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RESEARCH OPINION

A classification system for seed dormancy

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This paper is dedicated to Dr Marianna G. Nikolaeva, St. Petersburg, Russia, on the occasion of her 89th birthday (13 September 2003).

Abstract

The proposal is made that seed scientists need an internationally acceptable hierarchical system of classification for seed dormancy. Further, we suggest that a modified version of the scheme of the Russian seed physiologist Marianna G. Nikolaeva be adopted. The modified system includes three hierarchical layers – class, level and type; thus, a class may contain levels and types, and a level may contain only types. The system includes five classes of dormancy: physiological dormancy (PD), morphological dormancy (MD), morphophysiological dormancy (MPD), physical dormancy (PY) and combinational dormancy (PY + PD). The most extensive classification schemes are for PD, which contains three levels and five types (in the non-deep level), and MPD, which contains eight levels but no types. PY is not subdivided at all but probably should be, for reasons given. Justifications are presented for not including mechanical dormancy or chemical dormancy in the modified scheme. PD (non-deep level) is the most common kind of dormancy, and occurs in gymnosperms (*Coniferales*, *Gnetales*) and in all major clades of angiosperms. Since, first, this is the class and level of dormancy in seeds of wild populations of *Arabidopsis thaliana* and, secondly, Type 1 (to which seeds of *A. thaliana* belong) is also common, and geographically and phylogenetically widespread, it seems that biochemical, molecular and genetic studies on seed dormancy in this model species might have rather broad application in explaining the basic mechanism(s) of physiological dormancy in seeds.

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Introduction

Based on numerous studies, it is obvious that many seeds are dormant at maturity and, further, that there are various innate mechanisms (or combinations thereof) for delaying germination, i.e. kinds (generic sense, see below) of dormancy (Nikolaeva, 1969, 1977, 2001; Nikolaeva *et al*., 1985, 1999; Baskin and Baskin, 1989, 1998). Yet, most publications on seed dormancy have not indicated the kind of dormancy that is being investigated, or, if unknown at the outset of the study, the kind of dormancy the results suggest. Recent exceptions to this latter statement include papers by Vleeshouwers *et al*. (1995), Foley (2001) and Forbis and Diggle (2001). Vleeshouwers *et al*. (1995) and Foley (2001) made it clear in their articles that they would focus on physiological dormancy, and Forbis and Diggle (2001) used the results of their study to conclude that seeds of *Caltha leptosepala* have morphophysiological dormancy.

We suggest that not specifying the kind of seed dormancy in studies focusing on this subject may be somewhat analogous to not including the Latin name of the study organism in scientific articles. It certainly would seem to be analogous, for example, to a publication on whole-leaf photosynthetic characteristics of a plant that does not specify which carbon pathway [i.e. C_3, C_4, crassulacean acid metabolism (CAM), intermediates] it uses. Thus, we propose that the diversity of the kinds of seed dormancy needs to be structured, and the best way to do this is to have a comprehensive system of classification that is used by seed scientists worldwide, i.e. an internationally acceptable system.

Definition of dormancy

A *dormant* seed (or other germination unit) is one that does not have the capacity to germinate in a specified period of time 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 of embryo growth and radicle emergence after the mature seed has been dispersed. A freshly matured dormant seed (or other germination unit) is said to have *primary dormancy*, which develops during seed maturation on the mother plant (Hilhorst, 1995; Bewley, 1997a; Hilhorst *et al.*, 1998). A *non-dormant* seed (or other germination unit), on the other hand, is one that has the capacity to germinate over the widest range of normal physical environmental factors (temperature, light/dark, etc.) possible for the genotype. A non-dormant seed will not germinate, of course, unless a certain combination of physical environmental factors (temperature, light/dark, etc.), depending on the taxon and genotype (and perhaps the maternal environment and position in which it developed in the inflorescence), is present. The non-dormant seed that does not germinate because of the absence of one or more of these factors is said to be in a state of *quiescence* [enforced dormancy of Harper (1957, 1977) and pseudodormancy of Hilhorst and Karssen (1992), Koornneef and Karssen (1994) and Karssen (1995)]. Quiescence is included under ecodormancy of Lang *et al.* (1985, 1987) and Lang (1987). The seed will germinate when the appropriate set of environmental conditions is within its range of requirements for radicle emergence, providing it has not entered secondary dormancy (see below).

Whereas some authors (Bewley and Black, 1994) regard a seed to be dormant if the only environmental factor preventing it from germinating is absence of light, we, as well as others (Karssen, 1995; Vleeshouwers *et al.*, 1995), consider light to be just another environmental factor that some non-dormant (but quiescent) seeds require to germinate, like, for example, the presence of substrate moisture. In some cases, at least, whether light is regarded as a dormancy-breaking factor or as a germination-stimulating factor is a matter of semantics. For example, in Harper's scheme, light necessarily is a dormancy-breaking factor for light-requiring seeds in *enforced* dormancy, i.e. when the only thing preventing germination is absence of light. Following our reasoning, however, light is required to stimulate germination of non-dormant, light-requiring seeds.

However, in seeds of many species, dormancy is not an all or nothing stage in the plant's life cycle. Seeds of most species with non-deep physiological dormancy (non-deep PD, see below) go through a series of temperature-driven changes in their capacities for physiological responses to various factors between dormancy and non-dormancy (Bouwmeester and Karssen, 1992; Baskin and Baskin, 1998; see review by Probert, 2000): seed development $\rightarrow$ induction of primary dormancy (Sp) $\rightarrow$ mature seed (Sp) $\rightarrow Sc_1 \rightarrow Sc_2 \rightarrow Sc_3 \rightarrow Sc_4 \rightarrow Sc_5 \rightarrow$ non-dormancy (Sn) $\rightarrow Sc_5 \rightarrow Sc_4 \rightarrow Sc_3 \rightarrow Sc_2 \rightarrow Sc_1 \rightarrow$ Ss (secondary dormancy) $\rightarrow Sc_1 \rightarrow$ etc. $Sc_1 \rightleftharpoons Sc_5$ represent the five transitional physiological states the seed in this example undergoes between the state of primary dormancy (Sp) and the state of non-dormancy (Sn), or during relief of the state of Ss and its re-induction, i.e. the *dormancy continuum* (Baskin and Baskin, 1985). A seed in any of states $Sc_1 \rightleftharpoons Sc_5$ is in *conditional* or *relative dormancy* (see Vegis, 1964; Baskin and Baskin, 1998). A conditionally dormant seed is not capable of germinating in as wide a range of physical environmental conditions as is 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 the 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* (Baskin and Baskin, 1985).

Further, at maturity a seed already may be in one of the states of conditional dormancy ($Sc_1 \rightarrow Sc_5$) and may, or may not, enter dormancy (Ss). It may, however, change from one conditionally dormant state to another, e.g. cycle between Sc_2 and Sc_4, or it may become non-dormant and remain non-dormant, e.g. $Sc_4 \rightarrow Sc_5 \rightarrow$ Sn. Several other combinations of cycling between the various dormancy states have been documented (Baskin and Baskin, 1998).

Finally, a seed may be non-dormant at maturity (Sn), in which case, at least under natural or simulated natural conditions, it apparently remains in this state until it either germinates or dies. As such, a seed that is in the non-dormant state at maturity does not appear to have the capacity to change dormancy states, unlike those that are in the dormant state or in one of the states of conditional dormancy at maturity (Simpson, 1990; Baskin and Baskin, 1998). According to Simpson (1990, p. 129), 'Only seeds [of *Avena fatua*] that have the genetic capacity for primary dormancy can be induced into secondary dormancy … ' However, Khan (1994) did show that seeds of several cultivated vegetable species and *Impatiens novette*, which presumably were non-dormant at maturity, could be induced into dormancy by treating them with inhibitors of gibberellin biosynthesis. Dormancy in these species could be released by GA_{4+7}, and, in some of them, also by cold stratification.

With respect to a classification system for seed

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dormancy, we emphasize that the dormancy cycle is a series of dormancy states of the non-deep level of the class PD (see below). Thus, primary dormancy, conditional dormancy and secondary dormancy are not kinds (types, classes or levels, see below) of seed dormancy.

Mechanism of non-deep physiological dormancy

Since the Discussion of this paper will refer to some of the biochemical/molecular aspects of seed dormancy, it seems appropriate at this point to summarize briefly what is known about the mechanisms of seed dormancy. Seeds of the various model organisms (see below) in which dormancy has been investigated at the biochemical/molecular level had non-deep PD (Fig. 1), and some of them, e.g. potato (Pallais, 1995a, b; Alvarado *et al*., 2000) and *Nicotiana plumbaginifolia* (Jullien *et al*., 2000), were only conditionally dormant (see above). Thus, this summary pertains specifically to the mechanism of dormancy in seeds with non-deep PD.

There seems to be general agreement among plant physiologists/molecular biologists that the mechanisms of seed dormancy and germination involve the plant growth regulators abscisic acid (ABA) and gibberellins (GA). In the hormone-balance model, ABA (inhibitor) and GA (promoter) simultaneously and antagonistically regulate the onset, maintenance and termination of dormancy (Amen, 1968; Wareing and Saunders, 1971). However, this model has been revised based on studies of *Arabidopsis thaliana* (Karssen and Lacka, 1986; Karssen and Groot, 1987; Hilhorst and Karssen, 1992; Karssen, 1995). Thus, in the 'remote control' model, ABA (produced by the embryo) induces dormancy during seed development, and GA promotes germination of non-dormant seeds. Further, the amount of GA required for germination of ripe seeds is controlled by ABA concentrations during seed development. Thus, seeds with a low level of ABA produced during their development ('lightly dormant') require a low amount of GA to germinate, whereas those with a high concentration of ABA produced during seed development ('deeply dormant') require a high amount of GA to germinate. According to this model, GA and ABA do not interact directly. Results of Groot and Karssen (1992) on tomato, of LePage-Degivry *et al*. (1996) on annual sunflower and of Fennimore and Foley (1998) on wild oat support the revised version of the roles of ABA and GA in the regulation of seed dormancy and germination. Bewley (1997a) stated that 'GAs appear not to be involved in the control of dormancy *per se* but rather are important in the promotion and maintenance of germination, that is they act after the ABA-mediated inhibition of germination has been overcome.' The regulatory role of ABA in the induction of dormancy during seed development seems clear, whereas its role in maintaining dormancy is not, in part due to the presence of similar levels of endogenous ABA in dormant and non-dormant seeds. Therefore, the different effects of ABA in non-dormant and dormant seeds may reflect a difference in sensitivity to the hormone (Bewley, 1997a).

Recently, however, evidence has been presented for the involvement of both ABA and GA in dormancy-break in seeds of *Fagus sylvatica* (Nicolás *et al*., 1996; Lorenzo *et al*., 2002), *Arabidopsis* (Debeaujon and Koornneef, 2000), potato (Alvarado *et al*., 2000) and *Nicotiana plumbaginifolia* (Grappin *et al*., 2000; Jullien *et al*., 2000). Models for control of dormancy and germination in *Arabidopsis* (Debeaujon and Koornneef, 2000) and potato (Alvarado *et al*., 2000) show antagonistic interactions of ABA and GA by decreasing and increasing, respectively, embryo growth potential. In the model for potato, GA also acts (to promote germination) by inducing cell wall hydrolases, which cause endosperm weakening, thus allowing the seed to germinate (radicle protrusion) (Alvarado *et al*., 2000). In maize (White and Rivin, 2000; White *et al*., 2000) and sorghum (Steinbach *et al*., 1997), the balance between GA and ABA actions during seed development controls quiescence and maturation versus preharvest sprouting.

In addition to ABA and GA, a third plant hormone, ethylene, is involved in the regulation of seed dormancy and germination. Ethylene breaks dormancy and/or stimulates germination in the seeds of many species (Kępczyński and Kępczyńska, 1997; Matilla, 2000), apparently by decreasing the sensitivity of the seed to endogenous ABA. Thus, ethylene may promote germination by interfering with the action of ABA (Beaudoin *et al*., 2000; Ghassemian *et al*., 2000).

At the molecular level, studies, especially those on wild oats, have shown that specific ABA-responsive mRNAs and heat-stable proteins are upregulated and/or maintained in embryos of imbibed dormant seeds. Amounts of dormancy-associated transcripts remained high in embryos of dormant seeds, declined in initially non-dormant or in after-ripened seeds and disappeared during germination. Thus, the continuous presence of specific mRNAs and/or proteins seems to be required to maintain dormancy, which indicates that this phase of the life cycle is actively imposed (Morris *et al*., 1991; Goldmark *et al*., 1992; Dyer, 1993; Li and Foley, 1994, 1995, 1996, 1997; Johnson *et al*., 1995; Holdsworth *et al*., 1999). Accordingly, then, ' … the role of ABA in dormancy is not the suppression of gene expression but rather the induction of expression of specific genes involved in the blocking of embryo germination' (Garello *et al*., 2000). However, the

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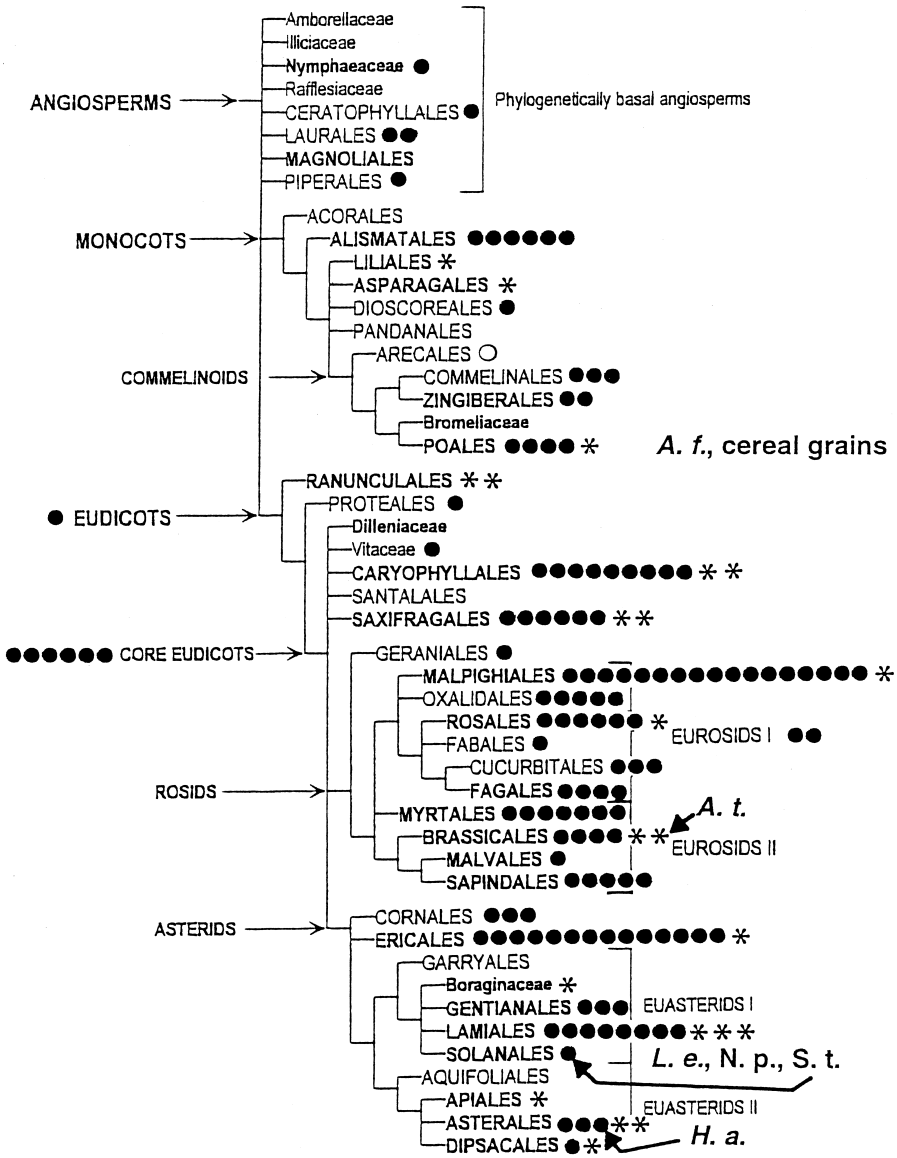

Figure 1. Ordinal phylogenetic position of seeds with physiological dormancy (PD). Each closed circle and each asterisk represents a family in which PD has been documented. In addition, an asterisk means that Type 1 non-deep PD [as occurs in the super model organism *Arabidopsis thaliana* (A. t.)] has been documented in a family. Other model organisms used in investigations on the molecular mechanisms of seed dormancy are indicated by initials: A. f., *Avena fatua*; H. a., *Helianthus annuus*; L. e., *Lycopersicon esculentum*; N. p., *Nicotiana plumbaginifolia*; S. t., *Solanum tuberosum*. Families with physiological dormancy combined with morphological dormancy (MPD), and those with physiological dormancy combined with physical dormancy (PY + PD), are not included on this diagram. The phylogenetic diagram is from the Angiosperm Phylogeny Group (1998), as modified by Bremer *et al.* (1999).

specific functions of these gene products in dormancy regulation are not known (Bewley, 1997a; Li and Foley, 1997; Garello *et al.*, 2000; Koornneef *et al.*, 2002). Li and Foley (1997) stated that ' … although several genes that are differentially expressed in imbibed dormant and nondormant embryos have been isolated, there is as yet no direct candidate for involvement in the maintenance or termination of seed dormancy' (also see Garello *et al.*, 2000). Nevertheless, non-deep PD in the seeds of gymnosperms (e.g. Jarvis *et al.*, 1996, 1997), monocots (e.g. Li and Foley, 1997; Holdsworth *et al.*, 1999) and dicots (e.g. Li and Foley, 1997; Koornneef *et al.*, 2002) appears to be controlled at the level of gene expression.

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Finally, seed dormancy is a typical quantitative genetic trait, involving many genes, influenced substantially by the environment during seed development, and exhibiting continuous (non-discrete) phenotypic variation. Further, it is controlled by nuclear genes, and also by maternal effects in some species and genotypes. Epistatic interactions may occur among loci (Li and Foley, 1997; Van der Schaar *et al*., 1997; Foley and Fennimore, 1998; Koornneef *et al*., 2000; Foley, 2001). Van der Schaar *et al.* (1997) stated that 'Of the traits with large genetic variation in nature, seed dormancy is probably one of the most complicated'.

A classification scheme of seed dormancy

Several schemes for classifying seed dormancy have been published, most notably those of Harper (1957, 1977), Nikolaeva (1969, 1977, 2001), Nikolaeva *et al.* (1985, 1999), Lang *et al.* (1985, 1987) and Lang (1987). Of the schemes available, Harper's has been the one used most frequently, especially in studies on seed ecology and whole-seed physiology. However, his system of innate, enforced (= quiescence; also could include conditional dormancy) and induced (about equivalent to secondary dormancy) is too restricted to accommodate adequately the diversity of the kinds of dormancy that occur among seeds (Baskin and Baskin, 1985, 1998). Vleeshouwers *et al.* (1995) and Thompson *et al.* (2003) have also discussed the inadequacy of the Harper system in describing seed dormancy. The Lang 'universal' system of endodormancy, paradormancy (initially called ectodormancy) and ecodormancy, which is intended to be used with all types of plant dormancy, not just seeds, is far too cumbersome to ever be applied to a representative sample of extant seed plants. Further, it is purely physiologically based. As such, his system does not give proper recognition to the importance of underdeveloped embryos or to water-impermeable seed (or fruit) coats, for example, as being important factors in the classification of seed dormancy. Further, the Lang system does not include intensities (i.e. levels) of dormancy (see below) or physiological patterns (i.e. types) of dormancy-break (see below). Finally, it is doubtful that his scheme could ever have significant utility in working out the biogeographic or phylogenetic relationships of seed dormancy. The shortcomings of the Lang system have been discussed in some detail by Simpson (1990), who states, 'The fact that terms indicating origin, degree and timing of control can occur in each of the categories [i.e. endo-, para- and eco-dormancy] indicates a lack of comprehensiveness of these classes in categorizing all aspects of dormancy' (Simpson, 1990, p. 43).

Nikolaeva's scheme, which we have modified slightly (Table 1), is the most comprehensive classification system of seed dormancy ever published. It can accommodate the diversity of the kinds of dormancy known to occur in seeds, regardless of evolutionary position (Baskin and Baskin, 1998; Nikolaeva, 1999), life form or biogeography (Baskin and Baskin, 1998, 2004a) of the taxon that produced them. Without Nikolaeva's system, it would have been impossible for us to synthesize information on seed dormancy from a phylogenetic, evolutionary or biogeographic point of view (Baskin and Baskin, 1998, 2004a). Further, the various kinds of dormancy in the Nikolaeva scheme fit nicely into a dichotomous key, based on seed (or fruit) coat permeability to water (i.e. impermeable versus permeable), embryo morphology (i.e. underdeveloped versus fully developed) and whole-seed physiological responses to temperature or to a sequence of temperatures (Baskin and Baskin, 1998, 2004b).

With a classification scheme comes a need for stratification of the hierarchical system into layers. Thus, we propose to use class, level and type of seed dormancy. As such, a class may contain levels and types, and a level may contain only types. Further, we

Table 1. A classification system for seed dormancy (modified from Nikolaeva, 1977; Baskin and Baskin, 1998). This system does not include seeds with undifferentiated embryos

A. Class –	Physiological dormancy (PD) Levels – deep, intermediate, non-deep Types – 1, 2, 3, 4 and 5 (of non-deep PD, see Fig. 2)
B. Class –	Morphological dormancy (MD) (does not include seeds with undifferentiated embryos)
C. Class –	Morphophysiological dormancy (MPD) Levels – non-deep simple, intermediate simple, deep simple, deep simple epicotyl, deep simple double, non-deep complex, intermediate complex and deep complex (see Table 3) (does not include seeds with undifferentiated embryos)
D. Class –	Physical dormancy (PY) (probably needs to be subdivided, see text)
E. Class –	Combinational dormancy (PY + PD) Level – non-deep PD (probably both Type 1 and Type 2 are represented)

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use 'kind' of seed dormancy in a generic sense, i.e. in reference to any layer in the hierarchical system of dormancy classification, perhaps similar to the use of the word 'taxon' in plant systematics.

Germination of seeds with undifferentiated embryos at maturity (i.e. as few as two cells, see Baskin and Baskin, 1998), such as those of the *Orchidaceae* and some or all taxa of at least 14 other angiosperm families (*sensu* the Angiosperm Phylogeny Group (APG), 1998; Baskin and Baskin, 1998, 2004a), is a specialized field of study. Nikolaeva (1969, 1977) did not include seeds with undifferentiated embryos in her classification system of seed dormancy, and neither have we included them in the scheme presented in this paper. Thus, we will not comment further on dormancy in this type of seed, except to say that: (1) by definition, they have a morphological (or morpho-anatomical) component of dormancy, and some also have a physiological component; and (2) phylogenetically they occur widely in flowering plants, i.e. phylogenetically basal angiosperms, monocots and eudicots (Baskin and Baskin, 2004a).

Physiological dormancy

Following Nikolaeva (1977), we recognize three levels of PD: deep, intermediate and non-deep. Characteristics for each of the three seed dormancy levels are summarized in Table 2. The great majority of seeds with PD have non-deep PD. Further, based on patterns of change in physiological responses to temperature during dormancy break, five types of non-deep PD are recognized (Fig. 2).

The starting point (1.0) on the *x*-axis in Fig. 2 is the (fully) dormant condition. Values <1.0 to >0.0 represent the continuum of stages toward dormancy break (see under Definition of dormancy) 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). Dormancy cycling, discussed earlier in this paper, is a physiological characteristic of these three types of PD. 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 (Fig. 2). Instead, seeds appear to proceed from the dormant state (1.0) to the non-dormant state (0.0) without going through the continuum of states exhibited by seeds with Types 1, 2 and 3, at least with regard to widening of their temperature responses for germination. Thus, during dormancy-break, seeds with Type 4 gain the ability to germinate only at high temperatures, and those with Type 5 gain the ability to germinate only at low temperatures.

Seeds of the great majority of species with non-deep PD that we have studied belong to either Type 1 or Type 2, and only a few have Type 3. Further, seeds with Type 4 or 5 appear to be even more uncommon than those with Type 3. We have documented Type 4 in the temperate deciduous forest shrub *Callicarpa americana* (*Verbenaceae*) of south-eastern USA (Baskin and Baskin, unpublished manuscript) and Type 5 in two North American hot desert winter annuals, *Eriastrum diffusum* (*Polemoniaceae*) and *Eriogonum abertianum* (*Polygonaceae*) (Baskin *et al*., 1993), and in the eastern North American strict biennial *Gentianella quinquefolia* (*Gentianaceae*) (Baskin and Baskin, unpublished manuscript).

Morphological dormancy

In seeds with morphological dormancy (MD), the embryo is small (underdeveloped) and differentiated, i.e. cotyledon(s) and hypocotyl–radicle can be

Table 2. 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
GA does not promote germination
Seeds require *c*. 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 for dormancy break
Dry storage can shorten the cold stratification period
Non-deep
Excised embryo produces normal seedling
GA promotes germination
Depending on species, cold (*c*. 0–10°C) or warm (≥15°C) stratification breaks dormancy
Seeds may after-ripen in dry storage
Scarification may promote germination

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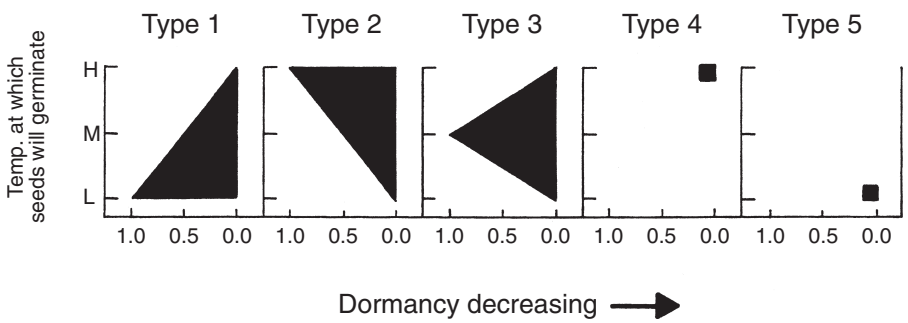

Figure 2. Types of non-deep physiological dormancy in seeds (see text for explanation). (Modified from Baskin and Baskin, 2004a.)

distinguished (Baskin and Baskin, 1998). Embryos in seeds with MD are not physiologically dormant and do not require a dormancy-breaking pretreatment *per se* in order to germinate; thus, they simply need time to grow to full size and then germinate (radicle protrusion). The dormancy period is the time elapsed between incubation of fresh seeds and radicle emergence. Under appropriate conditions, 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 d.

Morphophysiological dormancy

Seeds with this kind of dormancy have an underdeveloped embryo with a physiological component of dormancy. Thus, in order to germinate they require a dormancy-breaking pretreatment. In seeds with morphophysiological dormancy (MPD), embryo growth/radicle emergence requires a considerably longer period of time than in seeds with MD. There are eight known levels of MPD, based on the protocol for seed dormancy break and germination (Table 3).

Physical dormancy

Physical dormancy (PY) is caused by one or more water-impermeable layers of palisade cells in the seed or fruit coat (Baskin *et al*., 2000). Typically, dormancy break in seeds with PY, under both natural and artificial (except mechanical scarification) conditions, has been assumed to involve the formation of an opening ('water gap') in a specialized anatomical structure on the seed (or fruit) coat, through which water moves to the embryo (Baskin *et al*., 2000). Recently, however, Morrison *et al*. (1998) have presented evidence that, in some taxa of Fabaceae, dormancy break by heating may occur through the disruption of the seed coat in a region(s) other than the strophiole (lens).

Mechanical or chemical scarification will also promote germination in seeds with non-deep physiological dormancy (Table 2). Thus, it is not unusual for an investigator to report that seeds of a particular taxon have water-impermeable seed-coat (physical) dormancy, when, in fact, this is not the case. Almost without exception in such studies, lack of water uptake was not documented by comparing imbibition in scarified versus non-scarified seeds, and

Table 3. Eight levels of morphophysiological dormancy (Baskin and Baskin, 1998; Walck *et al*., 1999) and temperature, or temperature sequence, required to break them

	Temperature required[a]		
Type of MPD[b]	To break seed dormancy	At time of embryo growth	GA_3 overcomes dormancy
Non-deep simple	W or C	W	+[c]
Intermediate simple	W + C	W	+
Deep simple	W + C	W	+/–
Deep simple epicotyl	W + C	W	+/–
Deep simple double	C + W + C	W	?
Non-deep complex	C	C	+
Intermediate complex	C	C	+
Deep complex	C	C	–

[a]W, warm stratification; C, cold stratification.
[b]MPD, morphophysiological dormancy.
[c] +, yes; +/–, yes/no; –, no.

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further seeds were of plant taxa not known to have PY (see Baskin *et al*., 2000). Dormancy break by scarification in seeds with non-deep PD appears to be related to weakening (lowering resistance to radicle penetration) of the embryo covering layer, thus allowing the radicle to penetrate it. Compared to intact seeds of wild-type tomato (*Lycopersicon esculentum* cv. Moneymaker), detipped seeds (removal of endosperm plus testa layers opposing the radicle) germinated in a polyethylene glycol (PEG) solution that had a more negative (by *c*. 0.5 MPa) osmotic potential (Groot and Karssen, 1992).

Further, intact ABA-deficient *sitiens* (sit^w) mutant seeds of this tomato cultivar germinated at a faster rate and to a higher percentage than did intact seeds of the wild-type on PEG solutions of –0.3 to –1.5 MPa osmotic potential. However, at low water potentials seeds of the wild type, from which the testa had been removed at the micropylar region, germinated at a similar rate and to a similar percentage as those of intact sit^w. It was concluded that the difference in germination of intact sit^w and wild type ' … was solely dependent on a structural alteration in the mutant testa [much thinner in sit^w than in wild type], making it more delicate and lessening its resistance to penetration by the radicle' (Hilhorst and Downie, 1995).

Combinational dormancy

In seeds with (PY + PD), the seed (or fruit) coat is water impermeable and, in addition, 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 winter annuals, e.g. *Geranium* (*Geraniaceae*) and *Trifolium* (*Fabaceae*), have some conditional dormancy (e.g. Sc_3, Sc_4, Sc_5, see 'Definition of dormancy') and will come out of dormancy (after-ripen) in dry storage or in the field within a few weeks after maturity, even while the seed coat remains impermeable to water (Baskin and Baskin, 1998). Embryos in such genera as *Cercis* (*Fabaceae*) and *Ceanothus* (*Rhamnaceae*) are more deeply dormant (but still non-deep) and thus require a few weeks of cold stratification, i.e. after PY is broken and seeds imbibe water, before they will germinate.

A caveat

Whether a seed is dormant or non-dormant may vary within species and individuals. Thus, a portion of a seed collection may contain seeds that are dormant, as well as those that are non-dormant or conditionally dormant (in the case of seeds with non-deep PD). For example, in many *Fabaceae* the majority of seeds in a sample are water-impermeable, i.e. they have PY, but a low to moderate percentage of them are water-permeable, i.e. they are non-dormant. Further, seeds within a sample may differ in class or level of dormancy. For example, although most seeds (true seed + endocarp) of *Rhus aromatica* have (PY + PD), some of them have PY only (Li *et al*., 1999). In three species of *Aristolochia* subgenus *Siphisia*, a portion of the seeds had MD and a portion had deep simple MPD (Adams, 2003). Some seeds of *Frasera caroliniensis* have deep complex MPD and others non-deep complex MPD. Further, the proportion of seeds of *F. caroliniensis* with these two levels of dormancy varies between: (1) years within the same population; and (2) freshly matured seeds and those that overwinter on the parent plant (Threadgill *et al*., 1981; Baskin and Baskin, 1986, unpublished data). Finally, depending on the population from which seeds of *Empetrum hermaphroditum* were collected in Sweden, 62–78% of them had intermediate PD, while the others had non-deep PD (Baskin *et al*., 2002). Nikolaeva (Nikolaeva, 1977; Nikolaeva *et al*., 1985) was well aware that seeds of a species could have more than one kind of dormancy. For example, seeds of *Tilia cordata* have either (PY + PD) or PD only (Nikolaeva *et al*., 1985).

Evolutionary trends in seed dormancy

Based on information in Baskin and Baskin (1998), Nikolaeva (1999) and Baskin *et al*. (2000), we plotted the five classes of dormancy on Takhtajan's (1980) phylogenetic diagram for the subclasses and orders of angiosperms (not shown). The general evolutionary trends were: (1) MD/MPD are basal for the angiosperms as a whole and for several of the subclasses; (2) thus PD, PY and (PY + PD) are derived; (3) PY and (PY + PD) are the most phylogenetically restricted classes of seed dormancy (they also are the only ones not found in gymnosperms); and (4) PD is the most evolutionarily advanced and phylogenetically widespread class of dormancy, occurring in all ten subclasses. This broad evolutionary sequence is supported by results of a recent study by Forbis *et al*. (2002), who showed that the (low) embryo size to seed size ratio (E:S) has increased between ancestral and derived angiosperms (and gymnosperms). They concluded that the underdeveloped embryo (thus MD/MPD) is primitive among angiosperms (and gymnosperms), and that the other classes of dormancy and of non-dormancy are derived conditions. Forbis *et al*. (2002) argue on ecological grounds that the most primitive class of dormancy is MD, which agrees with the conclusion reached by Baskin and Baskin (1998).

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Discussion

It will be noted that this classification scheme does not recognize mechanical dormancy or chemical dormancy as kinds of dormancy *per se,* thus differing from that of Nikolaeva (1969, 1977) and Nikolaeva *et al.* (1985, 1999). We view mechanical dormancy as a component of physiological dormancy. Thus, a covering layer (or layers) restrains embryo growth (germination) due to low growth potential of the embryo in an intact dormant or in an intact conditionally dormant seed. Subjecting the intact seed (or other germination unit) to a dormancy-breaking protocol causes the growth potential ('expansive force') of the embryo to increase to the point when the radicle (usually) can break through the cover layer(s), the resistance of which to force has not changed (Bewley and Black, 1994; Baskin and Baskin, 1998; Debeaujon and Koornneef, 2000). Even Nikolaeva (Nikolaeva *et al*., 1985) shows that, in seeds of most species in which mechanical restriction of the embryo-covering layers plays a role in seed dormancy, mechanical restriction is combined with physiological dormancy. In only a few species does she indicate that seed dormancy is due only to mechanical restriction of the embryo.

Softening at the tip of the endosperm (distinct endosperm cap or micropylar endosperm in some species, but not in *Nicotiana tabacum*), or of the perisperm envelope, has been demonstrated in seeds of several species of dicots (Leubner-Metzger *et al*., 1995; Welbaum *et al*., 1995; Bewley, 1997b; Sánchez and de Miguel, 1997; Baskin and Baskin, 1998, pp. 30–33; Hilhorst *et al*., 1998; Leubner-Metzger, 2003). This weakening of the endosperm (or perisperm) lowers its resistance to radicle penetration, which, combined with an increase in the growth potential of the embryo (e.g. de Miguel and Sánchez, 1992; Sánchez and de Miguel, 1997; Alvarado *et al*., 2000), allows the seed to germinate. However, the events leading to this decrease in resistance of embryo cover layers appear, in most cases reported, to be part of the germination process in non-dormant seeds and not part of a dormancy-breaking process *per se.* Exceptions to this statement may possibly occur in seeds of the gymnosperms *Picea glauca* (*Pinaceae*) and *Chamaecyparis nootkatensis* (*Cupressaceae*). Downie and Bewley (1996) and Downie *et al.* (1997) demonstrated that a 3-week cold stratification treatment of seeds of *P. glauca* lowered the force required for the radicle to puncture the embryo covers (megagametophyte, nucellus and seed coat). However, they did not test the effect of cold stratification on growth potential of the embryo. Ren and Kermode (1999) showed that dormancy in seeds of *C. nootkatensis* could be broken by a warm, followed by a cold, stratification treatment, which also caused a mechanical weakening of the megagametophyte. In addition, the growth potential of the embryo also increased during the dormancy-breaking treatment. However, they concluded that maintenance of dormancy in seeds of this species is due primarily to the restraint imposed by the megagametophyte. Thus, as far as we are aware, it has not been demonstrated conclusively that modification of embryo cover structures (only) in water-permeable seeds via natural means, such as warm or cold stratification, is required for germination (Baskin and Baskin, 1998).

Chemical dormancy, as used in this paper, refers to the inhibition of germination by organic compounds or by inorganic compounds/ions present in fleshy and dry fruits and/or in the covering layer(s) of seeds. In the sense of Nikolaeva (1969, 1977), chemical dormancy is due to presence of inhibitors in the pericarp. Thus, chemical dormancy does not include the active components of the metabolic machinery *per se* of the seed. However, metabolic pathways involving promoters, inhibitors and membrane changes are involved in the biochemistry and biophysics of dormancy break and of dormancy induction (dormancy cycling) in seeds with physiological dormancy (Hilhorst, 1993, 1998; Derkx and Karssen, 1994; Hilhorst *et al*., 1996; Hilhorst and Cohn, 2000), and thus also in the physiological component of those with morphophysiological or combinational dormancy. In contrast to chemical dormancy, the causes of which are *exogenous*, physiological dormancy is *endogenous* (Nikolaeva, 1969, 1977).

There is no doubt that the presence of a fleshy pericarp is inhibitory to seed germination in some plants. For example, Burrows (1993, 1995, 1999 and other papers) has shown that intact fleshy pericarps delay/prevent germination of seeds of many native New Zealand woody species under near-natural conditions. However, although substances in the pericarp inhibit seed germination via chemical and/or osmotic effects, the chemical/physical nature of the inhibitors rarely has been identified (Nikolaeva, 1969). In the fleshy fruited cultivated species *Cucumis melo* (Welbaum *et al*., 1990) and *Lycopersicon esculentum* (Berry and Bewley, 1992), precocious germination of the developing seed was prevented by low water potential of the fruit tissue. However, although lack of germination of some seeds may be due only to inhibitors in the pericarp, in most cases (as with mechanical resistance of the embryo cover layers) their influence is combined with physiological dormancy of the embryo (Nikolaeva, 1969; Nikolaeva *et al*., 1985). We suggest that dormancy status of the seeds should be evaluated after they are released from the fleshy pericarp, i.e. determine the kind of dormancy for the germination unit. Thus, seeds that

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are prevented from germinating only by the unfavourable environment within fleshy fruits would be in a state of quiescence, i.e. no innate dormancy. In the case of dry fruits, in particular, the germination unit may include the true seed enclosed within part (e.g. endocarp of *Anacardiaceae*) or all of the pericarp (e.g. achenes, mericarps, nuts, etc.).

Although water-soluble germination inhibitors, such as ABA and coumarin, have been isolated from embryo cover layers and from fruits of many plant species, it is not at all clear what role, if any, they play in regulating germination under field conditions (Mayer and Poljakoff-Mayber, 1989; Bewley and Black, 1994). According to Mayer and Poljakoff-Mayber, only for the legume *Trigonella arabica* (*Fabaceae*), which has PY (Gutterman, 1993), has it been shown that coumarin occurs in inhibitory concentrations. Further, they state that ' … the presumed functions of inhibitors in fruits are by no means finally proven, and in fact they are very difficult to prove unequivocally' (Mayer and Poljakoff-Mayber, 1989, p. 225). Bewley and Black (1994, p. 213) point out that ' … the discovery of an inhibitor in a seed does not necessarily mean that it functions in the dormancy mechanism'. They pose four questions that must be answered in order to show that an inhibitor in seeds plays a role in maintaining dormancy. Then, they state (p. 213), 'Unfortunately, in no case do we know the answers to all or even most of these questions'. Finally, Simpson (1990, p. 78) states that ' … the case for involvement of growth inhibitors from hulls in caryopsis dormancy [in grasses] is not yet established'.

Neither is there much hard evidence (proof!) that seed dormancy in nature is regulated by the presence of inorganic compounds/ions in fruits or in seed covering layers. In several species of *Atriplex* (*Chenopodiaceae*), for example, salt concentration in the bracteoles has been proposed to impose seed dormancy under natural conditions, since leaching these salts from the bracteoles of the one-seeded fruits stimulated germination (Beadle, 1952; Koller, 1957; Osmund *et al*., 1980). However, Mandák and Pyšek (2001) have shown that this is not the case with the salt steppe species, *A. sagittata*. Even the highest salt concentration (1.484 mg l^{-1}) of NaCl in the bracteoles of this species did not inhibit germination. They state, 'Our model suggests that bracteole salt may not be important [in preventing seed germination] for *A. sagittata* in the field because the first autumn rain is probably sufficient to leach almost all their sodium and chloride'. Thus, the presence of salt in the bracteoles of this summer annual species does not act as a rain gauge (*sensu* Went, 1949; Gutterman, 2000). More recently, Garvin and Meyer (2003) concluded that soluble inhibitors are not an important component of the dormancy mechanism in germination units of the western North American salt desert species, *Atriplex confertifolia*.

Further, our combinational dormancy class contains only a few of Nikolaeva's combined dormancy types (types, *sensu* Nikolaeva). Her combined dormancy category consists of various combinations [a matrix (see Nikolaeva, 1969, p. 13) of endogenous (morphological, physiological, morphophysiological) and exogenous (physical, chemical, mechanical) dormancy types (types, *sensu* Nikolaeva)]. However, since we do not recognize chemical or mechanical dormancy as kinds of dormancy *per se* (Table 1), and underdeveloped embryos are not known to occur in seeds with water-impermeable seed (or fruit) coats (Baskin *et al*., 2000), the only combination left in the matrix in the class category is physical dormancy × physiological dormancy, thus (PY + PD). Theoretically, then, it is possible to have three subtypes in this class of dormancy: (PY + non-deep PD), (PY + intermediate PD) and (PY + deep PD). However, it appears that seeds of most species with (PY + PD) have non-deep PD; perhaps those of some species have intermediate PD (see Table 1).

Modification or expansion of the classification scheme presented here may need to be made from time to time to accommodate new kinds of seed dormancy. Along this line, for example, we believe that further study is needed on the classification of seeds with PY. With regard to the water-impermeability in seeds or other germination units with PY, there is considerable variation in the developmental origin of the palisade or palisade-like water-impermeable layer(s), and in the origin and anatomy of the specialized areas ('water gaps') that 'open' and allow water to move to the embryo (Baskin *et al*., 2000). It even appears that some species of *Fabaceae* with PY do not have a lens (Gunn, 1984, 1991).

Further, and perhaps more importantly, with regard to the establishment of any additional layer(s) of classification for seeds with PY, there is quite a bit of variation in the response of seeds in this dormancy class, both to the quality and quantity of laboratory and of field protocols that stimulate seeds to germinate (Baskin and Baskin, 1998). For example, even two *Senna* species in the same section of subfamily *Caesalpinioideae* (*Fabaceae*) differ, both qualitatively and quantitatively, in their responses to several dormancy-breaking treatments in the laboratory (Baskin *et al*., 1998). Further, whereas fire was completely ineffective in breaking dormancy in the two *Senna* species, it was quite effective in stimulating germination of seeds of *Iliamna corei* (*Malvaceae*) (Baskin and Baskin, 1997) and those (seed = true seed + endocarp) of *Rhus glabra* (*Anacardiaceae*) (Baskin *et al*., 2000).

Morrison *et al*. (1992) have shown that 34 species of south-eastern Australian *Fabaceae* fit into three

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more-or-less distinct groups at the subfamily–tribal level, based on percentages of freshly matured seeds that are dormant, and on their ability to come out of PY (or not) during dry storage in the laboratory. The three groups are: (1) high dormancy both before and after 3.5 years of dry storage in the laboratory, i.e. high–high; (2) low–low; and (3) high–low. Further, in a study on 16 of the 34 species, Morrison *et al.* (1998) demonstrated that the route of water entry into heat-treated (to break dormancy) seeds of nine of the species was via the (disrupted) lens only, whereas in the other seven species, it was via disrupted regions of the seed coat other than the lens, providing what seems to be evidence that seed coat impermeability is not localized at the lens in some legumes with PY. Water entry into all eight species in the high–high group (*Mimosoideae*: *Acacieae*; *Faboideae*: *Mirbelieae*), plus *Pultenia flexilis* (*Faboideae*: *Mirbelieae*) in the low–low group, was via the lens only. On the other hand, water entry into seeds of all six species in the high–low group (*Faboideae*: *Bossiaeae*; *Faboideae*: *Phaseoleae*), plus *Aotus ericoides* (*Faboideae*: *Mirbelieae*) in the low–low group, was via areas on the seed coat other than the lens. Interestingly, structure of the testa in the high–low group differs from that in the other two groups (Morrison *et al.*, 1998). We agree with Morrison *et al.*'s (1998) statement, that ' … testa-imposed dormancy does not represent a single dormancy mechanism in legumes, as is often assumed when dormancy is broken artificially'.

In a recent study of physical dormancy in 35 species of the family *Geraniaceae*, including *Erodium*, *Geranium* and *Pelargonium*, Meisert (2002) recognized three categories of dormancy, based on the proportion of water-permeable and water-impermeable coats in samples of fresh seeds. Water-permeability versus water-impermeability of the seeds of 18 of these species was tested again after 2 years of dry storage at 20°C. In the Meisert PY° category, which included *E. manescavii* and three *Pelargonium* species, 100% of the seeds were permeable (non-dormant) at maturity. In the PY^{80} category (1–80% with impermeable seeds), dormancy persisted during 2 years of storage in a proportion of the seeds of four species, while in three (*Geranium*) species it did not (i.e. 0% of the seeds with PY after 2 years). In the PY^{100} category (>80% with impermeable seeds), dormancy persisted in 51–100% of the seeds for 2 years in dry storage in nine species, while in two species (*G. canariense*, *E. cicutarium*) all seeds were permeable after 2 years. There was a general positive correlation between proportion of fresh seeds with impermeable coats and thickness of the water-impermeable and mechanical layers. Thus, Meisert (2002) concluded that ' … species with a high percentage of impermeable seeds have a closed chalazal slit [see Meisert *et al.*, 1999] and form a thick mechanical and impermeable layer'. Even so, all impermeable seeds of two species in the PY^{100} category became permeable during storage, while no impermeable seeds in seven species in this category did so. This pattern of retention/loss of impermeability during storage also occurred in seeds of species in the PY^{80} category. Thus it seems that the proportion of freshly matured seeds with water-impermeable versus water-permeable coats may not be a good predictor of kind (level or type?) of dormancy (with regard to maintenance and breakage) in *Geraniaceae*. It is quite clear, however, that ' … physical dormancy is a diversely differentiated feature in *Geraniaceae*, with regard to both percentage of impermeable seeds at maturity and maintenance of dormancy under particular conditions' (Meisert, 2002). Thus, lack of a single dormancy-breaking mechanism in plant families with PY suggests a need for subdivision of the PY class into lower layers in the hierarchy (Table 1).

Undoubtedly, then, there is quite a bit of diversity in dormancy at the (whole-seed) physiological, morphological and anatomical levels. Thus, the question arises: where does the plethora of studies on the molecular biology and genetics of seed dormancy in such model species as *Arabidopsis thaliana* (Koornneef *et al.*, 2002) fit into the scheme of things? Will results of studies on this species allow us to make broad generalizations about the basic mechanisms of seed dormancy? We think so – in part. First of all, seeds of wild populations of *A. thaliana* have non-deep PD (Baskin and Baskin, 1972, 1983, 1998; Ratcliffe, 1976; Tables 1 and 2), which is the most common kind of seed dormancy on Earth and in all of the world's major terrestrial biomes except matorral, where it is of about equal importance with PY (Baskin and Baskin, 2004a). Furthermore, seeds of *A. thaliana* have Type 1 (Ratcliffe, 1976; Baskin and Baskin, 1983; Figs 1 and 2), and most species with PD have either Type 1 or Type 2, non-deep PD (Baskin and Baskin, 2004a). In addition, PD (of the non-deep type) is found in both gymnosperms (*Coniferales*, *Gnetales*) and throughout the angiosperms, i.e. in the phylogenetically basal group, monocots and eudicots (Baskin and Baskin, 2004a). It is essentially the only kind of dormancy found in the phylogenetically advanced families *Poaceae* and *Asteraceae*. These two families alone contain >30,000 species or >10% of the extant angiosperms (Mabberley, 1997; Thorne, 2000).

Other model systems for studying the biochemistry, molecular biology and/or genetics of seed dormancy include *Avena fatua* (e.g. Li and Foley, 1997; Foley and Fennimore, 1998; Holdsworth *et al.*, 1999; Foley, 2001), *Helianthus annuus* (LePage-Degivry *et al.*, 1996), *Lycopersicon esculentus* (Hilhorst *et al.*, 1998), *Nicotiana plumbaginifolia* (Jullien *et al.*, 2000), *Nicotiana tabacum* (Leubner-Metzger, 2003), *Solanum tuberosum* (Alvarado *et al.*, 2000) and the cereals barley

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(*Hordeum vulgare*), oats (*Avena sativa*), rice (*Oryza sativa*) and wheat (*Triticum aestivum*) (Foley and Fennimore, 1998; Corbineau and Côme, 2000). Freshly matured seeds of these species that are dormant also appear to have non-deep PD. The high to low pattern of change in temperatures at which seeds can germinate during dormancy break indicates that at least two of these species, *Solanum tuberosum* (Pallais, 1995a, b; Alvarado *et al*., 2000) and *Helianthus annuus* (Baskin and Baskin, unpublished data), have Type 2 non-deep PD (Fig. 2).

Thus, it seems likely that unravelling the biochemical, molecular and genetic mechanisms of physiological dormancy in seeds of *A. thaliana*, and in those of the other model systems, could be a major step in understanding dormancy, both geographically and phylogenetically. Further, it may also contribute to understanding the mechanism of the physiological component of dormancy of seeds with combinational dormancy and of those with morphophysiological dormancy.

However, it seems reasonable to think that the biochemistry and molecular biology of the five types of non-deep PD may not be the same qualitatively and/or quantitatively. For example, seeds of winter annuals, such as *A. thaliana*, which have Type 1 non-deep PD, come out of primary dormancy during the high temperatures of summer, and seeds that do not germinate in autumn are induced into secondary dormancy by low temperatures during winter (Baskin and Baskin, 1983; Derkx and Karssen, 1994). On the other hand, seeds of summer annuals, such as common ragweed *Ambrosia artemisiifolia*, which have Type 2 non-deep PD, come out of dormancy during winter (cold stratification), and seeds that do not germinate (e.g. while buried in soil) in spring are induced into secondary dormancy by the increasing temperatures of late spring/early summer (Baskin and Baskin, 1980). Surely, then, the biochemical and molecular mechanisms of dormancy break in Types 1 and 2 are not exactly the same. Further, it seems reasonable that both of these types may differ from non-deep PD Types 3, 4 and 5 and from the intermediate and deep PD levels, as well as from the physiological component of MPD (of which there are eight levels, Table 3) and of combinational dormancy, although it appears that the physiological component of the latter dormancy class is of the non-deep type.

Undoubtedly, use of an 'official' classification scheme of seed dormancy would facilitate communication among seed scientists by providing a framework for interpretation of results at all layers in the hierarchy of biological organization. It would allow the investigator to determine where, in the system of the diversity of the kinds of seed dormancy, he/she is working. In addition, it may encourage biochemists and molecular biologists working on seed dormancy to use the comparative approach in attempting to define dormancy at these layers of study. There is certainly enough information on the biochemistry and molecular biology of seed dormancy in a phylogenetically diverse group of seed plants (gymnosperms, monocots, dicots) to begin to make comparisons at these levels of enquiry. A comprehensive seed dormancy classification system based on the initial scheme of Nikolaeva (1969) and its various modifications (Nikolaeva, 1977, 2001; Nikolaeva *et al*., 1985, 1999) is certainly essential in studies on the ecology, biogeography and evolution of seed dormancy (Baskin and Baskin, 1998; Nikolaeva, 1999).

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