Seed dormancy in commercial vegetable and flower species

Robert L. Geneve
Department of Horticulture
University of Kentucky
Lexington, KY 40546

Introduction

Following seed dissemination from the plant, orthodox seeds exhibit one of three conditions. A seed may be non-dormant and germinate immediately; it may be non-dormant and quiescent; or the seed may be dormant. Quiescent seeds are inhibited from germinating because the environment is unsuitable (i.e., the seed is dry or the temperature is outside the range that permits germination). Dormancy differs from quiescence because dormant seeds fail to germinate even when environmental conditions (water, temperature, and aeration) are suitable for germination.

Seed dormancy is a common condition found in many species. It is an adaptation that allows a species to determine the timing of germination for seeds in a population. Some species use environmental cues (such as drought vs. rainfall, or winter temperatures) to synchronize germination for most seeds at a particular time of the year. Other species are adapted for asynchronous germination over an extended time. This allows periodic germination and the establishment of a persistent seed bank. Domestication of crop plants has led to the reduction or elimination of seed dormancy to fit cropping schedules. Although this is true of most of the major agronomic crops, many vegetable and flower species still exhibit forms of seed dormancy that impact crop and seed production, and complicate seed testing. The purpose of this review is to describe the categories of seed dormancy and identify examples of vegetable and flower genera that exhibit seed dormancy.

CATEGORIES OF SEED DORMANCY

Propagators of cultivated plants long recognized that germination-delaying phenomena existed in seeds. The first recorded discussion of seed dormancy was by Theophrastus in ~300 B.C. (Evenari 1984). He recognized that most seeds germinated less after time in storage, while

others germinated at a higher percentage. Since that time, numerous scientific articles increased our knowledge about seed dormancy. Numerous attempts at defining the different kinds of seed dormancy have been attempted. An early system of classification was formulated by Crocker (1916), who described seven dormancy types based on treatments used to overcome them. Subsequently, Nikolaeva (1977) defined dormancy based primarily upon physiological controls. More recently, a universal terminology for dormancy was proposed (Lang 1987) that used the terms eco-, para-, and endo- dormancy to refer to dormancy factors related to the environment (eco), physical or biochemical signals originating external to the affected structure (para), and physiological factors inside the affected structure (endo). Baskin and Baskin (1998) have extended the dormancy classifications of Nikoleva to include additional specialty types.

In this review, dormancy conditions for vegetable and flower genera will be described using aspects of each system (Baskin and Baskin 1998; Crocker 1916; and Nikolaeva 1977). Major categories are primary and secondary dormancy. Within primary dormancy there are three recognized groups. These include: (1) exogenous; (2) endogenous; and (3) combinational dormancy (Hartmann et al. 1997). Exogenous dormancy is imposed by factors outside the embryo. These include maternal tissues (seed coat or pericarp) or mechanical resistance imposed on the radicle from the endosperm. Endogenous dormancy is related to dormancy factors within the embryo. Combinational dormancy includes a combination of exogenous and/or endogenous dormancy. These dormancy factors must be relieved sequentially to allow germination. Secondary dormancy is induced in certain non-dormant seeds when the germination environment is unfavorable for germination. Representative vegetable and flower genera for each of these categories is found in Table 1.

EXOGENOUS DORMANCY

The tissues enclosing the embryo can impact germination by (1) inhibiting water uptake; (2) providing mechanical restraint to embryo expansion and radicle emergence; (3) modifying gas exchange (i.e. limit oxygen to the embryo); (4) preventing leaching of inhibitors from the embryo; and (5) supplying inhibitors to the embryo (Bewley and Black 1994).

Seed coverings that impose exogenous dormancy are the endosperm, perisperm, outer

integuments of the seed coat or the remnant of the fruit pericarp. These may become hard, fibrous, or mucilaginous during dehydration and ripening. The most common form of exogenous dormancy occurs in seeds with “hard” seed coats that become suberized and impervious to water. Macrosclereid cells of the outer integument become rearranged, coalesce, incorporate suberin deposits, and develop external cutin coverings (Rolston 1978). Hard seeds are characteristic of members of the *Cannaceae, Convolvulaceae, Fabaceae, Geraniaceae,* and *Malvaceae*. Flower genera exhibiting hard seeds are listed in Table 2. This type of dormancy allows dry seed to be successfully stored for many years, even at warm storage temperatures. Germination in hard seeds can be increased by any method that can soften or “scarify” the covering (Hartmann et al. 1997). Hardseededness can be variable in a population of seeds. It is increased by environmental (dry) conditions during seed maturation, and environmental conditions during seed storage (Baskin and Baskin 1998). Harvesting slightly immature seeds and preventing them from completing desiccation can reduce hardseededness.

In nature, impervious seed coats are softened by microorganisms in the soil during warm periods of the season or by passage through digestive tracts of birds and mammals (Crocker 1948). They may be broken through mechanical abrasion, alternate freezing and thawing, and in some species, by fire. In crop species, any method that abrades or softens the seed coverings allows for germination. The most common commercial treatments are mechanical abrasion for large seed lots and concentrated sulfuric acid (15 to 60 min.) for smaller seed lots.

In other species such as cucumber (*Cucumis*) and spinach (*Spinacia*), mucilaginous layers on the seed coverings can restrict gaseous exchange (Bewley and Black 1982). These layers of integument and remnants of the endosperm and nucellus remain physiologically active during ripening and after the seed is separated from the plant. Such physiologically active layers maintain primary dormancy, mainly because this semipermeable nature restricts aeration and inhibitor movement.

For a number of species, the embryo can be removed from the seed coat of a dormant seed and germinate normally. In such instances, the seed coverings are the primary barrier to germination. The physical strength of the endosperm, perisperm or seed coverings have been

shown to restrict germination in cultivated crops like *Beta, Capsicum, Lactuca, Lycopersicon* and *Cucumis* (Dutta et al. 1994; Watkins and Cantliffe 1983; and Welbaum et al. 1995. Dormancy in these species is overcome when the seed coverings weaken, the embryo increases in growth potential or a combination of seed covering and embryo effects. It has been clearly demonstrated in *Lactuca* (Ikuma and Thimann 1963) and *Lycopersicon* (Still and Bradford 1997) that conditions that break dormancy are related to a weakening in the strength of the endosperm cells surrounding the radicle. This is accompanied by an increase in enzyme activity of cell wall degrading enzymes in the endosperm, particularly β-mannanase (Black 1996).

Chemicals that accumulate in fruit and seed covering tissues during development and remain with the seed after harvest can also act as germination inhibitors (Evenari 1949). Proving their function as germination controls does not necessarily follow, however. Nevertheless, germination can sometimes be improved by prolonged leaching with water, removing the seed coverings, or both (Nikolaeva 1977). Fleshy fruits, or juices from them, can strongly inhibit seed germination as in *Cucumis*, and *Lycopersicon* species. Likewise, chemicals extracted from dry fruits and fruit coverings, such as those in *Beta,* can inhibit germination. Some of the substances associated with inhibition are various phenols, coumarin, and abscisic acid (Bewley and Black 1982). Dormancy in *Iris* seeds is due to a water and ether-soluble germination inhibitors in the endosperm, that can be leached from the seeds with water or avoided by embryo excision (Arditti and Pray 1969). Inhibitors have been found in the seeds of such vegetable and flower families as *Polygonaceae*, *Brassicaceae, Chenopodiaceae, Linaceae* (*Linum*), *Lamiaceae (Lavendula), Portulaceae (Portulaca),* and *Violaceae* (Atwater 1980).

Endogenous Dormancy

Seeds with endogenous dormancy fail to germinate because of factors associated with the embryo. It can be confusing to distinguish between certain types of endogenous dormancy and some forms of exogenous dormancy, because removal of the seed coat (or pericarp) often allows the embryo to germinate in seeds with endogenous dormancy. There are two types of endogenous dormancy – morphological and physiological (Table 3).

Morphological dormancy is where the embryo has not completed development at the time the

seed is shed from the plant. The embryo must complete development prior to germination. Seeds with morphological dormancy can have either rudimentary or undeveloped embryos (Atwater 1980). Species with rudimentary embryos have little more than a proembryo embedded in a massive endosperm. These are found in *Ranunculaceae* (*Anemone, Ranunculus*), *Papaveraceae* (*Papaver, Romneya),* and *Araliaceae* (*Aralia, Fatsia*). Effective aids for inducing germination include (a) exposure to temperatures of <15^{o}C, (b) exposure to alternating temperatures, and (c) treatment with chemical additives such as potassium nitrate or gibberellic acid.

Seeds with undeveloped embryos have embryos that are torpedo shaped and up to one-half the size of the seed cavity. Important families and genera in this category include *Umbellifereae (Daucus), Primulaceae* (*Cyclamen, Primula*), and *Gentianaceae* (*Gentiana*). Warm temperatures (> 20^{o}C) favor germination, as does gibberellic acid treatment. Orchids have rudimentary embryos, but they are not considered dormant in the same sense as others in this category and special aseptic methods are used for germination.

The second type of endogenous dormancy is physiological dormancy. This involves physiological changes within the embryo that results in a change in its growth potential (Baskin and Baskin 1971) that allows the radicle to escape the restraint of the seed coverings. Physiological dormancy includes non-deep, intermediate and deep categories. By far, endogenous, non-deep physiological dormancy is the most common form of dormancy found in seeds (Baskin and Baskin 1998). This type of dormancy includes species that require light or darkness to germinate and species that must undergo an “after-ripening” period of dry storage to lose dormancy.

Seeds that either require light or dark conditions for germination are termed photodormant (Table 4). The basic mechanism of light sensitivity in seeds involves phytochrome (Bewley and Black 1994, Taylorson and Hendricks 1977). Exposure of the imbibed seed to red light (660 to 760 nm) usually stimulates germination, while far-red light (760 to 800 nm) or darkness causes a physiological change that inhibits germination (Van derWoude 1989). This was first demonstrated in the classic studies by Borthwick and co-workers at the USDA in Beltsville MD using lettuce seeds (Evanari 1984). This established the concept of photoreversibility and eventually the discovery of the different forms of phytochrome.

For some seeds, there is a distinct light and temperature for alleviating photodormancy. A light requirement can be offset by cool temperatures and sometimes by alternating temperatures. Lettuce (*Lactuca*) seeds generally require light to germinate, however, they lose this requirement and can germinate in darkness if the temperature is below 23^{o}C. Seeds may also lose their requirement for light after a period of dry storage.

In some cases, very low fluence rates are required to induce germination as in *Celosia* (Dixit and Amritphale 1996). In other cases, increasing the irradiance level (up to 150 μmol $\cdot$ sec^{-1} $\cdot$ m^{-2}) impacts the time required to satisfy photodormancy. This can be seen in common bedding plants such as *Begonia* (Carpenter et al. 1995) and *Impatiens* (Carpenter et al. 1994).

"After-ripening" is the time required for seeds in dry storage to lose dormancy. It is the general type of primary dormancy found in many freshly harvested seeds of herbaceous plants (Atwater 1980; AOSA 1993, Baskin and Baskin 1998). This type of dormancy is often transitory and disappears during dry storage, so it generally not a problem by the time the grower sows the seeds. It is however, a problem with seed testing laboratories requiring immediate germination. In seed testing laboratories, such seeds respond to various short-term treatments, including short periods of chilling, alternating temperatures, and treatment with potassium nitrate and gibberellic acid (AOSA 1993).

For most cultivated grasses, vegetables, and flower crops, nondeep physiological dormancy may last for one to six months and disappears with dry storage during normal handling (Table 5). Cucumber (*Cucumis*) displays nondeep physiological dormancy and is typical of many crops. Cultivated cucumber (*Cucumis sativus* var. *sativus*) has been selected over many years of breeding for a short dormancy period. It loses dormancy in dry storage at room temperature after several weeks (15 to 30 days). The hardwickii cucumber (*Cucumis sativus* var. *hardwickii*) is considered a wild progenitor species of the cultivated cucumber and it can maintain dormancy for 60 to 270 days (Weston et al. 1992). The time for dormancy release for hardwickii seeds in dry storage is shorter at warmer temperatures (180 days at 17^{o}C vs. 75 days at 37^{o}C). This negative relationship between after-ripening time and temperature is consistent within a species and has been modeled by Roberts (1965). He showed that time (log) to 50 % germination was linear with temperature. The time to dormancy release was also reduced by raising the seed moisture content

during storage (up to15 % moisture). Both these responses are typical of seeds with nondeep physiological dormancy.

Seeds with intermediate and deep physiological dormancy are characterized by a requirement for a one to three (sometimes more) month period of chilling, while in an imbibed and aerated state. This is a common dormancy type tree and shrub seeds and some herbaceous plants of the temperate zone (Crocker 1948). Seeds of this type ripen in the fall, overwinter in the moist leaf litter, and germinate in the spring. This requirement led to the horticultural practice of "stratification", in which seeds are placed between layers of moist sand or soil in boxes (or in the ground) and exposed to chilling temperatures, either out-of-doors or in refrigerators.

Temperature is the most important factor controlling stratification. The most effective temperature near freezing (1 to 10^{o}C). The time required to stratify seeds results from the interaction of the genetic characteristics of the seed population, seed development environment and the stratification environment (i.e., temperature). As a result, variability can occur within a seed lot and between different seed lots of the same species collected in different years or different locations.

Flower species that exhibit endogenous, intermediate physiological dormancy are usually herbaceous perennials (Table 6). These include species that require stratification for germination (such as *Aconitum* and *Gentiana)* and species where germination is improved (either higher percentages or faster germination rate) by brief periods of chilling temperatures. The latter is illustrated by purple coneflower (*Echinacea purpurea*) where germination percentage and rate of emergence was improved in 5 of 6 seed lots by a 10 day treatment of either 5 or 10 ^{o}C (Wartidininghsih and Geneve 1994).

Combinational dormancy

The third category of dormancy is combinational (also called double) dormancy. This dormancy condition combines two (or more) types of primary dormancy. Examples include exo-endodormancy (seed coat dormancy and intermediate physiological dormancy), or morphophysiological dormancy (an rudimentary embryo combined with physiological dormancy). To induce germination, all blocking conditions must be eliminated in proper sequence. The most

common form of combinational dormancy in flower and vegetable crops is morphophysiological dormancy (Table 7). This includes epicotyl dormancy, one of the most fascinating dormancy patterns found in seeds.

Seeds with morphophysiological dormancy may require simply warm (> 15^{o}C) or cold (1-10^{o}C) conditions during which time the embryo develops and then breaks physiological dormancy. More complex forms of morphophysiological dormancy require extended cycles of warm and cold temperatures to satisfy dormancy. In some species, there is a difference between cultivated and wild forms with respect to combinational dormancy. For example, in *Anemone*, cultivated 'de Caen' seeds showed only morphological dormancy (required only warm treatment), while wild populations of *A. coronaria* displayed morphophysiological dormancy and required warm followed by cold stratification (Horovitz et al. 1975).

Seeds with epicotyl dormancy have separate dormancy conditions for the radicle and epicotyl (Baskin and Baskin 1998, Crocker 1948, Nikoleava 1977). These species fall into two subgroups. In one group, only the epicotyl is dormant. Seeds initially germinate during a warm period of one to three months to produce root and hypocotyl growth but then require one to three months of chilling to enable the epicotyl to grow. This group includes seeds from various *Lilium* species, *Paeonia, Cimicifuga, and Asarum.* The dormancy breaking response of the epicotyl to chilling is sensitive to the stage of radicle growth (Barton and Chandler 1957). For *Paeonia*, 85% of the epicotyls exposed to 7 weeks of chilling grew if the radicle had reached 4 cm in length. In contrast, only 40 % of the epicotyls were released from dormancy under the same conditions with smaller 2-3 cm radicles.

In the second group, seeds require a chilling period followed by a warm period for the radicle to grow, then a second cold period to release the epicotyl from dormancy. In nature, such seeds require at least two full growing seasons to complete germination. Examples include *Trillium* and *Convallaria*. In some cases, a population of seeds can display either simple morphophysiological dormancy or epicotyl morphophysiological dormancy (Barton 1944). This has been shown for both *Sanguinaria* and *Polygonatum*. In these species, the seed population was split almost equally between the two types of dormancy.

Secondary Dormancy

In nature, primary dormancy is an adaptation to control the time and conditions for seed germination. Secondary dormancy is a further adaptation to prevent germination of an imbibed seed when environmental conditions are not favorable for seedling growth. These conditions can include unfavorable temperatures, prolonged light or darkness, water stress, or anoxia. These are involved in the seasonal rhythms (conditional dormancy) and prolonged survival of weed seeds in soil banks (Baskin and Baskin 1998). Induction of secondary dormancy is illustrated by classical experiments with freshly-harvested seeds of *Lactuca* (Khan 1980). If germinated at 25°C, the seeds required light, but if imbibed for two days in the dark, excised embryos germinated immediately, illustrating that only primary dormancy was present. If imbibition continued for as long as eight days, however, excised embryos did not germinate since they had developed secondary dormancy. Release from secondary dormancy can be induced by chilling, sometimes by light, and in various cases, treatment with germination-stimulating hormones, particularly gibberellic acid.

Nemophilla seeds require darkness to germinate. If these seeds are exposed to light for a period of time, they enter secondary dormancy and will no longer germinate in the dark without a chilling treatment (Chen 1968).

For some species, such as lettuce (*Lactuca*), celery (*Apium*), and pansy (*Viola*), germination at high temperatures (> 25°C) can induce thermodormancy (Table 8). This should not be confused with the thermal inhibition most seeds experience when the temperature exceeds the maximum temperature for germination. Seeds experiencing thermodormancy will not germinate when the temperature returns to near optimum temperatures, while thermal-inhibited seeds will germinate when temperatures are lowered. Commercially important crops that are prone to thermodormancy (such as summer-sown lettuce or pansy) can be primed prior to sowing to avoid germination problems (Cantliffe 1991; Carpenter and Boucher 1991).

CONCLUSIONS

Seed dormancy can be a factor in the successful germination and stand establishment of some flower and vegetable crops. It is a particular problem for accurately testing freshly harvested

seeds. The tables included in this review are not all inclusive and, unfortunately, some of the species included in a particular dormancy category had to be inferred from non-primary research. Definitive studies have only been completed for a limited number of vegetable and flower species. Also, the seed development and germination environment plays a critical role in dormancy induction of a particular seed lot and can complicate determining the dormancy status of a species . This review has been an attempt to bring together dormancy information concerning vegetable and flower seeds. Hopefully, it will serve as a stimulus to further refine our knowledge concerning dormancy in these important economic crops as additional scientific information becomes available.

Table 2. Flower genera containing seeds that have exogenous dormancy and require seed coat scarification.

Abutilon	*Convolvulus*	*Lespedeza*
Amorpha	*Indigofera*	*Lupinus*
Baptisia	*Geranium*	*Thermopsis*
Cistus	*Lathyrus*	

Table 3. Flower genera containing seeds that have endogenous, morphological dormancy.

Anemone	*Gentiana*	*Primula*
Apium	*Hemerocallis*	*Ranunculus*
Cyclamen	*Hosta*	*Romneya*
Eryngium	*Papaver*	

Table 4. Vegetable and flower genera containing seeds that have endogenous, non-deep physiological dormancy and require light or darkness for germination.

Light				**Dark**	
Amaranthus	*Catharanthus*	*Gaillardia*	*Nicotiana*	*Allium*	*Nigella*
Achillea	*Capsicum*	*Gloxinia*	*Oenothera **	*Cyclamen*	*Phacelia**
Alyssum	*Celosia*	*Helenium*	*Petunia*	*Exacum*	*Schizanthus*
Anagalis	*Centranthus*	*Iberis*	*Platycodon*	*Nemophilla*	
Antirrhinum	*Cleome*	*Impatiens*	*Portulaca*		
Apium	*Coreopsis*	*Kalanchoe*	*Primula*		
Aquilegia	*Cosmos*	*Lobelia*	*Ranunculus**		
Aster	*Daucus*	*Lobularia*	*Salvia*		
Begonia	*Dianthus*	*Lactuca**	*Silene*		
Borago	*Doronicum*	*Lychnis*	*Sinningia*		
Browallia	*Epilobium**	*Lythrum*	*Viola*		
Caladium	*Eschscholtzia*	*Mimulus*	*Verbena*		
Campanula	*Eustoma*	*Monarda*			

* Genera with loose the need for light or darkness to germinate after a period of dry storage.

Table 5. Vegetable and flower genera containing seeds that have endogenous, non-deep physiological dormancy and require a period of dry storage (after-ripening) for germination.

Alstromeria	*Coreopsis*	*Helianthus*	*Oenothera*
Antirrhinum	*Cosmos*	*Helichrysum*	*Petunia*
Brassica	*Cucumis*	*Impatiens*	*Portulaca*
Calendula	*Daucus*	*Lactuca*	*Solanum*
Capsicum	*Eschscholzia*	*Linum*	*Viola*
Celosia	*Festuca*	*Lycopersicon*	
Cleome	*Gypsophilla*	*Nicotiana*	

Table 6. Flower genera containing seeds that have endogenous, physiological dormancy and benefit from chilling stratification. Obligate species require stratification, while facultative species have seeds that will germinate without stratification but stratification increases germination rate.

Obligate			**Facultative**	
Aconitum	*Dodecatheon**	*Mertensia*	*Antirrhinum*	*Rudbeckia*
Arum	*Doronicum**	*Penstemon*	*Aquilegia*	*Lobelia*
Aruncus	*Eranthis*	*Primula*	*Asclepias*	*Salvia*
Aster	*Gentiana*	*Pulsatilla*	*Delphinium*	
*Bergenia**	*Helianthemum**	*Thalictrum**	*Echinacea*	
Brodieia	*Hemerocallis**	*Tiarella**		
Chionodoxa	*Hyacinthus*	*Tricyrtis*		
*Chrysopsis**	*Lavandula*	*Trollius*		
Dictamnus	*Liatris*	*Tulipa*		

* Genera with seeds that are not dormant as freshly harvested seeds, but require treatment after a period of storage.

Table 7. Flower genera containing seeds that have combinational dormancy. These species require a period of warm stratification for continued development of an immature embryo or to stimulate radicle growth and cold stratification for an endogenous, physiological dormancy prior to germination.

Warm followed by cold stratification			Cold, followed by warm, then cold stratification	
*Actea**	*Eryngium*	*Mertensia*	*Convallaria*	*Polygonatum**
Anemone	*Helleborus*	*Sanguinaria**	*Sanguinaria**	*Smilacina*
*Asarum**	*Jeffersonia*	*Trollius*	*Trillium**	
*Cimicifuga**	*Lilium**	*Tulipa*		
Eranthis	*Paeonia**			
Erythronium	*Polygonatum**			

* indicates species that exhibit epicpotyl morphophysiological dormancy.

Table 8. Vegetalve and flower genera with seeds that commonly exhibit secondary dormancy.

Thermodormancy		Light induced dormancy	
Apius	*Lactuca*	*Nemophila*	*Nigella*
Nemophila	*Viola*	*Phacelia*	

Table 1. Catagories of seed dormancy in vegetable and flower seeds.

Types of Dormancy	Causes of Dormancy	Conditions to Break Dormancy	Representative species of flower and vegetables
1. Exogenous dormancy Physical	Impermeable seed coat	Scarification	*Baptisia, Lupinus*
Chemical	Inhibitors in seed coverings	Removal of seed coverings (fruits) Leaching seeds	*Beta, Iris*
Mechanical 2. Endogenous dormancy	Seed coverings restrict radicle growth	Removal of seed covering Cold stratification	*Lactuca*
Morphological Rudimentary Undeveloped	The embryo is not fully developed at the time the seed sheds from the plant Small undifferentiated embryo Small differentiated embryo less than ½ size of seed	Warm or cold stratification Cold stratification and potassium nitrate Warm stratification and gibberellic acid	 *Anemone*, Ranunculus *Daucus, Cyclamen*
Physiological	Factors within embryo inhibits germination		
Nondeep	Positively photodormant Negatively photodormant	Red light Darkness	*Lactuca, Primula* *Cyclamen, Nigella*
	After-ripening	Short period of dry storage	*Cucumis, Impatiens*
Intermediate	Embryo germinates if separated from the seed coat	Moderate periods (up to 8 weeks) of cold stratification	*Aconitum, Gentiana*
Deep	Embryo does not germinate when removed from seed coat or will form a physiological dwarf	Long periods (> 8 weeks) of cold stratification	*Dictamnus*
3. Combinational dormancy	Combinations of different dormancy conditions that		

Types of Dormancy	Causes of Dormancy	Conditions to Break Dormancy	Representative species of flower and vegetables
	must be satisfied sequentially		
Morphophysiological	Combination of underdeveloped embryo and physiological dormancy	Cycles of warm and cold stratification	*Helleborus, Mertensia*
Epicotyl	Radicle is non-dormant and growth begins when temperature and water permit, but epicotyl is dormant	Warm followed by cold stratification	*Asarum, Paeonia*
Epicotyl and radicle	Radicle is dormant and growth begins after chilling stratification treatment, but epicotyl is dormant	Cold stratification followed by warm followed by a second cold stratification	*Convallaria, Trillium*
Exo-endodormancy	Combinations of exogenous and endogenous dormancy conditions. Example : physical (hard seed coat) plus intermediate physiological dormancy.	Sequential combinations of dormancy releasing treatments. Example : scarification followed by cold stratification.	No vegetable or flower genera in this category
4. Secondary dormancy			
Thermodormancy	After primary dormancy is relieved, high temperature induces dormancy	Growth regulators or cold stratification	*Apium, Lactuca, Viola*
Conditional dormancy	Change in ability to germinate related to time of the year	Chilling stratification	Not applicable for cultivated conditions

LITERATURE CITED

Arditti, J. and P. R. Pray. 1969. Dormancy factors in iris (*Iridaceae*) seeds. Amer. J. Bot. 56(3):254-59.

Association of Official Seed Analysts. 1993. Rules for testing seeds. J. Seed Tech. 16:1-113.

Atwater, B. R. 1980. Germination, dormancy and morphology of the seeds of herbaceous ornamental plants. Seed Sci. and Tech. 8:523-73.

Barton, L.V. 1944. Some seeds showing special dormancy. Contr. Boyce Thomp. Inst. 13:259-271.

Barton, L. V. and C. Chandler. 1957. Physiological and morphological effects of gibberellic acid on epicotyl dormancy of tree peony. Contr. Boyce Thomp. Inst. 19:201-14.

Baskin, J.M. and C.C. Baskin. 1971. Effect of chilling and gibberellic acid on growth potential of excised embryos of *Ruellia humilis*. Planta 100:365-69.

Baskin, J.M. and C.C. Baskin. 1998. *Ecology, Biogeography and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA.

Bewley, J. D. and M. Black. 1982. *Physiology and Biochemistry of Seeds in Relation to Germination.* Vol. 2. Springer-Verlag, New York.

Bewley, J. D., and M. Black. 1994. *Seeds: Physiology of development and germination.* Plenum Press, New York.

Black, M. 1996. Liberating the radicle: A case for softening-up. Seed Sci. Res. 6:39-42.

Cantliffe, D.J. 1991. Benzyladenine in the priming solution reduces thermodormancy of lettuce seeds. HortTechnology 1:95-99.

Carpenter, W.J. and J.F. Boucher. 1991. Priming improves high-temperature germination of pansy seed. HortScience 26:541-44.

Carpenter, W.J., E.R. Ostmark and J.A. Cornell. 1994. Light governs the germination of *Impatiens wallerana* Hook. F. seed. HortScience 29:854-57.

Carpenter, W.J., E.R. Ostmark and J.A. Cornell. 1995. Irradiance level and

duration required to terminate the dormancy of *Begonia x seperflorens* seed. HortScience 30:252-254.

Chen, S.S. C. 1968. Germination of light-inhibited seed of *Nemophila insignis*. Am. J. Bot. 55:1177-1183.

Crocker, W. 1916. Mechanics of dormancy in seeds. Amer. J. Bot. 3:99-120.

Crocker, W. 1948. Growth of plants. Reinhold, New York.

Dixit, S. And D. Amritphale. 1996. Very low fluence response in the induction and inhibition of seed germination in *Celosia argentea*. Seed Sci. Res. 6:43-48.

Dutta, S., K.J. Bradford and D.J. Nevins. 1994. Cell wall autohydrolysis in isolated endosperms of lettuce (*Lactuca sativa* L.). Plant Physiol. 104:263-268.

Evenari, M. 1949. Germination inhibitors. Bot. Rev. 15:153-94.

Evenari, M. 1984. Seed physiology: its history from antiquity to the beginning or the 20th Century. Bot. Rev. 50:119-142.

Ikuma, H. And K.V. Thimann. 1963. The role of the seed-coats in germination of photosensitive lettuce seeds. Plant & Cell Physiol. 4:169-185.

Hartmann, H.T., D.E. Kester, F. T. Davies, Jr., and R. L. Geneve. 1997. *Plant Propagation: Principles and Practices*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. Sixth edition.

Horovitz, A., S. Bullowa and M. Negbi. 1975. Germination characteristics in wild and cultivated anemone. Euphytica 24:213-220.

Khan, A.A. 1980. Hormonal regulation of primary and secondary dormancy. Israel J. Bot. 29:207-224.

Lang, G. A. 1987. Dormancy: A new universal terminology. HortScience 22:817-820.

Nikolaeva, M. G. 1977. Factors affecting the seed dormancy pattern. In *The physiology and biochemistry of seed dormancy and germination*, A. A. Khan, ed. Amsterdam: North-Holland Publishing Co., pp. 51-76.

Roberts, E.H. 1965. Dormancy in rice seed. IV. Varietal responses to storage and germination temperatures. J. Expt. Bot. 16:341-349.

Rolston, M. P. 1978. Water impermeable seed dormancy. Bot. Rev. 44:365-396.

Still, D. W. and K.J. Bradford. 1997. Endo-beta-mannanase activity from individual tomato endosperm caps and radicle tips in relation to germination rates. Plant Physiol. 113:21-29.

Taylorson, R. B., and S. B. Hendricks. 1977. Dormancy in seeds. Ann. Rev. Plant Physiol. 28*:* 331-354.

Van derWoude, W. 1989. Phytochrome and sensitization in germination control. pp. 181-90. *In : Recent Advances in the Development and Germination of Seeds.* R.B. Taylorson (ed.). Plenum Press, New York.

Watkins, J.T. and D.J. Cantliffe. 1983. Mechanical resistance of the seed coat and endosperm during germination of *Capsicum annuum* at low temperature. Plant Physiol. 72:146-150.

Welbaum, G.E., W.J. Muthui, J.H. Wilson, R.L. Grayson and R. D. Fell. 1995. Weakening of muskmelon perisperm envelope tissue during germination. J. Exp. Bot. 46:391-400.

Weston, L.A., R.L. Geneve and J.E. Staub. 1992. Seed dormancy in *Cucumis sativus* var. *hardwickii* (Royle) Alef. Scientia Hort. 50:35-46.

Wartidininghsih, N. And R.L. Geneve. 1994. Osmotic priming or chilling stratification improve seed germination of purple coneflower (*Echinacea purpurea*). HortScience 29:1445-1448.