

Seed Germination Ecology of Hawaiian Native Plants

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Propagation of native Hawaiian species from seeds is important in the conservation of rare species and in production of plants needed for restoration projects. However, seed dormancy can be a problem in accomplishing these goals. In this document, nondormancy and dormancy are compared, and each of the five classes of dormancy is described. A dichotomous key is provided to distinguish nondormancy and the five classes of dormancy. Using data from Alvin Yoshinaga (unpublished), Culliney and Koebele (1999), and laboratory studies by Baskin & Baskin on seeds of 38 species (unpublished), nondormancy or class of dormancy has been determined or inferred for 153 species of native Hawaiian plants.

Dormancy Terminology

If freshly-matured seeds germinate to high percentages (≥ 80) over a range of test conditions and these percentages do not increase after seeds have been given a dormancy-breaking treatment, we conclude they are **nondormant**. On the other hand, if no seeds germinate at any condition after 4 weeks, we conclude they are **dormant**. However, if fresh seeds germinate to high percentages at some conditions and not others after 4 weeks, they may be nondormant or **conditionally dormant**. If the seeds germinating only at limited conditions are nondormant, dormancy-breaking treatments will not result in any change in the range of conditions over which they will germinate. On the other hand, if seeds are conditionally dormant, the percentage and rate of germination as well as the range of conditions over which they germinate will increase following a dormancy-breaking treatment.

There are five classes of seed dormancy: physiological, morphological, morphophysiological, physical, and combinational. A closer look at these five classes will help explain why fresh seeds do not germinate and provide insight into how dormancy is broken in nature.

Physiological dormancy (PD) means that there is a “physiological problem” in the embryo that prevents it from generating enough push power or growth potential to overcome the mechanical constraint of the seed coat and other covering tissues (if present). Dormancy break occurs at cool (0.5-10°C/33-50°F) wet, warm (≥ 15 °C/59°F) wet, or warm dry conditions, depending on the species; seeds of a few species require warm followed by cool conditions to become nondormant. After the embryo becomes fully nondormant, it has sufficient growth potential to push through all the layers that surround it.

In seeds with **morphological dormancy (MD)**, the embryo is undifferentiated or differentiated but underdeveloped (not fully grown). In those seeds with undifferentiated

embryos, “differentiation” and growth must precede the appearance of cotyledon(s) and a radicle. However, in those seeds with a differentiated, underdeveloped embryo, the embryo must grow to a species-specific critical length before the radicle emerges. Embryos will grow within 4 weeks or less in seeds placed on a moist substrate at appropriate temperatures [some seeds require low (15/6, 20/10EC or 59/43, 68/50°F) and others high (25/15EC or 77/59°F) temperatures] and in light or in darkness, depending on the species.

Morphophysiological dormancy (MPD) is a combination of MD and PD. Although there is some evidence that seeds with undifferentiated embryos, e.g., some temperate-zone orchids (Ballard, 1987; Ichihashi, 1989) have PD, much of the research on seeds with MPD has been done on those with differentiated, underdeveloped embryos (Baskin and Baskin, 1998). In seeds with both an underdeveloped embryo and PD, PD has to be broken and the embryo must grow prior to the time of radicle emergence. Depending on the species, PD is broken before or during the period of embryo growth.

In seeds with **physical dormancy (PY)**, germination is prevented because the seed coat (sometimes the fruit coat, e.g. *Rhus*) is impermeable to water. Impermeability is due to the presence of one or more palisade layers of lignified cells, or macrosclereids, in the seed coat or in the innermost layer of the fruit wall (i.e., the endocarp) as in the case of *Rhus*. PY occurs in 15 plant families, but not all members of all of these families have impermeable seed/fruit coats. For example, PY in the Anacardiaceae appears to be restricted to the *Rhus* complex. In 12 of the 15 families, a specialized structure (“water gap”) has been identified in the impermeable seed or fruit coat. There are several kinds of water gaps, and they are dislodged or disrupted in response to environmental cues, especially temperature, thus creating an entry point for water (Baskin *et al.*, 2000).

Seeds with **combinational dormancy** have both an impermeable seed or fruit coat and PD of the embryo. In at least some species of *Geranium*, *Malva*, *Ornithopus*, *Sicyos*, *Stylosanthes*, and *Trifolium*, PD is broken before PY is broken. However, in at least some species of *Ceanothus*, *Cercis*, *Cotinus*, *Koeleruteria*, *Rhus*, and *Tilia*, PY is broken before PD is broken. *Rhus sandwicensis* appears to have PY only.

A DICHOTOMOUS KEY FOR CLASSES OF SEED DORMANCY

If fresh seeds are dormant, it is very helpful, especially from a plant propagation perspective, to know what kind of dormancy they have. Thus, a key to distinguish the five classes of seed dormancy has been developed using information on (1) the developmental state/size of the embryo, (2) whether the seed/fruit coat is permeable to water, and (3) whether the seed germinates within about 4 weeks (Table 1). It is assumed that studies begin with freshly-matured seeds and that seeds are incubated at temperatures (e.g., daily alternating temperature regimes of 20/10 and/or 25/15°C, = 68/50 and/or 77/59°F) appropriate for germination.

Table 1. A dichotomous key to distinguish nondormancy and the five classes of seed^a dormancy (modified from Baskin and Baskin, in press).

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1. Embryo undifferentiated or if differentiated it is underdeveloped **2**
 2. Embryo not differentiated **SPECIALIZED TYPE OF MORPHOLOGICAL OR MORPHOPHYSIOLOGICAL DORMANCY**
 2. Embryo differentiated but underdeveloped **3**
 3. After seeds are placed on a moist substrate, the embryo grows, and seeds germinate in 4 weeks or less **MORPHOLOGICAL DORMANCY**
 3. After seeds are placed on a moist substrate, the embryo does not grow, and seeds do not germinate in about 4 weeks **MORPHOPHYSIOLOGICAL DORMANCY**
 1. Embryo differentiated and fully developed **4**
 4. Seeds imbibe water
 5. Seeds germinate in about 4 weeks **NONDORMANT**
 5. Seeds do not germinate in about 4 weeks **PHYSIOLOGICAL DORMANCY**
 4. Seeds do not imbibe water **6**
 6. Scarified seeds germinate in 4 weeks or less **PHYSICAL DORMANCY**
 6. Scarified seeds do not germinate in 4 weeks **COMBINATIONAL DORMANCY**

^aNatural dispersal/germination unit may be a seed, or it may be a seed covered by one or more layers of the pericarps or other structures.

Studies on seed dormancy

In our studies on Hawaiian montane species, seeds are sown on moist sand or filter paper and placed in light (14 hr daily photoperiod) in three incubators, each set on a different daily alternating temperature regime: 15(day)/6(night), 20/10, and 25/15°C (59/43, 68/50, and 77/59°F). Thus far, studies have been done, or are in progress, on seeds of 38 species. We have learned enough about all 38 species (marked with an asterisk in Table 2) to be confident about the presence *vs.* absence of dormancy, and, when dormancy is present, to identify the class of dormancy.

Nondormancy is found in only two of the 38 species, and one of these species (*Colubrina oppositifolia*) has some seeds that have a short period of physical dormancy. That is, although many seeds imbibed within 1-2 days after being placed on wet sand, others

required up to 3 weeks to imbibe. Physiological dormancy is found in 26 species, physical dormancy in six species, the combination of physical and PD in one species, and morphophysiological dormancy in three species. None of the 38 species had morphological dormancy.

After 4 weeks or less at high temperatures (25/15°C), fresh seeds of 13 of the 26 species with PD had germinated at low to high percentages (depending on the species). Of these, none had germinated at low (15/6 or 20/10°C) temperatures after 4 weeks or less. However, high germination percentages were obtained for seeds of these 13 species by incubating them continuously at 25/15°C, (and frequently also at 20/10 and 15/6°C) for 8-14 weeks. In the other 13 species whose seeds had PD, no germination was recorded after 4 weeks, and studies are in progress for many of these species to determine the environmental conditions required for dormancy break and germination.

Only six of the 38 species had water-impermeable seed or fruit coats (physical dormancy). Detailed studies on *Dodonaea viscosa* revealed that seeds made permeable by dipping them into boiling water germinated slower than those that were mechanically scarified. It appears that the slow rate of imbibition and thus germination, following opening of the “water gap” in the seed coat, could serve as a rain gage in nature. Seeds of *Alphitonia ponderosa* had both PY and PD, *i.e.*, combinational dormancy.

Seeds of *Argemone glauca*, *Cheirodendron trigynum* and *Ilex anomala* have small embryos (that must grow prior to germination), as well as PD; thus, they have morphophysiological dormancy. PD was broken and embryo growth and germination occurred during 12 or more weeks of incubation at 20/10 and 25/15°C for *C. trigynum* and *I. anomala* seeds, respectively.

Seeds with PD can be divided into two categories: (1) none of the fresh seeds germinated at daily alternating temperature regimes of 15/6, 20/10, or 25/15°C after 4 weeks, and (2) a low to high percentage of fresh seeds germinated over a limited range of temperatures (usually only at 25/15°C) within 4 weeks, *i.e.*, a portion of the seeds were conditionally dormant. Seeds of species in Category No. 1 are relatively difficult to germinate, and we are using the “move-along experiment” technique (Baskin and Baskin 2003) to help identify the environmental conditions needed to break dormancy. This technique is a double phenology experiment, and it involves moving seeds along the seasonal gradient of temperatures that occurs in a given habitat. Species in Category No. 2 are relatively easy to germinate, with seeds requiring only continuous incubation, especially at high (25/15°C) temperatures, for an extended period of time (8 to 14 or more weeks, depending on the species).

Studies on seeds of *Dodonaea* and *Rhus*

A manuscript resulting from studies on *Donodaea viscosa* has been accepted for publication in *Seed Science Research* (March 2004). The abstract (slightly modified) from this paper is given in the following paragraph:

“Dormancy in seeds of *Dodonaea viscosa* is due to a water-impermeable seed coat (physical dormancy, PY). Thus, mechanically-scarified seeds imbibed water (*ca.* 95% increase in mass) and germinated to high percentages over a wide range of temperature regimes in both white light and darkness, whereas nonscarified seeds did not take up water. Dry heat at 80-160°C and dipping in boiling water for 1-60 seconds also broke dormancy in a high percentage of the seeds, and continuous far-red light was not inhibitory to germination. However, dry storage in the laboratory for >1 year did not overcome dormancy. Seeds made water-permeable (by dipping them in boiling water) both imbibed water and germinated at a much slower rate than those made water-permeable by mechanical scarification. We suggest that boiling opened the “water gap” in the seed coat (not yet described in Sapindaceae but present in other taxa with PY) and that water entered the seed only through this small opening, thereby accounting for the slow rate of imbibition and subsequent germination. Physical dormancy now has been shown to occur in seeds of this polymorphic, worldwide species from Australia, Brazil, Hawaii, Mexico, and New Zealand. The low amount of dormancy reported for seed lots of *D. viscosa* in China, India, and Pakistan probably is due to collecting seeds before they dried to the critical moisture content for development of water-impermeability of the seed coat. Germination of nondormant seeds over a wide range of temperatures and in white light, far-red (leaf-canopy shade) light, and darkness are part of the germination strategy of *D. viscosa* and of other taxa whose seeds have PY at maturity.”

Studies on *Rhus sandwicensis* are still in progress. The focus of the present research is on the long period of time required by some seeds in the population to imbibe water and germinate after they have been given a heat (*i.e.*, boiling water) treatment. Some heat-treated seeds are still imbibing and germinating, although it has been 110 days since the treatments were given.

Dormancy Database

For several years, Alvin Yoshinaga has been investigating seed storage of Hawaiian species, and as a part of this work he has tested freshly-matured seeds (as well as those that have been stored for various periods of time) of many montane species. The presence *vs.* absence of dormancy has been determined or inferred for seeds of the montane species in Alvin’s database, and if dormancy was present the class of dormancy has been determined or inferred. To make determinations about dormancy *vs.* nondormancy and about the class of dormancy, one needs to know: (1) the rate and percentage of germination of seeds sown under natural or near-natural environmental conditions, and (2) the physical characteristics of embryos and seed (or fruit) coats of members of the same family, and preferably of the same genus, as the one under investigation.

In addition, we were able to make dormancy determinations for in a few species using information in Culliney and Koebele (1999). Also, information from our current

studies of Hawaiian montane species (see below) has been added to the list. Thus, we now have information on 153 Hawaiian species (Table 2).

Table 2. Nondormancy or class of dormancy in seeds of Hawaiian species.

CD = conditional dormancy, MD= morphological dormancy, MPD = morphophysiological dormancy, ND= nondormant, ND/PD = part at the seeds were nondormant but others were physiologically dormant, PD = physiological dormancy, PY = physical dormancy, PY + PD = combination of physical and physiological dormancy, ? = further verification is needed, * = one of the 38 species that has been (or is currently being) studied.

References/Sources of information: B = Baskin & Baskin; C&K = Culliney & Koebele; Y = Yoshinaga.

Fahrenheit temperatures: 15/6°C = 49/43°F; 20/10°C = 68/50°F; 25/15°C = 77/59°F.

Germination times: Days after sowing when germination was first noted, last noted, test was terminated.

(Body of table 2 attached as separate spreadsheet file)

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