Dormancy-Unlocking Seed Secrets[1]

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Abstract-It is difficult, if not impossible, to know a priori what type of treatment is needed to break seed dormancy. However, knowing the reason(s) why seeds are dormant may offer clues about what seeds need for dormancy release. An evaluation of the habitat in which a particular species is found also may point to the most effective dormancy treatment if the requirements for a particular species are unknown. Dormancy may be due to: unfavourable climatic conditions, immaturity, a light requirement, genetic variation, or protection against predation. Depending upon the type of dormancy, stratification, light, leaching, scarification, growth regulators, or high 0 2 concentrations may be used to promote germination. Treatments such as stratification may have to be modified to meet the particular physiological requirements of different species. Five different types of stratification are presently used to release dormancy of forest trees.

WHY DO WE NEED TO UNDERSTAND SEED DORMANCY?

"What folks here really need - is just to look at a seed and know what kind of treatment it needs to germinate."

This sentiment frequently has been expressed by those attempting to grow plants from seeds when little or nothing is known about their germination requirements. Understandably, they wish the answers could be handed to them on a silver platter. Unfortunately, there is no silver platter, but there may be other means of obtaining the information they require. One approach is to try to determine the most probable reason for dormancy, then to apply a suitable treatment to satisfy the dormancy requirement. To do this, however, requires some understanding of seed dormancy, and the context in which dormancy occurs.

WHAT IS SEED DORMANCY?

Dormancy is a naturally occurring phenomenon of many plants to maximize the chances that seeds will germinate at an appropriate time. Dormancy may be defined as:

the physical or physiological condition of a viable seed that prevents germination even in the presence of otherwise favorable germination conditions.

Thus, seeds are considered dormant when they fall to germinate even though they have adequate light and water, and suitable temperatures for growth (which for temperate species are usually in the range of 15 to 30^{o}C). Alternately, dormancy can be defined as:

a seed characteristic, the degree of which defines what conditions should he met to make the seed germinate.

This definition mav be more useful in understanding dormancv because it suggests that dormancy is variable, rather than constant, which is the situation that we generally encounter in the native populations of many species.

WHAT ARE THE TYPES OF DORMANCY?

In the very simplest sense, the fundamental cause of dormancy is the inability of the embryo axis to overcome the constraints acting against it. These constraints may originate from within the embryo (endogenous or embryo dormancy) or from the tissues surrounding the embryo (exogenous or coat-imposed dormancy) (Table 1). Understanding whether dormancy originates from within or outside of the seed helps to determine the most appropriate dormancy treatment. Some seeds have both endogenous and exogenous dormancy, and may require a combination of treatments.

Table 1. Types of seed dormancy

Types of Dormancy	Cause of Dormancy
Exogenous	***Coat-imposed***
Physical	impermeability
Chemical	inhibitors
Mechanical	restraint
Endogenous	***Embryo-imposed***
Morphological	immaturity
Physiological	metabolic requirement

WHY DOES DORMANCY OCCUR?

Dormancy is a biological mechanism to ensure that seeds will germinate at a time and under conditions that will optimize the chances for the growth and survival of the next generation. The reasons for dormancy will vary, depending upon the species and their environment. The following section describes a variety of situations in which dormancy enhances a species' chances for survival.

Unfavorable climatic conditions for germination

Dormancy strategies may differ according to the characteristics and the timing of critical events of individual life cycles. For example, long-lived species such as pines, which require almost three years from cone bud initiation to seed maturation, would not be expected to have the same dormancy characteristics as small herbaceous annuals that germinate, flower, and set seed within three months.

Pattern 1. Maturation culminates in dormancy

In many tree species, seed maturation is accompanied by the induction of a state of dormancy (Figure 1). This is an advantage for tree seeds of temperate regions that mature in late summer to early fall, since immediate germination would leave vulnerable seedlings exposed to harsh winter conditions.

Biological Stage	Dormancy	Germination		
		Hydration	Activation	Emergence
Mature Seeds →				Germinants
Natural regeneration	Seed banks	Seeds soaked by fall rains	Overwinter in soil	Warm conditions in spring
Artificial regeneration	Storage (-18 C, <10%mc)	Soak in water	Stratification (2-5 C, >25%mc)	Sow in nursery

Figure 1. Comparison of the major stages of seed maturation, dormancy and germination in the natural and artificial regeneration of tree seedlings.

In nature, dormant tree seeds remain inactive until favorable growing conditions occur the following spring, although some may remain dormant for two growing seasons or more. Once dormancy is broken, however, seeds of this type generally do not re-enter the dormant state.

Pattern 2. Cyclic dormancy. Buried seeds of small herbaceous plants and grasses exposed to natural seasonal temperature changes may exhibit annual cycles of dormancy and non-dormancy. For example, fresh and buried witchgrass seeds that are dormant in early October become nondormant during late autumn and winter (Baskin and Baskin 1985). During spring and summer, however, seeds progressively lose their ability to germinate, as they gradually re-enter dormancy (Figure 2).

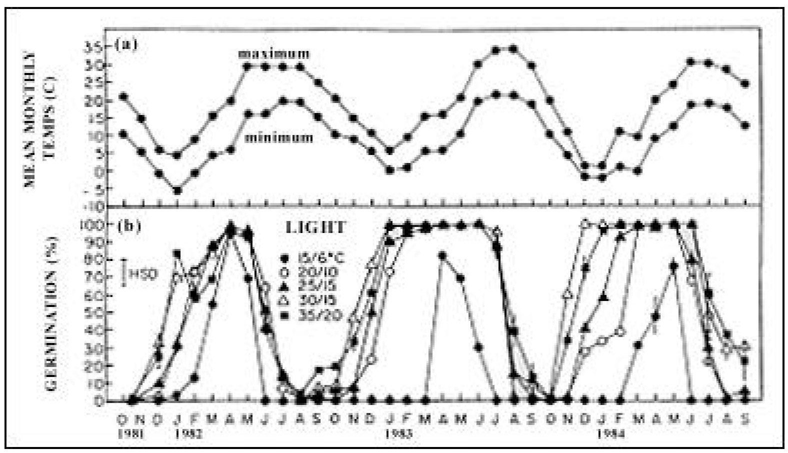

Figure 2. Witchgrass seeds (*Panicum capillare*) exhibit alternating cycles of dormancy and non-dormancy (Baskin and Baskin 1985) (a) mean maximum and minimum temperatures monitored at the test site in Lexington, KY. (b) germination of fresh and buried (2 to 35 months) seeds in controlled environment chambers under various temperatures. Fourteen hr light was given during the high temperature period.

Incomplete development

Immaturity may result in poor germination. Seeds may be immature because they have been harvested too early, or because they were collected from high elevation or high latitude areas that experience shortened growing seasons. Although, strictly speaking, immaturity is not a type of dormancy, it is mentioned here because some treatments for breaking dormancy have been modified to treat immature seeds (see below).

Light requirement

Small seeds lack the reserves to physically reach the soil surface if they are too deeply buried in the soil. To prevent germination of buried seeds, many small seeds have an inherent light-sensing mechanism which responds to the red and far-red portions of the light spectrum. Such seeds germinate when exposed to red light. Red light is predominant in full sunlight, so exposure to red light acts as an environmental signal that seeds are on or near the surface of the soil. Germination is prevented if seeds are in darkness, or exposed to far-red light. Light that is rich in far-red light is characteristic of the illumination that seeds would receive under a dense forest canopy.

This light mechanism is common in spring ephemerals that germinate and bloom early in the year. Typically, these species are found on the forest floor of hardwood forests, and the response to light ensures that they germinate and complete their reproductive cycles before the hardwood canopy closes.

Genetic variation (or, not putting all your eggs in one basket)

Wild oats (*Avena fatua*) produce seeds every year, but dormancy can vary among different members of the same population, with some individuals remaining viable in the soil up to seven years after they are produced (Naylor and Jana 1976). Variable dormancy has also been observed in seeds of white spruce (*Picea glauca* Moench.Voss)(Wang 1976) and Japanese red pine (*Pinus densiflora* Sieb. and Zucc.)(Asakawa and Funita 1966) that were produced by the same trees in different years.

The expression of dormancy in natural seed populations is known to be under genetic control (Naylor 1983, Edwards and El-Kassaby 1995), so variable dormancy possibly represents an evolved survival strategy to extend germination over many years and different environmental conditions. Variable dormancy ensures that, no matter what the present environment, at least some members of the population will survive and produce seeds for the next generation-a kind of an insurance policy against environmental change. It is conceivable that variable dormancy is an universal phenomenon in natural populations of most plant species.

Protection against predation

Physical dormancy is common in many dry regions of the world - from deserts to the dry tropics. Many species inhabiting these areas have seed coats or pericarps that are very hard or impermeable to water to protect the seeds from insects and other predators.

Protection against time (seed longevity)

In regard to their capability for long storage, seeds can be classified as either orthodox or recalcitrant. Orthodox seeds, e.g., the seeds of most temperate trees, gradually dry as they mature. The progressive induction of dormancy is an integral part of this maturation drying. As a consequence, orthodox seeds have the ability to remain viable for long periods in a desiccated state (less than 10% moisture content). Recalcitrant seeds remain at a relatively high moisture content (me) once they are mature, and typically are produced by species native to moist tropical regions. Characteristically, the seeds are nondormant, because environmental conditions such as temperature and moisture are always suitable for germination. Recalcitrant seeds usually germinate soon after maturity, and rarely can be stored beyond three months (Chin 1990). Many orthodox seeds need dormancy-release treatments to germinate, but recalcitrant seeds do not.

Legume seeds are orthodox seeds with very hard seed coats that are impermeable to water and gases. They are masters of longevity; lupine seeds found in a lemming burrow by a Yukon mining engineer were able to germinate and produce healthy, flowering plants after 10,000 years (Porsild *et al*. 1967). No conifer seeds can match this feat, but they still can be successfully stored for many years (at - 18^{o}C and 5-9% me). Under these storage conditions, germination in some British Columbia collections of Douglas fir, white spruce, lodgepole pine, and yellow pine seeds has remained high (more than 80%) even after 30 years (Leadem 1996).

WHEN TO RELEASE DORMANCY?

When the me of a mature seeds falls to 5-10% (<5% me will result in death), it can remain viable over long periods (Figure 1). With this degree of dehydration, however, metabolic activity is virtually nonexistent (Figure 1). Seeds must again become physiologically active, i.e., hydrated, by soaking in water for several hours to several days before any dormancy-release treatment is given.

HOW TO BREAK DORMANCY?

Once they are physiologically active, dormant seeds can be stimulated to germinate using treatments that emulate natural conditions or satisfy certain physiological requirements. A list of the different types of dormancy treatments, and a brief description of how they are assumed to break seed dormancy are summarized in Table 2. A more complete discussion of the various dormancy-release treatments are given below.

Table 2. Dormancy-release treatments

Treatment	Description
Stratification	Moist chilling at 2-5^{o}C; removes metabolic blocks, weakens seed coats, increases germination-promoter levels
Light	Exposure to specific wavelengths; stimulates the phytochrome system
Leaching	Soaking in water; removes inhibitors from seed coats
Scarification	Chemical (sulphuric acid) or mechanical (abrasion) treatment; breaks down seed coats
Plant growth regulators	Enhance natural levels in favor of germination, or trigger other metabolic pathways leading to germination
High oxygen concentrations	Supply respiration; remove metabolic blocks

Stratification

Stratification is the most consistently effective dormancy release treatment for many tree seeds. Stratification enables seeds to germinate more quickly and completely, and can sometimes eliminate the need for other special conditions, such as light. The choice of a suitable dormancy-release treatment can broaden the range of environmental conditions, e.g., temperature, under which germination can occur (Figure 3). Even when the total germination percentage does not change, the germination of most tree seeds is more rapid after they have been stratified (Figure 4). Damaged seeds, or those of low vigor, may deteriorate during stratification (Leadem 1986); in such cases, the seeds should be sown without chilling.

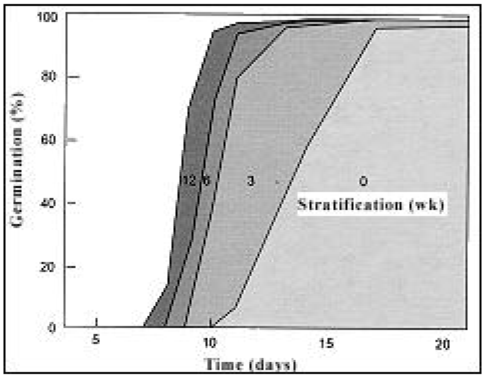

Figure 3. Germination of western hemlock seeds after stratification for 0, 3, 6, and 12 weeks (Edwards 1973)

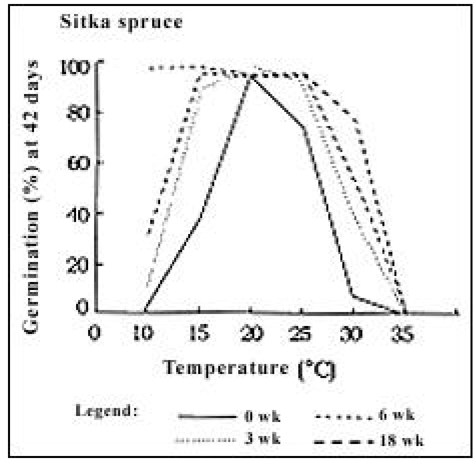

Figure 4. Germination of Sitka spruce seeds at different temperatures after stratification for 0, 3, 6, 18 weeks (Jones and Gosling 1994)

Stratification simulates winter conditions by exposing moist seeds to cold temperatures. Seeds are soaked in water (hydrated) usually for 24 h, drained, then placed in a plastic bag or other container, and refrigerated (2 to 5C) for several weeks (Table 3).

Table 3. Procedure for traditional stratification

Process	Soak	Stratify	Incubate
Time	24 or 48 h	3 to 4 wk	3 to 4 wk
Temperature	20 to 25^{o}C	2 to 5^{o}C	20 to 25^{o}C
MC	to>30%	30 to 60%	30 to 60%

Traditional stratification techniques may be insufficient to stimulate germination in some conifer species. The true firs (amabilis, grand, noble, and subalpine) respond best to a two-part stratification called stratification-redry (Edwards 1985, Leadem 1986, Tanaka and Edwards 1986, Leadem 1989). *Abies* seeds that receive the stratification-redry treatment are able to germinate more quickly and more completely (Figure 5).

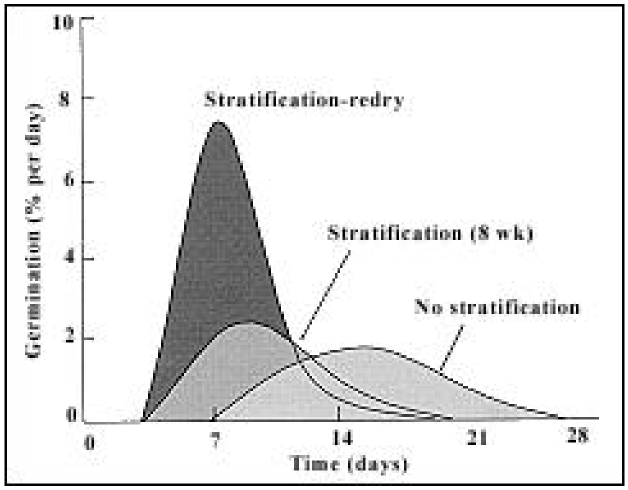

Figure 5. The rate of germination of amabilis fir seeds after 0 to 8 weeks stratification-redry treatment (Leadem 1986)

For the stratification-redry treatment, seeds are hydrated for 48 h and then stratified for 4 weeks at 2^{o}C to 5^{o}C; seed mc is high, usually above 40% (Table 4).

Table 4. Procedure for Stratification-Redry

Process	Soak	Stratify	Redry	Stratify	Incubate
Time	48 h; change after 24 h	4 wk	4 to 8 h	12 wk	3 to 4 wk
Temperature	20 to 25^{o}C	2 to 5^{o}C	20 to 25^{o}C	2 to 5^{o}C	20 to 25^{o}C
MC	to >30%	30 to 60%	25 to 30%	25%	25 to 60%

The seeds are then dried to 25-30^{o}C mc and chilled for an additional 12 weeks. Moisture is a critical factor in the application of the stratification-redry treatment. *Abies* seeds require very long stratification, but also have the capability to germinate at the temperatures used for stratification. With the stratification-redry treatment, seeds receive the extended chilling they require, but emergence of the radicle (i.e., evident germination) is prevented because seed me is kept at low levels. The stratification-redry treatment has also been found effective for some sources of Douglas-fir seeds, but not for other tree species, perhaps because the correct redry me has not been found.

Some seeds, such as *Acer macrophyllum*, require extended stratification, but the optimum duration for individual seed sources is unknown. An empirical procedure for seeds with variable dormancy is to place the hydrated seeds (> 30% me) at 2^{o}C to 5^{o}C, and maintain them at low temperatures until about 5% of the seeds germinate (Table 5). For *Acer macrophyllum*, this is about 60 to 120 days (J. Zasada, pers. comm. 1996). Germination of the least dormant individuals at low temperatures generally indicates that dormancy also has been released in the remaining, more dormant seeds, and that the seeds are ready to be transferred to warmer temperatures for testing or seedling production.

Table 5. Stratification procedure for seeds with variable dormancy

Process	Soak	Stratify	Incubate
Time	48 h; change after 24 h	X wk* (*5% germ.) X=60-120 d	3 to 4 wk
Temperature	20 to 25^{o}C	2 to 5^{o}C	20 to 25^{o}C
MC	to>30%	30 to 60%	30 to 60%

A variation of the preceding method is the compound stratification treatment used for *Pinus monticola* and for immature seeds (Table 6). The treatment is referred to as compound stratification because the seeds are exposed to both warm and cold temperatures. The usual combination used for *Pinus monticola* is 30 days "warm" stratification (20^{o}C to 25^{o}C) followed by 60 days "cold" stratification (2^{o}C to 5^{o}C). However, the duration of warm stratification may vary, depending upon the seed source. Thus, seeds are kept under warm conditions until about 5% of the seeds show evidence of germination, and then they are transferred to cold temperatures (D.W.G. Edwards pers. comm. 1996). Compound stratification also works well on *Chamaecyparis nootkatensis*.

Table 6. Procedure for compound stratification (warm + cold)

Process	Soak	Stratify-w	Stratify-c	Incubate
Time	48 h; change after 24 h	X wk* (*5% germ); X=3-5 wk	6 wk	3 to 4 wk
Temperature	20 to 25^{o}C	20 to 25^{o}C	2 to 5^{o}C	20 to 25^{o}C
MC	to>30%	30 to 60%	30 to 60%	30 to 60%

A procedure developed for beechnuts and other European hardwood seeds by Suszka et al. (1996) may also prove effective for removing the dormancy of North American hardwood seeds. It is similar to both the "variable dormancy" and "stratification -redry" treatments described above (Tables 4/5). It involves hydrating the seeds to a predetermined mc ("Y"), depending on the species (e.g. 30% mc for beechnuts), then chilling the seeds at this mc for X+2 weeks (Table 7). The duration of treatment (expressed in weeks), is represented as "X", or the time when 10% of the seeds have germinated. This length of stratification is sufficient to break dormancy, but germination is prevented because moisture levels are controlled during the chilling period.

Table 7. Procedure for variable dormancy of deeply dormant hardwood seeds

Process	Soak	Stratify	Incubate
Time	Until mc = Y	X + 2 wk X = 1 to 8 mo.	3 to 4 wk
Temperature	20 to 25°C	2 to 5°C	20 to 25°C OR
MC	(e.g., Y = 30%)	Y% mc	store @2-5°C, 10% mc

After treatment, the seeds can either be sown, or re-dried to below 10% mc and stored for several years (Muller and Bonnet-Masimbert 1989; Muller et al. 1990). They can be sown at any time and they will germinate readily as they are no longer dormant. This dormancy-breaking treatment is usually applied after storage, but it can also be applied before storage, i.e., immediately after collection. The time period "X" can be considered to be an indication of the degree of seed dormancy, and potentially could be used to compare the dormancy levels of different seed sources. The period "X" is 1 to 3 months for beechnuts (*Fagus sylvatica*), 5 to 6 months for wild cherries, (*Prunus sativum*), and 6 to 8 months for ash (*Fraxinus* spp.) (Muller 1993, Suszka et al. 1996).

Light

Some seeds require light to stimulate gennination, but, as with other dormancy-release treatments, the seeds must be fully hydrated to respond. The light stimulus is received through the phytochrome system, which operates as an on/off switch for many physiological processes in plants (Figure 6). Germination is usually stimulated by exposure to red light (660 nm) and inhibited by exposure to far-red light (730 nm). The intensity of light required to activate the phytochrome system is low, and 1 to 51x (comparable to bright moonlight) can be sufficient.

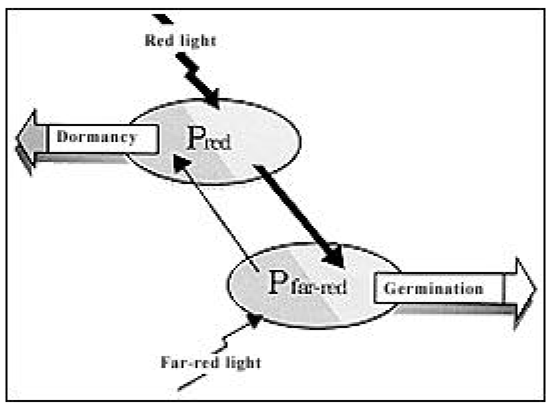

Figure 6. Absorption of far-red light converts the pigment phytochrome$_{far\ red}$ (usually the active form) back to phytochrome$_{red}$ (the inactive form). This reaction is reversible, depending on the relative amounts of red and far-red light. In sunlight, red light is predominant, whereas far-red light is predominant in canopy-filtered light.

Seeds lying on or near the soil surface receive enough light to trigger germination if all other conditions have been satisfied. In the nursery, the light requirement is generally met during the routine handling of hydrated seeds.

The light requirement for germination may be affected by treatments such as stratification. For example, unstratified seeds of species that require light for germination will germinate in darkness once they have been stratified.

Leaching

The coats of some seeds contain inhibitors that must be leached, or washed out. In temperate regions, seeds are leached naturally when they fall to the ground and are drenched by fall rains. This is a mechanism also found in desert species, which use the leaching of inhibitors in the coats by rainfall as an environmental signal that sufficient water is present for germination and growth.

Scarification

Scarification is an important technique for breaking the dormancy of many hard-seeded legume tree species, e.g., *Acacia*, *Leucaena*, *Albizia*, that are an important component of tropical forests. Hard seed coats are a means of protecting seeds from fungal and insect attack under conditions of high temperatures and high humidity. Mechanical or chemical degradation of the seed coat is necessary for germination, and in nature, is often facilitated by seeds passing through the intestinal tract of birds and other animals. When seeds or fruits are eaten by animals, enzymes in the digestive system assist in breaking down the seed coats so that seeds can germinate. Thus, in a very general sense, predation might be considered a dormancy-release treatment!

Tropical species such as teak (*Tectona grandis*) may be scarified by alternate drying and soaking. The seeds are soaked in water, then left in direct sunlight for several days. This cycle may be repeated many times, or until evidence of coat degradation is apparent. Hard seed coats also may be degraded by partial fermentation or by exposure to light-to-moderate fire. The seeds are burnt after they are covered with a layer of grass (Willan 1984). Few temperate forest species require scarification [Schopmeyer (1974) does not recommend it for any British Columbia trees], but seed coats are sometimes clipped to facilitate the germination of hard-seeded pines (Hoff and Steinhoff in press, Leadem 1985). Species common to some desert zones sometimes are mechanically scarified by tumbling, wire brushes, or hot water soaks.

Plant growth regulators

Application of plant growth regulators (especially gibberellic acid and cytokinin) have been shown to enhance germination of hardwoods, but have limited effectiveness for conifer species (Leadem 1987).

CONCLUSION - IS THERE A "SILVER PLATTER"?

The short answer is "no", but practically speaking, it may be possible to offer an "aluminium platter". The aluminium platter is an approach for determining the type of dormancy a particular species exhibits, by examining the type of habitat in which the seeds are found. From this, a probable reason for dormancy may be surmised, and the appropriate treatment applied (Table 8).

Table 8. Habitat and dormancy treatment (The Aluminium Platter)

Habitat of origin	Dormancy treatment
Temperate region by cold winters	Stratification
Short growing season (alpine, boreal forest)	Warm + cold stratification
Understory species, small seeds	Light
Dry climate (grassland, desert)	Leaching, scarification
Warm, high humidity	Scarification

The essence of this approach is to evaluate the general climatic pattern of the region in which the species naturally occurs. Are environmental conditions fairly uniform during the year, or is the climate characterized by cold, near-freezing temperatures during the winter months? In tropical regions where the climate is relatively uniform, the seeds may be nondormant, and require no treatment. However, in temperate regions that experience a range of temperatures during the year, stratification is probably needed to break dormancy.

In northern or high elevation areas that are very cold or covered by snow for most of the year, the growing season may not be long enough for seeds to mature naturally. In such cases, a period of warmth may be needed to promote embryo growth and complete the maturation process, so compound stratification should be used. On the other hand, small seeds and those of understory species in deciduous forests would probably respond to light treatment. If the species naturally occurs in dry grasslands or desert areas, the seeds may require leaching or scarification to germinate.

The above inquiries likely will only provide part of the information needed to propagate plants from seeds. Other factors may have to be considered, such as the physical properties of the seeds, or whether the seeds are usually subject to predation. The type of predator may offer clues as to the type of dormancy treatment required. Hard seeds which have evolved to resist predation by insects and molds generally require mechanical or chemical scarification, but other seeds, enclosed in a fleshy fruit that is eaten by birds and other animals, often need extended stratification to germinate.

In some instances, treatments that are known to be effective for closely-related species may be successfully applied.

Sometimes even logic, and trial-and-error will fall to provide the required answers. Once all other avenues have been explored, we may have to accept that, at least for the present, some seed secrets will remain hidden from our view.

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LITERATURE CITED

Asakawa, S. and K. Fujita. 1966. Studies on the management of seed stands. 1. The establishment of experimental seed stands of *Pinus densiflora* and *Larix leptolepis* and the results obtained for three years (1962 to 1964). Bull. Gov. Forest Exp. Stn. 184: 81134, Tokyo, Japan.

Baskin, J.M. and C.C. Baskin. 1985. Seasonal changes in the germination responses of buried witchgrass (*Panicum capillare*) seeds. Weed Science 34: 22-24.

Chin, H.F. 1990. Storage of recalcitrant seeds: Past, present and future. pp. 89-92. *In*.- JW. Turnbull. Tropical tree seed research: Proc. International Workshop, Forestry Training Centre, Gympie, Qld., Australia, August 21-24, 1989. Aust. Centre. International Agric. Res. Proceedings No. 28,156p.

Edwards, D.W.G. 1973. Effects of stratification on western hemlock germination. Can. J. For. Res. 3(4):522-527.

Edwards, D.W.G. 1985. Special prechilling techniques for tree seeds. J. Seed Technol. 10(2): 151-171.

Edwards, D.W.G. and Y.A. El-Kassaby. 1995. Douglas-fir genotypic response to seed stratification. Seed Science & Technol. 23: 771-778

Hoff, R.J. and R.J. Steinhoff. In Press. Cutting stratified seed of western white pine to determine viability or increase

germination. Tree Plant. Notes.

Jones, S.F. and P.G. Gosling. 1994. "Target moisture content" prechill overcomes the dormancy of temperate conifer seeds. New. For. 8: 309-32 1.

Leadem, C.L. 1985. Seed dormancy in three *Pinus* species of the inland mountain west. *In*: Proc. Symp. "Conifer tree seed in the inland mountain west", Missoula, Montana, August 5-7,1985, pp. 117-124.

Leadem, C.L. 1986. Stratification of *Abies amabilis* seeds. Can. J. For. Res. 16:755-760.

Leadem, C.L. 1987. The role of plant growth regulators in the germination of forest tree seeds. In Hormonal control of tree growth. S.V. Kossuth and S.D. Ross (editors), Martinus Nijhoff Publishers, Dordrecht., Chap. 4, pp. 61-93.

Leadem, C. L. 1989. Stratification and quality assessment of *Abies lasiocarpa* seeds. Canada-British Columbia FRDA Report 095, ISSN 0835-0752, 18 p.

Leadem, C.L. 1996. A guide to the biology and use of forest tree seeds. B.C. Min. For., Victoria, B.C. Land Manage. Handb. 3 0, 20 p.

Muller, C. 1993. Combination of dormancy-breaking and storage for tree seeds: new strategies for hardwood species. *In* Dormancy and barriers to germination, Proc. Intemat. Symp. IUFRO Proj. Group P2.04-00 (Seed Problems.) Victoria, British Columbia, Canada, April 23-26, 199 1. D.G.W. Edwards (compiler and editor). Can. For. Serv., Pac. For. Centre, Victoria, B.C. pp. 79-85.

Muller, C. and M. Bonnet-Masimbert. 1989. Breaking dormancy before storage: a great improvement to processing of beechnuts. Seed Sci. Technol. 17: 15-26.

Muller, C., M. Bonnet-Masimbert, and E. Laroppe. 1990 Nouvelles voies dans le traitement des graines dormantes de certains feuillus: hêtre, frêne, merisier. Rev. For. Fr. 42(3):329-345

Naylor, J.M. 1983. Studies on the genetic control of some physiological processes in seeds. Can. J. Bot. 61: 3561-3567.

Naylor, J.M. and S. Jana. 1976. Genetic adaptation for seed dormancy in *Avena fatua*. Can. J. Bot. 54: 306-312

Porsild, A.E., Harington, C.R., and G.A. Mulligan. 1967. Science 158:113-114.

Schopmeyer, C. S. (technical coordinator). 1974. Seeds of woody plants in the United States. U.S. Dept. Agric. For. Serv., Washington, D.C. Agric. Handb. No. 450,883 p.

Suszka, B., C. Muller, and M. Bonnet-Masimbert. 1996. Seeds of forest broad-leaves. From harvest to sowing. Translated by A. Gordon. Institute National de la Recherche Agronomique, Paris. 297 p.

Tanaka, Y., and D.G.W. Edwards. 1986. An improved and more versatile method for prechilling *Abies procera* Rehd. seeds. Seed Sci. & Technol. 14: 45 7-464

Wang, B.S.P. 1976. Dormancy and laboratory germination criteria of white spruce seed. *In*: Proc. 2nd Int. Symp. Physiology of seed germination, Tokyo, Japan. Govt. For. Exp. Sm., Min. Agric. Forestry of Japan. pp. 179-188.

Willan, R.L. 1984. (Compiler) A guide to forest seed handling (with special reference to the tropics) Danida Forest Seed Centre, DK-Humlebaek, Denmark. Draft Edition.