

Symposium

The natural history of soil seed banks of arable land

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This article briefly reviews how long weed seeds can live in the soil and what happens to them during burial. Freshly matured seeds of many weeds are water-permeable, but those of others are water-impermeable. Water-permeable seeds may have morphological, physiological, or morphophysiological dormancy, with physiological dormancy (PD) being the one most commonly found in buried weed seeds. Further, nondeep PD is very common in buried weed seeds, and many of them exhibit annual dormancy cycles in response to seasonal temperature changes. The time of year when seeds are nondormant varies with the species, i.e., autumn, spring, or spring to summer. A light requirement for germination plays an important role in preventing nondormant seeds from germinating in the soil. To germinate, soil disturbance that exposes seeds to light must occur at a time of year when seeds are nondormant. Buried seeds of some species come out of dormancy and remain nondormant regardless of seasonal changes in environmental conditions; however, a light requirement for germination prevents them from germinating in the soil. Water-impermeable seeds have either physical dormancy (PY) or a combination of PY and PD, with PY being the most common, e.g., in members of the Fabaceae and Malvaceae. Seeds with PY have a water gap in the seed coat that opens in response to an environmental signal, thereby allowing water to enter. When disturbance brings seeds to the soil surface, temperatures that are higher than those in the soil can cause the water gap to open. Consequently, the water gap indirectly serves as a depth sensor. A challenge for the future is to use information about buried weed seeds to better manage weeds in crops, and modeling is an important step in that direction.

Key words: Buried weed seeds, dormancy cycling, physical dormancy, physiological dormancy, weed emergence modeling.

In *The Origin of Species*, Charles Darwin (1859 [1892]) describes how he collected a cup of soil from the edge of a pond and then kept it moist in his study for 6 mo, during which time, 537 seeds germinated. These observations by a great naturalist indicate much curiosity about seeds in the soil and probably reflect an eagerness of many people to better understand the sudden appearance of a species in places where they previously had not seen the plant growing. No doubt, people have been aware of the presence of weed seeds in agricultural soils for centuries and wondered how long they could live. In the mid-1800s, various burial experiments to determine longevity of seeds were being conducted (see Brenchley 1918), and by the late-1800s, methods for determining soil seeds banks were being tested (Kropáč 1966).

Since the mid-1900s, numerous studies have been conducted to determine the size of the weed seed bank in arable soils in many parts of the world, and the numbers sometimes are staggering (Table 1). Thus, it is no wonder that scientists began what has turned out to be a fascinating “journey” to understand buried weed seeds. Much of this research has been directed toward answering four questions: (1) How long can weed seeds live in the soil? (2) What happens to seeds in the soil? (3) What is the dormancy state of buried seeds? (4) What controls the timing of germination of buried weed seeds? In this article, we review information addressing each of these questions and consider future directions of research on buried weed seeds.

Longevity of Weed Seeds in the Soil

The most accurate way to determine longevity of seeds in the soil is to bury them, wait for various periods of time, dig up samples, and check for viability. Many studies of this type have been conducted (see table 7.5 in Baskin and Baskin 1998a), but from a weed-seed perspective, the two most famous ones were initiated by W. J. Beal in 1879 and J.W.T. Duvel in 1902, using 23 and 107 species, respectively. The Beal experiment has continued for 120 yr (Telewski and Zeevaart 2002), but unfortunately, the Duvel experiment had to be terminated after only 39 yr (Toole and Brown 1946). Combining data from both studies, the list of weeds for which some seeds were alive after 39 or 40 yr is impressive: velvetleaf (*Abutilon theophrasti* Medik.), redroot pigweed (*Amaranthus retroflexus* L.), common ragweed (*Ambrosia artemisiifolia* L.), chinagrass [*Boehmeria nivea* (L.) Gaudich], black mustard [*Brassica nigra* (L.) W.D.J. Koch], shepherd's-purse [*Capsella bursa-pastoris* (L.) Medik.], common lambsquarters (*Chenopodium album* L.), hedge bindweed (*Convolvulus sepium* L.), jimsonweed (*Datura stramonium* L.), pitted morningglory (*Ipomoea lacunosa* L.), Virginia pepperweed (*Lepidium virginicum* L.), dwarf mallow (*Malva rotundifolia* L.), common eveningprimrose (*Oenothera biennis* L.), Scotch thistle (*Onopordum acanthium* L.), common pokeweed (*Phytolacca americana* L.), broadleaf plantain (*Plantago major* L.), Kentucky bluegrass (*Poa pratensis* L.), hedge smartweed (*Polygonum scandens* L.), common purslane (*Portulaca oleracea* L.), rough cinquefoil (*Po-*

TABLE 1. Maximum number of seeds in arable soils from various parts of the world.

Country	Seeds	Reference
	No. m ⁻²	
Argentina	55,750	D'Angela et al. 1988
Australia	17,300–646,000	McIntyre 1985
Bavaria	2,500–20,000	Albrecht and Forster 1996
Canada	300–30,000	Légère and Samson 2004
Ethiopia	20,740	Teketay 1997
India	8,205	Baig 2002
Malaysia	930,910	Sahid et al. 1995
Norway	17,600	Sjursen 2001
Poland	44,569	Symonides 1986
United Kingdom	26,000	Marshall and Arnold 1994
	50,000	Moss 1985
	69,490	Brenchley and Warington 1930
United States	137,700	Schweizer and Zimdahl 1984

tentilla norvegica L.), curly dock (*Rumex crispus* L.), broad-leaf dock (*Rumex obtusifolius* L.), bristly foxtail [*Setaria verticillata* (L.) P. Beauv.], green foxtail [*Setaria viridis* (L.) P. Beauv.], black nightshade (*Solanum nigrum* L.), moth mullein (*Verbascum blattaria* L.), and common mullein (*Verbascum thapsus* L.). In the Beal experiment, some seeds of common eveningprimrose, curly dock, and moth mullein were alive after 80 yr (Darlington and Steinbauer 1961), and after 120 yr, 32 seeds of moth mullein and two of a *Verbascum* sp. germinated and produced normal plants (Telewski and Zeevaert 2002).

In some studies, the age of seeds in the soil has been inferred based on information about age of the site. For example, Ødum (1965) found viable seeds of common lambsquarters and corn spurry (*Spergula arvensis* L.) in a Danish Iron Age archeological site in a layer dated at 1700 yr. Frequently, ages of seeds are estimated using knowledge of the agricultural history of a site. For example, Brenchley (1918) found seeds of arable weeds, such as parsley-piert [*Alchemilla arvensis* (L.) Scop.], spreading orach (*Atriplex patula* L.), *Brassica* sp., *Papaver* sp., and prostrate knotweed (*Polygonum aviculare* L.), 7.5 to 20 cm below the soil surface in the 40th year after a field had been sown to permanent pasture, suggesting that the seeds had been in the soil for 40 yr or longer.

Thompson and Grime (1979) distinguished four types of soil seed banks. In Types I and II, all seeds either germinate or die within 1 yr following maturation and dispersal, and these types are called “transient seed banks.” In Types III and IV, some seeds are still viable (but not germinated) 1 yr after maturation and dispersal, and these types are called “persistent seed banks.” Seeds of many species form persistent seed banks; however, the length of time they can be in the persistent seed bank varies with the species. Thus, Bakker et al. (1996) distinguished short-term (1 to < 5 yr) and long-term (≥ 5 yr) persistent seed banks.

Fate of Seeds in the Soil

Harold A. Roberts, working at the National Vegetable Research Station, Wellesbourne (England), began experi-

ments in 1953 to understand the fate of weed seeds in soil (Roberts, 1962). Some of his studies involved the use of plots in fields, whereas others were conducted in open-ended, glazed earthenware cylinders sunk into the ground, with the rim 8 cm above the soil surface. These cylinders were filled with soil, and known numbers of seeds were incorporated into each. Over the years, he determined fates of seeds of many species at different depths and in response to soil disturbance, rainfall, and management and cropping regimes (Roberts and Feast 1972; Roberts and Neilson 1981). He also determined yearly and seasonal patterns of germination in relation to cultivation and rainfall (Roberts 1984; Roberts and Potter 1980).

Schafer and Chilcote (1969) published a conceptual model for the persistence (P) and depletion (D) of seeds (S) in the soil seed bank.

$$S = P_{ex} + P_{end} + D_g + D_n \quad [1]$$

In this model, S equals the sum of all seeds; P_{ex} equals living, nondormant seeds that are prevented from germinating by some unfavorable environmental factor such as darkness; P_{end} is living seeds that do not germinate because they are dormant; D_g is seeds that germinate in the soil (in situ) and, thus, are no longer part of the persistent seed bank; and D_n equals nonviable seeds. Then, E. H. Roberts (1972) expanded the Schafer and Chilcote model:

$$S = P_{inn} + P_{ind} + P_{enf} + D_{gd} + D_{ge} + D_{ni} + D_{na} + D_{np} \quad [2]$$

where S is the sum of all seeds, P_{inn} is innately dormant (dormant at seed maturity), P_{ind} is induced dormancy (seeds are nondormant at maturity but became dormant after entering the seed bank), and P_{enf} equals enforced dormancy (environment prevents germination); D_{ge} equals seeds that germinate, and seedlings become established; D_{gd} equals seeds that germinate and die; D_{ni} equals seeds that were dead at the time they were buried; D_{na} equals seeds that died as a consequence of aging; and D_{np} equals seeds killed by predators or pathogens. Schafer and Chilcote (1970) added dormancy (D)/nondormancy (ND) reversibility, i.e., $D \leftrightarrow ND$, to their model. Thus, by the early 1970s, we had a basic model of what could happen to seeds while they are in the soil. However, the details of the changes that seeds themselves can undergo with respect to their state of dormancy were not added to the model until after much work had been done, in the 1970s and 1980s, on dormancy cycling (or not) in buried seeds. See Baskin and Baskin (1998b) for a conceptual model that also includes dormancy cycling.

Dormancy States of Buried Seeds

An important, early discovery about buried seeds was made by Brenchley and Warington (1930, 1933) as they monitored seedling emergence from numerous soil samples taken from arable land and maintained in a nonheated greenhouse at Rothamsted Research Station, Harpenden, Hertfordshire, U.K. These scientists documented the occurrence of germination periodicity. That is, although soil samples were watered and disturbed regularly, seedlings of many species appeared only during specific periods within the growing season. Thus, it became clear that buried seeds of

many species were not in a constant state of readiness to germinate, i.e., nondormant.

The first direct evidence that buried seeds of some species undergo changes in their dormancy state was obtained by Courtney (1968), Schafer and Chilcote (1970), and Taylorson (1970). Additional evidence was provided by Stoller and Wax (1974), Karssen (1980/1981), and Baskin and Baskin (1980). In these studies, seeds were buried under natural environmental conditions in humid, temperate regions of the Northern Hemisphere, and at intervals, samples of them were exhumed and tested for germination. It was found that seeds germinated to high percentages at some times of the year, but little or no germination occurred at other times of the year, depending on the species.

Seeds in the soil seed bank are either water-permeable or water-impermeable. Within each of these categories, seeds can be dormant, but dormancy can be broken, resulting in nondormant seeds. "Dormant" (D) seeds are defined as those that fail to germinate within about 30 d when tested over a range of environmental conditions. The reason for limiting the length of the germination test to 30 d is that after about 30 d, seeds of some species begin to come out of dormancy (Baskin and Baskin 1998a). "Nondormant" (ND) seeds are defined as those that germinate to high percentages ($\geq 80\%$), within 30 d, over the widest range of environmental conditions possible for the species or genotype.

Water-Permeable Seeds

The classes (kinds) of dormancy that may be present in water-permeable seeds include morphological, physiological, and morphophysiological, and each of these will be examined from a weed-seed perspective.

Morphological Dormancy (MD)

In seeds with MD, the embryo is undifferentiated, as in the parasitic weed *Orobanch* spp., or it is differentiated but quite small (underdeveloped), as in members of the carrot family (Apiaceae), such as poison hemlock (*Conium maculatum* L.), wild carrot (*Daucus carota* L.), and wild parsnip (*Pastinaca sativa* L.). Seeds of *Orobanch* have a special kind of MD, in that, the embryo never produces cotyledons or a radicle. Instead, the embryo of *Orobanch* develops into a germ tube, the lower end of which penetrates the host and becomes the haustorium and the upper portion swells to form a tubercle that gives rise to stems (Baskin and Baskin 1998a, p. 460). In seeds with a differentiated, underdeveloped embryo, like those of poison hemlock, the small embryo in mature seeds has cotyledons and a radicle, but the embryo must grow (within the confines of the endosperm) before radicle emergence occurs (Baskin and Baskin 1990a). The length of the dormancy period is the time required for embryo growth and is usually about 30 d or less if seeds are exposed to moderate temperatures, moisture, and light (or darkness in some species).

Physiological Dormancy (PD)

Seeds with PD have a "physiological inhibiting mechanism" in the embryo that prevents it from exerting enough growth potential (or push power) to overcome the mechan-

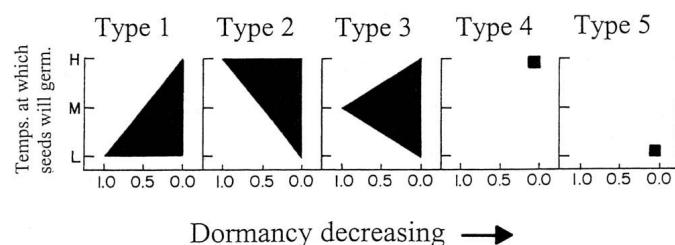


FIGURE 1. Types of nondeep physiological dormancy in seeds. Abbreviations: L, low temperature; M, intermediate temperature; H, high temperature; 1.0, seeds dormant; 0.0, seeds nondormant, and between 1.0 and 0.0, seeds are in conditional dormancy (with permission from Baskin and Baskin, 2004).

ical resistance of the seed coat and of the endosperm or parts of the pericarp, if present. Based on effect of gibberellins on dormancy break, whether or not embryos excised from dormant seeds will grow and produce a normal seedlings, and the relative amount of time required for dormancy to be broken, three levels of PD have been distinguished: nondeep, intermediate, and deep (Nikolaeva, 1969). Most weeds of arable land in temperate regions have seeds with nondeep PD (Baskin and Baskin 1998a).

Depending on the species, nondeep PD is broken by cold stratification (imbibed seeds at 0 to 10 C) or by warm stratification (imbibed seeds at ≥ 15 C). However, seeds of many species, especially those that come out of dormancy during warm stratification, will also after-ripen (come out of dormancy) in dry storage at room temperatures (Baskin and Baskin 1998a). Many, but not all, seeds with nondeep PD exhibit a widening of the temperature range over which they will germinate as the breaking of dormancy takes place. A widening of the temperature range for germination means that seeds pass through a series (continuum) of transitional stages known as *conditional dormancy* (CD) as they go from D to ND (or from ND back to D). If seeds are conditionally dormant, they germinate to high percentages at some, but not at all, of the conditions possible for the species. As the length of the dormancy-breaking treatment increases, the range of conditions over which seeds will germinate increases. Finally, seeds are ND and can germinate over the full range of conditions possible for the species or genotype. As dormancy is broken, the temperature range for germination and sensitivity to light and hormones may increase, whereas sensitivity to soil moisture may decrease (Baskin and Baskin 1998a). Also, many, but not all, seeds with nondeep PD exhibit dormancy cycles in response to seasonal temperature cycles in temperate regions (see below).

Five types of nondeep PD (Types 1, 2, 3, 4, and 5) have been identified, and three of them (Types 1, 2, and 3) occur in arable weeds of temperate regions (Figure 1), with Types 1 and 2 being by far the most common. Thus, we will discuss Types 1 and 2 in detail and only briefly describe Type 3, and our discussion will be limited to the temperate region. However, as more is learned about the dormancy-breaking and germination requirements of weeds of arable land in subtropical and tropical regions, we may discover that Types 4 and 5 are important.

In general, seeds of winter annuals have Type 1 nondeep PD, but a few perennials also have this type. In Type 1, seeds in the early stages of CD germinate only at low temperatures, but as dormancy break progresses, the maximum

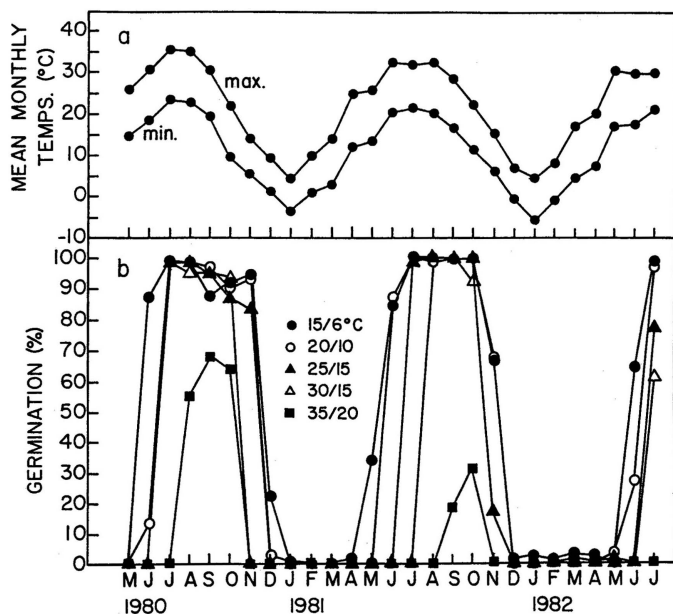


FIGURE 2. Annual dormancy/nondormancy cycle in buried seeds of the obligate winter annual, purple deadnettle. (a) Mean daily maximum and minimum temperatures that seeds were exposed to during burial. (b) Germination of seeds incubated at a 14-h daily photoperiod for 15 d following various periods of burial. Seeds incubated in darkness did not germinate (with permission from Baskin and Baskin, 1984a).

temperature at which seeds will germinate increases (Figures 1 and 2). ND seeds germinate to high percentages over a range of temperatures. D or CD seeds become ND when buried in moist soil at high (25/15 and 30/15 C day/night temperatures) but not at low temperatures (5 C or 15/6 C day/night temperature). Depending on the species, however, D seeds may become CD when buried at low temperatures, in which case they will be able to germinate at low, but not at high, temperatures (Baskin and Baskin 1984a). In the field, seeds of winter annuals are produced in spring and early summer, at which time, they are D or CD. If seeds are CD when dispersed, high temperatures in the habitat prevent them from germinating. Dormancy break occurs during summer as seeds are exposed to high temperatures, and they germinate in autumn when and if soil moisture and light requirements are fulfilled (Baskin and Baskin 1998a).

From a weed management perspective, what happens to seeds that fail to germinate in autumn is important. For some species, such as purple deadnettle (*Lamium purpureum* L.), the low temperatures in late autumn to early winter induce buried seeds into secondary dormancy (Baskin and Baskin 1984a). Thus, buried seeds are D in spring, and even if the soil is disturbed, germination does not occur (Baskin et al. 1986); this species is an obligate winter annual. In many winter annuals, however, low temperatures cause seeds to lose the ability to germinate at high, but not at low, temperatures; thus, they are capable of germinating in spring if exposed to light (Figure 3). Consequently, soil disturbance in spring promotes germination of species like henbit (*Lamium amplexicaule* L.) (Baskin et al. 1986); this species is a facultative winter annual. In some facultative winter annuals (Baskin and Baskin 1989a), the time when seeds enter CD may be delayed until late winter or early spring. Further, in henbit, germination in late summer to early autumn can

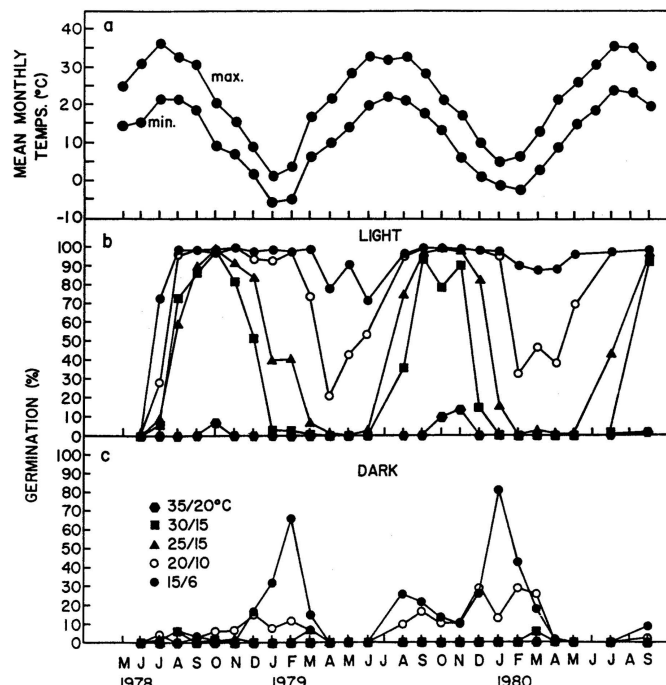


FIGURE 3. Annual conditional dormancy/nondormancy cycle in buried seeds of the facultative winter annual, henbit. (a) Mean daily maximum and minimum temperatures that seeds were exposed to during burial. (b) Germination of seeds incubated at a 14-h daily photoperiod for 15 d following various periods of burial. (c) Germination of seeds incubated in darkness following various periods of burial. (with permission from Baskin and Baskin, 1998a).

result in plants that produce seeds in autumn, and these seeds can enter CD during winter and germinate in spring (Baskin and Baskin 1984b). In Sweden, seeds of Shepherd's-purse and flixweed [*Descurainia sophia* (L.) Webb ex Prantl] that mature in late summer to early autumn enter ND and CD, respectively, during exposure to low habitat temperatures from late summer to spring, and seeds of both species can germinate in spring (Baskin et al. 2004). If all winter annuals behaved as obligate winter annuals, management efforts could be focused only on autumn; however, facultative winter annuals may require that control measures be undertaken in both autumn and spring.

In general, seeds of summer annuals and many perennials in temperate regions have Type 2. In Type 2 nondeep PD, seeds in the early stages of CD germinate only at high temperatures, but as dormancy break progresses, the minimum temperature at which seeds will germinate decreases (Figure 1). Finally, seeds become ND and can germinate to high percentages over a range of temperatures. D or CD seeds become ND when buried in moist soil at low (5 C and 15/6 C day/night temperature) temperatures. However, depending on the species, D seeds buried at high temperatures (20/10, 25/15, and 30/15 C day/night temperatures) may become CD; in which case, they germinate at high, but not at low, temperatures. In the field, seeds mature in late summer and autumn, and they are D or CD. If seeds are CD in autumn, low temperatures of the habitat prevent them from germinating (Baskin and Baskin 1998a). Seeds come out of dormancy during exposure to low temperatures during winter. By spring and early summer, depending on the species, seeds are capable of germinating at the lowest pos-

sible temperature for the species or genotype, temperatures in the habitat begin to increase, and thus, seeds germinate if their light and moisture requirements are fulfilled.

In a few summer annual weeds, such as common ragweed, darkness combined with increasing temperatures in late spring induce the ungerminated ND seeds into secondary D (Baskin and Baskin 1980). However, buried seeds of many temperate-zone summer annuals (e.g., *Amaranthus* spp. and common lambsquarters) are not induced into D in spring. Instead, entrance of seeds of many summer annual weeds into secondary D or CD may not occur until summer or autumn, depending on the species (e.g., Baskin and Baskin 1986). Thus, seeds germinate following soil disturbance throughout much of the growing season. It would be a dream-come-true for weed management if we could find a way to induce all ungerminated seeds of summer annuals into secondary D early in the warm growing season.

Type 3 nondeep PD is found in a few winter annuals, summer annuals, and perennials (Baskin and Baskin 1998a). In Type 3, seeds in the early phases of CD germinate only at intermediate temperatures. As dormancy break progresses, the maximum and minimum temperatures at which seeds will germinate increase and decrease, respectively, and ND seeds germinate over a range of temperatures. Type 3 has been reported in some temperate-zone members of the Asteraceae, Cyperaceae, Lamiaceae, Liliaceae, and Scrophulariaceae, but none of the species is considered to be a serious weed of arable land.

Although buried seeds of many weeds of arable land in temperate regions have nondeep PD and undergo annual D → CD → ND → CD → D or CD → ND → CD cycles, there are water-permeable seeds in the soil that do not exhibit cyclic changes in dormancy states. For example, freshly matured seeds of curly dock (Baskin and Baskin 1985) are conditionally dormant, and those of sulfur cinquefoil (*Potentilla recta* L.) (Baskin and Baskin 1990b) and Virginia pepperweed (Baskin and Baskin unpublished) are D. Dormancy in buried seeds of these three species is broken during summer or autumn, after which, seeds remain ND regardless of seasonal temperature cycles. These seeds require light for germination; consequently, germination of buried seeds does not occur until disturbance brings them to the soil surface. However, seeds can germinate at any time from early spring until late autumn if soil moisture, daily temperature fluctuation, and light requirements are fulfilled. Thus, as pointed out by Thompson et al. (2003), dormancy is not required for long-term persistence of seeds in the soil. In the Beal buried-seed experiment, seeds of curly dock were alive after 80 yr (Darlington and Steinbauer 1961), and presumably, they had been ND all that time.

In addition to a light requirement for germination, other factors of the burial environment may play a role in preventing ND seeds from germinating in the soil. Although seeds of various species fail to germinate when buried in soil, exhumed seeds will germinate to high percentages in darkness at certain times of the year (e.g., Baskin and Baskin 1989b, 1994; Baskin et al. 1996). The soil factors responsible for inhibiting germination are not well understood, but high concentrations of carbon dioxide (Yoshioka et al. 1998), low concentrations of oxygen (Benvenuti and Macchia 1995), and inhibitory volatile products of anaerobic

respiration (Holm 1972) could play a role in preventing germination of ND buried seeds.

Although seeds of many weeds of arable land are known to live for decades in the soil, germination of buried seeds can deplete this reserve. The percentage of in situ germination varies with the species, but it generally decreases with depth of burial and increases with frequency of soil disturbance (Roberts and Dawkins 1967). Large seeds are more likely to germinate during burial than small ones (Froud-Williams et al. 1984), and factors such as crop rotation, kind of plow, and type of soil also can influence in situ germination (Baskin and Baskin 1998a).

Morphophysiological Dormancy (MPD)

Although not common among weeds of arable land, some seed bank-forming species, such as poppy (*Papaver* spp.), have MPD. That is, the embryo is both underdeveloped (but differentiated) and has PD. Seeds of corn poppy (*Papaver rhoeas* L.) have Type 1 nondeep PD, which is broken during exposure to high temperatures in the field during summer (Baskin et al. 2002). In autumn, embryos grow if the physiologically nondormant seeds are exposed to light, and germination occurs after embryo growth is completed. If embryos do not grow, and seeds fail to germinate in autumn, seeds only enter CD during exposure to low (5/1 C day/night temperature, and 1 C) temperatures during winter. Consequently, seeds may germinate in spring if exposed to light. If seeds do not germinate while they are CD in spring, they become ND in summer and potentially would germinate the following autumn if exposed to light.

Water-impermeable Seeds

Seeds with water-impermeable seed (or fruit) coats have either physical or combinational dormancy, and both classes are found in weeds of arable land, with physical being much more common than combinational.

Physical (PY)

Seed (or fruit) coat impermeability to water is caused by the presence of one or more layers of palisade cells that are heavily lignified and impregnated with various water-repellent compounds. Water-impermeable seed (or fruit) coats are known to occur in at least some members of 15 flowering plant families: 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 Sarcolaenaceae (see Baskin et al. 2000). However, only the Convolvulaceae (including Cuscutaceae), Fabaceae, and Malvaceae are important as weeds with PY in arable land in temperate regions (Baskin et al. 2000, Baskin and Baskin 1998a). The impermeable layer is in the seed coat in these three families. In the Beal and Duvel buried seed experiments, seeds of weeds with PY that were alive after 39 or 40 yr include velvetleaf, dwarf mallow (Malvaceae), hedge bindweed, and pitted morningglory (Convolvulaceae) (Telewski and Zeevaart

2002; Toole and Brown 1946), and a few dwarf mallow seeds were alive after 120 yr (Telewski and Zeevaert 2002).

Despite claims in the literature, there is essentially no evidence that dormancy-break in seeds with PY occurs via degradation of the water-impermeable seed coat either by microbial decay or abrasion by soil particles (Baskin and Baskin 2000). A specialized “water gap” has been identified in the impermeable layer of Convolvulaceae, Fabaceae, and Malvaceae, but not yet in Cucurbitaceae (Baskin et al. 2000). From an anatomical perspective, there are several kinds of water gaps, but they all respond to appropriate environmental signals by moving or pulling apart, thereby, creating an entry point for water into the seed. For example, in a papilionoid legume seed, the palisade cells in the lens pull apart creating a water gap (Baskin, 2003), whereas in seeds of prickly sida (*Sida spinosa* L.) (Malvaceae), the chalazal plug is dislodged (Egley and Paul 1981).

An important signal from the environment that often promotes dormancy break and, thus, germination of seeds with PY is a shift from relatively low to high temperatures. In the agricultural setting, seeds with PY may be exposed to an upward shift in temperatures when the soil is disturbed, and seeds are moved from some depth in the soil to the surface. On the surface, seeds are subjected not only to higher temperatures but also to greater daily temperature fluctuations than they received in the soil, which may cause the water gap to open. Thus, the water gap, via its response to temperature, serves as a depth-detecting mechanism (Baskin and Baskin 1984c, 1998a).

A second temperature signal that may result in loss of PY of some weed seeds, e.g., *Trifolium* spp., is the upward temperature shift that occurs with the arrival of spring in temperate regions. Van Assche et al. (2003) demonstrated that seeds of five spring-germinating legumes incubated on a moist substrate at 5 °C for 2 mo germinated when moved to simulated early spring daily alternating temperature regimes of 15/6 or 20/10 °C day/night temperatures. However, few or no seeds germinated if they were incubated continuously at 5 °C or 15/6 or 20/10 °C day/night temperatures. Further, seeds shifted from 5 to 10 or 23 °C did not germinate, demonstrating that the daily alternating temperatures associated with early spring (following the low temperatures of winter) were an important part of the signal causing the lens on the seeds to open.

Regardless of the environmental signal that causes the water gap to open, imbibed seeds will germinate over a wide range of constant and alternating temperatures and in light, darkness (Baskin and Baskin 1998a), green light, and light with a high far-red : red (FR : R) ratio (Baskin et al. 2004). Further, once an opened water gap allows a seed to imbibe water, the seed can be dried (without loss of viability if drying occurs before radicle emergence), but it does not become water-impermeable again, i.e., the water gap does not close (Baskin et al. 2000, 2004).

Combinational Dormancy (PY + PD)

In this class of dormancy, the seed (or fruit) coat is impermeable to water, and the embryo has PD. Depending on the species, PD is broken by high (summer) or low (winter) temperature conditions. If PD is broken by high temperatures, dormancy break occurs before the seed becomes permeable. However, if PD is broken by low temperatures, the

seed coat becomes permeable during summer or autumn, and then the seed imbibes water. After the imbibed seed is cold-stratified during winter, it germinates in spring (Baskin and Baskin 1998a). Only a few weeds of arable land have PY + PD, and chayotillo (*Sicyos deppei* G. Don) (Brecht-Franco et al. 1992) and burcucumber (*Sicyos angulatus* L.) (Baskin et al. unpublished data; Mann et al. 1981) in the Cucurbitaceae are two of the most important ones. In both species, PD of the embryo was broken as seeds after-ripened in dry storage at room temperatures. Although about 30% of chayotillo seeds became water-permeable during 6 mo of dry storage (Orozco-Segovia et al. 2000), those of burcucumber remained water-impermeable after 1 yr of dry storage at room temperatures (Baskin et al. unpublished data). Mann et al. (1981) obtained an 11% increase in water-permeable seeds of burcucumber following an 18-wk period of cold stratification at 4 °C. However, seeds of this species germinated in the field from April to October (Smeda, 2001), indicating that seed coats became permeable throughout the growing season.

Heterogeneity in Species Response

Considerable variation may occur with respect to the percentage of dormant vs. nondormant seeds in different seed lots of the same species. Also, among the seeds that do germinate, there can be variation in the range of conditions over which they will germinate. Some of this variation is genetic, but much of it is related to the environmental conditions under which the seeds mature. For example, day length, light quality, mineral nutrition, age of mother plants, position on mother plants, temperature, soil moisture, and solar irradiance have been shown to influence responses of seeds (Baskin and Baskin 1998a).

In many of the species that produce dormant seeds, a small (sometimes large) proportion of them will be nondormant. However, within a species, all the dormant seeds usually have the same class of dormancy. Only rarely does a species produce seeds with two classes of dormancy. One example of a species with two classes of dormancy is corn poppy. In seeds of this species collected at different times during summer and autumn in Sweden, 1 to 6% of them had MD and the others MPD (Baskin et al. 2002).

Much of the within-species variation in germination requirements of freshly matured seeds is found in species whose seeds have nondeep PD. The variation in germination responses between and within seed lots of a species occurs because seeds are at different points in the continuum between D and ND when they mature (or when they are tested). If seeds are placed under appropriate conditions for dormancy break to occur, all of them will become ND, thereby eliminating the variation in germination responses (Baskin and Baskin 1998a).

Although all the freshly matured seeds of a species are dormant, they may vary in their behavior when buried in the soil, depending on the conditions under which they matured. For example, seeds of field violet (*Viola arvensis* Murr.) have nondeep PD, and all are dormant at maturity in spring (Baskin and Baskin 1995). However, seeds of this species that matured in 1981 exhibited an annual D/ND cycle when buried in soil for 33 mo, whereas those that matured in 1982 exhibited an annual CD/ND cycle while

buried for 20 mo. Further, more seeds had a D/ND cycle if collected in the same field in June than if collected in May; both were buried immediately after collection. Thus, the buried seed bank of field violet contains some seeds that cycle between D and ND and others that cycle between CD and ND.

Predicting Seedling Emergence and Future Research

Great advances have been made in our understanding of the basic ecology of seeds of arable weeds since the early 1900s. However, there are challenges for the future: (1) filling gaps in our knowledge about ecophysiology of buried weed seeds, and (2) making the already-acquired information useful to people who are attempting to manage weeds and grow crops. In trying to accomplish the latter goal, models that could accurately predict the kinds and numbers of weed seeds germinating in a field in a given year and the timing of seedling emergence are needed.

In trying to predict the size of field populations based on information about the soil seed bank of three summer annuals, Forcella (1992) found that sampling in spring was more reliable than sampling in autumn because many seeds died during winter. Also, greenhouse germination of seeds in soil samples was a better indicator of seedling emergence in spring than extracting and counting the number of seeds in soil samples. However, even when the size of the soil seed bank is known, the percentage of emergence varies with the species, year, weather patterns, and depth of burial (Forcella 1992; Mohler and Galford 1997). Thus, making a highly predictive model for weed seed emergence has proven to be a difficult task.

Grundy (2003) recently reviewed the modeling efforts to predict weed emergence and placed the models into two general categories: empirical and reductionist. Empirical modeling involves correlation of measurable factors such as date of plowing, soil temperatures, dormancy state of seeds, soil penetration resistance (Vleeshouwers and Kropff 2000), and hydrothermal time (i.e., soil moisture and temperature) (Ekeleme et al. 2005) to predict number and time of emergence of weed seedlings. However, an empirical model may only focus on one species in a limited area, e.g., common lambsquarters in southwestern Quebec, and a limited set of factors, such as air temperatures at the time of soil disturbance, to predict time of seedling emergence (Leblanc et al. 2003).

In reductionist modeling, a model is developed for each of the various aspects of seed ecology and physiology that ultimately may play a role in the germination of weed seeds. Thus, there are models for dormancy break (Batlla et al. 2003), dormancy cycling (Vleeshouwers and Boumeester 2001), changes in sensitivity of seeds to water potential (Batlla and Benech-Arnold 2004) and light (Batlla and Benech-Arnold 2005) as dormancy break occurs, and effects of seed density, weight, and shape on emergence from soil (Grundy et al. 2003).

As our understanding of the ecology of germination and recruitment processes has advanced, there have been improvements in the predictive accuracy of empirical modeling efforts. Whereas much of the early work on field germination and emergence was constrained to examining single

environmental factors, we now face the exciting prospect of examining the importance of multiple interacting factors. Could this multifactor approach lead to models that include the number of seeds in the soil, environmental factors (e.g., air temperatures, depth of burial, precipitation, and soil aeration, texture, and water potential), vertical and lateral seed movements during plowing (Colbach et al. 2000; Mohler and Galford 1997), and effects of farming practices, such as no-till (Colbach et al. 2005)? Also, the new type models should include seed factors (Forcella et al. 2000) and death of seeds due to in situ germination, pathogens, and predators (Roberts 1972; Schafer and Chilcote 1969, 1970). An attempt to develop a super multifactor model would, no doubt, quickly reveal to us that we need to learn more about the natural history of buried seeds in arable soils. For example, we need to know more about the effects of the soil gaseous environment on the control of dormancy break, dormancy induction, and germination (Dekker and Hargrove 2002) and differences in seeds of the same species collected in different locations (Grundy et al. 2003) or even at different times in the same year in a single population of a species (Baskin and Baskin 1995).

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