Annals of Botany **135**: 1059–1074, 2025
https://doi.org/10.1093/aob/mcae229, available online at www.academic.oup.com/aob

ANNALS OF
BOTANY
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RESEARCH IN CONTEXT

Fire and seed dormancy: a global meta-analysis

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Received: 2 October 2024 Returned for revision: 15 December 2024 Editorial decision: 20 December 2024 Accepted: 25 December 2024

- **Background and Aims** Fire-released seed dormancy (SD) is a key trait for successful germination and plant persistence in many fire-prone ecosystems. Many local studies have shown that fire-released SD depends on heat and exposure time, dose of smoke-derived compounds, SD class, plant lineage and the fire regime. However, a global quantitative analysis of fire-released SD is lacking. We hypothesized that fire-released SD is more prevalent in fire-prone than in non-fire-prone ecosystems, and in crown fire compared with surface fire ecosystems. Additionally, we expected to uncover patterns in the relationship between fire cues and SD classes at the global scale that mirror those identified in local or regional studies.
- **Methods** In total, 246 published germination studies from 1970 to 2022, encompassing 1782 species from 128 families, were used in our meta-analysis. Meta-analysis moderators included different fire cues, smoke application methods, smoke exposure duration and concentration, smoke compounds, fire-proneness, fire regimes and ecosystem types.
- **Key Results** Heat released physical, and smoke released physiological and morphophysiological dormancies. For SD release, heat and smoke acted synergistically, and karrikinolide (KAR_1) was the most effective smoke compound. Fire-released SD was more prevalent in fire-prone than in non-fire-prone regions, particularly under crown fire regimes. Fire-released SD occurred mainly in Mediterranean ecosystems, temperate dry forests and temperate warm ecosystems, whereas species from savannas and tropical grasslands, temperate grasslands and tropical rainforests generally responded negatively to fire.
- **Conclusions** Fire-released SD is strongly influenced by fire regimes, the latter having a significant role in shaping SD and germination patterns on a global scale. The synergistic effect of heat and smoke in dormancy release reveals more intricate interactions between fire cues than previously understood. Understanding these patterns is crucial in the context of shifting fire regimes driven by climate change, as they may disrupt plant life cycles, alter ecosystem functions, biodiversity and community composition, and provide key insights for biodiversity conservation and ecological restoration in fire-prone ecosystems.

Key words: Ecosystem responses to fire, fire regime, fire-released seed dormancy, germination, heat-shock, karrikinolide, seed dormancy, smoke.

INTRODUCTION

Fire is a major driver in shaping many ecosystems on Earth, and thus the present persistence and stability of many ecosystems are dependent on wildfires (Pausas and Keeley, 2009; He and Lamont, 2018; McLauchlan *et al.*, 2020). By introducing spatial and temporal variability, wildfires fundamentally contribute to enhancing global biodiversity (He *et al.*, 2019). However, at more localized scales, the impact of fire on biodiversity depends on the spatial heterogeneity of habitats, characteristics of fire regimes (including frequency and intensity) and type of ecosystem in question (Pausas and Ribeiro, 2017; Moritz *et al*., 2023).

Wildfires in fire-prone ecosystems significantly influence the evolution of adaptive mechanisms in plant species, ensuring their survival during a fire or stimulating post-fire recruitment (Gómez-González *et al*., 2011; Keeley *et al*., 2011). The diversity of these adaptations is influenced by the fire regime, since the prevalence of fire-adaptive traits varies across different ecosystems (Keeley and Pausas, 2022). For example, fire-released dormancy and the consequent post-fire stimulation of germination is a common adaptation in several Mediterranean-type ecosystems subjected to recurrent crown fires (Keeley *et al*., 2012), yet it is less frequently observed in tropical savannas where surface fires are dominant (Dayamba *et al*., 2008; Fichino *et al*., 2016).

The effects of fire on seed germination vary. For simplicity, we use the term 'fire cues' to refer to the various fire-related properties that release dormancy and stimulate germination. However, fire (through heat and smoke) not only provides the signal (cue) but also the mechanism for seed dormancy release as well as the optimal conditions for germination of shade-intolerant plants (Pausas and Lamont, 2022). Furthermore, different compounds produced during a wildfire may have either positive or negative impacts on seed germination, depending on the history of the lineage and the fire regime (Keeley and Fotheringham, 2000; Gómez-González *et al*., 2008; Jefferson *et al*., 2014). Heat- and smoke-induced dormancy release of seeds is particularly pronounced in Mediterranean ecosystems, where many species rely on seedling recruitment after fire from the existing soil seed bank (Keeley, 1991; Moreira *et al*., 2010; Tormo *et al*., 2014; Pausas and Lamont, 2022). Historically, various seed traits, especially those related to dormancy and germination, are expected to have been subject to selective evolutionary pressures imposed by fire, given their pivotal roles in the survival and reproduction of seeder plants in different fire-prone ecosystems (Keeley 1991, Gómez-González *et al*., 2011; Willis *et al*., 2014; Pausas and Lamont, 2022; Lamont and Pausas, 2023). Indeed, the widespread occurrence of fire-released seed dormancy across certain plant lineages supports this theory, underscoring the evolutionary interplay between fire regimes and plant reproductive strategies (Lamont *et al*., 2019).

Most spermatophytes (50–90 %) produce seeds that are dormant at maturity and after dispersal, germination does not occur even under seemingly appropriate environmental conditions (Baskin and Baskin, 2014; Kildisheva *et al*., 2020). For dormancy release and subsequent germination, seeds in different dormancy classes [physical (PY), physiological (PD), morphological (MD), morpho-physiological (MPD) and combinational (PY + PD); Baskin and Baskin, 2004] require exposure to specific environmental cues such as the heat or the smoke produced by fires (Keeley, 1991; Baskin and Baskin, 2014).

Early studies on fire focused on the role of heat in breaking dormancy in seeds with a water-impermeable seed or fruit coat i.e. seeds with physical dormancy (PY), also known as heat-released dormancy (Gill, 1975; Keeley and Keeley, 1987; Thanos *et al*., 1992; Keeley and Fotheringham, 2000). Seeds with PY have specialized anatomical features (water gaps) evolved to be dislodged or ruptured by the intense heat, thereby allowing water absorption and germination (Moreira and Pausas, 2012, 2018; Liyanage and Ooi, 2018). Furthermore, smoke (i.e. another fire cue) may have either stimulatory (Keeley and Pausas, 2018) or inhibitory effects (Gómez-González *et al*., 2008) on seed germination, suggesting that such dichotomous outcomes may be attributed to the specific identities of smoke-derived compounds. Indeed, smoke contains several compounds, such as karrikinolide (KAR_1) (Flematti *et al*., 2004; van Staden *et al*., 2004) and its analogues (KAR_2 to KAR_6), collectively known as karrikins (Flematti *et al*., 2009), which have been proven to enhance seed germination in many plant species. Other compounds, including cyanohydrin glyceronitrile, hydroquinone and the brassinosteroid precursor ergosterol, have also been found to break seed dormancy and stimulate seed germination (Flematti *et al*., 2011; Villedieu-Percheron *et al*., 2014; Kamran *et al*., 2017; Shayanfar *et al*., 2020). Additionally, some other gaseous chemicals in smoke, such as nitrogen oxides, nitric oxides, ethylene, carbon monoxide and carbon dioxide, can affect seed germination (Keeley and Fotheringham, 1998). Conversely, smoke also contains germination-inhibitory compounds, most notably a butenolide called 3,4,5-trimethylfuran-2(5H)-one (TMB) (Light *et al*., 2010). Smoke released from burning vegetation contains compounds that act as environmental signals, either independently or in conjunction with heat, leading to the breaking of seed dormancy and germination across a spectrum of species in both fire-prone and non-fire-prone ecosystems (Pierce *et al*., 1995; Keeley and Fotheringham, 1998; Moreira *et al*., 2010; Ferraz *et al*., 2013; Çatav *et al*., 2014, 2024; Abedi *et al*., 2018; Li *et al*., 2021). The occurrence of smoke-released seed dormancy in non-fire-prone ecosystems is only adaptive if the seeds also survive the heat of the fire, and may occur in lineages that experienced varied fire regimes in their evolutionary history (Lamont and He, 2017; Pausas and Lamont, 2022).

Various forms of smoke (aerosol smoke, smoke water and charred straw solution) at different concentrations and exposure times are used in germination experiments (Montalvo *et al*., 2002; Govindaraj *et al*., 2016; Abedi *et al*., 2018). However, care must be taken as different methods of making smoke and/or smoke solutions may lead to the underestimation of this process (Moreira and Pausas, 2018). The germination response to smoke can vary significantly among species, indicating species-specific sensitivities to different smoke concentrations (Moreira *et al*., 2010; Çatav *et al*., 2014). A critical unresolved question is whether there are global patterns in germination responses to various smoke application methods. Moreover, while regional research has begun to explore the interaction between seed dormancy classes and fire cues like heat and smoke (Moreira *et al*., 2010; Ferraz *et al*., 2013; Kazancı and Tavşanoğlu, 2019; Fernandes *et al*., 2021), a comprehensive global assessment is still lacking.

The individual or combined effects of different fire cues on seed germination vary (Keith, 1997; Tieu *et al*., 2001; Lamont and Pausas, 2023). Some studies have shown that the synergistic effects of heat and smoke on germination surpass their individual influences (Keith, 1997; Morris, 2000; Tavşanoğlu *et al*., 2017). While Lamont and Pausas (2023) recently summarized the combined effects of heat and smoke in fire-prone environments, a comprehensive quantitative analysis to assess the extent of these effects globally remains unexplored.

The majority of data on fire-released seed dormancy is derived from Mediterranean-type ecosystems, which are characterized by moderately frequent intense crown fires and specific plant families adapted to such fire regimes (Keeley and Fotheringham, 2000; Moreira and Pausas, 2018; Pausas and Lamont, 2022). In contrast, ecosystems like savannas and temperate grasslands under less intense but more frequent surface fires show a weaker germination response to fire (Pausas and Lamont, 2022). Limited studies in non-fire-prone environments, such as saline–alkaline grasslands (Li *et al.*, 2021), tropical rainforests (Ferraz *et al.*, 2013) and arid deserts (Pierce *et al.*, 1995), also indicate the positive role of fire cues in dormancy release. However, a quantitative comparison of seed germination responses to fire across fire-prone and non-fire-prone areas, and across crown and surface fire ecosystems has yet to be explored in detail (Pausas and Lamont, 2022; Lamont and Pausas, 2023). The diversity of ecosystems, each with its unique fire regime, suggests potential variability in germination responses to fire-related cues, a hypothesis that has not yet been fully examined on a global scale.

Here, we performed a global systematic review and meta-analysis to reveal the effects of fire on seed germination and their relationship with seed dormancy on the global scale, while also deciphering the different germination response patterns to fire cues across different ecosystems. Specifically, we have reviewed experiments that applied putative dormancy release treatments (heat, smoke, specific smoke compounds) to seeds and evaluated their effects by comparing germination between the treated and control seeds. We hypothesized that fire-released seed dormancy is more prevalent in fire-prone ecosystems than in non-fire-prone ones, and in crown fire ecosystems than in surface fire ecosystems, and that the specific effects of fire cues on dormancy release depend on the type and combination of fire cues and the class of seed dormancy. Additionally, we expected to uncover global patterns in the relationship between germination and smoke treatment and smoke components that may provide insights for application in restoration and conservation projects.

MATERIAL AND METHODS

Data collection

A database of published articles from 1970 to 2022 on the effects of fire cues on seed dormancy and germination was constructed through a search in the ISI Web of Science; with the steps documented in a PRISMA chart provided in Supplementary Data Fig. S1 (O'Dea *et al.*, 2021). The key words used in this survey included 'aerosol smoke + dormancy + germination', 'charred wood/straw + dormancy + germination', 'smoke water + dormancy + germination', 'ash + dormancy + germination', 'burning + dormancy + germination', 'smoke-derived compounds + dormancy + germination', 'fire + dormancy + germination', 'wildfire + dormancy + germination', 'heat shock + smoke + dormancy + germination', 'Kar + Karrikin + Karrikinolide + Karrikinolide and cyanohydrin + dormancy + germination', and 'Butenolide + dormancy + germination'. We also used information from two comprehensive surveys (Baskin and Baskin, 2014; Jefferson *et al.*, 2014). We only included published studies (journal articles and books); unpublished doctoral dissertations, conference abstracts and non-peer-reviewed literature (e.g. reports) were excluded. In total, 701 publications were extracted through a comprehensive literature search on the subject.

Each article was carefully reviewed, and 358 papers were excluded from the database due to improper definition of treatments and/or lack of relevant information, such as percentage of germination or ambiguity in the data numerical values. Also, 69 articles without primary data (such as reviews), 13 articles with data that were not retrievable, and 15 unpublished doctoral dissertations and conference abstracts were not included in our meta-analysis. In total, 246 publications were finalized for meta-analysis. All included studies met the following criteria: (1) an experimental design in which manipulated treatments were compared with a control, allowing for a comprehensive comparison across multiple studies, and (2) specified information regarding means and the number of replicates for each treatment was provided (Soltani *et al.*, 2018).

For germination percentage, the final database included 14 106 observations from 1782 plant species belonging to 128 plant families. The effects of fire-related cues on seed dormancy release across various plant families and lineages were determined based on the Angiosperm Phylogeny Group (APG IV, 2016; Jin and Qian, 2022).

Data extraction

In the first step, a standard spreadsheet was created to compile the necessary information from each study, including the journal and article titles, author(s), year of publication, country of seed origin, plant species and family, and germination percentage. Information from papers and Baskin and Baskin (2014) was used to categorize seed dormancy for each species and/or family. When information on seed dormancy was unavailable at the species level, the genus level was used based on available literature. If no information was available at both the species and genus levels, seed dormancy was reported in the 'unknown' group.

Meta-analysis procedures and calculations were performed using the 'metafor' package with the 'rma' function in R software (Viechtbauer, 2010; R Core Team, 2021). After extracting the necessary information, we calculated the actual effect size for each individual study (Gurevitch and Hedges, 1999; Osenberg *et al.*, 1999) to evaluate the effect of each treatment across different studies on a common scale of effect size in the meta-analysis. Quantifying the effect size for a treatment requires consistent interpretation and application of controls and treatments across relevant studies (Hedges *et al.*, 1999; Soltani *et al.*, 2018).

Since most studies did not report any measure of variance, a non-parametric method was used to weight the effect sizes based on the number of replications (Hedges *et al.*, 1999; Hoeksema and Forde, 2008).

The confidence interval (CI) was calculated using a bootstrapping procedure with the 'boot' package (Adams *et al.*, 1997). To facilitate interpretation, the results of the analyses on the effect size and CI were back-transformed and reported as the percentage change with treatment relative to the control. That is, positive and negative values indicate an increase and decrease in germination percentages after fire cues, respectively.

The effect size was considered significant when the 95 % CI did not overlap with zero. Likewise, differences between treatment categories were considered significant if their 95 % CIs did not overlap (Gurevitch and Hedges, 1999; Linquist *et al.*, 2013).

Before building the meta-analysis models, a heterogeneity test was conducted to determine whether a fixed effects model or a random effects model was appropriate, based on the indices of heterogeneity (Cochran's Q, I^2 and τ^2). Since most treatments (datasets) were not homogeneous (Philibert *et al.*, 2012; Nakagawa *et al.*, 2017), a random effects model was used to analyse the data.

Sensitivity analyses were conducted on the weighted mean effect sizes of each observation in the dataset using leave-one-out meta-analysis (Philibert *et al.*, 2012). In this procedure, each individual observation was removed from the dataset, and the models were re-fitted to the remaining data. Based on the changes in weighted mean effect sizes and the impact of removing each observation on the results, 24 observations were eliminated from the meta-analysis.

The data in this study displayed high variation; therefore, we examined the characteristics that may have influenced the results using the meta-analytic moderators (Supplementary Data Table S1). The moderators included fire cue components (heat, smoke, heat + smoke), different smoke application methods (aerosol smoke, smoke water and charred straw solution), various exposure times to smoke (0–5, 5–10, 10–30, 30–60 and 60–180 min), different smoke concentrations (1:1, 1:1–1:10, 1:10–1:100 and 1:100–1:1000, v/v), different smoke-derived compounds (KAR_1, butenolide, cyanohydrin glyceronitrile and nitrogenous components), different ecosystems (Mediterranean ecosystems, savannas and tropical grasslands, temperate dry forests, temperate grasslands, temperate warm ecosystems, temperate humid ecosystems, tropical and subtropical dry forests, and tropical rainforests), fire-proneness of these ecosystems (fire-prone or non-fire-prone) and fire regimes (surface and crown fire regimes).

Fire-prone ecosystems are those whose persistence and functioning are dependent on regular wildfires, whereas non-fire-proneness refers to natural ecosystems that rarely experience any wildfire. In the dataset, fire-proneness and fire regime were assigned to each ecosystem type based on available information about the fire regimes and climate types of the ecosystems where the seeds of the tested species were collected, using insights from various global and regional studies (Supplementary Data Table S2; Stern *et al.*, 2000; Peel *et al.*, 2007; Keeley *et al.*, 2012; Murphy *et al.*, 2013; Harrison *et al.*, 2021; Pausas, 2022; Pausas and Lamont, 2022). Specifically, savannas and tropical grasslands, Mediterranean ecosystems (except Chile), temperate dry forests, temperate grasslands, temperate warm ecosystems, and tropical and subtropical dry forests were considered fire-prone ecosystems (Table S2). Tropical rainforests, temperate humid ecosystems and Mediterranean-type ecosystems in Chile were classified as non-fire-prone (Table S2). Fire regime analysis was conducted only on fire-prone ecosystems, with savannas and grasslands (temperate or tropical) classified as surface fire ecosystems, and Mediterranean ecosystems, temperate warm ecosystems and temperate dry forests as crown fire ecosystems (Table S2).

The 246 articles used in our meta-analysis (Supplementary Data Table S3) span from 1970 to 2022, and mostly (61 %) come from Australia, Spain, USA and South Africa (Fig. 1).

RESULTS

Family-level response of seed germination to fire-derived cues

Our examination of 128 plant families revealed that Fabaceae, Poaceae and Asteraceae were the most frequently studied, representing 13.1, 9.2 and 9.4 % of the studies, respectively (Supplementary Data Table S4). Seed germination in 36 plant families responded positively to heat, with Solanaceae and Geraniaceae showing the highest increases in germination, by 39 and 37 %, respectively. In contrast, members of 58 families responded negatively to heat treatments. Moreover, seeds from 78 plant families responded positively to smoke treatments, while those of 31 families exhibited a negative germination response to smoke, highlighting distinctions between smoke-responsive and smoke-non-responsive families. Also, seeds from 25 and 13 plant families responded positively and negatively, respectively, to both heat and smoke.

Heat, smoke and their combined effects

Overall, fire-derived cues significantly increased germination percentage by 37.7 %, demonstrating the considerable stimulatory effect of fire cues on seed germination across a broad spectrum of plant families (Fig. 2A).

The analysis of 6400 observations across 100 families suggest that heat alone (considering all temperatures and exposure times tested) led to a 35.4 % reduction in seed germination compared to controls, whereas smoke alone ($n = 7028$) significantly increased germination by 156.0 %. Interestingly, the combination of heat and smoke yielded a synergistic increase in germination of 161.2 % ($n = 678$), surpassing the effects observed with either cue alone (Fig. 2B). To address potential bias due to the low number of observations for heat plus smoke compared to either cue alone, an additional analysis was conducted exclusively on studies that considered both individual and combined effects of heat and smoke (H, S, H + S) on seed germination and it was found that differences were significant (mean for H, S and H + S was −5.92, 139.41 and 169.40 %, respectively).

Effects of smoke type, concentration and exposure time

Different forms of smoke applications, such as aerosol smoke, smoke water and charred straw solution, had positive effects on seed germination (Fig. 2C). Aerosol smoke led to the most significant increase in germination (206.4 %; $n = 2035$), surpassing the effects of smoke water (146.3 %; $n = 2400$) and charred straw solution (99.3 %; $n = 550$). The efficacy of charred straw solution in enhancing seed germination across different families was generally lower than that of aerosol smoke or smoke water.

Aerosol smoke exposure for 60–180 min resulted in the greatest significant increase in seed germination, with a mean

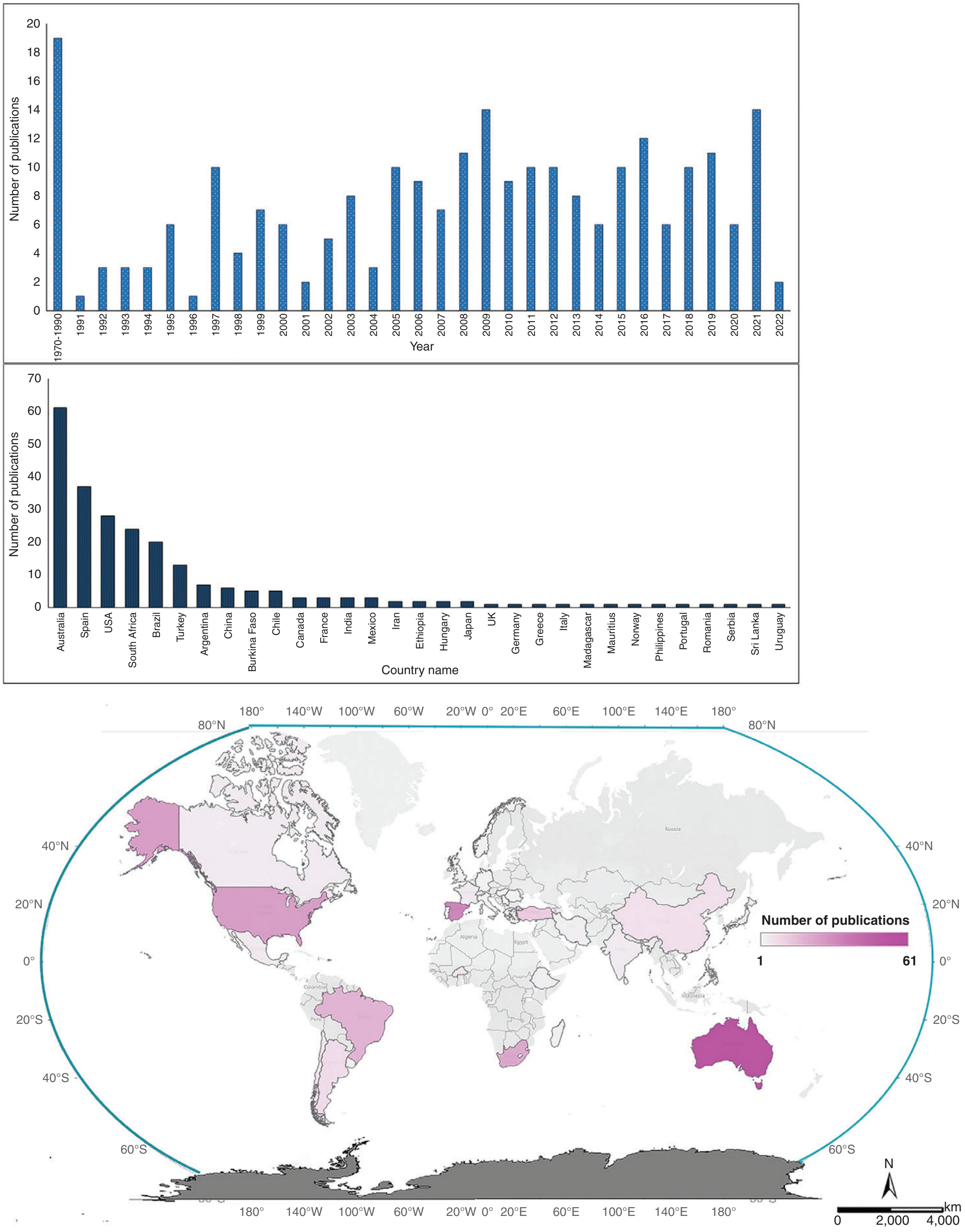

FIG. 1. Number of publications on fire cues based on year and seed origin country from 1970 to 2022 ($n = 246$), and a global distribution map of observations across different countries.

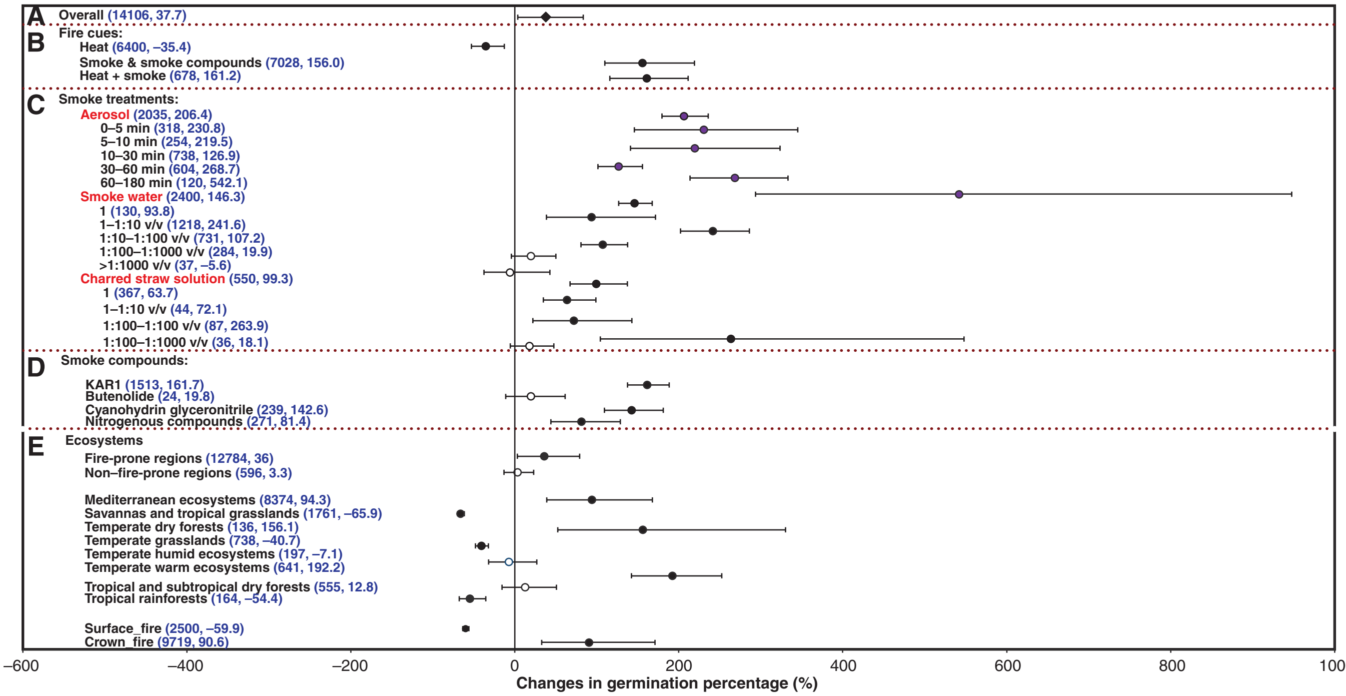

FIG. 2. A meta-analysis of the effects of fire cues on germination percentage. (A) Over all studies, (B) heat, (C) types of smoke treatment, (D) smoke-derived compounds and (E) different ecosystems. Each data point represents the percentage change as compared with the control. The first number in parentheses indicates the number of observations and the second represents the mean value. Symbols and bars show the mean response and 95 % confidence interval, respectively. Open circles indicate that estimates are not statistically significantly different from zero at α = 0.05, while filled symbols indicate significant differences. KAR_1, karrikinolide (3-methyl-2*H*-furo[2,3-*c*] pyran-2-one).

increase of 542.1 % as compared to the non-treated control seeds (Fig. 2C). For smoke water treatments, the lowest germination (mean = −5.6 %, not significantly different from 0) was observed with >1:1000 solutions (Fig. 2C). The most substantial germination increases, 241.6 and 107.2 %, were achieved with smoke water dilutions of 1:1–1:10 and 1:10–1:100 v/v, respectively. Regarding charred straw solution, the lowest germination occurred with dilutions of 1:100–1:1000 v/v (18.1 %) and the undiluted aqueous stock solution (63.7 %). Conversely, dilutions of 1:1–1:10 and 1:10–1:100 v/v significantly enhanced germination by 72.1 and 263.9 %, respectively (Fig. 2C).

Effects of smoke-derived compounds

The effect of smoke-derived compounds on seed germination varied significantly (Fig. 2D). KAR_1 exhibited the most significant stimulatory effect on seed germination, with an increase of 161.7 % (*n* = 1513), closely followed by cyanohydrin glyceronitrile at 142.6 % (*n* = 239) and nitrogenous compounds at 81.5 % (*n* = 271). The lowest germination compared to untreated control seeds was observed with butenolide (19.8 %; *n* = 24).

Responses across different ecosystems

Seed germination across various ecosystems demonstrated distinct responses to fire cues. Seeds from fire-prone regions showed the most significant increase in germination (36.0 %; *n* = 12 784). However, seed germination responses for non-fire-prone regions (3.3 %; *n* = 596) were not as significant as those of fire-prone regions (Fig. 2E). The significance appeared when disaggregating by ecosystem type or fire regime (Fig. 2E). Temperate warm ecosystems experienced the highest germination boost (192.2 %; *n* = 641), followed by temperate dry forest ecosystems (156.1 %; *n* = 136) and Mediterranean ecosystems (94.2 %; *n* = 8374). Conversely, fire cues led to a slight and non-significant increase and decrease in seed germination for species from tropical and subtropical dry forests (12.8 %; *n* = 555) and temperate humid ecosystems (−7.1 %; *n* = 197), respectively. Notably, there was a significant decline in germination percentages for species from savannas and tropical grasslands (−65.9 %; *n* = 1761), tropical rainforest (−54.4 %; *n* = 164) and temperate grasslands (−40.7 %; *n* = 738) following exposure to fire cues. Seed germination also varied in response to fire regimes (Fig. 2E): fire cues significantly stimulated seed germination in crown fire regimes (90.6 %; *n* = 9719) but not in surface fire regimes where germination was negatively impacted by fire cues (−60.0 %; *n* = 2500).

Germination responses of seeds with different dormancy classes

The meta-analysis highlighted significant variability in germination responses among seeds with different dormancy classes when exposed to fire-derived cues (Fig. 3). Germination of non-dormant (ND) seeds as well as those with MD, MPD and PD decreased by 78.7, 77.8, 44.3 and 44.8 %, respectively, after exposure to heat, whereas in the case of PY this treatment increased germination by 18.1 % (Fig. 3). A key finding was a significant increase in germination for seeds with MPD (343.6 %) and PD (204.3 %) following smoke treatment without heat. The application of both heat and different forms of smoke resulted in higher germination percentages in seeds with PD and PY (291.8 and 111.0 %, respectively) compared to the individual application of each treatment.

Different smoke application forms (aerosol smoke, smoke water and charred straw solution) were particularly effective in seeds with MPD (516.4, 634.9 and 400.3 % increase in aerosol, smoke water and charred straw solution, respectively) and PD (285.1, 161.6 and 172.5 % increase in aerosol, smoke water and charred straw solution, respectively), exhibiting a stronger effect than on other dormancy classes (Supplementary Data Fig. S2). Seeds with MD and PY displayed negative responses to these smoke forms (Fig. S2).

Differential responses were also noted in how seed dormancy classes interacted with exposure times to aerosol smoke and concentrations of smoke water and charred straw solution (Supplementary Data Figs S3, S4 and S5). For MPD and PD, the highest germination responses to aerosol smoke were observed with exposure times of 60–180 min (Fig. S3). Among the different dormancy classes, MPD displayed in general the highest response to different concentrations of smoke water, with the 1:1–1:10 v/v dilution being the most effective in stimulating seed germination (Fig. S4). This response was similar in seeds with PD, where germination was most stimulated by 1:1–1:10 v/v dilutions. Seeds with PD also showed the greatest increase in germination when treated with more diluted charred straw solutions (Fig. S5).

Analysis of the effects of smoke-derived compounds on the germination of seeds with various dormancy classes revealed inhibitory impacts of butenolide on PD seeds, whereas other compounds increased germination of seeds with PD by 156.0–191.7 %. KAR_1 (191.7 %), nitrogenous compounds (187.8 %) and cyanohydrin glyceronitrile (156.0 %) had positive effects on germination of PD seeds. MPD seeds treated with these compounds also showed a positive germination response, although the effect was relatively less pronounced than in PD seeds. Meta-analysis revealed weak to no effects of smoke-derived compounds on seeds with other dormancy classes (Fig. 4).

Fire-related germination across ecosystems and seed dormancy classes

The germination response of seeds from different regions to heat and smoke varied and was influenced by seed dormancy classes (Fig. 5). In fire-prone regions, heat decreased the germination of ND seeds as well as those with MD, MPD and PD; the only exception was seeds with PY, which showed increased germination (Fig. 5). In non-fire-prone regions, however, heat increased germination of seeds with PD and PY.

Heat negatively impacted germination of PD seeds across several ecosystems including Mediterranean, savannas and tropical grasslands, and temperate grasslands, but its effect was positive in temperate warm ecosystems and tropical and subtropical dry forests (Fig. 6). ND, MD and MPD seeds generally showed negative responses to heat across all ecosystems. Among the ecosystem types with enough sample size ($n > 100$) for an objective evaluation, PY seeds from Mediterranean ecosystems (52.2 %; $n = 1688$), temperate warm ecosystems (162.2 %; $n = 158$), and tropical and subtropical dry forests (243.1 %; $n = 130$) showed positive germination responses to heat, but this fire cue reduced

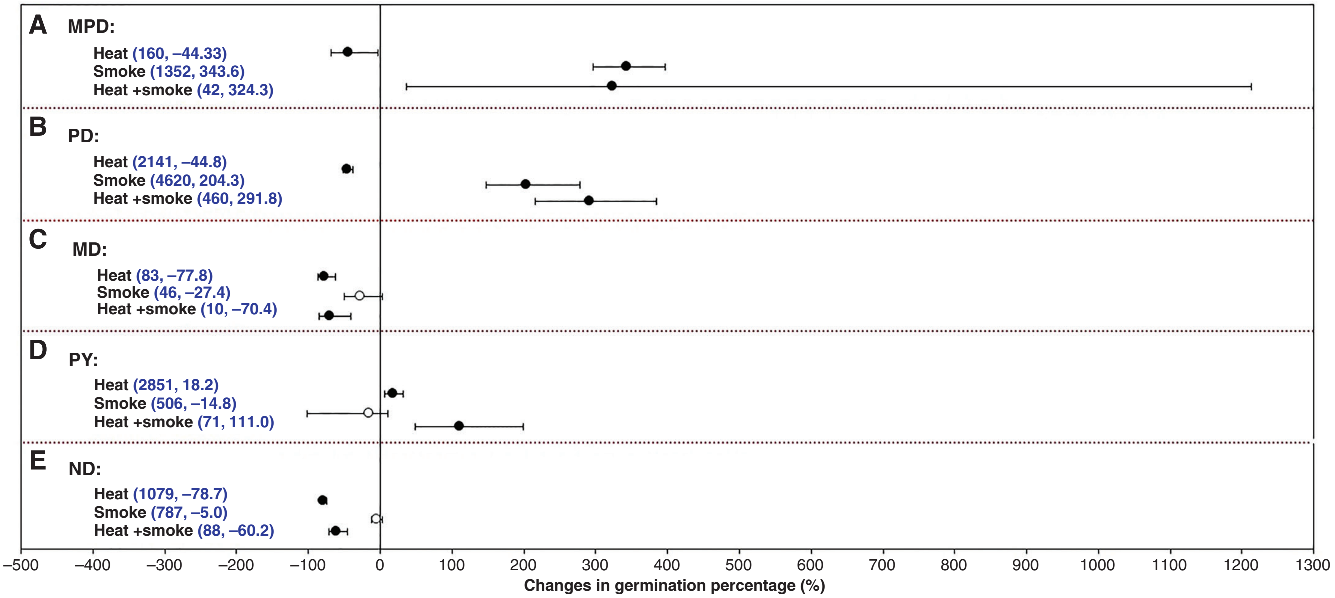

FIG. 3. Relative germination responses of non-dormant (ND) seeds and seeds with different classes of dormancy (MPD, PD, MD, PY) to fire cues (heat, smoke and heat + smoke). Each data point represents the percentage change compared with the control. The first number in parentheses indicates the number of observations and the second represents the mean value. Symbols and bars show the mean response and 95 % confidence interval, respectively. Open circles indicate that estimates are not statistically significantly different from zero at α = 0.05, while filled symbols indicate significant differences. ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MD/MPD, morphological dormancy/morphophysiological dormancy.

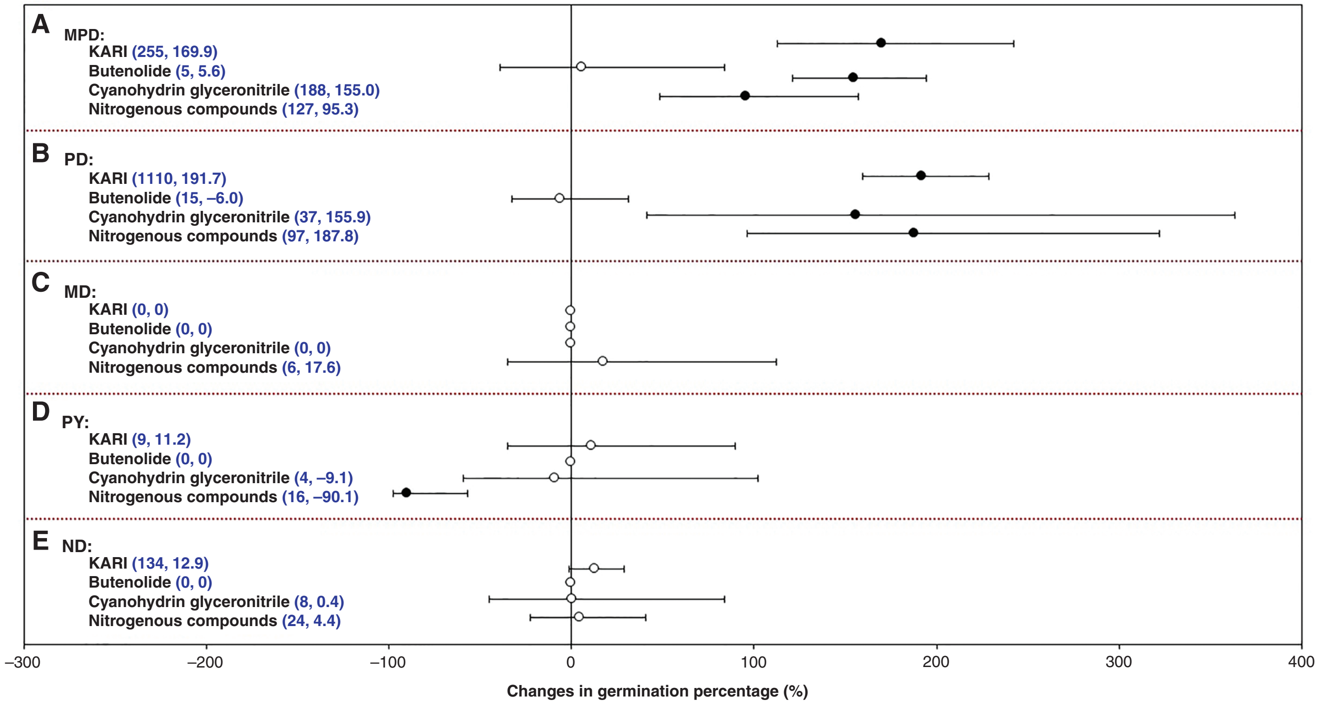

Fig. 4. Relative germination responses of non-dormant (ND) seeds and seeds with different classes of dormancy (MPD, PD, MD, PY) to smoke-derived compounds. Each data point represents the percentage change compared to the control. The first number in parentheses indicates the number of observations and the second represents the mean value. Symbols and bars show the mean response and 95 % confidence interval, respectively. Open circles indicate that estimates are not statistically significantly different from zero at α = 0.05, while filled symbols indicate significant differences. ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MD/MPD, morphological dormancy/morphophysiological dormancy.

germination of PY seeds in savannas and tropical grasslands (−66.8 %; *n* = 375).

Heat decreased the germination of ND, MD, MPD and PD seeds of species in regions with both crown and surface fire regimes (Fig. 7). Heat increased PY seed germination by 71.4 % (*n* = 2077) in regions under crown fire regimes, but decreased it by −64.6 % (*n* = 416) in regions under surface fire regimes.

In contrast to heat, smoke positively affected the germination of MPD and PD seeds in fire-prone regions (Fig. 5). MPD seeds (332.1 %; *n* = 1177) displayed greater germination responses to smoke in fire-prone areas than observed in PD seeds (230.0 %; *n* = 3733). Although MPD seeds showed a positive germination response to smoke in non-fire-prone areas (332.1 %; *n* = 25), the small sample size makes it uncertain whether this observation reflects a real trend. PD seeds showed a greater germination response to smoke in fire-prone (230.0 %; *n* = 3733) over non-fire-prone (7.5 %; *n* = 177) areas. Generally, the germination of ND, MD and PY seeds from fire-prone and non-fire-prone regions was not significantly affected by smoke (Fig. 5).

Smoke significantly enhanced the germination of MPD seeds only in Mediterranean ecosystems, although there are slight increases in other ecosystems except for temperate humid ecosystems (Fig. 6). On the other hand, smoke significantly enhanced the germination PD seeds across all ecosystems except for tropical rainforests, tropical and subtropical dry forests, and temperate humid ecosystems (Fig. 6). PY seeds, however, exhibited a positive response to smoke only in Mediterranean ecosystems (19.1 %; *n* = 295), but a negative response in savannas and tropical grasslands (−61.2 %, *n* = 107). ND seeds had negative responses to smoke in tropical rainforest (−45.0 %; *n* = 98) but were unaffected or had a slight positive response in other ecosystems (Fig. 6).

Smoke increased MPD and PD seed germination in regions under both surface and crown fire regimes, with greater effects in the latter (Fig. 7). This fire cue negatively affected ND and PY seed germination in regions with surface fire regimes but they showed an opposite response in regions with crown fire regimes. The effects of smoke on MD seeds from regions with surface and crown fire regimes were opposite to those of ND and PY seeds.

DISCUSSION

Pausas and Lamont (2022) set the framework for understanding the role of fire as a dormancy-release mechanism in fire-prone ecosystems. Here, we have provided a systematic quantitative review at the global scale to test some of their conclusions. Our meta-analysis showed the significant effect of fire-derived cues on seed germination, emphasizing the complexity and variability of responses across different ecosystems, fire regimes and seed dormancy classes. Moreover, we have established that fire regime is a crucial driver of dormancy release and germination in response to heat and smoke on a global scale. Remarkably, we found that smoke treatments, particularly aerosol smoke, universally stimulated seed germination, with pronounced effects in fire-prone regions and among seeds exhibiting PD and MPD. Conversely, heat treatments often reduced germination, except in seeds with PY,

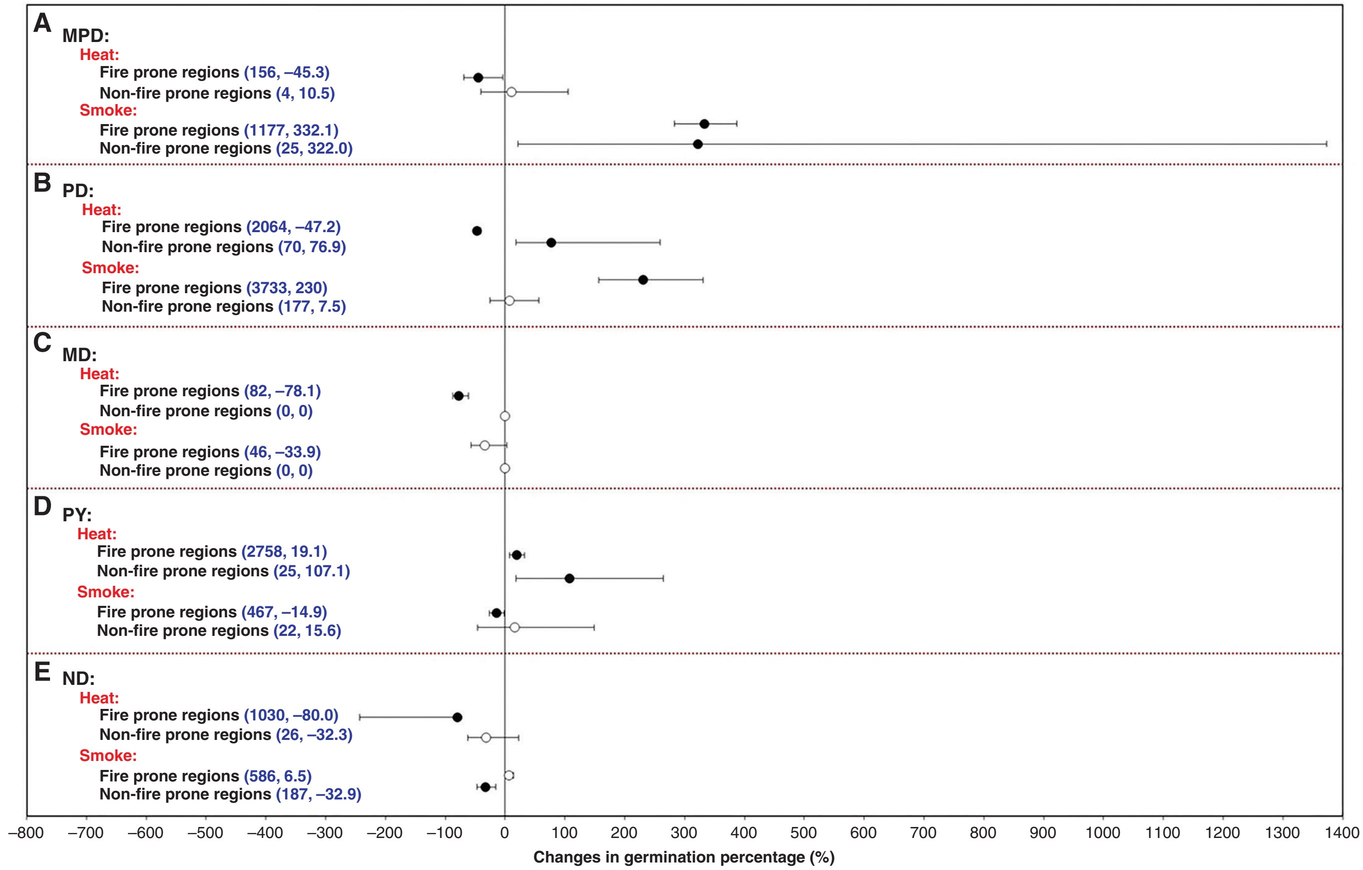

FIG. 5. Relative germination responses of non-dormant (ND) seeds and seeds with different classes of dormancy (MPD, PD, MD, PY) in fire-prone and non-fire-prone regions to heat and smoke. Each data point represents the percentage change compared with the control. The first number in parentheses indicates the number of observations and the second represents the mean value. Symbols and bars show the mean response and 95 % confidence interval, respectively. Open circles indicate that estimates are not statistically significantly different from zero at $\alpha = 0.05$, while filled symbols indicate significant differences. ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MD/MPD, morphological dormancy/morphophysiological dormancy.

where an increase was observed. Overall, the most fire-related stimulation of the germination was observed in crown fire ecosystems. All these findings, which are consistent with previous studies (Pausas and Lamont, 2022), highlight the complex relationship between fire and seed biology, underscoring the evolutionary capacity of plant species to adapt to specific fire regimes. Furthermore, our study provides a comprehensive global overview, revealing that germination responses to fire cues are not only species-specific but also influenced by the fire regimes present in ecosystems and the inherent dormancy mechanisms of seeds. This analysis sheds light on the adaptive strategies of plants in fire-prone environments and highlights the potential for applying fire cues in seed germination and conservation practices, and improves our understanding of how fire regimes shape fire-related traits.

Seed dormancy classes and response to heat and smoke treatments

The hypothesis that the synergistic effects of the combined heat + smoke treatment surpass their individual effects on seed germination was confirmed (Fig. 2A). Differential germination responses to fire-derived cues were linked to the interactive effects of these cues with the class of seed dormancy (Fig. 3). For instance, germination in ND, MD, MPD and PD seeds decreased after heat treatment, but it increased in seeds with PY. The negative effects of heat on PD seeds might involve the development of oxidative stress and accumulation of abscisic acid (ABA) (Huang *et al*., 2020), while in MD and MPD seeds, it might trigger programmed cell death in the embryonic axis (Castander-Olarieta *et al*., 2019). Smoke treatment notably enhanced germination in PD and MPD seeds compared with other dormancy classes. Furthermore, the combination of smoke and heat treatments had more pronounced effects on the germination of PD and PY seeds than either treatment alone. Lamont and Pausas (2023) suggested that the synergistic effect may result from heat and smoke activating distinct dormancy release mechanisms or contributing to various stages of a unified germination-promoting process. This suggests that seeds with a combination of physical and physiological dormancy (PY + PD) are particularly responsive to the synergistic effects of heat and smoke. The synergistic effect of heat and smoke on seed germination remains an underexplored area, requiring further research to elucidate the underlying mechanisms driving this combined effect. It is suggested that heat may disrupt the structural integrity of the seed coat (i.e. open the

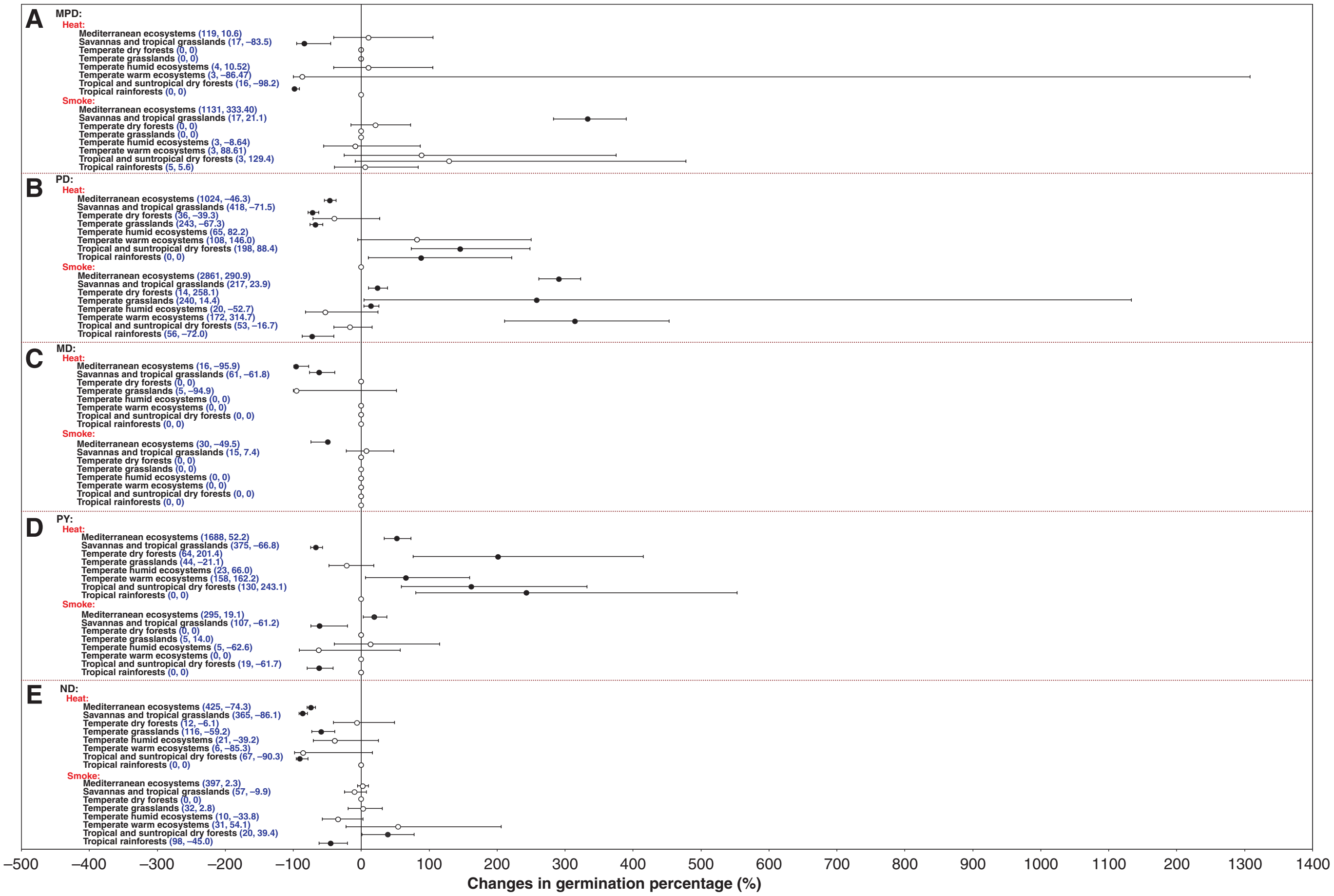

FIG. 6. Relative germination responses of non-dormant (ND) seeds and seeds with different classes of dormancy (MPD, PD, MD, PY) in different ecosystems to heat and smoke. Each data point represents the percentage change compared to the control. The first number in parentheses indicates the number of observations and the second represents the mean value. Symbols and bars show the mean response and 95 % confidence interval, respectively. Open circles indicate that estimates are not statistically significantly different from zero at α = 0.05, while filled symbols indicate significant differences. ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MD/MPD, morphological dormancy/morphophysiological dormancy.

water gap), facilitating imbibition and radicle emergence, particularly in larger seeds (Mackenzie *et al.*, 2016), or possibly facilitate the accumulation of optimal levels of reactive oxygen species (ROS) necessary to break seed dormancy (El-Maarouf-Bouteau and Bailly, 2008). Concurrently, smoke appears to remove physiological barriers, further enabling germination (Mackenzie *et al.*, 2016).

Seed dormancy release and fire cues dose/exposure time

Each of the smoke forms requires a threshold dose or exposure time to elicit a maximum germination response (Fig. 2C). Our meta-analysis also suggested that all types of smoke treatments have positive but differential effects on seed dormancy release and germination, in the order of aerosol smoke > smoke water > charred straw solution. In particular, seeds with PD and MPD benefit more from smoke treatments than those with other dormancy classes (Supplementary Data Fig. S2). The greater effectiveness of aerosol smoke in promoting seed germination compared with other smoke water-soluble forms might be explained by the presence of more germination-active compounds (Roche *et al.*, 1997), the release of gaseous compounds such as ethylene, ammonia and nitric oxide (NO) (Shaikh *et al.*, 1988; Bethke *et al.*, 2004; Gniazdowska *et al.*, 2010; Liu *et al.*, 2010), and the higher diffusion rate of germination-active gaseous compounds. The advantage of smoke water over charred straw solution could be linked to compositional differences, with smoke water potentially containing higher levels of nitrogenous compounds (van Staden *et al.*, 2000) and the presence of KAR_1 and KAR-like compounds, which are absent in charred straw solutions (Shayanfar *et al.*, 2020), along with other distinct compositional factors. From an ecological viewpoint, however, for aerosol smoke to be effective it might need to be dissolved in the semi-aqueous environment of an imbibed seed buried in the soil seed bank. Since water availability is a key driver of germination in post-fire environments (Céspedes *et al.*, 2012), it is likely that most seeds in the soil seed bank encounter smoke-derived compounds primarily through water infiltration during rainfall events after a fire, rather than direct exposure to aerosols during the fire itself. This suggests that smoke water might be a more realistic medium for delivering germination cues to soil-stored seeds in natural settings, but aerosol application may be most effective in management actions.

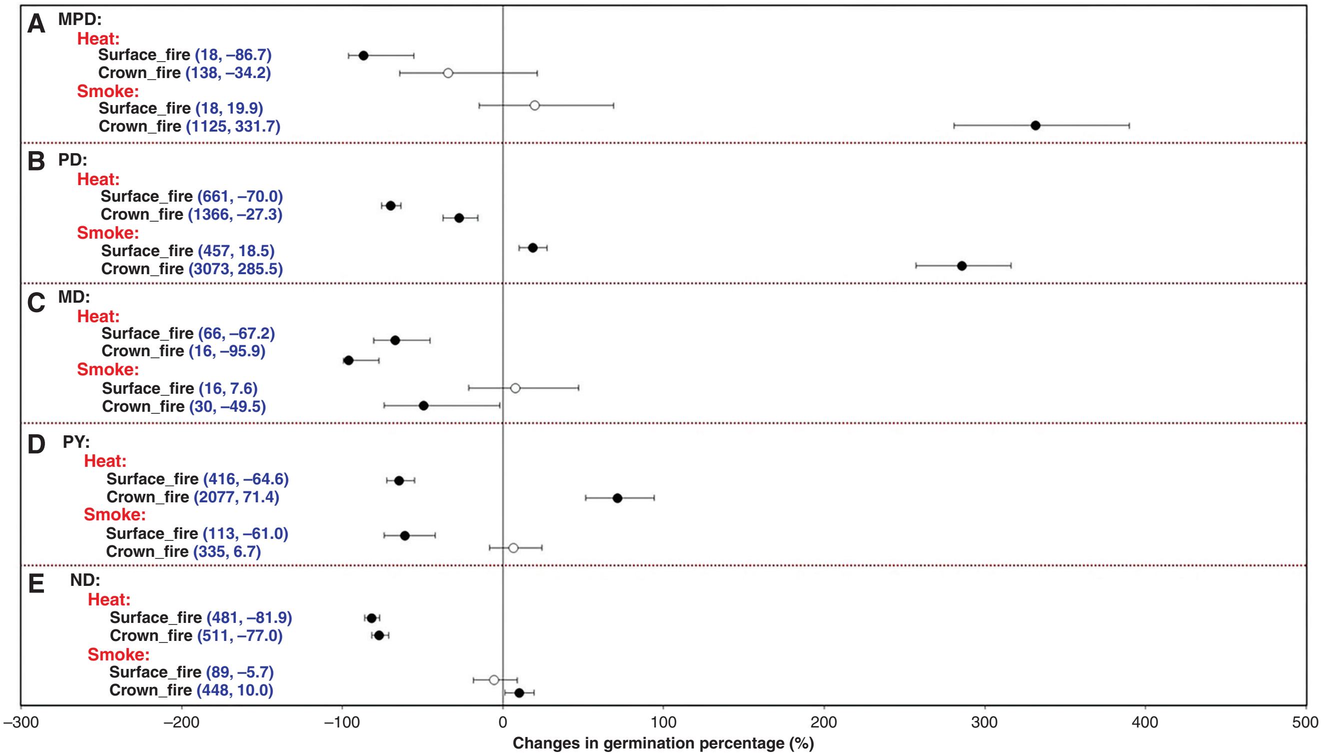

FIG. 7. Relative germination responses of non-dormant (ND) seeds and seeds with different classes of dormancy (MPD, PD, MD, PY) in surface and crown fire regimes to heat and smoke. Each data point represents the percentage change compared to the control. The first number in parentheses indicates the number of observations and the second represents the mean value. Symbols and bars show the mean response and 95 % confidence interval, respectively. Open circles indicate that estimates are not statistically significantly different from zero at α = 0.05, while filled symbols indicate significant differences. ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MD/MPD, morphological dormancy/morphophysiological dormancy.

For aerosol smoke treatments, the most significant increase in germination for seeds with MPD and PD was observed during exposure times of 60–180 min (Supplementary Data Fig. S3). Research practices vary in smoke exposure durations, which are often hard to align with natural fire events, and there is no consensus on the ideal exposure time to optimize seed germination. Hence, adjusting exposure times to match the ecological requirements of specific plant species and targeted ecosystems could enhance restoration efforts and deepen our understanding of plant recruitment after fire (Roche *et al.*, 1997; Hodges *et al.*, 2022).

In treatments using smoke water and charred straw solutions, seed germination was higher in dilution ranges of 1:1–1:10 and 1:10–1:100 compared with undiluted stock solutions and more diluted solutions (Fig. 2C). This pattern was particularly pronounced for seeds with MPD and PD (Supplementary Data Figs S4 and S5). The diminished germination effect from undiluted solutions, which may be reversible or irreversible depending on the concentration (Light *et al.*, 2002), could be attributed to potentially high concentrations of germination inhibitors and/or toxic chemicals (Brown, 1993; Drewes *et al.*, 1995; Baldos *et al.*, 2015; Abu *et al.*, 2016; Calabrese and Agathokleous, 2021). Additionally, highly diluted smoke solutions might not provide sufficient concentrations of compounds necessary for promoting germination (Light *et al.*, 2002), indicating a critical threshold for germination-active compounds is essential to break seed dormancy. A shortcoming of such analysis is the variability in smoke water and/or charred straw solutions across studies due to differences in preparation methods, which could affect seed germination responses. However, evidence suggests that smoke solutions derived from various plants do not significantly alter the germination response to smoke (Çatav *et al.*, 2012).

Germination active compounds from smoke and charred wood

Among the array of compounds in smoke known to promote germination, KAR_1 stands out for its pronounced effect, especially on seeds with PD (Fig. 2D). KAR_1 effectively releases dormancy in a wide range of species (Chiwocha *et al.*, 2009; Çatav *et al.*, 2018) possibly by promoting gibberellic acid (GA_3) synthesis while reducing ABA levels, enhancing ethylene sensitivity and/or production, improving water uptake, activating enzymes such as α-amylase, β-amylase and dehydrogenases during imbibition, and modulating antioxidant activity, thereby elevating various ROS forms necessary for dormancy release (Kępczyński, 2018; Sami *et al.*, 2021). Nitrogenous compounds in smoke also play a critical role in breaking seed dormancy and increasing germination percentages (Bethke *et al.*, 2006). The conversion of ammonium to nitrate and NO in burned areas significantly promotes seed germination (Keeley and Fotheringham, 1997, 1998; van Staden *et al.*, 2000). NO is known to enhance seed germination by reducing ABA levels, increasing gibberellin (GA) concentrations, and upregulating the expression of genes associated with ethylene and GA biosynthesis (Renata and Agnieszka, 2006; Bethke *et al.*, 2007; Zhang *et al.*, 2009). Following KAR_1 and nitrogenous compounds, cyanohydrin, also known as glyceronitrile, significantly promotes seed germination (Flematti *et al.*, 2011, 2013; Kępczyński and Sznigir, 2014; Tavşanoğlu *et al.*, 2017). It can generate cyanide, which acts to break seed dormancy (Lamont and Pausas, 2023). The remarkable germination-stimulating effect of glyceronitrile may also stem from its stability in the soil seed bank after fire (Pausas and Lamont, 2022), ensuring prolonged exposure of buried dormant seeds to this compound. Moreover, combined exposure to karrikins and cyanohydrins may have a synergistic effect in enhancing germination in various plant species (Çatav *et al*., 2018). Seed burial and moisture absorption initiate the dormancy release process, while exposure to glyceronitrile releases innate dormancy, facilitating germination (Lamont and Pausas, 2023). The stability of this compound makes it an advantageous tool in restoration efforts, especially in fire-prone areas.

Butenolide, also known as TMB, is another smoke-derived molecule that acts as a germination inhibitor and significantly reduces the germination-promoting effect of KAR_1 when both compounds are applied simultaneously (Fig. 2D). In a study on seeds of various weedy species, KAR_1 increased germination, while butenolide inhibited it, which was associated with decreased α-amylase activity (Papenfus *et al*., 2015). Butenolide also inhibits seed germination by increasing ABA levels and decreasing the activity of hydrolytic enzymes (Gupta *et al*., 2019). This compound holds potential for managing the germination of weedy seeds within seed banks. Papenfus *et al.* (2015) suggested that applying butenolide to the soil after crop establishment could create a weed-free interval, giving crops a competitive advantage over weeds that emerge later. The concentration of butenolide in the top 2–4 cm of soil is substantially higher (318 nmol g^{-1}) compared with KAR_1 (3.15 nmol g^{-1}), potentially preventing seed germination (Ghebrehiwot *et al*., 2013). However, rainfall can reduce soil concentrations of this inhibitory compound below levels that hinder germination, thereby allowing germination to proceed (Soós *et al*., 2019).

Fire regimes and ecosystem fire proneness

Our findings indicated that germination responses to fire cues vary significantly across seeds from different fire-prone regions and ecosystems. Specifically, seeds from Mediterranean ecosystems, temperate dry forests and temperate warm ecosystems displayed strong positive responses, while those from savannas and tropical grasslands and tropical rainforests responded negatively to fire cues (Fig. 2E). This is in agreement with Pausas and Lamont (2022) who noted that in fire-prone ecosystems, the presence of dense woody vegetation, subject to less frequent but more intense fires, significantly influences the evolution of fire-released seed dormancy mechanisms. Conversely, ecosystems dominated by grasses, such as savannas, which experience more frequent (surface) fires, tend to exhibit a weaker seed germination response to fire cues. The dynamics within non-fire-prone ecosystems are not well understood (Li *et al*., 2021), highlighting the need for detailed quantitative analyses, like the present study, to discern the specific effects of fire cues on seed dormancy release across different ecosystems.

In nearly all ecosystems, heat generally reduced germination in ND, MD, MPD and PD seeds (Fig. 6). Specifically, heat enhanced PY seed germination in Mediterranean ecosystems, temperate dry forests, temperate warm ecosystems, and tropical and subtropical dry forests. However, in savannas and tropical grasslands and temperate grasslands, this fire cue reduced germination. Our study also highlighted the varied responses of different dormancy classes to smoke in different ecosystems. Regardless of the ecosystem, seeds with MPD and PD universally showed positive germination responses to smoke, aligning with Pausas and Lamont's (2022) findings, with an exception of those from tropical rainforests. The effect was especially pronounced in PD seeds from Mediterranean ecosystems. Our analysis indicated that seeds with MPD are as reactive to smoke as those with PD. This adaptability to smoke in MPD seeds is logical since smoke primarily targets the PD component of MPD, allowing for subsequent embryo growth and overcoming MD.

So far, most global-level studies that downplayed the role of fire in the evolution of seed dormancy release (e.g. Rosbakh *et al*., 2023) have failed to fully provide a mechanistic understanding of processes shaping seed dormancy (Pausas *et al*., 2024). Our findings suggest that fire regime (surface versus crown fire ecosystems) significantly explains global fire-related germination patterns better than any other grouping used in our study. Specifically, in ecosystems with crown fires, heat was beneficial for germination of PY seeds, while smoke was more effective for MPD and PD seeds. On the other hand, the lack of fire-released seed dormancy in ecosystems with frequent, low-intensity surface fires such as savannas and tropical and temperate grasslands reflects the selection for other resilience mechanisms and traits such as resprouting, rather than seeding (Pausas and Keeley, 2014). The distinction between germination responses to fire in surface fire and crown fire ecosystems, as well as between fire-prone and non-fire-prone ecosystems, suggests that fire regime acts as a selective evolutionary force in seed dormancy release on a global scale (Pausas and Lamont, 2022).

Fire released seed dormancy across plant families

The distribution of dormancy classes is non-random but closely linked to specific lineages and the evolutionary role of fire in shaping seed dormancy (Pausas and Lamont, 2022). Our survey of 1782 species from 128 plant families also showed that plant families with certain classes of seed dormancy can be differentiated based on the sensitivity of their seeds to fire cues (Supplementary Data Table S4). For instance, MPD seeds with a positive response to fire cues were restricted to families such as Papaveraceae, Vitaceae and Stylidiaceae. These are distinct from families like Paeoniaceae, Liliaceae, Dasypogonaceae and Caprifoliaceae, which have seeds with MPD or MD that exhibit a negative or no response to fire cues. Similarly, PY seeds exhibit varied responses to fire cues, with positive responses in families like Geraniaceae and Cistaceae, and negative responses in Bixaceae. On the other hand, many plant families with PD seeds displayed fire-stimulated germination. Understanding the retention, gain or loss of fire-sensitivity traits in seeds of each lineage requires knowledge of their evolutionary history and interactions with various biotic and abiotic factors, especially fire, which has long-lasting effects on shaping plant communities.

Implications for conservation, restoration and management

The dependence of certain ecosystems on wildfires to sustain their biodiversity highlights the need for the conservation of fire regimes as well as the use of fire as a management tool (Kelly *et al*., 2020; Ulyshen *et al*., 2022). In addition, our study points to the potential use of heat and smoke to enhance germination in laboratory settings, offering valuable insights for incorporating fire-related germination cues into restoration projects for species with heat- or smoke-stimulated germination. However, changes in climate and land-use are intensifying fire regimes (increasing in frequency or intensity) in many ecosystems worldwide, including the emergence of novel fire-prone ecosystems at higher latitudes and altitudes (IPCC, 2022; Sayedi *et al*., 2024). Such changes in fire regimes could disrupt the plant life cycles adapted to current environmental conditions and fire regimes, as seed viability, dormancy release and post-fire seedling recruitment are highly influenced by various fire cues (Moreno and Oechel, 1991; Hanley and Lamont, 2000; Tormo *et al*., 2014; Çatav *et al*., 2018; Lamont *et al*., 2020). Over time, these disruptions may alter ecosystem functions and services as well as species diversity and the composition of local plant communities (Kelly *et al*., 2020; Grau-Andrés *et al*., 2024; Sayedi *et al*., 2024). To address these challenges, data on the structure and composition of different ecosystems (in both fire-prone and non-fire-prone areas), coupled with species-specific seed responses to fire and climate change projections, can be incorporated into simulations. Most studies on fire-related germination are based on laboratory experiments (e.g. Keeley and Fotheringham, 1998; Hanley, 2009; Moreira *et al*., 2010; Çatav *et al*., 2018; Kazancı and Tavşanoğlu, 2019; Fernandes *et al*., 2021), and the lack of studies testing germination under controlled field conditions, including fire temperatures and smoke applications, poses a challenge for applying these findings to conservation, restoration and management actions. Field applications (e.g. Roche *et al*., 1997; Tormo *et al*., 2014) are highly encouraged, as they can provide valuable insights into how laboratory results translate to natural conditions. Such studies, combined with simulations based on data from both laboratory and field experiments, could enhance our ability to predict species responses to altered functioning in existing and emerging fire-prone ecosystems. They may also help anticipate possible extinction events and provide essential guidance for conservation, restoration and fire management activities.

CONCLUSIONS

Our study faces inherent limitations due to existing knowledge gaps. For example, the class of seed dormancy is unknown for many plants. Additionally, the germination experiments with fire cues are probably biased in relation to species, families and ecosystems. Yet our analysis represents the current state-of-the-art on fire-released dormancy and germination across the globe. Below are some conclusions derived from this study:

(1) Our meta-analysis globally validates previous regional and overview studies and unveils new insights into seed responses to fire cues. We confirm the widespread synergistic impact of heat and smoke on seed dormancy release. Additionally, our findings support the hypothesis that fire regimes are a major driving force of seed dormancy release, particularly in crown fire ecosystems.

(2) We provide empirical evidence of a global disparity in fire-released seed dormancy between surface and crown fire ecosystems. Specifically, we confirm a positive germination response to fire in crown fire ecosystems and a negative response in surface fire ecosystems. These results highlight the importance of the fire regime rather than fire itself in shaping seed dormancy responses.

(3) In applying our results for breaking seed dormancy, fire cues and their various forms (e.g. heat, aerosol smoke, smoke water, charred straw solution) should be applied with defined exposure times and/or dosages. For larger-scale environmental applications, additional factors such as rainfall timing after fire, seed burial depth, post-fire plant diversity and the natural fire regime of the ecosystem must also be taken into account.

(4) Our study suggests that dormancy-release and germination responses of species across different ecosystems can be predicted by combining their seed dormancy class with the fire-proneness and the prevalent fire regime. When paired with results from laboratory germination experiments involving heat and smoke, this information can guide conservation, restoration and ecosystem management efforts.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following.

Table S1. Moderator analysis of the influence of fire cues on germination percentage. **Table S2.** Classification, definitions, fire regimes, and fire-proneness of ecosystem types included in the study. **Table S3.** List of studies included in the meta-analysis. **Table S4.** Response of non-dormant (ND) seeds and seeds with different classes of dormancy (MPD, PD, MD, PY) to heat and smoke in the surveyed plant families. **Fig. S1.** PRISMA chart showing the flow of information through the phases of the literature review. **Fig. S2.** Relative germination responses of non-dormant (ND) seeds and seeds with different classes of dormancy (MPD, PD, MD, PY) to different smoke treatments. **Fig. S3.** Relative germination responses of non-dormant (ND) seeds and seeds with different classes of dormancy (MPD, PD, MD, PY) to aerosol smoke at different exposure times. **Fig. S4.** Relative germination responses of non-dormant (ND) seeds and seeds with different classes of dormancy (MPD, PD, MD, PY) to different concentrations of smoke water. **Fig. S5.** Relative germination responses of non-dormant (ND) seeds and seeds with different classes of dormancy (MPD, PD, MD, PY) to different concentrations of charred straw solutions.

ACKNOWLEDGEMENTS

We thank all the researchers who have studied fire-related germination in various parts of the world, making this meta-analysis possible. We also thank the handling editor and two anonymous reviewers for their valuable comments, which helped improve the manuscript.

AUTHOR CONTRIBUTIONS

FGF and HRS presented the initial idea; FGF, HRS, CCB, ÇT and JGP performed the conceptualization; ZM, AS and FGF collected data; ZM, FGF, HRS and ÇT managed data handling and organization; ZM, FGF, ES, BT and MA performed the statistical analysis; ZM, FGF and HRS wrote the first draft of the manuscript; ZM, FGF, HRS, CCB, ÇT and JGP reviewed and edited the final version of the manuscript. All authors revised the final version.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY

The data underlying this article are available in the Figshare online data repository, at https://dx.doi.org/10.6084/m9.figshare.27988568.

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