Chapter 8

Determining Dormancy-Breaking and Germination Requirements from the Fewest Seeds

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A small number of seeds greatly limits the number, kind, and size of experiments that can be conducted to determine the dormancy-breaking and germination requirements of a species. For many species, problems related to a low number of seeds can be solved simply by returning to the field and collecting additional seeds. However, in some rare species (and sometimes also in common, widely distributed ones) with low seed production, it is undesirable or impractical to collect large numbers of seeds. However, even with a small number of seeds, it is possible to learn much about the germination biology of a species.

In this chapter, we show how information on seeds of other members of the family and on the life cycle (especially the phenology of seed maturation, dispersal, and germination) of the species under study may suggest the kind of dormancy present and how and when it is broken in nature. To facilitate seed germination studies, we describe how to differentiate the various general kinds of dormancy (or lack thereof). Because physiological dormancy is the most common and morphophysiological dormancy is the most difficult to break, much attention is devoted to these types of dormancy in this chapter. We have designed a move-along experiment involving a small number of seeds to determine the sequence of environmental conditions required to break dormancy in seeds with physiological or morphophysiological dormancy. We present our key for the eight known types of morphophysiological dormancy and discuss the use of data from the move-along experiment in identifying these types.

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he time of maturation, seeds of many species including *Chrysanthe-* *leucanthemum* L. (Baskin and Baskin 1988), *Agropyron repens* (L.) uv. (Williams 1971), and *Rumex obtusifolius* L. (Steinbauer and sby 1960) germinate over a wide range of environmental conditions; se seeds are nondormant (*sensu* Baskin and Baskin 1985) or nearly so. e seeds of concern to us in this chapter do not germinate at any condi- s when they are freshly matured and thus are dormant. Although it y not be too difficult to distinguish dormant from nondormant seeds, ntifying the kind of seed dormancy can be difficult. One of the best es to the kind of dormancy in seeds of a given species comes from infor- tion in the literature about other members of the family to which the ecies in question belongs.

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ysical Dormancy

eds of some species fail to germinate because the seed (or fruit) coat is permeable to water; this is called physical dormancy. Physical dormancy curs in members of several families, including the Anacardiaceae, Bix- eae, Cannaceae, Cistaceae, Cochlospermaceae, Convolvulaceae (includ- g Cuscutaceae), Cucurbitaceae, Dipterocarpaceae (subfamilies Mono- deae and Pakaraimoideae but not subfamily Dipterocarpoideae), baceae, Geraniaceae, Malvaceae (including Bombacaceae, Sterculi- eae, and Tiliaceae), Nelumbonaceae, Rhamnaceae, Sarcolaenaceae, and pindaceae (Baskin et al. 2000). However, it should be noted that in some these families, such as the Anacardiaceae, Fabaceae, Malvaceae, and amnaceae, not all taxa have physical dormancy (Baskin and Baskin 998). For example, in the Anacardiaceae only *Rhus*, *Cotinus*, and a few of e other 70 or so genera have physical dormancy (Baskin and Baskin, published data). The way to determine whether seeds or fruits are imper- eable to water is to weigh them, place them on a moist substrate for 24 ours, blot them dry, and reweigh. If seeds or fruits are impermeable to ater, the surest way to break dormancy is to cut a small hole in the seed or uit coat, preferably on the cotyledon end so as not to accidentally damage e radicle. Acid scarification or heat treatments often are used when it is

desirable to break physical dormancy in large quantities of seeds. Freshly matured seeds or fruits of some tropical members of the Anacardiaceae, Cucurbitaceae, Fabaceae, Malvaceae, and Sapindaceae are not only permeable to water but recalcitrant. That is, if water content of the seed or fruit decreases to less than about 25 percent of its air-dry weight (depending on the species), it will lose viability (Baskin and Baskin 1998).

In addition to an impermeable seed or fruit coat, the embryo in seeds of some species, including *Ceanothus sanguineus* Pursh, *Cercis* spp., *Rhus aromatica* Ait., and *Tilia* spp. (see Table 6.10 in Baskin and Baskin 1998 for complete list), is physiologically dormant. Therefore, germination does not occur until the seed or fruit coat becomes permeable and dormancy of the embryo has been broken. See Baskin and Baskin (1998) for a discussion of how physical dormancy is broken in nature. The remainder of this chapter is devoted to seeds and fruits whose coats are permeable to water.

Morphological Dormancy

This type of dormancy occurs in seeds with an undifferentiated embryo and in those with a differentiated but very small (underdeveloped) embryo. One or more (sometimes all) genera in the Balanophoraceae, Burmanniaceae, Ericaceae, Gentianaceae, Hydnoraceae, Lennoaceae, Monotropaceae, Orchidaceae, Orobanchaceae, Pyrolaceae, and Rafflesiaceae have either dwarf or micro seeds with small, undifferentiated embryos consisting of two or more cells, depending on the species (Baskin and Baskin 1998). In the presence of appropriate environmental stimuli, which may include exudates from roots of potential host plants (Parker and Riches 1993), cells of the embryo divide, and eventually a tissue emerges from the seed. Depending on the species, the "germinating" seed produces a tubercle, haustorium, or protocorm but not cotyledons or a radicle per se. Because germination of seeds with undifferentiated embryos often requires special media and/or stimulatory compounds (e.g., orchids and parasitic species), consultation with a specialist on the propagation of the genus or family in question increases the chance of growing the species from seeds.

In at least 55 plant families, including the Apiaceae, Araceae, Araliaceae, Berberidaceae, Illiciaceae, Liliaceae, Magnoliaceae, Papaveraceae, Ranunculaceae, Taxaceae, and Winteraceae (see Table 3.3 in Baskin and Baskin 1998 for a complete list of families), seeds have a fully differentiated (cotyledons and radicle present) but underdeveloped (small) embryo. The embryo must undergo elongation or growth before germination (i.e., radi-

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e emergence) occurs. Seeds with differentiated, underdeveloped embryos ay not require any special dormancy-breaking treatment to promote germination, and embryos begin to grow as soon as seeds are placed on a moist bstrate at appropriate temperature and light (or dark) conditions, depending on the species; these seeds have morphological dormancy (Baskin and skin 1998). After seeds are imbibed, the time required for completion of mbryo growth and emergence of the radicle varies from 6 (Jacobsen and essman 1979) to 30–45 (Baskin and Baskin 1986a) days.

ysiological Dormancy

rmancy (lack of germination under otherwise favorable conditions) in eds of many species is attributed to a physiological inhibiting mechaism in the embryo (Nikolaeva 1969, 1977); this is called physiological mancy. Physiological dormancy can be found in seeds with undifferiated embryos; differentiated, underdeveloped (small) embryos; or differntiated, fully developed embryos.

Physiological dormancy is the most common type of seed dormancy, d it occurs in numerous plant families whose seeds have differentiated, y developed embryos, including the Amaranthaceae, Asteraceae, Boraceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Cyperaceae, phorbiaceae, Lamiaceae, Poaceae, Rosaceae, and Scrophulariaceae skin and Baskin 1998).

There are three levels of physiological dormancy: nondeep, intermedi-, and deep (Nikolaeva 1969, 1977). Nondeep physiological dormancy is ken by 1–8 weeks of warm (≥15°C) or cold (0–10°C) stratification, pending on the species, and gibberellic acid (GA_3) promotes germina- (Baskin and Baskin 1998). Intermediate physiological dormancy is bro- by 8–14 weeks of cold stratification, but a period of dry storage at room peratures or warm stratification may reduce the length of the cold strat- tion period required to break dormancy; GA_3 can promote germina-. Deep physiological dormancy is broken by 10–16 weeks of cold strat- tion, but neither warm pretreatment nor GA_3 promotes germination.

rphophysiological Dormancy

n physiological dormancy occurs in seeds with undifferentiated yos or in those with differentiated, underdeveloped embryos, the seeds e morphophysiological dormancy. In the remainder of this chapter,

however, morphophysiological dormancy is used to refer only to seeds with differentiated, underdeveloped embryos.

Key to the General Types of Seed Dormancy

Although information about the types of dormancy found in a plant family can be very useful, germination studies of a specific species are aided by knowledge of the kind of dormancy occurring in the seeds of that species. To facilitate identification of the kind of dormancy, a key has been constructed (Figure 8.1). This key is based on the permeability of the seed or fruit coat to water; the characteristics and size of the embryo, which often may be obtained from the literature (e.g., see Martin 1946); and whether freshly matured seeds germinate within about 30–45 days at temperatures simulating those in the habitat at the time of seed maturation. It should be noted that freshly matured seeds of some species can germinate at temperatures higher or lower than those in the habitat at the time of seed maturation. Furthermore, in some species treatments that overcome physiological dormancy result in a decrease and/or increase in the temperature range for germination. A change in temperature requirements for germination means that the freshly matured seeds were in conditional dormancy. Conditional dormancy occurs in seeds with nondeep physiological dormancy, and it represents an intermediate state between dormancy and nondormancy (see "Dormancy Continuum" in Baskin and Baskin 1985).

Breaking Physiological and Morphophysiological Dormancy

Physiological and morphophysiological dormancy are the types of greatest concern (i.e., they can be the most difficult to break) in propagating many species from seeds. If seeds have either fully developed or underdeveloped embryos with physiological dormancy, they may require warm and/or cold stratification treatments before they will germinate. In both kinds of treatments, seeds are placed on a moist substrate. The range of effective temperatures for warm stratification is about 15–35°C (Baskin and Baskin 1986b), with 20–25°C being optimal for many species (Nikolaeva 1969). Many seeds that require exposure to high summer temperatures before they can germinate in autumn (especially those of winter annuals) also germinate after 1–3 months of dry storage at ambient room temperatures (Baskin and Baskin 1983). The range of effective temperatures for cold

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FIGURE 8.1.

Simplified key to general kinds of dormancy (or lack thereof) in freshly-matured seeds.

1. Seed or fruit coat not permeable to water. 2
   2. Germination occurs within about 2 weeks when seed or fruit coat is scarified. ..... PHYSICAL DORMANCY
   2. Germination does not occur within about 2 weeks when seed or fruit coat is scarified. ..... COMBINATION OF PHYSICAL AND PHYSIOLOGICAL DORMANCY

1. Seed or fruit coat permeable to water. 3
   3. Embryo not differentiated, or if differentiated it is underdeveloped (small). 4
      4. Embryo not differentiated. ..... SPECIALIZED TYPE OF MORPHOLOGICAL DORMANCY
      4. Embryo differentiated but underdeveloped (small). 5
         5. Seeds germinate within about 30 days at simulated autumn, spring, and summer habitat temperatures.[a] ..... MORPHOLOGICAL DORMANCY
         5. Seeds do not germinate within about 30 days at simulated autumn, spring, and summer habitat temperatures.[a] ..... MORPHOPHYSIOLOGICAL DORMANCY
   3. Embryo differentiated and fully developed (elongated). 6
      6. Seeds germinate within about 30 days at simulated autumn, spring, and summer habitat temperatures.[a] ..... NONDORMANT
      6. Seeds do not germinate within about 30 days at simulated autumn, spring, and summer habitat temperatures.[a] ..... PHYSIOLOGICAL DORMANCY

[a] In regions where winter temperatures are seldom or never below freezing, simulated winter habitat temperature also should be included.

stratification is about 0–10°C, with about 5°C being optimal for seeds of many species (Stokes 1965; Nikolaeva 1969). Depending on the species, some (rather slow) loss of dormancy may occur if seeds that normally come out of dormancy during a cold stratification treatment are stored dry at room temperatures (Baskin and Baskin 1998).

If it is concluded or suspected that seeds have physiological dormancy of a fully developed or of an underdeveloped embryo, the next step is to determine what dormancy-breaking treatments to use. These decisions are greatly facilitated by data on the phenological life cycle of the species, especially the timing of seed maturation, dispersal, and germination, and on environmental conditions in the habitat from the time of seed maturation until germination.

Physiological Dormancy in Seeds with Fully Developed Embryos

Summer is the natural time for loss of seed dormancy in winter annuals, and germination occurs in autumn. Seeds of various winter annuals have been shown to require exposure to high summer temperatures before they will germinate at autumn temperatures in autumn (Baskin and Baskin 1986b). As seeds come out of dormancy, the maximum temperature at which germination is possible increases (Baskin and Baskin 1985). Therefore, seeds of winter annuals subjected to natural (or simulated) summer temperatures for 2–3 months germinate at natural (or simulated) autumn temperature regimes. In some species, maximum germination does not occur until seeds are exposed to temperature regimes simulating those of late autumn and early winter (e.g., 15/6°C; Baskin and Baskin 1973).

If the species is a summer annual, the natural time for loss of seed dormancy is winter, and germination occurs in spring and/or summer. Seeds of various summer annuals have been shown to require exposure to cold stratification before they will germinate at spring temperatures in spring (Baskin and Baskin 1987). As seeds come out of dormancy, the minimum temperature at which germination is possible decreases (Baskin and Baskin 1985). Therefore, seeds of summer annuals subjected to 2–3 months of cold stratification germinate in spring and/or summer.

If the species is a perennial whose seeds mature in spring, the dormancy-breaking and germination requirements may be like those of a winter annual (Baskin et al. 1998). That is, the seeds require high summer temperatures for loss of dormancy, and nondormant seeds germinate in autumn. On the other hand, many spring-produced seeds of perennials require a cold stratification treatment for loss of dormancy and therefore do not germinate until the subsequent spring, such as *Mertensia virginica* (L.) Pers. (Baskin and Baskin 1998, unpublished data). Most autumn-produced seeds of perennials also require a cold stratification treatment for dormancy loss to occur (Baskin et al. 1993a, 1993b); therefore, nondormant seeds germinate in spring and/or summer (Baskin and Baskin 1988).

Morphophysiological Dormancy in Seeds with Underdeveloped Embryos

Germination does not occur in seeds with morphophysiological dormancy until physiological dormancy has been broken and the embryo has grown to some critical, species-dependent length, which may or may not equal the

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FIGURE 8.2.

Key to kinds of morphophysiological dormancy in seeds with differentiated, underdeveloped embryos.

1. Cold stratification (12–14 weeks) of freshly matured seeds results in emergence of radicle and epicotyl or only the radicle at simulated spring (e.g., 20/10°C, 15/6°C) temperatures. 2
   2. After cold stratification, both radicle and epicotyl emerge. 3
      3. Gibberellic acid substitutes for cold stratification in promoting germination. ..... INTERMEDIATE COMPLEX
      3. Gibberellic acid does not substitute for cold stratification in promoting germination. ..... DEEP COMPLEX
   2. After cold stratification, only the radicle emerges. Shoot (epicotyl) emerges after a period of warm stratification followed by a second period of cold stratification (i.e., shoot emerges the second spring). ..... DEEP SIMPLE DOUBLE
1. Cold stratification (12–14 weeks) of freshly matured seeds does not result in emergence of radicle or epicotyl. 4
   4. Warm stratification (8–12 weeks) of freshly matured seeds results in emergence of epicotyl and radicle or only the radicle at simulated autumn (e.g., 20/10°C, 15/6°C) temperatures. 5
      5. After warm stratification, radicle and epicotyl emerge at autumn temperatures. NONDEEP SIMPLE
      5. After warm stratification, only the radicle emerges at autumn temperatures (epicotyl emerges in spring). ..... DEEP SIMPLE EPICOTYL
   4. Warm stratification (8–12 weeks) of freshly matured seeds results in no emergence of radicle or epicotyl at autumn temperatures. 6
      6. Embryo growth (but not emergence of radicle or epicotyl) occurs at autumn temperatures. 7
         7. After embryo has grown, gibberellic acid promotes germination. ..... INTERMEDIATE SIMPLE
         7. After embryo has grown, gibberellic acid does not promote germination; seeds require cold stratification before they will germinate. ..... DEEP SIMPLE
      6. Embryo growth does not occur at autumn temperatures but does occur during a subsequent period of exposure to winter temperatures; seeds require cold stratification before they germinate (i.e., seeds require warm followed by cold stratification for germination). ..... NONDEEP COMPLEX

total length of the seed. Eight types of morphophysiological dormancy have been distinguished, based on the environmental conditions required for loss of physiological dormancy and growth of the embryo and on responses of seeds to GA_3 (Baskin and Baskin 1998). To facilitate identification of the various kinds of morphophysiological dormancy, we have developed a key (Figure 8.2).

Winter annuals whose seeds have morphophysiological dormancy germinate in autumn, like those of winter annuals whose seeds have only physiological dormancy (Baskin and Baskin 1990, 1994). Seeds of winter annuals have nondeep simple morphophysiological dormancy (Figure 8.2), and loss of physiological dormancy occurs while seeds are exposed to high temperatures in summer. However, loss of morphological dormancy (i.e., the embryo elongation that must precede radicle emergence) does not take place until physiological dormancy is broken and imbibed seeds are exposed to autumn temperatures. Furthermore, seeds of some species, such as *Chaerophyllum tainturieri* Hook., require light for embryo growth in autumn (Baskin and Baskin 1990). If seeds of *C. tainturieri* are in darkness in autumn, embryo growth does not occur, and seeds reenter physiological dormancy (secondary dormancy) as habitat temperatures decrease in late autumn (Baskin and Baskin 1990). In contrast, seeds of the winter annual *Corydalis flavula* (Raf.) DC. do not require light for embryo growth in autumn (Baskin and Baskin 1994). Therefore, after physiological dormancy is broken in summer, a high percentage of *C. flavula* seeds germinate even if they are buried.

Not much is known about morphophysiological dormancy in seeds of summer annuals, probably because few summer annuals are known to have morphophysiological dormancy. Seeds of the summer annual *Aethusa cynapium* L. are dormant at the time of maturation in autumn in England (Roberts and Boddrell 1985). Therefore, because seeds of *A. cynapium* have underdeveloped embryos (Martin 1946), it has been concluded that the seeds have morphophysiological dormancy (Baskin and Baskin 1998). However, the type of morphophysiological dormancy in *A. cynapium* seeds has not been determined. Cold stratification at 4°C or warm stratification at 30°C promotes germination of *A. cynapium* seeds. However, cold-stratified seeds germinated over a wide range of low to high temperatures (10/4°C, 20/4°C, 20/10°C, and 30/10°C), but warm-stratified ones did not germinate at low temperatures (Roberts and Boddrell 1985). The environmental conditions required for embryo growth in *A. cynapium* seeds are unknown. In the field, seeds of *A. cynapium* germinate primarily in spring, with some germination (≤10 percent) occurring in autumn (Roberts 1979). It is not known whether plants from autumn-germinating seeds of *A. cynapium* survive; therefore, we do not know whether this species can behave as a facultative summer annual. In some winter annuals, such as *Papaver* spp. (Roberts and Boddrell 1984), germination occurs mostly in

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autumn with plants behaving as winter annuals, but some seeds germinate in spring with plants behaving as summer annuals; these species are facultative winter annuals. Seeds of *Papaver* spp. have underdeveloped, physiologically dormant embryos and thus morphophysiological dormancy (Baskin and Baskin 1998).

Numerous perennial species have seeds with morphophysiological dormancy. Depending on the species, a period of exposure to conditions suitable for warm and/or cold stratification (hereafter these periods of exposure will be called warm stratification or cold stratification) may be required to break dormancy (Figure 8.2). Decisions about which dormancy-breaking protocol to use for seeds of a given species are aided by information on seed dispersal and germination of the species in the field. For example,

- If seeds are dispersed in spring and germinate in autumn, they may have nondeep simple morphophysiological dormancy and therefore require only warm stratification for dormancy loss (e.g., *Chaerophyllum tainturieri*; Baskin and Baskin 1990). It should be noted that another explanation for delay of germination until autumn is that seeds have only morphological dormancy, but they have a low temperature requirement for germination (e.g., *Isopyrum biternatum* [Raf.] T. & G.; Baskin and Baskin 1986a).
- If seeds are dispersed in autumn and germinate in spring, they may have deep complex morphophysiological dormancy and therefore require only cold stratification for dormancy break (e.g., *Heracleum sphondylium* L.; Stokes 1952). However, seeds might have deep simple double morphophysiological dormancy, with only the radicle emerging in spring after a period of cold stratification; shoot growth would not occur until the second spring (e.g., *Trillium grandiflorum* [Michx.] Salisb.; Barton 1944).
- If seeds are dispersed in spring and germinate the next spring, they may have deep complex morphophysiological dormancy and therefore require only cold stratification for dormancy break (e.g., *Delphinium tricorne* Michx.; Baskin and Baskin 1994a). The warm period to which seeds are exposed in summer is not required to break dormancy.
- If seeds that mature in summer are dispersed over a period of many months and germinate only in spring, they may have nondeep complex morphophysiological dormancy. These seeds would require

both warm and cold stratification to break dormancy. Seeds dispersed in summer and early autumn would be warm stratified before being cold stratified in winter and therefore would germinate in spring (e.g., *Osmorhiza longistylis* [Torr.] DC.; Baskin and Baskin 1984). Seeds dispersed too late in autumn to be warm stratified would not germinate until the second spring, after they had been warm stratified in summer and cold stratified in the subsequent winter. Cold stratification is effective in promoting germination of seeds with nondeep complex morphophysiological dormancy only if it follows warm stratification.

- If seeds mature in early autumn but do not germinate until the second spring (e.g., *Panax* spp.; Baskin and Baskin 1998), they may have deep simple morphophysiological dormancy. Seeds with this type of dormancy require three treatments (in sequence) before they will germinate: warm stratification in summer, a period at autumn temperatures for embryo growth, and cold stratification in winter. Seeds do not germinate in the field in the first spring after dispersal because they are dispersed too late in autumn to be exposed to a long enough period of warm stratification to complete the first phase of dormancy loss.

Move-Along Experiment

Over the years, we have developed an experimental design that allows one to learn much about the germination ecology of a species, even if little or nothing is known about its life cycle (Table 8.1). Eighteen dishes of seeds ([two treatments + four controls] × three replications) are used in this experiment, and seeds are placed on wet sand or soil. We prefer to use 50 seeds per dish, but the number per dish can be reduced if seed supplies are limited. This technique also is a good way to learn something about a species before a lot of time, energy, materials, and seeds is invested in large experiments. In our laboratory, seeds are exposed to 14 hours of light per day (40 µmol $m^{-2}s^{-1}$, 400–700 nm, cool-white fluorescent light). We use 30/15°C to simulate summer, 20/10°C and then 15/6°C to simulate decreasing temperatures in autumn, a constant temperature of 1 or 5°C (or sometimes 5/1°C) for winter, and 15/6°C and then 20/10°C to simulate increasing temperatures in spring. These temperature regimes generally approximate seasonal temperature changes in much of temperate eastern

Design for move-along experi
germination requirements of see
given a 14-hour daily pho

Temperature Regime (°C)		Time at Eac Temperature (weeks)
Series A	Series B	
30/15	5	12
↓	↓	
20/10	15/6[b]	4
↓	↓	
15/6[b]	20/10	4
↓	↓	
5	30/15	12
↓	↓	
15/6[b]	20/10	4
↓	↓	
20/10	15/6[b]	4
↓	↓	
30/15	5	12
↓	↓	
20/10	15/6[b]	4
↓	↓	
15/6[b]	20/10	4
↓	↓	
5	30/15	12

[a]Controls are seeds that remain on a we
duration of the experiment.
[b]If number of seeds is limited, 15/6°C can

North America (Wallis 1977), but
simulate conditions in other pa
peratures for the boreal regio
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diterranean region 15/10°C m
gime. In our studies, daily tem
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Controls for the experiment ar
perature regime. If seeds are n
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TABLE 8.1

Design for move-along experiment to determine dormancy-breaking and germination requirements of seeds; seeds are placed on a wet substrate and given a 14-hour daily photoperiod at each temperature regime.

Temperature Regime (°C)		Time at Each Temperature in Series (weeks)	Controls[a]			
Series A	Series B		5	15/6[b]	20/10	30/15
30/15	5	12				
↓	↓		↓	↓	↓	↓
20/10	15/6[b]	4				
↓	↓		↓	↓	↓	↓
15/6[b]	20/10	4				
↓	↓		↓	↓	↓	↓
5	30/15	12				
↓	↓		↓	↓	↓	↓
15/6[b]	20/10	4				
↓	↓		↓	↓	↓	↓
20/10	15/6[b]	4				
↓	↓		↓	↓	↓	↓
30/15	5	12				
↓	↓		↓	↓	↓	↓
20/10	15/6[b]	4				
↓	↓		↓	↓	↓	↓
15/6[b]	20/10	4				
↓	↓		↓	↓	↓	↓
5	30/15	12				

[a]Controls are seeds that remain on a wet substrate at 5°C, 15/6°C, 20/10°C, and 30/15°C for the duration of the experiment.
[b]If number of seeds is limited, 15/6°C can be omitted and time at 20/10°C increased to 6 weeks.

North America (Wallis 1977), but the temperatures easily can be modified to simulate conditions in other parts of the world. For example, to simulate temperatures for the boreal region, 15/10°C or 20/10°C might be used for the highest temperature regime, but to simulate temperatures for the Mediterranean region 15/10°C might be used for the lowest temperature regime. In our studies, daily temperature regimes are 12/12 hours, and lights come on in the incubators 1 hour before the beginning of the high-temperature period and remain on for 1 hour after the beginning of the low-temperature period.

Controls for the experiment are seeds incubated continuously at each temperature regime. If seeds are nondormant or if they have morphological dormancy, they will germinate at one or more of the temperature regimes. Also, seeds of some species may require a long period at a partic-

ular temperature for dormancy
of *Ceratiola ericoides* begin to
and continuous incubation on
mal for dormancy break and ge
al., unpublished data).

During an experiment, seed
to the next in each of the two
Therefore, the experiment is c
tells us whether warm stratificat
and Series B tells us whether cc
mancy break.

By moving seeds through Se
determine whether warm stratific
seeds can germinate. For examp
and *Zigadenus densus* (Desr.) Fe
dormancy, but warm stratification
(Table 8.2). Seeds kept at 5°C for
germinated at 5°C, but germinati
20/10°C than it was for those kep
growth occurred while seeds were

The information obtained fro
B allows one to use the key for typ
ure 8.2); however, additional infor
some types of dormancy. If seeds
response to GA_3 must be determi
diate or deep complex morphop
seeds that have not been cold stra
tened with water or with a solutio
water and incubated at 20/10°C f

To help distinguish between
nondeep complex morphophysi
whether embryos grow in autum
autumn, will the seeds germinate
in autumn (after seeds are warm
nation in autumn indicates that s
deep simple morphophysiological
to GA_3. Seeds (with elongated em
taining filter paper moistened wi

TABLE 8.2

Germination percentages (mean percentage ± SE) of seeds of Zigadenus leimanthoides *and* Zigadenus densus *moved through two series of temperature regimes. Imbibed seeds were exposed to 14 hours of light each day. Control seeds were kept continuously at 5°C, 20/10°C, and 30/15°C.*

	Zigadenus leimanthoides					*Zigadenus densus*				
	Moved		Controls			Moved		Controls		
Time (weeks)	Series A	Series B	5	20/10	30/15	Series A	Series B	5	20/10	30/15
12	30/15	5	5	20/10	30/15	30/15	5	5	20/10	30/15
	0	12 ± 2	4 ± 2	3 ± 1	0	0	5 ± 1	6 ± 2	0	0
	→	→	→	→	→	→	→	→	→	→
6	20/10	20/10	5	20/10	30/15	20/10	20/10	5	20/10	30/15
	0	97 ± 2	71 ± 2	13 ± 1	0	0	92 ± 6	65 ± 7	5 ± 1	0
	→	→	→	→	→	→	→	→	→	→
12	5	30/15	5	20/10	30/15	5	30/15	5	20/10	30/15
	97 ± 2	97 ± 2	99 ± 1	36 ± 3	0	8 ± 1	92 ± 6	98 ± 1	28 ± 9	0
	→	→	→	→	→	→	→	→	→	→
6	20/10	20/10	5	20/10	30/15	20/10	20/10	5	20/10	30/15
	97 ± 2	97 ± 2	99 ± 1	41 ± 3	1 ± 1	97 ± 1	92 ± 6	99 ± 1	34 ± 9	2 ± 1

Source: Data modified from Baskin et al. (1993b).

temperature for dormancy break and germination. For example, seeds of *Ceratiola ericoides* begin to germinate after about 90 days at 30/15°C, and continuous incubation on a wet substrate at high temperatures is optimal for dormancy break and germination of seeds of this species (Baskin et al., unpublished data).

During an experiment, seeds are moved from one temperature regime to the next in each of the two series of temperature regimes (Table 8.1). Therefore, the experiment is called a move-along experiment. Series A tells us whether warm stratification alone is sufficient for dormancy break, and Series B tells us whether cold stratification alone is sufficient for dormancy break.

By moving seeds through Series A and B concurrently, it is possible to determine whether warm stratification must precede cold stratification before seeds can germinate. For example, seeds of *Zigadenus leimanthoides* Gray and *Zigadenus densus* (Desr.) Fernald require cold stratification for loss of dormancy, but warm stratification does not have to precede cold stratification (Table 8.2). Seeds kept at 5°C for the duration of the experiment eventually germinated at 5°C, but germination was faster for seeds moved from 5°C to 20/10°C than it was for those kept continuously at 5°C (Table 8.2). Embryo growth occurred while seeds were at 5°C (Baskin et al. 1993b).

The information obtained from transferring seeds through Series A and B allows one to use the key for types of morphophysiological dormancy (Figure 8.2); however, additional information is needed for final decisions about some types of dormancy. If seeds germinate after cold stratification, their response to GA_3 must be determined to know whether seeds have intermediate or deep complex morphophysiological dormancy. Fresh seeds (i.e., seeds that have not been cold stratified) can be placed on filter paper moistened with water or with a solution of 100 or 1,000 mg/L GA_3 and distilled water and incubated at 20/10°C for 12 or more weeks (Baskin et al. 1992).

To help distinguish between intermediate simple, deep simple, and nondeep complex morphophysiological dormancy, we need to know whether embryos grow in autumn or in winter. Also, if embryos grow in autumn, will the seeds germinate when treated with GA_3? Embryo growth in autumn (after seeds are warm stratified in summer) but lack of germination in autumn indicates that seeds have either intermediate simple or deep simple morphophysiological dormancy, depending on their response to GA_3. Seeds (with elongated embryos) can be transferred to dishes containing filter paper moistened with 1,000 mg/L GA_3 ($GA_{4/7}$ may work as

well or better) to determine whether GA_3 will substitute for cold stratification in promoting germination. If GA_3 promotes germination, seeds have intermediate simple morphophysiological dormancy, but if GA_3 does not promote germination, seeds have deep simple morphophysiological dormancy. However, it should be noted that GA_3 promotes embryo growth (but not germination) in seeds with deep simple morphophysiological dormancy (Baskin and Baskin 1989). If seeds are warm stratified in summer and embryos fail to grow in autumn but do grow in winter, seeds have nondeep complex morphophysiological dormancy.

If seeds are moved through Series A and B concurrently and no germination occurs, there are several things to consider:

- The seeds may not be viable. A few seeds could be removed from the dishes and examined or tested to determine whether they are viable. We recommend excising the embryo and determining its degree of firmness and color. A firm, white embryo probably is alive; a soft, slightly tan or gray one is dead. In endospermous seeds, it is useful to compare the color of the embryo with that of the endosperm. If the embryo is darker than the white endosperm, the embryo is nonviable. Visual examination of embryos can be followed by tetrazolium tests (Grabe 1970). In our experience, firm, white embryos give a positive tetrazolium test, indicating viability, but soft, gray ones give a negative test. Furthermore, it should be noted that if seeds are dead or have low vigor, they often are attacked by fungi.
- Four weeks at 20/10°C may not be long enough for the embryo to become fully elongated. After 12 weeks of warm stratification at 30/15°C, seeds of *Jeffersonia diphylla* (L.) Pers. required 6 weeks at 20/10°C for completion of embryo growth (Baskin and Baskin 1989).
- A winter temperature of 5°C may be too high for effective cold stratification to occur (Baskin et al. 1995); therefore, 1°C or 5/1°C may be required to break dormancy.
- Seeds of some species may germinate to higher percentages in darkness than in light (Baskin and Baskin 1998).

We have emphasized the usefulness of the move-along experiment in determining the kind of morphophysiological dormancy; however, it can be helpful in studying seeds with fully developed but physiologically dormant embryos. For example, seeds of *Floerkea proserpinacoides* Willd. (Baskin et al. 1988) and *Cardamine concatenata* (Michx.) O. Schwarz

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Conclusions

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Baskin and Baskin 1994b) have fully developed embryos with physiological dormancy. Seeds of these two species need cold stratification before they will germinate. However, a period of warm stratification before the cold stratification treatment reduced the length of the cold stratification period required for 50 percent germination from 19 to 8 weeks in *F. proserpinacoides* and from 19 to 13 weeks in *C. concatenata* seeds. Thus, using Series A and B concurrently permits detection of species whose seeds have fully developed physiologically dormant embryos in which warm stratification reduces the cold stratification requirement for germination.

If seed supplies are limited, perhaps only Series A or B can be used. However, it sometimes takes longer to obtain seedlings using only one of the two series than it does when seeds are moved through Series A and B concurrently. Also, if Series A is used alone and seedlings are obtained after seeds have been exposed to 5°C for 12 weeks, one does not know whether warm stratification is a necessary part of the dormancy-breaking protocol. Thus, when Series A or B is used alone, seeds may germinate, but one is not conducting an experiment per se.

If the number of seeds is very limited, one could use only three dishes of seeds and move them each season of the year to simulated habitat temperatures (i.e., summer, autumn, winter, spring). We suggest starting with a temperature regime simulating temperatures in the habitat at the time of seed maturation and dispersal. However, this approach is not experimental. If seeds are locally produced, the same germination results may be obtained just as easily by planting seeds outdoors, where they would be exposed to natural temperature changes.

Conclusions

By knowing the family to which a species belongs, one can immediately obtain information about whether the seeds might have seed or fruit coats that are impermeable to water (= physical dormancy); an undifferentiated embryo (= specialized morphological dormancy); differentiated, underdeveloped (small) embryo (= morphological or morphophysiological dormancy); or a fully developed embryo (nondormancy or physiological dormancy). Regardless of the type of embryo, data from a move-along experiment make it possible to learn much about the dormancy-breaking and germination requirements of a species by using only a few hundred seeds.

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