PHYSIOLOGICAL, BIOCHEMICAL, AND GENETIC CHANGES IN SEED QUALITY DURING STORAGE

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Seldom are seeds harvested and immediately planted without undergoing at least a brief storage period. Exceptions would be certain seeds designated as "recalcitrant" (not readily storable) (45) which must be planted immediately, or viability is soon lost. Examples include many tropical plants as well as many of our temperate trees. The life span of these recalcitrant seeds may be of the order of a few days to several months (22). Another case where freshly harvested seeds may not undergo storage would be breeding materials where the object is to produce as many generations a year as possible. In this case, seeds are often harvested in an immature state and planted immediately. However, normally most seeds are stored several weeks or months before being planted. Longer storage periods, 1 to 5 years, are necessary for seeds which may be expensive or difficult to produce, or for those cultivars which are not produced every year due to lower demand by growers. Finally, germplasm banks, such as the USDA National Seed Storage Laboratory, may wish to preserve seeds for decades or even centuries (26).

Four factors must be considered in discussing seed storage. Time as a factor has already been mentioned. The other 3 factors, temperature, relative humidity (seed moisture content), and oxygen, have been discussed at great length by many authors (8, 22, 27, 43). With the exception of the recalcitrant species, 2 factors, time and oxygen level, have very little effect on storability if the optimum seed moisture content and storage temperature are observed. For example, Roberts and Ellis (48) predicted 95% survival of pea (*Pisum sativum* L.) seed after 1,090 years of storage at −20°C and 5% seed moisture content. If storage temperature is reduced further, the viability may be extended virtually indefinitely (25). The objective of this paper is not to discuss seed longevity, however, but to examine the physiological, biochemical, and genetic changes which might take place during storage. The changes to be discussed may be altered or even negated by alteration of the storage conditions.

Physiological changes

In this section I will discuss several gross changes in the physiology of seeds and seedlings resulting from storage of the seed. These changes usually affect either the germination of the seed or the growth of the resulting plant.

Induction and loss of dormancy. Probably the most important physiological change in seeds during storage concerns their viability or germination potential. Loss of viability with time is inevitable, although we have not yet established the limits of storage for any non-recalcitrant (orthodox) species. Seeds may lose germinability during storage for reasons apart from death; conversely, seeds may actually increase in germination during storage. The mechanism here is the induction and loss of dormancy. Storage condition is usually the controlling factor in this response.

Induction of dormancy during storage. Good storage conditions usually involve low temperatures and, more importantly, low relative humidities. Consequently, seeds may lose moisture during storage. Low seed moisture results in lowered germination in many kinds of seeds. Nutile and Woodstock (39) found that drying sorghum (*Sorghum bicolor* L.) seeds from 12 to 7% moisture content reduced germination by up to 65%, depending upon the temperature used to test the seed. Induction of hard seed, a form of dormancy, in certain cultivars of snapbeans and many other legumes, is common when seed moisture content is reduced (38, 42). Dry storage may also induce a secondary dormancy superimposed over a primary dormancy, as seen with seeds of hazel (*Corylus avellana* L.) (14, 15).

Storage at high humidity may also result in the induction of seed dormancy. Kosar and Thompson (29) stored lettuce (*Lactuca sativa* L.) seed at 10°C at relative humidities ranging from 0 to 100%. At very low humidities, seeds progressively developed dormancy (germination temperature = 24°C). Between 25 and 58% RH, little dormancy developed. At 67% RH and above, dormancy increased and seemed to precede seed death. Another case of induction of dormancy in lettuce was reported by Chowdhuri and Chatterjee (17). Seeds gradually lost germinability up to 150 days of storage and then gradually regained it after 1 year of storage. Unfortunately, the precise storage conditions were not specified.

Breaking dormancy during storage. Perhaps a more common result of storage is the breaking of dormancy. This may take the form of holding seeds in a moist condition and near freezing temperatures (after-ripening or stratification). However, dry storage can also result in loss of dormancy. Barton (9) lists over 40 species which after-ripen in dry storage. Many of those that respond to dry-storage after-ripening are capable of germination even when freshly harvested, but only in a narrow range of temperature or other environmental conditions. For example, after-ripening in dry storage, or dormancy of freshly harvested, seeds, is characteristic of many grasses, including some of our common cereals, such as oats, barley, wheat, rye, and rice. The period of dry storage needed for after-ripening varies from days to months. Many vegetable and flower seeds also exhibit this type of dormancy. For this reason, germination tests on fresh seed may not be reliable unless special methods are used to break the dormancy.

Shifts in germination requirements. Closely associated with the induction and loss of dormancy during storage is the shift in germination requirements for seeds during development, after-ripening, and storage. Vegis (54) has reviewed extensively the literature on changing temperature requirements for seed germination. Basically, there are 3 patterns seen in which the temperature range for germination is narrowed. Either the maximum or minimum germination temperature changes or both change, which results in the inability of the seeds to germinate at one or both of the temperature extremes.

Narrowed range for germination at low temperatures. In the first pattern, there is a gradual lowering of the maximum temperature at which germination can occur. The minimum temperature remains unchanged. Eventually, a point is reached where germination can occur only in a very narrow temperature range. In the extreme case, "true dormancy" results, and no germination can take place. Then the trend is reversed, and the seeds gradually recover their germinability, and the maximum germination temperature increases. The best examples of this type of behavior are the cereals. It has been known for many years that embryos of cereals can germinate at a very early developmental stage (7-14 days after fertilization). During the ripening process the caryopses lose the ability to germinate at high temperatures, but throughout maintain the ability to germinate at low temperatures. During after-ripening, the caryopses gradually recover the ability to germinate at high temperature. Seeds of many species and varieties of fruit trees in the family Rosaceae and many other perennials and winter annuals behave similarly.

Narrowed range for germination at high temperatures. The second type of pattern of temperature shift is the exact opposite of the first; in the second, the temperature range for germination is narrowed through an increase of the minimum temperature at which germination can occur. Freshly harvested seeds of *Amaranthus retroflexus* do not germinate at temperatures lower than 40°C. This dormancy disappears in dry storage, as is shown by a gradual lowering of the minimum temperature for germination. Seeds of *Thlaspi arvense* (penny-cress) only germinate within a range of 28-30°C. After stratification at low temperature, they gradually acquire the ability to germinate at lower and lower temperatures.

Narrowed range for germination at intermediate temperatures. The third pattern involves a narrowing in temperature range through both an increase in the minimum temperature and a decrease in the maximum temperature at which germination can occur. Vegis (53, 54) cites numerous examples of this type of behavior, including seeds of *Rumex crispus, Viola tricolor arvensis, Chenopodium album,* and *Taraxacum megalorhizon.*

Production of abnormal seedlings. Another physiological change during storage is the production of abnormal seedlings. As seeds deteriorate in storage, the number of abnormal seedlings slowly increases as germination (recorded as percent normal seedlings) declines. Rapid aging may result in fewer abnormals as the population passes quickly from normal seedlings to dead seeds. Certain types of abnormal seedlings are most prevalent and usually involve seedlings with no roots or no shoots. Generally these die before they become established plants in the field. Other abnormals survive, but have delayed growth and, in the case of many vegetables, mature late and thus do not contribute to the yield. Baldheads in beans are a classic example. Toole and Toole (52) reported an increase in physiological baldheads during warehouse storage; however, under controlled

storage conditions "the most evident change in a seedling was loss of vigor indicated by a very slender stem, a weak primary root, and small leaves. Definite injury to any one tissue was not observed."

In studies of aging-induced abnormal seedlings in onions (*Allium cepa* L.) Clark (18) observed that abnormal seedlings failed to form sharply bent knees, and many had blunt, undeveloped primary roots. "The failure of knee formation was found to be associated with the failure of critical cells of the cotyledon to enlarge and cause the cotyledon to bend. Dwarfed primary roots were found to be associated with the failure of root cells to elongate."

Physiological necrosis, or red cotyledons, in lettuce is another seedling abnormality which has been linked to storage conditions. Bass (11) showed that under poor storage conditions, red cotyledons developed rapidly, and that combinations of high temperature (21°C) and low relative humidity (30-50%) produced more physiological necrosis than combinations of 21°C with 70 and 90% RH. Storage at −12°C and 70% RH prevented red cotyledon development for over 4 years.

Liquid nitrogen as a storage medium is currently being studied at the National Seed Storage Laboratory (50, 51). Although most seeds studied can withstand exposure to the ultracold temperatures (−196°), certain species, notably flax (*Linum usitatissimum* L.), sesame (*Sesamum indicum* L.), and filberts (*Corylus* sp.) have resulted in some seed and seedling abnormalities. The damaging effects of the liquid N_2 on flax appear to be related to seed moisture content.

Effects on plant growth and yield. Plant growth. The most noticeable effect of seed storage on plant growth is a gradual reduction in seed viability and in the vigor of those seedlings which do survive. This loss in vigor may be manifested in many different ways. Slower germination of aged seeds is often used as a vigor test. Not only is there a delay in germination, but the rate of root elongation may also be reduced (2, 24). Shoot growth can also be slowed in the early stages of plant development. Growth habit may also be altered as a result of seed storage. Harrison (24) showed a delay in tillering of barley (*Hordeum vulgare* L.) plants from deteriorated seed, but tillering rates in plants from control and deteriorated seeds were similar. Another interesting effect of seed aging was found on the flowering habit of squash (*Cucurbita pepo* L.) plants (5). Plants from seeds stored for 1 or 2 years produced significantly fewer male flowers and lower male: female flower ratios than plants from freshly harvested seeds. This often resulted in higher yields from the stored seed.

Yield. Of greatest economic importance is the effect of seed storage on yield. Conflicting reports in the literature make a general conclusion difficult. First, the effects of storage on reduced population size in the field must be discounted. This can be done in either of 2 ways. The control and stored seeds may be overplanted and then thinned to a uniform stand. Alternatively, the seeds may be started in a greenhouse and transplanted to the field to give a uniform stand. This second technique was used by Barton and Garman (10) to compare yields of aster (*Callistephus chinensis* (L.) Nees), verbena (*Verbena teucroides* Gill. & Hook, now *V. plantensis* K. Spreng.), pepper (*Capsicum frutescens* L.), tomato (*Lycopersicon esculentum* Mill.), and lettuce from fresh and stored seeds. No effects of storage on yield were found for aster, verbena, and pepper. Stored tomato seeds with only 6% germination resulted in significantly lower yield than fresh seeds, while aged lettuce seeds actually resulted in higher head weights than fresh seeds. More recently, Abdalla and Roberts (2) found that, although early growth, in aged seeds of barley, broadbeans (*Vicia faba* L.), and peas was lowered compared with that of fresh seeds, this early inhibition did not persist; under normal field conditions, initial low rates of growth were compensated for at later stages of development. Thus, they found that, providing initial seed viability was not less than 50%, final yields were not significantly affected.

Biochemical changes

This topic is discussed by Abdul-Baki elsewhere in this series of symposium papers and in an extensive review (3). However, there are 4 topics which I would like to mention briefly in connection with biochemical changes during storage.

Auto-oxidation of lipids. Auto-oxidation of lipids is a non-enzymatic reaction involving the production of free radicals from the action of light and other radiation on unsaturated fats. These free radicals can then combine with oxygen to form various hydroperoxides; these can eventually lead to inactivation of enzymes, denaturation of proteins, and disruption of nucleic acids (23, 28). Artificially aged (high humidity and high temperature storage conditions) seeds were used to demonstrate lipid oxidation with increased aging (21) and also to demonstrate that applying a negative potential ("cathodic protection") to the seeds to reduce free radicals could result in their longer survival in storage than during storage of unprotected seeds (12, 40).

Loss of membrane integrity. Changes in the structure of lipids, particularly those making up the membranes, lead to loss in integrity of the membrane. Leaching of nutrients in damaged or aged seeds has formed the basis for vigor tests for pea (16, 30) and other seeds (31). Dr. Abdul-Baki has covered membrane integrity in greater detail in his symposium article.

Loss or reduction of enzyme activity. Numerous studies have correlated reduced vigor and/or germination with lowered biochemical activity in aged seed (3, 4, 41). The ability of the embryo to synthesize enzymes for mobilization of food reserves is reduced; this results in slower initial growth of seedlings, as mentioned earlier. Most of these studies have employed rapid aging techniques, and care must be taken to separate out effects of microorganisms in studies involving high seed moisture and elevated storage temperature (20).

Failure of repair mechanisms. One of the more popular recent ideas to explain death of seeds in storage is the failure of cellular repair mechanisms. Some age-induced damage is repaired during early germination (13); however, under low temperatures, and more particularly at low seed moisture contents, which are the preferred storage conditions, deteriorative changes may still take place inside the cells. Such changes are auto-oxidation of lipids, mutation, or denaturation of enzymes. Repair enzymes cannot function in the absence of sufficient water content, whereas under high seed moisture contents, under special conditions, as shown in lettuce, ash (*Fraxinus americana* L.), and barley, longevity is increased (55, 56, 57) and repair of genetic damage takes place (19). "Recalcitrant" seeds, which normally have high moisture contents, nevertheless cannot be stored for very long. Much more work is needed in this area before a full biochemical explanation of seed deterioration is possible.

Genetic changes

During prolonged storage, as in the case of germplasm preservation, genetic changes become increasingly more important. These changes may take the form of induced mutations, such as chromosomal aberrations, or natural selection within a heterogeneous population.

Chromosomal aberrations. For many years it has been recognized that mutations occur more frequently in plants grown from aged seed. Navashin (36, 37) was the first to observe the increased rate of chromosomal aberrations in root tips from aged seeds of *Crepis tectorum* L. This observation has been confirmed by many studies in several other species (7, 32, 44, 46). The induction of chromosomal aberrations and other genetic changes in seeds during storage has caused some concern among germplasm workers, and a recommendation has been made that the seeds should not be allowed to drop more than 5-10% in viability before the stocks are regenerated (47). With respect to induced chromosomal aberrations in aged seed, Murata (32) studied in detail the fate of the aberrations during the growth of barley (*Hordeum vulgare* L.) plants resulting from aged seed. His results clearly demonstrated that aging-induced chromosomal aberrations are eliminated during the growth and reproductive stages of the plant and thus are of little consequence in altering the genetic makeup of the next generation (32, 34, 35).

Of greater consequence to the seed is the effect of chromosomal aberrations on the normal germination of individual seeds. As described earlier, one consequence of storage is the production of increasing numbers of abnormal seedlings. In studies with pea (*Pisum sativum* L.), a close correlation was found between seed deterioration and the normal onset of mitosis in root tips of the germinating seeds (33). Mitosis was not only delayed in aged seeds, but the mitotic index was reduced. Disruption of the normal mitotic cycle, either because of induction of chromosomal aberrations or some other mechanism, is a natural consequence of seed deterioration.

Point mutations. Unlike chromosomal aberrations, point mutations may occur during seed storage and, if they are non-lethal, could gradually accumulate in a given population. Information on this particular topic is limited and, unfortunately, has usually been obtained on chlorophyll deficiency mutations, which are generally recessive lethal mutants (1, 46). Detailed studies are needed before it can be concluded that point mutations present a serious threat to the genetic integrity of a seed population. From the standpoint of germplasm preservation, accumulation of mutations during several cycles of seed aging and regrowing may actually be beneficial, as it adds to the total genetic variability of a species, which is one of the goals of germplasm conservation.

Population shifts. A more serious threat to the genetic makeup of a population of seeds consists of natural selection. Heterogeneous

populations (which many germplasm accessions are) undergo selection both during storage and during regeneration (6, 49). Genetic shifts in mixed populations may result from differential survival in storage, productivity differences, environmental selection, including the effects of weather conditions and pathogens, maturity differences, outcrossing, and finally, simple human error.

Conclusions

An obvious conclusion from the above review of physiological, biochemical, and genetic changes in seeds during storage is that storage time, per se, is not the critical factor influencing the change. Rather, it is the storage condition. Virtually every change noted was associated with a condition leading to or causing loss of viability. The solution, then, is to increase seed longevity. Attempts to prolong seed storage life have recently centered on the use of liquid nitrogen (LN_2) as a storage medium (25, 50, 51). The temperature of LN_2 is $-196°C$. At this temperature, presumably all biochemical activity is reduced to essentially zero. Deteriorative changes noted above should thus be eliminated. Genetic changes, however, may still take place, and this factor will have to be studied carefully before LN_2 storage is is adopted on a routine basis.

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ASSESSMENT OF SEED QUALITY[1]

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The assessment of seed quality continues to attract increasing attention from the seed industry. Farmers believe that seed quality information will enable them to make economic decisions regarding the cost of seeds, earliness of planting, quantity of seeds to plant, and the anticipated uniformity of stand. Seedsmen believe that seed quality information will aid them in monitoring seed quality during the various processing phases of seed production. Seed quality tests might reveal where loss in seed viability occurs during combining, cleaning, drying, storing, bagging, etc. and may pinpoint adverse practices which could subsequently be improved. The accurate assessment of seed quality could have a significant impact on improving seed performance, which would culminate in important economic considerations for the farmer and seedsman alike. This report will attempt to clarify what seed quality is, what constraints are imposed on seed quality testing, how seed quality tests are assessed, how seed quality tests can be standardized, and what the future of seed quality testing may be.

What is seed quality?

The Federal Seed Act dictates that seed quality is determined by 2 principle factors: seed purity and germination. Seed purity tells the seedsman and consumer how much unwanted material is present in the desired pure seed and specifies the nature of each containment. Seed germination is intended to assess how viable the purchased seed is and is defined as, *"the emergence and development from the seed embryo of those essential structures which, for the kind of seed in question, are indicative of the ability to produce a normal plant under favorable conditions"* (1). However, this definition and the general philosophy of germination testing have proven inadequate for assessing potential field emergence for the 2 following reasons:

1. The definition refers to the ability of a seed to produce a normal plant under *favorable* conditions. When seeds are germinated, only optimum test conditions such as substrate, moisture, temperature, light, and adequate testing time are employed to insure that maximum germination percentages are obtained. Unfortunately, optimum conditions are rarely encountered in the field and it is not surprising that field emergence is often less than that predicted by the germination test.

2. The germination test fails to take into account the progressive nature of seed deterioration. A seed is considered germinable when it has fulfilled the criteria established by the definition for the production of a normal plant. Therefore, seeds are classified as either germinable or non-germinable with no distinctions provided for "strong" or "weak" germinable seeds. Such information would be useful since we can forecast that "weak" seeds will soon deteriorate and be classified as non-germinable. Germination testing, therefore, does not provide a complete evaluation of seed lot deterioration or quality.

These inherent weaknesses of the seed germination test have been with us a long time and have resulted in dissatisfaction among seedsmen and farmers. Consequently, interest has been spurred to develop another or supplemental parameter of seed quality. This component is now known as seed vigor and will occupy the major portion of this discussion. Unfortunately, there are many misconceptions concerning seed vigor. This is exemplified by the array of definitions proposed for seed vigor which were recently collated by Heydecker (7). Because of this confusion, it is important that seed vigor be formally defined. The 2 major seed testing organizations, the International Seed Testing Association (ISTA) and the Association of Official Seed Analysts (AOSA) have charged their vigor testing committees with proposing a specific definition for seed vigor. In May, 1977, at the Madrid, Spain meetings, the ISTA group proposed the following definition for seed vigor: *"Seed vigor is the sum total of those properties of the seed which determines the potential level of activity and performance of the seed or seed lot during germination and seedling emergence".* Included among the aspects of performance were: 1) biochemical processes and reactions during germination such as enzyme reactions and respiratory activity, 2) rate of

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