12 Seeding and Seedling Establishment

Many crops begin the production cycle as a seed. Some crops are directly planted in the production field while others are started in a more protected environment such as a greenhouse, high tunnel or cold frame. In all cases, a productive crop must begin from viable, pure, high quality seed. While no standardized international laws to ensure that only high quality, true-to-name seed is sold to growers, many countries have laws regulating seed commerce. Within these laws, issues of seed purity, viability and other measures of quality are addressed. Since it would be impossible to examine all the seed laws in various countries, this section will be limited to a discussion of seed quality issues.

Seed Viability

The most widely accepted measure of seed quality is viability which is measured by testing germination. General rules for seed testing have been adopted by many organizations and usually include at least the following:

1. Four 100 seed samples should be tested for each sample.
2. A suitable substrate such as blotters, towels, sand, etc. should be used as a germination medium.
3. Depending on the test species, seed should be germinated at 20/30°C night/day temperature or 20°C or 15°C constant temperature for a specific duration.
4. Light conditions for germination are also species dependent, as is KNO_3 treatment.
5. Some seeds may need pre-chilling for a specific number of days at 5 or 10°C.
6. Some seeds (onions (*Allium cepa*), asparagus (*Asparagus officinalis*), carrots (*Daucus carota*), buttercups (*Ranunculus*), poppies (*Papaver*), columbine (*Aquilegia*)) may need to mature before testing to allow embryos to complete development.
7. Normal seedling status is based on an accepted definition for the species as well as published drawings for comparison.

A germination test does not totally express viability. It merely estimates the percentage of seeds capable of growing under the prescribed conditions. Some seeds of the lot may be alive but still dormant. To clarify the viability/germination/dormancy status of a seed lot, particularly species that exhibit strong seed endodormancy or to estimate viability alone, seed technologists use the tetrazolium (TZ) test (Peters, 2000).

Imbibed seeds are soaked in a solution of 2,3,5-triphenyl tetrazolium chloride (TTC) dissolved in water. In some species, seeds are cut or seed coats removed to facilitate testing. Living tissues of the seed produce hydrogen (H^+) ions that convert the TTC molecules to an insoluble red dye called formazan. Dyed tissue indicates living, viable tissue. Results are ready in a few hours or a day or two, depending on species.

The percentage viability is indicated by the percentage of seeds exhibiting a red color. When coupled with a standardized germination test, an estimate of the percentage of dormant seeds in the lot can be estimated by subtracting the percentage germination from the percentage viable seed obtained with the TZ test.

The main drawback of the TZ test is that it is more labor intensive than a simple germination test. Additionally, most seed laws do not allow a TZ test as a substitute for a standard germination test.

Seed Purity

Purity is an important attribute of any seed sample. The purity of a seed lot describes its physical composition, verifying that it is the species in question and describing any other crop seed, weed seed, and noxious weed seeds that might be in the sample. It also identifies soil, insects, plant material, and any

other foreign material that might have contaminated the sample. Purity analysis also provides a measure of confidence to the grower that what they have purchased is true to name and unadulterated.

Identification of the amount of pure live seed (PLS) in the sample allows a grower to adjust seeding rates for maximum productivity and utilization of land.

The purity test examines 2500 seeds to establish purity and 25,000 seeds to estimate noxious weed contamination. The sample is examined by hand and sorted into its component parts: (i) pure seed; (ii) other crop seed; (iii) weed seed including seeds, florets, bulblets, tubers or sporocarps of plants normally considered weeds; and (iv) inert matter. Noxious weeds vary from region to region and are categorized as restricted or prohibited. The presence of prohibited noxious weeds renders the entire lot unfit for sale. Restricted weeds found must be listed on the seed label.

Seed Purity and GMOs

As more and more growers utilize genetically modified organisms (GMO) as their choice of seed, conventional and organic growers must be given a mechanism for ensuring that their crops are not contaminated with GMOs. The 'unavoidable' contamination of normal seed lots with GMO seed is called adventitious or technically unavoidable mixing and leads to the production of an admixture. The ability of farmers to choose conventional, organic or GMO seeds with a specified level of purity is called coexistence, and is becoming increasingly difficult (Endres, 2005).

Admixtures can develop due to pollen drift, commingling during harvest or transportation and storage, or from volunteer plants from previous growing seasons. Although precautions are taken to avoid the production of admixtures, a number of historical contaminations have occurred and for many growers, are as unacceptable as contamination with a chemical toxin.

One notable admixture controversy was the StarLink corn (*Zea mays*) fiasco of the late 1990s. StarLink corn were varieties of Bt corn patented by Aventis Crop Sciences, now a part of Bayer AG that was intended for animal feed only. Bt is a naturally occurring soil bacterium, *Bacillus thuringiensis*, and the gene inserted into StarLink corn from the Bt produces a protein, the Bt delta endotoxin, that kills Lepidoptera larvae, most notably, the European corn borer (*Ostrinia nubilalis*). Bt corn is used as an alternative for insecticidal control of the European and south-western corn borer (*Diatraea grandiosella*). The restriction on StarLink corn was due to a possible allergic reaction by some individuals to the specific strain of the delta endotoxin produced in the StarLink corn. StarLink corn was found in food destined for humans and around 30 people had allergic reactions related to eating contaminated corn products. However, the US Centers for Disease Control found no evidence that allergic reactions were due to the StarLink corn. Even so, consumers have a right to know where their food is coming from and what is in it. Since 2004, no corn samples have been found to be contaminated with StarLink corn.

Another admixture incident occurred when volunteer genetically altered corn plants were harvested with non-GMO soybeans contaminating 500,000 bushels of soybeans. The USDA and the Food and Drug Administration (FDA) ultimately received $250,000 in penalties form Prodigene Inc., the company responsible for the mishap, to defray the cost of removing the contaminated soybeans from the market (Endres, 2005).

Whether or not you favor GMO crops, the above two examples highlight the need for regulations ensuring that products labeled as organic or non-GMO have not been inadvertently contaminated with GMOs. A major part of the controversy is about who should pay for any testing associated with identifying instances of contamination and who is liable should a crop become contaminated.

The classic example of Percy Schmeiser vs Monsanto and the contamination of Schmeiser's fields with Roundup Ready Canola was finally settled out of court in 2008, with Monsanto agreeing to pay to clean up Schmeiser's fields (Hartley, 2008).

But the problem doesn't stop with seeds. Think about this: the European Union has banned the importation of Canadian honey because producers cannot guarantee that it is not contaminated with GM pollen (Smyth *et al*., 2002).

The Seed Label and Seed Certification

To ensure full disclosure regarding the status and composition of a seed lot, most seed laws require specific information to appear on the seed label (USDA NRCS, 2009) (Fig. 12.1). As part of the label, seeds are identified as: (i) breeder seed; (ii) foundation seed;

Fig. 12.1. A typical seed label.

(iii) registered seed; or (iv) certified seed. Each level of certification recognizes a specific degree of genetic purity, seed identity, and a minimum level of quality.

Breeder seed is seed that is produced and directly controlled by the breeder and its sole purpose is for generating seeds of the other certified classes. Foundation and registered seeds are seeds directly produced from breeder or foundation seed. Certified seed is produced from breeder, foundation or registered seed. Certification classes are often identified by tag color.

Most growers purchase cultivars of either registered or certified seed. A fairly new type of seed is becoming available called 'Per-Varietal Germplasm' and is often used with native species. These seeds have not been released as a cultivar, but are ready for adoption by growers without the extensive field testing needed for cultivar certification. These seeds are often called ecotypes since they have most of their original genetic identity and their range of adaptation and performance traits have not been examined.

Besides identifying the type of seed for sale, all seed for sale whether certified or non-certified, usually is labeled with information that includes:

1. The species and/or common name and the cultivar or variety that distinguishes the seeds from other similar kinds. If it is a mixture, each specific component above 5% is listed. If the cultivar or variety is not indicated, the label will state 'variety not indicated' or VNI.
2. The lot number with a defined quantity of seeds that must fall within a defined acceptable range.
3. The location where the seed was produced.
4. The net weight of the contained seeds.
5. The percentage purity indicating the amount of pure seed, inert matter, other crop seed, and weed seeds. The total for these four components must equal 100%.
6. The percentage germination.
7. The percentage of dormant seed.
8. The percentage of hard seed. This is seed that fails to imbibe water during the germination test.
9. The percentage of total viable seed (TVS). This is the total of the percentage germination plus the percentage hard seed plus the percentage dormant seed. It reflects the maximum germination that might be expected.
10. PLS (pure live seed) is the percentage of pure seed × the percentage of TVS. This gives a measure of the amount of PLS in the sample.
11. The germination test date.
12. Any restricted noxious seeds indicating the number of seeds per kilogram and the weed name. Many regions have weeds identified as restricted or prohibited. The number of restricted weed seeds per kilogram is limited while prohibited seeds are not allowed at any level. In fact, most seed tests must explicitly state that no prohibited noxious weeds are present in the seed lot.
13. Any seed treatment, which is usually an inoculant or a pesticide.
14. The name and address of the seed company responsible for the analysis included on the label.
15. Any other information including disclaimers, limited warranties, etc.

Germination

Seeds are an amazingly packaged, pre-programmed plant, ready to grow and flourish if given the

right environment. Upon removal from the mother plant either within a fruit or naked, a seed is usually dry and mature and may possess barriers to growth that we call dormancy. The complex nature of seed dormancy was covered in Chapter 10, this volume. For germination to proceed, dormancy must be eliminated. Once dormancy has been removed from the seed, external factors control germination including water, light, temperature, and sometimes nitrate.

A typical dry, mature seed consists of a desiccation-tolerant sporophyte surrounded by a seed coat, or endosperm and a seed coat, depending on the species. Many of the physiological and physical changes associated with germination have been studied using model systems that include peas (*Pisum sativum*), *Arabidopsis thaliana*, cress (*Lepidium sativum*), and tobacco (*Nicotiana tabacum*). Peas store most of their seed food reserves as proteins and starch within the embryo's cotyledons, having no endosperm when seeds are mature. *A. thaliana* and cress have a thin endosperm layer, and tobacco has a thick endosperm layer surrounding the embryo.

Most dry seeds have a water content of about 10% (Weitbrecht *et al*., 2011). Most of the water in a seed is bound and very little is available for metabolic activities. Even so, seeds are not metabolically quiet during the stage between harvest and sowing, often called after-ripening (dry storage of mature seeds at room temperature). After-ripening is characterized by a general improvement in germination percentage and rate with the relaxation of specific temperature, light, or nitrate requirements normally needed to stimulate germination. Even though the process occurs in dry seed, a minimum moisture content, albeit extremely low, is required and is species dependent. Small pockets of free water may exist in many seeds to allow for RNA transcription in specific tissues or organs during after-ripening (Weitbrecht *et al*., 2011). Oily seeds have a lower minimum moisture threshold for after-ripening than starchy seeds. After-ripening will not occur in very high humidity storage.

The exact mechanisms of after-ripening are not known (Finch-Savage and Leubner-Metzger, 2006). During after-ripening, reactive oxygen species (ROS) are formed, accumulate and oxidize proteins. Glutathione works as an antioxidant to protect the seed from ROS oxidation during after-ripening and tocopherol protects membrane lipids from oxidation by ROS during after-ripening. Ascorbic acid seems to play only a very minor role in ROS protection of seeds. It has been proposed that oxidation by ROS early during after-ripening leads to progression through after-ripening and a loss of dormancy, but later may lead to oxidative damage and loss of viability (Bailly, 2004; Oracz *et al*., 2007, 2009). Dry seeds contain abundant mRNAs that survive desiccation and play a role in the metabolic passage through after-ripening and the preparation for and initiation of the metabolism of germination itself.

Factors affecting germination – water

Dry seeds may persist for many years. When planted in the soil or some other growing medium with sufficient water content, germination begins with the imbibition of water. The extremely low water potential of dry seeds leads to a rapid initial uptake of water called phase I that is present in both living and dead seeds. It is a purely physical absorption of water due to water potential gradients. The seed rapidly swells and may change size and shape. There is often leakage of a large quantity of solutes, caused by damage to membranes during rapid rehydration. Various metabolic processes are initiated to repair this damage. Over time the activity of these repair mechansims is reduced and seed viability decreases.

When water uptake in phase I declines and changes in seed size and shape are completed, the seed enters phase II of water uptake. In phase II, water content remains stable as inbibition has reached a plateau. During phase II the embryo begins to elongate. Some species such as *Arabidopsis, Lepidium* and *Nicotiana* possess what is called 'two-step germination': the seed coat (testa) ruptures followed by rupture of the endosperm. Other species without an endosperm such as *Pisum* exhibit 'one-stage germination' where only a testa requires rupturing. Both types of germinating seeds exit phase II and enter phase III, a period of increased water uptake, following the testa rupture. Phase III includes endosperm rupture in two-step germinators and radicle protrusion in both two- and one-step germinators.

Membrane proteins called aquaporins transport water and small molecules across membranes and help cell-to-cell water and solute movement in seeds. They may help regulate the distribution of water within a germinating seed as well as testa rupture. Testa rupture in species where it has been

studied begins at the micropyle. An increase in seed size due to cell expansion and not cell division helps create pressure on the testa leading to its rupture. In species in which it has been studied, cell division does not occur in the embryo during germination. Completion of germination is marked by the protrusion of the radicle through the seed-covering layers (Weitbrecht *et al*., 2011).

Factors affecting germination – light

Germination is often regulated by light via the pigment phytochrome. Exposure to red light after imbibition leads to the formation of P_{fr} which triggers metabolic processes in the seed that facilitate embryo growth. Seed must be imbibing water to sense the light exposure; dry seeds do not respond. If exposure to red light is immediately followed by exposure to far-red light, germination will not occur. Alternately exposing seeds to red and far-red light always results in a response linked with exposure to the most recent light exposure: red light causes germination, far-red prevents it. This is a classic physiology experiment using lettuce seed. Seed and seedling responses to light were covered in Chapter 8, this volume.

Other species in which germination requires exposure to light include *Ageratum, Begonia, Browallia, Impatiens*, and *Petunia*. These seeds should be sown on the surface of the germinating medium and only lightly covered. Seed packets or catalogs provide light requirements for germination.

Depth of planting in the soil and existing canopy cover can greatly influence germination in light-sensitive species via phytochrome mediation (Botto *et al*., 1996; Shinomura *et al*., 1996). Recall from Chapter 8, this volume, the three different types of phytochrome-mediated plant responses based on light levels: (i) the very low fluence response (VLFR); (ii) the low fluence response (LFR); and (iii) the high irradiance response (HIR) (Furuya and Schäfer, 1996). Both VLFR and LFR can be triggered by pulses of light lasting only seconds while the HIR requires much longer exposure, usually several hours. LFR reactions are photoreversible with far-red light and controlled mainly by phytochrome B while VLFR reactions are not and are regulated primarily by phytochrome A. HIR reactions are not photoreversible.

The germination of most light-sensitive seeds is via a LFR-type reaction with exposure to red light. This is the type of response that allows seeds to detect their depth in the soil or their position under an existing canopy and whether they are in the shade or light. For *Arabidopsis* and possibly many other species, this LFR reaction is mediated by phytochrome B and phytochrome E (Hennig *et al*., 2002).

Seeds of many species that are imbibed in the dark often remain photo-dormant and acquire a VLFR phytochrome response mechanism controlled by phytochrome A. These seeds are extremely sensitive to red light and germinate with only a few seconds of very low levels of red light (Smith, 1982). Many weed species utilize this mechanism. When imbibed seeds are deep in the soil, they remain dormant. When disturbed via cultivation and exposure to red light, even only briefly, they resume germination. Remember, germination starts with imbibition, thus even though the seeds are photo-dormant before exposure to red light, they are in the process of germinating. This is a good example of the complexity of the process and how dormancy and germination often overlap in many cases. They are not discrete, separate processes.

Not all seeds germinate in the light. In seeds that can germinate in the dark, exposure to far-red light for long periods inhibits germination via an HIR reaction mediated by phytochrome A. This is the phytochrome response observed in seeds underneath a dense canopy of leaves. The canopy absorbs much of the red light in incoming solar radiation, thus seeds on the ground or buried slightly received a prolonged exposure to far-red-rich light (Smith and Whitelam, 1990). The blue-light-mediated HIR reaction controlled by phytochrome A may or may not have a function in germination.

Factors affecting germination – temperature

Temperature can have a profound effect on both the rate and the percentage of germination by affecting at least three different physiological processes (Roberts, 1988). The first mechanism related to seed germination significantly affected by temperature is seed longevity. As seeds age, their viability decreases and the rate of deterioration is mostly affected by moisture content and temperature. Each species has a different genetically predetermined limit to viability that no alteration of storage conditions can change. In general, the Q10 for the rate of seed deterioration or loss of the ability to germinate is around 2 at –10°C increasing to 10 at 70°C

(Roberts, 1988). Storage of seeds at a low temperature generally minimizes the loss of viability within genetically predetermined constraints.

A second mechanism of temperature control of germination is temperature's effects on dormancy release. The Q10 for loss of dormancy in dry seeds is relatively constant at 2.5–3.8 over a wide range of temperatures up to 55°C. Hydrated seeds are different. Higher temperatures often prolong dormancy or induce a secondary dormancy. Lower temperatures, especially in the range from –1°C to 10°C often remove dormancy through the process of stratification. Low temperatures only infrequently induce a secondary dormancy in imbibed seeds. Alternating temperatures generally remove dormancy and promote germination in imbibed seeds. The level of dormancy release is related to: (i) amplitude; (ii) mean temperature; (iii) the thermoperiod; and (iv) the number of cycles (Thompson *et al*., 1977).

The third way temperature influences germination is through effects on the rate of germination. The percentage germination is primarily determined by the first two mechanisms. In general, once dormancy and any imposed secondary dormancy have been removed the rate of germination is positively related to increase in temperature between the base temperature and the optimum temperature. Germination will not occur below the base temperature and reaches a maximum rate (minimum number of days to germinate) at the optimum temperature. Above the optimum up to the temperature at which germination will not occur (often called the ceiling), the rate of germination is negatively related to temperature.

Most species have an optimum temperature for seed germination and that temperature is often related to climatic adaptation. Those species adapted to cool climates germinate at lower temperatures while those adapted to warmer climates germinate at higher temperatures. Some of the regulation of germination by temperature may be tied to phytochrome, particularly in light-sensitive species. Different forms of phytochrome are more prevalent at different temperatures (Heschel *et al*., 2008). This area of phytochrome–temperature–germination interaction is relatively new and growing (Franklin, 2009).

Factors affecting germination – nitrate

Nitrate (NO_3^-) stimulates germination in many dormant seeds. One hypothesis for nitrate's involvement in seed germination is as follows. Nitrate is reduced to nitrite or hydroxylamine and nitric oxide may be produced from nitrite. All three substances inhibit the decomposition of hydrogen peroxide (H_2O_2) to water and oxygen by the enzyme catalase. The inhibition of catalase leaves some hydrogen peroxide available for peroxidase activity. Peroxidase is responsible for catalyzing the oxidation (removal of electrons) by hydrogen peroxide of many substrates in living cells. Some seeds, such as barley and rice, show a shift from the Embden-Meyerhof-Parnas pathway of glucose utilization (primarily generation of ATP through glycolysis) to the pentose phosphate pathway (generation of NADPH and five-carbon sugars) as they break dormancy and begin to germinate (Hendricks and Taylorson, 1974). The pentose phosphate pathway uses $NADP^+$ as an oxidant (electron remover) which may be limited by the rate of regeneration of $NADP^+$ by reoxidation of NADPH. Nitrate and its reduction products may regulate this reoxidation process.

More recently it has been suggested that nitrate reduces seed dormancy by reducing abscisic acid (ABA) levels (Matakiadis *et al*., 2009). Nitrate reduces ABA levels in imbibed seeds when nitrate is included in the germination medium and also results in lower ABA levels in dry seeds of plants supplied with nitrate during seed development (Alboresi *et al*., 2005). A specific gene (CYP707A2) controlling seed ABA levels that responds to exogenous nitrate has been identified in *Arabidopsis* (Matakiadis *et al*., 2009). In addition, nitrate can initiate production of nitric oxide (NO), a potent signaling molecule (Bethke *et al*., 2006). Again, the complex interaction of dormancy and germination are exposed here. Nitrate appears to relieve dormancy and stimulate germination through effects on ABA and carbohydrate metabolism.

Hormones and germination

ABA induces and maintains the dormant state in most seeds (Kucera *et al*., 2005). During germination the endogenous level of ABA of both dormant and non-dormant seeds declines rapidly during imbibition (Weitbrecht *et al*., 2011). Overexpression of the genes responsible for ABA synthesis increases seed ABA content and enhances dormancy while delaying germination (Lindgren *et al*., 2003; Nambara and Marion-Poll, 2003). ABA-deficient mutants exhibit vivipary (Koornneef and Karssen, 1994; Thompson *et al*., 2000; White *et al*., 2000)

providing further evidence that ABA inhibits germination. ABA inhibits germination at least in part by preventing the transition from phase II to phase III water uptake which then prevents both testa and endosperm rupture as well as radicle emergence (Kucera, *et al*., 2005; Muller *et al*., 2006). When either ABA synthesis or seed sensitivity to ABA are reduced experimentally, germination is enhanced (Kucera *et al*., 2005).

Jasmonic acid decreases and indole acetic acid (IAA) increases during *Arabidopsis* germination (Preston *et al*., 2009). Nitrate seems to regulate both gibberellin (GA) and ABA metabolism in germinating seeds (Alboresi *et al*., 2005) and accelerates the reduction in seed ABA levels during imbibition (Ali-Rachedi *et al*., 2004).

While ABA induces dormancy and inhibits germination, GA promotes germination and counters the effects of ABA. GA has two specific roles during germination: (i) it increases the growth potential of the embryo, which promotes embryo elongation; and (ii) it weakens the tissues surrounding the radicle thereby removing the mechanical constraint to radicle protrusion (Kucera *et al*., 2005). During seed development a large store of inactive GA or precursors accumulate and germination proceeds according to the balance of ABA:GA (active forms). ABA inhibits GA biosynthesis in early germination. Both red light and cold stratification induce GA production and break dormancy in *Arabidopsis* and lettuce (*Lactuca sativa*) (Kucera *et al*., 2005). GA levels are relatively high in dry, mature seeds and biosynthesis of GA is localized in the radicle, hypocotyls, and micropylar endosperm during later germination (Ogawa *et al*., 2003). GA also promotes vivipary (White *et al*., 2000).

Ethylene promotes germination and counteracts ABA's inhibitory effects in many species (Kucera *et al*., 2005; Holdsworth *et al*., 2008; Linkies *et al*., 2009; North *et al*., 2010). Increased ethylene evolution during germination is often observed with many seeds (Matilla, 2000) and a peak of ethylene evolution is often observed as germination is completed. Germination is inhibited if seeds are treated with ethylene biosynthesis inhibitors (Sisler and Serek, 2003; Kucera *et al*., 2005). It is likely that ethylene promotes germination by promoting radial cell expansion of the hypocotyl, increasing seed respiration, increasing embryo water potential, and promoting endosperm rupture (in seeds with two stage germination) (Leubner-Metzger *et al*., 1998; Kucera *et al*., 2005).

Brassinosteroids (BR) work with GA in promoting cell elongation and germination and in counteracting the inhibitory effects of ABA (Kucera *et al*., 2005). BR may act by stimulating GA and ethylene biosynthesis, but this hypothesis is still in question. Cytokinins are abundant in developing seed and seem to play a major role in promoting cell division and development in the embryo and enhancing sink strength of fruit (Kucera *et al*., 2005). While much is known about the involvement of auxin in the first stages of embryo development, information describing the role of auxins in germination is sparse.

Nitric oxide (NO) is a potent signaling molecule in plants (Šírováa *et al*., 2011) so it is no surprise that it is implicated in regulating germination (Zhenga *et al*., 2009). Treating wheat seed with NO by imbibing them in a solution producing NO led to increased germination rate, increased coleoptile and radicle weight, and enhanced respiration and ATP production. NO also increased anti-ROS enzymes, helping protect germinating seeds from the deleterious effects of excessive ROS such as hydrogen peroxide and superoxide anions.

ROS also play a regulatory role in seed germination. Excessive levels of ROS in seeds lead to oxidative damage in cells and a decrease in seed viability. However, cellular signaling relies on at least a minimal level of ROS. The state in between a minimal and an excessive level is called the oxidative window for seed germination (Bailly *et al*., 2008), the state in which germination will proceed.

While specific germination responses to plant hormones and signaling molecules have been described here, keep in mind that germination is regulated by the complex interaction of these compounds. In addition, while much is known regarding hormonal regulation of dormancy and germination, much remains to be understood regarding this incredibly important process.

Metabolism of germination

Metabolism is reactivated with water imbibition during phases I and II of germination. A great deal of work has been performed to determine whether the increase in metabolism associated with germination is due to newly formed enzymes or due to enzymes stored in the seed. In *Arabidopsis*, translation of mRNA is required for germination while inhibition of transcription of DNA to RNA does not inhibit germination (Rajjou *et al*., 2004). Tobacco (*N. tabacum*), however, proceeds to testa

rupture but requires transcription to complete endosperm rupture (Leubner-Metzger, 2003). Thus it appears that the initial metabolism activated by water imbibition during germination is via stored enzymes or their mRNA, but completion of germination may require newly synthesized enzymes.

Upon imbibition, a sharp increase in oxygen uptake and carbon dioxide evolution by the seed is observed, but then quickly stagnates until the end of phase II (Bewley, 1997). A sharp increase in ATP production is concomitant with imbibition (Benamar *et al*., 2008) and levels increase as mitochondria are repaired or synthesized during the early stages of germination. Stored sugars, lipids, and proteins provide substrates for energy production.

Some practical implications for seed dormancy and germination

Dormancy and germination are intimately linked and the practical implications for such an interaction are worth discussing. In many crops, a certain level of seed dormancy at harvest is desired to prevent viviparous germination either while on the parent plant or after harvest. However, for some crops, such as those used for sprouting or where germination is crucial to their economic use (malted barley, *Hordeum vulgare*, for example), dormancy is not desirable. When seeds are used for propagation rather than food or feed, dormancy is not desirable as rapid and uniform germination are necessary elements of productive culture. As long as environmental factors such as light, temperature, and moisture can be carefully regulated during storage, dormancy is not needed.

Since many seeds exhibit dormancy after harvest, a number of seed treatments have been developed to improve germination upon planting. Treatments include: (i) a period of after-ripening; (ii) stratification; (iii) heat treatment to simulate fire; (iv) scarification; (v) hormone treatments; and (vi) priming. Each species may have specific treatments to enhance removal of dormancy and/or enhance germination. Many of the treatments that improve germination may also reduce storability.

As novel methods of weed control are developed for low-input operations, better understanding of the complex nature of weed seed dormancy and germination integration is imperative. Many weed species cycle in and out of dormancy allowing them to remain viable for years in the soil, while at the same time, being ready to germinate under specific environmental conditions. This weed seed bank in the soil is often difficult to deal with in many weed control strategies.

Seeding and factors affecting establishment

With an understanding of the basic physiology behind seed dormancy and germination, now consider the physical act of planting seed for horticultural production. While many seeds are sown directly into the production field, there are also many crops that are started in the greenhouse and transplanted to the production field. We will examine both approaches.

Greenhouse seeding

Seedlings started in the greenhouse may be directly sown into the cell trays in which they will grow while in the greenhouse or they may be sown in a germinating flat and transplanted into production trays a week or two after germinating. The first approach requires seed large enough for singulation. The second approach requires labor skilled enough for transplanting seedlings. Transplanting seedlings also subjects seedlings to the stress of a disturbed root system. With either approach, appropriate containers and an appropriate medium are needed.

CONTAINERS Most commercial containers for seedling production in the greenhouse are plastic, Styrofoam®, or a sustainable material such as wood, compressed fiber, or peat moss. Some greenhouse operators use homemade soil blocks and avoid the use of a container altogether. Soil blocks are labor intensive and are mostly used in smaller operations.

Styrofoam® and plastic are the most widely used trays with plastic being preferred over Styrofoam®. This is because: (i) Styrofoam® trays are generally more expensive than plastic; (ii) they insulate the root systems of seedlings leading to slower growth; and (iii) they may also promote algal growth and disease development. In addition, Styrofoam® trays cannot be nested like plastic inserts for storage. Plastic seedling trays normally consist of two parts:

1. An outer tray measuring 28 × 53 cm (11 × 21 in), also called the standard 1020 tray, with or without holes for drainage. Trays with drainage holes are usually recommended.

2. The second component is called an insert, which is normally placed inside the tray to increase sturdiness. Inserts can be used without the outer support tray, however this is not recommended. The inserts are identified by a number indicating the number of plugs per insert or standard 1020 tray.

Standard inserts are available in 24, 36, 38, 50, 72, 98, 128, 200, 288, 406, 512, 600, and 800 sizes (Fig. 12.2). Individual cells range from 2.5 to 6.3 cm (1–2.5 in) deep and are either round or square. Other sizes are available for special needs. Inserts from 24 to 72 are often called finishing or transplant trays. Higher count inserts (98–800) are often called plug trays. Plants germinated in plug trays must be transplanted into finishing trays.

Many growers opt to purchase plugs and finish them off in their own greenhouse after transplanting to larger cell sizes, typically in the 24–72 cell size. Specialty nurseries grow seedlings in the 400–800 tray size for just this market. Other growers prefer growing their own seedlings. With this approach, they don't have to rely on the cultivars available from commercial plug producers. They can direct seed into production trays or transplant young seedlings from germination flats (standard 1020 trays can be used as germination trays) or their own plug trays. There are a wide variety of devices available for seeding greenhouse trays and their costs vary considerably. With machine-seeded flats, flat sizes may be 400, 500, 600, or 800 cells per flat. Many smaller growers sow seed in plug trays by hand or using hand-held devices.

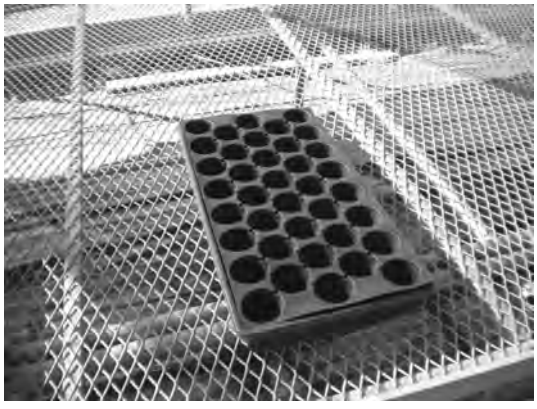

Fig. 12.2. A standard 38-cell insert for greenhouse seeding or transplanting.

Selection of finishing tray size is based on: (i) the species; (ii) the number of seedlings required; and (iii) the greenhouse space available for production. Larger cells are much less likely to suffer from stress-induced premature flower formation. Even though retail sales may prefer smaller transplants with flowers, ultimate field performance is best with transplants that have not been prematurely induced to flower. This is true for both flowering annuals and vegetable transplants. Thus, it is best to go with the largest cell size that can be accommodated in the available space.

Larger cells result in faster maturing seedlings but take up more room per seedling in the greenhouse and are therefore more expensive to produce. There is no evidence that cell size influences final yield as long as cells are well watered. Smaller cells dry out more readily than larger cells, thus are more prone to stress should watering become compromised.

Organic growers may benefit from larger cell sizes due to greater nutrient availability per seedling in larger cells. Organic transplant production is complicated by the lack of a high-nitrogen water-soluble fertilizer for application during the later stages of greenhouse production when nutrient supply from the growing medium has been exhausted. Fish emulsion is the classic fertilizer used in organic transplant production. It is relatively low in nitrogen (about 5%) and often has an unpleasant odor. In non-organic seedling production, there are many high-nitrogen, water-soluble fertilizers available for use.

MEDIA There are many growing media available for use in greenhouse transplant production and a description here of all of them would not be possible. However, a good greenhouse medium should posses certain attributes pertaining to: (i) drainage; (ii) chemical properties such as pH and soluble salts content; (iii) sterility; and (iv) nutrient availability.

Greenhouse media must be well drained. Larger particle sizes provide better drainage, but require more frequent watering. Additionally, smaller particles facilitate easier plug cell filling. Poorer drainage of smaller particle sizes can be accounted for by less frequent watering.

A good greenhouse medium should have a pH of 5.5–6.5, and have a balanced, low level of nutrients. Excess nutrients can lead to succulent, tender growth that is difficult to harden off before field transplanting. Soluble salts should be in an acceptable range indicated by electrical conductivity values

between 0.4 and 0.6 μS/cm for an extract made by mixing one part soil with two parts distilled water.

Greenhouse media should be free of plant pathogens but does not necessarily have to be sterile. Most soil-less mixes are purchased pre-sterilized or their components are purchased before mixing on site.

The base components of a good growing medium include several of the following: peat moss, perlite, vermiculite, coconut coir, rice hulls, screened bark, compost, and sterilized soil. Peat moss, coir or compost normally provide the bulk of the medium, and perlite, vermiculite, bark or rice hulls are added for drainage. There are many recipes for seedling media available online. The key to success is to use the highest quality materials available and mix the media carefully, paying close attention to pH of the final mix and measure lime and fertilizer amendments carefully.

In many regions, commercially prepared mixes are available that are quite affordable and often do not cost much more than the separate components used to make a mix on site (Fig. 12.3). Mixes are also now widely available that conform to organic production regulations. Organic mixes made on site should contain significant amounts of good quality compost if possible to ensure adequate nutrition of seedlings.

Fig. 12.3. A bale of standard potting medium for greenhouse production of transplants. Most commercial media are a mixture of ingredients which may include peat moss, pine bark, coir, rice hulls, vermiculite, perlite, lime, starter nutrients, a wetting agent, and other proprietary ingredients.

FERTILIZING SEEDLINGS Most greenhouse seedlings require some nutrients to supplement those available from the growing medium. The quality and field productivity of spring-grown greenhouse transplants is linearly related to fertility levels (Vavrina *et al.*, 1998). In non-organic production systems, this is easily accomplished with a balanced water-soluble fertilizer. Many formulations are available from greenhouse supply firms. Organic production systems are more problematic. Nitrates are the nutrient most needed by greenhouse seedlings (Van Iersel *et al.*, 1998), and most organic nitrogen sources provide slowly available, low levels of nitrates to seedlings. In addition, most organic sources of nitrogen do not supply nitrate directly. The nitrogen is normally in a more complex form, such a protein, which must be broken down into ammonium (mineralization) then converted to nitrate by bacteria in the medium (nitrification). Ammonium can be taken up and used directly by plants, however, most nitrogen is utilized as nitrate. Too much ammonium under low light or cool soil conditions (<12°C) can be toxic to seedlings.

Most organically produced transplants are fertilized with fish emulsion fertilizer or compost tea on a fairly frequent basis soon after seedling emergence. Fertilizing with a low level of nitrogen at every watering is possible. However, to avoid over fertilizing, every week or every other week is often more suitable.

WATERING SEEDLINGS The key to watering greenhouse-grown seedlings is to prevent drying out and water stress while at the same time avoiding overwatering, which is also stressful and may lead to root rot and epinasty. Common sense and observation are the best tools. A good rule of thumb is to water an hour or two after sunrise and then check the greenhouse again just after noon, especially on warm sunny days. Avoid watering late in the day to avoid night-time humidity problems and increased disease potential. The growing medium should be allowed to dry nearly to the point of wilting before rewatering. Apply enough water to thoroughly wet the medium, but do not overwater. Just because

water flows from container drainage holes does not mean that the medium has been thoroughly wetted. If the growing medium dries out too much, it often pulls away from the side of the container and water flows around the root ball and out of the container rather than through it.

When making watering decisions consider: (i) the seedlings' stage of production; (ii) the greenhouse temperature; and (iii) the current weather conditions outside (is it sunny or cloudy?). Pay very close attention to germination flats as they are easy to overwater. But never let germination flats or seedling flats dry out completely either.

HARDENING OFF TRANSPLANTS Before setting in the field, transplants are gradually conditioned to tolerate harsher conditions found in the field as compared with the greenhouse. Hardening off is usually accomplished over a 1–2 week period. It consists of increasing daily exposure to field conditions which includes: (i) higher direct sunlight; (ii) less frequent watering; and (iii) exposure to wind. Night-time temperatures should be considered when hardening off sensitive crops.

There are various approaches used to accomplish the same goal. Transplants are often moved outside to a semi-protected area for several hours a day for a few days to acclimate them to outdoor conditions. The daily length of exposure is gradually increased and protection gradually removed such that by the end of the second week, transplants have spent several days and nights outside, under conditions similar to the production field.

Moving transplants in and out of the greenhouse during the first stages of hardening is labor intensive. Therefore, hardening may be accomplished in an area outside the greenhouse that is protected from the direct outside environment with some sort of shade cloth or in a lath house. Gradually the protection is removed.

TEMPORARY STORAGE OF TRANSPLANTS Sometimes field planting of transplants must be delayed due to circumstances beyond the control of the grower such as inclement weather. Additional fertilization is often ineffective in maintaining slow growth of seedlings because root volume has been filled. If held in the greenhouse, such transplants are often stressed to the point that they flower prematurely thereby greatly reducing productivity in the field. Flats of such seedlings can be temporarily held in a state of 'suspended animation' allowing a grower more time to prepare the production field.

The temperature and length of storage depends on the species being held (Gast and Stevens, 1994). All species store better with exposure to light of at least 5 foot candles when stored in cold-storage facilities (Fig. 12.4). Supplemental light is not

Fig. 12.4. Plug plants held in a cooler until suitable conditions for planting occur.

needed when stored in cold frames or cool greenhouses. *Botrytis* can become a major problem in stored plugs, especially with lushly growing plugs. After storage, plugs should be slowly warmed to 15–20°C (60–70°F) under low light conditions before transplanting.

Since most growers do not have the luxury of access to many different temperatures for temporary storage of plugs, some general recommendations were made by Gast and Stevens (1994) and are listed in Table 12.1.

Field seeding

Many crops are directly seeded in the production field rather than being transplanted from greenhouse-grown seedlings. Field-seeded crops do not experience the luxury of a controlled environment during germination which is the most crucial event during stand establishment. In order to maximize germination success, proper seed bed preparation, seed spacing, depth of soil coverage, and irrigation following planting are crucial.

SEED BED PREPARATION The seed bed should be well tilled before sowing unless no-till seeding is practiced. The main mistake made during seed bed preparation is over preparing the soil for sowing. The idea that a seed bed must be prepared to create good seed-to-soil contact is somewhat misleading. While it is true that good seed-to-soil contact allows capillary water in the soil to flow towards the seed and surround it, most of the water imbibed by seeds is in a vapor form. Only about 10% of a seed's surface is in contact with liquid water during imbibition in soil that is near field capacity. It is more important to ensure that soil moisture losses are minimized during germination by covering the seeds adequately with either soil, mulch or both.

Excess tilling leads to extremely fine soil which is likely to form a hard, compact crust when the soil dries following post-planting irrigation. While this crust does reduce water loss from the soil, the force required to break this crust is often much greater than a germinating seedling can generate. Seedling emergence is then severely compromised.

DEPTH OF PLANTING Some seeds such as lettuce (*L. sativa*), require light for germination and should be sown shallowly. Light-regulated germination is most often controlled by phytochrome. The seed must be covered with enough soil to create a microclimate that supports water imbibition but not so much soil that light penetration is severely decreased. When seeds are covered with enough soil to promote imbibition, enough red light can penetrate the layer to induce the formation of P_{fr} and signal the commencement of germination.

Depth of seeding must also consider seed size and the ability of the seed to supply energy during germination via reserves until emergence and the inception of photosynthesis. If planted too deeply, a seed may exhaust all stored food before it can emerge from the soil and photosynthesize. However, if seeds are not planted deeply enough, poor seedling anchorage will result leading to poor stand establishment.

SPACING In-row seed spacing should be based on final plant densities required to optimize yield as well as whether or not seedlings will be thinned. Seeding density must also consider germination percentage. Seed lots with low germination should be seeded more densely to compensate for reduced germination and thinned if needed.

Between-row spacing is often determined by equipment requirements. In situations where hand labor is mostly utilized, between-row spacing is determined by optimum plant densities and management requirements. In both instances, spacing should utilize the land area to: (i) optimize yield; (ii) ease management; and (iii) protect the soil from wind and water erosion.

METHOD OF SEEDING Seed can be sown by hand or by using various types of seeders that are available from a number of sources. Even in small operations, the use of mechanized seeding can save time as well as reduce seed costs by more efficient and even placement of seeds during sowing.

Seed technology

Many crops are mechanically planted with precision seeders to: (i) reduce the number of seeds used per acre; (ii) reduce labor requirements for seeding; and (iii) reduce seedling thinning after germination. Many seed technologies have been developed to make precision planting easier, enhance germination, improve stands after germination, and improve uniformity at harvest. Seed technologies include: (i) mechanical seed treatments; (ii) pelleted seed; (iii) seed encrusting; (iv) film coating; (v) seed priming; (vi) seed-lot upgrading; (vii) artificial seeds; and (viii) genetic use restriction technology (GURT).

Table 12.1. Recommended temperatures and storage times (in dark and light) for plugs and seedlings of various flowering annuals and annual vegetables (after Gast and Stevens, 1994).

Species	Cultivar	Optimum storage temperature (°C)	Maximum storage time (weeks)	
			In the dark	With light[a]
Ageratum	'Blue Danube'	7.2	6	6
Alyssum	'New Carpet of Snow'	7.2	–[b]	3
	'New Carpet of Snow'	2.5	5	6
Fibrous begonia	'Viva'	7.2	–	1
	'Vodka'	5.0	6	6
Tuberous begonia	'Nonstop Scarlet'	7.2	–	6
	'Nonstop Scarlet'	5.0	3	6
Celosia	'Cherry Red'	7.2	–	1
	'Cherry Red'	10.0	2	3
Coleus (*Solenostemon*)	'Multicolor Rainbow'	7.2	–	2
Cyclamen	'Giselle', 'Sylvia'	7.2	–	6
Dahlia	'Amore', 'Figaro'	7.2	–	6
	'Amore', 'Figaro'	5.0	2	5
Geranium (*Pelargonium*)	'Pinto Red'	7.2	–	4
	'Pinto Red'	3.0	4	4
Impatiens	'Accent Lilac', 'Accent Red Star', 'Super Elfin Orange'	7.2	–	2
	'Accent Orange'	7.5	6	6
Lobelia	'Blue Moon'	7.2	–	5
	'Blue Moon'	5.0	6	6
Marigolds (*Tagetes*)	'Scarlet Sophia'	7.2	–	5
	'Hero Yellow'	5.0	3	6
New Guinea Impatiens (*Impatiens* × *hawkeri*)	'Kientzler Series', 'Paradise Series'	12.5	2	3
Pansy (*Viola*)	'Majestic Yellow'	7.2	–	6
	'Majestic Yellow'	2.5	6	6
Pepper (*Capsicum*)	'Better Bell'	7.2	–	2
Petunia	'White Flash'	7.2	–	5
	'Ultra Red'	3.0	6	6
Portulaca	'Double Mix'	7.2	–	5
	'Fuschia'	7.5	5	5
Salvia	'Red Hot Sally', 'Red Pillar'	7.2	–	4
	'Red Hot Sally'	5.0	6	6
Tomatoes (*Solanum lycopersicum*)	'Better Boy'	7.2	–	4
	'Rutgers'	7.5	3	3
Verbena	'Showtime Mix'	7.2	–	4
	'Romance Mix'	7.5	1	1
Vinca	'Bright Eyes', 'Grape Cooler', 'Little Linda', 'Little Pinkie', 'Polka Dot', 'Pretty 'n' Rose'	7.2	–	3
	'Peppermint Cooler'	10.0	5	6

[a] At least 5 foot candles of light.
[b] –, Indicates this has not been tested at this temperature in the dark.

Mechanical seed treatments

Mechanical seed treatments are treatments that improve a seed's reproductive quality by: (i) scarring or removing the seed coat; (ii) removing the hardened pericarp; or (iii) sorting into defined sizes or densities. All of these treatments improve water imbibition or facilitate mechanical seed planting.

As an example, consider the combination of several mechanical technologies used in sugarbeet seed production (*Beta vulgaris*). Beet seeds are really fruit (schizocarps) where the dried, hardened pericarp surrounds one or more seeds with rather rough projections from the globular fruit. In order to facilitate precise mechanical planting, these projections are removed by polishing the seed. A second step sorts the polished seeds into different sizes, allowing precise placement in the field. A third technology, monogerm cultivars, may be employed; these contain only one seed per fruit, thus eliminating the need for post-emergence thinning.

Pelleted seed

Seed pelleting adds a coating of an inert material such as clay to irregularly shaped or very small seeds (Fig. 12.5). By transforming irregularly shaped or long seeds into round, easily singularized seeds, precise mechanical planting can be achieved (Fig. 12.6).

Improvements have been made in pelleting seeds to increase oxygen permeability at planting, including pellets which split open upon hydration. Different coating materials can vary pellet density for increased precision. Heavier pellets tend to drop quickly from the metering device to the soil with little pellet bounce in the furrow allowing faster tractor speeds during planting. Seed protectants are often incorporated into the pellet. Protectants applied in this manner reduce the total amount of chemical applied per hectare and is very target specific.

Fig. 12.5. Pelleted, primed lettuce (*Lactuca sativa*) (left) seed compared with non-pelleted seed (right).

Seed encrusting

Encrusting adds weight to a normally lightweight seed to enable more precise mechanical planting by encasing the seed in an inert material. The overall seed shape may or may not be modified. Many sweet corn cultivars have light-weight, irregularly shaped seeds that are difficult to mechanically plant. Encrusting adds weight and improves their shape for handling by mechanical planters. Encrusting is less expensive than pelleting.

Film coating

Some seeds, such as those of the *Brassica*, are large and regularly shaped and do not require pelleting. In these cases, protective chemicals can be applied in a film of synthetic polymer. Polymers have the advantage of producing a thin coat of tightly adhered protectant, preventing loss of the material while adding little to the weight of the seeds. Additionally, reduced worker exposure to the chemical and its dust improves worker safety.

A rather novel use of thin polymer coating is the use of temperature-sensitive water-permeable films which only allow imbibition once the soil temperature has reached a certain minimum. This prevents germination before soil environmental conditions are favorable for continued seedling growth.

Seed priming

An increasingly common practice in horticultural production is seed priming. Seed priming consists of precisely controlled water imbibition allowing germination to begin. At a precisely defined stage before radicle emergence and before desiccation tolerance is lost, germination is halted and the seed is dried for later planting. Once planted, germination is completed with radicle emergence.

Since many of the physiological processes of germination are well under way in primed seeds, the metabolic phase of germination is greatly shortened, thus germination time and time to emergence in the field is reduced by up to 50% compared with non-primed seeds. Additionally, priming increases the effective temperature range for germination, thereby allowing germination at less than optimal temperatures. Priming also promotes the proliferation of root hairs, which may lead to more efficient nutrient and water uptake. In crops such as lettuce and celery, priming releases the seeds from phytochrome-induced

Fig. 12.6. A nice stand of lettuce (*L. sativa*) achieved by mechanical planting of primed and pelleted seed.

dormancy. Priming also improves the final stand of many commercial crops which promotes uniformity at maturity.

A beneficial side effect of priming is the reduction of several seed-borne pathogens, including *Xanthomonas campestris* in *Brassica* seeds and *Septoria* in celery (*Apium graveolens*). The likely causes of this reduced pathogen load is the water potential the organisms are exposed to during priming, sensitivity to priming salts, or oxygen concentration.

A major disadvantage of primed seed is that they have a shorter shelf life and are more expensive than their non-primed counterparts.

Seeds can be primed in several ways and though different, all achieve the same results. The key to priming is slow and controlled imbibition. Most commercial priming methods are proprietary. Osmo-priming (osmo-conditioning) is the standard method for priming seeds. Seeds are soaked in a water solution where water potential is precisely controlled with polyethyleneglycol or potassium chloride. A variation of this method, matrix-priming (matrix-conditioning) includes hydrating seeds in a matrix such as vermiculite or absorbent polymers.

Soaking seeds in warm water overnight is a simple method of hydro-priming. Seeds primed this way are not dried, but rather, planted immediately. Many growers hydro-prime long germinating or difficult seeds, for example carrots (*D. carota*) and beets (*B. vulgaris*), in an attempt to hasten germination. Care must be used as some crops cannot be primed, such as green bean (*Phaseolus vulgaris*).

THE PHYSIOLOGY OF SEED PRIMING The uptake of water during imbibition occurs in three stages. Stage I is imbibition where there is a rapid initial water uptake due to the seed's low water potential. During this phase, proteins are synthesized using existing mRNA and DNA and mitochondria are repaired. In stage II, there is a slow increase in seed water content, and physiological activities associated with germination are initiated, including synthesis of proteins by translation of new mRNAs and synthesis of new mitochondria. Stages I and II are the foundations of successful seed priming where the seed is brought to a seed moisture content that is just short of radicle protrusion. There is a rapid uptake of water in stage III where the process of germination is completed culminating in radicle emergence.

Priming induces rRNA synthesis and the repair of DNA damaged during normal seed ageing. Many enzymes involved in metabolic processes involved in germination are also synthesized or induced. This includes enzymes responsible for mobilization of storage proteins (peptidases), carbohydrates (α and β amylases), and lipids (isocitrate lyase) that are particularly needed after radicle emergence.

Other enzymes that increase during priming include catalase and superoxide dismutase, both free-radical scavengers important in minimizing cell damage. Priming induces osmotic stress in seeds, thus low-molecular-weight heat shock proteins often appear during priming. They may help maintain the proper folding of other proteins, facilitating entry into proteolytic pathways when needed during germination.

The priming process is stopped just prior to radicle emergence so that the seed's desiccation tolerance is not lost. Cell enlargement is responsible for radicle emergence and cell division begins after emergence commences. Cell division is not affected by priming; however, priming does advance the cell cycle up to mitosis, so the seed is 'ready to go' once it is planted. In addition, primed seeds have increased levels of ATP compared with non-primed counterparts and the levels remain high for 4–6 months after drying. Upon planting and imbibition, primed seeds are 'loaded' with ATP energy

compared with non-primed seeds making the primed seeds more vigorous during germination.

Priming can also release seeds from dormancy in certain crops. Many seeds of cultivars of lettuce (*L. sativa*) are thermodormant at high temperatures (30–35°C). The embryos of lettuce seeds are enclosed in an endosperm that is two to four cell layers thick, with cell walls composed primarily of glactomannan polysaccharides through which the radicle must penetrate for germination to be complete. The enzyme endo-β-mannase is the enzyme responsible for endosperm weakening and it requires ethylene for activation. High temperatures inhibit ethylene production and thereby inhibit cell wall loosening and radicle protrusion. Priming somehow improves ethylene production by the embryo, enhancing the activity of the cell-wall-loosening enzyme. Some seeds such as tomato (*Solanum lycopersicum*), carrot (*D. carota*) and cucumber (*Cucumis sativus*) do not require ethylene for germination. Priming enhances loosening of cell walls in these species as well, allowing germination at less than optimal temperatures. Enzymes regulating cell wall loosening are probably activated by the priming process.

Seed-lot upgrading

Viable seeds are often more dense than non-viable ones. By separating seed lots by density, improved germination rates nearing 100% can be obtained by removing the non-viable seeds based on their lower density. Sorted seed can also be primed, improving their performance even more.

Artificial seeds

New technologies in cell culture and regeneration allow large-scale somatic embryo production. Somatic embryos are vegetatively derived clones. The embryos can be placed in a gel-like matrix of agar, gum or dextrans and surrounded by an artificial seed coat. The 'seeds' can then be used for propagation much like normal seeds.

Genetic use restriction technology (GURT)

GURT, commonly known as terminator technology, is a controversial issue in contemporary agriculture. Whether you support or oppose GURT is not germane to this text. Rather, knowledge of the basic mechanisms of GURT will provide the information needed to argue either way intelligently.

The technology was developed by the Agricultural Research Service of the USDA and Delta and Pine Land Company in the 1990s. Monsanto Company, the world's largest seed company pledged not to commercialize this technology in 1999. In 2006, Monsanto bought Delta and Pine Land Company.

GURTs are a range of strategies designed primarily to impede transgene movement. There are two major types of GURTs: (i) T-GURTs (trait-GURTs); and (ii) V-GURTs. T-GURT plants are such that they possess some form of genetic enhancement but the level of expression of the trait is controlled via application of a proprietary chemical treatment. T-GURT plants are fertile, produce viable seed, and the enhanced gene is passed on from generation to generation. The gene's expression is under control of the developing company via its proprietary chemical. If a farmer purchased T-GURT seed from Company X, he or she would also have to purchase the proprietary chemical from Company X to induce the desired trait. The farmer could save seed for planting the next season; however, the desired trait would not be expressed lacking the proprietary chemical.

V-GURT plants prevent transgene movement by producing sterile seeds. If a farmer purchased V-GURT seeds, he or she could not save the seed for the next growing season, since it would produce sterile plants which would not produce fruit or seeds. The farmer would have to purchase new seeds annually. This is no different from the current practice of buying hybrid seed.

GURTs can prevent transmission of transgenes out of their desirable domain, thereby limiting the flow of genes into the wild. GURTs also protect proprietary germplasm. Even though this is one of the more controversial aspects of the issue, it is no different from seed companies protecting their germplasm by developing proprietary hybrids which have been used for years in world agriculture.