最大值在1:1浓度下达到87%, 同对照相比提高了30% (Çatav <i>et al.</i> , 2014). The maximum germination percentage reached 87% at the concentration of 1:1, which was 30% higher than the control (Çatav <i>et al.</i> , 2014).
禾本科 Poaceae	野燕麦 <i>Avena fatua</i>	SW (1:10 000, 1:1 000, 1:100) $T (15, 20, 25, 30\text{ }^{\circ}\text{C}) \times \text{KAR}_1$ ($10^{-7}, 10^{-8}, 10^{-9}, 10^{-10}\text{ mol}\cdot\text{L}^{-1}$)	萌发率最大值在1:100浓度下达到90%。KAR ₁ 在15–30 °C 范围内可显著提高种子萌发率(Kępczyński <i>et al.</i> , 2006, 2010). The maximum germination percentage reached 90% at the concentration of 1:100. KAR ₁ significantly increased seed germination in the range of 15–30 °C (Kępczyński <i>et al.</i> , 2006, 2010).
蔷薇科 Rosaceae	<i>Adenostoma fasciculatum</i>	SW (1:100, 1:500, 1:1 000)	萌发率在1:500浓度下超过90%。显著高于对照(Keeley <i>et al.</i> , 2005). The germination percentage was over 90% at the concentration of 1:500, which was significantly higher than the control (Keeley <i>et al.</i> , 2005).
紫草科 Boraginaceae	<i>Eriodictyon crassifolium</i>	SW (1:100, 1:500, 1:1 000)	萌发率在1:500浓度下超过80%。显著高于对照(Keeley <i>et al.</i> , 2005). The germination percentage was over 80% at the concentration of 1:500, which was significantly higher than the control (Keeley <i>et al.</i> , 2005).
血皮草科 Haemodorraceae	<i>Anigozanthos flavidus</i>	SP ₁ (5.00, 10.00, 25.00, 50.00, 75.00, 100.00, 200.00, 300.00, 400.00, 500.00 $\mu\text{mol}\cdot\text{L}^{-1}$)	萌发率最大值在50.00和200.00 $\mu\text{mol}\cdot\text{L}^{-1}$ 下达到95%, 比对照增加了67% (Downes <i>et al.</i> , 2013). The maximum germination percentage reached 95% at 50.00 and 200.00 $\mu\text{mol}\cdot\text{L}^{-1}$, which was 67% higher than the control (Downes <i>et al.</i> , 2013).

KAR₁, karrikinolide; SP₁, glyceronitrile; SW, 烟水; T, 温度。
KAR₁, karrikinolide; SP₁, glyceronitrile; SW, smoke water; T, temperature.

些物种均不会对热信号响应。Çatav等(2014)发现烟水处理显著增加了地中海地区唇形科植物种子的萌发, 其中*Lavandula stoechas*的萌发率从69%增加到经1:100的烟水处理后的95%。植物源烟促进了欧洲温带地区小果亚麻荠(*Camelina microcarpa*)、荠(*Capsella bursa-pastoris*)、播娘蒿(*Descurainia Sophia*)和长叶车前(*Plantago lanceolata*) 4种草本植物种子的萌发(Mojzes & Kalapos, 2014)。

相近类群的植物种子萌发对于烟信号的响应并不完全一致。在同一种群的不同个体水平上, 芸香科植物*Boronia floribunda*种子萌发对不同烟水浓度的响应在个体间存在显著差异, 此外, 相同烟处理下, 个体间萌发开始的时间也存在显著差异(Ma *et al.*, 2018)。在同一物种不同种群水平上, SP₁和烟水处理分别显著提高了*Anigozanthos flavidus*的12和8个种群的萌发率(Ma *et al.*, 2020)。

对于不易发生火烧的生态系统出现的萌发对于植物源烟的响应现象, Flematti等(2004)认为烟雾中的生物活性物质是刺激种子萌发的重要原因。KARs和SP₁作为烟信号中影响种子萌发的主要生物活性物质已经被广泛验证(表2)。Daws等(2007)发现来自不易发生火烧生态系统中的18种杂草的种子经KAR₁处理后, 8种杂草的萌发率显著提高, 这表明KAR₁作为萌发刺激物质具有广泛的适应性。但

KARs对种子萌发影响的作用机制尚不明确。KARs同植物激素独脚金内酯具有结构上的相似性, 但是植物对于二者的响应却不一致(Waters *et al.*, 2014)。KARs处理使拟南芥(*Arabidopsis thaliana*)种子的萌发率显著增加, 科研人员借助该物种丰富的基因组学资源发现了影响KARs作用机制的两个重要基因MAX2和KAI2 (Nelson *et al.*, 2012; Waters *et al.*, 2014)。Gupta等(2019)发现烟水和KAR₁通过降低脱落酸水平和增强水解酶活性显著促进光敏植物莴苣(*Lactuca sativa*)种子萌发, 并缓解了萌发对于光照的需求。植物源烟的组成成分复杂, 环蕊木科植物*Gyrostemon racemiger*种子萌发对烟水响应, 但是对KAR₁和SP₁不响应, 这表明烟信号中依旧存在一些新的微量萌发刺激物质尚未确定(Downes *et al.*, 2013)。因此, 未来需要进行更多的实验来探讨植物种子萌发对于火烧信号的响应情况, 特别是要选择不同生境中的特有物种, 以此来帮助分离和确定烟信号中影响种子萌发的特定化学物质。

火烧后土壤中的营养物质的组成和有效性会发生显著变化。氮以铵态氮或有机氮的形式随雨水进入到土壤中, 随后被硝化细菌转化为硝酸盐。一些研究表明, 这类含氮化合物(主要是亚硝酸盐和硝酸盐)能有效地打破许多植物种子的休眠或者促进其萌发(Baskin & Baskin, 2014)。例如, 硝酸盐显著

促进了禾本科植物 *Emmenanthe penduliflora* 的种子萌发(Thanos & Rundel, 1995)。Pérez-Fernández和

Rodríguez-Echeverría (2003)发现, 亚硝酸钠处理显著提高了鸭茅(*Dactylis glomerata*)、*Cistus ladanifer*

表3 物理信号和化学信号交互对种子萌发的影响
Table 3 Effects of interaction of physical and chemical cues on seed germination

科名 Family	物种 Species	实验设计 Experiment design	响应类型 Response type	主要发现 Main findings
豆科 Fabaceae	<i>Harpalyce</i> sp.	SW (1:1) × HS (100 °C-1 min)	增效作用 Positive effect	萌发率最大值在烟水和热激交互处理下达到32%。同对照、烟水和热激处理相比分别提高了19%、27%、25% (Zirondi <i>et al.</i> , 2019)。 The maximum germination percentage reached 32% at the interactive treatment, which was increased by 19%, 27%, and 25% respectively compared with the control, smoke water, and heat shock treatments (Zirondi <i>et al.</i> , 2019).
豆科 Fabaceae	<i>Mimosa leioccephala</i>	SW (1:1) × HS (100 °C-1 min)	增效作用 Positive effect	萌发率最大值在烟水和热激交互处理下达到35%。同对照、烟水和热激处理相比分别提高了26%、21%、28% (Zirondi <i>et al.</i> , 2019)。 The maximum germination percentage reached 35% at the interactive treatment, which was increased by 26%, 21%, and 28% respectively compared with the control, smoke water, and heat shock treatments (Zirondi <i>et al.</i> , 2019).
豆科 Fabaceae	<i>Mimosa somnians</i>	SW (1:1) × HS (100 °C-1 min)	增效作用 Positive effect	萌发率最大值在烟水和热激交互处理下达到27%。同对照、烟水和热激处理相比分别提高了13%、6%、13% (Zirondi <i>et al.</i> , 2019)。 The maximum germination percentage reached 27% at the interactive treatment, which was increased by 13.0%, 6%, and 13.0% respectively compared with the control, smoke water, and heat shock treatment (Zirondi <i>et al.</i> , 2019).
豆科 Fabaceae	<i>Acacia angustissima</i>	SW × HS (120 °C-5 min)	等效作用 Equivalent effect	萌发率在交互处理和热激处理之间无显著差异(Zuloaga-Aguilar <i>et al.</i> , 2011)。 There was no significant difference in germination percentage between the heat shock treatment and the interactive treatment (Zuloaga-Aguilar <i>et al.</i> , 2011).
豆科 Fabaceae	<i>Calliandralo ngipedicellata</i>	SW × HS (120 °C-5 min)	减效作用 Negative effect	萌发率在热激处理下达到最大值, 显著高于烟水和热激的交互处理(Zuloaga-Aguilar <i>et al.</i> , 2011)。 The germination percentage reached the maximum at the heat shock treatment, which was significantly higher than the interactive treatment (Zuloaga-Aguilar <i>et al.</i> , 2011).
菊科 Asteraceae	白紫千里光 <i>Senecio albopurpureus</i>	(Smoke-60 min) × HS (80 °C-5 min)	减效作用 Negative effect	萌发率在热激和烟交互处理下达到最小值, 显著低于热激、烟和对照处理(Gonzalez & Ghermandi, 2012)。 The germination percentage reached the minimum at interactive treatment, which was significantly lower than the control, heat shock, and smoke treatments (Gonzalez & Ghermandi, 2012).
天门冬科 Asparagaceae	<i>Dichopogon strictus</i>	SW (1:10) × HS (80 °C-1 h)	增效作用 Positive effect	新鲜种子的萌发率最大值在烟水和热激交互处理下达到72%。同对照、烟水、热激处理相比分别提高了22%、19%、31% (Hodges <i>et al.</i> , 2019)。 The maximum germination percentage reached 72% at the interactive treatment, which was increased by 22%, 19%, and 31% respectively compared with the control, smoke water, and heat shock treatments (Hodges <i>et al.</i> , 2019).
天门冬科 Asphodelaceae	<i>Dianella revoluta</i>	SW (1:10) × HS (80 °C-1 h)	减效作用 Negative effect	新鲜种子的萌发率在烟水和热激处理下达到33%, 同烟水处理相比下降了5% (Hodges <i>et al.</i> , 2019)。 The germination percentage reached 33% at the interactive treatment, which was 5% lower than the control (Hodges <i>et al.</i> , 2019).
车前科 Plantaginaceae	<i>Penstemon barbatus</i>	SW (1:10) × HS (100 °C-30 min)	等效作用 Equivalent effect	在烟水处理下萌发率最大值达到63%, 但与烟水和热激交互处理无显著差异(Abella, 2006)。 The maximum germination percentage reached 63% at the smoke water treatment, there was no significantly difference with the interactive treatment (Abella, 2006).
翡若翠科 Velloziaceae	<i>Vellozia alutacea</i>	SW × HS (100 °C-5 min)	减效作用 Negative effect	萌发率在烟水和热激交互处理下显著低于烟水处理(Fernandes <i>et al.</i> , 2021)。 The germination percentage at the interactive treatment was significantly lower than the smoke water treatment (Fernandes <i>et al.</i> , 2021).
翡若翠科 Velloziaceae	<i>Vellozia resinosa</i>	SW × HS (100 °C-5 min)	减效作用 Negative effect	萌发率在烟水和热激交互处理下显著低于烟水处理(Fernandes <i>et al.</i> , 2021)。 The germination percentage at the interactive treatment was significantly lower than the smoke water treatment (Fernandes <i>et al.</i> , 2021).
翡若翠科 Velloziaceae	<i>Vellozia epidendroides</i>	SW × HS (100 °C-5 min)	减效作用 Negative effect	萌发率在交互处理下显著低于热激处理(Fernandes <i>et al.</i> , 2021)。 The germination percentage at the interactive treatment was significantly lower than the heat shock treatment (Fernandes <i>et al.</i> , 2021).
翡若翠科 Xyridaceae	<i>Xyris pilosa</i>	SW × HS (100 °C-5 min)	等效作用 Equivalent effect	萌发率在交互处理和烟水处理之间无显著差异(Fernandes <i>et al.</i> , 2021)。 There was no significant difference in germination percentage between the smoke water treatment and the interactive treatment (Fernandes <i>et al.</i> , 2021).

SW, 烟水; HS, 热激。
SW, smoke water; HS, heat shock.

等植物种子的萌发率。

2.3 物理与化学信号的交互作用

物理和化学信号共同作用影响种子萌发的现象普遍存在(表3)。根据萌发率将交互作用的效果分为增效作用、等效作用、减效作用3种类型。增效作用: 物理和化学信号共同作用下, 萌发率高于单独施加两种处理。*Harpalyce* sp.和*Mimosa leioccephala*在热激和烟信号交互作用下取得了更高的萌发率, 其中*Harpalyce* sp.的萌发率在烟水和热激交互处理下达到最大值32%, 同对照、烟水和热激相比分别提高了19%、27%、25%(Zirondi *et al.*, 2019)。等效作用: 物理和化学信号共同作用下, 萌发率与施加单独处理的效果无显著差异。*Acacia angustissima*在热激单独处理下与交互处理无显著差异, *Penstemon barbatus*在烟水单独处理下与交互作用无显著差异(Abella, 2006; Zuloaga-Aguilar *et al.*, 2011)。减效作用: 物理和化学信号共同作用下, 萌发率显著低于单独施加处理的效果。*Vellozia alutacea*, *Vellozia resinosa*和白紫千里光(*Senecio albopurpureus*)等物种在热激和烟信号交互作用下萌发率受到了显著的抑制(Gonzalez & Ghermandi, 2012; Fernandes *et al.*, 2021)。

物理和化学信号交互作用对种子萌发的影响可能受火烧信号的强度以及种子休眠类型等多种因素影响。复合休眠的物种在热激打破种子的物理休眠后, 烟水可以促进种子生理休眠的释放, 起到增效作用(Auld & Ooi, 2009)。物理休眠的种子通常会受到热量的刺激而萌发, 而由于种皮的不透水性, 可能会导致对烟没有响应以起到等效作用。高浓度的

烟信号和高强度的热激会使种子失去活性, 降低种子萌发率(Ferraz *et al.*, 2013; Liyanage & Ooi, 2015)。因此, 当物理和化学信号互作超过了打破种子休眠所需的阈值就会使种子失去活性或者再次进入休眠状态, 起到减效作用(Gonzalez & Ghermandi, 2012)。

2.4 火烧信号与种子休眠类型之间的关系

在易发生火烧的生态系统中, 种子的休眠特性是影响火烧后土壤种子库持久性和幼苗建植的关键。Baskin和Baskin (2014)将植物种子的休眠类型划分为生理休眠、物理休眠、复合休眠、形态休眠和形态生理休眠。大量研究表明多种休眠类型与火烧信号存在紧密联系(图3)(Cao *et al.*, 2020; Collette & Ooi, 2021)。一般情况下, 火烧产生的高温可以打破物理休眠种子的不透水层, 刺激种子萌发。但是也有部分物理休眠的植物种子萌发并不受热激效应影响, 因为不同物种的温度生态幅存在明显差异(Baskin & Baskin, 2014)。烟、烟水、火烧灰等化学信号可以促进种子生理休眠和形态生理休眠的释放, 刺激种子萌发。但是部分具有生理或者形态生理休眠的种子只有在经过一段时间的后熟处理后, 才能对烟信号产生萌发响应(Flematti *et al.*, 2015)。对于复合休眠的种子而言热激打破物理休眠后, 化学信号可以促进种子生理休眠的释放(Auld & Ooi, 2009)。特别值得关注的是火烧信号与种子休眠类型之间并非是严格对应的, 例如, Mackenzie等(2016)发现90 °C-10 min的热激处理显著促进了具有生理休眠的芸香科植物*Boronia serrulata*种子的萌发。部分物理休眠的种子可能会因为烟水呈酸性, 影响其种皮渗透性而打破休眠(Moreira & Pausas, 2018)。

图3 火烧信号与休眠类型之间的关系。

Fig. 3 Relationships between fire cues and dormancy classes.

3 火烧信号在实践中的应用

烟信号可以通过提高种子萌发率、促进幼苗生长发育、增强幼苗活性来增加新生个体的数目和生物多样性指数以实现退化生态系统的恢复。澳大利亚西部 *Banksia* 林地是火烧易发的地区, 其恢复地区萌发植物的总数增加了4–48倍, 物种多样性增加了3倍(Rokich & Dixon, 2007)。化学信号在农业和园艺育苗上的应用可以通过对种子或者幼苗施加气态烟、烟水、KAR₁等方式实现。烟水对于黄瓜(*Cucumis sativus*)、番茄(*Lycopersicon esculentum*)、*Gladiolus* × *hybridus* 和金盏花(*Calendula officinalis*) 4种园艺植物种子的萌发和幼苗生长具有显著的促进作用(Elsadek & Yousef, 2019)。Sparg等(2006)发现烟和烟水处理显著提高了玉米(*Zea mays*)的萌发率, 增强了幼苗活力。将烟水和KAR₁直接喷施在幼苗表面可以促进咖啡黄葵(*Abelmoschus esculentus*)和番茄幼苗的生长发育, 具体表现在根长、苗长、叶片的数量、总叶面积和茎粗的增加(Kulkarni *et al.*, 2011)。种子萌发和幼苗建植是植物重要的生活史阶段, 也是对外界环境因子最敏感的时期。将烟或烟水用作种子引发剂, 为提高种子在盐碱、干旱等逆境条件下萌发和幼苗建植提供了有效的方法。烟水处理增加了玉米中K⁺和Ca²⁺的含量, 减少了Na⁺的含量, 使玉米的萌发率从70%增至93%, 根和幼苗的干鲜质量也有增加(Waheed *et al.*, 2016)。用烟水和KAR₁对芝麻科植物 *Ceratothera triloba* 种子进行引发, 提高了在极端温度、干旱和盐碱等胁迫环境下种子的萌发率(Masondo *et al.*, 2018)。但目前植物种子萌发和幼苗建植的引发技术大部分处于实验研究阶段, 较少应用于田间实践, 并且缺乏对不同类型引发剂作用效果的比较和作用机理的深入探讨。

4 总结和展望

火是陆地生态系统的重要组成部分, 也是影响许多生态过程的关键因子。本文系统地总结了近年来不同类别的火烧信号及其交互作用对种子萌发影响的研究。为了进一步理解火烧信号对种子萌发的影响, 我们建议未来的研究可以从以下4个方面入手:

(1)深入探讨烟信号的作用机理。借助模式植物拟南芥丰富的基因组学资源, 人们对于KARs影响

种子萌发的作用机理有了更深层次的了解。但是拟南芥并非是易发生火烧生态系统中的典型物种。对于必须借助火烧信号才能实现萌发的植物来说, 其对于KARs的响应机制是否同拟南芥一致尚未确定。KARs作为植物源烟中主要的萌发刺激物质, 探究其作用机理对于揭示植物生长发育调控新途径具有重要意义。今后需要通过分子生物学、多组学联合分析等技术手段, 深入探讨烟信号对种子萌发及幼苗生长的作用机制。

(2)在全球变化的背景下, 探究不断变化的火烧情势对种子萌发的影响。火烧情势反映了影响特定生态系统的火烧的大小、频率、扩散速度等特征。以增温、CO₂浓度升高、极端天气频发等为主要特征的全球变化对火烧事件产生了重要影响。例如, 在过去的半个世纪里, 加拿大森林地区火烧发生的强度、火烧季节开始和结束的时间均发生了显著的变化(Hanes *et al.*, 2019)。生物对于火的适应实质是对不同火烧情势的适应(Keeley *et al.*, 2011)。植物种子萌发如何响应全球变化背景下火烧情势的改变应是未来研究的热点和重点。

(3)开展火烧信号同环境因子互作影响种子萌发的系统研究。水分、氧气、光照、温度等环境因子决定种子是否萌发。当前, 火烧信号对种子萌发影响的研究多集中于单一火烧信号或者两种不同类别的火烧信号的交互实验, 火烧信号与环境因子互作的探究实验较少。开展火烧信号与环境因子互作的研究可以更好地反映自然环境中的真实条件, 有助于更加全面地理解种子萌发对于火烧信号的响应情况。

(4)加强火烧信号的合理应用。火烧信号作为重要的生态系统管理工具, 特别是火烧产生的化学信号, 在农业和园艺育苗、提高种子抗逆性和生态恢复等方面具有重要的应用潜力。但目前的研究多限于实验室内小范围的控制实验, 如何规模化利用烟信号为农业和园艺业的发展提供技术支撑还需要进行深入探讨。

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