

Classification, Biogeography, and Phylogenetic Relationships of Seed Dormancy



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Summary

Seeds of the majority of plant taxa in all major biomes of the world except tropical rainforest and tropical semi-evergreen forest are dormant at maturity. Dormant seeds can be classified into one of five classes: physiological (PD, low growth potential of the embryo); morphological (MD, small undifferentiated or small differentiated, but underdeveloped, embryo); morphophysiological (MPD, underdeveloped, physiologically-dormant embryo); physical [PY, water-impermeable palisade or palisade-like layer(s) of cells in seed (or fruit) coat]; and combinational [(PY+PD), water-impermeable seed (or fruit) coat + physiologically dormant embryo]. Classes of dormancy can be layered further into levels and levels into types. Mechanical dormancy is an aspect of physiological dormancy, and evidence for chemical dormancy as a kind of dormancy *per se* is weak at best. A dichotomous key to the five classes of dormancy, based on laboratory procedures for dormancy-break, is presented. PD is the most common class of dormancy in all major terrestrial biomes except matorral, where PD and PY are about equally important numerically. Worldwide, MD, MPD, and (PY+PD) are unimportant numerically compared to PD and PY. PD occurs widely among gymnosperms, dicots, and monocots. MD and MPD are present in several families of gymnosperms and in phylogenetically basal angiosperms, monocots, eumagnoliids, and eudicots, but they are not present in the rosids. Fourteen of the 15 angiosperm families in which PY is known are dicots, and six of them belong to the *Malvales* (excepting *Malvaceae s.l.*). *Canna* (*Cannaceae*) is the only monocot taxon in which PY has been documented, and no gymnosperm has PY. There is no obvious relationship between seed dormancy and plant life form or geographical range.

Introduction

A *dormant* seed (or other germination unit) is one that will not germinate under any combination of normal physical environmental factors (temperature, light/dark, *etc.*) that otherwise is favourable for its germination – i.e., after the seed becomes non-dormant. In the case of morphological dormancy, delay of germination (dormancy) is due to the requirement for a period during which the embryo completes growth. A freshly-matured dormant seed is said to have *primary dormancy*.

A *non-dormant* seed (or other germination unit), on the other hand, will germinate over the widest range of normal physical environmental factors possible for the genotype (and considering maternal effects). The non-dormant seed that does not germinate because of the absence of one or more of these physical environmental factors is said to be in a state of *quiescence* (= enforced dormancy of Harper, 1957). The seed will germinate when the appropriate combination of environmental conditions is within its range of requirements for radicle emergence, providing it has not entered secondary

dormancy (see below). Whereas some authors regard a seed to be dormant if the only environmental factor preventing it from germinating is absence of light, we consider such a seed to be quiescent. Thus, light is just another environmental factor that some non-dormant (but quiescent) seeds require to germinate, like, for example, presence of substrate moisture.

However, in seeds of many species, dormancy is not an all or nothing stage in the plant's life cycle, i.e., not plus or minus, black or white, on or off. Seeds of many species with non-deep physiological dormancy go through a series of changes in their capacities for physiological responses to various factors between dormancy and non-dormancy (Baskin and Baskin, 1998): seed development \rightarrow primary dormancy (Sp) \rightarrow Sc₁ \rightarrow Sc₂ \rightarrow Sc₃ \rightarrow Sc₄ \rightarrow Sc₅ \rightarrow non-dormancy (Sn) \rightarrow Sc₅ \rightarrow Sc₄ \rightarrow Sc₃ \rightarrow Sc₂ \rightarrow Sc₁ \rightarrow Ss (secondary dormancy) \rightarrow Sc₁ \rightarrow etc. Sc₁ \rightleftharpoons Sc₅ represents transitional physiological states a seed undergoes between primary dormancy (Sp) and non-dormancy (Sn) or during relief of Ss and its reinduction, i.e., the *dormancy continuum*. A seed in any of stages Sc₁ \rightleftharpoons Sc₅ is in *conditional or relative dormancy* (see Vegis, 1964; Baskin and Baskin, 1998). A conditionally dormant seed will germinate in a narrower range of physical environmental conditions than will a non-dormant seed. Conditions required for germination gradually become wider and wider between Sp \rightarrow Sn and narrower and narrower between Sn \rightarrow Ss, which represents re-entrance of the non-dormant seed into dormancy, now called *secondary dormancy* (Ss). Thus, seeds with non-deep physiological dormancy may cycle between dormancy and non-dormancy – the *dormancy cycle*.

The purpose of this chapter is to present an overview of the classification, biogeography, and phylogenetic relationships of seed dormancy and to update/revise material published in Baskin and Baskin (1998). We have: (1) made some adjustments in the seed dormancy classification scheme, (2) added 1,670 species to the database on the biogeography of seed dormancy, and (3) used modern phylogenetic trees to examine evolutionary relationships of seed dormancy.

Classification of Seed Dormancy

In this chapter, we use a three-tiered hierarchal system of dormancy classification: class, level, and type. Thus, a class may contain levels and types, and a level may contain types. Further, we use “kind” of seed dormancy in a generic sense, i.e., in reference to any layer in the hierarchal system of dormancy classification, perhaps similar to the use of the word “taxon” in plant systematics. The five classes of dormancy and the endogenous and/or exogenous factor(s) responsible for maintaining each of them is (are) outlined in Table 28.1. It should be noted that this classification scheme does not recognize mechanical or chemical as kinds of dormancy *per se*, thus differing from that of Nikolaeva (1969, 1977). We view mechanical dormancy as a component of physiological dormancy (Bewley and Black, 1994; Baskin and Baskin, 1998) and conclude that evidence for chemical dormancy in nature is weak at best (Mayer and Poljakoff-Mayber, 1989; Bewley and Black, 1994; Baskin and Baskin, 1998).

Table 28.1 Classes of seed dormancy (modified from Nikolaeva, 1977 and Baskin and Baskin, 1998)

Class of dormancy	Cause(s) of dormancy
A. Physiological, PD	low growth potential of embryo, which cannot overcome mechanical constraint of seed (or fruit) coat
B. Morphological, MD	small differentiated (but underdeveloped), or small undifferentiated, embryo that simply needs time to grow (or grow/differentiate) before seed germinates, i.e., growth (or growth/differentiation) period = period of dormancy
C. Morphophysiological, MPD	combination of underdeveloped (or undifferentiated) and physiologically-dormant embryo
D. Physical, PY	water-impermeable layer(s) of palisade or palisade-like cells in seed (or fruit) coat
E. Combinational, (PY + PD)	water-impermeable seed (or fruit) coat and physiologically-dormant embryo

Table 28.2 A dichotomous key to the five classes of dormancy (or lack thereof) in freshly-matured seeds (modified from Baskin and Baskin, in press). It is assumed that incubation conditions are appropriate for non-dormant seeds to germinate.

1. Seed/fruit coat not permeable to water; embryo fully developed 2
 2. Germination occurs within about 2 weeks (usually much less time) when seed/fruit coat is scarified PHYSICAL DORMANCY
 2. Germination does not occur within about 2 weeks (usually not even within a somewhat longer period of time) after seed/fruit coat is scarified, although seed becomes fully imbibed within a few hours following scarification COMBINATION OF PHYSICAL AND PHYSIOLOGICAL DORMANCY
1. Seed/fruit coat permeable to water; embryo either fully developed or underdeveloped 3
 3. Embryo not differentiated, or if differentiated, underdeveloped (small) 4
 4. Embryo not differentiated SPECIALIZED TYPE OF MORPHOLOGICAL or MORPHOPHYSIOLOGICAL DORMANCY
 4. Embryo differentiated but underdeveloped (small) 5
 5. Embryos in freshly-matured seeds begin to grow (elongate) within a period of a few days to 1–2 weeks, and seeds germinate within about 30 days MORPHOLOGICAL DORMANCY
 5. Embryos in freshly-matured seeds do not begin to grow within a period of even a few weeks, and seeds do not germinate within 30 days MORPHOPHYSIOLOGICAL DORMANCY
 3. Embryo differentiated and fully developed (elongated) 6
 6. Seeds do not germinate within about 30 days PHYSIOLOGICAL DORMANCY
 6. Seeds germinate within about 30 days NON-DORMANT

1. A Dichotomous Key to Seed Dormancy Classes

Our dichotomous key provides some essential information about the causes(s) of dormancy in each of the five classes and how it is broken in intact seeds or other dispersal units (Table 28.2). However, additional comments will be made on dormancy and dormancy-break for each of the five classes under laboratory conditions.

1.1. Physical dormancy

Physical dormancy is caused by (a) water-impermeable layer(s) of palisade or palisade-like cells in the seed or fruit coat (Figure 28.1; Baskin *et al.*, 2000). Dormancy-break in seeds with PY under both natural and artificial (except mechanical scarification) conditions typically has been assumed to involve the formation of an opening (“water gap”) in a specialized anatomical structure on the seed (or fruit) coat (Figure 28.1) through which water moves to the embryo (Baskin *et al.*, 2000). Recently, however, Morrison *et al.* (1998) have presented evidence that dormancy-break by heating in some taxa of *Fabaceae*

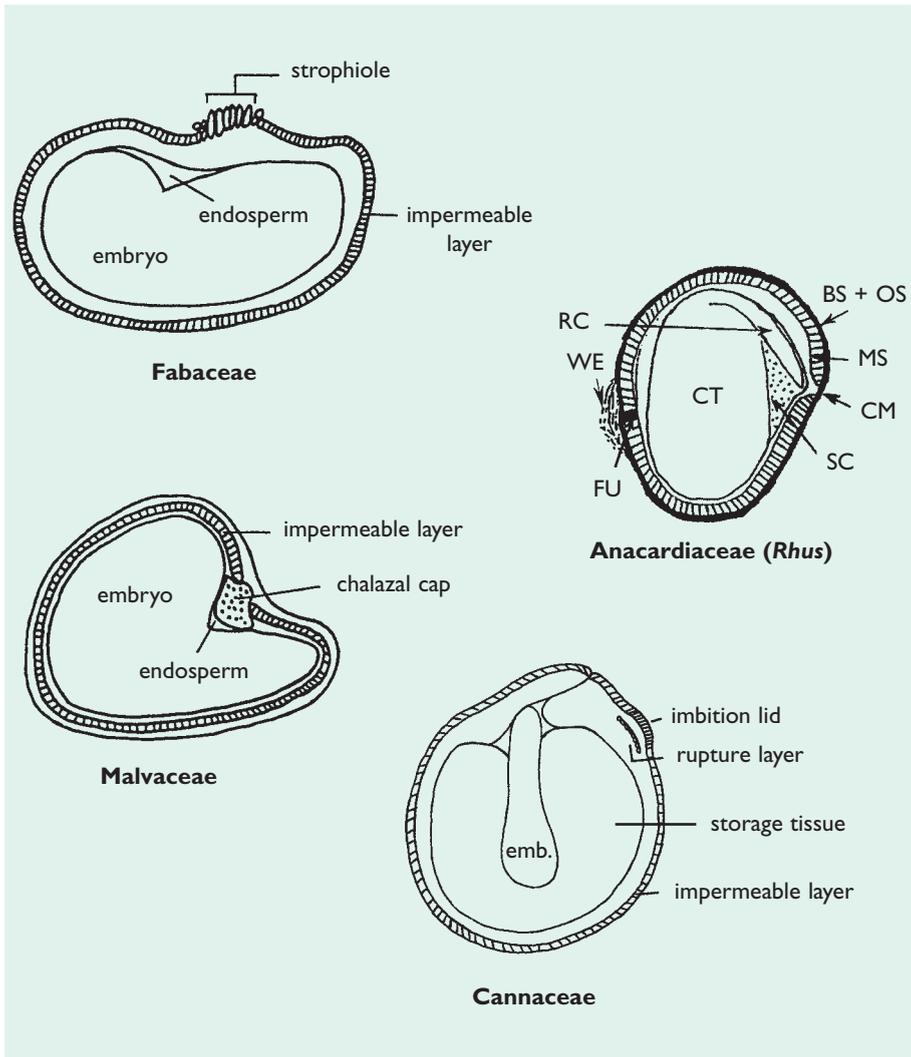


Figure 28.1 Anatomy of the germination unit (seed + endocarp in *Rhus* and seed only in *Cannaceae*, *Fabaceae*, and *Malvaceae*). The specialized 'water gap' areas are 'carpellary micropyle' (CM) in endocarp of *Rhus*, and imbibition lid, strophiole (lens), and chalazal cap in seeds of *Cannaceae*, *Fabaceae*, and *Malvaceae*, respectively. For *Rhus*: BS, brachysclereids; CM, carpillary micropyle; CT, cotyledon; FU, funiculus; MS, macrosclereids; OS, osteosclereids; RC, radicle; SC, seed coat; WE, whitish exudate. BS, MS, and OS are the three water-impermeable layers in the endocarp of *Rhus*. [*Fabaceae* and *Malvaceae* from Baskin and Baskin (1998), with permission; *Anacardiaceae* from Li et al. (1999), with permission; *Cannaceae* modified from drawings and photographs in Grootjen and Bouman (1988).]

Table 28.3 Summary of the relative effectiveness of various treatments in breaking dormancy in seeds of *Senna marilandica* and of *S. obtusifolia*. – = negative effect, 0 = no effect, + = slightly effective, +++++ = very effective (from Baskin *et al.*, 1998, with permission)

Treatment	<i>S. marilandica</i>	<i>S. obtusifolia</i>
Acid scarification	++++	++++
Boiling	+	++++
Burning ^a	0 or -	0 or -
Dry heat	0	++
Dry storage ^a	0	0 or -
Ethanol	++	++++
Freezing and thawing ^a	0	0
High temperature incubation	0	++++
Mechanical scarification	++++	++++
Temperature shifts	0 or -	0 or -
Wetting and drying	0	0

^a From Nan, 1992

may occur through disruption of the seed coat in (a) region(s) other than the lens. The lens is assumed to be an environmental ‘signal detector’ in legumes (Baskin *et al.*, 2000); however, we certainly agree with Morrison *et al.* (1998) that their observations make it difficult to understand the ecological role of the lens in these species.

Effects of various methods for overcoming PY in seeds of *Senna obtusifolia* and *S. marilandica* (*Fabaceae*: *Caesalpinioideae*, section *Chamaefistula*) are listed in Table 28.3. It can be seen that: (1) mechanical scarification (with a scapel) and scarification with concentrated sulphuric acid were very effective for both species; (2) dipping seeds into boiling water or incubating them at high temperatures (35/20, 40/25°C) broke dormancy in seeds of the pantropical/subtropical annual, *S. obtusifolia*, but not in those of the native temperate eastern North American polycarpic perennial, *S. marilandica*; (3) ethanol was less effective in *S. marilandica* than in *S. obtusifolia*; (4) dry heat was moderately effective in *S. obtusifolia*, but completely ineffective in *S. marilandica*; and (5) neither burning (fire), dry storage, freezing/thawing, temperature shifts, nor wetting/drying were effective in either species. Thus, even seeds of these two species of *Senna* in the same section of the genus responded differently to several methods typically used to overcome PY under laboratory conditions.

Mechanical or chemical scarification also will promote germination in seeds with non-deep physiological dormancy. Thus, it is not unusual for an investigator to

report (or imply) that seeds of a particular taxon have water-impermeable seed coat dormancy, when, in fact, this is not the case. Without exception in such studies, water uptake (or lack thereof) was not documented by comparing imbibition in scarified vs. non-scarified seeds. To determine if seeds have PY, one should compare water uptake in mechanically-scarified and non-scarified (control) seeds (or other germination units). Seeds that are scarified properly (by whatever method used) will imbibe water, whereas non-scarified seeds, or (usually) only a small percentage of them, will do so. That is, the impermeability barrier usually fails to develop in a small number of seeds in a seed lot of a species in which the majority of seeds have PY (see Morrison *et al.*, 1992).

1.2. Morphological dormancy

In seeds with MD, the embryo is either small (underdeveloped) and undifferentiated or small (underdeveloped) and differentiated, i.e., cotyledon(s) and radicle can be distinguished (Figure 28.2). Germination of seeds of underdeveloped, undifferentiated embryos is a specialized field of study. Thus, we do not wish to comment on dormancy in this group, except to say that, by definition, seeds of all taxa have a morphological (or a morpho-anatomical!) component of dormancy, and in addition some also have a physiological component of dormancy (Baskin and Baskin, 1998).

In seeds with non-dormant, underdeveloped, differentiated embryos, the embryos simply need time to grow to full size and then germinate (radicle protrusion). The dormancy period is the time required for completion of embryo growth, after which the radicle emerges. Our arbitrary cut-off time for assigning seeds to MD is about 30 days. Thus, seeds that take significantly longer than 30 days to germinate are considered to have MPD.

1.3. Morphophysiological dormancy

Seeds with this kind of dormancy have an underdeveloped embryo that has a physiological component of dormancy. There are eight known levels of the MPD class based on the protocol for seed dormancy break and germination (Baskin and Baskin, 1998).

1.4. Combinational dormancy

In seeds with (PY+PD), the seed (or fruit) coat is water-impermeable and the embryo is physiologically dormant. The physiological component appears to be at the non-deep level in all examples with which we are familiar (Baskin and Baskin, 1998). Embryos of freshly matured seeds of some taxa of winter annuals (e.g., *Geranium*, *Trifolium*) have a low amount of conditional dormancy and will come out of dormancy (after-ripen) in dry storage, or in the field, within a few weeks after seed maturity, even while the seed coat remains impermeable to water. Embryos in such genera as *Cercis* and *Ceanothus* are more deeply dormant (but still non-deep), and thus the seeds require a few weeks of cold stratification, i.e., after PY is broken and seeds imbibe water, before they will germinate (Baskin and Baskin, 1998).

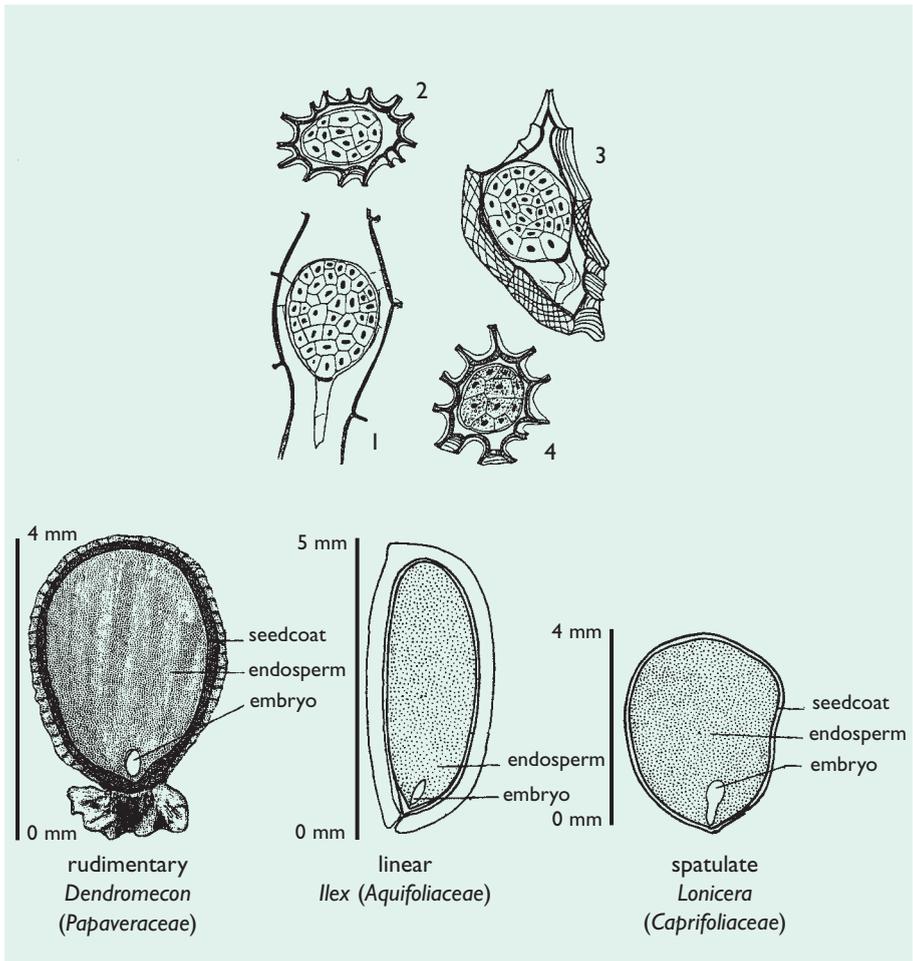


Figure 28.2 (Top) Undifferentiated embryos of *Orchidaceae* 1. *Dactylorhiza*; 2, 3. *Ophrys*; 4. *Anacamptis* (from Burgeff, 1936, scale not given). (Bottom) Underdeveloped but differentiated embryos in three dicotyledonous families (from Schopmeyer, 1974)

1.5. Physiological dormancy

Following Nikolaeva (1977), we recognize three levels of PD: deep, intermediate, and non-deep. Characteristics of each level are summarized in Table 28.4. Further, based on pattern of change in temperature requirements for germination during the dormancy-breaking period, five types of non-deep PD are recognized (Figure 28.3).

Table 28.4 Characteristics of dormancy in seeds with deep, intermediate, and non-deep physiological dormancy (from information in Baskin and Baskin, 1998)

Deep

- Excised embryo produces abnormal seedling.
- Gibberellic Acid (GA) does not promote germination.
- Seeds require ca. 3–4 months of cold stratification to germinate.

Intermediate

- Excised embryo produces normal seedling.
- GA promotes germination in some (but not all) species.
- Seeds require 2–3 months of cold stratification to break dormancy.
- Dry storage can shorten the cold stratification period.

Non-deep

- Excised embryo produces normal seedling.
- GA promotes germination.
- Depending on species, cold (ca. 0–10°C) or warm ($\geq 15^\circ\text{C}$) stratification breaks dormancy.
- Seeds may after-ripen in dry storage.
- Scarification may promote germination.

The starting point on the x-axis in Figure 28.3, 1.0, is the (fully) dormant condition. Values <1.0 to >0.0 represent the continuum of stages during dormancy break (see chapter Introduction) in types 1, 2, and 3. During progression from dormancy to non-dormancy, the temperature range at which seeds can germinate gradually increases (y-axis): (1) from low to high (Type 1), (2) high to low (Type 2), or (3) medium to both high and low (Type 3). Additionally, in seeds with non-deep dormancy types 1, 2, and 3, sensitivity to other factors, such as Pfr and plant growth regulators, increases during progression of dormancy-break (Baskin and Baskin, 1998).

On the other hand, limited knowledge of seeds with types 4 and 5 suggests that they do not exhibit a distinct continuum of changes during dormancy-break (Figure 28.3). Instead, seeds appear to proceed from the dormant (1.0) to the non-dormant (0.0) state without going through the continuum of changes (<1.0 to >0.0) exhibited by seeds with types 1, 2, and 3. As such, release of dormancy in types 4 and 5 may be controlled by an “on/off” switch *vs.* a “cam” switching mechanism in types 1, 2, and 3.

Seeds of the great majority of species with PD that we have studied belong to the non-deep PD level. Further, a high percentage of them have either Type 1 or Type 2 and only a few Type 3. Seeds with types 4 and 5 appear to be even

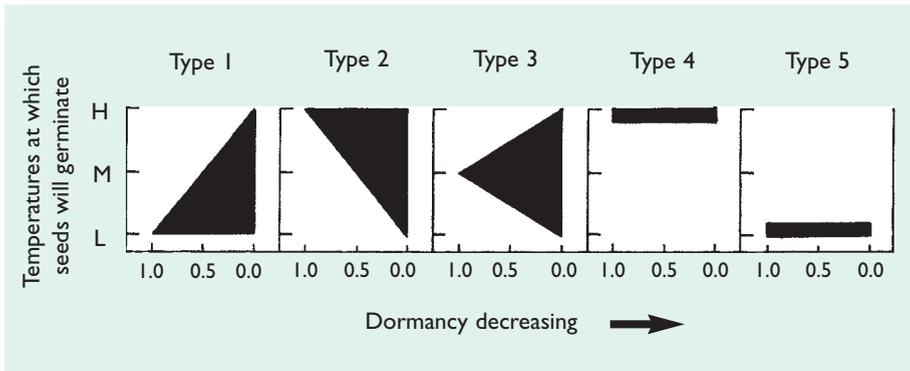


Figure 28.3 Types of non-deep physiological dormancy (based on information in Baskin and Baskin, 1998)

more uncommon than those with Type 3, but many additional species, especially those from warm deserts and tropical savannas, need to be studied. We have documented Type 4 in the temperate deciduous forest shrub *Callicarpa americana* (*Verbenaceae*) of southeastern USA (Baskin and Baskin, unpublished data) and Type 5 in the North American hot desert winter annual *Eriastrum diffusum* (*Polemoniaceae*) (Baskin *et al.*, 1993).

2. Maternal and Position Effects on Seed Dormancy

In wild taxa, it is expected that the seed population (seed lot) produced in a given year will exhibit differences in degree of dormancy. That is, the degree of dormancy is not uniform among seeds in the population. It is well known that the environment (temperature, soil water, soil nutrients, photoperiod, light quality) of the mother plant during seed development can influence dormancy of the seeds produced (Baskin and Baskin, 1998). Thus, degree of dormancy in a seed population may differ from year to year, or even between seasonal cohorts within a population.

In freshly matured seeds of the winter annual *Arenaria patula* var. *robusta* (*Caryophyllaceae*) of southeastern USA, which have non-deep PD, proportions of dormant and conditionally dormant seeds varied significantly from year to year over a three-year period within a population in a rocky-thin soil habitat in central Kentucky. Germination percentages at several temperatures generally were higher in 1971 and 1972, when the amount of rainfall during the 30 days preceding seed maturity was 37 and 63 mm, respectively, than in 1973, when rainfall during the 30 days preceding maturity was 183 mm (Baskin and Baskin, 1975). In *Ononis sicula* and *Trigonella arabica*, two annual legumes that grow in the Negev Desert of Israel, the proportion of seeds with PY was much higher when mother plants were grown under a short- than under a long-day

photoperiod. Thus, a higher proportion of seeds matured under a long-day photoperiod were non-dormant (Gutterman, 1993). Finally, in the long-lived monocarpic perennial, *Frasera caroliniensis* (*Gentianaceae*), a species of woodlands and glades in eastern North America, the proportion of seeds with deep, complex and non-deep, complex levels of MPD can vary from year to year (Threadgill *et al.*, 1981; Baskin and Baskin, 1986, unpublished data). However, we have not attempted to determine if there is a relationship between dormancy type and seed maturation environment.

Position of seeds in fruits and in inflorescences, and (in amphicarpic plants) whether they are produced above or below ground, also can influence dormancy status of the seed (Gutterman, 2000).

World Biogeography of Seed Dormancy

Perhaps “biome” would be more appropriate to use in our discussion of the biogeography of seed dormancy than would “major vegetation zone” (Figures 28.4 and 28.5) Whereas Walter’s (1979) vegetation zones refer only to climax or potential natural vegetation types, our database for his zones includes both climax and developmental (successional) stages of vegetation (Baskin and Baskin, 1998, and unpublished data).

1. Dormant vs. Non-dormant Seeds

Relative proportions of species with dormant, and non-dormant, freshly-matured seeds among the major terrestrial biomes on earth (*sensu* Walter, 1979) are shown in Figure 28.4. Relative proportions of dormant and non-dormant seeds of 3,580 species reported in Baskin and Baskin (1998) are compared with those of 5,250 species, i.e., after an additional 1,670 species were added to the database. Except for tropical montane vegetation, there was little change in relative proportion of dormant and non-dormant seeds after the addition of the 1,670 species. The relatively large change in proportion of species with dormant and non-dormant seeds in tropical montane vegetation probably was due to the small sample (only 18 species) available in Baskin and Baskin (1998). In fact, tropical montane was not included in Figures 12.1 or 12.2 of Baskin and Baskin (1998) because data were available for only 18 species, and the 3,580 species in Baskin and Baskin (1998) did not include the 18 species from tropical montane. Tropical montane is included in Figure 28.4 of this chapter. However, we have data for only two tropical subalpine species and no data for tropical alpine species, thus these vegetation zones are not represented in Figure 28.4. Of the 1,670 species added to our database, 1,282 (76.8%) were from tropical/subtropical zones; 614 (36.8%) of these were

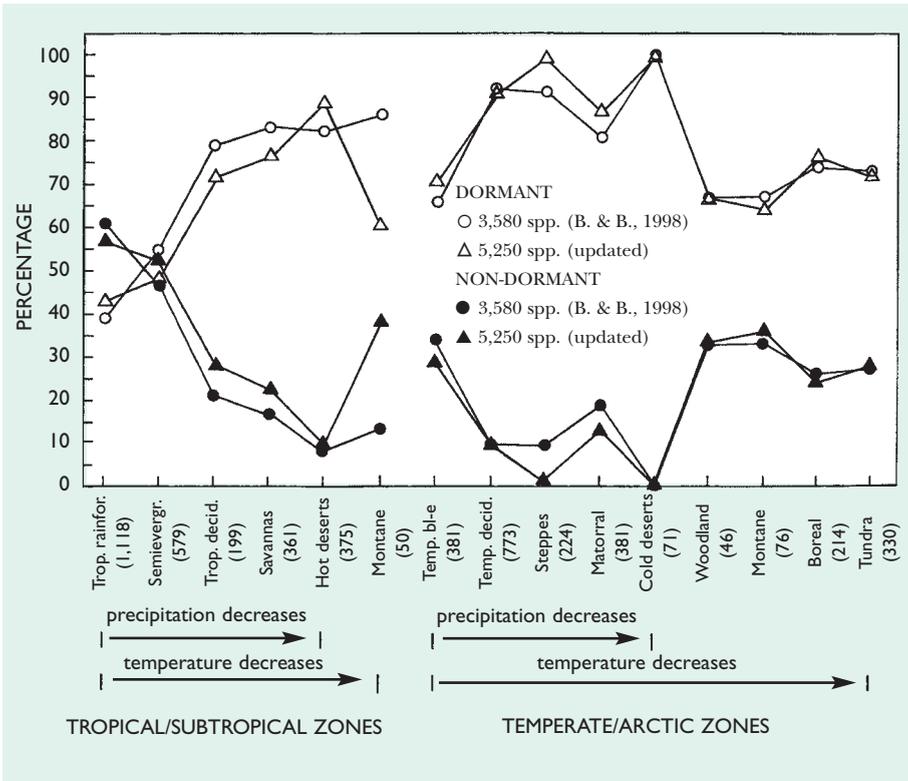


Figure 28.4

Comparison of the world biogeography of seed dormancy (all classes), and of non-dormancy, based on the 3,580 species in Fig. 12.1 of Baskin and Baskin (1998, with permission) vs. 5,250 species (i.e., after addition of 1,670 species to the database in Baskin and Baskin, 1998)

from tropical rainforest and 370 (22.2%) from tropical semi-evergreen forest. The greatest increase in number of species for temperate/arctic vegetation zones was in broadleaved evergreen forest (176) and matorral (185).

Clearly, freshly-matured seeds of the majority of plant taxa in all major terrestrial biomes of the world, except tropical rainforest and tropical semi-evergreen forest, have some kind of dormancy. Our data indicate that about 60% of the seeds of tropical rainforest and about 50% of those of tropical semi-evergreen forest are non-dormant at maturity. A very high proportion ($\geq 85\%$) of seeds of hot deserts, temperate deciduous forests, steppes, matorral, and cold deserts are dormant at maturity (Figure 28.4).

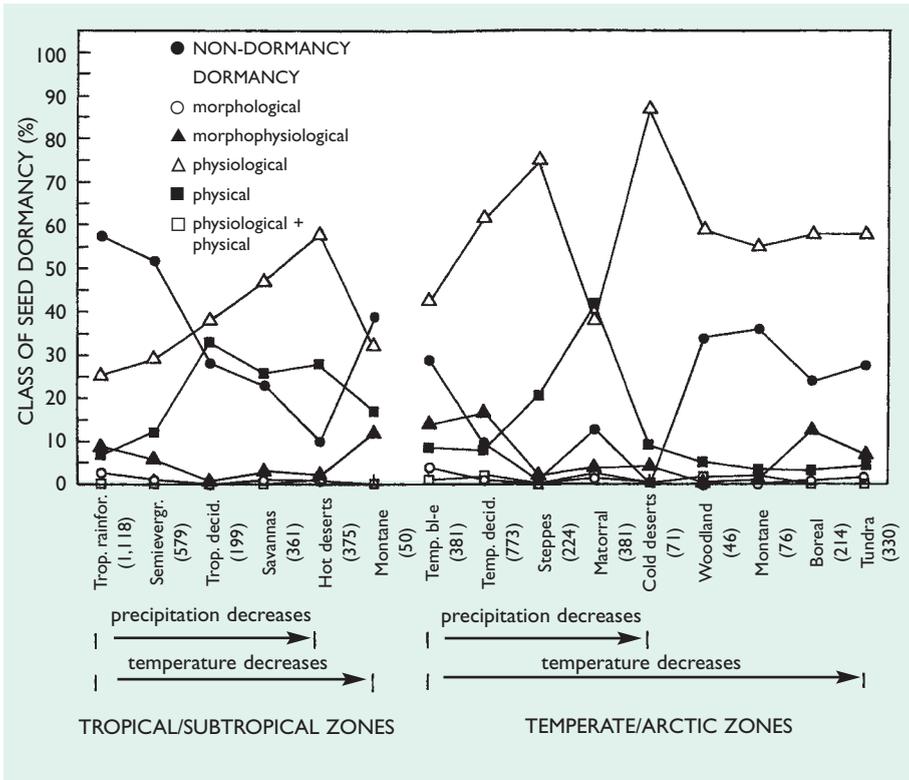


Figure 28.5 World biogeography of the five classes of seed dormancy, and of nondormancy, based on 5,250 species (updated from Baskin and Baskin, 1998)

2. Classes of Seed Dormancy

Proportions of non-dormant seeds and each of the five classes of dormant seeds (i.e., percentage non-dormant + percentage in each of five dormancy classes = 100) for each of Walter’s major vegetation zones, excluding tropical alpine and tropical subalpine (see above), are shown in Figure 28.5. The proportions of non-dormant seeds in Figure 28.5 are the same as those in Figure 28.4 for the 5,280 species. The proportion of dormant seeds for each vegetation type in Figure 28.4 is broken down into the five classes of dormancy in Figure 28.5.

Physiological dormancy is the most common class of seed dormancy in all of Walter’s vegetation types except matorral. In matorral, the proportion of taxa with PY is slightly higher than that of those with PD (Figure 28.5). The second

Table 28.5 Angiosperm families with PY or with PY and (PY + PD) (from information in Baskin et al., 2000)

Families	PY	(PY + PD)
<i>Anacardiaceae</i>	x	x
<i>Bixaceae</i>	x	
<i>Cannaceae</i>	x	
<i>Cistaceae</i>	x	
<i>Cochlospermaceae</i>	x	
<i>Convolvulaceae^a</i>	x	
<i>Cucurbitaceae</i>	x	x
<i>Dipterocarpaceae^b</i>	x	
<i>Fabaceae</i>	x	x
<i>Geraniaceae</i>	x	x
<i>Malvaceae^c</i>	x	x
<i>Nelumbonaceae</i>	x	
<i>Rhamnaceae</i>	x	x
<i>Sarcocaulaceae</i>	x	
<i>Sapindaceae</i>	x	x

^a Including *Cuscutaceae*, which has species with water-impermeable seed coats

^b Including subfamilies *Monotoideae* and *Pakaraimoideae*, but not subfamily *Dipterocarpoideae*

^c Including *Bombacaceae*, *Sterculiaceae*, and *Tiliaceae*, all of which have some species with water-impermeable seed coats

most common kind of dormancy is PY. On the basis of vegetation types, PY is second to PD in all tropical/subtropical types shown in Figure 28.5 except tropical rainforest, where it is in about equal proportion to MPD. In temperate/arctic zones, PY is about equal to PD in matorral, and it is second in importance to PD in steppes, cold deserts, woodland, and montane. However, of the latter four vegetation types, the proportion of species with PY is <10% except in steppes (*ca.* 20%) and cold deserts (*ca.* 10%).

MPD is second to PD in temperate broadleaved evergreen, temperate broadleaved deciduous, boreal, and tundra vegetation types. In all tropical/subtropical and temperate/arctic vegetation types, however, the proportion of taxa with MPD is <20%. The proportion of species with MD, and of those with (PY+PD), ranges from 0.0 to <5% across world vegetation zones. The relatively low importance of a class of dormancy, such as MPD, in a life form group in a given habitat, for example, may be obscured by averaging across a vegetation type. Thus, whereas seeds of only about 8% of the 773 species representing the temperate broadleaved deciduous forest biome type are in this dormancy class, seeds of 45 of 68 (66.2%) species of mesic forest herbs of the eastern North American portion of this biome that have been studied have MPD (Baskin and Baskin, 1998, and unpublished data).

Phylogenetic Relationships of Seed Dormancy

1. Physical Dormancy

Physical dormancy is known to occur only in angiosperms (Baskin *et al.*, 2000). Within the angiosperms, it occurs only in one order and one family of monocots and in eight orders and 14 families of eudicots (*sensu* APG, 1998). Six of the nine orders and 13 of the 15 families in which PY occurs are in the rosids (Figure 28.6, Table 28.5).

2. Combinational Dormancy

Dormancy caused by the combined effects of a water-impermeable seed (or fruit) coat and a physiologically-dormant embryo is known in only six orders and seven families, all of which are eudicots (Figure 28.6, Table 28.5).

3. Seeds with Underdeveloped, Undifferentiated Embryos

This kind of embryo (Figure 28.2) appears to occur only in flowering plants, where it is represented in phylogenetically basal angiosperms, monocots, and eudicots; it apparently is not present in the eumagnoliids (Figure 28.7). Underdeveloped, undifferentiated embryos occur in at least 15 families (*sensu* APG, 1998). They are represented in the asterids by six families but apparently do not occur in the rosids (Baskin and Baskin, unpublished data).

4. Seeds with Underdeveloped, Differentiated Embryos

Unlike underdeveloped, undifferentiated embryos, underdeveloped, differentiated embryos occur in gymnosperms as well as in angiosperms. In gymnosperms, they are found in *Ginkgoales*, *Cycadales*, and in some non-*Pinaceae* conifers (Figure 28.7), such as *Podocarpus* and *Taxus* (Baskin and Baskin, 1998). Among flowering plants, underdeveloped, differentiated embryos occur in the phylogenetically basal angiosperms (including *Amborella*), monocots, eumagnoliids, and eudicots (Figure 28.7). Within the angiosperms, they occur in at least 22 orders and 54 families (*sensu* APG, 1998). Like seeds with underdeveloped, undifferentiated embryos, those with underdeveloped, differentiated embryos do not appear to occur in the rosids (Baskin and Baskin, unpublished data).

MD and/or MPD occur in both gymnosperms and angiosperms. Like the phylogenetic distribution of taxa with underdeveloped, differentiated embryos (Figure 28.7), those with MPD occur from the most primitive to the most advanced groups. Thus, MPD is present in all major clades except the rosids, which cannot have this class of seed dormancy because none of them has underdeveloped embryos.

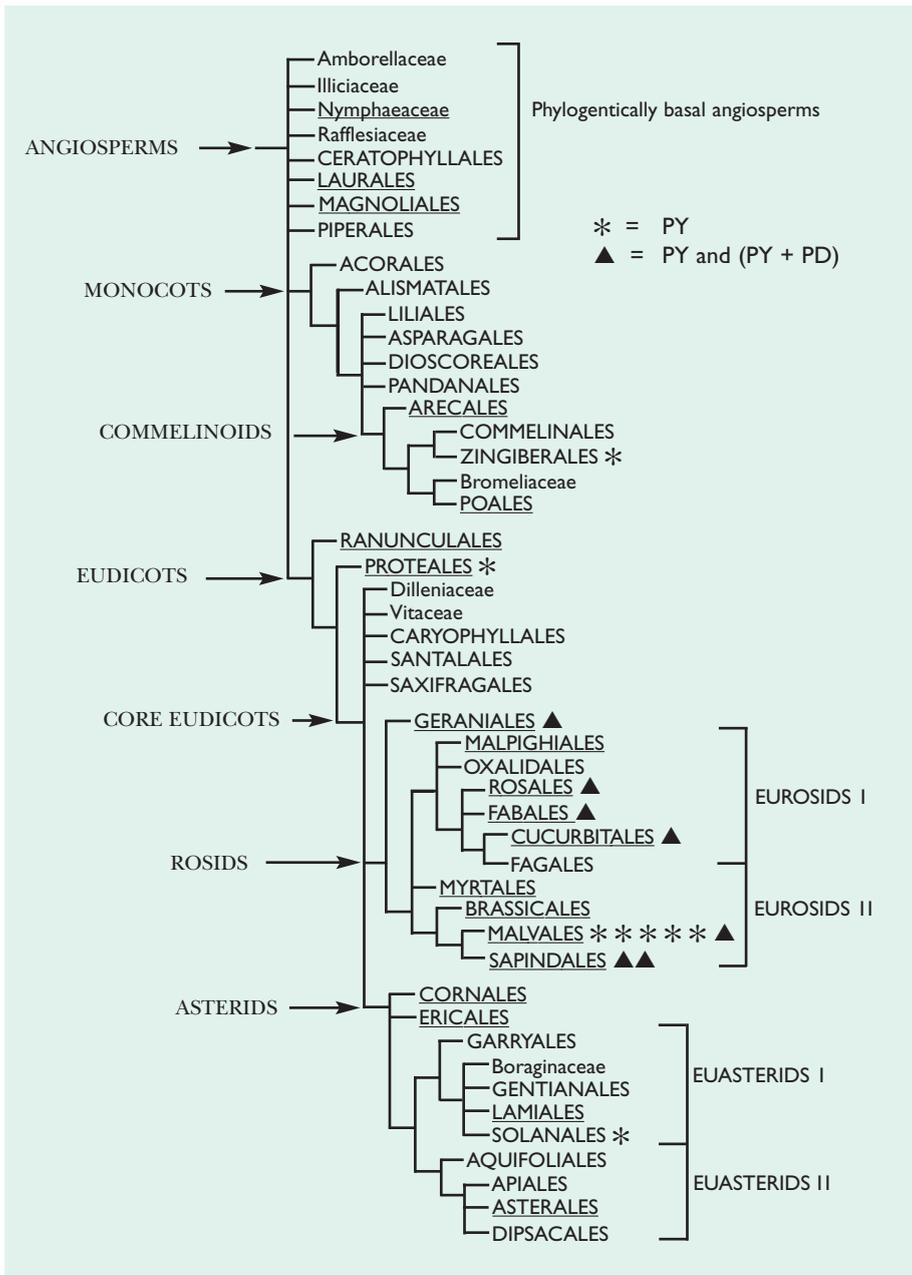


Figure 28.6 Ordinal phylogenetic position of plant families with PY or with PY and (PY + PD) (phylogenetic diagram from Angiosperm Phylogeny Group as modified by Bremer *et al.*, 1999). Orders with recalcitrant seeds are underlined. Each asterisk or triangle represents a family. PY, physical dormancy; (PY + PD), combination of physical and physiological (PD) dormancy (modified Baskin *et al.*, 2000, with permission).

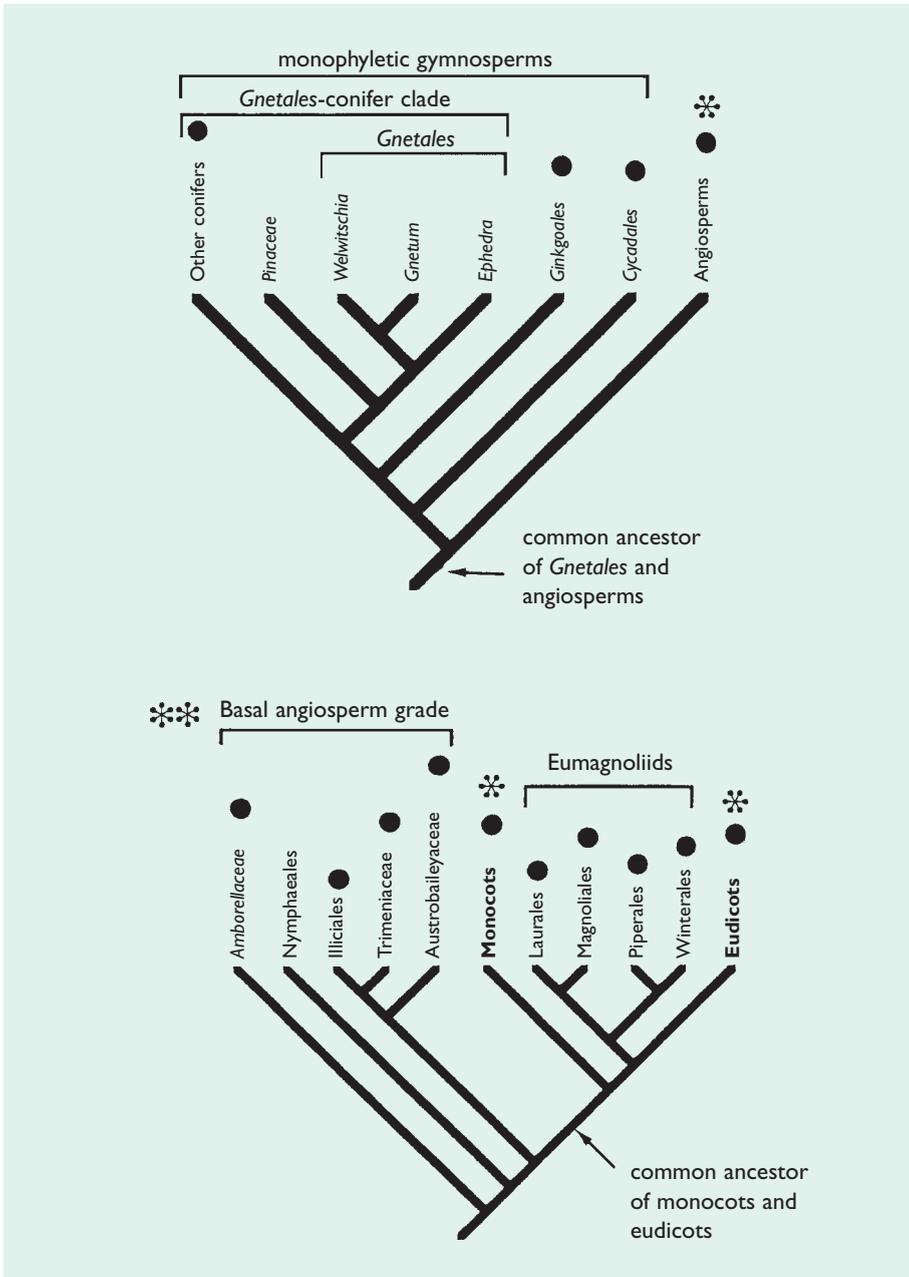


Figure 28.7 Phylogenetic position of underdeveloped embryos in high-level taxa of seed plants (top), and in phylogenetically-basal angiosperms, monocots, eumagnoliids, and eudicots (bottom). *, undeveloped, undifferentiated embryo; •, underdeveloped, differentiated embryo. (Phylogenetic diagrams from Friedman and Floyd, 2001, with permission; embryo information from Baskin and Baskin, 1998, and unpublished data).

5. Physiological Dormancy

Physiological dormancy occurs in gymnosperms and in all major clades of angiosperms. According to our database, seeds of the great majority of angiosperm taxa in this dormancy class have the non-deep level of PD. The five types within the non-deep PD level also are not phylogenetically constrained (Figure 28.8). This is especially true for types 1 and 2, which our studies indicate occur far more frequently than types 3, 4, or 5. Even so, types 3, 4, and 5 have been documented in monocots and in eudicots (Figure 28.8).

6. Within Family Variation in Seed Dormancy

Class, level, and/or type of seed dormancy may vary within a family and even within lower levels in the taxonomic hierarchy. Examples within four families of eudicots will be used to illustrate this variation. In *Anacardiaceae*, freshly matured seeds can be non-dormant or have PD, PY, or (PY+PD). Further, PY and (PY+PD) are found only in a few genera of the tribe *Rhoeae*, and seeds of members of the other four tribes of this family, and even those in some *Rhoeae*, are either non-dormant or have PD. Finally, within the genus *Rhus* both PY and (PY+PD) are found in subgenus *Lobadium*, whereas only PY occurs in subgenus *Rhus* (Baskin *et al.*, 2000, and unpublished data). Seeds of *Caprifoliaceae* can have MD and at least five types of MPD (Hidayati, 2000). Seeds of *Fabaceae* can be non-dormant or have PY and (PY+PD), and perhaps even PD in some tropical genera that produce drupes (See Baskin *et al.*, 2000). In *Rhamnaceae*, seeds may be non-dormant or have PD, PY, or (PY+PD) (Baskin and Baskin, 1998, and unpublished data).

An interesting case of variation occurs in the monocot order *Zingiberales*. PY is found only in the monotypic family *Cannaceae* (*Canna*), and members of the other seven families in the order are non-dormant or have PD (Baskin and Baskin, unpublished). In fact, this is the only monocot group with PY (Figure 28.6), and thus it represents a seemingly “strange phylogenetic occurrence” of this class of dormancy.

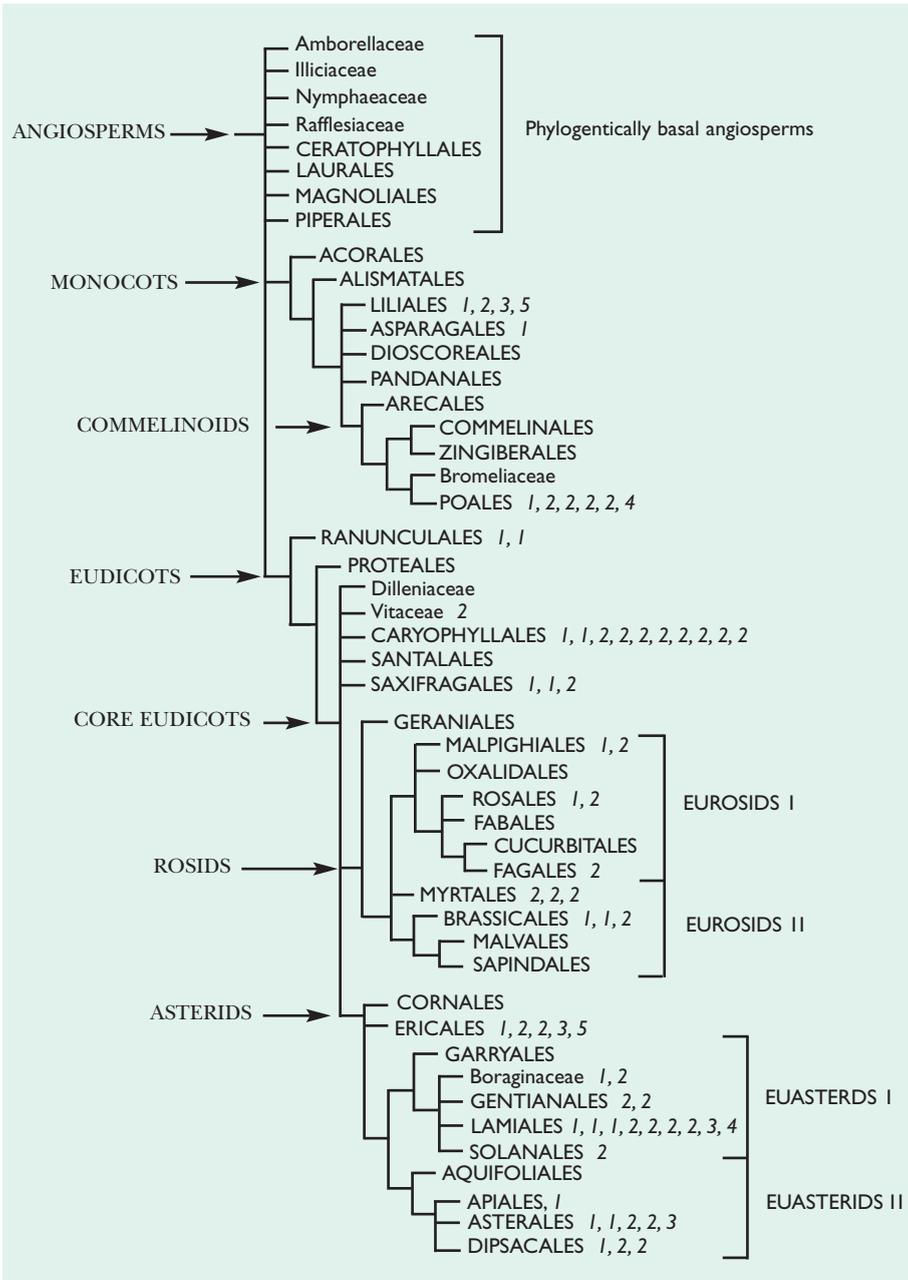


Figure 28.8

Ordinal phylogenetic position of seeds with the five types of non-deep physiological dormancy. Each digit represents a family (e.g., 10 families in *Caryophyllales*). 1, 2, 3, 4, and 5 are the five types of non-deep physiological dormancy (see Figure 28.3). (Phylogenetic diagram from Angiosperm Phylogeny Group as modified by Bremer *et al.*, 1999; data on type of dormancy from Baskin and Baskin, 1998, and unpublished data).

Life Form and Geographical Distribution:

Relationships with Seed Dormancy Class

1. Life Form

There is no obvious relationship between life (growth) form and seed dormancy class for any of Walter's major vegetation types of the world (Baskin and Baskin, 1998), as illustrated for the Temperate Deciduous Forest Biome (Figure 28.9). Thus, it can be seen that, for the most part, each of the five classes of dormancy are proportionally fairly evenly distributed across growth forms (trees, shrubs, lianas and herbs).

A comparison can be made between the occurrence of MPD and of PY for the entire biome with that of herbs in mesic habitats in the North American Eastern Deciduous Forest (EDF), which is a part of the Temperate Deciduous Forest Biome type. For the EDF, seeds of 66% of 68 mesic herbs studied had MPD (Baskin and Baskin, 1998, and unpublished data), whereas for the biome type the percentage was only about 15 (Figure 28.9). On the other hand, whereas seeds of only one (*Geranium maculatum*) of 68 (1.5%) species of mesic herbs in the EDF had PY (Baskin and Baskin, 1998), 10% of those in the entire biome had PY (Figure 28.9).

2. Geographic Range

There does not seem to be a relationship between geographic range of species and class, level, or type of seed dormancy, as illustrated by narrowly-endemic *vs.* geographically-widespread taxa. *Echinacea tennesseensis* (Asteraceae) is a US federally-endangered species endemic to redcedar (*Juniperus virginiana*) glades in three counties in the Central Basin of Tennessee. This species has never been collected from the wild outside the three counties where there are presently about 12 populations. Its very close relative, *E. angustifolia* var. *angustifolia*, occurs throughout a large portion of the central North American grasslands (prairies), from southern Canada to southcentral Texas, USA. Both taxa produce many viable, sexual seeds that have non-deep PD and essentially identical requirements for dormancy-break and germination (Baskin *et al.*, 1997).

Iliamna corei is a US federally-endangered and extremely narrow endemic known only from a single population, on Peters Mountain in the Ridge and Valley Physiographic Province of Giles County, Virginia. The geographic range of *I. rivularis*, a species very closely related to *I. corei*, extends from southern British Columbia and southwestern Alberta, Canada, south to Oregon, Utah, and Colorado, USA, and like seeds of other temperate-zone members of *Malvaceae*, those of *I. corei* and *I. rivularis* have PY. Further, it seems that for both species the only factor that breaks dormancy in nature is heat from fire (Baskin and Baskin, 1997).

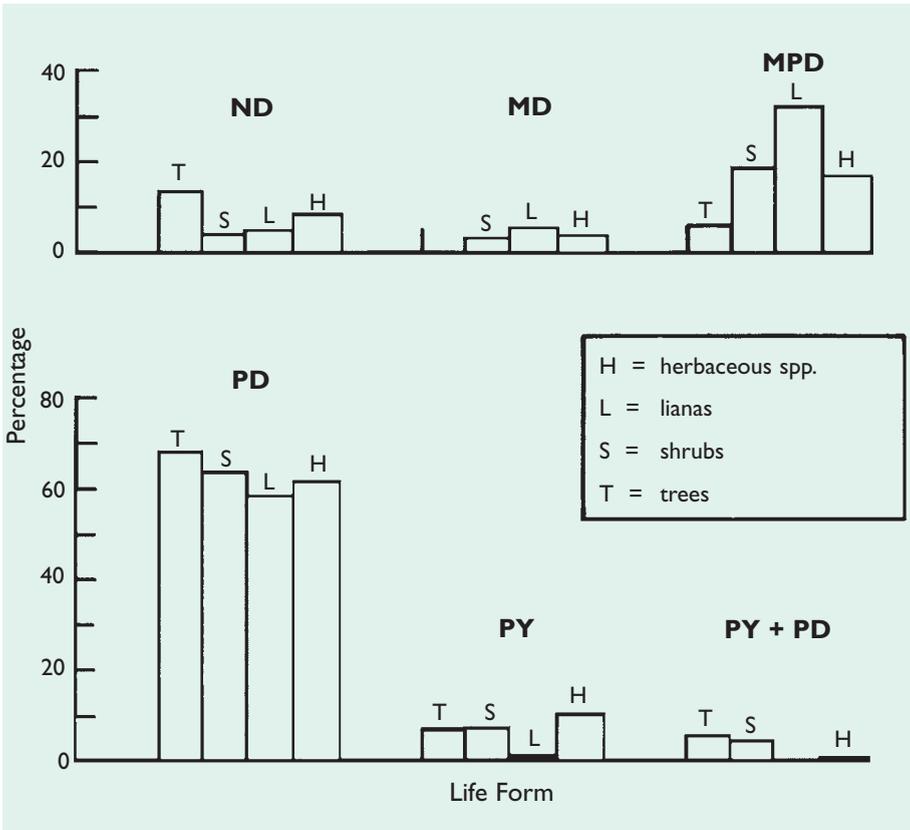


Figure 28.9 Distribution of kinds of dormancy among seed plant life forms within the Temperate Deciduous Forest Biome (extracted from Baskin and Baskin, 1998). ND, non-dormant; MD, morphological dormancy; MPD, morphophysiological dormancy; PD, physiological dormancy; PY, physical dormancy; (PY + PD), combinational dormancy.

Results from these and other studies we have done on seed dormancy and germination of narrowly-endemic taxa from several plant families (see Baskin and Baskin, 1988) lead us to the preliminary conclusion that kind of dormancy *per se* has little, if anything, to do with differences in the distribution of narrowly-endemic vs. geographically-widespread taxa.

Future Research and Other Needs

Much remains to be learned about classification, phylogeny, and biogeography of seed dormancy. Some issues we think need to be addressed to advance these fields of inquiry are discussed in this section of the chapter.

1. Classification

First and foremost, the diversity of kinds of seed dormancy needs to be put into a structural framework, and the best way to do this is to develop a comprehensive scheme of classification that can be used by seed scientists worldwide. Several schemes for classifying seed dormancy have been published (e.g., Harper, 1957; Nikolaeva, 1969, 1977, 1985; Lang, 1987). Of the schemes available, Harper's continues to be the one used most frequently. However, this system is too simple to accommodate the diversity of kinds of dormancy that occurs among seeds (see Baskin and Baskin, 1985, 1998). Nikolaeva's scheme, which we have modified somewhat, is the most comprehensive classification system of seed dormancy ever published. It can accommodate the diversity of kinds of dormancy known to occur in seeds, regardless of the evolutionary position, life form, or biogeography of the taxon that produced them (Baskin and Baskin, 1998, this chapter; Nikolaeva, 1999). Further, the various kinds of dormancy in the Nikolaeva scheme fit nicely into a dichotomous key based on a combination of whole-seed physiological responses (Table 28.2; Baskin and Baskin, in press).

With a classification scheme comes a need for stratification of the hierarchal system into layers. We have used class, level, and type of seed dormancy in this chapter, but our scheme may need to be modified/improved. For example, are three layers in the hierarchy enough, and is(are) there (a) more appropriate name(s) for any, or all, of the layers?

2. Phylogenetic Relationships

In extensive studies on phylogenetic relationships of the kinds of seed dormancy, Nikolaeva (1999) found it informative, in an evolutionary sense, to analyse patterns (trends) of seed dormancy in large taxa (*sensu* Takhtajan's classification system, e.g., see Takhtajan, 1980, 1998). Thus, it seems very worthwhile to summarise briefly her results. This English-language paper by Nikolaeva is an overview of several of her more extensive Russian-language papers.

In class *Magnoliopsida*, the primitive subclasses *Magnoliidae* and *Ranunculidae* have a predominance of underdeveloped embryos and thus MD and MPD. The more advanced subclasses *Hamamelididae* and *Caryophyllidae*, on the other hand, practically lack species with underdeveloped embryos, and PD is prevalent.

Although subclasses *Dilleniidae*, *Rosidae*, and *Lamiidae* exhibit a wide range of kinds of seed dormancy, including MD and MPD, they generally have PD, and also PY in the *Dilleniidae* (*Malvales*) and *Rosidae* (e.g., *Fabales*, *Sapindales*). In *Asteridae*, the most advanced subclass of dicots, large embryos and non-deep PD or ND are predominant (Nikolaeva, 1999).

Class *Liliopsida*, subclass *Alismatidae*, although thought to be primitive, generally have large embryos and PD, whereas small embryos, MD, and MPD are characteristics of subclass *Arecidae*. In subclass *Liliidae*, embryos of *Orchidaceae* are undifferentiated and have a special pattern of dormancy, while embryos in the evolutionary advanced family *Poaceae* are fully-developed, and the seeds are physiologically dormant (Nikolaeva, 1999).

In the gymnosperms, primitive families (*Ginkgoaceae*, *Podocarpaceae*, *Taxaceae*, *Cycadaceae*) have underdeveloped embryos and either MD or MPD, while the advanced families (*Pinaceae*, *Taxodiaceae*, *Cupressaceae*, *Ephedraceae*) have well-developed embryos and PD (Nikolaeva, 1999).

Based on patterns of seed dormancy and germination for >3,000 taxa, Nikolaeva (1999) concluded that, "The patterns of seed dormancy differed in large taxa (as classified by Takhtajan) and evolved *in parallel* (emphasis added) in the various classes and even divisions." This statement certainly is not contradicted by results we obtained by plotting the various kinds of dormancy onto modern phylogenetic trees for orders and higher taxonomic units. It seems that at the ordinal level, PY and (PY+PD) are considerably more phylogenetically constrained than are the other three classes of seed dormancy.

Nevertheless, perhaps the next step in our attempt to understand the phylogeny of seed dormancy is to plot the positions of the various classes, levels, and types of dormancy on phylogenetic trees below the rank of order. Along this line, our preliminary results of a literature survey show that PY in the *Zingiberales* (eight families) occurs only in an evolutionary advanced family (*Cannaceae*) and in the family *Anacardiaceae* (ca. 75 genera) only in an advanced group of closely related genera (*Rhus* and allies)

Thus far, our attempt to determine phylogenetic relationships of the kinds of dormancy has concentrated on the highest layer (i.e., class) in the hierarchy of the suggested classification scheme of seed dormancy. And although type of dormancy within the non-deep PD level is known for species in a good number of families (Figure 28.8), most of the species studied are native to the Northern Hemisphere Temperate Zone (Laurasia). Thus, only a very small percentage of the taxa represented in Figure 28.8 are native to the Southern Hemisphere (Gondwana). Additional information is needed on type of non-deep PD for species in other vegetation zones in both the northern and southern hemispheres. Further, we have not yet begun to sort out the phylogenetic relationships of the deep and intermediate levels of PD or of the levels and types within MD, MPD, PY, or (PY+PD).

3. Biogeography

Our dataset for the occurrence of the classes of seed dormancy and of non-dormancy in the major terrestrial biomes of the world include only 5,250 species of the about 250,000 extant species of seed plants (*sensu* Mabberley, 1997). Thus, Figures 28.4 and 28.5 are based on only about 2% of the seed plants (gymnosperms plus angiosperms). Further: (1) tropical montane, cold desert, woodland, and temperate montane biomes are represented by less than 100 species each (Figures 28.4 and 28.5); and (2) tropical alpine and tropical subalpine zones are not included on Figures 28.4 and 28.5, because we have an insufficient amount of data on seed dormancy in these vegetation types. Thus, information on the kinds of seed dormancy in additional taxa from these six biomes is highly desirable.

We are pleased that, except for tropical montane vegetation, adding classes of dormancy or of non-dormancy for 1,670 additional species to the database in Baskin and Baskin (1998) had only minor effects on the proportional distribution of classes of dormancy, or of non-dormancy, both within and between Walter's vegetation zones. However, we believe that the "models" in Figures 28.4 and 28.5 need further testing, and of course proportions of seed dormancy classes, and of non-dormancy, in the six vegetation zones presently represented by fewer than 100 species each need to be based on larger samples. Our goal is to increase overall sample size from 2% to a minimum of 4% of the extant species of seed plants on earth.

Finally, we only just have begun to sort out biogeographical patterns for the various levels and types of seed dormancy. At present, the database is not available to determine, with much confidence, biogeographic patterns for most levels or types of seed dormancy. Obviously, then, much more research is needed on within-class taxonomy of seed dormancy of many more species in all terrestrial biomes on earth.

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