A seed is a ripened ovule. At the time of separation from the parent plant it consists of an embryo and stored food supply, both of which are encased in a protective covering. The activation of the metabolic machinery of the embryo leading to the emergence of a new seedling plant is known as germination. This chapter describes the various conditions that determine the success of germination and initial growth of the seedling.

THE GERMINATION PROCESS

For germination to be initiated, three conditions must be fulfilled (31, 67):

First, the seed must be viable; that is, the embryo must be alive and capable of germination.

Second, the seed must be subjected to the appropriate environmental conditions: available water, proper temperature regimes, a supply of oxygen, and sometimes light.

Third, any primary dormancy condition present within the seed (35) must be overcome. Internal processes leading to removal of primary dormancy are collectively known as after-ripening and result from the interaction of the environment with the specific primary dormancy condition. After-ripening requires a period of time and sometimes specific methods of seed handling. Even in the absence of primary dormancy and/or if the seeds are subjected to adverse environmental conditions, a secondary dormancy can develop and further delay the period when germination takes place (26, 68, 75).

Stages of Germination

Germination is divided into several consecutive but overlapping stages (19, 31):

Stage 1—Activation

Imbibition of water. Water is absorbed by the dry seed and the moisture content increases
rapidly at first, then levels off (see Fig. 6-1). Initial absorption involves the imbibition of water by colloids of the dry seed. Water softens the seed coverings and causes hydration of the protoplasm. The seed swells and the seed coats may break. Imbibition is a physical process and can take place even in dead seeds.

In triggering germination, water absorption shows three stages: (a) an initial increase to 40 to 60 percent of water (fresh weight basis) equivalent to 80 to 120 percent dry weight (water content/initial dry weight), (b) a slow (lag) period after which the radicle emerges (germination), followed by (c) a further increase to 170 to 180 percent (dry weight basis) as the seedling grows (Fig. 6-1).

Synthesis of enzymes. As the seed absorbs water, enzyme activity begins to appear within a matter of hours. Activation results in part from reactivation of stored enzymes, previously formed during development of the embryo, and, in part, from synthesis of new enzymes as germination starts (19, 69). Synthesis requires the presence of specifically programmed RNA molecules (see box). Some of these appear to have been formed during seed development, conserved during the ripening process and available to initiate germination. Others are apparently formed after germination starts. Energy for these processes is obtained from the high-energy phosphate bonds in adenosine triphosphate (ATP) present in mitochondria. Some ATP is conserved in the dormant seed and reactivated as the seed absorbs moisture.

Cell elongation and emergence of the radicle. The first visible evidence of germination is emergence of the radicle, which results from enlargement of cells rather than from cell division (17, 19, 56). Emergence of the radicle can occur within a few hours or a few days after the initiation of germination and marks the end of stage 1.

Stage 2—Digestion and Translocation

Fats, proteins, and carbohydrates stored in the endosperm, cotyledons, perisperm, or female gametophyte (conifers) are digested to simpler chemical substances, which are translocated to the growing points of the embryo axis. The existing cell systems have been activated and the protein-synthesizing system is functioning to produce new enzymes, structural materials, regulatory compounds, hormones, and nucleic acids to carry on the cell functions and synthesize new materials. Water uptake and respiration now continue at a steady rate.

Stage 3—Seedling Growth

In the third stage, development of the seedling plant begins with cell division at the two ends of the embryo axis, followed by the expansion of the seedling structures. The initiation of cell division in the growing points appears to be independent of the initiation of cell elongation (17, 56).

The embryo consists of an axis bearing one or more seed leaves, or cotyledons. The growing point of the root, the radicle, emerges from the base of the embryo axis. The growing point of the shoot, the plumule, is at the upper end of the em-
BIOLOGICAL CONTROL
IN GERMINATION AND DORMANCY

Control of embryogenesis, germination, and dormancy have revolved around three different biological concepts: (a) the transfer of specific genetic information from the genes to the proteins to specific metabolic systems characteristic of particular stages of development; (b) the balance and interplay among different endogenous hormone systems, involving primarily abscisic acid, gibberellin, and cytokinin; and (c) phase transition in cell membranes at specific temperatures (19).

(a) Embryogenesis originates in the single-celled zygote (see Chaps. 1 and 3), which is described as being totipotent, that is, it contains all the genetic information needed to produce the embryo and the seedling plant and its subsequent development. How the information codes of the gene specified by the DNA (deoxyribonucleic acid) of the cell are transferred into embryo and seedling development determines the pattern and unique outcomes of the germination sequence for particular plants (29). These pathways are mediated through the activity of biologically active compounds known as RNAs (ribonucleic acids), differing from DNA in specific molecular structure. Specific stages in this sequence involve the transcription of specific DNA sequences to transfer RNA (tRNA), the processing to messenger RNA (mRNA), transport from the nucleus to the cytoplasm to join into structures (ribosomes) where it is known as ribose RNA (rRNA), and degradation and translation to direct the synthesis of specific proteins. Proteins are complex nitrogen-containing compounds that act as enzymes, serve as intermediates to other complex metabolites, and become storage products and/or structural compounds.

(b) Much research indicates that endogenous hormones are directly involved in various aspects of RNA transcription and translation and may turn on and off various key metabolic steps, most of which are not understood (88). For instance, the presence of cytokinin and gibberellins is associated with embryo enlargement phases of development, whereas inhibitors (particularly abscisic acid) along with dehydration have been associated with the maintenance of the embryonic phase and the prevention of premature germination. Germination initiation, breakdown of storage products, and seedling growth have been associated with gibberellins, whereas cytokinins are effective in neutralizing the inhibitors.

Sometimes an applied hormone can have a direct effect in overcoming or inducing dormancy, as described on page 148. In other cases, for example, in embryo dormancy of apple (27), a hormone may have only a partial effect and all three are involved.

(c) Further research emphasized biophysical effects of cell membranes in growth inhibition, activation, and dormancy control. Evidence is provided in the correlation of cell and membrane changes from liquid to gels at specific temperatures (19), shifts which are similar to dormancy responses to temperature. Inner layers of the testa and the remnants of the endosperm and/or nucellus have restricting effects that are released with alteration or removal of the membranes, shifting temperatures, or subjecting seeds to anerobiosis (11).

bryo axis, above the cotyledons. The seedling stem is divided into the section below the cotyledons—the hypocotyl—and the section above the cotyledons—the epicotyl.

Once growth begins from the embryo axis, fresh weight and dry weight of the new seedling plant increase but total weight of storage tissue decreases. The respiration rate, as measured by
oxygen uptake, increases steadily with advance in growth. Storage tissues of the seed eventually cease to be involved in metabolic activities except in plants of which the cotyledons emerge from the ground and become active in photosynthesis. Water absorption increases steadily as new roots explore the germination medium and the fresh weight of the seedling plant increases.

The initial growth of the seedling follows one of two patterns. In one type—epigeous germination—the hypocotyl elongates and raises the cotyledons above the ground. In the other type—hypogeous germination—the lengthening of the hypocotyl does not raise the cotyledons above the ground, and only the epicotyl emerges (Figs. 6-2 and 6-3).

**FIGURE 6-2** Seed germination in dicotyledonous plants. *Top:* Epigeous germination of cherry. The cotyledons are above ground. *Below:* Hypogeous germination of peach. The cotyledons remain below ground.
QUALITY OF SEEDS

A method of judging viability is essential in successful seed propagation. A dead or dying seed is characterized by a gradual decline in vigor, and necrosis or injuries may appear in localized areas of the seed coat. But the difference between a live seed and a dead one is not always distinct (63, 106). Viability is expressed by the germination percentage, which indicates the number of seedlings produced by a given number of seeds. Additional characteristics of high-quality seed are prompt germination, vigorous seedling growth, and normal appearance (2). Vigor of seed and seedling is an important attribute of quality but is difficult to measure (90, 92). Low germination percentage, low germination rate, and low vigor are often associated. Low germination can be due to genetic properties of certain cultivars (43), incomplete seed development on the plant, injuries during harvest, improper processing (41) and storage (104), disease, and aging. Loss in viability is usually preceded by a period of declining vigor (121).

Seeds with low vigor may not be able to withstand unfavorable conditions in the seed, such as attacks by disease organisms. The seedlings may lack the strength to emerge if they are planted too deeply or if the soil surface is crusted. Field survival of low-vigor seeds is likely to be less than a laboratory germination percentage test would indicate.

Measurement of Seed Quality

If one measures the time sequence of germination of a given lot of seeds, or the emergence of seedlings from a seed bed, one usually finds a pattern like the germination curve shown in Fig. 6-3. There is an initial delay in the start of germination, then a rapid increase in the number of seedlings that germinate, followed by a decrease in the rate of appearance. When viability is less than 100 percent, the end point may not be exact.

Germination is measured on two parameters—the germination percentage and the germination rate. Vigor may be indicated by measurements, but seedling growth rate and physiological appearance also must be considered.
Sometimes abnormally growing seedlings result from low seed quality (63).

Statements of germination percentage should involve a time element, indicating the number of seedlings produced within a specified length of time. Germination rate can be measured by several methods. One determines the number of days required to produce a given germination percentage. Another method calculates the average number of days required for radicle or plumule emergence as follows:

Mean days =

\[ \frac{N_1T_1 + N_2T_2 + \ldots + N_rT_r}{\text{total number of seeds germinating}} \]

Values are the numbers of seeds germinating within consecutive intervals of time; \( T \) values indicate the times between the beginning of the test and the end of the particular interval of measurement. Kotowski (79) has used the reciprocal of this formula multiplied by 100 to determine a coefficient of velocity. Gordon (54) has suggested the term germination resistance as the time (hours or days) to average germination, based on seeds that germinate.

Czabator (38) has suggested another measurement for seeds of woody perennials in which germination may be slow: the germination value (\( GV \)). It includes both the germination rate and percentage. To calculate \( GV \), a germination curve, as shown in Figure 6-4, must be obtained by periodic counts of radicle or plumule emergence. The important values on the curve are \( T \)—the point at which the germination rate begins to slow down—and \( G \)—the final germination percentage. These points divide the curve into two parts—a rapid phase and a slow phase. Peak value (\( PV \)) is the germination percentage at \( T \), divided by the days to reach that point. Mean daily germination (MDG) is the final germination percentage divided by number of days to reach final germination. For example:

\[ GV = PV \times MDG \]
\[ = \frac{68}{13} \times \frac{85}{34} \]
\[ = 5.2 \times 2.5 \]
\[ = 13.0 \]

DORMANCY: REGULATION OF GERMINATION

When a seed is separated from the plant, it invariably has primary dormancy (see Chap. 3). This not only prevents immediate germination but also regulates the time, conditions, and place that germination will occur. In nature, different kinds of primary dormancy have evolved to aid survival of the species (78, 118, 120, 131) by programming the time of germination for particularly favorable times in the annual seasonal cycle.

Secondary dormancy is a further survival mechanism that can be induced under unfavorable environmental conditions and may further delay the time that germination occurs. Knowl-
edge of the ecological characteristics of the natural
habitat of a species can aid in establishing treat-
ments to induce germination (102, 132).

In cultivation, domestication of seed-propa-
gated cultivars of many crop plants, such as grains
and vegetables, has undoubtedly included selec-
tion for sufficient primary dormancy to prevent
immediate germination of freshly harvested seed
but not enough to cause problems in propagation.
Dormancy facilitates storage, transport, and han-
dling. After-ripening changes take place with nor-
mal dry storage handling of most agricultural,
vegetable, and flower seed to allow germination
to proceed whenever the seeds are subjected to
normal germinating conditions. Problems can oc-
cur when seed testing is attempted on freshly har-
vested seeds. Seeds of some species are sensitive
to high-temperature and light conditions related
to seed dormancy (see p. 115). Many weed seeds
persist in soil due to either primary or secondary
dormancy and provide "seed banks" that pro-
duce extensive weed seed germination whenever
the soil is disturbed (19).

Practical problems occur with nursery propa-
gation of seeds of many tree and shrub species. 
These require specific treatments to overcome
dormancy by satisfying the requirements needed
to bring about germination (see Chaps. 18 and
19).

Kinds of Primary Seed Dormancy

Propagators of cultivated plants have long recog-
nized these germination-delaying phenomena and

CONCEPTS OF DORMANCY

Dormancy in a general sense has been de-
defined as "a temporary suspension of visible
growth of any plant structure containing a
meristem" (82). It includes growth cessation
due to both internal (physiological) and exter-
nal (environmental) factors. Seed technolo-
gists, however, have restricted seed dor-
mancy to internal conditions that prevent
germination after the seed is subjected to fa-
vorable environmental conditions (5). If ger-
mination occurs immediately upon exposure
to favorable conditions, the seed is said to be
quiescent.

A seed is unique in being a combination
of tissues of two plant generations, the em-
broyo (and endosperm) being the new genera-
tion, whereas the enclosing tissues are from
the parental generation. Seed dormancy is
more than a cessation of growth but may in-
clude the transition from an embryonic phase
of development to a juvenile seedling phase.
Consequently, the point of reference in
applying dormancy terminology to seeds is
the triggering of germination in the entire em-
broyo, including both root and shoot elonga-
tion.

A system of dormancy terminology has

been proposed (83) that could be applied to
any plant structure, including seeds. Table
6–1 lists the kinds of seed dormancy de-
scribed in this chapter and relates them to
this terminology.

Ecodormancy. Dormancy due to one or
more unsuitable factors of the environment
which are nonspecific in their effect. In seeds
this term is equivalent to "quiescence" (5,
19, 26, 67, 123).

Paradormancy. Dormancy due to physi-
cal factors or biochemical signals originating
external to the affected structure for the ini-
tial reaction, as in apical dominance or bud
scale effects. In the seed, the control would
come from any of the enclosing structures
surrounding the embryo, not restricted to
biochemical signals. This category could be
identified by prompt germination and normal
seedling growth following excision of the
embryo.

Endodormancy. Dormancy regulated by
physiological factors inside the affected
structure. (Rest period in buds would be an
example.) In seeds, this type is present if em-
broyo excision fails to produce either prompt
germination or normal seedling growth.


<table>
<thead>
<tr>
<th>Kind of Seed Dormancy</th>
<th>Description</th>
<th>Eco-dormancy</th>
<th>Para-dormancy</th>
<th>Endo-dormancy</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>Quiescence</td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>I. Nondormancy</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Physical</td>
<td>Seed coat</td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mechanical</td>
<td>Seed coat</td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inhibitor</td>
<td>Seed coat</td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morphological</td>
<td>Undeveloped embryo</td>
<td>x</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Physiological</td>
<td>Active membranes</td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thermodormancy</td>
<td>Active membranes</td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Photodormancy</td>
<td>Active membranes</td>
<td>x</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Intermediate</td>
<td>Combination</td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Embryo</td>
<td>Internal</td>
<td>x</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Double</td>
<td>Internal</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Various</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>II. Primary Dormancy</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Various</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>III. Secondary Dormancy</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

have learned to manipulate different kinds of seed dormancy through the adoption of appropriate pregermination and handling procedures discovered by trial and error (see Chap. 7).

Much scientific thought has gone into defining a uniform terminology for different kinds of seed dormancy. An historically early system for seeds was formulated by Crocker in 1916 (35, 36) who described seven kinds based primarily on treatments to overcome them. Subsequently, Nikolaeva (97) has defined a system based predominately upon physiological controls of dormancy. Atwater (6) has shown that morphological characteristics, including both seed morphology and types of seed covering, characteristic of taxonomic plant families could be associated with dormancy categories particularly significant in seed testing.

**Seed Coat Dormancy**

**Physical dormancy (seed coat dormancy).** Dormancy is produced by seed coverings that are impervious to water. This type can preserve the dry seed for many years, even at warm temperature. Germination can be induced by any method that can soften or scarify the covering (Fig. 6–5).

Physical dormancy is a genetic characteristic of certain plant families, including Leguminosae, Malvaceae, Cannaceae, Geraniaceae, Chenopodiaceae, Convolvulaceae, and Solanaceae. Among cultivated crops, hardseededness is found chiefly in the herbaceous legumes, including clover and alfalfa, as well as many woody legumes (Robinia, Acacia, Sophora, etc.). Hardseededness is also increased by environmental (dry) conditions during seed maturation, and environmental conditions during seed storage. Drying at high temperatures during ripening will increase hardseededness. Harvesting slightly immature seeds and preventing them from drying can reduce or overcome hardseededness in some cases.

Impermeability of the seed coat is due to a layer of palisade-like macrosclereid cells, especially thick-walled on their outer surfaces and coated with a layer of waxy, cuticular substances (103) (see Fig. 6–5). Disintegration of the “caps” of such cells, or mechanical stress separating the cells, may allow water to enter and produce germination (25, 87). In some legume species, the
point of attachment (hilum) of the seed acts as a one-way valve during ripening by opening to allow water to escape in a dry atmosphere but closing in a moist atmosphere to prevent water uptake (66). In *Albizia lophantha* (40) a small opening (strophiola) near the hilum is sealed with a cork-like plug, which can be dislodged with vigorous shaking or impaction (57) or by exposure to dry heat as in a fire (40).

In nature, impervious seed coats are softened by action of microorganisms in the soil during warm periods of the season or by passage through the digestive tracts of birds and mammals (36). They may be broken through mechanical abrasion, alternate freezing and thawing, and in some species by fire. In cultivation any method to break, soften, abrade, or remove the seed coverings is immediately effective (Chap. 7).

**Mechanical dormancy (hard seed coats).** Some seed enclosing structures, such as shells of walnut (36), pits of stone fruits (97), and stones of olive (32), are too strong to allow embryo expansion during germination. Water may be ab-
FIGURE 6-5 (cont.) Left top, middle, bottom: Liquid N₂ scarification shows cracked surfaces plus remnants of waxy surface. Right top, middle, bottom: Immersion in boiling water for 1 minute shows destruction of seed coats and separation of macrosclereid cells. Bar length (top left and right) = 100 μm; (middle left and right) = 10 μm; and (bottom left and right) = 5 μm. (Courtesy of Liu, Khatamian, and Fretz (87)).

sorbed but the difficulty arises in the cementing material that holds the dehiscent layers together, as shown in walnut. Softening primarily comes from soil microorganisms which are favored by nonsterile media and warm temperatures (36).

Chemical Dormancy
(or Inhibitor Dormancy)

Chemicals that accumulate in fruit and seed covering tissues during development and remain with the seed after harvest can be shown to act as germination inhibitors (49). 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 (45, 97). Some examples are the following:

1. Fleshy fruits, or juices from them, can strongly inhibit seed germination. This occurs in citrus, cucurbits, stone fruits, apples, pears, grapes, and tomatoes. Likewise, dry fruits and fruit coverings, such as the hulls of guayule, Penni-
setum ciliare, wheat, as well as the capsules of mustard (Brassica), can inhibit germination. Some of the substances associated with inhibition are various phenols, coumarin, and abscisic acid.

2. Specific seed germination inhibitors play a role in the ecology of certain desert plants (78, 128, 129). Inhibitors are leached out of the seeds by heavy soaking rains which would in turn provide sufficient soil moisture to ensure survival of the seedlings. Since a light rain shower is insufficient to cause leaching, such inhibiting substances have been referred to as "chemical rain gauges."

3. Dormancy in iris seeds is due to a water- and ether-soluble germination inhibitor in the endosperm, which can be leached from the seeds with water or avoided by embryo excision (4).

4. Inhibitors are described as causing the rudimentary and undeveloped embryo, described in morphological dormancy. Their effect must be counteracted before embryo development proceeds (6, 97).

Inhibitors have been found in the seeds of such families as Polygonaceae, Chenopodiaceae (Atriplex), Portulacaceae (Portulaca), and other species in which the embryo is peripherally located (see beet seed, Fig. 3–8). Likewise, seeds of a group of such families as Cruciferae (mustard), Linaceae (flax), Violaceae (violet), and Labiatae (Lavandula) have a thin seed coat with a mucilaginous inner layer that contains inhibitors (6).

**Morphological (Rudimentary and Undeveloped) Dormancy**

Dormancy occurs in some seeds in which the embryo is not fully developed at the time of seed dissemination. Enlargement of the embryo occurs after the seeds have imbibed water and before germination begins. The process of embryo enlargement is favored by a period of warm temperatures.

1. Atwater (6) has distinguished between two groups of embryos that are found in herbaceous flower crops. Seeds of some species have rudimentary embryos with little more than a proembryo embedded in a massive endosperm. These are found in various families, such as Ranunculaceae (anemone, ranunculus), Papaveraceae (poppy, Romneya), and Araliaceae (ginseng, fatsia). Germination-inhibiting chemicals also occur in the endosperm and become active at high temperatures. Effective aids for inducing germination include (a) exposure to temperatures of 15°C (59°F) or below, (b) exposure to alternating temperatures, and (c) treatment with chemical additives such as potassium nitrate or gibberellic acid.

A second category includes seeds with undeveloped embryos which are torpedo shaped and up to one-half the size of the seed cavity. Important families and species in this category include Umbelliferae (carrot), Ericaceae (rhododendron, heather), Primulaceae (cyclamen, primula), and Gentianaceae (gentian). Other conditions, such as semipermeability of the inner seed coats and internal germination inhibitors, may be involved. A temperature of about 20°C (68°F) favors germination, as does gibberellic acid treatment.

2. Certain temperate zone woody plants such as holly (Ilex) and snowberry (Symphoricarpus) have rudimentary embryos but, in addition, have other types of dormancy, such as hard seed coats and dormant embryos, which must be overcome (97) for germination to occur.

In seeds of some species, subsequent chilling is also required for germination after the warm embryo development period. Various temperate zone trees fall into this category, including Fraxinus (ash) and Euonymous species (97).

3. Various tropical species, many of which are monocots, have seeds with undeveloped embryos that require an extended period at high temperatures for germination to take place. For example, seeds of various palm species ordinarily require storage for several years to germinate, but this period can be reduced to three months by holding the seeds at temperatures of 38 to 40°C (100 to 104°F), or to 24 hours by excising the embryos and germinating them aseptically. Gibberellic acid (1000 ppm) has accelerated germination in palm seed, but a seed coat treatment is needed to assure penetration of the chemical (96). Other examples include Actinidia, whose seed requires two months' warmth, and Annona squamosa seed, which requires three months' warmth (97).

4. Orchids have both rudimentary embryos and undeveloped seeds. They are not considered dormant in the same sense as others in this cate-
Physiological Dormancy

This term refers to a general type of primary dormancy that exists in many, if not most, freshly harvested seeds of herbaceous plants. This type of dormancy is often transitory and tends to disappear during dry storage (5, 19, 92, 97, 117), so that it generally is gone before germination. Consequently, it is primarily a problem with seed-testing laboratories that need 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/or gibberellic acid (see p. 148).

For most cultivated cereals, grasses, vegetables, and flower crops, physiological dormancy may last for one to six months and disappears with dry storage during normal handling procedures. For many noncultivated plants physiological dormancy may not only last longer but can develop into secondary dormancy, particularly if the moist seeds are buried in the ground.

Physiologically dormant seeds tend to have more specific environmental requirements for germination than when they become nondormant. Freshly harvested seeds of cocklebur or amaranth, for example, germinate only at high temperatures, about 30°C (86°F). In freshly harvested seeds of other species, such as some cultivars of lettuce and celery, germination is inhibited at temperatures above 25°C (77°F). Such heat sensitivity is called thermodormancy (see p. 127). [This type has also been called relative dormancy by other authors (19).]

Seeds of many species that have temperature sensitivity also have light sensitivity (photodormancy). Seeds of some plants, including lettuce and many flower crops, require light to germinate, whereas others require darkness (see p. 128).

Control of physiological dormancy appears to reside in the semipermeability of the physiologically active seed coverings (inner seed coat, remnants of nucellus and/or endosperm, perisperm, or endosperm) which surround the embryo (50). These layers allow water uptake but apparently control other aspects which are not well understood.

A great deal of research has been done to determine the mechanism for the control of dormancy and germination in these seeds. Early research with cocklebur showed that the semipermeable membranes restricted gaseous exchange, limiting oxygen uptake and preventing carbon dioxide escape (50). Later experiments showed that the membranes also restricted the leaching of germination inhibitors from within the embryo which kept the embryo dormant (127). In lettuce, experiments have shown that the two-cell-layered endosperm is sufficiently resistant to prevent penetration by the dormant embryo (19). Current concepts are that germination is controlled through the interchange of (a) endogenous inhibitors and hormones, including gibberellins, cytokinin, and abscisic acid (see p. 119) and (b) specific environmental requirements, such as temperature (see p. 127) and light (see p. 129).

Intermediate Dormancy

Intermediate dormancy is a term used primarily with various conifer species whose seeds respond to chilling (see below) but do not have an absolute requirement (97, 117). Chilling greatly increases the rate, but seeds will eventually germinate. These seeds have a large storage tissue surrounding the embryo (see Fig. 3–8). The control of dormancy appears to be in the enclosing seed coverings (80, 97) since the embryo itself is capable of prompt germination if excised from the seed.

Physiologically Deep Dormancy (Embryo Dormancy)

Embryo dormancy involves controls within the embryo itself. It is characterized by a requirement for a period of one to three months' chilling while in an imbibed and aerated state. Dormant embryos are most common in seeds of trees and shrubs and some herbaceous plants of the temperate zone (36). Here seeds ripen in the fall, overwinter in the moist leaf litter on the ground, and germinate in the spring. Nursery propagators have known since early times that such seeds re-
quired moist-chilling (32, 84, 97, 123). 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 (see Chap. 
7).

Since germination in seeds with embryo dormancy is controlled by both the seed covers and 
endogenous conditions within the embryo, it represents a combination of both para- and endodormancy (82). Endodormancy appears to be biologically equivalent to the "rest period" of buds of temperate-zone plants. Evidence for seed cover control is that removal of the seed coats and other coverings can shorten the stratification requirement and sometimes induce immediate germination (Fig. 6-5). Evidence for a dormant embryo is that the excised embryo usually will not germinate normally and the seedling produced may be abnormal. The relative response is the basis for the "excised embryo" viability test (36, 97) (see p. 140). Responses include enlargement and greening of the cotyledons; short thickened radicle growth, no epicotyl development, or lack of normal root systems. Typically, unchilled excised embryos develop into physiological dwarfs (36, 32) (Fig. 6-6).

Biological changes that take place progressively within the seed during moist-chilling are included in the general term of after-ripening.

These require moisture, aeration, chilling temperature, and time. Many studies have been made of the gross changes occurring during the moist-chilling treatment without a clear understanding of the fundamental control process emerging.

**Moisture.** The dry dormant seed absorbs moisture by imbibition to around 50 percent (84, 97). In some seeds, a hard bony endocarp enclosing the seed reduces water uptake, provides inhibitors, and delays the initiation of after-ripening (45). Sometimes mechanically removing the covers, subjecting the seeds to warm moist nonsterile conditions prior to germination, leaching, and early harvest without drying prior to stratification, reduces stratification time. The seed moisture content should remain relatively constant during stratification. Dehydration stops the after-ripening process (59) and the seeds may revert to secondary dormancy (124). When the end of the chilling period is reached, the seeds absorb water rapidly (84), the seed coats "crack," and the radicle eventually emerges, sometimes even at low temperatures (see Fig. 6-13A). Drying at this stage can cause injury to the seed.

**Aeration.** The amount of oxygen needed is related to temperature (33). At high temperatures the moist seed coverings of dormant, imbibed seeds restrict oxygen uptake because of (a) low oxygen solubility in water, and (b) oxygen fixation by phenolic substances in the seed coats. At chilling temperatures, however, the embryo's oxygen requirement is low and oxygen is generally adequate. If the temperature is increased, the oxygen requirement of the embryo increases, the solubility of oxygen is less, and the amount fixed by the phenols increases.

**Temperature.** Temperature is the single most important factor controlling after-ripening of seeds with dormant embryos. The most effective temperature regimes for moist-chilling are similar to those during the winter and early spring of the natural environment of the species. Temperatures somewhat above freezing [2 to 7°C (35 to 45°F)] are generally most effective (i.e., shows fastest rate of after-ripening) with a slower rate at higher and lower temperatures with a minimum of -5°C (23°F) (112). Higher temperatures can

![FIGURE 6-6 Physiological dwarfing of epicotyls of almond seedlings. Left shows normal development.](image-url)
FIGURE 6–7 Effect of temperature during germination (radicle emergence) on both the rate and percentage of germination in apple seeds previously stratified at 3°C for 65 days. (Data from deHaas and Schander [39].)

slow the after-ripening of the most dormant seeds but can speed up the sprouting of those approaching germination (Fig. 6–7). Above a particular maximum temperature, known as the compensation temperature, secondary dormancy can develop (1, 110, 111, 113, 124). For apple, this point has been determined to be 17°C (62°F) (1), but it apparently varies with individual species (115) and different stages of after-ripening (116).

Toward the end of the after-ripening period, the maximum temperature for germination gradually increases and the minimum temperature gradually decreases. This period has been called postdormancy (93).

Physiological dwarfing in excised nonafter-ripened embryos has been shown to result from exposure of the apical meristem to warm germination temperatures (99). In peaches, temperatures of 23 to 27°C (73 to 81°F) and higher produced symptoms of physiological dwarfing, but at lower temperatures the seedlings grew normally. In almonds, exposing incompletely stratified seed to high temperatures subsequently induced physiological dwarfing in the seedling.

Pinching out the apex can circumvent dwarfing by forcing lateral growth from non-dwarfed lower nodes. Dwarfing has also been offset by exposing seedlings to long photoperiods or continuous light (32, 81), provided that this action is taken before the apical meristem becomes fully dormant. Repeated application of gibberellic acid has also overcome dwarfing (14, 15, 52). Some experiments have shown that systematic removal of the cotyledons from the dormant embryo can induce germination and overcome physiological dwarfing, suggesting the existence of endogenous inhibitors present within the cotyledons (19).

Time. The time required to after-ripen seeds with dormant embryos results from the interaction of (a) the genetic characteristics of the seed population (70, 71, 112, 131), (b) the conditions during seed development sometimes (123), (c) the environment of the seedbed, and (d) the management of seed handling. There is a correlation between the seed chilling requirements and the bud chilling requirements of the plants from which the seeds were taken (107). In studies with almond, a high quantitative correlation was shown between the mean of the seedling populations and the mean of both the seed and pollen parents (70) but a low correlation between the individual seed and the buds of the new plant coming from the embryo (71). This difference suggests that the dormancy involves both a genetic component within the embryo and a maternal component from the seed parent. As a result a great deal of variability in individual seed germination time can occur within a given seed lot and between different seed lots of the same species collected in different years and different locations.
Under controlled temperature conditions, germination curves show a characteristic pattern \((39, 110)\), illustrated in Fig. 6-7. In temperate climates under field conditions, the most effective regimes are a warm fall, cool wet winter, and a cool spring where soil temperatures gradually increase as the season advances. The concept of postdormancy is an adaptation to this pattern \((93)\). If premature periods of high temperatures occur in nature, secondary dormancy can prevent germination during a dry and possibly hot summer period. In nurseries these conditions can delay germination until the second spring.

**Epicotyl Dormancy**

Some seeds have separate after-ripening requirements for the radicle, hypocotyl, and epicotyl \((16, 36, 97)\). These species fall into two subgroups.

1. Seeds that initially germinate during a warm period of one to three months to produce root and hypocotyl growth but then require one to three months' chilling to enable the epicotyl to grow. This group includes various lily \((Lilium)\) species, *Viburnum* spp., peony \((Paeonia)\), black cohosh \((Cimifusa racemosa)\), and *Hepatica acutiloba*.

2. Seeds that require a chilling period to after-ripen the embryo, followed by a warm period for the root to grow, then a second cold period to stimulate shoot growth. In nature, such seeds require two full growing seasons to complete germination. Examples include *Trillium* and certain other native perennials of the temperate zone (see Chap. 19).

**Double Dormancy**

Double dormancy combines two (or more) kinds of dormancy, such as seed coat dormancy and a dormant embryo (some tree legumes), or a rudimentary embryo and a dormant embryo \((Ilex)\). To produce germination all blocking conditions must be eliminated in proper sequence. Seed coats must be modified to allow water to penetrate to the embryo; after-ripening of the embryo can then take place. Warm followed by cold stratification generally overcomes these situations.

This type of dormancy is characteristic of species of trees and shrubs in families having seeds with hard seed coats but whose plants grow in cold winter areas. In nature, various agents of the environment—those that affect physical dormancy—soften the seed coat when the seed falls to the ground, then the seeds are chilled as they overwinter.

**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 if other environmental conditions are not favorable \((19, 35, 68, 75)\). These conditions can include unfavorably high temperatures, temperatures too low, prolonged darkness \((skotodormancy)\), prolonged white light \((photodormancy)\), prolonged far-red light, water stress, and anoxia. These conditions are particularly involved in the seasonal rhythms and prolonged survival of weed seeds in soil \((19)\).

Induction of secondary dormancy is illustrated by experiments with freshly-harvested seeds of lettuce \((75)\). If germinated at 25°C \((77°F)\) the seeds require light, but if imbibed with water for two days in the dark, excised embryos germinate immediately, illustrating that only primary dormancy was present. If imbibition continues for as long as eight days, however, excised embryos will not germinate since they have then 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 gibberelic acid.

Secondary dormancy can come into play in some instances in cultivated crops but prolonged dry storage may prevent its occurrence. Seeds with a dormant embryo undergoing moist-chilling may be affected if shifted to high temperatures too quickly (see p. 145). The term could apply to hardseededness that could develop in storage in seeds of some species, such as beans and other legumes.

**Control of Dormancy and Germination**

Much experimental evidence supports the concept that specific endogenous growth promoting
and inhibiting compounds are involved directly in control of seed development, dormancy, and germination (19, 21, 73, 84, 101). Evidence for hormone involvement comes from correlations of hormone concentration with specific developmental stages, effects of applied hormones, and the relationship of hormones to metabolic activities.

**Specific Germination Hormones**

**Gibberellins.** Gibberellins (GA) comprise the class of hormones most directly implicated in the control and promotion of seed germination (see Fig. 6–8). While there are many molecular variations of gibberellin, the one most widely used experimentally and commercially is gibberellic acid (GA₃), but GA₄,⁷ is also active. These compounds occur at relatively high concentrations in developing seeds but usually drop to a lower level in mature dormant seeds, particularly in dicotyledonous plants. Applied gibberellins can relieve certain types of dormancy, including physiological dormancy, photodormancy, and thermidormancy.

Gibberellins appear to play a role in two different stages of germination. One occurs at the initial enzyme induction in their transcription from the chromosomes. The second is at Stage III in the activation of reserve food mobilizing systems. In barley, for instance, gibberellins appear in the embryo with imbibition, are translocated to the three- to four-cell-layered aleurone surrounding the endosperm and induce *de novo* alpha-amylase enzyme synthesis. The alpha-amylase enzyme then moves to the endosperm. Starch is converted to sugar, which is then translocated to the growing points to provide energy for seedling development.

**Abscisic acid (ABA).** This naturally occurring compound is an important growth-regulating compound not only in seed germination but in plant growth in general (125, 126). ABA appears to play a role in preventing "precocious germination" of the developing embryo in the ovule (51, 69). High inhibitor levels have been considered responsible for the lack of development in rudimentary embryos (6) (see p. 114).

ABA tends to increase with maturation of the fruit and may prevent vivipary and induce primary dormancy. It has been isolated from the seed coats of dormant peach, walnut, apple, rose, and plum, but it decreases during stratification (Fig. 6–13).

![Figure 6–8 Chemical structure of plant growth regulators involved in germination.](attachment:image.png)

**FIGURE 6–8** Chemical structure of plant growth regulators involved in germination.
Application of ABA can inhibit germination of nondormant seed and offset the effects of applied gibberellic acid. In general, inhibition is temporary and disappears when seeds are shifted to an ABA-free solution.

**Cytokinins.** These naturally occurring compounds (119) have the basic chemical structure of an N8-substituted adenine (see Fig. 6–8). Synthetic cytokinins available for experimental use include benzyladenine, kinetin, and others. In addition, cytokinin activity is shown by such compounds as thiourea and diphénylurea (119) (see also p. 148).

Cytokinin activity tends to be high in developing fruits and seeds, but decreases and becomes difficult to detect as the seeds mature. In seed germination, cytokinin is believed to play the effect of inhibitors, notably ABA. It has been described, therefore, as playing a “permissive” role in germination in allowing gibberellic acid to function (73). It is believed to be active, therefore, at a different germination stage than gibberellins.

**Ethylene.** Ethylene gas (72) is an important, naturally occurring hormone involved in many aspects of plant growth. Response to ethylene treatment of dormant seeds of snowberry (Symphoricarpos), honeysuckle (Lonicera), and similar species, as well as seeds of corn and other cereals, was demonstrated many years ago. Ethylene production from germinating bean and pea seed was shown in 1935. Later work demonstrated that ethylene is a natural germination-promoting agent for certain kinds of seeds. Ethylene apparently has a limited role in seed germination but has been shown to stimulate germination in subterranean clover (Trifolium subterraneum) (48), Virginia-type peanut (Arachis hypogaea), and witchweed (Striga asiatica) (47).

**Other compounds.** Certain other compounds are known to stimulate seed germination, but their role is not clear. Use of potassium nitrate has been an important seed treatment in seed-testing laboratories for many years without a good explanation for its action. Thiourea overcomes certain types of dormancy, such as the seed coat inhibiting effect of deep embryo-dormant Prunus seeds as well as the high-temperature inhibition of lettuce seeds (119). The effect of thiourea may be due to its cytokinin activity in overcoming inhibition. Two other naturally occurring substances, fusiconic and cotylenic (74), have been reported to mimic the combination of GA plus cytokinin.

**Interactions of Hormones and Dormancy**

Dormancy may involve interactions among specific hormones, as described in the following experimental examples.

1. **Rudimentary embryos** (see p. 114) (Fig. 3–8A) (60, 61). Imbibed seeds of Trollius ledebourii have inhibitors in the testa which prevent expansion of the embryo (61) (Fig. 6–9). Germination begins with rupture of the seed coverings, enlargement of the embryo, radicle growth, and digestion of proteins in the endosperm. This inhibitory effect can be removed by leaching and/or testa removal or overcome by application of gibberellin.

2. **Physiological dormancy.** Figures 6–10 and 6–11 show the interaction of exogenous hormones with light (photodormancy) (73, 76) and temperature (thermodormancy) (114) with ‘Grand Rapids’ lettuce seed. GA promotes germination, ABA inhibits it, and cytokinin counteracts the effect of the ABA. The relationship is an example of a “permissive” effect of cytokinin to allow GA stimulation of germination by offsetting ABA inhibition. Figure 6–12 illustrates dormancy control in cocklebur (76).

3. **Embryo dormancy.** The hormonal changes that occur during the two to three months of chilling of seeds with dormant embryos have received much attention.

In the peach (Prunus persica), two separate aspects of germination are affected: (a) initiation of radicle elongation, and (b) epicotyl elongation (134, 135). Figure 6–13 combines data from a number of experiments to show a three-phase pattern of seed response to chilling at 5°C (41°F). During phase 1 (0 to 30 days) no germination response occurs in intact seeds during chilling, after transfer to 25°C (77°F) at weekly intervals, or if presoaked with GA. In phase 2 (30 to 45 days) seeds being chilled do not germinate but seeds transferred to 25°C (77°F) show increasing ger-
FIGURE 6-9 Germination in *Trollius* (Ranunculaceae family), an example of a seed with a rudimentary embryo. Germination in a dormant seed (a) is preceded by dissolution of the enclosing seed covering (b) and elongation of the embryo (c). These changes take place slowly (60 days) during germination on filter paper in a germinator. If the seeds are treated with GA, germination time in the germinator was shortened but not all seeds germinated. If the testae were removed (TR), germination was complete within 30 days. However, if the seeds were presoaked for 11 days and testae removed, germination was complete within 10 days. If the seeds with the last treatment were also treated with GA, germination was complete within five days. The results are interpreted that endogenous inhibitors were present in the testa and embryo to delay germination.

Hormone concentrations are correlated to the responses described. Freshly harvested peach seed (42, 86), as well as other species, including walnut (89), plum (85), apple (111), and hazelnut (133), have a high concentration of ABA in both testae and a lesser amount in the cotyledons. ABA concentration drops to near zero during phase 1. Treatment of excised embryos with ABA prevents germination. Physical contact of the testa with the embryo axis has been sufficient to inhibit germination and/or to produce dwarfing (60, 85). Experimental treatment of intact peach seeds with a
cytokinin benzylaminopurine (BAP) has overcome the inhibiting effect of the testa and allowed germination to occur (108).

The concentration of gibberellin-like compounds is low in phase 1 in intact seeds held at chilling temperatures (first 30 days) but shows a sharp increase in phase 2, indicating that the ability to synthesize gibberellins is either present (53) or there is a change from an inactive form to a free form [as shown in apple (20)]. Introduction of an inhibitor of gibberellin synthesis (paclorbidazole) at the beginning of phase 2 decreased gibberellin synthesis sharply but only slightly decreased the germination percentage. Epicotyl and seedling elongation was strongly inhibited, indicating a separation between the radical and epicotyl response during chilling.

These results support the concept that inhibitors (undoubtedly ABA) are present in the testa as well as the cotyledons in the dormant seed. These disappear during the early stages of dormancy (or are neutralized by cytokinins). Gibberellins are either synthesized at the chilling temperatures or are converted to an available (or unbound form), allowing radicle emergence (germination) to take place at warmer temperatures (27, 91). Epicotyl elongation is a more localized phenomenon which either has a higher threshold for gibberellin or involves a different control system.

Research with filbert (Corylus avellana) seeds has illustrated separation of growth-inhibiting and growth-promoting hormonal systems in control of germination. At the time of ripening, the intact
FIGURE 6-11 Hormonal effects on high-temperature dormancy 'Grand Rapids' lettuce seed. Seed pre-soaked for 24 hours at 20°C overcame thermodormancy to allow germination to proceed during subsequent exposure to 35°C (a). Nonpresoaked seed remained dormant at high temperature (b), but kinetin removed most of the dormancy (c). Ethylene had limited but significant effect without (d) or with kinetin (e). (Redrawn from Sharples (114).)

- Kinetin
+ Kinetin

FIGURE 6-12 Germination of cocklebur (Xanthium). Two buds are shown at A, each of which contains two seeds (B and C); the smaller one is dormant but the other is not. Early experiments showed that low permeability to gases was a dormancy inducing factor. Later experiments (127) showed that the smaller, dormant, seed contains two water-insoluble inhibitors that prevent germination. If these are removed by leaching, or if the seed is subjected to high oxygen pressure, then germination will occur. The two seeds also differ in seed coat strength and the germinating forces required to rupture them. Treatment with kinetin or ethylene (74) will stimulate germination of both seeds, while abscisic acid will inhibit it. (From Khan et al. (76.).)

ENVIRONMENTAL FACTORS AFFECTING SEED GERMINATION

Water

Water content is a major controlling factor programming the embryonic phase to the juvenile seedling phase, controlling seed longevity (Chap. 5), initiating germination, and ensuring the survival and health of the seedling. During storage it
FIGURE 6–13 (A) Germination trends during stratification of peach (53). Germination was low in imbibed seed held continuously at warm temperatures (i.e., 20°C (77°F)), but germination began to occur rapidly after 55 days in seed held continuously at cool temperatures. When stratified seed was shifted to warm termination temperatures, sprouting began to occur at about 30 days with increasing amounts with increasing stratification time.

(cont.)
is convenient to consider water on the fresh weight basis (water content/fresh weight). During germination it may be convenient to use the dry weight basis (water content/dry weight of seed).

**Water Potential**

The absorptive power of the dry seed (19) during stage 1 is measured by its water potential, which in a dry seed can be as low as $-100$ MPa. Negative potential comes from the matric potential (i.e., colloidal structure of the embryo, storage areas, and seed coverings) and the osmotic potential (solute concentration) of the living cells of the seeds. Opposed to these are the pressure (turgor) potential of the cell wall, which has a positive potential. Water moves into the seed following a gradient from high (outside the seed) to low potential (inside the seed).

Water movement has been measured in units of barometric pressure called a bar, but later usage is for the term "megapascal (MPa)," where $-1$ MPa = $-10$ bar. Pure water equals 0, whereas water with solutes present has a negative potential. Water moves from high potential (least negative) to low potential (most negative).

The rate of water movement into the seed is also dependent on similar properties of the germination medium. The matric potential measures the ability of the water to move by capillarity through the pores of the soil or other germination medium to the seed. Rate of movement depends upon (a) the pore structure (texture) of the germo-

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An initial GA soak increased the germination rate. (Paclobutrazol, an inhibitor of gibberellin synthesis, applied to seeds at 28 days decreased final germination percentage by 36, 25, and 27 if shifted to the warm temperature after 7, 14, and 28 days, respectively, of additional chilling. Elongation growth of the seedling was severely curtailed by paclobutrazol.) (8) Correlations to hormone concentrations in seeds. Many separate studies show that ABA is initially high in the dormant seeds, but the levels drop sharply within the first 30 days. Data from Lin and Boe (85), Lipe and Crane (86), and others is superimposed on the graph. In the peach study (53), GA concentration was low during the first 30 days but increased dramatically after 30 to 45 days of stratification. Paclobutrazol sharply reduced GA concentration when applied at 28 and 35 days. (Redrawn from Gianfagna and Rachmiel (53).)
nation medium, (b) the soil packing, and (c) the closeness and distribution of the soil–seed contact. As moisture is removed from the soil by the imbibing seed the area nearest the seed becomes dry and must be replenished by water in pores farther away. Consequently, a firm, fine-textured seedbed closely compacted to the seed is important in maintaining a uniform moisture supply.

Osmotic potential in the soil solution depends upon the presence of solutes (salts). Excess soluble salts (high salinity) in the germination medium may exert strong negative pressure (exosmosis) and counterbalance the osmotic pressure in the seeds. Salts may also produce specific toxic effects. These may inhibit germination and reduce seedling stands (7). Such salts originate in the soil and other materials used in the germination medium, the irrigation water, or excessive fertilization. Since the effects of salinity become more acute when the moisture supply is low and the concentration of salts thereby increased, it is particularly important to maintain a high moisture supply in the seedbed, where the possibility of high salinity exists. Surface evaporation from subirrigated beds can result in the accumulation of salts at the soil surface even under conditions in which salinity would not be expected. Planting seeds several inches below the top edge of a sloping seedbed can minimize this hazard (18).

Water stress can reduce the germination percentage (44, 58). Most kinds of seed germinate equally well over the range of available soil moisture, from field capacity (FC) to permanent wilting percentage (PWP) (7). Germination of some seeds, particularly those with dormancy problems (e.g., beet, lettuce, endive, or celery), is inhibited as moisture levels are decreased. Such seeds apparently contain inhibitors and require leaching. Seeds of other species (e.g., spinach), when exposed to excess water, produce extensive mucilage that restricts oxygen supply to the embryo (64); an inhibitor is also present (6). In these cases germination improves with less moisture.

Moisture stress strongly reduces the rate of seedling emergence from a seedbed. This decline in emergence rate occurs as the available moisture decreases to a level approximately halfway through the range from FC to PWP (Fig. 6–15) (7, 44, 58). Once the seed germinates and the radicle emerges, the water supply to the seedling depends on the ability of the root system to grow into the germination medium and the ability of the new roots to absorb water.

** Priming and Seed Soaking 

This process refers to procedures designed to initiate germination before planting in order to shorten the time of emergence, improve the uniformity of stand, and circumvent some adverse conditions in the seedbed.

**Soaking.** Seeds are sometimes soaked in water before planting to speed up germination. Seeds of most herbaceous species could benefit

![FIGURE 6–15 Effect of different amounts of available soil moisture on the germination (emergence) of 'Sweet Spanish' onion seed in Pachappa fine sandy loam. (From Ayres (7.)](attachment:image.png)
from eight hours of soaking but may be injured by soaking periods of 24 hours or more. Large seeds are particularly vulnerable to prolonged soaking (98). Excess water may be trapped between cotyledons and suffocate the embryo (64). Harmful results have been attributed to the effects of microorganisms and to a reduced oxygen supply (12, 13). If soaking is to be prolonged, the water should be changed at least once every 24 hours. Dormant seeds of woody plants can be reached for longer periods without injury (98).

Fluid drilling (55, 109). In this process, seeds are pregerminated under controlled conditions. They are then planted with special machines to protect the seed from drying and injury. These seeds may be mixed in special gels (see p. 79).

Osmotic priming (osmoconditioning). Osmotic priming uses a pretreatment with an external high osmotic solution to decrease the osmotic potential within the seed. This allows metabolic activities leading to germination but prevents or delays the emergence of the radicle (22, 28, 64, 74, 77). An inert compound, polyethylene glycol (PEG 6000) is usually used, but some systems use salt solutions of NaCl or KNO₃, although these may be toxic to some kinds of seeds (24).

**Temperature**

Temperature is, perhaps, the most important environmental factor that regulates the timing of germination, partly due to dormancy control and partly due to climate adaptation. Temperature control is also essential in subsequent seedling growth. Dry, uninjured seeds can withstand extremes of temperature. For disease control, seeds can be placed in boiling water for short periods without killing them. In nature, frost fires are often effective in overcoming dormancy without damaging the seeds.

### Effects on Germination

Temperature affects both germination percentage and germination rate (79). Germination rate is invariably low at low temperature but increases gradually as temperature rises, similar to a chemical rate-reaction curve (78). Above an optimum level, where the rate is most rapid, a decline occurs as the temperatures approach a lethal limit where the seed is injured.

Germination percentage, unlike the germination rate, may remain relatively constant, at least over the middle part of the temperature range, if sufficient time is allowed for germination to occur.

Three temperature points (minimum, optimum, and maximum), varying with the species, are usually designated for seed germination (46). Minimum is the lowest temperature for effective germination. Maximum is the highest temperature at which germination occurs. Above this, the seed either is injured or goes dormant. Optimum temperatures for seed germination fall within the range at which the largest percentage of seedlings are produced at the highest rate. The optimum for nondormant seeds of most plants is between 25 and 30°C (77 and 86°F).

Seeds of different species, whether cultivated or native, can be categorized into temperature requirement groups. These are related to their climatic origin:

**Cool-temperature tolerant.** Seeds of many kinds of plants, mostly native to temperate zones, will germinate over a wide temperature range from about 4.5°C (40°F) (or sometimes near freezing) up to the lethal limit—from 30°C (86°F) to about 40°C (104°F). The optimum germination temperature is usually about 24 to 30°C (77 to 86°F). Examples include broccoli, carrot, cabbage, alyssum, and others.

**Cool-temperature requiring.** Seeds of some cool-season species and cultivars adapted to a Mediterranean climate require low temperatures and fail to germinate at temperatures higher than about 25°C (77°F). Species of this group tend to be winter annuals in which germination is prevented in the hot summer, but takes place in the cool fall when winter rains commence. This category involves thermodormancy (also called relative dormancy) (19) (see p. 115), which is present in many species with physiologically dormant seeds. It tends to disappear with after-ripening at dry
storage. Examples include various vegetables, such as celery, lettuce, and onion, as well as some flower seed—coleus, cyclamen, freesia, primula, delphinium, and others (6).

**Warm-temperature requiring.** Seeds of another broad group fail to germinate below about 10°C (50°F) (asparagus, sweet corn, and tomato) or 15°C (60°F) beans, eggplant, pepper, and cucurbits). These species originated primarily in subtropical or tropical regions. Other species, such as lima bean, cotton, soybean, and sorghum, are also susceptible to “chilling injury” when exposed to temperatures of 10 to 15°C (50 to 60°F) during initial imbibition. Planting in a cold soil can injure the embryo axis and result in abnormal seedlings (62, 100).

**Alternating temperatures.** Fluctuating day-night temperatures give better results than constant temperatures for both seed germination and seedling growth. Use of fluctuating temperatures is a standard practice in seed-testing laboratories, even for seeds not requiring it. The alternation should be a 10°C (18°F) difference (122). This requirement is particularly important with dormant, freshly harvested seeds (3). Seeds of a few species will not germinate at all at constant temperatures. It has been suggested that one of the reasons imbibed seeds deep in the soil do not germinate is that soil temperature fluctuations disappear with increasing soil depth (102).

**Effects on Seedling Growth**

The optimum temperature may shift after germination begins since seedling growth tends to have different temperature requirements than seed germination. In the nursery or laboratory the usual practice is to shift the seedlings to a somewhat lower temperature regime following germination in order to prepare the plants for transplanting and to reduce disease problems in the seed bed.

If seeds are germinated and the seedlings grown at high temperatures, it is important that other environmental conditions be favorable. Plants should have increased light, preferably long photoperiods, adequate fertilization, and sterile conditions to eliminate disease pathogens. Increased carbon dioxide is also a useful component of this system.

**Aeration**

Exchange of gases between the germination medium and the embryo is essential for rapid and uniform germination. Oxygen (O₂) is essential for the respiratory processes in the germinating seed. Oxygen uptake can be measured shortly after imbibition of water begins. Rate of oxygen uptake is an indicator of germination progress and has been suggested as a measure of seed vigor (79). In general, O₂ uptake is proportional to the amount of metabolic activity taking place.

Oxygen supply is limited where there is excessive water in the soil medium. Poorly drained outdoor seed beds, particularly after heavy rains or irrigation, can have the pore spaces of the soil so filled with water that little oxygen is available to the seeds. The amount of oxygen in the germination medium is affected by its low solubility in water and its slow diffusability into the medium. Thus, gaseous exchange between the germination medium and the atmosphere, where the O₂ concentration is 20 percent, is reduced significantly by soil depth and, in particular, by a hard crust on the surface, which can limit oxygen diffusion (58).

Carbon dioxide (CO₂) is a product of respiration and under conditions of poor aeration can accumulate in the soil. At lower soil depths increased CO₂ may inhibit germination to some extent but probably plays a minor role, if any, in maintaining dormancy. In fact, high levels of CO₂ can be effective in overcoming dormancy in some seeds (78).

Seeds of different species vary in their ability to germinate at very low oxygen levels, as occurs under water (94, 95). Seeds of some water plants germinate readily under water, with germination inhibited in air. Rice seeds can germinate in a shallow layer of water. At low oxygen levels, rice seedlings, however, develop differently than those of other monocots. Shoot development is stimulated and the plumule grows to extend up through the water into the air; root growth is suppressed.
and poor anchorage results unless the water layer is drained away (30).

Light

Light has been recognized since the mid-nineteenth century as a germination-controlling factor (37). Recent research demonstrates that light acts in both dormancy induction and release and is a mechanism that adapts plants to specific niches in the environment often interacting with temperature. Light can involve both quality (wavelength) and photoperiod (duration).

Light is recognized to be a factor in the following situations:

1. Certain epiphytic plants, such as mistletoe (Viscum album) and strangling fig (Ficus aurea), have an absolute requirement for light and lose viability in a few weeks without it.

2. Most of the light-sensitive species fall into the category of physiological dormancy (including most grasses, various herbaceous vegetable and flower species, and various weed and native species). Light-sensitive seeds are characterized by being small in size, in which a shallow depth of planting would be an important factor favoring survival. Otherwise, if covered too deeply, the epicotyl may not penetrate the soil. Some important flower crops include aliyssum, begonia, calceolaria, coleus, Kalanchoe, primrose, and Sanpaulia (10).

3. Many conifer seeds with intermediate dormancy have light sensitivity (see Table 7-1).

4. Germination is inhibited by light in a small number of species, such as Phacelia, Nigella, Allium, Amaranthus, and Phlox. Some of these are desert plants where survival would be enhanced if the seeds were located at greater depths, where adequate moisture might be assured. Some flower crops are listed as dark requiring, including calendula, delphinium, pansy, annual phlox, and annual verbena (10).

5. Photoperiodism affects seeds of some woody plants as eastern hemlock (Tsuga canadensis) (115) and birch (19).

Light Quality

The basic mechanism of light sensitivity in seeds involves a photochemically reactive pigment called phytochrome, widely present in plants (19, 117). Exposure of the imbibed seed to red light (660 to 760 nm) causes the phytochrome to change to phytochrome (P) (or P), which stimulates germination. Exposure of the seed to far-red light (760 to 800 nm) causes a change to the alternate form (P), which inhibits germination. Both of these changes are instantaneous and can be repeated indefinitely, the last treatment being the one that is effective. In darkness a slow change to P occurs and prevents germination.

The membranes of the seed coat and/or the endosperm appear to act as the light sensors; if removed, the light control disappears. A light requirement can be offset by cool temperatures and sometimes by alternating temperatures. The control mechanism is complex and involves both (a) an initial physical reaction utilizing lower than physiological moisture levels, and (b) a physiological reaction requiring full imbibition and linkage to the hormonal regulation of the seed. Treatments with hormones can offset the light effect, as illustrated in Figs. 6-10 and 6-11.

Use of artificial lighting should take into account the potential effect of rays of particular wavelengths (19). White fluorescent lamps tend to be rich in the red rays and favorable to germination, whereas incandescent lamps tend to be rich in the infrared (far-red) rays and could result in dormancy.

In nature. The light quality reaching the seed can have an impact even during development. Green fruits transmit light rich in infrared rays, which can induce dormancy in the seeds as they mature (19). Experiments have shown that seeds of Arabidopsis are dormant if the plant is exposed to incandescent light before harvest and nondormant if fluorescent lights are used.

Furthermore, seeds of some plants (Chenopodium album) are dormant if plants are exposed to long days and nondormant if exposed to short days (19). In natural sunlight, red wavelengths dominate over far-red at a ratio of 2:1, so that the phytochrome tends to remain in the active P form. Under a foliage canopy, far-red is dominant.
and the red/far-red ratio may be as low as 0.12:1.00 to 0.70:1.00, which can inhibit seed germination (102). Red light penetrates less deeply into the soil than far-red, so that the red/far-red ratio becomes lower with depth until eventually darkness is complete (118). Imbibed lightsensitive seeds buried in the soil will remain dormant until such time as the soil is cultivated or disturbed so as to expose them to light. Similarly, seedling survival is not favored if the seed germinates in close proximity to other plants, where there would be intense competition for light, nutrients, and water by the already established plant population.

In cultivation. Light sensitivity in cultivated cultivars is primarily a property of freshly harvested, physiologically dormant seeds and tends to disappear during after-ripening in dry storage as these seeds lose their primary dormancy. Consequently, light sensitivity is a problem encountered mainly in seed-testing laboratories for most cultivated crops. Light is a standard aspect of the test. Nevertheless, light exposure may be beneficial for some cultivars as lettuce as well as some flower seeds (10) and conifers (111).

Light sensitivity can be induced in secondary dormancy by exposing imbibed nonsensitive seeds to conditions inhibiting germination, such as high temperature, high osmotic pressure, or germination-inhibiting gases (130). Light requirements should be met in seed-priming procedures.

Light and Seedling Growth

Light of a relatively high intensity is desirable to produce sturdy, vigorous plants, particularly if transplanting is involved. Low light intensity results in etiolation and reduced photosynthesis and poor seedling survival if transplanted.

High light intensity, on the other hand, often results in high temperatures that produce heat injury to the seedling, particularly at the soil level, in a manner resembling “damping-off” fungi attacks. Shading is desirable for many kinds of plants during their early seedling growth out-of-doors to avoid heat injury. Use of supplementary artificial light is described in Chap. 2.

Disease Control during Seed Germination

The control of disease during seed germination is one of the most important tasks of the propagator. The most universally destructive pathogens are those resulting in “damping-off,” which may cause serious loss of seeds, seedlings, and young plants (9). In addition, there are a number of fungous, virus, and bacterial diseases that are seedborne and may infect certain plants (8). In such cases, specific methods of control are required during propagation. (See the discussion of sanitation in Chap. 2, p. 37.)

Damping-Off

Damping-off is a term long used to describe the death of small seedlings resulting from attacks by certain fungi, primarily Pythium ultimum and Rhizoctonia solani, although other fungi—for example, Botrytis cinerea and Phytophthora spp.—may also be involved. Mycelia from these organisms occur in soil, in infected plant tissues, or on seeds, from which they contaminate clean soil and infect clean plants. Pythium and Phytophthora produce spores that are moved about in water.

The environmental conditions prevailing during the germination period will affect the growth rate of both the attacking fungi and the seedling. For instance, the optimum temperature for the growth of Pythium ultimum and Rhizoctonia solani is between approximately 20 to 30°C (68 and 86°F), with a decrease in activity at both higher and lower temperatures. Seeds that have a high minimum temperature for germination (warm-season plants) are particularly susceptible to damping-off, because at lower or intermediate temperatures (less than 23°C or 75°F) their growth rate is low at a time when the activity of the fungi is high. At high temperatures, not only do the seeds germinate faster, but also the activity of the fungi is less. Field planting of such seeds should be delayed until the soil is warm. On the other hand, seeds of cool-season plants germinate (although slowly) at temperatures of less than 13°C (55°F), but since there is little or no activity of the fungi, they can escape the effects of damping-off. As the temperature increases, their susceptibility increases, because the activity of the fungi is relatively greater than that of the seedling.
The control of damping-off involves two separate procedures: (a) the complete elimination of the pathogens during propagation, and (b) the control of plant growth and environmental conditions, which will minimize the effects of damping-off or give temporary control until the seedlings have passed their initial vulnerable stages of growth.

If damping-off begins after seedlings are growing, it may sometimes be controlled by treating that area of the medium with a fungicide. The ability to control attacks depends on their severity and on the modifying environmental conditions (see Chap. 2).

Symptoms resembling damping-off are also produced by certain unfavorable environmental conditions in the seedbed. Drying, high soil temperatures, or high concentrations of salts (see Fig. 6-16) in the upper layers of the germination medium can cause injuries to the tender stems of the seedlings near the ground level. The collapsed stem tissues have the appearance of being "burned off." These symptoms may be confused with those caused by pathogens. Damping-off fungi can grow in concentrations of soil solutes high enough to inhibit the growth of seedlings. Where salts accumulate in the germination medium, damping-off can thus be particularly serious.

REFERENCES


123. Vilters, T. A. 1972. Seed dormancy. In Seed bi-


SUPPLEMENTARY READING


