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From oversight to insight: integrating epicotyl emergence to redefine germination and enhance the seed dormancy framework

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Abstract

The seed science community currently defines germination as radicle emergence of 2 mm from the dispersal unit. Consequently, most seed researchers abruptly terminate germination experiments after radicle emergence, concluding that the seed has germinated. However, this approach underestimates epicotyl dormancy and often leads to dormancy misclassification, or worse, a failure to identify epicotyl dormancy altogether. To address these limitations, we propose extending germination studies to the point of first leaf emergence; we term this the "full germination" period. Our methodology involves germinating fully matured, freshly collected seeds and depending on the time required for radicle emergence, the seeds are categorized into (1) viviparous, where seeds germinate prematurely while they are still attached to the parent plant or within the fruit; (2) Morphological dormancy (MD) or Non-dormant (ND), where seeds germinate within 30 days; and (3) physiological dormancy (PD) and morphophysiological dormancy (MPD), where germination does not occur within 30 days. The absence of shoot emergence within 30 days following radicle protrusion indicates the presence of epicotyl dormancy. Thus, species initially classified as ND, MD, or viviparous may be miscategorized if shoot emergence is not assessed. Likewise, seeds exhibiting PD or MPD may possess an additional epicotyl dormancy component, possibly leading to placing them in incorrect subclass or level. A comprehensive assessment of shoot development is imperative for accurate dormancy characterization. We strongly recommend monitoring seed germination until first true leaf emergence should be adopted to ensure correct conclusions about dormancy, plant life cycles and ecological adaptations.

Introduction

Since Crocker's (1916) first detailed work on seed dormancy, thousands of research articles and hundreds of books have been published on this topic, which increased our understanding significantly in several areas. Now, we have a more acceptable definition of dormancy. Baskin and Baskin (2004, 2014, 2021) define "*a dormant seed (or other germination unit) is one that does not have the capacity to germinate in a specified period of time* (30 days) *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*." Likewise, despite several attempts that had been made to classify seed dormancy in the past (Bewley et al., 2013; Harper, 1977; Vleeshouwers et al, 1995), the use of Russian seed physiologist Marianna G. Nikolaeva's (1969) classification system modified by Baskin and Baskin (Baskin and Baskin, 2004, 2021) has become the most useful system because it not only refers to what causes dormancy (hampers germination) but also what conditions have to be met in the field before dormancy is broken.

The five classes proposed by Baskin and Baskin (2004, 2014, 2021) include: (i) physiological dormancy (PD), in which embryos lack the potential to elongate due to either innate constraints or thick water-permeable seed coat/endocarps preventing elongation; (ii) morphological dormancy (MD), where seeds are dispersed with underdeveloped embryos requiring time to mature and develop, despite having distinct cotyledons and hypocotyl-radicles; (iii) morphophysiological dormancy (MPD), characterized by seeds with underdeveloped embryos that also possess PD, necessitating specific dormancy-breaking conditions to break both MD and PD before germination; (iv) physical dormancy (PY), where the palisade layer of lignified Malpighian cells in the seed/fruit coat becomes impermeable during maturation drying, preventing water uptake and hydration; and (v) combinational dormancy (PY + PD), where seeds exhibit both PY and PD, requiring conditions that break both dormancy classes before germination can occur. However, not all the spermatophytes produce dormant seeds, particularly those inhabiting tropical-wet and aquatic environments, produce non-dormant (ND) seeds that germinate almost immediately after dispersal when they receive favourable conditions for seed germination (Baskin and Baskin, 2014, 2021). Furthermore, some species in extreme environments such as mangroves, produce seeds that germinate prematurely while they are still attached to the parent plant or within the fruit, even before dispersal (Farnsworth, 2000). This phenomenon involves the continuous growth of the embryo without entering a dormant state. These seeds are known as viviparous or crypto-viviparous (Wijayasinghe et al, 2019).

The transition from seed to seedling, with a specific focus on the epicotyl, has been a subject of longstanding interest in plant biology (e.g., Engelmann, 1880). Although the phenomenon of epicotyl dormancy, characterized by a temporal separation between radicle emergence and subsequent shoot development, has been recognized for some time, this particular form of dormancy has received comparatively limited attention across a diverse range of species. In the recently updated dormancy classification system, Baskin and Baskin (2021) included epicotyl dormancy under PD subclass 2 and recognized two levels: Level 1. Nondeep, in which the seeds are non-dormant, i.e., radicle emerges quickly, but the shoot emergence is delayed; and Level 2. Deep, which contains seeds that show both root emergence delay and delay for shoot emergence after root emerged. In addition, the palm seeds with MDare included under Class 2. Morphological [B] subclass 6. Specialized E (palms) also have known cases of epicotyl dormancy (the alphabets and subclass numbers refer to the dormancy classes proposed by Baskin and Baskin, 2021). Further, MPDalso includes three levels, namely nondeep epicotyl, deep epicotyl, and double dormancy. Epicotyl dormancy can be present independently in species otherwise characterized by ND or occur in species with other established dormancy classes. Regardless of this, the defining feature of epicotyl dormancy is the delayed development of the shoot system, frequently necessitating specific environmental cues or treatments to facilitate shoot establishment. This intricate relationship underscores the need for more rigorous investigations into the physiological and ecological understanding of epicotyl dormancy.

Most seed researchers terminate their germination experiments abruptly after the first visible signs of germination, which is radicle emergence to 2 mm, based either on the International Seed Testing Association recommendation (ISTA, 2024) or a general understanding that a germinated seed is no longer part of "seed research." A major problem with this approach is that studies concluding the dispersal units are ND underestimate the presence of dormancy, particularly epicotyl dormancy. Obviously, this oversight needs to be addressed for various reasons. Firstly, understanding epicotyl dormancy informs us of the adaptive strategy used by some species to survive adverse environmental conditions (Jaganathan, 2021; Jaganathan and Phartyal, 2024). Desiccation sensitive (DS) seeds avoid desiccation stress in the seed state, but the growing radicle can penetrate deep into the soil, which retains moisture from rainfall for a long time. Secondly, epicotyl dormancy might be a risk-minimizing strategy to reduce competition during the growing season. A delayed emergence in the shoot may allow the growing seedlings to absorb more nutrients when all other species have already started photosynthesis. Thirdly, our understanding of the distribution of dormant seeds in several habitats often ignores epicotyl dormancy, and a reassessment might offer a varied perspective on the ecological significance of dormancy in relation to climate. For example, in DS species, epicotyl dormancy may synchronize shoot emergence with the wet season. Finally, the hormonal pathways, mainly, gibberellins (GAs) and abscisic acid (ABA) in ND and comparatively in dormant seeds, can be better understood. This is especially crucial when epicotyl dormancy occurs with other forms of dormancy, and our understanding of the biochemical and molecular mechanisms involved is not complete (Chen et al, 2024).

The traditional definition of germination, focusing solely on radicle emergence, is insufficient to capture the complexities of epicotyl dormancy. This limitation is particularly significant as epicotyl dormancy is a key component of various dormancy classes including ND, MD, PD, and MPD. Thus, by relying solely on radicle emergence, researchers may overlook or misclassify important dormancy mechanisms, potentially leading to an incomplete understanding of seed biology and ecology. To address this problem in all species, including agricultural and wild species, this work proposes that continuing seed germination studies until the first leaf emergence is critical for understanding dormancy complexity and capturing novel insights into evolutionary ecology and trait coexistence. We call this as "full germination" period, i.e., from sowing to first leaf emergence. To this end, we have developed a detailed methodology from the onset of germination experiments (Fig. 1). Our method involves germinating fully matured seeds (immediately after collection) across a wide range of temperature and light conditions, separating them into three distinct groups based on germination timing: (1) Viviparous seeds, which by definition exhibit visible germination at the time of dispersal, as evidenced by radicle emergence; (2) ND or MD seeds that achieve more than 50% germination under any single combination of temperature and light within 30 days; and (3) PD or MPD seeds that fail to achieve 50% germination under any combination of temperature and light within 30 days. More importantly, our goal here is not to attempt an exhaustive review of epicotyl dormancy, but to show as many examples as possible that monitoring seed germination until the emergence of first leaves is essential.

Group 1- viviparous/ cryptoviviparous seeds

The viviparous seeds with emerged radicles must be monitored for germination across a wide range of temperature and light conditions. If seeds are truly non-dormant, shoot emergence occurs within 30 days. If shoot emergence is delayed beyond 30 days, the seeds exhibit PD-subclass 2: epicotyl dormancy. Further, because the radicle already emerged indicating the absence of PD, these species have nondeep PD with subclass epicotyl dormancy. While this type of dormancy remains less explored in the literature, some true mangrove species have viviparous seeds where the hypocotyl elongates and emerges, piercing both the seed and fruit coats before the dispersal. However, the epicotyl emerges once the seed is firmly established on a stable shoreline. During the dispersal, shoot stays dormant. Wijayasinghe et al (2023) unequivocally reported a significant delay in shoot emergence following radicle emergence in *Aegiceras corniculatum* (Primulaceae), a crypto-viviparous (radicle emerge piercing the seed coat but not piercing the fruit coat, prior to dispersal) mangrove species. This finding suggests that viviparous and cryptoviviparous species may exhibit epicotyl dormancy, overturning the standard notation that all viviparous seeds are non-dormant. Thus, viviparous seeds are either (truly) ND or PD with subclass-epicotyl Level 1 (i.e., radicle ND).

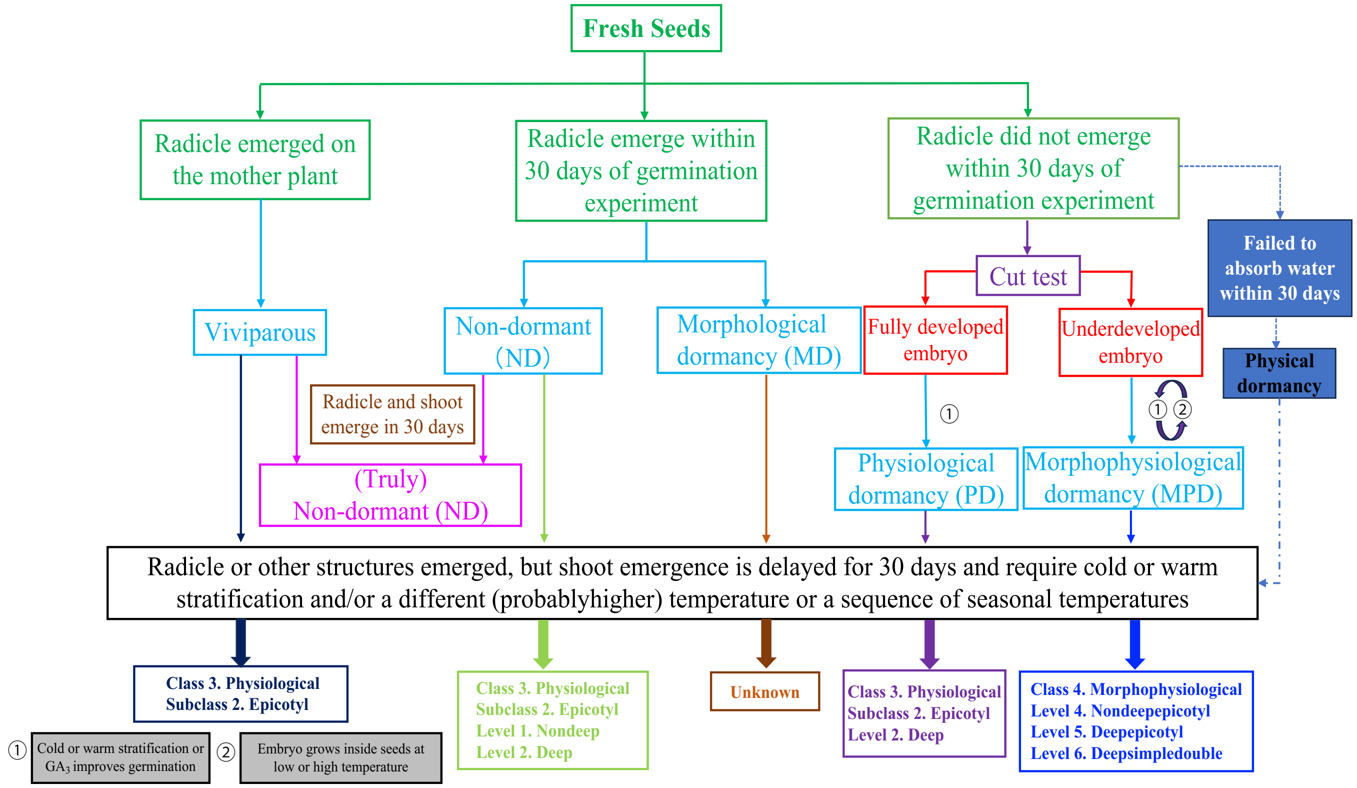

Figure 1. A decision tree for classifying seed dormancy types based on radicle emergence and embryo development patterns. Seeds are initially sorted into three groups according to the time required for germination, 1) radicle emerged on the mother plant (Viviparous); 2) radicle emerged within 30 days at any temperature or light conditions (Non-dormant, ND or Morphological dormant, MD); and 3) radicle did not emerge within 30 days at any temperature or light conditions (Physiological dormant, PD or morphophysiological dormant, MPD). A cut test is then used to distinguish PD and MPD seeds. Depending on the interval between radicle emergence and shoot emergence, seeds are redefined as truly ND or as having epicotyl dormancy. If epicotyl dormancy is observed, seeds are assigned to the appropriate class, subclass, and levels. In PD and MPD seeds, if shoot emergence is delayed the growing seedlings should be monitored until first leaves and assigned to the appropriate class, subclass and levels (also see Baskin and Baskin, 2021).

Group 2- non-dormant and morphological dormancy

The second group of seeds that germinated within 30 days are either ND or MD. Post-radicle emergence, germinated seeds must be evaluated at a wide-range of temperature and light gradients. This is because, shoot emergence may require specific conditions and testing at one or two conditions may fail to provide the precise set of conditions. If shoot emergence is delayed for more than 30 days under any temperature-light combination, these seeds have some component of epicotyl dormancy. Therefore, seeds initially classified as ND are not (truly) ND and may possess PD with subclass-epicotyl of varying levels, necessitating leaf emergence monitoring for definitive non-dormancy classification. For example, Farmer (1977) and Allen and Farmer (1977), showed that acorns of *Quercus alba, Q. prinus*, and *Q. ilicifolia* germinate in autumn with immediate root growth, but shoot emergence is delayed until spring. When freshly collected acorns germinate at typical fall soil temperatures (10°-15°C), root growth occurs, while shoot emergence requires a period of cold stratification. This adaptation establishes roots before winter while protecting the vulnerable shoot from frost damage. Thus, the roots of these acorns are non-dormant, but the epicotyl is dormant, i.e., Level 1: Non-deep, Subclass 2- Epicotyl of Class Physiological Dormancy. Jaganathan and Phartyal (2024) stated that many Fagaceae acorns reported to be ND could have epicotyl dormancy, and long-term monitoring of the shoot emergence is important.

Although Fagaceae species have been discussed extensively for the presence of epicotyl dormancy, an increasing number of studies show this could be much more common in other families. Jayasuriya et al (2010) reported that seeds of *Humboldtia laurifolia* needed approximately 2 weeks for radicle emergence, but subsequent shoot development take about 1-2 months. A similar pattern was described for *Cynometra cauliflora*, which requires approximately 2 weeks for radicle emergence, followed by shoot development that occurs after an additional 4-6 weeks (Jayasuriya et al, 2012). Thus, both these species of Fabaceae have non-deep epicotyl PD due to their delayed shoot emergence after root development. In contrast, *Brownea coccinea* (Fabaceae) demonstrates a more pronounced epicotyl dormancy, where the radicle emerges within about 2 weeks, but the shoot may take up to 8 weeks or more to appear (Jayasuriya et al, 2012). For *Chionanthus retusus* (Oleaceae), which exhibits deep epicotyl dormancy, the radicle typically emerges within 1 week, but shoots may take up to 3 months to develop fully (Chien et al, 2004). Likewise, *Lecythis ampla* (Lecythidaceae) and *Platonia insignis* (Clusiaceae) also germinated within 30 days, yet shoot growth required up to 240 days (Mourão & Beltrati, (1995c)).

In some ND and dormant seeds, the seed reserves are moved to the extending radicle, creating a bulge or corm-like structure, from which the shoot emerges after some time. For instance, in *Polygonatum sibiricum* (Asparagaceae) seeds, radicle emerges at 25 °C (over 30 to 60 days) with the development of a corm structure, but 60 days of cold-stratification is necessary to break epicotyl dormancy, with longer root lengths (2.5 cm) significantly enhancing shoot emergence timing at 25 °C (Liao et al, 2021).

We propose that long-term studies tracking complete seedling ontogeny in species exhibiting MD are essential for a comprehensive understanding of their germination and growth processes. It has been described in *Bhesa nitidissima* (Centroplacaceae) and *Gaertnera walkeri* (Rubiaceae) (Athugala et al, 2018); and *Strychnos benthamii* (Loganiaceae) ((Muthuthanthirige et al, 2020), that the underdeveloped embryos, indicated by an embryo-to-seed length ratio of ≤ 0.5 had T_{50} (time to 50% germination) of less than 30 days. When radicle emergence is considered the criterion for germination, these species could be categorized as having MD. However, despite optimal germination conditions, the emergence of the shoot from seeds of these three species takes longer than 30 days. This extended period before shoot emergence suggests that they should be classified as having MD epicotyl dormant seeds. However, more studies are needed to further divide them into levels and types.

Group 3- physiological dormancy (PD) or morphophysiological dormancy (MPD)

In ND seeds, terminating germination experiments immediately after radicle emergence could lead to incorrect dormancy classification; otherwise, species having PD with subclass epicotyl (Fig. 1). A similar problem could be evident in seeds with PD and MPD, where one could have applied dormancy-breaking treatment(s), and terminating the experiments with successful radicle emergence underestimates the presence of epicotyl dormancy. For instance, in *Nothapodytes nimmoniana* (Icacinaceae) and *Symplocos cochinchinensis* (Symplocaceae) warm stratification at 25 °C combined with gibberellic acid (GA_3) treatment led to the radicle emergence within 46-100 days and 28 days, respectively. However, epicotyl emergence was significantly delayed in both species. If the radicle has PD along with epicotyl having dormancy, these species would be Level 2. Deep, Subclass 2 Epicotyl of Class PD, with Type 1 or 3. This has also been shown to occur in several Fagaceae species, particularly in *Quercus* (Jaganathan and Phartyal, 2024) and *Castanopsis* species (Li et al, 2023). Thus, studying “full germination” is critical to understand the dormancy mechanisms.

Several species with MPD also have been reported to have epicotyl dormancy. At family level, this has been studied extensively in Rannunculaceae. Seeds of *Helleborus thibetanus* exhibits MPD with epicotyl dormancy requiring sequential treatment: 6 weeks at 15°C (or GA_3) for radicle emergence and 4 weeks at 4°C (or GA_3) for epicotyl emergence, albeit only in $> 13\%$ seeds (Gong et al, 2024). The requirement of cold and/or warm stratification for radicle and shoot emergence appears to be wide-spread in species with MPD with epicotyl dormancy. Similarly, working with *Anemone nemorosa* from northern Italy, Mondoni et al (2008) reported that the seeds have underdeveloped embryos requiring growth before germination and a physiological component delaying germination, involving epicotyl emergence. Thus, these seeds have deep, simple epicotyl MPD, which require cold-stratification for shoot emergence.

Studies in three *Crocus ser. Verni* (Iridaceae) of Mediterranean and temperate climate showed that the seeds exhibit nondeep simple MD, requiring warm stratification (20–25°C) followed by cool temperatures (~10°C) for embryo growth and radicle emergence in November, while shoot emergence in March depended on species-specific processes (Carta et al, 2014). For *C. neapolitanus*, adapted to temperate climates, shoot emergence and epicotyl dormancy breaking required cold stratification, whereas the sub-Mediterranean *C. etruscus* and Mediterranean *C. ilvensis* relied on gradual development under natural temperature fluctuations. These variations in dormancy mechanisms reflect ecological adaptations to different climatic conditions, highlighting the influence of phylogeny on dormancy evolution within the *Crocus* genus. Indeed, nondeep simple MPD has been reported in several other Iridaceae species, e.g., *Crocus alatavicus* (Fu et al, 2013).

Many temperate *Viburnum* (Viburnaceae) species exhibit deep simple epicotyl MPD, requiring a sequence of warm and cold stratification. Initial warm temperatures, typically around 20/10°C to 25/15°C, promote embryo growth, with embryo length increasing significantly before radicle emergence (Hidayati et al, 2005; Baskin et al, 2008; Phartyal et al, 2014). Radicle emergence itself is also optimized at approximately 20/10°C, often requiring several weeks to months, e.g., 24 weeks for 50% emergence in *V. betulifolium* (Chien et al, 2011). Subsequent shoot emergence is strictly dependent on a prolonged period (≥12 weeks) of cold stratification at 5°C following radicle emergence. In contrast, some species, like *V. tinus* (Karlsson et al, 2005) and *V. odoratissimum* (Baskin et al, 2008), exhibit non-deep simple epicotyl MPD, requiring shorter periods of warm stratification for both radicle and shoot dormancy release. If the experiments were terminated after radicle emergence, the seeds would have been misclassified as MPD, and the critical role of the epicotyl would have remained uncharacterized.

In *Paeonia ostii* (Paeoniaceae), radicle emergence occurs in autumn, but shoot emergence is delayed until late winter, requiring cold stratification (Zhang et al, 2022). Seeds of *Paeonia peregrina* exhibit MPD, which requires warm stratification and GA_3 for growth of the embryo and radicle emergence, followed by cold stratification for shoot development (Prijić et al, 2024). Many Paeoniaceae species, including *P. ludlowii* seeds require fluctuating temperatures – cold, warm, and cold – to break dormancy, with the radicle emerging in the first year and the plumule (shoot) developing in the second year (Zhang et al, 2019). Furthermore, it appears that epicotyl becomes sensitive to cold stratification only after the root has reached a certain length, and that exogenous application of gibberellic acid (GA_3) or scarification can enhance embryo growth and germination rates, but this requires to be tested in a wide range of species (Hao et al, 2014).

Investigations on MPD with subclass double dormancy have been less studied, but available evidence shows root and shoot emergence can take up to two years (Adams et al, 2003). For instance, *Convallaria keiskei* (Asparagaceae) exhibits deep simple double MPD, requiring two years for complete germination: roots emerge in the first spring, followed by embryo growth, and shoots emerge in the second spring, with cold stratification being essential for shoot emergence (Kondo et al, 2015). Seeds of *Trillium camschatcense* (Melanthiaceae) also have simple double deep MPD, which requires cold stratification for radicle emergence, followed by a second winter for shoot emergence (Kondo et al, 2019). These cases further exemplify the need for reporting “full germination.” Furthermore, it is not easy to infer which species might have epicotyl dormancy, as some families have very less species documented (Fu et al, 2013; Rhie et al, 2019) compared with well-studied genera or families (Baskin et al, 2009).

Physical dormancy

One would argue that the germination failure in the protocol developed may occur due to the presence of a water-impermeable seed coat. However, to the best of our knowledge, epicotyl dormancy has not been reported in PY species (Jaganathan, 2025). While we recommend conducting an imbibition test when seeds fail to germinate within 30 days, monitoring seeds until first leaf emergence is critical (Fig. 1). The imbibition test quantifies water uptake by comparing initial seed mass with subsequent mass changes under controlled moisture conditions. Seeds with PY exhibit complete impermeability; consequently, showing no measurable water absorption. Thus, slower water absorption could be caused by the physical barrier of thick endocarps. In this case, physical barrier is not equal to PY, and should not be misinterpreted as PY.

Conclusion

The complexity of seed dormancy mechanisms necessitates a paradigm shift in germination studies methodology, specifically advocating for the extension of experimental observations until the first true leaf emergence. Many studies articulated that casual observation of leaf emergence led to subsequent detailed investigations on epicotyl dormancy (Jayasuriya et al, 2010; Kondo et al, 2015). Our methodological refinement makes casual observation in to systematic process, thereby bridging the temporal dissociation between radicle protrusion and shoot emergence in species exhibiting epicotyl dormancy. We also suggest reporting the "full germination" period, and standardizing germination reporting protocols to include the comprehensive germination period, defined as the interval from seed sowing to first true leaf emergence. This is particularly crucial to enhance our understanding of germination ecophysiology and facilitate more accurate comparisons across species and studies. Whenever possible, we suggest documenting distinct temporal parameters for both radicle protrusion and shoot emergence, as these represent physiologically distinct developmental phases.

In seeds lacking epicotyl dormancy, whether initially dormant or non-dormant at dispersal, shoot emergence typically occurs within 30 diurnal cycles post-radicle protrusion (Baskin and Baskin, 2021). However, delayed shoot emergence exceeding this temporal threshold strongly indicates epicotyl dormancy, necessitating specific dormancy-breaking treatments for successful shoot system development. The germination process in epicotyl dormant seeds involves initial radicle emergence followed by subsequent shoot development, each phase characterized by distinct thermophysiological requirements and temporal dynamics. This physiological complexity is further modulated by the underlying dormancy classification. Seeds exhibiting PD with Subclass 2 Epicotyl can be further differentiated into nondeep (Level 1) and deep (Level 2). These seeds demonstrate successful radicle emergence but exhibit temporally delayed shoot development, requiring specific environmental conditions such as cold or warm stratification regimes or elevated temperature exposure for complete germination. In contrast, MPD represents a more intricate category, encompassing nondeep epicotyl, deep epicotyl, and deep simple double, each characterized by distinct physiological and morphological barriers to germination. Thus, our proposal that monitoring seed germination until the emergence of the first leaves provides a systematic approach for categorizing the diverse mechanisms governing seed dormancy, will provide more nuanced understanding with significant implications for both theoretical seed biology and practical horticultural applications.

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References

Adams CA, Baskin JM and Baskin CC (2003) Epicotyl dormancy in the mesic woodland herb *Hexastylis heterophylla* (Aristolochiaceae). *Journal of the Torrey Botanical Society* **130**, 11–15.

Allen R and Farmer Jr RE (1977) Germination characteristics of bear oak. *Southern Journal of Applied Forestry* **1**, 19–20.

Athugala YS, Jayasuriya K, Gunarathne A and Baskin CC (2018) Diversity of epicotyl dormancy among tropical montane forest species in Sri Lanka. *Plant Biology* **20**, 916–925.

Baskin CC, and Baskin JM (2014) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Second edn. San Diego: Elsevier.

Baskin CC, Chen S-Y, Chien C-T and Baskin JM (2009) Overview of seed dormancy in Viburnum (Caprifoliaceae). *Propagation of Ornamental Plants* **9**, 115–121.

Baskin CC, Chien C-T, Chen S-Y and Baskin JM (2008) Germination of *Viburnum odoratissimum* seeds: a new level of morphophysiological dormancy. *Seed Science Research* **18**, 179–184.

Baskin JM and Baskin CC (2004) A classification system for seed dormancy. *Seed Science Research* **14**, 1–16.

Baskin JM and Baskin CC (2021) The great diversity in kinds of seed dormancy: a revision of the Nikolaeva–Baskin classification system for primary seed dormancy. *Seed Science Research* **31**, 1–29.

Bewley JD and Black M (1994) *Seeds: Physiology of Development and Germination*. Springer.

Bewley JD, Bradford KJ, Hilhorst HWM and Nonogaki H (2013) *Seeds: physiology of development, germination and dormancy* (3rd edn). New York, Springer.

Carta A, Probert R, Moretti M, Peruzzi L and Bedini G (2014) Seed dormancy and germination in three *Crocus* ser. Verni species (Iridaceae): implications for evolution of dormancy within the genus. *Plant Biology* **16**, 1065–1074.

Chen Y, Liu P, Wang Y, Xu T, Li J, Pei Z, Zhang Y, Li G and Yang Q (2024) Characteristic of epicotyl dormancy and its hormonal regulation in Chinese cork oak (*Quercus variabilis*). *Plant Physiology and Biochemistry* **215**, 109041.

Chien C-T, Chen S-Y, Tsai -C-C, Baskin JM, Baskin CC and Kuo-Huang -L-L (2011) Deep simple epicotyl morphophysiological dormancy in seeds of two *Viburnum* species, with special reference to shoot growth and development inside the seed. *Annals of Botany* **108**, 13–22.

Chien C-T, Kuo-Huang -L-L, Shen Y-C, Zhang R, Chen S-Y, Yang J-C and Pharis RP (2004) Storage behavior of *Chionanthus retusus* seed and asynchronous development of the radicle and shoot apex during germination in relation to germination inhibitors, including abscisic acid and four phenolic glucosides. *Plant and Cell Physiology* **45**, 1158–1167.

Crocker W (1916) Mechanics of dormancy in seeds. *American Journal of Botany* **3**, 99–120.

Engelmann G (1880) The acorns and their germination. *Transaction of the Academy of Science of St. Louis* **4**, 190–192.

Farmer RE (1977) Epicotyl dormancy in white and chestnut oaks. *Forest Science* **23**, 329–332.

Farnsworth E (2000) The ecology and physiology of viviparous and recalcitrant seeds. *Annual Review of Ecology and Systematics* **31**, 107–138.

Fu Z, Tan D, Baskin JM and Baskin CC (2013) Seed dormancy and germination of the subalpine geophyte *Crocus alatavicus* (Iridaceae). *Australian Journal of Botany* **61**, 376–382.

Gong X, Cao X, Chen C, Peng Y, Zhang J, Shi X and Du L (2024) Nondeep simple epicotyl morphophysiological dormancy in seeds of *Helleborus thibetanus* (Ranunculaceae). *Scientia Horticulturae* **338**, 113685.

Hao H-P, He Z, Li H, Shi L and Tang Y-D (2014) Effect of root length on epicotyl dormancy release in seeds of *Paeonia ludlowii*, Tibetan peony. *Annals of Botany* **113**, 443–452.

Harper JL (1977) *Population Biology of Plants. Population Biology of Plants*. London, UK: Academic Press.

Hidayati SN, Baskin JM and Baskin CC (2005) Epicotyl dormancy in *Viburnum acerifolium* (Caprifoliaceae). *The American Midland Naturalist* **153**, 232–244.

ISTA. 2024. International Rules for Seed Testing. International Seed Testing Association.

Jaganathan GK (2021) Ecological insights into the coexistence of dormancy and desiccation-sensitivity in Arecaceae species. *Annals of Forest Science* **78**, 1–14.

Jaganathan GK, and Phartyal SS (2024) A classification system for germination in desiccation-sensitive Fagaceae acorns: with a special focus on physiological and epicotyl dormancy. *Botanical Journal of the Linnean Society* **207**(3), 197-207. https://doi.org/10.1093/botlinnean/boae049

Jaganathan GK (2025) Mutual exclusivity in seed traits: implications for conservation and ecology. *Botany Letters* 1-10. https://doi.org/10.1080/23818107.2025.2521293

Jayasuriya KG, Wijetunga AS, Baskin JM and Baskin CC (2010) Recalcitrancy and a new kind of epicotyl dormancy in seeds of the understory tropical rainforest tree *Humboldtia laurifolia* (Fabaceae, Ceasalpinioideae). *American Journal of Botany* **97**, 15–26.

Jayasuriya KG, Wijetunga AS, Baskin JM and Baskin CC (2012) Physiological epicotyl dormancy and recalcitrant storage behaviour in seeds of two tropical Fabaceae (subfamily Caesalpinioideae) species. *AoB Plants* **2012**, ls044.

Karlsson LM, Hidayati SN, Walck JL and Milberg P (2005) Complex combination of seed dormancy and seedling development determine emergence of *Viburnum tinus* (Caprifoliaceae). *Annals of Botany* **95**, 323–330.

Kondo T, Narita M, Phartyal SS, Hidayati SN, Walck JL, Baskin JM and Baskin CC (2015) Morphophysiological dormancy in seeds of *Convallaria keiskei* and a proposal to recognize two types of double dormancy in seed dormancy classification. *Seed Science Research* **25**, 210–220.

Kondo T, Walck JL and Hidayati SN (2019) Radicle emergence with increased temperatures following summer dispersal in *Trillium camschatcense*: a species with deep simple double morphophysiological dormancy in seeds. *Plant Species Biology* **34**, 45–52.

Li J, Jaganathan GK, Kang H and Liu B (2023) The CO-OCCURRENCE of physiological and epicotyl physiological dormancy in three desiccation-sensitive Castanopsis (Fagaceae) acorns from China with specific reference to the embryonic axis position. *Forests* **14**, 2330.

Liao D, An R, Wei J, Wang D, Li X and Qi J (2021) Transcriptome profiles revealed molecular mechanisms of alternating temperatures in breaking the epicotyl morphophysiological dormancy of *Polygonatum sibiricum* seeds. *BMC Plant Biology* **21**, 370.

Mondoni A, Probert R, Rossi G, Hay F and Bonomi C (2008) Habitat-correlated seed germination behaviour in populations of wood anemone (*Anemone nemorosa* L.) from northern Italy. *Seed Science Research* **18**, 213–222.

Mourão KSM, and Beltrati CM (1995c) Morfologia dos frutos, sementes e plantulas de Platonia insignis Mart (Clusiaceae). III. *Germinacao e plantulas. Acta Amazônica* 25, 47–53.

Muthuthanthirige DL, Wijetunga WAS and Jayasuriya KG (2020) Epicotyl morphophysiological dormancy and storage behaviour of seeds of *Strychnos nux-vomica. Strychnos Potatorum and Strychnos Benthamii (Loganiaceae). Seed Science Research* **30**, 284–292.

Nikolaeva MG (1969) *Physiology of Deep Dormancy in Seeds. Izdatel'stvo Nauka, Leningrad* Translated from Russian by Z. Shapiro. Washington, DC: National Science Foundation.

Phartyal SS, Kondo T, Fuji A, Hidayati SN and Walck JL (2014) A comprehensive view of epicotyl dormancy in *Viburnum furcatum*: combining field studies with laboratory studies using temperature sequences. *Seed Science Research* **24**, 281–292.

Prijić Ž, Mikić S, Peškanov J, Zhang X, Guo L, Dragumilo A, Filipović V, Anačkov G, Marković T (2024) Diversity of treatments in overcoming morphophysiological dormancy of Paeonia peregrina Mill. seeds. *Plants* **13**, 2178.

Rhie YH, Lee SY and Kim KS (2019) Deep simple epicotyl morphophysiological dormancy in seeds of *Gymnospermium microrrhynchum* (S. Moore) takht., a rare species in Korea. *Horticultural Science and Technology* **37**, 669–677.

Vleeshouwers L, Bouwmeester H and Karssen C (1995) Redefining seed dormancy: an attempt to integrate physiology and ecology. *Journal of Ecology* **83**, 1031–1037.

Wijayasinghe MM, Jayasuriya KG, Gunatilleke C, Gunatilleke I and Walck JL (2019) Effect of salinity on seed germination of five mangroves from Sri Lanka: use of hydrotime modelling for mangrove germination. *Seed Science Research* **29**, 55–63.

Wijayasinghe MM, Jayasuriya KG, Gunatilleke C, Gunatilleke I and Walck JL (2023) Seed dormancy diversity of the mangrove plant community in Sri Lanka to assist in direct seeding and seedling transplanting restoration. *Seed Science Research* **33**, 107–117.

Zhang K, Pan H, Baskin CC, Baskin JM, Xiong Z, Cao W, Yao L, Tang B, Zhang C and Tao J (2022) Epicotyl morphophysiological dormancy in seeds of *Paeonia ostii* (Paeoniaceae): seasonal temperature regulation of germination phenology. *Environmental and Experimental Botany* **194**, 104742.

Zhang K, Yao L, Zhang Y, Baskin JM, Baskin CC, Xiong Z and Tao J (2019) A review of the seed biology of Paeonia species (Paeoniaceae), with particular reference to dormancy and germination. *Planta* **249**, 291–303.