

RESEARCH OPINION

Are wildfires an adapted ecological cue breaking physical dormancy in the Mediterranean basin?

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Abstract

Many studies have claimed that fire acts as the chief ecological factor cueing dormancy break in seeds with a water-impermeable seed coat, i.e. physical dormancy (PY), in Mediterranean ecosystems. However, a proposal is made that seasonal temperature changes must be viewed as more meaningful dormancy-breaking cues because: (1) fire is erratic and may break PY in seasons during which seedlings cannot complete their life cycle; (2) fire may not occur for long periods, thereby only providing an opportunity for dormancy break and germination once in every several years; and (3) if fire opens the specialized anatomical structures called 'water gaps', in seconds, their evolutionary role of detecting environmental conditions becomes irrational. Although fire breaks dormancy in a proportion of seeds, given the risk of seed mortality and the post-fire environment providing cues for dormancy break, it is suggested that fire might possibly be an exaptation.

Keywords: adaptation, dry heat, exaptation, germination timing, high temperature, post-fire environment, seasonal temperature, water-impermeable seed coat, water gap

Physical dormancy (PY) in seeds is caused by a water-impermeable seed coat, which develops at the final stage of maturation drying, due to the palisade layer of lignified Malpighian cells (Rolston, 1978; Baskin *et al.*, 2000; Baskin and Baskin, 2004; Baskin and Baskin, 2014). In the many genera belonging to the 18 angiosperm families that are known to produce PY

seeds, the impermeable nature of the seed coat does not allow the seeds to germinate until a range of environmental conditions is present, including high summer temperature, temperature fluctuations, freeze–thaw cycle, low temperature and a fire-opened specialized region of seeds called a 'water gap', which serves as the water entry point (Baskin *et al.*, 2000; Baskin and Baskin, 2014). However, PY can also be broken by non-natural treatments such as acid scarification, mechanical scarification, dry and wet heat (e.g. 100°C), radiation, pricking, nicking of the seed coat, etc. (reviewed in Rolston, 1978; Baskin and Baskin, 2014). After breaking of PY, seeds eventually begin to germinate, provided that the embryo does not have any physiological dormancy (PD). Seeds with both PY and PD have combinational dormancy (PY + PD) (*sensu* Baskin and Baskin, 2004) and germination of these species in natural environments is delayed until both forms of dormancy have been alleviated (Baskin and Baskin, 2014). However, unlike seeds with PD, which can cycle between dormant and non-dormant states several times before germination, once the impermeable seed coat is made permeable to water, the PY seeds cannot become impermeable again (Baskin and Baskin, 2014).

Fire has been claimed to act as the chief ecological factor breaking PY in species adapted to the Mediterranean ecosystem (Moreira and Pausas, 2012). Such claims are generally supported by studies showing that there is a surge of germination following fire events in the natural environment, and empirical treatment of PY seeds with temperatures equivalent to those of fire (*c.* >80°C), resulting in dormancy break (see below). However, consideration of fire as an ecological cue, breaking PY, needs some refinement from an evolutionary and ecological perspective. The purpose of this opinion paper is to suggest that seasonal temperatures are more meaningful dormancy-breaking signals in PY species than fire *per se*, which might possibly be an exaptation, i.e. a shift in the

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function of a trait during evolution (for a full explanation of the term, see Bradshaw *et al.*, 2011).

Information available on the role of fire in breaking PY comes mainly from the following categories of studies: (1) direct field observation of germination of PY species following fire (Christensen and Muller, 1975; Walters *et al.*, 2004; Auld and Denham, 2006); (2) subjecting PY seeds to artificial fire in soil (Mucunguzi and Oryem-Origa, 1996; Walters *et al.*, 2004); and (3) treating PY species with simulated fire temperature in the laboratory, mostly dry heat (Rincker, 1954; Martin *et al.*, 1975; Mallik and Gimingham, 1985; Thanos and Georghiou, 1988; Hodgkinson and Oxley, 1990; Auld and O'Connell, 1991; Herranz *et al.*, 1998; Gashaw and Michelsen, 2002; Williams *et al.*, 2003; Ooi *et al.*, 2014). Based on these studies, it is clear that temperatures ranging from 80 to 200°C, for a duration of 30 s to 60 min, may alleviate PY in a majority of – but not all – species, although the optimum temperature and duration resulting in dormancy loss is species specific. Furthermore, there is a consensus that fire increases the soil temperature to levels required for breaking PY in the top layer of soil of the Mediterranean ecosystem (Auld and O'Connell, 1991; Bradstock and Auld, 1995) and that the seeds of many species become non-dormant following fire (Floyd, 1966; Keeley and Fotheringham, 2000).

However, the temperature during prolonged fire may be considerably higher at the soil surface (e.g. 0–2 cm), which may kill seeds (Auld, 1986; Herranz *et al.*, 2000), or very low at depths (e.g. >5 cm), having negligible effects on dormancy break (Auld and Denham, 2006). Thus, it seems likely that seeds persisting at a depth of approximately 2–5 cm tend to benefit from fire. Nonetheless, a less intense or a short fire may play an important role in safely breaking dormancy of seeds found at the soil surface (0–2 cm). The length and intensity of fire in natural environments, and the soil temperature during burning, may be determined by several factors, including location, soil type, fuel availability, season, wind, fire-free intervals and severity of fire (reviewed in Keeley *et al.*, 2011a). It has been observed routinely that temperatures as high as 150°C on the burning soil surface are common, and could break dormancy effectively in many species of Fabaceae (Herranz *et al.*, 1998), Malvaceae (Chawan, 1971) and Cistaceae (Thanos and Georghiou, 1988; Herranz *et al.*, 2000) only if the duration was <1 min, whereas longer exposure completely killed all the species. More frequently, seeds also experience a less intense, but very long, burning in the Mediterranean climate. These conditions, killing seeds, have also been clearly described for a variety of species (Hodgkinson and Oxley, 1990; Keeley, 1991; Auld and O'Connell, 1991; Doussi and Thanos, 1994; Rivas *et al.*, 2006).

Because loss of PY in seeds subjected to temperatures equivalent to fire in the laboratory is straightforward, compared to the longer and highly specific summer- or fluctuating temperatures required, many workers have been tempted to conclude that fire is the most important factor breaking PY. For example, Moreira and Pausas (2012) showed that fire conditions simulated by heating PY seeds of *Fumana thymifolia*, *Cistus salvifolius*, *C. albidus*, *C. parviflorus*, *C. creticus* and *Ulex parviflorus* at 100°C, 120°C or 150°C for 5 min, broke dormancy in all the species tested, whereas treatments simulating summer conditions (30 daily cycles of 3 h at 31°C, 4 h at 43°C, 3 h at 33°C and 14 h at 18°C) only improved germination in *U. parviflorus*. Thus, those authors concluded: 'despite the fact that some species with physical seed dormancy in fire-prone ecosystems may have a fraction of seeds with fire-independent germination, our results support the hypothesis that temperature thresholds that break physical dormancy are better explained as a response to fire than as a response to the summer temperatures'. Similarly, Ooi *et al.* (2014) have conducted an intriguing study that compared the fire-related temperatures with summer conditions in the Mediterranean basin of south-eastern Australia. Of the 14 PY species tested in their study, six species did not release dormancy unless the temperature was 100°C for 10 min, but similar durations at 60°C and 80°C reduced dormancy in four species each. All the species that required 100°C remained dormant when incubated at summer conditions of 55/20°C for 30 d, but species that had overcome dormancy at 60°C and 80°C exhibited significant improvement in germination under summer conditions. However, these studies have overlooked the fact that the summer seasons in a Mediterranean environment last longer than 1 month (Baeza and Roy, 2008; Santana *et al.*, 2012; Ana Rey, pers. comm.). Evidence is growing that PY break under Mediterranean summer conditions, not only by high summer temperatures but also by fluctuating temperatures, occurs only after 1 month (see below).

The same might be said for the studies comparing the loss of PY in seeds treated at different temperatures, ranging from 20°C to 150°C, for a duration of less than 1 h only (Cushwa *et al.*, 1968; Auld and O'Connell, 1991; Tarrega *et al.*, 1992; Herranz *et al.*, 1998, 2000; Gashaw and Michelsen, 2002; Rivas *et al.*, 2006; Moreira *et al.*, 2010). As one might expect, depending on the species, only temperatures above 80°C broke dormancy effectively. At temperatures below 80°C only very few species overcame dormancy. Thus, these studies must be viewed from the standpoint of unravelling the temperature, and duration required at higher temperature, to break dormancy, instead of whether or not lower temperatures can alleviate dormancy in 1 h, because there is no way that seeds exposed to 40–70°C are relieved from dormancy,

as such a trait would reduce the fitness of plants in their natural environment.

To date, only little attention has been directed towards understanding PY loss in Mediterranean species under ecologically relevant conditions. Many Australian PY species belonging to the Fabaceae became non-dormant between 15 and 75°C in a few months if the temperature fluctuated by at least 15°C, with fewer cycles needed at higher temperature (Quinlivan, 1961, 1966, 1968). Likewise, impermeability of the seed coat of nine tropical coastal sand-dune legumes collected from Mexico was lost during incubation at 20°C diurnal fluctuation, but only after 45 d (Moreno-Casasola *et al.*, 1994). Seeds of many Fabaceae species growing in New South Wales decreased their dormancy under fluctuating temperatures, but the degree of fluctuation required was species specific (Lodge *et al.*, 1990). In the case of *Malva parviflora* collected in an Australian Mediterranean environment, seeds became permeable within 3 months when stored at a fluctuating temperature of 50/20°C, but seeds stored at a constant temperature of 37°C remained dormant after 2 years (Michael *et al.*, 2006). An important point relevant in the context of the breaking of PY by fluctuating temperature is that the requirement for a 15°C temperature fluctuation does not mean that seeds subjected to these cycles for a shorter length of time may also effectively break dormancy, indicating that the temperature duration prevalent in the environment is required. In *Trifolium subterraneum*, for example, seeds exposed to daily fluctuations of 20/54°C broke dormancy within 3 months, but fluctuations of 23/60°C with cycle lengths lasting only for 15 min to 1 h failed to break dormancy (Hagon, 1971), indicating that environmental conditions guide dormancy loss.

Even less is known about the role of high summer temperatures in breaking PY of Mediterranean species. However, evidence exists to suggest that high summer temperatures make the seed coat permeable to water. For example, seeds of *T. subterraneum* collected from a Mediterranean environment of Australia lost dormancy on experiencing summer temperatures, both in the soil and the laboratory (Quinlivan and Millington, 1962). In northern Australia, several *Stylosanthes* species progressively lost dormancy during summer, with daytime temperatures rising above 50°C, and began to germinate during the subsequent rainy season (McKeon and Mott, 1982; McKeon and Brook, 1983). While more detailed studies are still to be conducted on the wide range of Mediterranean species, data available from tropical regions somewhat support the dominant role of high summer temperatures in breaking PY (Van Assche and Vandeloos, 2006; Cook *et al.*, 2008; Jaganathan and Liu, 2014b).

Another possible PY-breaking route in Mediterranean soil is wet heat. Summer rain keeps seeds

moistened in the soil, and high temperatures on subsequent days heat the soil, providing conditions favouring dormancy alleviation. Two lines of evidence support this idea. First, seeds buried deep in the soil (but experiencing temperature fluctuations, e.g. 2–5 cm deep) come out of dormancy more quickly than seeds on the top (see Loi *et al.*, 1999; Taylor and Revell, 2002), and this is possibly attributed to the longer moisture-holding capacity of soil at depth. Second, PY seeds incubated under moist conditions with temperatures equivalent to natural conditions provide cues for dormancy alleviation (e.g. Hu *et al.*, 2009).

Bradshaw *et al.* (2011) concluded that there is no evolutionary relationship between fire and PY, but Keeley *et al.* (2011b), arguing against this viewpoint, suggested ‘...in some plant lineages physical dormancy might well have originated in response to fire, and in other lineages it was appropriated by species suddenly cast into a fire prone setting’. However, when viewed from an evolutionary standpoint, PY break cued by fire seems to offer no, and sometimes reduced, ecological fitness. According to Baskin and Baskin (2014), ‘although seeds of a (PY) species may germinate over a period of years, the germination season each year is about the same’. Given the ability to establish long-term persistent seed banks, seasonal control of dormancy alleviation not only allows only a proportion of PY seeds to germinate every year but also synchronizes germination with the most favourable time for seedling establishment. Thus, the mechanism of distributing germination at a particular time of the year would ensure that at least some seedlings would complete their life cycle (Probert, 2000; Van Assche *et al.*, 2003).

Since PY loss is irreversible, the seasonal control of dormancy alleviation in many species occurs in two distinctive steps: (1) a preconditioning step, which makes seeds sensitive; and (2) actual dormancy breaking under environmental conditions, to ensure that dormancy is broken only during the most favourable time for germination and seedling establishment. In some species, such as *Melilotus albus*, *Medicago lupulina*, *Lotus corniculatus* and *Trifolium repens*, seeds are preconditioned during constant cold, wet winter temperatures, and the opening of the water gap then synchronizes with the germination at spring temperatures (Van Assche *et al.*, 2003). On the other hand, seeds of many species, including *T. subterraneum* and *Ornithopus compressus*, are made sensitive by summer conditions but only become non-dormant with temperature fluctuations with a minimum of 20°C, mostly with daytime temperatures reaching above 50°C (Taylor, 1981; Taylor and Revell, 1999). Studies on *Ipomoea lacunose* (Jayasuriya *et al.*, 2008) and *I. hederacea* (Jayasuriya *et al.*, 2009) demonstrated that seeds can precondition at a lower constant or lower alternating temperature; and at a

higher constant or higher alternating temperature, or at lower temperature, the seed coat becomes water-permeable. Seeds of *Geranium carolinianum* required summer temperatures for preconditioning, and dormancy was broken during the autumn conditions (Gama-Arachchige *et al.*, 2012). However, there is increasing evidence that if the specific dormancy-breaking cues for the seeds are not met, the preconditioning step is reversed and seeds wait for next year. Thus, until this final cue the dormancy breaking does not take place and the specialized areas present in seeds ('water gap'), e.g. the lens in Fabaceae, are kept closed. This suggests that species with PY not only prevent asynchronous germination but also control the timing of germination.

In this context, there are several ecological factors that argue against the notion that seed dormancy in fire-prone environments is broken only by fire. First, in contrast to the seasonal dormancy-breaking cue, fire in the wild is erratic, and fire-related PY loss can thus occur at any time of the year in a Mediterranean climate (see the discussion in Moreno *et al.*, 2011). Unlike the strict environmental conditions controlling PY break under seasonal changes, a 'water gap' opens within seconds during fire, thereby leaving the non-dormant seeds in highly risky, uncertain post-fire environmental conditions (Auld and O'Connell, 1991; Céspedes *et al.*, 2012, 2014; Santana *et al.*, 2012). These seeds might germinate asynchronously during discontinuous summer rain, which signals a 'falsified germination cue', and the developing seedlings perish due to the absence of continuous water (Baskin *et al.*, 2004; Michael *et al.*, 2006; De Luis *et al.*, 2008; Santana *et al.*, 2012). Second, although most fires occur during the dry summer seasons, many studies have demonstrated that these seeds do not germinate until the following growing season (Auld and Denham, 2006; Buhk and Hensen, 2006; Moreira *et al.*, 2010; Santana *et al.*, 2012). As such, this raises the question of the extent to which the post-fire environment breaks PY because the passage of fire clears the standing vegetation, and seeds present in the exposed soils can experience higher summer temperatures, possibly leading to dormancy breaking before the growing season (Warcup, 1980; Auld and O'Connell, 1991; Baker *et al.*, 2005; Auld and Denham, 2006; Buhk and Hensen, 2006; Michael *et al.*, 2006; Luna *et al.*, 2007; Santana *et al.*, 2012; Jaganathan and Liu, 2014a). Third, if one accepts fire as the evolved factor cueing PY loss, wildfires in many Mediterranean ecosystems can occur only once in several years. In Catalonia, Spain, historical data available on fire return intervals, demonstrate that some sites were not burnt for 31 years (Lloret *et al.*, 2003). Mouillot *et al.* (2003) showed that a 8752 km² fire-prone area of central Corsica (France) has a fire return interval of 20 years, but that 47% of the area was not burnt once between 1957 and

1997. Keeley *et al.* (2011a) noted that California chaparral has an average fire return interval of 15 years, although recent historical data suggest no fire for longer periods than this average. Further, based on Keeley *et al.* (1999), they stated that 'wildlands in southern California have an average fire rotation interval of 36 yrs, but the actual fire return interval can vary from fires every few years at some sites to fires every 100 yrs at other sites'. Also, simulation models and dendrochronology studies estimate that events of fire are highly stochastic, with irregular return intervals (reviewed by Keeley *et al.*, 2011a). In addition, fire should not occur too frequently and there must be enough fire-free intervals for PY seeds that germinate following fire to complete their life cycle and disperse seeds (Buhk *et al.*, 2007; Ooi, 2012).

Further, the increased germination of many species in the post-fire environment is also attributed to the effect of smoke, resulting from burnt vegetation. De Lange and Boucher (1990) first demonstrated that some of the chemical factors found in smoke triggered germination in *Audouinia capitata*. Subsequently, several workers have made it clear that smoke or smoke water improves germination in seeds of many families (see reviews in Dixon *et al.*, 1995; Staden *et al.*, 2000). However, the specific role of smoke in PY break has not been studied to any great extent. In order to demonstrate that smoke can break PY, the permeability and viability of seeds must be checked before and after smoke treatment. However, a literature survey indicates no evidence for this. Furthermore, it is not clear whether smoke breaks dormancy or stimulates germination in many of the smoke-responsive species, and our understanding of how seeds respond to smoke is rudimentary. Nevertheless, in the PY-broken seeds, some compounds present in smoke, such as karrikinolide (a type of butenolide), might play a role in germination during the growing season (Moreira *et al.*, 2010).

Taking all the evidence together, it does not make good sense from evolutionary and ecological points of view to support the claim that dormancy loss in fire-prone Mediterranean ecosystems are cued only by fire, which is an extremely unpredictable event in terms of season, return interval and intensity. However, in no way would this mean that fire has no ecological significance in breaking PY, or in other processes such as the release of a canopy seed bank, but claiming that PY of seeds in fire-prone environments is only broken during fire seems not compelling. Obviously, this issue requires more long-term studies under ecologically meaningful conditions, taking into account high summer temperatures (e.g. 60°C) and fluctuating temperatures (e.g. 20/50°C), particularly in species that have highly specific high-temperature requirements, e.g. *Iliamna corei* (Baskin and Baskin, 1997). Nonetheless, it is clearly an over-simplification to state that results from seeds treated in the laboratory at

temperatures equivalent to fire (for only a sufficient time to break dormancy), and germinated in appropriate conditions, adequately confirm the situation in the real-life natural environment. Thus, as stated by Baskin and Baskin (2000), 'to ensure continuation of the species, (PY) dormancy-break must be fine-tuned to the environment in such a way that seeds germinate only when conditions are suitable for the plant to become established and eventually complete its life cycle. In species with PY, this can only be accomplished by physical-environmental signal detectors in the seed (or fruit) coat.'

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Conflict of interest

None.

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