Seed Dormancy in Commercial Vegetable and Flower Species

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INTRODUCTION

This paper is a review of seed dormancy in vegetable and flower seeds. Due to page constraints only a portion of it appears here. A complete discussion of this topic including tables on individual species with different dormancy types has been previously published (Geneve, 1998).

Following seed dissemination from the plant, orthodox seeds exhibit one of three conditions. A seed may be nondormant and germinate immediately; it may be nondormant 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. 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.

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. 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. Baskin and Baskin (1998) have extended the dormancy classifications of Nikoleva to include additional specialty types and forms the basis for the system presented here for horticultural crops.

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). Representative vegetable and flower genera for each of these categories are 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., limiting 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. Hard seeds are characteristic of members of the *Cannaceae, Convolvulaceae, Fabaceae, Geraniaceae,* and *Malvaceae*. Germination in hard seeds can be increased by any method that can soften or "scarify" the covering (Hartmann et al., 1997).

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 maintain primary dormancy, mainly because this semipermeable nature restricts aeration and inhibitor movement.

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). Fleshy fruits, or juices from them, can strongly inhibit seed germination as in *Cucumis* and *Lycopersicon* species. Some of the substances associated with inhibition are various phenols, coumarin, and abscisic acid (Bewley and Black, 1982). 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.

Morphological Dormancy is where the embryo has not completed development at the time the seed is shed from the plant. 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 *Umbelliferae (Daucus), Primulaceae* (*Cyclamen*, *Primula*), and *Gentianaceae* (*Gentiana*). Warm temperatures ($> 20^{o}$C) favor germination, as does gibberellic acid treatment.

The second type of endogenous dormancy is **physiological dormancy**. This involves physiological changes within the embryo 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**. The basic mechanism of light sensitivity in seeds involves phytochrome (Bewley and Black, 1994; Taylorson and Hendricks, 1977). For some seeds, there is a distinct light and temperature for alleviating photodormancy. Lettuce (*Lactuca*) seeds generally require light to germinate, however, they lose this requirement and can germinate in darkness if the temperature is below 23°C. Seeds may also lose their requirement for light after a period of dry storage.

"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 is generally not a problem by the time the grower sows the seeds. For most cultivated grasses, vegetables, and flower crops, nondeep physiological dormancy may last for 1 to 6 months and disappears with dry storage during normal handling.

Seeds with intermediate and deep physiological dormancy are characterized by a requirement for a 1- to 3-month period (sometimes more) of chilling, while in an imbibed and aerated state. This is a common dormancy type for tree and shrub seeds and some herbaceous plants of the temperate zone (Crocker, 1948). 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 is near freezing (1 to 10°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).

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 (a rudimentary embryo combined with physiological dormancy). To induce germination, all blocking conditions must be eliminated in proper sequence.

Seeds with **morphophysiological** dormancy may require simply warm (> 15°C) or cold (1 to 10°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. 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 1 to 3 months to produce root and hypocotyl growth but then require 1 to 3 months of chilling to enable the epicotyl to grow. This group includes seeds from various *Lilium* species, *Paeonia, Cimicifuga,* and *Asarum.*

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.

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	Seed coverings restrict radicle growth.	Removal of seed covering. Cold stratification.	*Lactuca*
2. Endogenous dormancy			
Morphological	The embryo is not fully developed at the time the seed sheds from the plant.	Warm or cold stratification.	
Rudimentary	Small undifferentiated embryo.	Cold stratification and potassium nitrate.	*Anemone*, *Ranunculus*, *Daucus*, *Cyclamen*
Undeveloped	Small differentiated embryo less than ½ size of seed.		
Physiological	Factors within embryo inhibits germination.		
Nondeep	Positively photodormant.	Red light.	*Lactuca*, *Primula*,
	Negatively photodormant.	Darkness.	*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 must be satisfied sequentially.		
Morphophysiological	Combination of underdeveloped embryo and physiological dormancy.	Cycles of warm and cold stratification.	*Helleborus, Mertensia*
Epicotyl	Radicle is nondormant 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 beginsafter 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.

In nature, such seeds require at least two full growing seasons to complete germination. Examples include *Sanguinaria*, *Trillium*, and *Convallaria*. In some cases, a population of seeds can display either simple morphophysiological dormancy or epicotyl morphophysiological dormancy (Barton, 1944).

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).

For some species, such as lettuce (*Lactuca*), celery (*Apium*), and pansy (*Viola*), germination at high temperatures (> 25°C) can induce **thermodormancy**. 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).

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