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Seed dormancy in ornamental plants: A review

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ABSTRACT

Seed is the first input used in transfer of genetic traits in ornamental plants production. Seed dormancy is a physiological phenomenon in plants, which is caused by external or internal factors, and prevents seed germination, even in optimal conditions. Seed dormancy in flower crops impacts both seed production and germination. It can also complicate assessment of seed quality by the seed analyst who requires prompt germination to evaluate a seed lot. Flower crops display diverse mechanisms for seed dormancy like hard seed coat, immature, rudimentary embryo and inhibitors. It can be broken by soil melting and freezing, microorganism's activity, forest fires, soil activity and being eaten by animals, in normal conditions. This review surveys and categorizes the different seed dormancy conditions found in flowering plants. Flower genera are listed according to dormancy type. Categories of dormancy include primary and secondary dormancy. Within primary dormancy, examples of flower genera can be found that display exogenous, endogenous and combinational dormancy. Secondary dormancy can be an important problem in selected flower seeds. Specific examples are given for each type of dormancy along with methods to alleviate dormancy.

Key word: Flowers genera, Leaching, Scarification, Seed dormancy

The diversification of agriculture has given rise to many agri-based industries which have boosted the Indian economy (Das *et al*. 2012, Tiwari and Mishra 2012). The adoption of new crops and technologies having commercial potential is needed to strengthen the socio-economic status of developing countries like India (Dixit *et al.* 2013, Kumar *et al*. 2014). In commercial floriculture, flower seed production is considered one of the profitable and remunerative enterprises (Chauhan *et al.* 2010, Ganesh *et al.* 2014).This high value, labour intensive enterprise, taken up by small farmers, will help to reduce their poverty and lead them to live a respectful life (Kumar *et al*. 2011, Kumar *et al*. 2014). However, this sector is still in a nascent stage of development and accounts for a negligible share in the global exports (Tiwari *et al.* 2015a). Flowering annuals are usually grown for landscaping and commercially for seed production under Northern Indian climatic conditions. The demand of flowers hybrid seeds is soaring in the Indian market due to their high production potential. To ensure the use of good quality seeds, it is required to be available on time and place at reasonable prices. The cost of production in countries like USA, UK, France, Germany and Japan goes high due to energy expenses in mitigating extreme cold temperature and high labour costs (Modak *et al*. 1997). Due to this, various foreign seed companies have started outsourcing their seed production on contractual basis in different parts of the country especially Punjab, Karnataka, Andhra Pradesh and Maharashtra (Chauhan *et al*. 2010). As a result, Indian flower seed market is under the domination of global seed business (Gupta 2014). In India about 800 ha area is under flower seed production and Punjab contributes around half of the area with an estimated annual earnings of ₹ 6 crores (Tiwari *et al.* 2014a). Realizing the ground reality of safeguarding the national interest of self sufficiency, import substitution, and export promotion of good quality flower seeds, there is a need to strengthen the production technology of flowers to ensure higher seed yield with better quality.

The process of germination represents a very risky step in the lifecycle of a plant. The majority of seed-bearing plants disperse seeds that are desiccation tolerant which means they can withstand drying and remain viable in the soil for months or even years. In contrast, most seedlings are highly vulnerable. At the seedling stage, most of the plant's features are poorly established; the roots are small, scant and have limited access to water, the leaves are small limiting their ability to capture light, protective structures / compounds are often missing or minimal and the process of seedling growth limits the plant's resources. Considering this move from robust seed to vulnerable seedling, it is not surprising that many plants try to ensure that seed germination takes place at just the right moment, in just the right place.

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Hilhorst (1992) summarized this idea in his definition of dormancy as a device for optimizing the distribution of germination over time and place.

Originally, it was assumed that dormancy enabled seeds to survive long periods of environmental conditions unfavorable for germination (Li *et al*. 2012). However, unfavorable conditions would lack germination stimulation features, preventing germination regardless of whether or not the seeds were dormant. Better supported is the suggestion that dormancy enables seeds to survive short periods of favorable conditions; when germination stimulating factors are present, but prevailing conditions are not suitable for subsequent seedling growth and plant development. In other words, the seeds have evolved to postpone germination until a time and place that not only supports germination, but also maximizes seedling establishment and growth (Cao *et al*. 2014). Because dormant seeds don't germinate, dormancy was, for many years, considered to be some sort of seed defect or inactivity that meant that even a viable seed simply could not germinate (Garces *et al*. 2014, Mortensen and Grasser 2014). However, studies have shown that viable seeds, including dormant seeds, continually sense and respond to their environment, so dormant seeds are not inactive or defective (Juliette *et al*. 2012). As scientists have learnt more, seed dormancy behaviour has been split into several types.

Seed dormancy is a common condition found in many species of flowering plants. It is an adaptation that allows a species to determine the timing of germination for seeds in a population. A seed may be non-dormant and germinate immediately, it may be non-dormant (Chiba and Koyama 2012) and quiescent; or the seed may be dormant (Rolhauser *et al*. 2013). Quiescent seeds are inhibited from germinating because the environment is unsuitable. Dormancy differs from quiescence because dormant seeds fail to germinate even when environmental conditions (water, temperature, and aeration) are suitable for germination. 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 (Andujar *et al.* 2012). Although this is true of most of the major agronomic crops, many flower species still exhibit forms of seed dormancy that impact crop and seed production, and complicate seed testing. Refinement of the production technology to ensure higher seed yield with better quality is prerequisite to harness the export potential of flower seed. Propagators of cultivated plants long ago recognized that germination-delaying phenomena existed in seeds. The first recorded discussion of seed dormancy was by Theophrastus in ~300 B.C. (Ittu *et al*. 2014). Despite the fact that many researchers study dormancy, there is no unambiguous definition of the phenomenon, perhaps because it is manifest and broken in different ways in different species (Steven *et al*. 2015, Cross *et al*. 2015). For the sake of simplicity, seed dormancy, conceived as the temporary failure of an intact viable seed to complete germination under favourable conditions, is developed during the last period of embryogenesis and prevents germination during periods unfavourable to seedling growth and development. Therefore, seed dormancy is an adaptive mechanism to ensure plant survival (Tielborger *et al*. 2012). The purpose of this review is to describe the categories of seed dormancy and identify examples of flower genera that exhibit seed dormancy. This review categorizes the different seed dormancy conditions found in flower crops. Specific examples are given for each type of dormancy along with methods to alleviate it.

CATEGORIES OF SEED DORMANCY

Numerous attempts at defining the different kinds of seed dormancy were attempted (Footitt *et al*. 2015). The universal terminology for dormancy was proposed by Lang (1987) as eco-(environment) para-(physical or biochemical signals originating external to the affected structure) and endo- (physiological factors inside the affected structure dormancy). Geneve (2013) have grouped two broad categories, i.e. primary and secondary dormancy. Within primary dormancy, there are three more groups: (1) exogenous; (2) endogenous and (3) combinational dormancy (Duddu *et al*. 2014). Exogenous dormancy is imposed by factors outside the embryo (Wen *et al*. 2013). Combinational dormancy includes a combination of exogenous and/or endogenous dormancy. These dormancy factors must be relieved sequentially to allow germination (Otroshy *et al*. 2010). Secondary dormancy is induced in certain non-dormant seed when the germination environment is unfavorable for germination. In this review, dormancy conditions of flower genera will be described by using various aspects of each system. Representative flower genera for each of these categories are given in Table 1.

Mechanism of exogenous dormancy

The seed coat-imposed dormancy (hard seededness) is either due to the impermeability of the coat to water and/or gases, the mechanical prevention of radicle extension, or the seed coat preventing inhibitory substances from leaving the embryo or by supplying inhibitors to the embryo.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 (Tiryaki and Topu 2014).

Seed coverings that imposed exogenous dormancy are the endosperm in iris seed, perisperm in *Opuntia tomentosa*, outer integuments of the seed coat in *Grevillea linearifolia, G. buxifolia, G. sericea* and *Geranium carolinianum* (Gama *et al.* 2011) or the remnant of the fruit pericarp in *Harpagophytum procumbens* (Jordaan 2011). These may become hard, fibrous, or mucilaginous (Karin *et al.* 2011)

Table 1 Categories of seed dormancy in ornamental plants seeds

Types of dormancy	Causes of dormancy	Conditions to break dormancy	Representative genera of flower
Exogenous : Due to external factors (either seed structure or chemicals in seed coat have the cause)			
Physical	Impermeable seed coat	Scarification	*Baptisia*, *Lupinus*
Chemical	Inhibitors in seed coverings	Removal of seed coverings (fruits) Leaching seeds	*Iris,* Viola
Mechanical	Seed coverings restrict radicle growth	Removal of seed covering Cold stratification	*Echinacea purpurea,Rosea* spp.
Endogenous : embryo itself			
Morphological	The embryo is not fully developed at the time the seed sheds from the plant	Warm or cold stratification	*Narcissus pseudonarcissus Galanthus nivalis*
Rudimentary	Small undifferentiated embryo	Cold stratification and potassium nitrate	*Anemone*, Ranunculus
Undeveloped	Small differentiated embryo less than ½ size of seed	Warm stratification and gibberellic acid	*Daucus, Cyclamen*
Physiological	Factors within embryo inhibits germination	Cold or warm stratification are required before germination can take place	
Nondeep	Positively photodormant Negatively photodormant	Red light Darkness	*Lactuca*, *Primula Cyclamen*, *Nigella*
	After-ripening	Short period of dry storage	*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*
Combinational : Combinations of different dormancy conditions that must be satisfied sequentially			
Morphophysiological	Combination of under developed embryo and physiological dormancy	Cycles of warm and cold stratification	*Helleborus*, *Mertensia*
Epicotyl	Radicle is non-dormant and growth begins when and water permit, temperature 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*
Secondary dormancy			
Thermodormancy	After primary dormancy is relieved, high temperature induces dormancy	Growth regulators or cold stratification	*Apium*, *Lactuca*, *Viola*

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 (Kosma *et al.* 2014).

Physical dormancy is caused by one or more water impermeable layers of palisade cells in the seed (or fruit) coat along with a closed chalaza and micropyle and is known to occur only in angiosperms. One monocot and 16 eudicot (monophyletic clade of flowering plants) families have been inferred to contain species that have physical dormancy. Out of the 16 eudicots, occurrence of physical dormancy in Dipterocarpaceae, Sarcolaenaceae and Sphaerosepalaceae has been based only on seed-coat anatomy (Horn 2004). Seeds with physical dormancy cannot imbibe water even under favourable environmental conditions due to a water-impermeable layer(s) of cells. Specialized structures are involved in occlusion of the water gaps. The breaking of physical dormancy involves disruption or dislodgement of water-gap structures, which act as environmental signal detectors for germination. Once the

closed water gap opens, a seed can imbibe water rapidly and germinate under a wide range of conditions. Water-gap anatomy, morphology, origin and location differ among families as well as within the same family. Moreover, anatomy and morphology of the seed (or fruit) coat in the water-gap region differ from those of the rest of the seed (or fruit) coat. Nine different water-gap types were characterized in seven (excluding Geraniaceae) of the 17 angiosperm families with PY. The presence of a hard and impermeable seed coat is regarded as a widespread cause of seed dormancy in leguminous flowering species such as in *Lupinus albus* L. and *Trifolium pretense* (Tiryaki and Topu 2014) and in some other important ornamental plant families such as Geraniaceae (*Pelargonium* sp.), Oleaceae (*Jaminum* spp.), *Jasminum fructicans*, and Malvaceae (*Abutilon theophrasti*) (Schutte *et al*. 2014). Seed-coat thickness improved the explanatory power of logistic regression models for seed-size effects on both seed-bank persistence and dormancy (Schutte *et al*. 2014). Flower genera exhibiting hard seeds are listed in Table 2.

MECHANISM OF 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 – physiological and morphological.

Morphological endogenous dormancy

Morphological dormancy (MD) is an endogenous dormancy, associated with the seed embryo. These seeds have fully differentiated embryos that need to grow more before seed germination, or the embryos are not differentiated into different tissues at the time of fruit ripening. This is one of the most common seed dormancy which occurs by seeds intrinsic properties (Mousavi *et al.* 2011**)**. It may be due to inhibitor material in the seed, and should be reduced or removed before germination. Physiological changes such as: embryos maturity, response to growth regulators, changes in temperature, exposure to light, eliminates genetic dormancy. Environmental conditions existing at the time of seed development and maturity affect genetic dormancy duration. Flower genera containing seeds that have endogenous morphological dormancy are *Anemone, Cyclospermum (Apium), Cyclamen, Diervilla, Eryngium, Gentiana, Ginkgo, Hemerocallis, Lolium, Magnolia, Primula,* Manglietia, *Papaver.*

Table 2 Genera of ornamental plants having exogenous seed dormancy and require seed coat scarification

Ornamental plant genera	Ornamental plant genera	Ornamental plant genera
Abutilon	*Elaeagnus*	*Morus*
Acacia	*Epilasia*	*Opuntia*
Alberta	*Geranium*	*Rosa*
Amaranthus	*Grevillea*	*Sophora*
Abrus	*Harpagophytum*	*Spartium*
Argyreia	*Iliamna*	*Thermopsis*
Baptisia	*Indigofera*	*Trifolium*
Brachiaria	*Ipomoea*	*Urena*
Calycotome	*Iris*	*Viola*
Cassia	*Jasminum*	
Cistus	*Koelpinia*	
Convolvulus	*Kosteletzkya*	
Crataegus	*Lathyrus*	
Desmodium	*Lupinus*	
Echinacea	*Mauritia*	

Physiological endogenous dormancy

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 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 2010, Tiwari *et al.* 2010). 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. Dormancy due to inhibitors is based upon the fact that germination and growth promoting enzymes and hormones can be inhibited, thus preventing germination. Inhibitors, such as abscisic acid may be at sufficient level to counteract growth promoting enzymes, such as gibberellins. Usually it is the balance or ratio between inhibitors and promoters that needs to be tipped in the favor of those that will allow germination to proceed. These inhibitors are found in the endosperm, cotyledons, or other food storage tissue. Sometimes these chemicals are found in the outer coverings of the seed or fruit. Many of these chemicals are water soluble and can be leached from the seed, thus shifting the balance towards the growth promoting chemicals and allowing it to germinate. Others must be degraded into other forms or chemicals to reduce their concentration. With inhibitors that are found within the embryonic axis, it is temperature (and sometimes light) that generally controls this shift. Temperature may also favor the production of growth promoting hormones and enzymes in the embryonic axis. Cool temperatures generally shift the balance of promotors and inhibitors towards promoting germination (Erker 2010). Physiological dormancy (PD) is the most common expression of seed dormancy and is caused by the physiological inhibiting mechanism (PIM) of the seed embryo. This is the most abundant form of seed dormancy in angiosperm plants. PD is classified into three levels, i.e. Non-deep, Intermediate, and Deep. Genera of ornamental plants containing seeds having endogenous, non-deep physiological dormancy which require light or darkness for germination are enlisted in Table 3.

Table 3 Genera of ornamental plants containing seeds having endogenous, non-deep physiological dormancy

Genera	Reference	Genera	Reference
Achillea	Pirbalouti and Golparvar 2006	*Gaillardia*	Yin *et al.* 2014
Alyssum	Hosseini *et al.* 2010	*Gloxinia*	Yu *et al.* 2000
Amaranthus	Leon *et al.* 2006	*Helenium*	Gonzalez *et al.* 2011
Anagalis	Jayasuriya *et al.* 2009	*Iberis*	Copete *et al.* 2009
Antirrhinum	Benvenuti 2010	*Impatiens*	Iwamoto and Ishida 2005
Apium	Baninasab 2011	*Kalanchoe*	Chikhale *et al.* 2004
Aquilegia	Russell 2011	*Lobelia*	Carol *et al.* 2005
Aster	Washitani *et al.* 1997	*Lychnis*	Partzsch 2011
Begonia	Jian *et al.* 2012	*Lythrum*	Flanagan *et al.* 2010
Borago	Anna *et al.* 2014	*Mimulus*	Flanagan *et al.* 2010
Browallia	Magnani *et al.* 1994	*Monarda*	Kan and Dryagina 1996
Caladium	Sanchez *et al.* 2015	*Nicotiana*	Jerome *et al.* 2005
Campanula	Levitskaya 2015	*Oenothera*	Walck and Hidayati 2007
Catharanthus	Lalonde and Saini 1992	*Petunia*	Girard 1990
Celosia	Ferreira *et al.* 2012	*Platycodon*	Mei *et al.* 2015
Centranthus	Mack *et al.* 2015	*Portulaca*	Ali and Ansari 2000
Cleome	Zharare 2012	*Ranunculus*	Karami and Khui 2007
Coreopsis	Norcini and Aldrich 2007	*Romulea*	Swart *et al.* 2011
Cosmos	Dubey *et al*. 2002	*Salvia*	Khakpor 2011
Dianthus	Roychowdhury *et al.* 2012	*Silene*	Mira *et al.* 2011
Dipteronia	Tang *et al.* 2012	*Scrophularia*	Nurse *et al*. 2008
Doronicum	Mondoni *et al.* 2012	*Sinningia*	Yu *et al.* 2000
Epilobium	Akbari and Azizian 2006	*Verbena*	Brandel and Schutz 2003
Echinops	Baskin *et al.* 2014	*Viola*	Prochazka and Dvorak 2006
Eschscholtzia	Benvenuti *et al.* 2004	*Nigella*	Rouhi *et al.* 2012
Acer	Li *et al.* 2009	*Phacelia*	Patterson *et al.* 2013
Cyclamen	Burun and Sahin 2009	*Psammochloa*	Ying *et al.* 2004
Cotinus	Deng *et al.* 2010	*Suaeda*	Lei *et al.* 2008
Exacum	Magnani *et al.* 1994		
Schizanthus	Leon and Munoz 2013		

Table 4 Genera of ornamental plants containing seeds having endogenous, non-deep physiological dormancy and require a period of dry storage (after-ripening) for germination

Genera	Reference	Genera	Reference
Acanthocarpus	Commander *et al.* 2009	*Gypsophila*	Copete *et al.* 2007
Amaranthus	Omami *et al.* 1992	*Helichrysum*	Paraikovic *et al.* 2008
Anthocercis	Commander *et al.* 2009	*Impatiens*	Iwamoto and Ishida 2005
Asparagus	Conversa *et al.* 2010	*Linum*	Ashrafi *et al.* 2013
Antirrhinum	Gupta *et al.* 2015	*Lolium*	Ichihara *et al.* 2009
Brassica	Benincasa *et al.* 2012	*Lithospermum*	Chantre *et al.* 2009
Calendula	Eberle *et al.* 2014	*Nicotiana*	Jerome *et al.* 2005
Celosia	Zheng *et al.* 2009	*Oenothera*	Walck and Hidayati 2007
Cleome	Ochuodho and Modi 2005	*Petunia*	Estrada-Melo *et al.* 2015
Coreopsis	Zhang *et al.* 2014	*Physaria*	Cruz *et al.* 2012.
Cosmos	Dubey *et al*. 2002	*Portulaca*	
Cornus	Tylkowski 1992, Tiwari *et. al*. 2014b	*Theobroma*	Voigt *et al.*1995
Dioscorea	Commander *et al.* 2009	*Thryptomene*	Commander *et al.* 2009
Eschscholzia	Montalvo *et al.* 2002	*Viola*	Prochazka and Dvorak 2006
Eremophila	Commander *et al.* 2009	*Zygophyllum*	Commander *et al.* 2009
Festuca	Stanisavljevic *et al.* 2010		

For most cultivated grasses and flower crops, non-deep physiological dormancy may last for one to six months and disappears with dry storage during normal handling (Table 4).

Table 5 Ornamental plants genera having obligatory chilling stratification requirement due to endogenous, physiological seed dormancy

Genera	Reference	Genera	Reference
Aconitum	Yuan *et al.* 2011	*Hemerocallis**	Suzuki *et al.* 2003
Arum	Williams 1997	*Hyacinthus*	Ramon *et al.* 2006
Aruncus	Wang *et al.* 2009	*Lavandula*	Macchia *et al.*1996
Aster	Gettys and Werner 2001	*Liatris*	Parks and Boyle 2002
*Bergenia**	Noronha *et al.* 1997	*Mertensia*	Skarpaas *et al.* 2002
Brodieia	Wang *et al.* 2011	*Penstemon*	Kitchen and Meyer 1991
Chionodoxa	Daskalyuk *et al.* 1999	*Primula*	Moustafa *et al.* 2002
Dictamnus	Debska *et al.* 2013	*Thalictrum*	Walck *et al.* 1999
*Dodecatheon**	Bessler and Zimmer 1994	*Tiarella**	Wang *et al.* 2009
*Doronicum**	Noronha *et al*. 1997	*Tricyrtis*	Zhang *et al*. 2014
Eranthis	Gonzalez and Villalobos 1988	*Trollius*	Hitchmough *et al.* 2000
Gentiana	Millaku *et al.* 2012	*Tulipa*	Rouhi *et al.* 2012
*Helianthemum**	Zaman *et al.* 2009		

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

Table 6 Ornamental plants genera having facultative endogenous, physiological seed dormancy that seeds will germinate without stratification but stratification increases germination rate

Genera	Reference	Genera	Reference
Antirrhinum	Montero *et al.* 1990	*Echinacea*	Qu and Widrlechner 2012
Aquilegia	Russell 2011	*Lobelia*	Baskin and Baskin 2012
Asclepias	Balogh *et al.*	*Rudbeckia*	Baradaranrad and Aruee 2013
Delphinium	Baskin and Baskin 1994	*Salvia*	Khakpor *et al.* 2011

Flower species that exhibit endogenous, intermediate physiological dormancy are usually herbaceous perennials (Table 5). 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 (Table 6).

MECHANISM OF COMBINATIONAL/DOUBLE 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 exoendodormancy (seed coat dormancy and intermediate physiological dormancy), or morpho-physiological dormancy (a rudimentary embryo combined with physiological dormancy).To induce germination, all blocking conditions must be eliminated in proper sequence.

Morpho-physiological dormancy (MPD)

Morphological dormancy (MD) is often found in combination with physiological dormancy (PD) and is known as morpho-physiological dormancy or combined dormancy; MD + PD or MPD. It occurs due to either seed embryo is rudimentary or linear (under developed) or seeds require physiological dormancy to be alleviated, even after the seed embryo has fully developed. *Rubus* seed has a deep double dormancy that restricts germination due to seed coat structure and chemical composition. This study evaluated the seed coat structure of three species with thin (*R. hoffmeisterianus* Kunth & C D Bouche), medium (*R. occidentalis* L.) and thick (*R. caesius* L.) seed coats. The three species exhibited distinctive seed-coat cell composition. The very thin testa (0.086 mm) of *R. hoffmeisterianus* had little exotesta (surface) reticulation; with the meso- and endotesta composed of sclereids of homogenous shape and size. *R. occidentalis* had a thick testa (0.175 mm) and a highly reticulate exotesta; the meso- and endotesta were composed of several diverse types of sclereids. *R. caesius* had the thickest seed coat (0.185 mm) but only moderate exotesta reticulation; the meso- and endotesta were composed of large, irregular, loosely arranged sclereids. *R. occidentalis*, a medium size seed, was the most heavily lignified with seed-coat thickness similar to *R. caesius*, the largest seed. Proanthocyanidins (PAs) from dry seed of six *Rubus* species were extracted and quantified by high performance liquid chromatography. *R. hoffmeisterianus*, a thin only slightly hard seed, had half the PA (0.45 µ g/seed) of *R. occidentalis* with a thick, extremely-hard seed coat and diverse sclereids (1.07 µ g/seed). PA content and sclereid composition both appear to contribute to seed coat hardness and resulting seed dormancy. The effectiveness of sulfuric acid for *Rubus* seed scarification is likely due to degradation of PAs in the testa (Wada *et al*. 2011). Niimi *et al.* 2006 reported that seeds of Christmas rose (*Helleborusniger*) had a heart-shaped embryo when dispersed from parent plants. That embryo developed rapidly to the torpedo stage

at 25º C, after which no further development occurred. When seeds with a torpedo-stage embryo were held at 15º C, the embryos developed to the cotyledon stage, but no further germination occurred. Similar phenomena in the course of embryo development were observed in seeds held in a non-heated polyethylene house, in which the embryos developed to the torpedo stage at 20º C or more, while further development to the cotyledon stage was attained only at temperatures of 15º C or less. Seeds with a cotyledon-stage embryo rarely germinated until they were treated at 4º C for more than 8 weeks. These results suggest that seeds of *H. niger* have a deep, simple morpho-physiological dormancy caused by the combination of rudimentary embryos and a physiological dormancy that can be broken by cycles of warming and chilling. Genetic dormancy decreases with increasing age of seed (Mandujano *et al*. 2005, Sarmadnia 1997). Light, wavelength, and day duration have an impact on seeds germination, which have a physiological dormancy. Seed dormancy in lettuce is broken down with placing the seeds in red light (670 nm). Some plant species seeds, respond to short days and some react to long days (Kathryn 2004). Continuous light may inhibit germination in some seeds such as onions and leeks. The most common form of combinational dormancy in flower crops is morpho-physiological dormancy (Table 7).

According to Baskin and Baskin (1998), the Amaryllidaceae have under developed linear embryos that are fully differentiated, thus they need to grow before the seed germinates. Nevertheless, data on embryo growth requirements are particularly scarce in this family. However, Copete *et al.* 2011, concluded that seeds of N. hispanicus have deep simple epicotyl morpho-physiological dormancy (MPD), with the dormancy formula C1bB (root) – C3 (epicotyl).This includes epicotyl dormancy, one of the most fascinating dormancy patterns found in seeds. Seeds with morpho-physiological dormancy may require simply warm (> 15ºC) or cold (1-10^{0}C) conditions during which time the embryo develops and then breaks physiological dormancy. More complex forms of morpho-physiological 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 morpho-physiological dormancy and required warm followed by cold stratification (Horovitz *et al.* 1975).

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)

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

*Indicates species that exhibit epicpotyl morpho-physiological dormancy. (*Source:* http://www.uky.edu/Projects/SeedBiology/research/.

Epicotyl-dormancy: Seeds with epicotyl dormancy have separate dormancy conditions for the radicle and epicotyls (Baskin and Baskin 1998, 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. 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 morpho-physiological dormancy or epicotyl morpho-physiological dormancy. 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.

The most common kind of epicotyl dormancy described is epicotyl morpho-physiological dormancy (MPD) that occurs in some seeds with an under developed embryo. However, epicotyls dormancy has also been identified in a few species whose seeds have a fully developed embryo: *Quercus alba*, *Quercus prinus* (Pasquini 2012), *Quercus ilicifolia*, *Platonia insignis*, *Chionanthus retusus*, *Calophyllum brasiliensis*, *Lecythis ampla*, *Garcinia kola* and *Humboldtia laurifolia* (Jayasuriya *et al.* 2012). Thus, this kind of epicotyl dormancy cannot be classified as a level of MPD. Baskin and Baskin (2004) referred to the acorns of the white oaks as having a pecialized kind of epicotyl dormancy, thus distinguishing it from epicotyl MPD. Jayasuriya *et al.* (2010) reported still another kind of epicotyl dormancy in seeds of *H. laurifolia* (Fabaceae, subfamily Caesalpinioideae), in which the shoot needs to grow to a considerable length inside the seed before it can

emerge.

SECONDARY DORMANCY

Secondary dormancy can occur in seeds which previously have had no dormancy, or it can be imposed upon seeds which already possess primary dormancy (Karssen 1980/81, Hilhorst 2007). It is not as common a phenomenon as it is in ornammental grasses (Simpson 1990). ABA has been widely implicated in the imposition and the maintenance of seed dormancy. Expression of this dormancy during grain imbibition is associated with maintenance of ABA at high levels, while embryo ABA content decreases sharply in non-dormant and dormant grains placed in conditions which allow germination. In addition, the responsiveness of embryos to ABA depends on the dormancy state, embryos isolated from dormant grains being more sensitive to ABA than those isolated from non-dormant grains. To our knowledge, there is no clear evidence of ABA involvement in secondary dormancy, although it is likely. However, conditions that maintain ABA synthesis are also effective in the induction of secondary dormancy in *Arabidopsis* and *Brassica napus*, and treatment of oat seeds with fluridone prevents the induction of thermodormancy, suggesting that ABA synthesis is involved in this phenomenon. In the latter species, embryo sensitivity to ABA was also reinforced in secondary dormant grains as compared with primary dormant grains. ABA content results from a balance of ABA biosynthesis and catabolism. In *Arabidopsis* seeds, the expression of the ABA 80-hydroxylase (ABA80OH) gene is greater in embryos from non-dormant seeds than in those isolated from dormant seeds, suggesting that it may be considered as a key gene controlling ABA catabolism (i.e. a decrease in ABA embryo content) during imbibition, and consequently dormancy. The 9-cis-epoxycarotenoid dioxygenase (NCED) gene family which plays a critical role in ABA synthesis is also implicated, in particular AtNCED6 and AtNCED9, in induction of primary dormancy during seed development. However, the link between expression of both HvNCED1 and HvNCED2 and dormancy remains unclear (Millar *et al.* 2006). Polyethylene glycol treatment induces secondary seed dormancy in *Brassica napus* L. cultivar 'AC Excel' (ACE), but not in 'DH12075' (DH). Gene expression, metabolite profiles, and hormone profiles were obtained from seeds of both cultivars following polyethylene glycol 8000 treatment. ACE seeds were more transcriptionally active: 28 genes were up-regulated in both cultivars and 10 and 158 genes were specifically upregulated in DH and ACE, respectively. Non-targeted metabolite analyses combined with gene expression analyses showed significant differences in lipid, sugar, and phenylpropanoid metabolism between the cultivars. Abscisic acid (ABA) levels were higher and many ABA-inducible genes were expressed more in ACE. An association of ABA with secondary dormancy was supported by the observation that secondary dormancy was induced by polyethylene glycol 8000 in *Arabidopsis* wild-type seeds, but was reduced in ABA-deficient and ABA-insensitive mutants. Therefore, secondary dormancy appears to be realized through an active ABA-related mechanism that may involve changes in primary and secondary metabolism (Fei *et al.* 2009). Jan *et al*. (2003) reported that neither ethylene nor 1-aminocyclopropane-1-carboxylic acid (ACC) was able to prevent the induction of secondary dormancy of *Amaranthus caudatus* at 45º C. Both ethylene ($4.5 \times 10^{-9} – 4.5 \times 10^{-7}$ M) and ACC (10^{-3}–10^{-2} M) removed secondary dormancy at 25º C, although ethylene was much more effective. The presence of ethylene for only 10 h was sufficient to remove secondary dormancy in almost all seeds. Incubation of secondary dormant seeds for up to 5 d at 25º C did not change sensitivity to ethylene. The breaking of secondarydormancy by ethylene was prevented by 2,5-norbornadiene (NBD; $1.5 \times 10^{-5} – 3 \times 10^{-4}$ M), indicating the physiological action of ethylene. Abscisic acid (ABA; $10^{-4} – 10^{-3}$ M) increased the requirement for exogenous ethylene. It is suggested that secondary dormancy in A. caudatus seeds might be related to insufficient ethylene production associated with an insufficient amount of ACC. Secondary seed dormancy in oilseed rape is a phenomenon that allows seeds to survive in the soil for many years without germination (Schatzki *et al.* 2013). Inheritance of secondary dormancy may be related to seed longevity (SL) in the soil. Genetic reduction in secondary dormancy and SL could provide a mean to reduce the frequency of volunteer plants and especially the dispersal of transgenic oilseed rape. Heritability was high for secondary dormancy and moderate for germination rate and SL.

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). If germinated at 25^0C, 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 pansy (*Viola*), germination at high temperatures (> 25^0C) can induce thermodormancy. 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 pansy) can be primed prior to sowing to avoid germination problems.

Seed dormancy can be a factor in the successful germination and stand establishment of some flower 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 were completed for a limited number of 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 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.

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