Afterripening, Rest Period, and Dormancy

BRUCE M. POLLOCK AND
VIVIAN KEARNS TOOLE

SEED MATURITY and seed germination follow in direct sequence in the life of a plant, but normally they are separated in time and space.

The interval may be a few hours or many years. It may be a few inches or thousands of miles.

The function of the seed is to carry its embryo plant through the hazards of time and space to a time and place where the new plant can grow, flower, and in its turn produce seeds.

It is of advantage to the seed to remain in an inactive condition until it reaches a favorable time and place for germination: A young plant is vulnerable to lack of water and extremes of heat and cold—hazards that the embryo plant within the seed is adapted to withstand. In the nongrowing condition, the water content of the tissue is relatively low, the protoplasm of the cells is protected from damage, and the metabolic rate is low. Thus the seed can survive on its nutrient reserves for a long period.

DELAYED GERMINATION is not accidental. It is the result of physiological mechanisms that keep the seed in a nongerminating state.

The term "dormancy" is used to describe two inactive conditions. One results from an unfavorable environment. The other is due to internally imposed blocks. For example, germination may be delayed by inadequate water supply or unfavorable temperature. In some seeds, however, germination is prevented by blocking mechanisms within the seed. They must be removed before the germination can occur.

The terms "rest" and "rest period" also have been used to describe seeds and buds that are inactive because of these internal blocks.

One should be aware of this confusion in terminology when he reads about seeds and germination, but he need not think the dual terminology is an exercise in scientific semantics. Our scientific terminology has to be precise. Often in writings it is difficult to tell whether the investigator was working with seeds that were "dormant" because they were dry or cold, or with seeds that were "dormant" because of blocks. It is simple to write on paper a definition of "dormancy" or "rest," but it is more difficult to apply the definitions to a seed or a seed lot.

An example illustrates the problem. The seed of silver maple (*Acer saccharinum*) can germinate as soon as it falls from the parent tree. You are familiar with the appearance of seedlings in early summer under the trees. This seed is "inactive dormant" at the time of maturity, but it is not "resting" or "blocked dormant," because it germinates as soon as it reaches the water supply in the soil.

At the other extreme, the seed of the apple tree (*Pyrus malus*) is "resting" or "blocked dormant" at maturity. It will not grow even under good conditions for germination until it has undergone changes, known as afterripening, to remove the germination blocks.

If one defines these two extremes as "dormant" and "resting" and then attempts to apply these definitions to other seeds, difficulties arise. Take the lettuce seed (*Lactuca sativa*). It germinates promptly in total darkness if it is planted in moist soil at 57° F. It does not contain a germination block. If the same seed is planted at 84°, however, it remains inactive. If, following 84° for a few days, the temperature drops to 57°, the seed still cannot germinate. Exposure of the imbibed seed to the high temperature induced the formation of a block that did not exist previously. This block may be removed by an exposure to red light.

Can one then easily apply a rigid definition of dormancy or rest to describe a lettuce or similar seed?

Obviously not, without qualifying the definition by listing carefully the conditions under which germination was attempted. The variety of the lettuce and the previous history of the seed also are important—not all varieties behave in the way we described, nor do all lots of one variety.

GERMINATION BLOCKS are relative, not absolute.

Close examination of some seeds, such as the sour cherry (*Prunus cerasus*), has disclosed that growth is not completely stopped, even in a blocked seed at a low temperature. Cells of the root and shoot can divide, and the whole embryonic axis grows slightly at a time when the seed cannot germinate even under good conditions.

This observation and the fact that something obviously does occur during afterripening to permit subsequent germination show that the blocks are only relative.

A blocked seed is like an automobile with its motor running at idling speed but with the gears disengaged—there is no motion.

Germination blocks are variable. Gardeners and farmers know that all the viable seeds they plant do not germinate. The proportion of those that do germinate varies with conditions of germination. A major reason for the variability is that all seeds are not genetically identical.

Conditions required for germination are the expression of the seed's heredity as influenced by environment during seed formation, maturity, and germination.

We do not know, even for a single kind of seed, exactly what are the critical environmental factors, when they act, or how they may be controlled experimentally or in commercial practice.

The result of the interaction of genetic and environmental factors is extreme variability in the rate at which germination of different kinds of seeds and different seeds of one kind begins.

The germination of seeds has a continuous range from prompt growth over a wide range of environmental conditions to sluggish growth over a narrow range of environmental conditions. Most farmers, scientific workers, seedsmen, and gardeners recognize this variability. It is the variability of Nature.

A species survives because of blocks that delay germination. They tend to spread germination over a period of years. One unfavorable growing season does not obliterate a species.

Consider weeds. All farmers and gardeners see how weeds emerge in soil clean cultivated for many years. Some may have been introduced recently by animal carriers or the wind, but most were already present in the soil from previous years. These seeds had germination blocks that previously prevented germination.

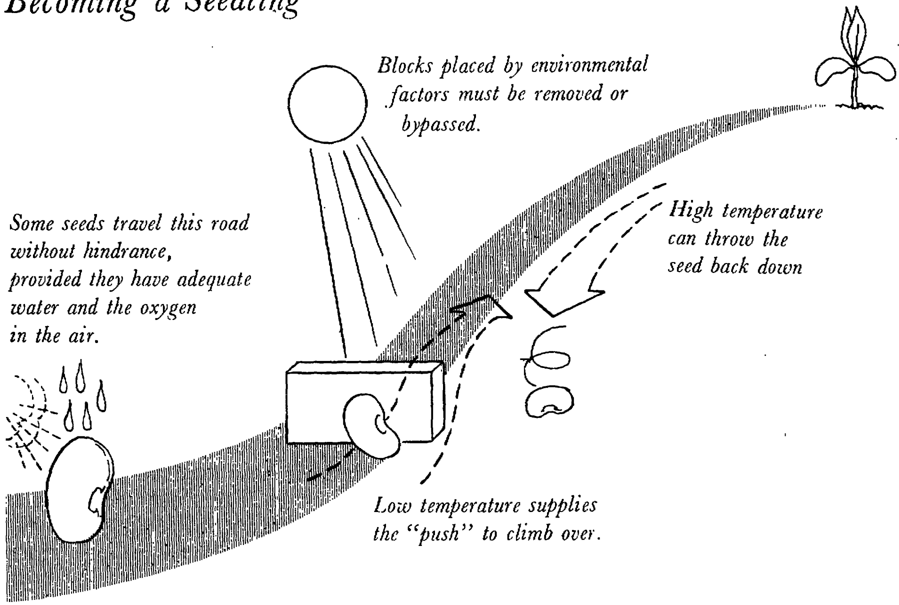
Blocked seeds are more obvious and more extreme in wild plants than in most of our cultivated forms. One inherited difference between seeds is the ability to develop germination blocks.

Through the years, man has tended to select seeds that give relatively prompt germination. The result is that some of our cultivated plants cannot survive without man to protect the seeds by proper storage until a favorable season for germination. In a sense, man has substituted himself for the germination blocks that probably were present in the ancestors of our common cultivated plants.

The term "block" is a convenient name for a mechanism that restricts germination. Blocks act through a number of different physiological mechanisms. Some blocks are simple and well understood. Others are complex and almost completely unknown.

The end result is the same in all instances: The seed is held in a nongrowing condition.

Germination is the Road a Seed Must Travel Before Becoming a Seedling



THE MOST complete block to germination is in seeds that have seedcoats impermeable to water. These hard seeds are common in the waterlily, mallow (cotton, okra), and legume (beans, clovers) families.

During ripening and drying of red and white clover seeds (*Trifolium pratense* and *T. repens*), the seedcoat becomes impermeable to water when the moisture content of the seed has reached a low level. The impermeable seedcoat has a fissure along the groove of the hilum, which functions as a hygroscopic valve. When the seeds are surrounded by dry air, the fissure opens and permits water vapor to escape. The fissure closes in moist air. Thus the seeds can dry further through outward diffusion of water vapor, while reentry of water is prevented. Such seeds remain impermeable to water until the seedcoat is somehow broken. If water cannot enter, the first steps toward germination are prevented.

Some germination blocks are localized. Many blocks affect the whole embryo. Seeds of the apple are blocked and germinate only after undergoing a period of afterripening while moist at a temperature around 40°. Imbibed seeds that have been chilled for 2 to 3 months germinate promptly and produce normal seedlings.

The embryo in seed of the tree peony (*Paeonia suffruticosa*) has a root that will grow under normal germinating conditions. The shoot, however, is blocked and requires exposure to low temperature to permit growth. The chilling is not effective until after the root has grown. Seeds of the tree peony ripen in late summer, and the winter temperature is too low to permit germination. The root therefore cannot grow until spring. The required chilling is received during the next winter, and the shoot emerges above ground the second spring, 18 months after the seed matures.

The seed of *Trillium grandiflorum*, a wild flower found in the woods in early spring, requires chilling to remove the block to root growth and then a period of moderate temperature to permit root growth. This must be followed by a second period of chilling to remove a shoot block, and a second moderate temperature period for shoot growth.

CONDITIONS for removing blocks have been studied for many years, but we need to know much more about how blocks are removed naturally and how they may be removed artificially to produce plants out of their normal environment and season or to measure viability of seed in the laboratory.

One way to remove blocks is by a natural combination of time and exposure to the elements. A hard seedcoat may be softened in the soil by alternate freezing and thawing or wetting and drying. Micro-organisms may use the seedcoat as a source of nutrients and thus rot it off. At the same time, low soil temperature may meet a requirement for chilling.

Mere drying for a period induces changes that permit germination in some seeds. This is afterripening in the dry condition and is used often in the preparation of crop seeds.

A hard seedcoat may be artificially removed or its effect minimized by scarification. Seeds are scarified mechanically by blowing them against abrasive points or rubbing them over an abrasive surface. Chemical scarification with acid or hot water is used frequently in the case of such seed as black locust (*Robinia pseudoacacia*) and the dropseed grasses (*Sporobolus*).

The leaching action of water removes the blocks in some seeds. Desert plants are noteworthy in this respect. A seed in a desert needs enough water to germinate and much more to become established. It must be able to distinguish between a small amount of water and a large amount. The seed does this by means of inhibitors that are removed only by a large amount of water—an amount that will moisten the soil enough for the plants to become established.

Light initiates changes that permit germination of some seeds. The farmer when he plows his field and the gardener who spades a garden assists the germination of weed seeds by turning new seeds to the surface, where the light requirement is satisfied. A new crop of weeds is assured after each cultivation.

The conditions against which blocks protect the seed often are the same ones that serve to remove the blocks. This is closely related to the alternation of seasons a seed encounters.

Consider an annual plant of the Temperate Zone, such as ragweed (*Ambrosia artemisiifolia*), whose seeds mature in the late summer. It is not winter hardy. If the seeds germinate immediately upon maturity, the new plant will be killed by freezing during winter. Germination is blocked, however, and the block must be removed by some mechanism. This mechanism is controlled by exposure to low temperature during winter. Thus the seed is prevented from growing until the low temperature renders growth possible. The same low temperature that removes the block permits growth the following summer as the seed is warmed. The same condition occurs in the buds of trees.

Germination blocks are reversible. Afterripened seeds are ready to germinate. If they are in a place where they receive a deficiency of oxygen, an excess of water, or a temperature that is too high for germination, however, they will revert quickly to the blocked condition.

Afterripening also is reversible—undoubtedly a major factor in the longevity of weed seeds and a factor that often is overlooked in germinating seeds for garden purposes.

For example, seeds that have been afterripened carefully in a refrigerator may be planted at a high temperature, 76° or higher, and revert to the blocked condition instead of germinating. The seeds of pine, rose, apple, cocklebur, and many others are known to revert to the blocked condition—"secondary dormancy."

Blocks may be physical or chemical.

Physical blocks are caused by the structures surrounding the embryo.

Chemical blocks are of two types—inhibiting chemicals in tissues surrounding the seed and an inhibition within the embryo itself.

Many seeds have more than one block. In the subterranean clover (*Trifolium subterraneum*), a hard coat is present in addition to a chemical block within the embryo.

PHYSICAL BLOCKS are associated with the structure of the seedcoats and other tissues surrounding the embryo.

These tissues usually are considered to function primarily to protect the embryo from mechanical damage and from attack by micro-organisms. They may also act as germination blocks. The seedcoat of some seeds is so hard that it mechanically prevents expansion of the embryo. In others, the seedcoat is so impervious to water that the seed remains dry internally even though it is immersed in water.

The seedcoat and surrounding membranes also may act as blocks by preventing the entry of oxygen into the embryo or possibly the discharge of carbon dioxide. Most seeds require an abundant supply of oxygen during germination. Membranes restrict the oxygen supply in some seeds, and the resulting change in seed metabolism imposes a block.

Chemical blocks may be present in tissues surrounding the embryo. We commonly find that seeds do not germinate until freed from the outermost covering, the ovary or fruit wall. Seeds do not normally germinate within the fruit. Occasionally germination occurs on the parent plant. These viviparous seedlings may be economic problems, as in the case of some varieties of soft wheat. It may be that soft wheats lack an inhibitor that is present in seeds of hard wheat.

Germination-inhibiting chemicals in fruits may account somewhat for the failure of seeds to germinate in the fruit. Inhibitors are also known in the seedcoats and the other membranes around the embryo.

More than 120 sources of germination inhibitors were listed in an article in 1949. Many more are described each year. The chemical nature of many of these compounds is known. Most inhibitors are nonspecific. They block germination in many kinds of seeds besides those of the plant in which the inhibitor is found.

A word of caution concerning inhibitors: Inhibitors may be isolated from most or all seeds and other plant parts. The mere isolation of a chemical does not prove that it acts to inhibit germination in the seed. Many actively growing plant parts are excellent sources of the inhibitors found in seeds. We consider this problem later.

We assume that embryo blocks are chemical. Blocks in the seedcoat and membranes are simple and well understood in comparison with blocks within the embryo. It is perhaps even misleading to suggest that the embryo blocks are chemical, although our increasing understanding of growth and metabolism indicates that most growth phenomena result from chemical processes.

We must be careful, however, not to assume that the embryo blocks are necessarily caused by growth-inhibiting chemicals. They may result equally from a deficiency of some essential compound. The effect of afterripening might then be to permit the accumulation of the missing compound to the level that would permit germination. When seed of the loblolly pine (*Pinus taeda*), for example, is kept 2 weeks at a low temperature, some substance apparently accumulates that permits germination when the seed is stimulated by light.

Many investigators believe that inhibitors cause embryo blocks. Their evidence is not always sound, because it is extremely difficult to isolate and identify an inhibitor. It cannot be isolated until an active compound can be measured outside the plant. Since its chemical properties cannot be known until after isolation, some plant response, or bioassay, must be used for measurement.

The best test for an inhibitor would be to inhibit afterripened seeds of the kind from which it was isolated. But how can one be sure that a compound will enter the undamaged embryo? To overcome this difficulty, investigators frequently test isolated compounds by their effect on cell elongation in isolated sections of stem tissue. But what evidence is there that a germination inhibitor acts by directly blocking cell elongation?

Even the isolation of an inhibitor is not direct evidence that it actually functions as an inhibitor in the seed. When a chemical is extracted, it is torn from its normal location and form in the cells.

Cyanide, a powerful (and deadly to animals) inhibitor, is a common constituent of many seeds. It is an obvious candidate for a compound that can control germination. In the embryo, however, it occurs in a chemical complex known as emulsin, a glucoside. In this form it has no growth-inhibiting properties. Free cyanide is formed only when the cells are damaged. Many investigations have failed to give adequate evidence that cyanide actually functions as a germination inhibitor.

There is a rigorous test that should be used to decide whether an extracted compound functioned in the seed as an inhibitor. The true inhibitor should change in quantity parallel to changes in the physiological condition of the seed. If the seed is strongly blocked, a germination inhibitor should be present in high concentration. As the block is removed, the concentration of inhibitor should decline to a minimum when germination is most prompt. If afterripening is reversed by high temperature or lack of oxygen, the concentration of inhibitor should increase.

With the present state of our knowledge, we can conclude that growth-inhibiting chemicals may very well control germination. They are not the only possible mechanism, however. Much more intensive research will be required to establish their nature.

Changes in cellular organization exemplify a type of mechanism that has not yet been investigated enough as a possibility for controlling germination.

Modern biology recognizes that cells of animals and plants are similar in that they contain large numbers of complex chemical compounds. The compounds are not distributed at random within the cells.

They exist in definite chemical and physical combinations in parts of the cell, such as mitochondria and microsomes, which are too small to be seen with ordinary microscopes. Even powerful electron microscopes can only suggest how they are arranged.

We know that the processes of respiration, photosynthesis, and protein synthesis depend on such structures.

In the seed, is it possible that germination may fail because the compounds within these structures are incompletely or improperly joined? We have no direct information yet on this possibility, but we should not ignore it.

Many uncertainties and unknowns exist in our understanding of the mechanism of germination blocks.

What, in fact, do we know?

We know that we can distinguish between blocks that seem to yield easily to removal and those that require much more strenuous efforts. Light, for example, stimulates the germination of many seeds, and this same mechanism controls other plant growth responses, including flowering.

We know that the light reaction results from a pigment that may absorb either red or far-red light. Although the pigment has been isolated from seedlings, we do not know how it is coupled to germination.

We know that other factors also can stimulate germination. Virginia runner-type peanut seeds (*Arachis hypogaea*) are blocked at maturity. They germinate within 48 hours if exposed to air containing a minute amount of ethylene gas.

Some kinds of seed respond to environmental factors much more sluggishly. They do not seem to require a true stimulus. Time is important; the essential processes are slow. This is the case with low temperature.

We know that low temperature is required to remove the blocks in many seeds. This may require a few days to several months. High temperature can regenerate the block.

Since chemical reactions depend on temperature, increasing in rate with increasing temperature, we assume that temperature must influence one type of chemical reaction differently than does another. The specific reactions involved are completely obscure, however. Why low temperatures should be required is difficult for us to understand.

Interaction between blocks is common. Blocks that can be removed by stimuli (such as light) and blocks that can be removed by long exposure to low temperatures may be interdependent. Artificially applied chemicals can interact with light and temperature.

We know that these interactions exist. We know that germination is controlled by "blocks." It seems reasonable therefore to visualize germination proceeding by a number of alternate pathways. These pathways may be closed by blocks imposed and removed by various environmental conditions. Some of the pathways are temperature sensitive. Some are light sensitive. Some can be controlled by applied chemicals. Some cannot be.

The idea of alternate pathways is not unique.

Biochemistry has shown that chemical reactions in cells and organisms are brought about by enzymes. The rate of activity of these enzymes is controlled by many factors, including temperature. We do know that a cell may have several pathways of producing or utilizing a required chemical. These are alternate pathways of synthesis or destruction.

Are these also alternate pathways of germination? This question cannot now be answered, but we strongly suspect that the answer is yes.

Why bother with these complexities of mechanism? Are they important? Are they worth the time and energy spent in studying them? The answers to these questions must be yes.

Understanding in a scientific sense leads to control. Control of germination is of enormous practical importance. Think of agriculture without weeds!

We recognize that germination is a critical stage in the life of each plant. Natural mechanisms exist that control germination. An understanding of these mechanisms would provide us with the scientific basis upon which control of germination could be based.

With this knowledge we might cause, or prevent, germination at will. We also could probably control the storage life of seeds.

There is another reason for understanding the mechanism of germination. Scientists since 1930 have come to recognize that all cells, whether they are bacterial, insect, plant, or human, are essentially the same. Blocks to growth are not unique to plants; they are known to exist in many, if not all, organisms.

An understanding of the mechanisms of germination blocks in seeds could contribute to a larger understanding and control of growth in the other organisms.

BRUCE M. POLLOCK *is Leader of Vegetable Seed Investigations for the Crops Research Division of the Department of Agriculture. He has done postdoctorate research in the Cytochemical Department of the Carlsberg Laboratory in Copenhagen, Denmark, and was associate professor of biological sciences and horticulture at the University of Delaware.*

VIVIAN KEARNS TOOLE *is a plant physiologist doing research on seed physiology in the Vegetables and Ornamentals Research Branch, Crops Research Division, Agricultural Research Service. She holds degrees from the University of North Carolina and the George Washington University.*