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RESEARCH OPINION

Evolutionary considerations of claims for physical dormancy-break by microbial action and abrasion by soil particles†

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Abstract

Books and review articles in various areas of ecology and seed and plant biology continue to report that dormancy-break in seeds (and fruits) with water-impermeable coats (i.e. physical dormancy) occurs via soil-microbial action and/or abrasion by soil particles. However, there is little evidence in the scientific literature to support these assumptions, which, in fact, do not make good evolutionary sense for two related reasons. First, several types of anatomically specialized water-restriction structures have evolved as part of the seed or fruit coat of taxa with physical dormancy. These structures act as 'signal detectors' of physical-environmental changes that cause seeds (and fruits) to become water-permeable only at these sites, in seasons and habitats in which there is a good chance that some seedlings will become established. Second, seed (and fruit) coat breakdown by microbial action or by abrasion likely would occur in seasons and habitats in which seedlings could not survive, thus lowering the fitness (λ) of the plant taxa in question.

Keywords: abrasion and physical dormancy, evolution and physical dormancy, microbes and physical dormancy, signal detectors and physical dormancy

There is good supporting evidence from laboratory and field studies that dormancy-breaking and germination requirements in nature are responses of seeds to specific environmental cues. For example, dormancy in many species of spring-germinating plants is broken by moist, low temperature conditions during winter and in fall-germinating plants by exposure to the high temperatures during summer. Germination of buried nondormant seeds may be inhibited until they are brought to the soil surface by ploughing, animal burrowing or other disturbances. At the soil surface, exposure to sunlight and/or an increase in the amplitude of daily temperature fluctuations often stimulates the seeds to germinate. Seeds inhibited by a low R/FR photon ratio (thus low P_{fr}/P_{total}) under a plant canopy respond to an increase in the R/FR photon ratio (thus high P_{fr}/P_{total}) when a gap is formed in the canopy (Baskin and Baskin, 1998).

The statement is often made in books and review articles in ecology and seed and plant biology that dormancy-break in seeds with water-impermeable seed (or fruit) coats, i.e. physical dormancy (PY), is cued to microbial action and/or to abrasion by soil particles (Table 1). For example, Mayer and Poljakoff-Mayber (1989, p. 76) state that, "… in nature most seeds [with water-impermeable coats] become permeable to water when the seed coat is broken down or punctured by mechanical abrasion, microbial attack …" However, we found only weak support in the scientific literature for breakage of PY by soil microbial action and no support for breakage of it by abrasion. *Albizia julibrissin* seeds incubated in sterilized and nonsterilized native soil for 7 days germinated to 30% and 11%, respectively. Further, after 30 days seeds of this species germinated to 1%, 3% and 3% in the presence of the soil fungi *Fusarium* sp., *Rhizoctonia* sp. and *Pythium* sp., respectively; 2% of the seeds germinated in the control. After 60 days, germination was 10%, 22%, 5% and 3%, respectively, and after 90 days, 21%, 38%, 7% and 9%, respectively (Gogue and Emino, 1979). Seeds of *Vigna minima* kept on blotters soaked with a soil suspension had imbibed after 168 h, whereas those on blotters moistened with distilled water remained nonimbibed after 30 days (Gopinanthan and Babu, 1985). These

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Table 1. Examples of books and review articles published in 1977–1999 in which it is stated that dormancy-break of seeds with physical dormancy in nature is by microbial action and/or by abrasion by soil particles

Method(s) of dormancy-break		
Microbial action	Abrasion	Reference
Introductory botany texts		
x	x	Stern, 1994
x	x	Moore *et al*., 1998
	x	Raven *et al*., 1999
Plant physiology text		
x	x	Salisbury and Ross, 1992
Plant population biology texts		
	x	Harper, 1977
x		Silvertown and Doust, 1993
Plant physiological ecology texts		
x		Fitter and Hay, 1987
x		Larcher, 1995
x		Lüttge, 1997
x		Lambers *et al*., 1998
Seed biology texts		
x	x	Fenner, 1985
x	x	Mayer and Poljakoff-Mayber, 1989
	x	Gutterman, 1993
x	x	Bewley and Black, 1994
Reviews		
x	x	Rolston, 1978
x		Van Staden *et al*., 1989
x		Vásquez-Yanes and Orozco-Segovia, 1993
x		Boesewinkel and Bouman, 1995
x	x	Geneve, 1998

authors concluded that microbes in the soil suspension soften the seed coat of *V. minima* at the lens (strophiole). However, other studies have shown that soil microbes have no effect on rendering impermeable seeds permeable. Aitken (1939) found no significant difference in germination of *Trifolium subterraneum* seeds incubated for 12 months in the presence of fungi, root nodule bacteria and seed coat saprophytes and in those incubated in the control. The proportion of impermeable seeds of *Abutilon theophrasti* incubated in the dark at 28°C for 4 days with *Fusarium oxysporum* alone and in combination with various germination stimulants, herbicides or insecticides generally did not differ significantly from that of the control (Kremer and Schulte, 1989).

According to Halloin (1983), " … the seed coat is the most important component of resistance of seeds to deterioration." With regard to species with PY, the water-impermeable seed coat appears to be highly resistant to decomposition by soil microorganisms. Fungi invade the mature seeds of permeable-seeded lines of cotton through the chalazal slit (Halloin, 1983), the only area on the seed coat of cotton (Simpson *et al*., 1940) and other species of Malvaceae (Baskin and Baskin, 1998; Baskin *et al*., 2000) that is (or later becomes) permeable to water. Seeds of impermeable-seeded lines, however, in which the chalazal slit is plugged (Baskin and Baskin, 1998; Baskin *et al*., 2000) are not invaded by fungi (Halloin, 1983). Thus, seeds of permeable-seeded lines of cotton quickly deteriorate in the soil, whereas those of impermeable-seeded lines form a persistent seed bank from which plants " … appear in fields for years following cropping with these lines" (Halloin, 1983). Some seeds of the impermeable-seeded species of wild cotton *Gossypium thurberi* produced in Arizona in 1963 germinated in the field each year over an 8-year period, 1965–1972 (Endrizzi, 1974).

The fact that seeds of hardseeded lines of cotton and of many wild taxa with impermeable seed coats (Baskin and Baskin, 1998) can remain dormant and viable in the soil for many years strongly suggests that seed coat breakdown by soil-microbial decomposition as a cue for overcoming dormancy is unlikely. According to Kremer (1993), only a low percentage of seeds in the soil are killed by microbial attack, and thus most of them "… persist for many years in the presence of millions of soil microorganisms that apparently are unable to exploit the potentially nutrient rich sources within the seeds."

There is quite a bit of information on prevention of colonization (attack) of the seed surface by soil microbes. Kremer *et al*. (1984) identified a characteristic group of fungi associated with the water-impermeable seed coat of *Albutilon theophrasti* that prevented the establishment of soil microbes on the seed surface (Kremer, 1986a). Further, compounds with antifungal properties have been shown to occur on seeds of various species with PY: *Abutilon theophrasti* (Kirkpatrick and Bazzaz, 1979; Kremer, 1986b), *Colutea* spp. (Aguinagalde *et al*., 1990), *Ipomoea hederacea* (Kirkpatrick and Bazzaz, 1979), *Medicago arborea* and *M. strasseri* (Perez-Garcia *et al*., 1992). Finally, bacteria isolated from the seed coats of *Abutilon theophrasti* and *I. hederacea* inhibited the growth of several fungal species (Kremer, 1987).

There are also a few reports that microorganisms promote germination in seeds with water-permeable coats (Humphrey Jones and Waid, 1963; Probert, 1981; van Leeuwen, 1981; Guttridge *et al*., 1984). However, as in seeds with water-impermeable coats, those with water-permeable coats also produce chemical compounds with antifungal properties (e.g. Warr *et al*., 1992). Thus, Kremer (1993) concluded that, "In nature soil microorganisms may not be a significant factor in breaking seed dormancy, primarily due to deterioration resistance mechanisms …"

We know of no data to support the often-made suggestion (Table 1) that PY in nature is broken by mechanical abrasion. The idea may have originated with F.W. Went (1948, 1955), who observed that leguminous trees grow along desert washes in the Mojave Desert of California, USA. Thus, he conjectured that seeds are mechanically scarified in the rapidly flowing water during desert floods by " … the grinding action of sand and gravel" (Went, 1955).

Two aspects of the evolutionary biology of PY argue against breakage of dormancy in seeds (or fruits) with water-impermeable coats by these methods. The first of these is that in taxa with PY, water passes through the initially impermeable layer(s) of the seed or fruit coat only at a specialized anatomical region and only after it has been disrupted, e.g. lens (strophiole) in seeds of Leguminosae, bixoid chalazal apparatus in seeds of Malvales, imbibition lid in seeds of Cannaceae, carpellary micropyle in endocarp of fruits of *Rhus* (Anacardiaceae) (Baskin and Baskin, 1998; Li *et al*., 1999; Baskin *et al*., 2000). No such specialized anatomical areas are known to serve as environmental signal detectors in seeds (or fruits) of taxa which do not contain species with PY. Specialized areas (opercula or germination lids) do occur in a variety of seeds (and fruits) with permeable coats (e.g. Hill, 1933, 1937; Werker, 1997), but to our knowledge they do not serve as environmental signal detectors. Certainly, such seeds are not impermeable to water. For example, seeds (true seed plus endocarp) of *Sclerocarya birrea* subsp. *caffra* (Anacardiaceae, tribe Spondideae) first imbibe water, and then the radicle breaks through the operculum (von Teichman *et al*., 1986).

The second aspect is that plant life history strategy with the highest fitness value (λ) will include germination at the most suitable time(s) of the year, and in the most favourable circumstance(s), that result in the highest probability for survival and reproduction. Such a seed germination strategy requires that the seed dormancy-breaking response be cued to qualitative or quantitative changes in a physical-environmental factor(s). Three examples of these changes are: (1) high daily fluctuation in temperature at the soil surface during summer in pastures in the Mediterranean region of Australia that breaks dormancy in winter annual legumes (Quinlivan, 1971; Mckeon and Mott, 1982); (2) increase in daily fluctuation in temperature at the soil surface, following formation of gaps in tropical rain forests, that breaks PY in seeds of gap-colonizing species (Vásquez-Yanes and Orozco-Segovia, 1982); and (3) heat from fire that kills forest vegetation and breaks PY in shade-intolerant perennials that are early-successional colonizers (from soil seed bank) of the burned area (Baskin and Baskin, 1997). The anatomy of tissue disruption in the specialized area on the seed (or fruit) coat by high or high fluctuating temperatures, thereby allowing passage of water into the seeds, is well documented, especially in the seed coat of Leguminosae (e.g. Dell, 1980; Hanna, 1984; Van Staden *et al*., 1989) and in the endocarp of the genus *Rhus* (Anacardiaceae, tribe Rhoeae) (Li *et al*., 1999). The anatomy and histochemistry of disruption of the chalazal plug (i.e. dormancy-break) in the water-impermeable seeds of *Sida spinosa* (Malvaceae) has been studied in considerable detail by Egley (1989), Egley and Paul (1981) and Egley *et al*. (1986).

Thus, it simply does not make good evolutionary sense for a critical event in the life history of a plant, such as dormancy-break, that requires coupling of physical/chemical changes in a highly specialized anatomical area of the seed (or fruit) coat with a change in a physical environmental factor, to be regulated by potentially ever-present processes such as microbial activity or movement of soil particles. When the specialized anatomical areas ('water gaps') in the seed (and fruit) coats of species with PY are viewed as products of evolution that function as physical-environmental 'signal detectors', it seems even more unrealistic to regard microbial action or abrasion by soil particles as causes of dormancy-break in seeds (or fruits) with this type of dormancy.

Further, once PY is broken (1) seeds can germinate over a wide range of temperatures in both light and dark, (2) the seed (or fruit) coat cannot revert to impermeability and (3) the nondormant embryo cannot be induced into dormancy (Baskin and Baskin, 1998). The nondormant seed is 'committed' to germinate or die. Thus, to ensure continuation of the species, 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. It seems inconceivable that either microbial action or abrasion by soil particles could serve such a role.

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