

REVIEW

Seed dormancy revisited: Dormancy-release pathways and environmental interactions

Byron B. Lamont¹  | Juli G. Pausas² 

¹Ecology Section, School of Life and Molecular Sciences, Curtin University, Perth, Western Australia, Australia

²CIDE-CSIC, Consejo Superior de Investigaciones Científicas, Valencia, Spain

Correspondence

Byron B. Lamont

Email: protea2@hotmail.com; b.lamont@curtin.edu.au

Funding information

Generalitat Valenciana, Grant/Award Number: PROMETEO/2021/040; Curtin University of Technology

Handling Editor: P. William Hughes

Abstract

1. Many internal (inherent) and environmental (imposed) factors control seed dormancy and germination that we divide into three basic dormancy-release pathways: Maternal structures and embryo physiology control inherent dormancy that is broken by various types of scarification and physiological changes, followed by imposed-dormancy release when the prevailing environment is replaced by certain 'standard' conditions that stimulate germination (Pathway 1); imposed dormancy prevails even if inherent dormancy is broken or not applicable that is released when replaced by certain 'standard' environmental conditions which stimulate germination (Pathway 2); and release from inherent dormancy by light/dark or cold stratification is contingent on the pre-existence of certain environmental conditions that stimulate germination (Pathway 3).
2. On-plant seed storage (serotiny) and frugivorous seeds are recognized here as representing special types of physical dormancy, as their properties are consistent with those of hard diaspores. Warm stratification does not require seeds to be moist as it is just a physical response. Heat may promote germination of non-hard, as well as hard, seeds as it may increase their permeability further.
3. Levels of germination gauge the net effect of inherent- and imposed-dormancy release so that it is only possible to identify the extent of inherent-dormancy release when conditions for germination are optimal (imposed dormancy has been annulled). While imposed dormancy may be protracted after inherent dormancy is broken by heat or chilling during the dry or cold seasons, release from both states may effectively coincide if smoke chemicals or light are received during the (wet) growing season.
4. We suggest reserving the term secondary dormancy for seeds that return to (inherent or imposed) dormancy due to changed environmental conditions. Under seasonal climates, fluctuations in environmental conditions can lead to secondary dormancy and even dormancy cycling.
5. We recognize four types of functional interactions between any two environmental factors that induce inherent-dormancy release: binary interactions are ineffective, only one stimulus is effective, both are effective but non-additive, or

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

both are additive/synergistic. Two environmental stimuli that individually break dormancy but have no additive effect must be affecting the same process; this was demonstrated here for some interactions between heat and smoke.

6. The three dormancy-release pathways, together with internal, seasonal and stochastic interactions, are coordinated by the non-dormant seed to ensure maximum germination under optimal conditions. To ignore any aspect outlined here leads to an impoverished understanding of the disparate seed ecology of species adapted to different stressful and disturbance-prone habitats.

KEYWORDS

cold/warm stratification, heat and smoke, karrikin, photoperiod, phytochrome, primary seed dormancy, scarification, seasonality

1 | INTRODUCTION

Seeds can be assigned to two basic dormancy classes: inherent (an inherited property of the organism) and imposed (controlled by properties of the surrounding environment) (Baskin & Baskin, 2021; Considine & Considine, 2016). However, recent reviews do not differentiate between these two classes of dormancy nor discuss the mechanisms by which seed dormancy is overcome (Baskin & Baskin, 2021; Carta et al., 2022; Gioria et al., 2020; Zhang et al., 2022). Distinguishing these two dormancy classes should provide greater insights into the factors that enable a plant's life cycle to begin. Thus, our aim here is to outline the different types of dormancy in the context of physicochemical processes responsible for maintaining dormancy followed by environmentally controlled release of dormancy that allows germination to proceed. While we note that climate (mean total and seasonal temperatures and rainfall) is usually held to be the key to the evolution of seed dormancy (Gioria et al., 2020; Zhang et al., 2022), regular fluctuations in growing conditions on an *intra-annual* scale can only explain the evolution of imposed (environmentally delayed) dormancy. In association with extended seed longevity, inherent dormancy (internally delayed) more likely arose because of *inter-annual* variations in conditions suitable for seedling recruitment, on the expectation of infrequent but guaranteed events in some years that can serve to both break dormancy and be taken advantage of by stored seeds for germination. These include exposing seeds to light through soil disturbance or tree-fall, unusually wet seasons that wash out inhibitors, extended bouts of cold or warmth, or fire with its heat pulses and novel chemicals in smoke that align with optimal (postfire) recruitment conditions. It is the operation and relationship of these mechanisms that we examine here.

While reviewing the literature, we became aware of limitations in current terminology and disparities in the scope of the concept of seed dormancy and conditions that enable seeds to germinate. Sometimes, seeds can return to their original state that has been called secondary dormancy, but imposed dormancy is also often described as secondary. Logic suggests that any seed that will not germinate under standard conditions of moisture, temperature and air

should be regarded as inherently dormant, not just those yet to receive certain temperature treatments as envisaged by some authors (Walck et al., 2011). We also realized that three dormancy-release pathways, rather than the usual two, can arise from different combinations of the two dormancy classes. Since seed dormancy is usually considered as just under climate control, non-soil-stored seeds subject to frugivory or fire-caused heat release (serotiny) have been ignored in global syntheses, but there is a case for considering them as examples of physical dormancy (Pausas et al., 2022). Understanding their functional relationship is challenging when two or more environmental factors interact to break dormancy. Special attention is therefore given to how moisture, cold, light, summer warmth, and fire-type heat and smoke interact with each other to coordinate dormancy release. Research on mechanisms of seed-dormancy release has been especially well studied in fire-prone ecosystems, as it is here that dormancy is most adaptive and widespread (Pausas & Lamont, 2022); thus, many of our examples relate to the role of heat and smoke. We finish by placing the various dormancy-release types in an interseasonal context and suggest relevant topics for future research.

2 | DORMANCY CLASSES AND RELEASE PATHWAYS

Seed dormancy is a state of metabolic inactivity that prevents the embryo from growing and thus the seed from germinating (Considine & Considine, 2016). This fits within the general concept of suspension of activity (quiescence) without needing to outline the cause (Rohde & Bhalerao, 2007). When seed dormancy is examined in more detail, we see that two distinct classes can be identified, inherent and environmentally imposed (Pausas & Lamont, 2022). First, we outline these two seed-dormancy classes explaining how dormancy is maintained and then describe mechanisms of dormancy release that allow germination to proceed. These classes exist independently of each other but can relate in different chronological order to produce three pathways that we describe in the second half of this section.

Morphological dormancy due to immature embryos is not specifically examined in this review as it is neither environmentally controlled nor metabolically inactive and might be better considered as post-release embryo maturation and only apparently dormant ('pseudodormancy').

The embryo is surrounded by various layers of tissues and structures that support and protect it and thus maintain its viability over an extended time that has allowed seed dormancy to evolve (Figure 1). All seeds are exposed to periods of dry air or soil (low water potentials), low or high temperatures and sometimes anoxia, all of which impose environmental dormancy on the seeds. The supra-embryonic layers insulate them from the deleterious effects of these adverse conditions (Lamont & Milberg, 1997). On the other hand, these layers prevent germination even when the external conditions are otherwise suitable, whereas non-dormant seeds germinate once the embryo is moist, aerated and exposed to mild temperatures. The layers wrapped around the embryo represent the biotic maternal environment and are responsible for maintaining inherent dormancy via their physical or physiological properties that are distinct from embryo control (Adkins et al., 2002). The embryo (\pm endosperm) itself forms the biotic internal environment and may possess physiological properties that also control dormancy. Thus, dormancy release requires the breaking of both inherent and environmentally imposed dormancy (Figure 1). A detailed description of these two dormancy classes is as follows.

2.1 | Inherent dormancy

Inherent refers to that class of dormancy where germination cannot commence even if external conditions are otherwise suitable. Physicochemical reasons include (a) the seed is either impermeable to water and/or oxygen; (b) necessary metabolic cofactors are not available, either needing to be provided from the surroundings, such as exudates produced by potential host roots, or internally synthesized in response to external stimuli, such as phytochrome red in response to sunlight; or (c) these cofactors

are prevented from acting by inhibitory chemicals within or surrounding the seed, such as salt in *Atriplex* bracteoles (all described in detail below). It is a genetically based property of the seed (innate/inherited) that requires special conditions to be met before dormancy is broken (Table 1). In the past, this type of dormancy has often been referred to as primary, or simply dormancy with no prefix, but we prefer the more descriptive term, *inherent dormancy*, to distinguish it from the imposed dormancy class, and use this term routinely here.

Inherent dormancy has both direct (proximate) and indirect (ultimate) components: *direct* as properties of the diaspore serve to maintain dormancy in the present, and *indirect* in anticipation of rare, but certain, future conditions when (1) a suitable agent for breaking dormancy will become available and (2) successful germination and seedling establishment are more likely. Dormancy is futile unless it is also coupled with a way of breaking it that increases the seed's fitness. The word 'cue' is often used to describe the agent of release, for example, fire cue, but it is more than just a signal of dormancy change that is the usual meaning of the word, as it also creates the conditions suitable for germination so that 'stimulus' is more apt. The stimuli for inherent dormancy release are varied and are examined further in later sections. Here, we note that they cover periods of extreme diurnal temperatures, momentary fire-type heat and other forms of scarification such as stomach acids, light/dark (photo-period), smoke chemicals, removal from anoxia and leaching out of chemical inhibitors that prevent germination even when ambient conditions are otherwise suitable. These are specific requirements and their absence or deficiency is responsible for the maintenance of inherent dormancy at the species, and even population, level. We now consider the two types of inherent dormancy, physical and physiological.

2.1.1 | Physical dormancy

Physical dormancy is that type of inherent dormancy where the seed coat is impermeable to water and/or oxygen such that metabolism cannot occur and the seed cannot germinate even if hydrothermal

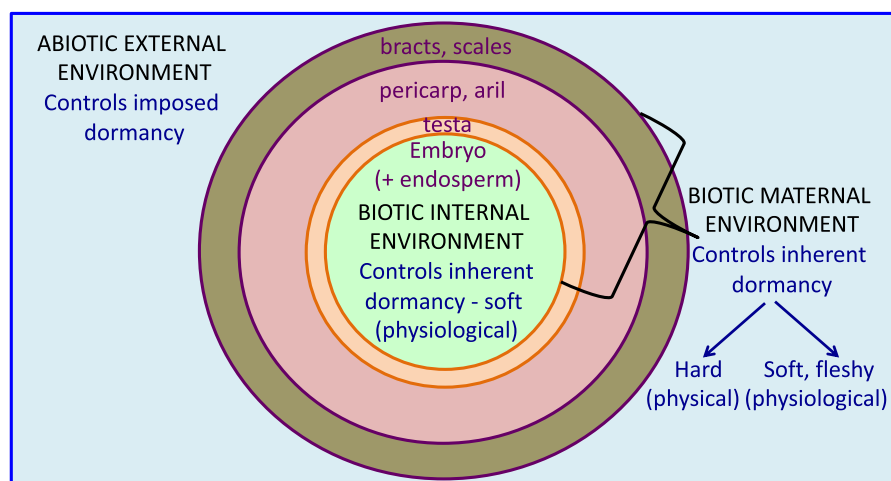


FIGURE 1 Relationship between seed structure and environmental control of dormancy and germination. Note that sometimes mature seeds may remain embedded within the surrounding pericarp, bracts or scales that may prevent interaction with the external environment and thus maintain inherent dormancy. The layers covering the embryo may be hard and impermeable, maintaining physical dormancy, or semipermeable or even fleshy and maintain dormancy through physiological mechanisms.

TABLE 1 Descriptions of the two classes of seed dormancy based on dormancy-maintenance and environmental-release mechanisms. Serotiny is treated as conforming to the inherent-dormancy class. The need for embryo maturation ('morphological dormancy') is excluded from this scheme as its apparent dormancy release is not stimulus dependent.

Dormancy class	Inherent	Imposed
Basis of dormancy	Internal/endogenous—genetic control (structural, physiological)	External/exogenous—abiotic (environmental)
Mechanism of dormancy control	Hard, impermeable/weakly permeable seed coat or cone, embryo bone dry, presence of respiratory inhibitors, need for (activated) cofactors for enzyme production, or inhibitory chemicals stored in the seed, fruit or infructescence, need for host root exudates for endoparasites, need for mycorrhizal fungi (orchids, ericas)	Drought (low water potential), extreme diurnal temperatures, anoxia (waterlogging)
Duration of dormancy	Indefinite (equal to seed longevity) or gradually lost over time (years)	Depends on weather, climate seasonality and substrate
Stimuli that can break dormancy	Heat, warm stratification (dry), dry conditions—branch death (serotiny), smoke/charate chemicals (karrikins, cyanoglycerile, syringaldehyde, NO _x , ethylene), light/dark, rain (leaching), frugivory, seed coat decay agents, moist soil, mild temperatures, aeration, anaerobiosis, leaching out of chemical inhibitors, presence of host root exudates for endoparasites, presence of mycorrhizal fungi	Moist soil (not required by mistletoes), mild temperatures, aeration, light (mistletoes only)
Mechanism of dormancy release	Seed-coat fractured or water gap opened, pericarp ruptured/ cone opens to release seeds, cofactor links to proteins to produce hydrolytic enzymes (hydrolases), inhibitors removed	Respiration and other metabolic processes now enabled as hydrolases activated
Seed-coat permeability	Impermeable to moderately permeable	Moderate to high
Type of dormancy to be broken	Inherent followed by imposed if prevailing at the time (inherent and imposed sometimes broken in rapid succession)	Imposed (inherent already broken or seed lacks inherent dormancy)

conditions are otherwise suitable (Figure 1). Physical dormancy appears to have preceded physiological dormancy historically (Pausas & Lamont, 2022) and there is a high probability that hard seeds were already present in the Rhamnaceae as far back as its estimated crown age of 260 million years ago (He & Lamont, 2022). The sources of physical-dormancy release can be categorized as heat and other stimuli (non-heat).

Heat

The best-known causes of inherent dormancy are hard, impermeable seed coats, usually the testa but sometimes including the dry pericarp fused to the testa (Figure 1). Dormancy is broken when the coat is fractured (scarified) or a special pore is opened (water gap) to enable water and oxygen uptake. It is clear for two widespread clades with physical dormancy (Figure 2) that (a) the water gap is associated with hard seeds consistent with its function and (b) both are a feature of fire-prone biomes in particular, with their relative abundance in surface-fire (savanna) systems somewhat less than in crown-fire (warm temperate) systems, consistent with other aspects of their fire-released dormancy (Pausas & Lamont, 2022). The displacement of the plug (variably corresponding to the pleurogram/ lens/oculus) is a response to heat, although all anatomical studies to date have been based on wet heat as fracturing is stronger than with dry heat for study purposes (Burrows et al., 2018; Erickson, 2015; Gama-Arachchige et al., 2013; Nandi, 1998). Burrows et al. (2018) noted the absence of lens 'popping' among two non-fire-prone acacias when heated, but the structure was retained among another

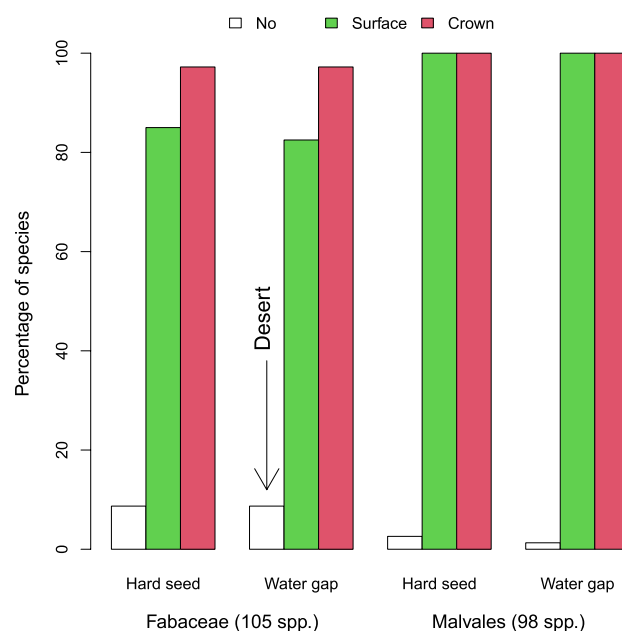


FIGURE 2 Percentage of hard seeds (vs. non-hard seeds) and water-gap-forming structures (vs. their absence) among Fabaceae and Malvales from species in non-fire-prone (usually rainforests with some deserts; $n = 100$ species), surface-fire (grasslands, savannas; $n = 56$) and crown-fire (shrublands, woodlands, forests; $n = 47$) habitats. The association between having hard seeds and a water gap is highly significant ($p < 0.0001$; Chi sq test) for both clades. See Lamont and Pausas (2023) and Data Sources for data and references.

three acacias in desert environments. Perhaps the lens is displaced here in response to summer heat and might still have a function in ensuring rapid response to bouts of rain in deserts (imposed-dormancy release).

Scarification is only relevant to hard seeds that lack the seed-coat structures to produce a water gap and its necessity under natural conditions is usually speculative as comparative empirical studies are few (Baes et al., 2002). Most studies have involved scratching the surface of the seed or applying sulfuric acid and it is seldom as effective in breaking dormancy as dislodgement of the water gap by heat (Bell et al., 1993). While it may be a convenient tool for breaking dormancy in horticulture, we question the ecological significance of studies that use artificial scarification as if it were equivalent to processes that occur in nature without examining any role for fire-type heat (Carta et al., 2022; Wyse & Dickie, 2018; Zhang et al., 2022; Figure 2). Equally, the use of boiling water to simulate fire is also of dubious ecological value as it overestimates its efficacy, although it is a convenient method for showing the operation of the water gap (Burrows et al., 2018).

About 1% of the world's seed-bearing flora is estimated to store mature seeds on the mother plant, called serotiny (Lamont et al., 2020). Its dormancy is usually regarded as environmentally imposed but there is a strong case for treating all cases of seeds stored within their fruits or bracts/scales as inherently dormant. For example, the mother plant has genetic control over the structure of the scale-complex, pericarp and/or testa, which may be hard and impermeable to water and/or air, and thus creates physical dormancy in the woody pericarp of flowering plants or cone of conifers among plant-stored seeds in much the same way as soil-stored seeds (illustrated in Figure S2). No matter how moist, mild or aerated the surrounding conditions are, the seed remains insulated and will not germinate. Serotinous seeds are air dry but whether anoxia also plays a role in maintaining dormancy, as it does in *Leucospermum* (Brits & Manning, 2019), is unknown. Fire-type heat is effective in dormancy release in all cases of hard caryopsis, hard-testa and woody-pericarp/cone-imposed dormancy as the seeds can now absorb water (Figure S2). In the first case, the seed coat fractures (Brits & Manning, 2019); in the second, special tissues are dislodged to form a water gap (Burrows et al., 2018); and in the third, the pericarp splits along special suture lines or the bracts reflex to release the seeds whose entire testa is highly water permeable (Lamont et al., 2020; Lamont, Gómez Barreiro, et al., 2022). However, environmental dormancy may still be imposed as dispersed serotinous seeds usually join the first two in dry soil and all must await the first substantial wet-season rains at mild-cool temperatures before they can begin to germinate.

Other stimuli

Scarification through scratching the surface of the seed coat was noted under 'Heat' above. It is more likely that the seed coat decays over time through physical processes, for example, diurnal temperature fluctuations or saprophytic microbial processes, rather than scratching by sharp soil particles (Zalamea et al., 2015).

More important are ingestion and defecation of dry seeds (Manzano et al., 2005) or fleshy fruits (Cochrane et al., 2005) that are ingested by birds, mammals or reptiles that may break physical dormancy (Renison et al., 2010; Traveset et al., 2001). Digestion appears to scarify certain seeds via acid conditions in the gut, as inorganic acids may be effective in dormancy release among hard seeds by increasing their permeability in several families (Tibugari et al., 2013; Traveset & Verdú, 2002). This raises another possible function of seed dormancy not discussed here: dispersal of dormant seeds away from the parent to potentially more favourable recruitment microsites, which is a form of bet-hedging (Pausas et al., 2022).

2.1.2 | Physiological dormancy

Physiological dormancy is that type of inherent dormancy in which metabolic requirements have yet to be met and germination cannot proceed even if there is no environmentally imposed dormancy. Since the embryo must be capable of metabolic activity for physiological-dormancy release the seed coat must be at least semipermeable to water and, in some cases, to oxygen. It is broken when respiration inhibitors are leached out of the seed, or essential cofactors are received from the surrounds (e.g. strigolactone exuded by the roots of a potential host of the holoparasite, *Striga*; Yoneyama et al., 2010), or their synthesis is induced by a change in the surrounding environment.

Smoke-released dormancy is a type of physiological dormancy that is maintained until chemical byproducts in smoke or ash from the combustion of plant matter combine with specific stored proteins. The protein complex breaks dormancy by catalysing production of hydrolytic enzymes required for initiating metabolic activity (Figure 3)—this dormancy type is somewhat complex and is discussed further under 'Smoke-released dormancy' (below). *Inhibitor-released dormancy* includes chemical inhibitors/osmotica in the berry matrix surrounding tomato-related (Solanaceae) seeds that are annulled once the seed is removed from the fruit (Berry & Bewley, 1992). Sodium chloride, osmotica and/or saponins must be washed from the supporting bracteoles of saltbushes, especially *Atriplex* species (Chenopodiaceae), before release from dormancy is possible (Khan & Ungar, 2000; Muñoz-Rodríguez et al., 2012). The naked embryos (seed coats are absent) in mistletoe (Loranthaceae) berries are embedded in mucilage bearing high levels of dissolved carbon dioxide that enforce dormancy until the seed is removed by frugivorous birds when germination begins immediately in the presence of light (Lamont, 1982).

2.2 | Imposed dormancy

The second class of dormancy is a response to conditions imposed by the external environment that must be annulled and replaced by suitable conditions for the initiation of germination.

1. Dormancy release via radiant heat

Environmental stimulus			Seeds dormant	Dormancy release	Germination promotion (temperature suitable, water adequate)	
Location:	Vegetation	Heat source	Soil	Seed	Embryo/endosperm	Germinant (post-fire)
Combustion Radiant heat Hot summer				Increased perm. Pore opening (water gap), seed coat fracturing and tearing	Enzymes activated Catalytic α/β hydrolases e.g. starch \rightarrow maltose protein \rightarrow amino acids	Embryo growth respiration, metabolism, cell elongation
Hard/(non-hard) seeds { Non-hard seeds			Inherent dormancy	Imposed dormancy	Non-dormant	
				Dry seeds	Moist seeds	
			Dormant	Non-dormant		

2. Dormancy release via smoke chemicals

Environmental stimulus				Seeds dormant	Dormancy release	Germination promotion (temperature suitable, water adequate)	
Location:	Plant matter	Fire	Smoke	Soil	Seed	Embryo/endosperm	Germinant (post-fire)
Substrates: hemicellulose, cellulose Pyrolysis alkylbutenolides?				Transport volatile or in water	Enzymes synthesised KAI2 + MAX2 proteins + karrikins + other cofactors	Enzymes activated Catalytic α/β hydrolases e.g. starch \rightarrow maltose protein \rightarrow amino acids	Embryo growth respiration, metabolism, cell elongation
karrikins (pyranbutenolide)						Non-dormant	
Non-hard seeds					Dry seeds	Moist seeds	
				Dormant	Non-dormant		

3. Dormancy release via sunlight

Environmental stimulus			Seeds dormant	Dormancy release	Germination promotion (temperature suitable, water adequate)	
Location:	Vegetation	Sunlight	Soil	Seed	Embryo/endosperm	Germinant (post-fire)
Long photoperiod Red light			Irradiation	Enzymes synthesised Phytochrome Red converted to Phytochrome Far-red + NOx* + ABA suppression	Enzymes activated Catalytic α/β hydrolases e.g. starch \rightarrow maltose protein \rightarrow amino acids	Embryo growth respiration, metabolism, cell elongation
*can be supplied in smoke or ash Non-hard seeds			Inherent dormancy	Imposed dormancy broken already	Non-dormant	
					Moist seeds	

FIGURE 3 Flow diagrams for examples of dormancy-release pathways in response to three environmental stimuli. Text in blue refers to the process involved, the four coloured columns refer to the sequence of events under each heading to the column. (1) shows how radiant heat is produced via plant-based combustion or sometimes via high summer temperatures (warm stratification) to rupture the seed coat or dislodge the water gap tissues. Once suitable hydrothermal conditions arise, imposed dormancy is broken, gibberellins are produced to catalyse the activation of hydrolytic enzymes to initiate germination. Note that many semipermeable seeds are also heat responsive and inherent dormancy may be broken when they are dry or, among some savanna species, when they have already imbibed. perm. = permeability. This is an example of Pathway 1. (2) shows production of karrikins from the combustion of plant matter, their linkage to other compounds to produce hydrolytic enzymes, possibly via production of gibberellins (inherent-dormancy release), that are activated once hydrothermal conditions are suitable to produce respiratory substrates and initiate cell elongation (imposed-dormancy release). Note that only the first phase is completed if aerosol smoke is applied and the second phase may be delayed for months before the wet seasons starts (Pathway 1), but that the smoke chemicals may only act once they are absorbed in soil water at the start of the wet season (Pathway 3). Adapted from Lamont et al. (2019). (3) shows a species that requires long days to receive sufficient red light to convert phytochrome red to phytochrome far-red to break inherent dormancy in the presence of other cofactors. Note that this is only possible when the seeds are moist and usually under mild temperatures, that is, it depends on prior release from imposed dormancy (Pathway 3).

We refer to this class as *imposed dormancy* as we consider the usual word, secondary, is inappropriate. For example, it may be the only form of dormancy preventing germination among many (otherwise non-dormant) seeds, while it must already be broken before seeds can respond to light, and so cannot be considered secondary in a temporal sense nor minor in a functional sense (Figure 3). Instead, we suggest that the term *secondary dormancy* be reserved for return to the dormant state following the introduction of earlier or new inhibitory conditions that re-impose seed dormancy.

In defining imposed dormancy, it is necessary for there to be agreement on what (standard) conditions are required for dormancy release. It is generally accepted that these cover (1) a supply of sufficient water to ensure full imbibition, (2) moderate temperatures that can maximize embryo growth rate and (3) sufficient oxygen for maximum embryo growth rate (Table 1; see Figure S3 for a field example). In the absence of any of these, dormancy is maintained. The minimum, optimum and maximum levels of these (usually temperature) will also be genetically based, and in that sense creates a link with inherent dormancy. Since these 'cardinal' requirements vary genotypically and phenotypically, there cannot be a general quantitative definition of their levels, only agreement on what the relevant factors are; they are determined by the species and population under consideration (Ghebrehewot et al., 2009). *Dormancy cycling* may occur when seeds that have previously broken inherent or imposed dormancy return to that state (*secondary inherent/imposed dormancy*) following conditions that annul the current dormancy-release state (Baskin & Baskin, 1985). An example is the seasonal cycling of temperatures suitable for germination that cause seeds to drift in and out of imposed dormancy (Mackenzie et al., 2016).

2.3 | Dormancy-release pathways

After examining the sequences under which the two dormancy classes are usually broken we see that they fall into three distinct, but related, dormancy-release pathways (Figure 4). These are now discussed in turn here.

2.3.1 | Inherent-imposed-dormancy-release pathway (1)

Numerous groups of internal and external factors serve to maintain inherent dormancy, whether or not the surrounding environment is moist, aerated and at mild temperatures (Table 1). Inherent dormancy is usually broken while the seed is still in a state of imposed dormancy, for example, fire-type heat (inherent-dormancy release) acting on dry seeds (imposed dormancy maintained) (Figures 1 and 2, Figure S1). But for germination to proceed, imposed dormancy must also be broken at some (later) stage (see Section 2.2). Seeds remain under environmentally-imposed dormancy after inherent-dormancy release but will germinate as soon as suitable hydrothermal conditions prevail. Thus, inherent-dormancy release followed by imposed-dormancy release becomes the *inherent-imposed-dormancy-release pathway* (Pathway 1 in Figure 4).

2.3.2 | Imposed-dormancy-release pathway (2)

Alternatively, many seeds are produced that lack inherent dormancy (non-dormant) but encounter an environment that does not meet their germination requirements on release from the mother plant so that they remain under imposed dormancy (see Section 2.2). Thus, the second pathway involves imposed-dormancy release with no further barriers to germination and defines the *imposed-dormancy-release pathway* (Pathway 2 in Figure 4). [A reviewer suggested that it might be termed pathway 1B as distinct from 1A, but it is simply part B of a possible pathway (A + B). We refer to B as Pathway 2 since it may also apply to inherently non-dormant seeds that do not need to pass through part A].

2.3.3 | Imposed-inherent-dormancy-release pathway (3)

Certain stimuli are only effective in breaking inherent dormancy once imposed dormancy is broken, especially requiring the seed to

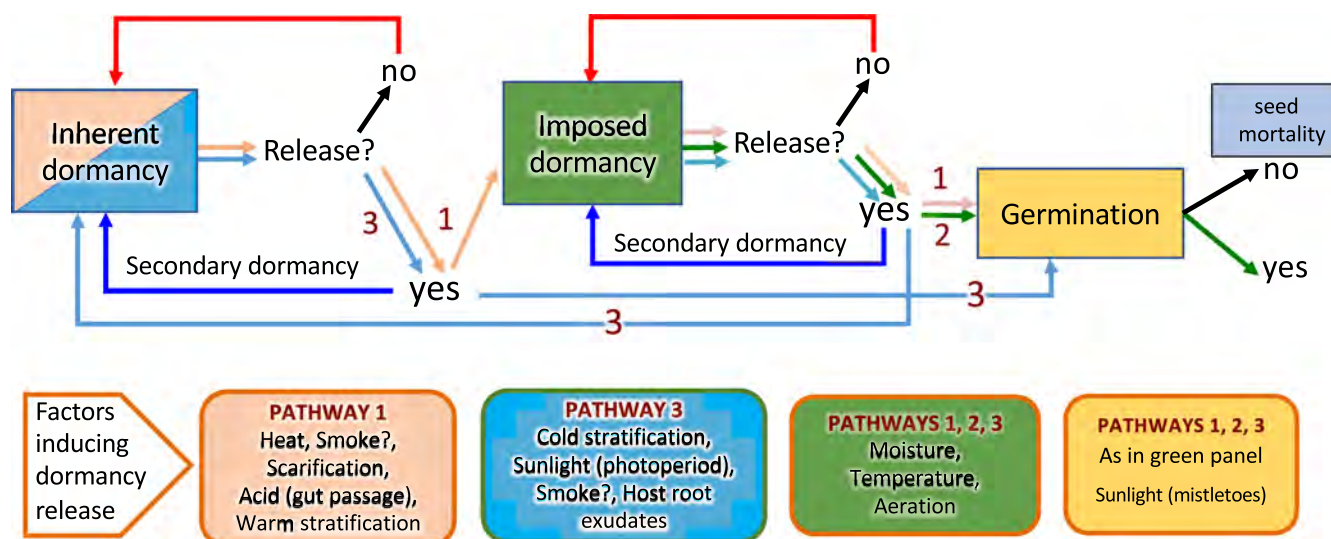


FIGURE 4 In terms of a time sequence, usually (Pathway 1, pink arrows) inherent dormancy is broken first by certain environmental stimuli (pink panels) followed by imposed-dormancy release by a different set of 'standard' stimuli (green panels) and then germination (grey panel). If seeds lack inherent dormancy then only imposed-dormancy release applies (Pathway 2, green arrows). Also common are partial or complete imposed-dormancy release that is required before inherent-dormancy release by quite different environmental stimuli (pale blue panels) is possible (Pathway 3, pale blue arrows). Note how the blue arrows arise from the imposed dormancy panel, move to the inherent dormancy panel, then bypass the imposed dormancy panel to the germination panel, provided prior imposed dormancy-release was complete. Should certain conditions arise before germination has commenced, such as extreme dryness, then seeds may become secondarily dormant (dark blue arrows).

be imbibed and aerated, and sometimes at mild temperatures as well (Table 1; Figure 3). That is, the sequence is critical: in this case, imposed dormancy must be broken *before* inherent-dormancy release is possible. Thus, there is a need to recognize a further category, the *imposed-inherent-dormancy-release pathway* (Pathway 3 in Figure 4). It is that pathway where release from inherent (physiological) dormancy is contingent on prior complete or partial release from imposed dormancy before the seed can germinate.

This pathway applies to light/dark-released, cold-released and host-chemical-released dormancy types in particular. In the past, photoperiod-controlled dormancy has been variously placed under imposed dormancy or considered unrelated to dormancy as it only serves to 'promote' germination of non-dormant seeds (Baskin & Baskin, 2021; Walck et al., 2011). The former interpretation (breaking imposed dormancy) is inappropriate as light is not universally required by seeds to germinate, unlike moisture, mild temperatures and oxygen. For example, light is only beneficial for species with small seeds that signals the seed is near the soil surface (Smith, 2000). In fact, light/dark-released dormancy involves the highly specialized phytochrome-pigment system that oscillates between the red and far-red forms and requires seeds to be imbibed before the pigments are photoreceptive. Inherent dormancy is maintained until the imbibed seed is exposed to a threshold period of dark/light to convert phytochrome FR/R to phytochrome R/FR respectively as a cofactor for initiating metabolic activity via gibberellins (Figure 3; Vleeshouwers et al., 1995). And the latter interpretation (that the seed is non-dormant) is not applicable either, as, even if phytochrome conversion has resulted in production of active gibberellins,

germination may still not occur if imposed-dormancy release was not complete, such as seasonal temperatures are still too low for germination to occur.

Cold-released dormancy is a type of physiological dormancy that is maintained until the seed is exposed to periods of cold (e.g. ~5°C for 2 months) that promotes production of cofactors, such as hydrogen cyanide from cyanoglycosides, required for initiating metabolic activity (Dziewanowska et al., 1979). Since the seed must already be imbibed and aerated for this to occur (i.e. imposed dormancy must be released first) it fits into the third pathway. Other dormancy-release types following this pathway include seeds of endoparasites or spores of mycorrhizal fungi that require certain host-root exudates, such as strigolactones, to break dormancy but must already be under suitable conditions for germination before they can respond (Al-Babili & Bouwmeester, 2015). Since smoke chemicals may be absorbed by both dry and moist seeds, it is unclear at present if the relevant pathway is 1 or 3, but it is certainly not 2 (see Section 3) (Figure 3).

3 | SMOKE-RELEASED DORMANCY

The above considerations lead to the concept of *dormancy syndrome* (Pausas & Lamont, 2022): a correlated suite of traits that is coordinated to maintain (inherent) seed dormancy during storage, execute seed-dormancy release in response to specified environmental stimuli and respond quickly once (imposed) dormancy conditions are removed. Relevant sequences are given in Figures 3 and

5 and Figure S1. In fire-prone ecosystems, there are two dominant syndromes: heat-released dormancy and smoke-released dormancy. Although the significance of smoke-released dormancy was only recognized 30 years ago (de Lange & Boucher, 1990), much is now known about the role of smoke chemicals in promoting germination. It has often been regarded as 'just' a germination cue (Thompson & Ooi, 2013) but Figure 3 shows that it is intimately involved in the biochemistry of dormancy release. Early research was based on aerosol smoke, and some researchers continue to use free smoke, whereas it is now routine to use aqueous smoke (smoke-water). Dry seeds in petri dishes exposed to smoke for a few minutes to hours can absorb chemicals in smoke that promote germination of imbibed seeds later (Keeley & Fotheringham, 1998; Mackenzie et al., 2016; Roche et al., 1997; Figure S3). Smoke-water is often more effective but this may be due to the greater likelihood of seeds absorbing the chemicals as they are taken up with the water solvent during imbibition (Montalvo et al., 2002).

It is possible that inherent dormancy is broken even when the seed is dry as it must be asked how else could the smoke chemicals be retained? Cao et al. (2021) showed that the poorly water-soluble, smoke-derived, dormancy-breaking syringaldehyde was readily adsorbed by seeds of the fire ephemeral, *Nicotiana attenuata* (Solanaceae), and noted that its 'seeds may rapidly sense the smoke cue shortly after wildfires [i.e. break inherent dormancy?] and commence germination immediately when the abiotic...conditions are suitable [i.e. break imposed dormancy]'. Thus, there is a clear two-step process in the action of smoke chemicals (Figure 3.2) but to what extent stage 1 can be undertaken by non-imbibed seeds has yet to be demonstrated (i.e. what exactly does 'seeds...rapidly sense the smoke cue' mean biochemically?).

If an external source of water is required and smoke chemicals only enter with the soil water at the start of the wet season then the two steps may occur in rapid succession, effectively concurrent. If conditions remain unsuitable for germination after smoke-chemical absorption, then dormancy may be further imposed for some months, for example, when winter temperatures are too low (Mackenzie et al., 2016).

Once moist and temperatures are mild, the synthesized enzymes catalyse the degradation of large, stored molecules (starch, fats, proteins) into their monomers that act as substrates for respiration and other metabolic activities. Cell elongation begins in response to the now activated GA₃ and the radicle expands. This is consistent with studies that show karrikins may replace the role of gibberellins in promoting germination (radicle elongation) of seeds once moist (Gardner et al., 2001). These processes need to be separated from the ability of smoke chemicals to *hasten* the rate of germination in some species, just as it may enhance seedling growth (Hodges et al., 2021; Moreira et al., 2010). Here, smoke chemicals simply serve to *supplement* the embryo's supply of hydrolytic enzymes and total germination may not be affected.

Part of the dilemma with terminology in this field of research is that dormancy release is usually regarded as synonymous with germination. The level of germination is used as a surrogate for the extent of dormancy release as direct evidence is only possible if optimal (complete) germination conditions can be created. Even fractures in the seed coat may only be superficial and no guarantee that physical dormancy has been broken (Tran & Cavanagh, 1980). The problem is highlighted in Figure 5. Here, the incubation temperature dictates the extent to which germination reflects actual dormancy release. Since all seeds were previously subjected to karrikin (Merritt

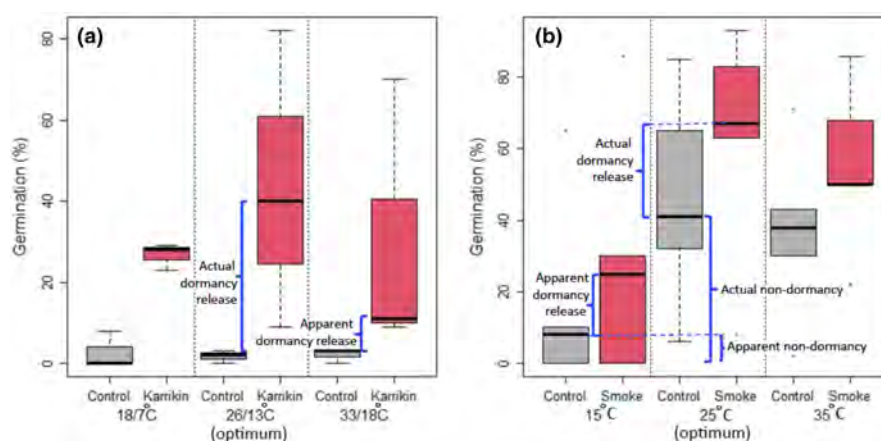


FIGURE 5 Two studies that highlight the potential disparity between level of inherent-dormancy release and level of germination as an index of it, using a range of temperatures for germination following treatment with 0.1 mg/kg karrikin [a, for three daisies (Asteraceae), collated from Merritt et al., 2006] or smoke-water [b, for five smoke-responsive grasses (Poaceae), collated from Ghebrehewot et al., 2009]. Thus, while inherent dormancy is broken in all treatments to some extent, dormancy imposed by the different temperature regimes dictates the extent to which germination reflects this. Seasonal switching from one temperature regime to another leads to the concept of (imposed) dormancy cycling. Note that the fraction of non-dormant seeds will also appear to differ between the temperature treatments so the actual level of inherent dormancy that can be broken by smoke chemicals is best estimated by subtracting the highest level of non-dormancy (controls) from the highest level of germination (smoke response). Estimates of inherent dormancy levels will therefore improve the more temperature regimes that are used per experimental treatment. Boxplots represent the median (horizontal thick line), the first and third quartiles (box), and the 1.5 interquartile range (whiskers). See Lamont and Pausas (2023) and Data Sources for data and references.

et al., 2006) or smoke–water (Ghebrehewot et al., 2009) all have broken inherent dormancy, but this can only be detected under optimal germination conditions (moderate temperatures).

This is another example where the two steps of smoke-chemical action are clearly separated when conditions do not promote germination (high or low temperatures) but they do coincide under optimal conditions (moderate temperatures). Hence, studies need to have taken measures (e.g. using a range of incubation-temperature treatments) to ensure that imposed dormancy has been completely broken when germination is used to quantify inherent dormancy release. As an aside, the same optimal conditions are required to correctly state the initial level of non-dormancy (Figure 5). When the actual (experimentally highest) level of non-dormancy is taken into account, a substantial fraction of dormant seeds is still shown to have been released from inherent dormancy by smoke chemicals. Of course, it is essential that initial seed viability is also considered (Lamont, 2022).

4 | INTERACTIONS BETWEEN DORMANCY-RELEASE STIMULI

We now consider interaction effects between two environmental factors as they control inherent-dormancy release.

4.1 | Heat and smoke interactions

During a fire, seeds are subjected to both heat and smoke so it is of interest to see if, and how, they might interact. There are four types of interactions that should apply to all binary interactions between all environmental stimuli (Table 2). *Type 1*: some seeds lack inherent dormancy and germinate as soon as conditions are

suitable. Soil-stored seeds not responsive to either fire property are by far the minority in fire-prone ecosystems, falling to <5% in some Mediterranean-type regions (Carthy et al., 2018; Enright et al., 2007). By contrast, lack of responses to heat or smoke is a notable feature of serotinous seeds, especially if they are winged, since they are released from their supporting structures after fire (He et al., 2016; Lamont et al., 2020; Newton et al., 2021). We list nine taxa among soil-stored species that germinate in the absence of smoke or heat, including the succulent-fruited Asparagaceae, that resulted from our brief review of worldwide, fire-prone floras (Table S1).

Type 2A: exclusively smoke-responsive seeds have weakly to moderately permeable seed coats (Lamont, Gómez Barreiro, et al., 2022; Moreira et al., 2010). Smoke-released dormancy has been recorded widely among the world's fire-prone floras, especially among graminoids, forbs and woody shrubs (Pausas & Lamont, 2022, Table S1). Here, it is clearly an alternative to fire-type heat in dormancy release that does not enhance germination any further when applied with smoke among the 10 examples given in Table S1. The reverse is true for seeds that are only heat-responsive (*Type 2B*). They appear impermeable initially as there is no smoke response. Alternatively, they may simply not be smoke sensitive as, even when rendered permeable by heat, there is still no smoke response. While the Fabaceae is well known for its abundant species with hard, thick, impermeable seed coats, the presence of the grass, *Bromus berterianus*, is unexpected (Figuerola et al., 2009; Table S1). The few taxa observed in this category compared with the others probably reflect researchers considering it pointless to test for smoke responses among hard-seeded species.

That seeds are not always either smoke- or heat-responsive which is indicated by the next dormancy-release type where the presence of heat and smoke has an additive, even synergistic, effect (*Type 3*). This may reflect the interplay between smoke absorption

TABLE 2 Four dormancy-release types based on individual effects of fire-type heat (H), smoke (S) and additive effects (H + S) on germination compared with the control (C) that can be applied to all fire-prone species. Type 2A/B covers each environmental stimulus interacting with the other to produce different outcomes but they represent the same category (single effect). Notes within parentheses refer to the likely mechanism of dormancy release as supported by relevant literature cited in the text. Seeds whose germination is inhibited by fire-type heat or smoke are excluded from this scheme. Species examples with supporting references are given in Table S1.

Type	Pattern	Description
1	$C = H = S = (H + S)$	No effect. Neither H nor S required for promoting dormancy release (thin seed coat, already highly permeable)
2A	$C = H < S = (H + S)$	Single effect. S, but not H, promotes dormancy release (moderately thick, permeable seed coat—smoke chemical adsorption enables enzyme synthesis, possibly increases permeability)
2B	$C = S < H = (H + S)$	Single effect. H, but not S, promotes dormancy release (thick, impermeable seed coat—now rendered permeable)
3	$C < \max(H, S) < (H + S)$	Additive (or synergic) effect. H and S promote different dormancy-release processes, or contribute to different parts of the same process (moderately thick seed coat—increased permeability to smoke and water, smoke chemical absorption enables enzyme synthesis)
4	$C < (H, S) = (H + S)$	Replacement/non-additive effect. H and S promote dormancy release with no additive effect so must contribute to the same process (both increase permeability to water? See main text)

requiring permeable seed coats, and heat increasing permeability generally. This will promote smoke-chemical absorption, and possibly promote their physiological effect on dormancy release, so enhancing different steps in the germination process. Thus, among 30 species that were smoke and/or heat-responsive, Clarke et al. (2000) recorded seven that were both heat- and smoke-responsive. Since seeds must already be permeable to be smoke-responsive, this means that seeds do not need to be strictly impermeable to respond to heat—presumably heat here serves to make them even more permeable. Six possible relationship types exist between the control, heat and smoke categories that yield lower dormancy release than the combined effect of heat and smoke. Our brief literature search identified examples of all six scenarios (Table S1). In six of the 11 cases documented, the seeds appear to have been impermeable initially such that heat rendered them permeable and this then facilitated later uptake of smoke chemicals. In five cases, smoke (alone) was more effective than heat (alone), indicating that they were already permeable while heat may have increased their permeability, explaining their additive effect when applied together.

A special case of category 3 is where both heat and smoke can release dormancy but the net effect of heat and smoke together is no greater than either of them individually (Type 4). This appears uncommon in nature as we recorded only four species conforming to this category (Table S1). Nevertheless, when a sample of 20 species of *Leucadendron* (Proteaceae) was assessed for its heat and smoke effects, there was a small heat response and a large smoke response that was negligibly increased by heat plus smoke as seed-coat thickness increased (Figure 6). These trends were the opposite of that for

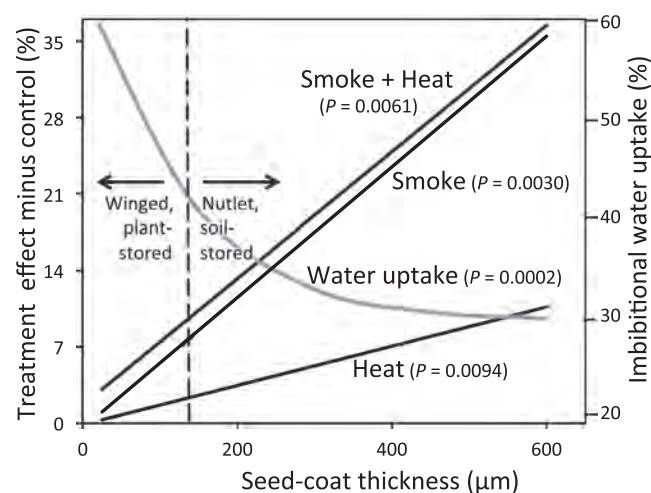


FIGURE 6 Relationship between seed-coat thickness of 20 *Leucadendron* species (Proteaceae) and effect of smoke water, heat (80°C for 20 min) and (smoke plus heat) on germination levels (inherent-dormancy release) compared with the controls, and % imbibition after 24 h. This is an example of type 4 in Table 2. Note the marked enhancing effect of smoke with increasing seed-coat thickness in contrast to heat with no additive effect when both were applied (implying that they contribute to the same process) and that even the thickest seeds (600 μm) were still (semi) permeable. Data available in Newton et al. (2021) and Lamont, Gómez Barreiro, et al. (2022).

imbibitional uptake with increase in seed-coat thickness, although even the seeds with maximum heat response showed limited water permeability. All three treatments had a negligible effect on the thin-walled serotinous seeds (as germination was already ~100%). There was no difference between smoke and heat plus smoke among the thickest-walled nutlets, bringing their germination levels almost up to that of the serotinous species.

The only logical explanation for the lack of an additive effect by heat plus smoke among Type 4 must be that they affect the same dormancy-release process. Since heat is only known to increase seed-coat permeability, it implies that smoke chemicals can (here, must) also be involved in permeability control. In this regard, there is some evidence that karrikins can act as 'aquaporins', increasing the ability of cells to absorb water (Footitt et al., 2019; Ghebrehiwot et al., 2008; Jain et al., 2008). This warrants further investigation as Table S1 and Figure 6 now provide independent support for the existence of such a dormancy-breaking mechanism among smoke chemicals. This is a completely different function than its generally accepted role as a cofactor in the synthesis of catalytic enzymes (Figure 3).

Six other heat-smoke scenarios are given in Table S1 (types 5–10) that we identified in the literature but are rare. For four, the individual effect of heat or smoke is greater than when they are combined that is no greater than the control. This appears maladaptive as the norm in nature is heat plus smoke. Seeds of three appear impermeable as there is only a heat effect that must be inhibited by smoke when they are applied together (as smoke can now be absorbed) to explain how these treatments fall back to the level of the control. For the remaining two, the inhibitory effect of heat or smoke is cancelled by the presence of the other that therefore appears adaptive. But it means that fire does not promote dormancy-release in these species. It may be telling that most examples in the last six categories are associated with savanna and Chilean floras where the seeds of most species are not fire-responsive (Pausas & Lamont, 2022).

4.2 | Interactions between light/dark and smoke

Light sensitivity may be important among seeds of herbs and shrubs in fire-prone woodlands (44%; Clarke et al., 2000), shrublands that rarely burn (36%; Tsuyuzaki & Miyoshi, 2009), weed-dominated herblands (89%; Milberg et al., 2000) and rainforests (49%; Figueroa, 2003) but not among fire-prone trees (5%; Clifford, 1953). Light sensitivity is especially adaptive among small seeds, which is a cue that they are near the soil surface or now exposed to sunlight (Milberg et al., 2000). Here, phytochrome R is gradually converted to phytochrome FR such that daylength becomes critical in breaking inherent dormancy (Vleeshouwers et al., 1995; Figure 3). Some seeds are dark sensitive, which acts as a cue that the seeds are buried. Here, phytochrome FR is converted to the active phytochrome R form to break dormancy, possibly leading to the production of GA₃. Other seeds from a population might be smoke or heat responsive that leads to an additive effect when they are kept in the

dark as well (Keith, 1997 found *Epacris stuartii* germination is greatest with dark + smoke + heat, Table S1). Note that the phytochrome system requires moist, mild conditions to operate (i.e. prior imposed-dormancy release), placing it in Pathway 3 (Figure 4).

For nine studies on the possible interaction between light and smoke (Figure S4), the median germination of the controls was 18%, tripling in the presence of smoke or light, and five times greater in the presence of light plus smoke. Thus, light and smoke have similar effects in promoting germination: smoke can replace the role of light in breaking dormancy but via different dormancy-release mechanisms and without any synergistic effects. Since fire increases light availability, especially in fire-prone forests, the additive effect of smoke and light is clearly adaptive as cues to the onset of suitable conditions for recruitment. Among the myriad of reasons suggested for why seeds in grassland savannas are less fire-responsive than crown-fire-prone vegetation is that light availability is less variable pre- and post-fire in savannas (Pausas & Lamont, 2022). However, some savanna studies cited here show marked light, as well as smoke, responses, indicating that low light may still be limiting recruitment (Leperlier et al., 2018; López-Mársico et al., 2019).

4.3 | Interactions between cold/warm stratification and fire

4.3.1 | Cold stratification

For regions with freezing winters that are also fire-prone in the warm part of the year, seeds might be expected to require both chilling and fire-related pretreatments to yield maximum levels of dormancy release. A strong bout of cold that heralds the onset of warmer growing conditions can be considered a driver of dormancy release via cold stratification, while fire maximizes the opportunities

for recruitment. The five hard-seeded species assessed in Figure 7a occur in uplands subject to low winter temperatures as well as fire but they showed little individual response to fire-type heat followed by cold. However, heat followed by stratification increased germination by a mean of seven times over heat alone. Since cold stratification is a metabolic process, it requires that seeds be kept moist (Section 2.3.2), whereas hard seeds are impermeable so that the synergistic outcome can be explained by heat fracturing the seed coat first, allowing water to enter and thus cold-stimulated respiration to commence (dormancy-release Pathway 1 followed by 3).

The Californian poppy, *Eschscholzia californica*, shows great variation in the elevation of its habitats but they are generally fire-prone. Across the 8 populations studied, smoke is more effective than cold and there is a marked additive effect such that the net germination on average is five times that of the controls (Figure 7b). This implies two processes, with smoke chemicals and cold promoting respiration but in contrasting ways with different seeds in the batch responding to one or the other. As most regions with severe winters rarely burn, few species will have fire-responsive seeds. Thus, Tsuyuzaki and Miyoshi (2009), working in the extreme north of the north island of Japan, recorded 6 species out of 44 that benefitted from cold stratification, none benefitted from heat, the germination of 11 was inhibited by smoke and the rest were non-dormant. In contrast, Clarke et al. (2000) examined 10 species of Fabaceae in fire-prone, upland grassy woodland of northern NSW, Australia, for which germination of eight responded significantly to heat (80°C for 15 min) compared with the controls while all showed no, or an inhibitory, response to chilling (5°C for 1 week). Tavsanoğlu (2011) recorded no effect of cold stratification on *Cistus creticus* in Mediterranean-climate Turkey compared with the nine times greater germination after heat and smoke. Similarly, Huffman (2006) showed that cold stratification did not promote germination of *Ceanothus fendleri* in California in contrast to a pretreatment at 90°C for 10 min. Taylorson (1975)

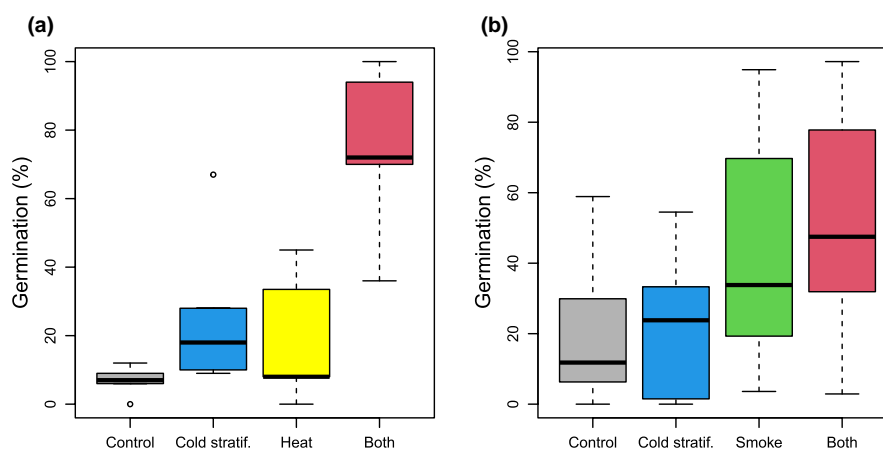


FIGURE 7 Summary of interaction between cold stratification (2 months at 5°C) and fire-related (boiling water) treatments for species that are subject to cold and fire with the fire treatment applied before the cold treatment when subjected to both (as would occur in nature). (a) Five shrub species (*Ceanothus*, *Discaria*, *Lupinus*, *Silphium*) treated with heat in five studies (cited in Data Sources). (b) 8 populations of *Eschscholzia californica* (Montalvo et al., 2002) treated with smoke. Boxplots represent the median (horizontal thick line), the first and third quartiles (box), and the 1.5 interquartile range (whiskers). Stratif., Stratification. Adapted from supplementary information in Pausas and Lamont (2022); see Lamont and Pausas (2023) and Data Sources for data and references.

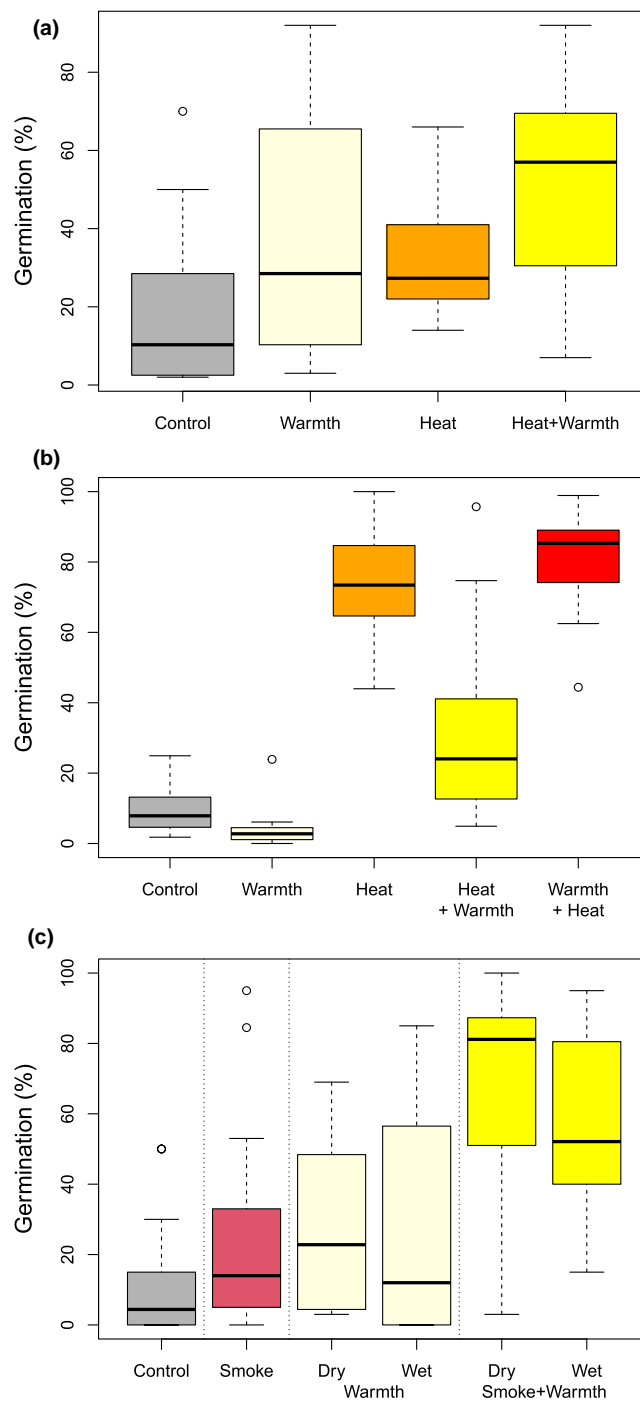
FIGURE 8 Relationship between warm stratification (bouts of summer-type temperatures) and fire (heat or smoke) on germination. (a) Germination of 12 shrub species in South Africa (*Leucadendron*), Spain (*Ulex*), Australia (*Dianella*) and New Zealand (*Pomaderris*) receiving fire-type heat (80–100°C for 10–20 min) and/or warmth [35–40°C (day)/20–40°C (night) for 1–2 months]. Collated from Haines et al. (2007), Zupo et al. (2016), Hodges et al. (2019) and Newton et al. (2021). (b) 12 species of Cistaceae native to the Iberian Peninsula, Spain, following 50/20°C daily for 2 months simulating bare soil after fire (that would require unlikely postfire arrival of the seeds), fire-type heat (100°C for 10 min) without summer heat (equivalent to a late autumn fire just prior to substantial rains), fire-type heat followed by extended summer heat (equivalent to early summer fire), summer heat associated with bare soil (rare) followed by late autumn fire just prior to substantial rains. Collated from Luna (2020) and Lamont, Burrows, et al. (2022). (c) Germination of 21 species of mainly Mediterranean-climate origin in South Africa and Australia following smoke–water treatment, bouts of warmth [35–40°C (day)/20–40°C (night) for 1–2 months] applied to moist seeds (late autumn), smoke plus warmth with seeds moist, bouts of warmth applied to dry seeds (summer) or smoke plus warmth with seeds dry. Note that different species were used for the wet and dry experiments preventing direct comparison. See Lamont and Pausas (2023) and Data Sources for data and references.

reported the imposition of secondary inherent dormancy by light in sorghum following its release by cold stratification perhaps as an adaptive response to the need to be buried in addition to passing through a cold winter.

4.3.2 | Warm stratification

Heat

The exposed surface soil heats up considerably following fire (Lamont, Burrows, et al., 2022). Therefore, if there is a protracted period of imposed dormancy before conditions are suitable for germination, it can be expected that this might have a supplementary role in seed-dormancy release. Four studies that examined the interaction between fire-type heat and warm stratification among 12 species showed minor effects of each but with a marked additive effect on germination, three times that of the control (Figure 8a). However, most studies show little interaction between summer-type and fire-type heat, with collation of 68 taxa germinating at ~10% with summer warmth but ~80% with fire-type heat (Pausas & Lamont, 2022)—here, there was little scope for an additive effect as the heat pulse was so effective (we prefer the term ‘heat pulse’ to the personified synonym, ‘heat shock’). Interestingly, the few savanna species examined did not show a positive heat-pulse response. Unlike most of the other interactions we have outlined here (Table 2), these two stimuli appear to have affected the same process—increasing seed-coat permeability (via scarification) that is the only role for heat that has ever been documented. In that case, it seems to be the sum of the two heat sources that is important in promoting dormancy release. It is worth noting that the fire-type



temperature threshold for dormancy release among two *Cistus* species is greater the warmer the dry season in which it occurs (Zomer et al., 2022). Thus, the minimum heat requirement tracks summer temperatures to maintain a critical interval between the two, confirming that heat release is a specific adaptation to a fire-prone environment.

Warm stratification is not always beneficial in promoting dormancy release. Luna (2020) undertook a novel pair of experiments that involved alternating the order of warmth and fire-type heat (Figure 8b). In all, 12 species of Cistaceae (*Cistus*, *Helianthemum*), native to the Iberian Peninsula, were subjected to 50/20°C daily for

2 months simulating bare soil after fire although, in the field, this would require the unlikely arrival of seeds from an unburnt area that had no effect. The fire-type heat treatment (100°C for 10 min) simulated conditions in late autumn fire just prior to substantial rains resulted in ~80% germination. Seeds were subjected to 50/20°C daily (such a high maximum is only likely to be associated with bare, postfire soil; Lamont, Gómez Barreiro, et al., 2022) before the heat treatment, possibly equivalent to a late autumn fire just prior to substantial rains, that resulted in a similar high level of germination to the heat treatment only. However, when these treatments were reversed, simulating an early summer fire followed by 2 months of warm bare soil, germination fell sharply (Figure 8b). Luna (2020) interpreted this as a type of dormancy cycling, although the concept is usually reserved for seasonal variation in imposed dormancy (Figure 5), with the dormancy-release mechanism involving contact with water. A more likely interpretation is that the seeds returned to dormancy with the ongoing shrinkage of the seeds as they continued to dehydrate (Lamont, Gómez Barreiro, et al., 2022). There is a precedent for such secondary dormancy among other hard-seeded species (Hagon & Ballard, 1970) but it relies on the plug of the water gap returning to its original position, which is not always possible with some hard seeds (Lamont, Gómez Barreiro, et al., 2022).

Smoke

Species whose germination is promoted by smoke are usually omitted from any discussion on the role of summer heat in breaking dormancy, but the six studies undertaken so far show a marked response to both may occur in the same species (Figure 8c). Responses among species treated with smoke and/or summer-type heat varied from essentially due to warm stratification (85% vs. 0% for the control) to essentially due to smoke (95% vs. 2%) but there is usually a marked interaction that is additive ('wet' seeds in Figure 8c) if not synergistic ('dry' seeds in Figure 8c). Under highly seasonal climates, a bout of warmth (summer-autumn) might herald the onset of cool, moist conditions (winter) suitable for germination. In the absence of fire, such annual dormancy-breaking activity (Merritt et al., 2007) would likely be maladaptive if it leads to marked germination in the interfire period when recruitment is unlikely; in practice the effect is not strong. However, the warm conditions used are more likely to prevail only after fire rather than before (Lamont, Burrows, et al., 2022), even though the sequence used in these experiments was to apply the smoke (water) after warm stratification. Either way, in association with fire (smoke), this dual environmental stimulus might prove to be a 'fail-safe' mechanism for promoting successful germination and recruitment.

These studies make it clear that summer warmth and smoke applied individually may alleviate inherent dormancy among some seeds in the batch and many more when applied together. This additive/synergistic effect can be envisaged as summer heat increasing seed-coat permeability and allowing greater smoke-chemical absorption following the first substantial rains and causing more seeds to break inherent dormancy. If that is so, then there should be no need for the seeds to be imbibed for successful warm stratification

since dry seeds will be adequate, as shown here (Figure 8c). However, Ma et al. (2020) noted that *Anigozanthos flavidus* (Haemodoraceae), included here, is considered to have morphophysiological dormancy. Their overall results show that the smoke chemical, glyceronitrile, is as effective as an extended period of wet warmth in breaking dormancy and that there is no additive effect (all averaging 85%–88%). This means that both stimuli must have affected the same process (Table 2) and the most likely explanation is that glyceronitrile promoted respiration of the non-dormant embryo and thus embryo growth equivalent to that occurring during warm stratification. This is then a case of a smoke chemical hastening the rate of growth of non-dormant embryos, rather than breaking dormancy as such, a phenomenon now well established (Hodges et al., 2019).

5 | SEASON-FIRE INTERACTIONS

Fire creates conditions that promote greatest release from inherent dormancy: interactions between heat, smoke, sunlight and/or temperature extremes peak as the blackened soil surface increases exposure to light and solar insolation and reradiation (Table S9 in Pausas & Lamont, 2022). Non-fire-related environmental stimuli are most effective in promoting germination when they work together with fire-related stimuli, not just because they activate most seeds but because, as we show here, they invariably have an additive effect (Figures 7, 8 and S5). Imposed dormancy is finally overcome as rain can now reach the mineral soil where the seeds are stored and any inhibitory compounds, such as polyphenolics, in the litter have been volatilized (He & Lamont, 2018). Timing of germination varies between (1) immediately after fire if the soil is moist (autumn) and (2) delays of 3–8 months over the dry summer until autumn-winter when the rains return and conditions are suitable for germination and imposed dormancy is annulled. Should rain be insufficient or temperatures above average (the 'greenhouse' effect), many seeds will remain dormant, leading to secondary imposed dormancy of 15 months or more, and even dormancy cycling. Seeds with greater drought tolerances or temperature thresholds might still germinate (Zomer et al., 2022) but their germinants are less likely to become recruits.

6 | RESEARCH NEEDS

The incentive for this review was the comment by a colleague that 'smoke does not break dormancy, it only promotes germination', a belief that can be traced to Thompson and Ooi (2013). This immediately raises questions about the limitations of language in conveying concepts—what do 'break dormancy' and 'promote germination' actually mean? And why would seed biologists see the need to distinguish what, to many, would appear to be synonyms? We show here that, in fact, promoting germination is shorthand for breaking two dormancy classes that involve quite different environmental stimuli and chemical pathways, and are therefore worth distinguishing.

Thus, the challenges for future research on smoke-related germination include: (a) resolving whether seeds must be imbibed before inherent dormancy can be broken by smoke chemicals (Pathway 3); (b) if so, how is it that dry seeds exposed to aerosol smoke before imbibition may germinate as well as those already imbibed (Pathway 1, Figure 4)?; and (c) corroborating the current evidence that karrikins can act as 'aquaporins', increasing the ability of cells to absorb water (Footitt et al., 2019; Ghebrehiwot et al., 2008; Jain et al., 2008; Table S1; Figure 6), to explain how smoke and heat may sometimes have a non-additive, replacement effect.

Other research needs cover (1) testing to what extent recognizing our third dormancy-release pathway is helpful in understanding seed-dormancy release in relation to cold and light; (2) accepting that only moisture, temperature and aeration are relevant to controlling imposed dormancy (contrast Walck et al., 2011); and (3) demonstrating to what extent seeds may re-enter inherent or imposed dormancy (and accepting that the term secondary dormancy should be confined to this phenomenon, which also implies accepting inherent and imposed terminology, or similar, rather than primary and secondary). A better understanding of secondary dormancy will require investigating the dynamics of the water gap among hard seeds (Lamont, Burrows, et al., 2022).

In conducting experiments designed to identify optimal conditions for breaking seed dormancy, researchers need to decide whether their approach is as a horticulturalist or ecologist. Scratching the seed surface, soaking in sulfuric acid (although this might simulate gut passage effects if that is likely) or using wet heat are relevant to the former but are no substitute for fire-type heat as required by the latter. When compared, their outcomes are rarely the same (Erickson, 2015; Melo Junior & De Andrade, 2019). Among non-fire-prone floras, it is seldom clear what environmental stimuli were responsible for the occasional bout of germination (bet-hedging), but it is more likely to be disturbance or exceptional climatic events rather than predictable climatic conditions, even if strongly seasonal (see Section 5 above, Pausas et al., 2022). Scratching and acid treatments may aim to simulate decay processes during soil storage but their effect in the soil is usually exaggerated (Zalamea et al., 2015). On the other hand, soil-storage experiments rarely last more than 12 months (Downes et al., 2015) that inadequately simulates decay processes. And, even then, seeking explanations for any change in dormancy, for example, showing that storage has led to increased permeability, are not undertaken so that a mechanistic explanation is not possible: it is often vaguely described as 'after-ripening' (Merritt et al., 2007).

Despite claims to the contrary, we question the ecological value of studies designed using crude surrogates for stochastic natural processes but are interpreted as satisfying them (Carta et al., 2022; Wyse & Dickie, 2018; Zhang et al., 2022). In particular, mean seasonal variation in rainfall and temperature give few reliable cues to inter-annual variability in growing conditions (Cowling et al., 2005) and ignore the occurrence of key dormancy-disrupting disturbances such as floods, heat waves, plagues of frugivores or granivores, or fire (Pausas et al., 2022). Our hope is that this review prompts new

research directed at ecologically realistic treatments and explanations of the mechanisms that maintain and break seed dormancy, and that takes into account the importance of interactive effects between environmental stimuli and the order in which they are applied.

7 | CONCLUSIONS

1. The two classes of seed dormancy can be overcome through three dormancy-release pathways: the first is controlled by the seed or parent plant (inherent dormancy) followed by the surrounding environment (imposed dormancy) both of which must be overcome before germination is possible (Pathway 1); the second is controlled just by the surrounding environment (imposed) that is broken by a change to standard conditions (Pathway 2); and the third requires prior (at least partial) imposed-dormancy release before inherent-dormancy release by a different set of environmental conditions is possible (Pathway 3).

2. According to these definitions, sunlight, diurnal temperature extremes (stratification), fire-type heat and other sources of scarification, smoke chemicals, certain root exudates, removal of stored metabolic inhibitors through leaching, gut passage and release from internally caused anoxia, may break inherent dormancy, whereas standard conditions of adequate moisture (high water potential), cool-moderate daily temperatures and aeration break environmentally imposed dormancy. Whether smoke chemicals break inherent dormancy while dry (Pathway 1) or only once moist (Pathway 3) is unclear at present.

3. On-plant stored (serotinous) and frugivorous seeds are recognized here as conforming with the requirements for physical dormancy, as all their functional traits are consistent with those of hard diaspores.

4. We suggest reserving the term secondary dormancy for seeds that return to inherent or imposed dormancy following a change in environmental conditions. Some seeds cannot return to secondary inherent dormancy as the physical or physiological change is permanent.

5. Under seasonal climates, seeds may oscillate between imposed and non-dormancy as the temperature fluctuates even though inherent dormancy has been broken (secondary imposed-dormancy cycling).

6. Heat may promote germination of non-hard (as well as hard) seeds, as it may increase their permeability further.

7. Warm stratification does not require seeds to be moist before it can occur but, as with wet heat, it may be more effective—it can be viewed as just a form of mild heat applied over an extended period.

8. There may be multiple co-acting stimuli for breaking inherent dormancy, usually affecting different processes (additive or synergistic effect). Two environmental stimuli that individually break dormancy but have no additive effect must be affecting the same process. This appears rare and was demonstrated here for the interaction between heat and smoke—the most likely interpretation is that they both served to increase seed permeability to water.

9. Positive interaction effects between fire-type heat and summer stratification, and between smoke and cold stratification, heat or sunlight on inherent dormancy, and the intense expression of imposed dormancy, are especially notable in strongly seasonal, temperate climates.

AUTHOR CONTRIBUTIONS

Byron B. Lamont conceived the project, reviewed the literature, prepared the tables and most of the figures, and wrote the first draft. Juli G. Pausas edited numerous drafts, refined concepts, prepared the remaining figures and collated the on-line data.

ACKNOWLEDGEMENTS

We thank colleagues and cited researchers who created the empirical background that enabled us to think through some of the key issues about seed dormancy unimpeded by previous interpretations, Jon Keeley for sharing ideas and the reviewers for their helpful comments on the manuscript. JGPs contribution to this study was undertaken within the framework of the FocScales projects (PROMETEO/2021/040; Generalitat Valenciana) while BBL is supported by a Curtin University of Technology pension. Open access publishing facilitated by Curtin University, as part of the Wiley - Curtin University agreement via the Council of Australian University Librarians.

CONFLICTS OF INTEREST

We declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data compiled for this paper are available in Dryad Digital Repository at <https://doi.org/10.5061/dryad.c59zw3rcd> (Lamont & Pausas, 2023). Also see Data Sources.

ORCID

Byron B. Lamont  <https://orcid.org/0000-0001-9279-7149>

Juli G. Pausas  <https://orcid.org/0000-0003-3533-5786>

REFERENCES

- Adkins, S. W., Bellairs, S. M., & Loch, D. S. (2002). Seed dormancy mechanisms in warm season grass species. *Euphytica*, 126(1), 13–20.
- Al-Babili, S., & Bouwmeester, H. J. (2015). Strigolactones, a novel carotenoid-derived plant hormone. *Annual Review of Plant Biology*, 66(1), 161–186. <https://doi.org/10.1146/annurev-arplant-043014-114759>
- Baes, P. O., de Viana, M. L., & Sühling, S. (2002). Germination in *Prosopis ferox* seeds: Effects of mechanical, chemical and biological scarifiers. *Journal of Arid Environments*, 50(1), 185–189. <https://doi.org/10.1006/jare.2001.0859>
- Baskin, J. M., & Baskin, C. C. (1985). The annual dormancy cycle in buried weed seeds: A continuum. *BioScience*, 35(8), 492–498. <https://doi.org/10.2307/1309817>
- Baskin, J. M., & Baskin, C. C. (2021). The great diversity in kinds of seed dormancy: A revision of the Nikolaeva–Baskin classification system for primary seed dormancy. *Seed Science Research*, 31(4), 249–277. <https://doi.org/10.1017/S096025852100026X>
- Bell, D. T., Plummer, J. A., & Taylor, S. K. (1993). Seed germination ecology in southwestern Western Australia. *The Botanical Review*, 59, 24–73. <https://doi.org/10.1007/BF02856612>
- Berry, T., & Bewley, J. D. (1992). A role for the surrounding fruit tissues in preventing the germination of tomato (*Lycopersicon esculentum*) seeds 1: A consideration of the osmotic environment and abscisic acid. *Plant Physiology*, 100(2), 951–957. <https://doi.org/10.1104/pp.100.2.951>
- Brits, G. J., & Manning, J. C. (2019). Seed structure and physiology in relation to recruitment ecology in *Leucospermum* (Proteaceae) in fynbos. *Australian Journal of Botany*, 67(4), 290–308. <https://doi.org/10.1071/BT18199>
- Burrows, G. E., Alden, R., & Robinson, W. A. (2018). The lens in focus—Lens structure in seeds of 51 Australian *acacia* species and its implications for imbibition and germination. *Australian Journal of Botany*, 66(5), 398–413. <https://doi.org/10.1071/BT17239>
- Cao, D., Schöttner, M., Halitschke, R., Li, D., Baldwin, G., Rocha, C., & Baldwin, I. T. (2021). Syringaldehyde is a novel smoke-derived germination cue for the native fire-chasing tobacco, *Nicotiana attenuata*. *Seed Science Research*, 31(4), 292–299. <https://doi.org/10.1017/S0960258521000271>
- Carta, A., Fernández-Pascual, E., Gioria, M., Müller, J. V., Rivièrè, S., Rosbakh, S., Saatkamp, A., Vandelook, F., & Mattana, E. (2022). Climate shapes the seed germination niche of temperate flowering plants: A meta-analysis of European seed conservation data. *Annals of Botany*, 129(7), 775–786. <https://doi.org/10.1093/aob/mcac037>
- Carthey, A. J. R., Tims, A., Geedicke, I., & Leishman, M. R. (2018). Broad-scale patterns in smoke-responsive germination from the south-eastern Australian flora. *Journal of Vegetation Science*, 29(4), 737–745. <https://doi.org/10.1111/jvs.12657>
- Clarke, P. J., Davison, E. A., & Fulloon, L. (2000). Germination and dormancy of grassy woodland and forest species: Effects of smoke, heat, darkness and cold. *Australian Journal of Botany*, 48(6), 687–699. <https://doi.org/10.1071/bt99077>
- Clifford, H. T. (1953). A note on the germination of *eucalyptus* seed. *Australian Forestry*, 17, 17–20.
- Cochrane, J., Friend, J., & Hill, S. (2005). Endozoochory and the Australian bluebell: Consumption of *Billardiera fusiformis* (Labill.) Payer (Pittosporaceae) seeds by three mammal species at two peoples bay nature reserve, Western Australia. *Journal of the Royal Society of Western Australia*, 88, 191.
- Considine, M. J., & Considine, J. A. (2016). On the language and physiology of dormancy and quiescence in plants. *Journal of Experimental Botany*, 67(11), 3189–3203. <https://doi.org/10.1093/jxb/erw138>
- Cowling, R. M., Ojeda, F., Lamont, B. B., Rundel, P. W., & Lechmere-Oertel, R. (2005). Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. *Global Ecology and Biogeography*, 14(6), 509–519.
- de Lange, J. H., & Boucher, C. (1990). Autoecological studies on *Audouinia capitata* (Bruniaceae). I. Plant-derived smoke as a seed germination cue. *South African Journal of Botany*, 56, 700–703.
- Downes, K. S., Light, M. E., Pošta, M., & van Staden, J. (2015). Fire-related cues and the germination of eight *Conostylis* (Haemodoraceae) taxa, when freshly collected, after burial and after laboratory storage. *Seed Science Research*, 25(3), 286–298. <https://doi.org/10.1017/S0960258515000227>
- Dziewanowska, K., Niedzwiedz, I., & Lewak, S. (1979). Hydrogen cyanide and cyanogenic compounds in seeds. III: Degradation of cyanogenic glucosides during apple seed stratification. *Physiologie Vegetale*, 17, 297–303.
- Enright, N. J., Mosner, E., Miller, B. P., Johnson, N., & Lamont, B. B. (2007). Soil versus canopy seed storage and plant species coexistence in species-rich shrublands of southwestern Australia. *Ecology*, 88, 2292–2304. <https://doi.org/10.1890/06-1343.1>

- Erickson, T. E. (2015). *Seed dormancy and germination traits of 89 arid zone species targeted for mine-site restoration in the Pilbara region of Western Australia* (PhD thesis). University of Western Australia. https://research-repository.uwa.edu.au/files/5293910/Erickson_Todd_2015.pdf
- Figueroa, J. A. (2003). Seed germination in temperate rain forest species of southern Chile: Chilling and gap-dependency germination. *Plant Ecology*, 166(2), 227–240. <https://doi.org/10.1023/A:1023286521721>
- Figueroa, J. A., Cavieres, L. A., Gómez-González, S., Montenegro, M. M., & Jaksic, F. M. (2009). Do heat and smoke increase emergence of exotic and native plants in the matorral of Central Chile? *Acta Oecologica*, 35(2), 335–340. <https://doi.org/10.1016/j.actao.2008.12.004>
- Footitt, S., Clewes, R., Feeney, M., Finch-Savage, W. E., & Frigerio, L. (2019). Aquaporins influence seed dormancy and germination in response to stress. *Plant, Cell & Environment*, 42(8), 2325–2339. <https://doi.org/10.1111/pce.13561>
- Gama-Arachchige, N. S., Baskin, J. M., Geneve, R. L., & Baskin, C. C. (2013). Identification and characterization of ten new water gaps in seeds and fruits with physical dormancy and classification of water-gap complexes. *Annals of Botany*, 112(1), 69–84. <https://doi.org/10.1093/aob/mct094>
- Gardner, M. J., Dalling, K. J., Light, M. E., Jäger, A. K., & van Staden, J. (2001). Does smoke substitute for red light in the germination of light-sensitive lettuce seeds by affecting gibberellin metabolism? *South African Journal of Botany*, 67(4), 636–640. [https://doi.org/10.1016/S0254-6299\(15\)31194-7](https://doi.org/10.1016/S0254-6299(15)31194-7)
- Ghebrehewot, H. M., Kulkarni, M. G., Kirkman, K. P., & Van Staden, J. (2008). Smoke-water and a smoke-isolated butenolide improve germination and seedling vigour of *Eragrostis Tef* (Zucc.) trotter under high temperature and low osmotic potential. *Journal of Agronomy and Crop Science*, 194(4), 270–277.
- Ghebrehewot, H. M., Kulkarni, M. G., Kirkman, K. P., & Van Staden, J. (2009). Smoke solutions and temperature influence the germination and seedling growth of south African Mesic grassland species. *Rangeland Ecology & Management*, 62(6), 572–578.
- Gioria, M., Pyšek, P., Baskin, C. C., & Carta, A. (2020). Phylogenetic relatedness mediates persistence and density of soil seed banks. *Journal of Ecology*, 108(5), 2121–2131. <https://doi.org/10.1111/1365-2745.13437>
- Hagon, M. W., & Ballard, L. A. T. (1970). Reversibility of strophilolar permeability to water in seeds of subterranean clover (*Trifolium subterraneum* L.). *Australian Journal of Biological Sciences*, 23, 519–528.
- Haines, L., Ennis, I. L., Blanchon, D. J., & Triggs, C. M. (2007). Propagating the pale-flowered kumarahou (*Pomaderris hamiltonii*) and kumarahou (*Pomaderris kumeraho*) from seeds. *New Zealand Journal of Botany*, 45(1), 91–100. <https://doi.org/10.1080/00288250709509706>
- He, T., Belcher, C. M., Lamont, B. B., & Lim, S. L. (2016). A 350-million-year legacy of fire adaptation among conifers. *Journal of Ecology*, 104, 352–363. <https://doi.org/10.1111/1365-2745.12513>
- He, T., & Lamont, B. B. (2018). Fire as a potent mutagenic agent among plants. *Critical Reviews in Plant Sciences*, 37(1), 1–14. <https://doi.org/10.1080/07352689.2018.1453981>
- He, T., & Lamont, B. B. (2022). Ancient Rhamnaceae flowers impute an origin for flowering plants exceeding 250-million-years ago. *IScience*, 25(7), 104642. <https://doi.org/10.1016/j.isci.2022.104642>
- Hodges, J. A., Price, J. N., Nicotra, A. B., Neeman, T., & Guja, L. K. (2021). Smoke and heat accelerate and increase germination in fire-prone temperate grassy ecosystems. *Ecosphere*, 12(12), e03851. <https://doi.org/10.1002/ecs2.3851>
- Huffman, D. W. (2006). Production, losses, and germination of *Ceanothus fendleri* seeds in an Arizona Ponderosa pine forest. *Western North American Naturalist*, 66(3), 365–373. [https://doi.org/10.3398/1527-0904\(2006\)66\[365:PLAGOC\]2.0.CO;2](https://doi.org/10.3398/1527-0904(2006)66[365:PLAGOC]2.0.CO;2)
- Jain, N., Ascough, G. D., & Van Staden, J. (2008). A smoke-derived butenolide alleviates HgCl₂ and ZnCl₂ inhibition of water uptake during germination and subsequent growth of tomato—Possible involvement of aquaporins. *Journal of Plant Physiology*, 165(13), 1422–1427. <https://doi.org/10.1016/j.jplph.2008.04.017>
- Keeley, J. E., & Fotheringham, C. J. (1998). Smoke-induced seed germination in California chaparral. *Ecology*, 79(7), 2320–2336. [https://doi.org/10.1890/0012-9658\(1998\)079\[2320:SISGIC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2320:SISGIC]2.0.CO;2)
- Keith, D. A. (1997). Combined effects of heat shock, smoke and darkness on germination of *epacris stuartii* Stapf., an endangered fire-prone Australian shrub. *Oecologia*, 112(3), 340–344.
- Khan, M. A., & Ungar, I. A. (2000). Alleviation of innate and salinity-induced dormancy in *Atriplex griffithii* Moq. var. *stocksii* Boiss. *Seed Science and Technology*, 28(1), 29–37.
- Lamont, B. B. (1982). Gas content of berries of the Australian mistletoe *Amyema preissii* and the effect of maturity, viscin, temperature and carbon dioxide on germination. *Journal of Experimental Botany*, 33(4), 790–798. <https://doi.org/10.1093/jxb/33.4.790>
- Lamont, B. B. (2022). Seed biologists beware: Estimates of initial viability based on ungerminated seeds at the end of an experiment may be error-prone. *Plant Biology*, 24, 399–403. <https://doi.org/10.1111/plb.13407>
- Lamont, B., & Pausas, J. (2023). Data from: Seed dormancy revisited: Dormancy-release pathways and environmental interactions [Dataset]. Dryad, <https://doi.org/10.5061/dryad.c59zw3rcd>
- Lamont, B. B., Burrows, G. E., & Korczynskij, D. (2022). High summer temperatures do not interact with fire to promote germination among seeds of Cistaceae: A reinterpretation of Luna (2020) with extra data on wet/dry conditions. *Plant Ecology*, 223, 141–149. <https://doi.org/10.1007/s11258-021-01172-y>
- Lamont, B. B., Gómez Barreiro, P., & Newton, R. J. (2022). Seed-coat thickness explains contrasting germination responses to smoke and heat in *Leucadendron*. *Seed Science Research*, 32, 70–77. <https://doi.org/10.1017/S0960258522000113>
- Lamont, B. B., He, T., & Yan, Z. (2019). Evolutionary history of fire-stimulated resprouting, flowering, seed release and germination. *Biological Reviews*, 94, 903–928. <https://doi.org/10.1111/brv.12483>
- Lamont, B. B., & Milberg, P. (1997). Removal of the testa during germination or establishment increases germinant mortality, decay and water loss. *Seed Science Research*, 7(3), 245–252. <https://doi.org/10.1017/S0960258500003597>
- Lamont, B. B., Pausas, J. G., He, T., Witkowski, E. T. F., & Hanley, M. E. (2020). Fire as a selective agent for both serotiny and nonserotiny over space and time. *Critical Reviews in Plant Sciences*, 39(2), 140–172. <https://doi.org/10.1080/07352689.2020.1768465>
- Leperlier, C., Riviere, J.-N. E., Allibert, A., Dessauw, D., Lacroix, S., & Fock-Bastide, I. (2018). Overcoming dormancy and light requirements in seeds of *Heteropogon contortus*, a target species for savanna restoration. *Ecological Engineering*, 122, 10–15. <https://doi.org/10.1016/j.ecoleng.2018.07.017>
- López-Mársico, L., Fariás-Moreira, L., Lezama, F., Altesor, A., & Rodríguez, C. (2019). Light intensity triggers different germination responses to fire-related cues in temperate grassland species. *Folia Geobotanica*, 54(1), 53–63. <https://doi.org/10.1007/s12224-019-09336-5>
- Luna, B. (2020). Fire and summer temperatures work together breaking physical seed dormancy. *Scientific Reports*, 10(1), 6031. <https://doi.org/10.1038/s41598-020-62909-9>
- Ma, H., Erickson, T. E., Walck, J. L., Merritt, D. J., Ma, H., Erickson, T. E., Walck, J. L., & Merritt, D. J. (2020). Interpopulation variation in germination response to fire-related cues and after-ripening in seeds of the evergreen perennial *Anigozanthos flavidus* (Haemodoraceae). *International Journal of Wildland Fire*, 29(10), 950–960. <https://doi.org/10.1071/WF19195>
- Mackenzie, B. D. E., Auld, T. D., Keith, D. A., Hui, F. K. C., & Ooi, M. K. J. (2016). The effect of seasonal ambient temperatures on fire-stimulated germination of species with physiological dormancy: A case study using *Boronia* (Rutaceae). *PLoS ONE*, 11(5), e0156142. <https://doi.org/10.1371/journal.pone.0156142>

- Manzano, P., Malo, J. E., & Peco, B. (2005). Sheep gut passage and survival of Mediterranean shrub seeds. *Seed Science Research*, 15(1), 21–28. <https://doi.org/10.1079/SSR2004192>
- Melo Junior, J. L. A., & De Andrade, J. L. (2019). *Morfometria, germinação e armazenamento de sementes* de Colubrina glandulosa Perkins (Ph.D. thesis). Universidade Federal de Alagoas. <http://www.repositorio.ufal.br/handle/riufal/6717>
- Merritt, D., Kristiansen, M., Flematti, G., Turner, S., Ghisalberti, E., Trengove, R., & Dixon, K. (2006). Effects of a butenolide present in smoke on light-mediated germination of Australian Asteraceae. *Seed Science Research*, 16(1), 29–36.
- Merritt, D. J., Turner, S. R., Clarke, S., & Dixon, K. W. (2007). Seed dormancy and germination stimulation syndromes for Australian temperate species. *Australian Journal of Botany*, 55, 336–344. <https://doi.org/10.1071/BT06106>
- Milberg, P., Andersson, L., & Thompson, K. (2000). Large-seeded spices are less dependent on light for germination than small-seeded ones. *Seed Science Research*, 10(1), 99–104. <https://doi.org/10.1017/S0960258500000118>
- Montalvo, A. M., Feist-Alvey, L. J., & Koehler, C. E. (2002). The effect of fire and cold treatments on seed germination of annual and perennial populations of *Eschscholzia californica* (Papaveraceae) in Southern California. *Madroño*, 49(4), 207–227.
- Moreira, B., Tormo, J., Estrelles, E., & Pausas, J. G. (2010). Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. *Annals of Botany*, 105(4), 627–635. <https://doi.org/10.1093/aob/mcq017>
- Muñoz-Rodríguez, A. F., Rodríguez-Rubio, P., Nieva, F. J., Fernández-Illescas, F., Sánchez-Gullón, E., Soto, J. M., Hermoso-López, V., & Márquez-García, B. (2012). The importance of bracteoles in ensuring Atriplex halimus germination under optimal conditions. *Fresenius Environmental Bulletin*, 21, 3521–3526.
- Nandi, O. I. (1998). Ovule and seed anatomy of Cistaceae and related Malvaceae. *Plant Systematics and Evolution*, 209(3/4), 239–264. 2.
- Newton, R. J., Mackenzie, B. D. E., Lamont, B. B., Gomez-Barreiro, P., Cowling, R. M., & He, T. (2021). Fire-mediated germination syndromes in *Leucadendron* (Proteaceae) and their functional correlates. *Oecologia*, 196, 589–604. <https://doi.org/10.1007/s00442-021-04947-2>
- Pausas, J. G., & Lamont, B. B. (2022). Fire-released seed dormancy—A global synthesis. *Biological Reviews*, 97(1612–1639), 1612–1639. <https://doi.org/10.1111/brv.12855>
- Pausas, J. G., Lamont, B. B., Keeley, J. E., & Bond, W. J. (2022). Bet-hedging and best-bet strategies shape seed dormancy. *New Phytologist*, 236, 1232–1236. <https://doi.org/10.1111/nph.18436>
- Renison, D., Valladares, G., & Martella, M. B. (2010). The effect of passage through the gut of the greater Rhea (*Rhea americana*) on germination of tree seeds: Implications for forest restoration. *Emu—Australian Ornithology*, 110(2), 125–131. <https://doi.org/10.1071/MU09090>
- Roche, S., Dixon, K. W., & Pate, J. S. (1997). Seed ageing and smoke: Partner cues in the amelioration of seed dormancy in selected Australian native species. *Australian Journal of Botany*, 45(5), 783–815. <https://doi.org/10.1071/bt96099>
- Rohde, A., & Bhalerao, R. P. (2007). Plant dormancy in the perennial context. *Trends in Plant Science*, 12, 217–223. <https://doi.org/10.1016/j.tplants.2007.03.012>
- Smith, H. (2000). Phytochromes and light signal perception by plants—An emerging synthesis. *Nature*, 407(6804), 585–591. <https://doi.org/10.1038/35036500>
- Tavsanoglu, C. (2011). Fire-related cues (heat shock and smoke) and seed germination in a *Cistus creticus* population in southwestern Turkey. *Ekoloji*, 20(79), 99–104. <https://doi.org/10.5053/ekoloji.2011.7913>
- Taylorson, R. B. (1975). Inhibition of Prechill-induced dark germination in *Sorghum halepense* (L.) Pers. seeds by Phytochrome transformations. *Plant Physiology*, 55(6), 1093–1097. <https://doi.org/10.1104/pp.55.6.1093>
- Thompson, K., & Ooi, M. K. J. (2013). Germination and dormancy breaking: Two different things. *Seed Science Research*, 23(1), 1. <https://doi.org/10.1017/S0960258512000190>
- Tibugari, H., Kaundura, F., & Mandumbu, R. (2013). Berchemia discolor response to different scarification methods. *J. Agric. Tech*, 9(7), 1927–1935.
- Tran, V. N., & Cavanagh, A. K. (1980). Taxonomic implications of fracture load and deformation histograms and the effects of treatments on the impermeable seed coat of acacia species. *Australian Journal of Botany*, 28(1), 39–51. <https://doi.org/10.1071/bt9800039>
- Traveset, A., Riera, N., & Mas, R. E. (2001). Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology*, 15, 669–675.
- Traveset, A., & Verdú, M. (2002). A meta-analysis of the effect of gut treatment on seed germination. In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed dispersal and Frugivory: Ecology, evolution and conservation* (pp. 339–350). CAB International.
- Tsuyuzaki, S., & Miyoshi, C. (2009). Effects of smoke, heat, darkness and cold stratification on seed germination of 40 species in a cool temperate zone in northern Japan. *Plant Biology*, 11(3), 369–378. <https://doi.org/10.1111/j.1438-8677.2008.00136.x>
- Vleeshouwers, L. M., Bouwmeester, H. J., & Karssen, C. M. (1995). Redefining seed dormancy: An attempt to integrate physiology and ecology. *Journal of Ecology*, 83, 1031–1037.
- Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K., & Poschlod, P. (2011). Climate change and plant regeneration from seed. *Global Change Biology*, 17(6), 2145–2161. <https://doi.org/10.1111/j.1365-2486.2010.02368.x>
- Wyse, S. V., & Dickie, J. B. (2018). Ecological correlates of seed dormancy differ among dormancy types: A case study in the legumes. *New Phytologist*, 217(2), 477–479. <https://doi.org/10.1111/nph.14777>
- Yoneyama, K., Awad, A. A., Xie, X., Yoneyama, K., & Takeuchi, Y. (2010). Strigolactones as germination stimulants for root parasitic plants. *Plant and Cell Physiology*, 51(7), 1095–1103. <https://doi.org/10.1093/pcp/pcq055>
- Zalamea, P.-C., Sarmiento, C., Arnold, A. E., Davis, A. S., & Dalling, J. W. (2015). Do soil microbes and abrasion by soil particles influence persistence and loss of physical dormancy in seeds of tropical pioneers? *Frontiers in Plant Science*, 5, 799. <https://doi.org/10.3389/fpls.2014.00799>
- Zhang, Y., Liu, Y., Sun, L., Baskin, C. C., Baskin, J. M., Cao, M., & Yang, J. (2022). Seed dormancy in space and time: Global distribution, paleo- and present climatic drivers and evolutionary adaptations. *New Phytologist*, 234, 1770–1781. <https://doi.org/10.1111/nph.18099>
- Zomer, M., Moreira, B., & Pausas, J. G. (2022). Fire and summer temperatures interact to shape seed dormancy thresholds. *Annals of Botany*, 129(7), 809–816. <https://doi.org/10.1093/aob/mcac047>
- Zupo, T., Baeza, M. J., & Fidelis, A. (2016). The effect of simulated heat-shock and daily temperature fluctuations on seed germination of four species from fire-prone ecosystems. *Acta Botânica Brasilica*, 30(3), 514–519. <https://doi.org/10.1590/0102-33062016abb0246>

DATA SOURCES

Additional references used in **Figures 2, 7a** and **8c**, **Figure S5** and **Table S1**.

Figure 2

- Ademoh, F. O., Muoghalu, J. I., & Onwumere, B. (2017). Temporal pattern of tree community dynamics in a secondary forest in southwestern Nigeria, 29 years after a ground fire. *Global Ecology and Conservation*, 9, 148–170. <https://doi.org/10.1016/j.gecco.2016.11.005>
- Arianoutsou, M., Diamantopoulou, J., & Margaris, N. S. (1980). Fire behaviour of *Ceratonia siliqua*. *Portugaliae Acta Biologica. Série A*, XVI(1–4), 67–74.

- Burrows, G. E., Alden, R., & Robinson, W. A. (2018b). The lens in focus—Lens structure in seeds of 51 Australian *Acacia* species and its implications for imbibition and germination. *Australian Journal of Botany*, 66(5), 398–413. <https://doi.org/10.1071/BT17239>
- Corral, R., Pita, J. M., & Pérez-García, F. (1990). Some aspects of seed germination in four species of *Cistus* L. *Seed Science and Technology*, 18(2), 321–325.
- Cruz, E. D., Queiroz, R. J. B., & de Carvalho, J. E. U. (2009). Métodos para superação da dormência em sementes de *Dinizia excelsa* Ducke. *Revista Brasileira de Sementes*, 31, 152–159. <https://doi.org/10.1590/S0101-31222009000400018>
- Dell, B. (1980). Structure and Function of the Strophilar Plug in Seeds of *Albizia lophantha*. *American Journal of Botany*, 67(4), 556–563. <https://doi.org/10.1002/j.1537-2197.1980.tb07684.x>
- Doran, J. C., & Gunn, B. V. (1986). *Treatments to promote Seed germination in Australian Acacias*. Proceedings of an International Workshop Held at the Forest Training Centre, 4–7 August 1986.
- Erickson, T. E. (2015b). *Seed dormancy and germination traits of 89 arid zone species targeted for mine-site restoration in the Pilbara region of Western Australia* (PhD thesis). University of Western Australia. https://research-repository.uwa.edu.au/files/5293910/Erickson_Todd_2015.pdf
- Erickson, T. E., Merritt, D. J., & Turner, S. R. (2016). Overcoming physical seed dormancy in priority native species for use in arid-zone restoration programs. *Australian Journal of Botany*, 64, 401–416. <https://doi.org/10.1071/BT16059>
- Gama-Arachchige, N. S., Baskin, J. M., Geneve, R. L., & Baskin, C. C. (2013b). Identification and characterization of ten new water gaps in seeds and fruits with physical dormancy and classification of water-gap complexes. *Annals of Botany*, 112(1), 69–84. <https://doi.org/10.1093/aob/mct094>
- Gashaw, M., & Michelsen, A. (2002). Influence of heat shock on seed germination of plants from regularly burnt savanna woodlands and grasslands in Ethiopia. *Plant Ecology*, 159, 83–93.
- Gunn, C. R. (1984). *Fruits and seeds of genera in the subfamily Mimosoideae (Fabaceae)* (Technical Bulletin No. 1681). US Department of Agriculture. <https://ageconsearch.umn.edu/record/157649/files/tb1681.pdf>
- Iroko, O. A., Rufal, S. O., & Wahab, W. T. (2021). Effect of Seed Size and Different Pretreatment Methods on Germination of *Albizia zygia* (DC.) J. F. Macbr. *Journal of Applied Sciences and Environmental Management*, 25(5), 815–818. <https://doi.org/10.4314/jasem.v25i5.19>
- Luckow, M., Fortunato, R. H., Sede, S., & Livshultz, T. (2005). The phylogenetic affinities of two mysterious monotypic mimosoids from Southern South America. *Systematic Botany*, 30(3), 585–602. <https://doi.org/10.1600/0363644054782206>
- Nandi, O. I. (1998b). Ovule and seed anatomy of Cistaceae and related Malvaceae. *Plant Systematics and Evolution*, 209(3/4), 239–264.
- Odjegba, E. E., Bankole, A. O., Sadiq, A. Y., Busari, I. O., & Layi-Adigun, B. O. (2021). Rapid assessment of the water chemistry of public water supply in Abeokuta, SouthWest Nigeria. *Journal of Applied Sciences and Environmental Management*, 25(5), Article 5. <https://doi.org/10.4314/jasem.v25i5.1>
- Pritchard, H. W., Haye, A. J., Wright, W. J., & Steadman, K. J. (1995). A comparative study of seed viability in *Inga* species: desiccation tolerance in relation to the physical characteristics and chemical composition of the embryo. *Seed Science and Technology*, 23, 85–100.
- Sajeevukumar, B., Sudhakara, K., Ashokan, P. K., & Gopikumar, K. (1995). Seed dormancy and germination in *Albizia falcata* and *Albizia procera*. *Journal of Tropical Forest Science*, 7(3), 371–382.
- Thompson, P. B. (1998). Seed physiology. In S. Appanah & J. M. Turnbull (Eds.), *Dipterocarps: Taxonomy, ecology and silviculture* (pp. 57–72). Center International Forestry Research.
- Ullah, F., Ahmad, M., Zafar, M., Jabeen, A., Sultana, S., Ghani, A., Luqman, M., Nazish, M., & Alam, F. (2019). Macromorphological and micromorphological seed features of selected taxa of Caesalpiniaceae using light and scanning electron microscopy. *Microscopy Research and Technique*, 82(7), 1073–1082. <https://doi.org/10.1002/jemt.23255>
- www.tropical.ferns.info/viewtropical.php?id=Archidendron+vaillantii,tropicalbotany.wordpress.com/December29,2013/inga-seeds-and-their-preparation-for-sowing

Figure 7

- Coates, F. (1996). *Ecological and biogeographical correlates of rarity in two narrow endemics in Tasmania: Spyridium microphyllum* (F. Muell. Ex Reisseck) Druce and *Spyridium obcordatum* (Hook. F.) W.M. Curtis (Ph.D. thesis). University of Tasmania.
- Kaye, T. N., & Kuykendall, K. (2001). Effects of scarification and cold stratification on seed germination of *Lupinus sulphureus* ssp. *Kincaidii*. *Seed Science and Technology*, 29(3), 663–668.

- McClain, K. (2016a). *Seed germination requirements for four fire-recruiter chaparral shrubs* [Senior Honours Projects 91]. John Carroll University. <http://collected.jcu.edu/honorspapers/91>
- Schramm, P., & Johnson, R. (1981). *Seed conditioning and germination of New Jersey tea* (*Ceanothus americanus*; *Rhamnaceae*). Proceedings of the 6th North American Prairie Conference, 15, 222–226.
- Stuurwold, J. E. (1972). *The effects of moist-heat treatments and stratification on germination of prairie plant seeds* (Honours thesis). Western Michigan University. https://scholarworks.wmich.edu/honors_theses/255

Figure 8c

- Baker, K. S., Steadman, K. J., Plummer, J. A., Merritt, D. J., & Dixon, K. W. (2005). Dormancy release in Australian fire ephemeral seeds during burial increases germination response to smoke water or heat. *Seed Science Research*, 15, 339–348.
- Hodges, J. A., Price, J. N., Nimmo, D. G., & Guja, L. K. (2019). Evidence for direct effects of fire-cues on germination of some perennial forbs common in grassy ecosystems. *Austral Ecology*, 44(7), 1271–1284. <https://doi.org/10.1111/aec.12806>
- Ma, H., Erickson, T. E., Walck, J. L., Merritt, D. J., Ma, H., Erickson, T. E., Walck, J. L., & Merritt, D. J. (2020b). Interpopulation variation in germination response to fire-related cues and after-ripening in seeds of the evergreen perennial *Anigozanthos flavidus* (Haemodoraceae). *International Journal of Wildland Fire*, 29(10), 950–960. <https://doi.org/10.1071/WF19195>
- McClain, K. (2016b). *Seed germination requirements for four fire-recruiter chaparral shrubs* [Senior Honours/Honors Projects 91]. John Carroll University. <http://collected.jcu.edu/honorspapers/91>
- Merritt, D. J., Turner, S. R., Clarke, S., & Dixon, K. W. (2007a). Seed dormancy and germination stimulation syndromes for Australian temperate species. *Australian Journal of Botany*, 55(3), 336–344. <https://doi.org/10.1071/BT06106>
- Newton, R. J., Mackenzie, B. D. E., Lamont, B. B., Gómez-Barreiro, P., Cowling, R. M., & He, T. (2021b). Fire-mediated germination syndromes in *Leucadendron* (Proteaceae) and their ecological correlates. *Oecologia*, 196, 589–604. <https://doi.org/10.1007/s00442-021-04947-2>
- Tieu, A., Dixon, K. W., Meney, K. A., & Sivasithamparan, K. (2001). The interaction of heat and smoke in the release of seed dormancy in seven species from southwestern Western Australia. *Annals of Botany*, 88, 259–265.

Figure 5S

- Afolayan, A. J., Meyer, J. J. M., & Leeuwener, D. V. (1997). Germination in *Helichrysum aureonitens* (Asteraceae): Effects of temperature, light, gibberellic acid, scarification and smoke extract. *South African Journal of Botany*, 63(1), 22–24. [https://doi.org/10.1016/S0254-6299\(15\)30687-6](https://doi.org/10.1016/S0254-6299(15)30687-6)
- Brown, N. A. C., & van Staden, J. (1997). Smoke as a germination cue: A review. *Plant Growth Regulation*, 22, 115–124.
- Clarke, P. J., Davison, E. A., & Fulloon, L. (2000b). Germination and dormancy of grassy woodland and forest species: Effects of smoke, heat, darkness and cold. *Australian Journal of Botany*, 48(6), 687–699. <https://doi.org/10.1071/bt99077>
- Collette, J. C., & Ooi, M. K. J. (2017). Germination ecology of the endangered species *Asterolasia buxifolia* (Rutaceae): Smoke response depends on season and light. *Australian Journal of Botany*, 65, 283–291. <https://doi.org/10.1071/BT17025>
- Keeley, J. E., & Fotheringham, C. J. (1998b). Smoke-induced seed germination in California chaparral. *Ecology*, 79(7), 2320–2336. [https://doi.org/10.1890/0012-9658\(1998\)079\[2320:SISGIC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2320:SISGIC]2.0.CO;2)
- Lepelier, C., Riviere, J.-N. E., Allibert, A., Dessauw, D., Lacroix, S., & Fock-Bastide, I. (2018b). Overcoming dormancy and light requirements in seeds of *Heteropogon contortus*, a target species for savanna restoration. *Ecological Engineering*, 122, 10–15. <https://doi.org/10.1016/j.ecoleng.2018.07.017>
- López-Mársico, L., Fariás-Moreira, L., Lezama, F., Altesor, A., & Rodríguez, C. (2019b). Light intensity triggers different germination responses to fire-related cues in temperate grassland species. *Folia Geobotanica*, 54(1), 53–63. <https://doi.org/10.1007/s12224-019-09336-5>
- Merritt, D. J., Turner, S. R., Clarke, S., & Dixon, K. W. (2007b). Seed dormancy and germination stimulation syndromes for Australian temperate species. *Australian Journal of Botany*, 55(3), 336–344. <https://doi.org/10.1071/BT06106>
- Ramos, D. M., Valls, J. F. M., Borghetti, F., & Ooi, M. K. J. (2019). Fire cues trigger germination and stimulate seedling growth of grass species from Brazilian savannas. *American Journal of Botany*, 106(9), 1190–1201. <https://doi.org/10.1002/ajb2.1345>

Table S1

- Abella, S. R. A. R., Springer, J. D. S. D., & Covington, W. W. C. W. (2007). Seed banks of an Arizona *Pinus ponderosa* landscape: Responses to environmental gradients and fire cues. *Canadian Journal of Forest Research*, 37(3), 552–567. <https://doi.org/10.1139/X06-255>
- Clarke, S., & French, K. (2005). Germination response to heat and smoke of 22 Poaceae species from grassy woodlands. *Australian Journal of Botany*, 53(5), 445–454. <https://doi.org/10.1071/BT04017>
- Fernandes, A. F., Oki, Y., Fernandes, G. W., & Moreira, B. (2020). The effect of fire on seed germination of campo rupestre species in the South American Cerrado. *Plant Ecology*, 222, 45–55. <https://doi.org/10.1007/s11258-020-01086-1>
- Figuerola, J. A., & Cavieres, L. A. (2012). The effect of heat and smoke on the emergence of exotic and native seedlings in a Mediterranean fire-free matorral of central Chile. *Revista Chilena de Historia Natural*, 85(1), 101–111.
- Figuerola, J. A., Cavieres, L. A., Gómez-González, S., Montenegro, M. M., & Jaksic, F. M. (2009b). Do heat and smoke increase emergence of exotic and native plants in the matorral of central Chile? *Acta Oecologica*, 35(2), 335–340. <https://doi.org/10.1016/j.actao.2008.12.004>
- Ghebrehewot, H., Kulkarni, M., Kirkman, K., & Van Staden, J. (2012). Smoke and heat: Influence on seedling emergence from the germinable soil seed bank of mesic grassland in South Africa. *Plant Growth Regulation*, 66(2), 119–127. <https://doi.org/10.1007/s10725-011-9635-5>
- Montalvo, A. M., Feist-Alvey, L. J., & Koehler, C. E. (2002b). The effect of fire and cold treatments on seed germination of annual and perennial populations of *Eschscholzia californica* (Papaveraceae) in Southern California. *Madroño*, 49(4), 207–227.
- Moreira, B., & Pausas, J. G. (2012). Tanned or burned: The role of fire in shaping physical seed dormancy. *PLoS ONE*, 7(12), e51523. <https://doi.org/10.1371/journal.pone.0051523>
- Thomas, P. B., Morris, E. C., & Auld, T. D. (2003). Interactive effects of heat shock and smoke on germination of nine species forming soil seed banks within the Sydney region. *Austral Ecology*, 28(6), 674–683.
- Williams, P. R., Congdon, R. A., Grice, A. C., & Clarke, P. J. (2003). Fire-related cues break seed dormancy of six legumes of tropical eucalypt savannas in north-eastern Australia. *Austral Ecology*, 28, 507–514.

Zirondi, H. L., Silveira, F. A. O., & Fidelis, A. (2019). Fire effects on seed germination: Heat shock and smoke on permeable vs impermeable seed coats. *Flora*, 253, 98–106. <https://doi.org/10.1016/j.flora.2019.03.007>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Flow diagram with details on environmental constraints operating at various steps in the three dormancy-release pathways.

Figure S2. Comparison of typical structure and mechanism of dormancy release of hard diaspores versus serotinous seeds.

Figure S3. Monthly means for variables related to breaking inherent and imposed dormancy of species in the Mediterranean Basin.

Figure S4. Studies that show aerosol (dry) smoke may be as effective as aqueous (wet) smoke in breaking inherent dormancy.

Figure S5. Interaction between smoke and light on seed germination.

Table S1. Taxonomic examples of the various seed-dormancy types in relation to their release by fire-type heat and/or smoke plus additive effects.

How to cite this article: Lamont, B. B., & Pausas, J. G. (2023). Seed dormancy revisited: Dormancy-release pathways and environmental interactions. *Functional Ecology*, 37, 1106–1125. <https://doi.org/10.1111/1365-2435.14269>