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# Seed survival in soil: interacting effects of predation, dormancy and the soil microbial community

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## Summary

**1.** *Plant defence theory* provides a robust framework for understanding interactions between plants and antagonists, and for interpreting broad patterns in the functional-trait composition of plant communities. However, this framework has been built almost entirely on traits expressed by seedlings and mature plants.

**2.** No equivalent *seed defence theory* exists that recognizes the distinct suite of natural enemies that seeds encounter, and the unique constraints to their response. Furthermore, most attention has been paid to insect and vertebrate seed predators active above ground, whereas microbes in soil also have large effects on seed survival, particularly for plants that recruit from soil seed banks.

**3.** We suggest that concurrent selection on seed dormancy and resistance to microbial antagonists should result in distinct *seed defence syndromes*. We predict that species with physical seed dormancy will rely on physical defences to exclude predators and pathogens, and rapid seed germination to escape pathogens at the emergence stage. In contrast, species with physiological seed dormancy will deploy a continuum of physical and chemical defences, depending on soil pathogen pressure and duration of seed persistence. Finally, seeds of some species persist in the soil in a non-dormant, imbibed state, and lack obvious chemical and physical defences. These seeds may be especially dependent upon protection from beneficial seed-inhabiting microbes.

**4.** Framing a general 'seed defence theory' may help to account for the distribution of seed dormancy types across ecosystems. We predict that physiological dormancy will be favoured in dry or well-drained environments where pathogen pressure is relatively low, germination cues are most unpredictable, and seedling recruitment success is most variable. In contrast, physical dormancy should be favoured in warm and moist environments where pathogen pressure is high, and where germination cues are a stronger predictor of recruitment success. Persistent, non-dormant seeds are restricted to relatively aseasonal environments where favourable conditions for recruitment can occur over most of the year.

**5.** *Synthesis*. Integrating seed defence and dormancy traits can provide new insights into selection on dormancy types, and will help elucidate major trends in seed ecology and evolution. Understanding how seeds are defended also may improve our ability to predict plant regeneration and help develop innovative management strategies for weedy and invasive species.

**Key-words:** physical dormancy, physiological dormancy, plant defence theory, plant–herbivore interactions, plant pathogens, seed-infecting fungi, seed persistence, soil seed bank

Development of plant defence theory represents one of the most significant contributions to ecology in the last 35 years (e.g. McKey 1974; Coley, Bryant & Chapin 1985; Herms & Mattson 1992). Drawing on the economics of resource

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acquisition and use, plant defence theory provides a framework for understanding the evolutionary and ecological dynamics of plant–herbivore and plant–pathogen interactions at multiple scales (e.g. Price *et al.* 1980; Agrawal 2007; Mangan *et al.* 2010). As a result, ecologists have gained new perspectives on life-history trade-offs and the distribution of functional traits within and among communities (e.g. Hubbell & Foster 1992; Pacala *et al.* 1996), distributions of plants along gradients of resource availability (e.g. Shure & Wilson 1993; Fine, Mesones & Coley 2004), and the success of introduced and invasive plant species in novel habitats (e.g. Blossey & Nötzold 1995; Callaway & Ridenour 2004).

To date, however, plant defence theory has focused almost entirely on seedlings and established plants, with little attention to how the theory should be applied to seeds. This is a critical gap in our current understanding of plant ecology: seeds are among the most heavily defended plant parts (Zangerl & Bazzaz 1992) and for many plant species they represent the most significant component of fitness (Blake 1935). Furthermore, seed dispersal and survival determines spatial patterns of recruitment and contributes to species coexistence (Hurtt & Pacala 1995; Nathan & Muller-Landau 2000). Yet, unlike plants after germination, which can adjust resource acquisition and allocation to track a changing environment and tailor their defence responses to individual threats, seeds must defend themselves with limited resources that dwindle over time (Bewley 1997). As a consequence, factors affecting seed survival may create strong, unfiltered selection on suites of characteristics – 'seed defence syndromes', analogous to defence syndromes of plants (Agrawal & Fishbein 2006).

Most consideration of seed defences has focused on selection on seed size, nutrition and the structural or chemical traits that influence predation rates prior to incorporation in the soil (e.g. Janzen 1969; Grubb *et al.* 1998; Moles, Warton & Westoby 2003). We suggest that, for most plant species, understanding how and when seeds are defended also requires attention to the fate of seeds in the soil. In particular, we propose that understanding selection on defensive traits of seeds that are either transient or persistent in the soil requires recognition of: (i) the distinction between quiescent seeds (seeds awaiting a suitable environmental cue for germination) and dormant seeds (seeds that fail to germinate even in the presence of extrinsic germination cues); (ii) the potential role of seed dormancy as a mediator of mechanisms of seed defence against natural enemies; and (iii) the potential for both beneficial and antagonistic interactions between seeds and microbial communities to determine seed survival in the soil.

## Distinguishing dormancy and seed persistence

Seeds persist in the soil when they remain viable and in an ungerminated state (Schafer & Chilcote 1969). Persistence can occur either through *dormancy*, where seeds maintain physical or physiological barriers to germination, or *quiescence*, where seeds have no such barriers: they are ready to germinate, but only do so when conditions are favourable (Vegis 1963;

Murdoch & Ellis 2000; Khurana & Singh 2001; Thompson *et al.* 2003). Numerous categories of seed dormancy have been recognized (Baskin & Baskin 1998). However, most species have either physical or physiological dormancy, or in some cases, a combination of both (e.g. *Cercis canadensis*; Geneve 1991). Whereas the essential role of these dormancy types is assumed to be similar, i.e. preventing germination during periods unfavourable for seedling survival, the incidence of physical versus physiological dormancy varies among habitat types and, we suggest, has implications for how seeds interact with natural enemies.

### PHYSICAL DORMANCY: DELAYING GERMINATION WHEN FIDELITY IS HIGH

Physically dormant seeds germinate when an impermeable seed coat or fruit wall is breached. Loss of seed impermeability usually follows high or fluctuating temperatures associated with fire (Hanley & Fenner 1998) or gaps in the overstorey vegetation (Vázquez-Yanes & Orozco-Segovia 1982). Dependence on exogenous factors to initiate germination suggests that physically dormant seeds should be limited in the ability to spread germination risk over multiple recruitment opportunities, although in a few taxa the responsiveness of seeds to dormancy-breaking cues varies seasonally (Van Assche, Debucquoy & Rommens 2003; Jayasuriya, Baskin & Baskin 2009). We suggest that physical dormancy may be most advantageous in 'high fidelity' environments i.e. those where disturbance events that cue germination are infrequent, and the probability of post-emergence recruitment success is high.

### PHYSIOLOGICAL DORMANCY: HEDGING BETS WHEN FIDELITY IS LOW

In some environments, favourable conditions for seedling emergence occur frequently (e.g. seasonal changes in temperature, moisture or light availability), but post-emergence survival is highly variable. From a seed's perspective these are 'low fidelity' environments because germination cues are poor predictors of post-emergence recruitment success. Physiological dormancy, in which a germination response to environmental cues is blocked by chemical inhibition of embryo growth, provides an endogenous mechanism that can distribute the receptivity to germination cues of a seed cohort over multiple years and further limit germination opportunities to favourable seasons within a year (Baskin & Baskin 1998). Physiological dormancy is common in these low-fidelity environments (e.g. Dekker & Hargrove 2002; Leon, Bassam & Owen 2006; Olvera-Carrillo *et al.* 2009).

## Sources of seed losses: predators and pathogens

To date, seed defensive traits mostly have been interpreted as adaptive against pre- and post-dispersal predators, including both insects and vertebrates (e.g. Janzen 1969; Crawley 1992). Seed predators are of undeniable importance, as predation

rates often exceed 90% of available seeds, with many documented effects on population growth rate (reviewed in Kolb, Ehrlen & Eriksson 2007). However, seed chemical and physical defences are also likely to be shaped by interactions with seed pathogens, which have a major impact on seed survival in the soil (e.g. Crist & Friese 1993; Dalling, Swaine & Garwood 1998; O'Hanlen-Manners & Kotanen 2004). Furthermore, chemical and physical traits interpreted as defences against predators may also be effective against pathogens. For example, hard seed and fruit walls in two arable weeds, *Abutilon theophrasti* and *Chenopodium album,* do not deter post-dispersal seed predators (Cardina *et al.* 1996; Carmona, Menalled & Landis 1999; Westerman *et al.* 2006), but are effective in preventing fungi from penetrating the seed (Kremer, Hughes & Aldrich 1984; Davis *et al.* 2008). Seeds may prevent lethal infection from pathogens via four mechanisms: (i) physical barriers that render seeds impermeable to pathogens; (ii) endogenous chemical defences of seeds; (iii) chemical defences of beneficial seed–microbial associations; and (iv) rapid seed germination.

### SEED PHYSICAL DEFENCES

Physical defences of seeds are most apparent in species with 'hard seeds', a term synonymous with physical dormancy, where the seed is impermeable to water until germination commences. Physical dormancy has already been suggested to play a defensive role, as rodents that rely on olfactory cues cannot detect buried seeds that remain impermeable (Van der Wall 1998). Here we suggest that physical dormancy also provides an effective barrier against microbial access to nutrient-rich seed contents. Physical defences may also extend to some seeds with physiological dormancy, as seed-enclosing structures may need to soften before the radicle can emerge (Baskin & Baskin 1998). Permeability of these structures may therefore also be sufficiently restrictive to prevent microbial access to the seed embryo.

### SEED CHEMICAL DEFENCES

Seeds contain a diversity of secondary chemicals, often at concentrations much higher than elsewhere in the plant (e.g. Berenbaum 1981; Terras *et al.* 1995). Synthesis of chemical defences is costly and potentially equivalent to the investment in seed physical defences (Zangerl & Berenbaum 1997). In most cases the relative effectiveness of chemical defences against different classes of seed predators and pathogens has not been assessed. Those considered to be effective against microbial infection in the soil include phenolic compounds (Scalbert 1991; Picman, Schneider & Picman 1995), anti-fungal proteins (Selitrennikoff 2001) and alkaloids (Veldman *et al.* 2007). Consistent with an antimicrobial role, chemical defences often are allocated primarily to seed coats rather than embryo or endosperm tissue (Berenbaum & Zangerl 1986; Suzuki & Waller 1987), and also may be present in fruit tissue (Cipollini & Stiles 1992; Tewksbury *et al.* 2008), protecting seeds from pathogen infection at the pre-dispersal stage.

### BENEFICIAL SEED–MICROBIAL ASSOCIATIONS

Not all fungi and bacteria inhabiting seeds are associated with seed death or damage (Kirkpatrick & Bazzaz 1979; Kremer 1986; Gallery, Dalling & Arnold 2007). Viable, asymptomatic seeds can harbour microbes that colonize internal tissues (Gallery, Dalling & Arnold 2007; see also Clay & Schardl 2002; Schardl, Leuchtmann & Spiering 2004) or the seed surface (Kremer 1986) prior to soil contact. The latter can be effective in preventing pathogen infection when seeds are incubated in soil (Kremer 1986, 1987). In turn, fungi present within seeds may include endophytes (fungi that occur within healthy seedlings and mature plants without causing disease) that are transmitted vertically from maternal plants, or horizontally transmitted strains that colonize seeds from the external environment (Gallery, Dalling & Arnold 2007). In some grasses (e.g. many Pooideae characteristic of temperate pastures and woodlands), seedborne endophytes in the Clavicipitaceae confer a variety of benefits to hosts after germination [e.g. protection against herbivores, drought resistance and enhanced root growth (Clay & Schardl 2002; but see Faeth & Fagan 2002)] and may alter interactions between seeds and other organisms (e.g., Knoch, Faeth & Arnott 1993). Although maternal transmission of endophytes is not considered to be common outside the specialized grass-endophyte symbiosis, Gallery, Dalling & Arnold (2007) showed that fungi present within seeds harvested directly from tree crowns in a tropical forest frequently represent genotypes consistent with endophytic fungi from healthy leaves of trees in the same habitat (Arnold & Lutzoni 2007; Gallery, Dalling & Arnold 2007). Members of these endophytic lineages have been shown to protect seedling tissues against microbial antagonists (Arnold *et al.* 2003; see also Clay & Schardl 2002), such that seed-borne fungi may play an important but often overlooked role in defence against soil-borne pathogens.

Seeds also may become infected by beneficial fungi after dispersal. In two studies in moist tropical forest in Panama, Gallery, Dalling & Arnold (2007) and Kluger *et al.* (2008) showed that seeds of pioneer species with quiescence are rapidly infected by diverse ascomycetous fungi after burial in the soil. Although all fungi in those studies were isolated from non-viable seeds, some fungal taxa were consistently associated with groups of seeds that had higher survival in the soil than expected by chance. Others were reliably associated with replicates with lower than expected germination (Gallery, Dalling & Arnold 2007) and others, including taxa known primarily as saprotrophs, had no observed effect (e.g. *Xylaria* spp.). We suggest that microbial communities present on seed exteriors may act as gatekeepers that prevent either pathogenic attack of seed contents or slow decay of hard seed enclosing structures. In contrast, fungi that initially colonize seed contents may enjoy a priority effect that limits subsequent pathogenic infection, and may be particularly important for seeds that lack physical barriers to microbial infection.

RAPID GERMINATION

Germination should be an especially sensitive period for seeds: protective structures enclosing the seeds are ruptured, providing access for bacteria and fungal hyphae. Furthermore, carbon-limited seedlings, particularly those lacking stored seed reserves, may be incapable of synthesizing the defensive chemicals found either in seeds or adult plants (Barton 2007; Elger *et al.* 2009). Just as rapid leaf expansion reduces opportunities for herbivores and pathogens to access poorly defended, immature tissues (Aide & Londoño 1989; Ernest 1989; Coley & Barone 1996), rapid germination may reduce the probability of pathogen infection. In an elegant study of the interaction between seed germination and fungi and oomycetes causing damping-off in agricultural crops, Leach (1947) showed that the severity of damping off depended on the ratio of pathogen and seedling growth rate, which in turn is influenced by temperature. More recently Beckstead *et al.* (2007) showed that growth rate also influences the outcome of interactions between an annual grass (*Bromus tectorum*) and a fungal pathogen of seeds (*Pyrenophora semeniperda*). In their study, recently harvested seeds germinated slowly as a result of physiological dormancy and usually were killed by the pathogen, whereas older, after-ripened seeds germinated fast and often escaped. Intriguingly, pathogens may be fundamentally constrained in their ability to respond adaptively to rapid germination: Meyer, Stewart & Clement (2010) showed that the mycelial growth rate of *P. semeniperda* genotypes is negatively correlated with their virulence.
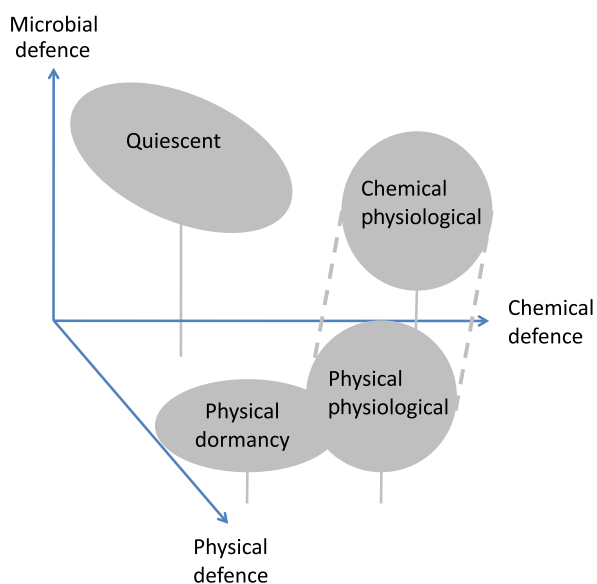


**Fig. 1.** Schematic illustration of the relative positioning of different dormancy types along axes describing seed investment in physical and chemical defences, and defences provided by beneficial seed-associated microbes. Dormancy types are quiescent (non-dormant), physical dormancy and physiological dormancy. Physiologically dormant seeds occupy a gradient of relative investment in chemical versus physical defences (see text).

## Seed defence syndromes: interactions among dormancy, persistence and defence

We predict that the three major types of persistent seeds commonly found in soil (physically dormant, physiologically dormant and quiescent) rely on distinct sets of defences, resulting in dormancy-defence syndromes (Fig. 1).

**1.** *Physical dormancy - physical defence syndrome*. If an impermeable seed coat prevents microbial access to seed reserves, then we predict that seeds with physical dormancy will allocate little to chemical defence. Endophytic fungi will also be absent from the interior of these seeds, or should be limited to those that colonize during seed development. However, physically dormant seeds may benefit from beneficial fungi and bacteria arrayed on the exterior of the seed. In the absence of chemical defences, we predict that physically dormant seeds must rely on rapid germination to escape soil pathogens. Along these lines, radicle emergence is often observed to occur quickly after water impermeable seed coats are compromised (Baskin & Baskin 1998).

**2.** *Physiological dormancy – a chemical and physical defence continuum*. We predict that seeds with physiological dormancy will vary in their investment in chemical versus physical defences depending on seed persistence and habitat type. In habitats where pathogen pressure is relatively low (e.g. arid ecosystems or well-drained, temperate agricultural fields) physical defences may be sufficient to ensure long-term seed persistence (Davis *et al.* 2008). For these species we predict that (i) seeds will be less permeable to bacteria and fungi than species that rely on chemical defences and (ii) that microbial and chemical defences, if present, will be arrayed on the exterior of the seed. In habitats where pathogen pressure is high (e.g. wet temperate and tropical habitats), then physical defences alone may be insufficient to prevent pathogen infection, and seed persistence is positively correlated with chemical defence investment (Hendry *et al.* 1994; Veldman *et al.* 2007). For species in these habitats, chemical defences will be deployed both on the seed exterior, and in embryo and endosperm tissues.

**3.** *Quiescence-microbial defence syndrome*. Most quiescent (i.e. non-dormant) seeds germinate within a few weeks of dispersal. However, small-seeded species that recruit in canopy gaps in tropical forests frequently have quiescent seeds capable of persisting a year or more in the soil (Dalling, Swaine & Garwood 1997). Quiescent seeds remain in the soil in an imbibed state and are capable of a rapid response to germination cues. We predict that in warm, moist tropical soils that are favourable for microbial growth, quiescent seeds may depend on defences produced by endophytic microbes present inside seeds. For example, quiescent *Cecropia* seeds in neotropical forest soils survive for up to 1 year despite an apparent lack of chemical and physical defences (Gallery, Dalling & Arnold 2007; U'Ren *et al.* 2009; Gallery, Moore & Dalling 2010). If defences are associated with specific fungal or bacterial taxa then we would expect (i) an association between seed mortality and the composition of the soil microbial community, as shown for agricultural weeds (Davis *et al.* 2006) and tropical forest pioneers (Gallery, Dalling & Arnold 2007); (ii) that fungi or bacteria

isolated from viable seeds incubated in the soil will inhibit the growth of pathogens in culture; and (iii) that inoculation of uninfected seeds with beneficial microbes will prolong survival in the soil.

## Implications of a seed defence theory

The link between dormancy and seed defence proposed here may explain some of the variation in the frequency of seed dormancy types observed across biomes. For example, physiological dormancy is most common in cold deserts, where it is present in *c.* 90% of species. Physiological dormancy declines in frequency in tropical biomes from 60% in hot deserts to *c.* 25% in tropical rainforests as rainfall increases (fig. 12.2 in Baskin & Baskin 1998). Some of this variability can be attributed to the greater representation of non-dormant species in wet and seasonally moist tropical forest, but does not account for the elevated frequency of physical dormancy in seasonal tropical forests and savannas (*c.* 35% of species) compared to temperate and arctic biomes (< 10% of species; Baskin & Baskin 1998).

We predict that physical dormancy should be particularly common in warm and moist environments where conditions are most conducive to fungal growth, and long-term seed persistence can best be achieved by preventing microbial access to nutrient-rich seed embryos. In contrast, in deserts, and in montane, boreal and tundra ecosystems, moisture availability or temperature limits fungal growth rates (Pietikäinen, Pettersson & Bååth 2005) and seeds should be at lower risk of pathogen infection while in the soil. In dry or cold environments where environmental cues are poor predictors of recruitment success, physiological dormancy may be advantageous, assuming that

there is a greater potential of this dormancy mechanism to distribute germination events through time (Fig. 2).

Understanding linkages between seed dormancy and defence also may assist in devising novel methods to manage regeneration. For weeds and invasive species with seeds that rely on physical defences, damage to seeds, either applied mechanically or by encouraging predispersal seed predators that pierce seed coats, may be effective in controlling seed populations in the soil by increasing losses to pathogens (Davis *et al.* 2008). For species with quiescent seeds or species with physiologically dormant seeds, altering the microbial environment of seeds may be an effective means of changing seed fate. Inoculating leaves with foliar endophytic fungi has been shown to decrease susceptibility of leaf tissue foliar pathogen infection (Arnold *et al.* 2003) and, the fact that many seed-infecting fungi are closely related to foliar endophytes (U'Ren *et al.* 2009) suggests that seed inoculations may have similar results.

The development of a framework for understanding seed defences, organized around putative syndromes of linked dormancy and defence mechanisms, remains to be verified through empirical tests of its predictions. Here we emphasize defensive characteristics of ungerminated seeds in the soil: however a more complete 'seed defence theory' will need to consider pre-dispersal risks, and in some cases, how persistent seed reserves are defended in developing seedlings (Dalling & Harms 1999; Green & Juniper 2004). Two approaches to research on seed defences appear especially promising. First, assays of the specificity of defence traits against predators and pathogens will reveal the extent to which chemical and physical defences have overlapping roles, and are primarily effective at either pre- or post-dispersal stages. Second, exploration of seed
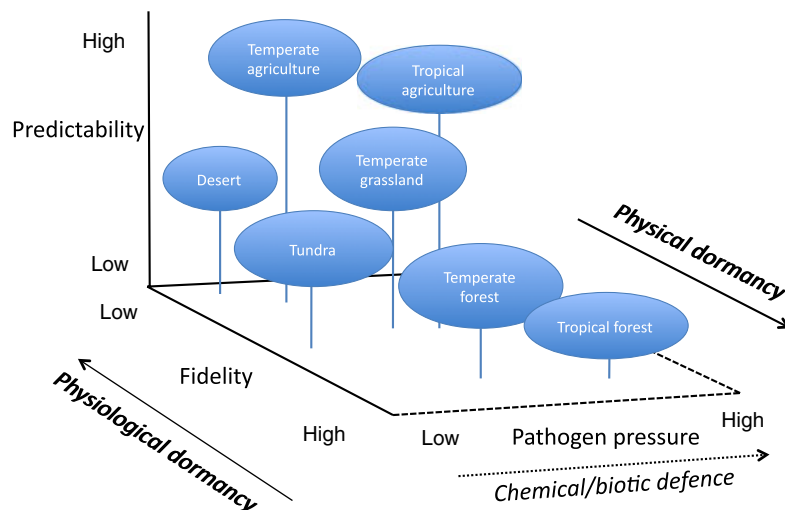


**Fig. 2.** Schematic illustration of the relative positioning of biomes and agricultural ecosystems according to axes of temporal *predictability* of recruitment opportunities, *fidelity* of recruitment opportunities (indicating whether germination cues are reliable indicators of seedling establishment conditions), and *pathogen pressure* associated with microbial attack in the soil. We predict that low fidelity will select for physiological dormancy, whereas high fidelity, particularly when combined with high pathogen pressure will select for physical dormancy. As pathogen pressure increases, seeds that persist in the soil also are predicted to be more strongly chemically defended, or may rely on beneficial seed-associated microbes to repel pathogens. Note: for clarity we depict biomes as occupying discrete regions of axis space, however, in reality ecosystem distributions are likely to overlap.

defences within a phylogenetic context will help us understand how individual defences are selected across ecosystems that vary in the activity of specific seed antagonists.

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