Reviews

Germinating Seeds of Wildflowers, an Ecological Perspective

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SUMMARY. Five kinds (classes) of seed dormancy are known: physiological (PD), morphological (MD), morphophysiological (MPD), physical (PY), and combinational (PY+PD). PD is the most common class in the major vegetation zones of the world followed by PY, MPD, MD, and (PY+PD). Each class is described, and a dichotomous key to identify them is presented. The environmental conditions required to break PD, MD, MPD, PY, and (PY + PD) and promote germination are discussed. To help determine which treatments to use for breaking dormancy in seeds with water-permeable seedcoats (PD, MD, MPD), a “move-along experiment” is recommended. Little or no convincing evidence for the role of microbes or mechanical abrasion by soil particles in breaking PY can be found in the literature. However, there is good evidence that the water plug or gap in the seed or fruit coat of seeds

with PY responds to environmental cues that permit timing of imbibition and germination to be well controlled in nature. Seeds of many species remain viable after passing through the digestive tracts of animals, with varying effects on germination.

The reasons why people might wish to germinate seeds of wildflowers, or of non-cultivated species in general, range from wanting to introduce interesting plants into the horticulture trade to propagating plants with medicinal value to producing plants needed for restoration projects. All too often, however, seeds of wild plants do not germinate, and little information is available on their dormancy-breaking and germination requirements in the literature, leading to frustration. The seed germination ecologist not only wants to germinate seeds of wild plants but seeks to understand what controls the timing of germination in nature. That is, what are the dormancy-breaking and germination requirements of the seeds? Obviously, horticulturists and seed ecologists share many common goals! In this paper, we provide a brief overview of dormancy-break and germination from an ecological perspective.

DORMANCY TERMINOLOGY. If freshly matured, viable seeds fail to germinate after 4 weeks at any of several combinations of environmental conditions (Baskin and Baskin, 1998), they are **dormant**. In germination tests that extend beyond 4 weeks, there is a possibility that dormancy loss will have occurred, thus making it impossible to determine if fresh seeds were dormant. On the other hand, if fresh seeds germinate to high percentages ($\geq 80\%$) over a range of test conditions

in 4 weeks or less, and this range does not increase after seeds have been given a dormancy-breaking treatment, they are **nondormant**, or perhaps morphologically dormant (see below). If fresh seeds germinate to high percentages at some conditions and not others after 4 weeks, they may be in a *state* of **conditional dormancy**, which appears to be found only in seeds with nondeep physiological dormancy (see below). If fresh seeds are in a state of conditional dormancy, the percentage and rate of germination, as well as the range of conditions over which they germinate, increase following a dormancy-breaking treatment.

We have compiled seed dormancy and germination data for 5250 species from the major vegetation zones of the world, and seeds of 69.6% of the species are dormant at maturity (Baskin and Baskin, 2003a). There are five kinds (classes) of seed dormancy: physiological, morphological, morphophysiological, physical, and combinational. A closer look at these five classes will help explain why fresh seeds do not germinate and provide insight into how dormancy is broken in nature.

Physiological dormancy (PD) means there is a “physiological inhibiting mechanism” in the embryo that prevents it from generating enough growth potential to overcome the mechanical constraint of the seedcoat and/or other covering layers. Dormancy break occurs at cool [about 0.5 to 10 °C (32.9 to 50.0 °F)] wet, warm [≥ 15 °C (59.0 °F)] wet, or warm dry conditions, depending on the species. After the embryo becomes fully nondormant, it has sufficient growth potential to push through all layers surrounding it. PD is the most common class of dormancy in all vegetation zones on earth except in the matorral (a type of vegetation dominated primarily by small-leaved, evergreen shrubs that occurs in a climate with cool, moist winters and hot, dry summers, i.e., Mediterranean-type climate), where PY is equally important (Baskin and Baskin, 2003a).

In seeds with **morphological dormancy** (MD), the embryo is undifferentiated, or it may be differentiated but underdeveloped (small). Although seeds with MD germinate in about 4 weeks, they differ from nondormant seeds because time is required for morphological changes

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and/or growth of the embryo to occur, prior to germination. In seeds with undifferentiated embryos (e.g., families Burmanniaceae, Orchidaceae, Orobanchaceae, and Rafflesiaceae) the embryo has no organs and is a mass of 2–100 or more cells. A radicle and cotyledon(s) are not formed, and the tissue that emerges from the germinated seeds enlarges to form a structure other than a seedling per se such as the protocorm in orchids and the hastorium in some of the parasitic plants. In seeds with a differentiated, underdeveloped embryo, a radicle and cotyledon(s) are present, but the embryo may be only ≤ 1 mm (0.04 inch) in length (e.g., some members of the families Apiaceae and Ranunculaceae). However, before the radicle emerges, the embryo must grow to a species-specific critical length, which may be an increase of 250% or more. If seeds with underdeveloped embryos have only MD, they do not require any pretreatment per se for the embryo to grow. (However, if the small embryo also has PD the seed has morphophysiological dormancy, and treatments will be required, see below.) If seeds with MD are placed on a moist substrate at appropriate temperatures [some seeds require low temperatures [day/night 15/6 °C (59.0/42.8 °F), 20/10 °C (68.0/50.0 °F)] and others high temperatures [25/15 °C (77.0/59.0 °F)] in light or in darkness, depending on the species, embryo growth and seed germination may occur in 4 weeks or less (Baskin and Baskin, 1998). Among the 5250 species for which germination data have been compiled, MD is not very common in any vegetation region on earth (Baskin and Baskin, 1998, 2003a). However, as we learn more about the biogeography of seed dormancy and germination, undoubtedly many additional species with MD (and also MPD) will be added to the list, especially for tropical regions in which there are many orchids.

Morphophysiological dormancy (MPD) is a combination of MD and PD. Although there is some evidence that seeds with undifferentiated embryos, e.g., some temperate-zone orchids such as showy lady's slipper (*Cypripedium reginae*) (Ballard, 1987) and ucho-ran (*Ponerorchis graminiflora*) (Ichihashi, 1989) also have PD (thus MPD), much of the research on this class of dormancy has been done on seeds with differentiated, underdevel-

oped embryos [e.g., families Apiaceae, Araceae, Araliaceae, Aristolochiaceae, Berberidaceae, Caprifoliaceae, Fumariaceae, Liliaceae, Papaveraceae, and Ranunculaceae (Baskin and Baskin, 1998)]. In seeds with both PD and an underdeveloped embryo, PD has to be broken, either prior to or after the embryo elongates, and the embryo must grow before the radicle can emerge. MPD is more common in temperate broadleaved evergreen forests and in temperate deciduous forests than in any other vegetation region on earth (Baskin and Baskin, 1998, 2003a). Seeds of many wildflowers [e.g., jack-in-the-pulpit (*Arisaema* spp.), wild ginger (*Asarum canadense*), larkspur (*Delphinium* spp.), dog's tooth violet (*Erythronium* spp.), twinleaf (*Jeffersonia diphylla*), sweet cicely (*Osmorhiza* spp.), bloodroot (*Sanguinaria canadensis*), celandine-poppy (*Stylophorum diphyllum*), and wake-robin (*Trillium* spp.)] in temperate deciduous forests have MPD; thus, this class of dormancy has long been of interest to horticulturists and ecologists.

In seeds with physical dormancy (PY), germination is prevented because the seedcoat (sometimes the fruit coat) is impermeable to water. Impermeability is due to the presence of one or more palisade layers of lignified cells in the seed or fruit coat (pericarp), e.g., the endocarp (innermost layer of the pericarp) of sumac (*Rhus* spp.) fruits is impermeable to water. Physical dormancy is known to occur in 15 plant families (*sensu* Angiosperm Phylogeny Group, 1998): Anacardiaceae, Bixaceae, Cannaceae, Cistaceae, Cochlospermaceae, Convolvulaceae (including Cuscutaceae), Curcubitaceae, Dipterocarpaceae (subfamilies Montoideae and Pakaraimoideae, but not Dipterocarpoideae), Fabaceae (subfamilies Caesalpinioideae, Mimosoideae, and Papilionoideae), Geraniaceae, Malvaceae (including Bombacaceae, Sterculiaceae, and Tiliaceae), Nelumbonaceae, Rhamnaceae, Sapindaceae, and Sarcocaulaceae (Baskin et al., 2000). However, not all members of most of these 15 families have impermeable seed/fruit coats. For example, in the Anacardiaceae PY is restricted to the sumac complex, and in the Fabaceae many tropical taxa have a water-permeable seedcoat. In 12 of the 15 families, a specialized structure ("water plug" or "water gap") has been

Fig. 1. Sagittal sections of a stylized seed of a Papilionoid legume [e.g., clovers (*Trifolium* spp.)]: (a) whole seed. (b) portion of the seedcoat showing water gap (lens) closed. (c) portion of the seedcoat showing lens open. CL, cleft; Cu, cuticle; E, embryo; H, hilum; L, lens; M, micro-pyle; P, impermeable palisade layer of seedcoat; RL, radicle lobe (from Baskin, 2003, with permission from *New Phytologist*).

identified in the impermeable seed or fruit coat. There are several kinds of these specialized structures, which hereafter are referred to as water gaps; one example is shown in Fig. 1. These structures are dislodged or disrupted in response to environmental cues such as heat from fire, high temperatures, or alternating temperatures, thereby creating an entry point for water into the seed (Baskin et al., 2000). From a world perspective, PY is the second (next to PD) most common class of dormancy (Baskin and Baskin, 1998; Baskin and Baskin, 2003a).

Seeds with **combinational dormancy** have both an impermeable seed or fruit coat and a physiologically-dormant embryo. In cranesbill (*Geranium* spp.), mallow (*Malva* spp.), bird's foot (*Ornithopus* spp.), bur-cucumber (*Sicyos* spp.), pencil-flower (*Stylosanthes* spp.), and clover (*Trifolium* spp.), PD is broken via afterripening before PY is broken; however, in redroot (*Ceanothus* spp.), redbud (*Cercis* spp.), smoke tree (*Cotinus* spp.), golden raintree (*Koelreuteria* spp.), sumac, and basswood (*Tilia* spp.), PY must be broken before PD can be broken via cold stratification, i.e., seeds must be imbibed (Baskin and Baskin, 1998).

Table 1. A dichotomous key to distinguish nondormancy and the five classes of seed² dormancy (modified from Baskin and Baskin, 2004).

1. Embryo undifferentiated or if differentiated it is underdeveloped	2
2. Embryo not differentiated	SPECIALIZED TYPE OF MORPHOLOGICAL OR MORPHOPHYSIOLOGICAL DORMANCY
2. Embryo differentiated but underdeveloped	3
3. After seeds are placed on a moist substrate, the embryo grows, and seeds germinate in 4 weeks or less.....	MORPHOLOGICAL DORMANCY
3. After seeds are placed on a moist substrate, the embryo does not grow, and seeds do not germinate in about 4 weeks.....	MORPHOPHYSIOLOGICAL DORMANCY
1. Embryo differentiated and fully developed	4
4. Seeds imbibe water	
5. Seeds germinate within about 4 weeks	NONDORMANT
5. Seeds do not germinate within about 4 weeks.....	PHYSIOLOGICAL DORMANCY
4. Seeds do not imbibe water	6
6. Scarified seeds germinate in 4 weeks or less.....	PHYSICAL DORMANCY
6. Scarified seeds do not germinate in 4 weeks	COMBINATIONAL DORMANCY

²Natural dispersal/germination unit may be a seed, or it may be a seed covered by one or more layers of the pericarp or other structures (e.g., bracts in some *Chenopodiaceae*).

From a world perspective, combinational dormancy is the rarest class of dormancy (Baskin and Baskin, 1998, 2003a).

A DICHOTOMOUS KEY FOR CLASSES OF SEED DORMANCY. If fresh seeds are dormant, it is very helpful, especially from a plant propagation perspective, to know what kind of dormancy they have before planning germination studies. Thus, a key to distinguish the five classes of seed dormancy has been developed using information on: 1) the developmental state/size of the embryo; 2) whether the seed/fruit coat is permeable to water; and 3) whether the seed germinates within 4 weeks or less (Table 1). It is assumed that studies begin with freshly matured seeds and that seeds are incubated at temperatures (e.g., daily alternating temperature regimes of 20/10 °C and/or 25/15 °C) appropriate for germination.

As a first step in using this key, seeds should be imbibed for 24 h at room temperatures and then cut open to expose the embryo using a dissecting microscope. The objective is to determine if the embryo has organs (if so, the embryo is differentiated), and if the embryo is fully developed (if so, the embryo will be as long as half or

more the full length of the seed).

Seed size can be useful in predicting information about the embryo. If a seed is ≤ 0.2 mm (0.008 inch) in length, it probably will have an undifferentiated embryo (Martin, 1946; Baskin and Baskin, 1998). Some seeds between 0.2 and 2.0 mm (0.08 inch) in length have undifferentiated embryos, but most do not. Differentiated, underdeveloped embryos usually occur in seeds that are greater than 2.0 mm in length; however, fully developed embryos can occur in seeds that are less than or greater than 2.0 mm.

BREAKING PHYSIOLOGICAL DORMANCY. In subtropical/tropical regions, PD is broken while seeds are exposed to warm wet (warm stratification) or warm dry (afterripening) conditions. However, in other climatic regions warm wet, warm dry, or cool wet (cold stratification) conditions may be required for dormancy loss to occur, depending on the species.

Three levels of PD have been distinguished: deep, intermediate, and nondeep (Nikolaeva, 1969). In general, seeds with deep PD require 10–16 weeks of cold stratification to become nondormant, while those with intermediate PD require 8–14 weeks of cold stratification to become

nondormant. However, a period of afterripening or of warm stratification may reduce the length of the cold stratification period required to break intermediate PD. Nondeep PD is broken in seeds of many species by 2–8 weeks of warm stratification (or sometime by 8–12 weeks of afterripening), but it is broken in seeds of other species by 2–10 weeks of cold stratification. Seeds of all species with PD in subtropical/tropical climatic regions, and most of those in other parts of the world, have nondeep PD.

Seeds with nondeep PD exhibit a continuum of changes as they go from dormancy (D) to conditional dormancy (CD) and finally to nondormancy (ND), i.e., $D \rightarrow CD \rightarrow ND$. Seeds coming out of dormancy exhibit various patterns in the temperatures at which they can germinate while in conditional dormancy. In the early phases of conditional dormancy, seeds of some species germinate to high percentages only at low (15/6 °C), others at high [30/15 °C (86.0/59.0 °F)], and still others at intermediate (20/10 °C) temperatures (Baskin and Baskin, 1998, 2003a). After seeds are nondormant, they will germinate over the full range of temperatures possible for the species, if light and moisture are not limiting. Thus, when working with dormant seeds of wild plants, it seems logical to test them over a range of temperatures after various periods of exposure to dormancy-breaking treatments such as cold stratification or warm stratification.

GERMINATING SEEDS AFTER PD IS BROKEN. Although seeds with deep or intermediate PD may germinate at the same low temperatures [e.g., 5 °C (41.0 °F)] at which dormancy is broken, the temperature regime required to break dormancy in seeds with nondeep PD frequently is not the optimal temperature for germination, especially while seeds are in conditional dormancy. For example, the optimal temperature for dormancy break in seeds of winter annuals is summer temperatures [e.g., 30/15 °C or 35/20 °C (95.0/68.0 °F)], but the only temperatures at which seeds will germinate when they are in the early phases of conditional dormancy are low autumn (e.g., 15/6 °C) temperatures. Later, after several months of exposure to high summer temperatures, seeds eventually become nondormant and thus gain the ability to germinate over

a wide range of temperatures including 25/15 °C and even sometimes 30/15 °C. Thus, if one were eager to obtain seedlings, it would be good to expose seeds to high summer temperatures for 1–2 months, and then test them at a low or moderate temperature. In many summer annuals, responses to temperature are just the reverse of what they are for a winter annual. That is, cold stratification breaks PD, but in the early phases of conditional dormancy, high temperatures (e.g., 30/15 °C) are optimal for germination (Baskin and Baskin, 1998).

After seeds with PD, and especially those with nondeep PD, have come out of dormancy (during exposure to either high summer or low winter temperatures) environmental factors other than temperature may play a role in promoting germination. For example, seeds of the summer annual hall's bulrush (*Schoenoplectus hallii*), a rare species occurring in occasionally-flooded sites, have nondeep PD and require cold stratification to come out of dormancy. This treatment can be given while seeds are buried in moist (but nonflooded) soil and exposed to natural temperature regimes in central Kentucky (Baskin et al., 2003). However, seeds do not germinate unless they are flooded and exposed to light, high temperatures, and ethylene. In contrast to the flooding requirement for germination of hall's bulrush seeds, there is a growing body of evidence, especially in South Africa, Australia, and California that smoke from fires can significantly increase germination of seeds of various species growing in fire-prone seasonally-dry sclerophyllous woodlands (Baskin and Baskin, 1998; Roche et al., 1998).

Another unique feature about many seeds with nondeep PD in the temperate zone is their ability to reenter dormancy (secondary dormancy), if they are prevented from germinating during their normal germination season. As they reenter dormancy, they go from nondormancy to conditional dormancy and then to dormancy (i.e., ND → CD → D). Depending on the species, seeds may go all the way into dormancy or stop at conditional dormancy. In the first case, seeds cycle between dormancy and nondormancy, and in the second case between conditional dormancy and nondormancy, until they either germinate or die. In the soil environment, darkness is an

important factor that prevents many buried seeds from germinating at the time of year when they are nondormant. Low temperatures of winter induce seeds of many winter annuals into secondary dormancy (or into conditional dormancy), and dormancy or conditional dormancy is broken the following summer. High temperatures of summer induce seeds of many summer annuals into secondary dormancy (or into conditional dormancy), and dormancy or conditional dormancy is broken the following winter (Baskin and Baskin, 1998).

BREAKING MORPHOPHYSIOLOGICAL DORMANCY. Eight levels of MPD have been identified on the basis of a high vs. low temperature requirement for embryo growth, warm and/or cold stratification requirements for dormancy break, and germination response of seeds to gibberellins (GA), in particular GA₃ (Nikolaeva, 1969; Baskin and Baskin, 1998, 2004). The levels of MPD are: nondeep simple, intermediate simple, deep simple, deep epicotyl simple, deep double simple, nondeep complex, intermediate complex, and deep complex (Baskin and Baskin, 2004).

In seeds with a "simple" level of MPD, temperatures of autumn or of spring are required for embryo growth. That is, embryos do not grow during cold stratification. PD is broken in some seeds with nondeep simple MPD [yellow fumewort (*Corydalis flavula*)] during summer, and embryo growth and germination occur in autumn (Baskin and Baskin, 1998). PD of seeds of other species with nondeep simple MPD [fairy-wand (*Chamaelirium luteum*)] is broken during winter, and embryo growth and germination occur in spring (Baskin et al., 2001). In seeds with deep simple MPD [ginseng (*Panax* spp.) and twinleaf], PD is partly broken in summer, embryo growth occurs in autumn, PD is completely broken during winter, and seeds germinate in spring (Baskin and Baskin, 1998). Intermediate simple MPD is not known in a wildflower per se, but it does occur in seeds of the woody species kakure-mino zoku (*Dendropanax japonicum*) (Grushvitzky, 1967). In nature, seeds with intermediate simple MPD have the same dormancy-breaking and germination requirements as those with deep simple MPD. However, in the laboratory GA₃ can be used to substitute for the cold stratification

requirement of seeds with intermediate simple MPD but not for that of seeds with deep simple MPD (Baskin and Baskin, 1998).

PD of the radicle is broken during summer in seeds with deep epicotyl MPD [wild ginger and hepatica (*Hepatica acutiloba*)], growth of the radicle and emergence from the seeds occur in autumn, PD of the epicotyl is broken during winter, and cotyledons emerge in spring (Baskin and Baskin, 1998). In seeds with deep simple double MPD [jack-in-the-pulpit and false solomon's-seal (*Smilacina racemosa*)], PD of the radicle is broken during winter, radicle growth and emergence occur in spring, PD of the epicotyl is broken the following winter, and shoot growth occurs the second spring (Baskin and Baskin, 1998).

In seeds with a "complex" level of MPD, cold stratification is required for embryo growth, i.e., embryos grow while seeds are being cold stratified. Seeds with nondeep complex MPD [yellow trout-lily (*Erythronium americanum*), white dog's tooth violet (*E. albidum*), and anise-root (*Osmorhiza longistylis*)] require summer (warm stratification) followed by winter (cold stratification) to break PD and promote growth of the embryos. Embryo growth occurs during winter, and seeds germinate in spring (Baskin and Baskin, 1998). In contrast, only cold stratification is required to break PD and promote embryo growth in seeds with deep complex MPD [dwarf larkspur (*Delphinium tricornis*) and tulip (*Tulipa* spp.)]; thus, seeds become nondormant during winter and germinate in spring (Baskin and Baskin, 1998). Cold stratification also is the only requirement for breaking intermediate complex MPD [celandine-poppy and globe-flower (*Trollius* spp.)]. However, GA₃ will substitute for the cold stratification requirement in seeds with intermediate complex MPD but not for that of seeds with deep complex MPD (Baskin and Baskin, 1998).

MOVE-ALONG EXPERIMENT. When confronted with dormant seeds of a wild species from the temperate zone, especially those with MPD, the big question is, "Do the seeds require warm stratification, cold stratification, or both to come out of dormancy and germinate?" If the seeds are permeable to water, we suggest using the move-along experiment (Baskin and

Baskin, 2003b). This method requires relatively few seeds, and it identifies the sequence of temperature regimes necessary for dormancy break and germination. Temperatures simulating those in the natural habitat during winter, summer, and autumn/spring are used. For species from temperate regions, an incubator or refrigerator set at about 5 °C can be used to simulate winter, while summer temperature can be obtained in an air-conditioned greenhouse or in an incubator (25/15 °C is warm enough). An environmental chamber to simulate early spring and late autumn and another to simulate late spring and early autumn is very helpful. We have used 5 °C for winter, 15/6 °C for early spring/late autumn, 20/10 °C for late spring/early autumn, and 25/15 °C (sometimes 30/15 °C) for summer. However, depending on where seeds are collected, other temperature regimes may be required to simulate habitat temperatures for different seasons of the year. The experiment consists of two move-along sequences that run concurrently and four controls (seeds kept continuously at 5, 15/6, 20/10, and 25/15 °C), and three replicates of 50 seeds each are used for each; 18 (6 conditions × 3 dishes) for the whole experiment. The two move-along sequences are:

1) 25/15 °C (12 weeks) → 20/10 °C (4 weeks) → 15/6 °C (4 weeks) → 5 °C (12 weeks) → 15/6 °C (4 weeks) → 20/10 °C (4 weeks) → 25/15 °C (12 weeks) → etc.

2) 5 °C (12 weeks) → 15/6 °C (4 weeks) → 20/10 °C (4 weeks) → 25/15 °C (12 weeks) → 20/10 °C (4 weeks) → 15/6 °C (4 weeks) → 5 °C (12 weeks) → etc.

All seeds are on a wet substrate and exposed to light each day, and they are checked for germination at 1- or 2-week intervals.

One of the most interesting wildflowers we have studied using the move-along experiment is cucumber-root [*Medeola virginiana* (Liliaceae, in the broad sense)] (Baskin and Baskin, 1998). Seeds of this species required warm + cold + warm + cold stratification, and then both the radicle and epicotyl emerged at the same time at spring temperatures, suggesting that they had a special kind of deep simple double MPD. From cucumber-root, we learned that it pays to continue the move-along experiment until germina-

tion occurs; in this species 20 months were required.

BREAKING PHYSICAL DORMANCY. Under laboratory conditions, mechanical scarification is a safe and effective way to make the seed or fruit coat permeable to water. Other methods used to make seeds permeable include acid scarification and heat treatments. Scarification with concentrated sulfuric acid, dipping in boiling water, or exposure to dry heat in an oven can make seeds permeable by disrupting the water gap. However, the response of impermeable seeds to boiling water and dry heat varies with the species, and neither treatment works for some species (Baskin and Baskin 1998, unpublished data; Baskin et al., 2000).

Timing of germination of seeds with PY in nature is controlled by responses of the seeds (and specifically the water gaps) to environmental cues, and temperature is the most important factor controlling the breaking of dormancy. However, while exposure to specific temperature regimes overcomes a “physiological problem” of the embryo in seeds with PD and MPD, it disrupts the water gap in seeds with PY (Fig. 1).

The temperature regimes required to break PY vary with the species. Seeds of towns ville stylo (*Stylosanthes humilis*) and caribbean stylo (*S. hamata*) (Fabaceae) became permeable during the dry hot season in Northern Australia and thus germinated when the wet season began (McKeon and Mott, 1982). In jonote tree [*Heliocarpus donnell-smithii* (Malvaceae, in the broad sense)], 67% of the seeds germinated when placed in a Mexican rainforest canopy gap with a 15 °C difference between day and night temperatures, but only 25% of them germinated when placed under the canopy with only a 5 °C daily temperature fluctuation (Vazquez-Yanes et Orozco-Segovia, 1982). The maximum daily temperature also was higher [about 38 °C (100.4 °F)] in the gap than in the forest [about 27 °C (80.6 °F)]. Recently, Van Assche et al. (2003) found that if impermeable seeds of various spring-germinating legumes were held at 5 °C for 2 months, high percentages of them became permeable and germinated if moved from 5 to 15/6 °C or from 5 to 20/10 °C. However, seeds moved from 5 °C to a constant temperature of 10 °C or 23 °C (73.4 °F) did not become per-

meable. Thus, germination in spring occurs only if seeds are subjected to low winter temperatures followed by low alternating temperature regimes of early spring. Any seeds buried in soil in spring would not be subjected to the daily alternating temperature regimes required to make them permeable, and consequently they would not germinate and thus remain in the soil seed bank.

Even after seeds are subjected to temperature regimes that promote opening of the water gap, they may require a number of days on a wet substrate before they imbibe water and germinate, e.g., 3–12 d were required for all the heat-treated seeds of ‘a’ali’i [*Dodonaea viscosa* (Sapindaceae)] collected in Hawaii to imbibe and 7–14 d for them to germinate (Baskin et al., 2004). Slow imbibition means that seeds of ‘a’ali’i cannot germinate unless the substrate is moist for 3 d or more; thus, it serves as a natural “rain gauge.” Once dormancy is broken in seeds of ‘a’ali’i and in those of other taxa with PY, germination can occur over a wide range of temperature and light (even high far red:red ratio) conditions (Baskin et al., 2004).

Many people have speculated that soil microbial action and/or abrasion by soil particles play a role in making seeds with PY water-permeable. In fact, many botany and plant physiology text books, as well as books and review articles on seeds, have stated that soil microbes and/or mechanical abrasion are responsible for seeds with PY becoming permeable (Baskin and Baskin, 2000). There are some problems with these explanations of the way in which PY is broken. 1) Only weak support can be found in the literature that microorganisms promote germination of seeds with PY (Baskin and Baskin, 2000). In fact, Kremer (1993) found evidence that soil microbes on the seed surface produced compounds which prevented the growth of fungi, thereby preventing breakdown of the seedcoat. 2) No experimental evidence is available to support the idea of mechanical abrasion as a means of breaking PY. 3) The books and papers in which microbes and abrasion were claimed to be the mechanisms for breaking PY make little or no mention of the fact that the water gap serves as a detector of environmental cues for germination at a time when conditions are suitable for seedling establishment. 4) It does

not make evolutionary and ecological sense for seed dormancy break to be controlled by factors (microbes and/or mechanical abrasion) that may act at any season of the year; that is, there is no mechanism for coordinating the loss of PY with favorability of the environment for seedling survival. Finally, one has to ask why an anatomically-complex water gap, such as the bixoid chalazal plug in members of several orders of the superorder Malvanae (Nandi, 1998), evolved, if it did not have a specific function, i.e., physical environmental signal detector for dormancy break.

EFFECTS OF ANIMALS ON SEEDS.

Many (but not all!) seeds eaten by animals pass through the digestive tract without losing viability. Depending on the species, passage of seeds with PY through a digestive tract may increase germination percentages, compared to control seeds (Baskin and Baskin, 1998); however, it is not clear why this treatment increases germination. Careful studies have ruled out abrasion as a dormancy-breaking factor. Further, prolonged exposure to the acidic contents of digestive systems does not result in 100% of the seeds becoming permeable. Another factor that may be involved is the warm, wet treatment seeds receive as they move through the digestive tract. Finally, Gill (1985) has suggested that the wet, high temperature conditions experienced by seeds in fecal material dropped in sunny locations could play a role in breaking PY.

Animals also eat fruits containing seeds without PY (i.e., seeds are permeable to water when they are eaten). Depending on the digestive system of the animal and the kind of seed, large numbers of viable seeds can be found in fecal or regurgitated material. Germination percentages of seeds collected from this fecal or regurgitated material may be equal to, less than, or greater than those of control seeds (Baskin and Baskin, 1998; Cochrane, 2003; Traveset et al., 2001; Schaumann and Heinken, 2002). It is not known why germination percentages of permeable seeds would be improved after they pass through an animal. One hypothesis is that the digestive system removes all the fruit material that could be attacked by pathogens that kill the seeds before they can germinate (Witmer, 1991). In fact, Witmer has suggested that the extinct dodo bird may have promoted germination of seeds of

the tambalacoque tree [*Calvaria* sp. (Sapotaceae)] not by making them permeable but by removing fruit material that promoted growth of pathogenic organisms. Germination also may be increased by hand-removal of fruit material from around seeds (Cowl- ing et al., 1997; Meyer and Witmer, 1998), and in some species germination is prevented (Burrows, 1999) or delayed (N. Hill, C. Baskin, and J. Baskin, unpublished data) unless the fruit material is removed. Research is needed to better understand the role of fruit material in regulating the timing of germination.

CONCLUDING THOUGHTS. Non-dormant seeds can germinate as soon as they are dispersed, if soil moisture, aeration, light/dark, and temperature requirements for germination are non-limiting. However, seeds with MD, PD, MPD, PY or PY+PD must undergo changes before they can germinate, and the timing of the occurrence of these changes depends on the class of dormancy and the environment.

Seeds with MD may germinate shortly after dispersal, if environmental conditions are suitable for embryo growth, but germination can be delayed for several months if the environment is not favorable. For example, seeds of false rue anemone (*Isopyrum biternatum*), which have MD and require relatively low temperatures (15/6, 20/10 °C) for embryo growth, are dispersed in mid- to late May, after temperatures are too high for embryo growth. Thus, embryo growth and germination are delayed until autumn, after temperatures have declined (Baskin and Baskin, 1986).

In seeds with PD, MPD, and PY+PD, the changes required to break PD take place slowly (frequently requiring several months), and they occur during the season of the year when environmental conditions are not favorable for seedling establishment. However, PD is broken by the end of the unfavorable season, thus seeds can germinate at the beginning of the favorable season for seedling establishment and growth. In contrast, dormancy break takes place relatively quickly in seeds with PY, although 1–2 weeks may be required in seeds of some species (e.g., Baskin et al., 2004). Further, the environmental factor resulting in dislodgement or pulling apart of the water gap may occur immediately prior to the time the habitat is favorable for

seedling establishment, e.g., a fire that exposes the soil surface to full sunlight. On the other hand, the environmental factor that causes the water gap to open may be associated with the favorable environment itself, e.g., the increased daily temperature fluctuations that occur when soil is disturbed during the growing season are a signal that seeds are near the soil surface and/or a light gap has been created.

Literature cited

- Angiosperm Phylogeny Group. 1998. An ordinal classification for families of flowering plants. *Ann. Missouri Bot. Garden* 85:531–553.
- Ballard, W. W. 1987. Sterile propagation of *Cypripedium reginae* from seeds. *Amer. Orchid Soc. Bul.* 56:935–946.
- Baskin, C.C. 2003. Commentary: Breaking physical dormancy in seeds—Focusing on the lens. *New Phytol.* 158:229–232.
- Baskin, C.C. and J.M. Baskin. 1998. Seeds: Ecology, biogeography, and evolution of dormancy and germination. *Acad. Press, San Diego*.
- Baskin, C.C. and J.M. Baskin. 2003b. When breaking seed dormancy is a problem, try a move-along experiment. *Native Plants J.* 4:17–21.
- Baskin, C.C. and J.M. Baskin. 2004. Determining dormancy-breaking and germination requirements from the fewest seeds, p. 162–179. In: E. Guerrant, K. Havens, and M. Maunder (eds.). *Ex situ plant conservation: Supporting species survival in the wild*. Island Press, Covelo, Calif.
- Baskin, C.C., J.M. Baskin, and E.W. Chester. 2001. Morphophysiological dormancy in seeds of *Chamaelirium luteum*, a long-lived dioecious lily. *J. Torrey Bot. Soc.* 128:7–15.
- Baskin, C.C., J.M. Baskin, E.W. Chester, and M. Smith. 2003. Ethylene as a possible cue for seed germination of *Schoenoplectus hallii* (Cyperaceae), a rare summer annual of occasionally flooded sites. *Amer. J. Bot.* 90:620–627.
- Baskin, J.M. and C.C. Baskin. 1986. Germination ecophysiology of the mesic deciduous forest herb *Isopyrum biternatum*. *Bot. Gaz.* 147:152–155.
- Baskin, J.M. and C.C. Baskin. 2000. Evolutionary considerations of claims for physical dormancy-break by microbial action and abrasion by soil particles. *Seed Sci. Res.* 10:409–413.
- Baskin, J.M. and C.C. Baskin. 2003a. Classification, biogeography, and phylogenetic relationships of seed dormancy, p.

- 517–544. In: R.D. Smith et al. (eds.). Seed conservation: Turning science into practice. Royal Bot. Gardens, Kew, U.K.
- Baskin, J.M., C.C. Baskin, and X. Li. 2000. Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biol.* 15:139–152.
- Baskin, J.M., B.H. Davis, C.C. Baskin, S. M. Gleason, and S. Cordell. 2004. Physical dormancy in seeds of *Dodonaea viscosa* (Sapindales, Sapindaceae) from Hawaii. *Seed Sci. Res.* 14:81–90.
- Burrows, C.J. 1999. Germination behaviour of seeds of the New Zealand woody species *Alseuosmia macrophylla*, *A. pusilla*, *Cordyline banksii*, *Geniostoma rupestre*, *Myrtus bullata*, and *Solanum aviculare*. *New Zealand J. Bot.* 37:277–287.
- Cochrane, E.P. 2003. The need to be eaten: *Balanites wilsoniana* with and without elephant seed-dispersal. *J. Trop. Ecol.* 19:579–589.
- Cowling, R.M., J.J. Midgley, D. Kirkwood, and S.M. Pierce. 1997. Invasion and persistence of bird-dispersed, subtropical thicket and forest species in fire-prone coastal fynbos. *J. Vegetation Sci.* 8:475–488.
- Gill, M. 1985. *Acacia cyclops* G. Don (Leguminosae-Mimosaceae) in Australia: Distribution and dispersal. *J. Roy. Soc. W. Austral.* 67:59–65.
- Grushvitzky, I.V. 1967. After-ripening of seeds of primitive tribes of angiosperms, conditions and peculiarities, p. 329–345. In: H. Borris (ed.). *Physiologie, Ökologie und Biochemie der Keimung*. Vol. 1. Ernst-Moritz-Arndt Universität, Greifswald, Germany.
- Ichihashi, S. 1989. Seed germination of *Ponerorchis graminifolia*. *Lindleyana* 4:161–163.
- Kremer, R.J. 1993. Management of weed seed banks with microorganisms. *Ecol. Applications* 3:42–52.
- Martin, A.C. 1946. The comparative internal morphology of seeds. *Amer. Midland Naturalist* 36:513–660.
- McKeon, G.M. and J.J. Mott. 1982. The effect of temperature on the field softening of hard seed of *Stylosanthes humilis* and *S. hamata* in a dry monsoonal climate. *Austral. J. Agr. Res.* 33:75–85.
- Meyer, G.A. and M.C. Witmer. 1998. Influence of seed processing by frugivorous birds on germination success of three North American shrubs. *Amer. Midland Naturalist* 140:129–139.
- Nandi, O.I. 1998. Ovule and seed anatomy of Cistaceae and related Malvaceae. *Plant System. Evol.* 209:239–264.
- Nikolaeva, M.G. 1969. Physiology of deep dormancy in seeds (translated from Russian by Z. Shapiro, National Science Foundation, Washington, D.C.). Izdatel'stvo "Nauka," Leningrad.
- Roche, S., K.W. Dixon, and J.S. Pate. 1998. For everything a season: Smoke-induced seed germination and seedling recruitment in a Western Australian *Banksia* woodland. *Austral. J. Ecol.* 23:111–120.
- Schaumann, F. and R. Heinken. 2002. Endozoochorous seed dispersal by martens (*Martes foina*, *M. martes*) in two woodland habitats. *Flora* 197:370–378.
- Traveset, A., N. Riera, and R.E. Mas. 2001. Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecol.* 15:669–675.
- Van Assche, J.A., K.L.A. Debucquoy, and W.A.F. Rommens. 2003. Seasonal cycles in the germination capacity of buried seeds of some Leguminosae (Fabaceae). *New Phytol.* 158:315–323.
- Vazquez-Yanes, C. and A. Orozco-Segovia. 1982. Seed germination of a tropical rain forest pioneer tree (*Heliocarpus donnell-smithii*) in response to diurnal fluctuation of temperatures. *Physiol. Plant.* 56:295–298.
- Witmer, M.C. 1991. The dodo and the tambalacoque tree: An obligate mutualism reconsidered. *Oikos* 61:133–137.