many important physical and chemical factors.

Details of the changes of simple organic constituents and respiratory processes of quiescent seeds have long been known. Information about complex organic compounds and seed hormones is just unfolding.

Other information and an understanding of facts already known must be sought.

We know enough about the manipulation of storage environments to minimize undesirable changes in most seeds for one or several years. Yet many so-called short-lived seeds do not retain their viability even under the best known procedures.

Perhaps the new research techniques and hypotheses will provide better ways to lengthen the lifespan and increase the germinative ability of the living seed.

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How Long Can a Seed Remain Alive?

CLARENCE R. QUICK

PEOPLE USED to think that 150 years was about the maximum lifespan of the most durably viable seeds.

Some years ago, however, a Japanese botanist found some viable lotus (waterlily) seeds in a layer of peat under a layer of windblown soil in a dry lakebed in Manchuria. A geologist classified the peat and loess layers of the lakebed as Pleistocene deposits, but this geologic period—the Ice Age—in general came to an end 10 thousand to 15 thousand years ago.

The ancient Manchurian seeds are the size of small hazelnuts. They have thick, horny seedcoats. They closely resemble the seeds of *Nelumbo nucifera*, the East Indian lotus.

Several germination tests were made on the seeds. Almost all of them grew, even after having lain around in museums for a decade or two.

Was the estimation of age of the peat somehow in error, or are these viable seeds actually hundreds of years old?

Preliminary tests on several whole seeds by the residual carbon 14 isotope method of dating organic carbon residues indicated that the seeds were between 830 and 1,250 years old. More tests on larger numbers of seeds are needed to determine the probable maximum age. The seeds are reasonably common in the peat, but the old lakebed is in China, and there seems to be no immediate way to get more of the seeds.

SEEDS sometimes are divided into three classes according to their lifespan under the best possible conditions.

Seeds may be microbiotic (a lifespan of less than 3 years), mesobiotic (3 to 15 years), or macrobiotic (more than 15 years).

Such a classification is convenient but arbitrary. It assumes that we know the optimum conditions for preservation of viability in many kinds of seeds, but that is not entirely correct, even for the many economically important kinds of seeds.

Many—perhaps most—kinds of seeds of Temperate Zone wild plants are best preserved if they are carefully and thoroughly dried, placed in airtight containers, and stored under moderate refrigeration.

Many others, particularly seeds of numerous plants of the wet Tropics, would be killed by this treatment. Some seeds are dead if they become thoroughly dry. Immature seeds and seeds from diseased or otherwise unvigorous plants commonly have less longevity than more normal seeds.

Obviously, adequate methods for storage and adequate methods for germination must be known specifically before maximum longevity of seed can be approximated.

Most of our knowledge of longevity of seed comes from germination tests with three general types of stored seed samples: Seeds recovered from planned length-of-storage tests, "finds" of old seed samples, and old herbarium collections. The third method has led to valuable results, but it is not generally recommended, especially by herbarium curators! Collection data and storage conditions, furthermore, are not likely to be known so explicitly for seeds from herbarium samples and from finds of old samples.

Carefully planned length-of-storage tests have been made on many species of seeds and under many conditions of storage. Storage conditions and tests are highly important, especially for crop seeds. In this chapter I discuss only the tests that resulted in germination of seeds of ages well beyond common lengths of commercial storage of crop seeds.

Paul Becquerel, a French botanist, in 1907 and again in 1934 gave reports on germination tests on about 500 species of old seeds from a storage room in a museum. Of 13 species of viable seeds more than 50 years old, 11 species were legumes. Two species of *Cassia* (Leguminosae), one with seeds viable after 158 years and one after 115 years, were outstanding.

A. J. Ewart, an Australian, in 1908 reported tests on some 1,400 species and varieties of old seeds. Of the 49 samples of viable seeds more than 50 years old, 37 were legumes. Seeds of one species each of *Hovea* and of *Goodia* were viable after 105 years. Both plants are legumes.

J. H. Turner, Kew Gardens, England, in 1933 reported viable seeds in samples of seven species of legumes that were 80 or more years of age. The genera were *Anthyllis*, *Cytisus*, *Lotus*, *Medicago*, *Melilotus*, and *Trifolium*.

The Gardeners' Chronicle, London, in 1942 reported viable seeds of *Albizzia julibrissin* (a legume) after 149 years of storage and of *Nelumbium speciosum* (a waterlily) after about 250 years.

Many other germination tests on old seeds have been reported.

Frits W. Went, of the California Institute of Technology, and Philip A. Munz, of Rancho Santa Ana Botanic Garden, Calif., in 1948 started an elaborate longtime longevity test on seeds of more than 100 native California plants. Samples were dried in vacuum desiccators, packed in small glass tubes (20 tubes per seed sample), evacuated in the tubes to 0.1 millimeter of mercury or less, sealed, and placed in an insulated but unrefrigerated storage room. It is proposed that the last set of these samples be tested for germination in A.D. 2307.

We used to read reports that plants grew from "mummy" grains and pease found in ancient Egyptian tombs. It was also suggested somewhat later that viable seeds of *Silene* (a pink) and of *Glaucium* (a poppy) may have remained dormant for some 2 thousand years in the soil under heaps of ancient mining and smelting debris in the Laurian area of Greece.

Seed physiologists now consider all such claims erroneous. In all tests of authentic seed from Egyptian tombs, the seeds were dead. They disintegrated promptly.

Farmers know that weed seeds can remain viable but dormant for many years in clean-cultivated land. Seeds of many garden plants react similarly to burial.

Seedlings of certain plants grow abundantly around old cow pads in pastures, an indication that some seeds can pass through the digestive system of grazing animals and remain viable, possibly to contaminate clean pastures. Sheep, horses, deer, bear, and rabbits are known to pass viable seeds. Some birds scatter many kinds of viable seeds. Other plant-eating and fruit-eating animals are presumed to do the same. Topsoil of fields and wildlands comes to contain considerable populations of viable seeds.

For example, 800 seedlings of field bindweed per acre emerged in 1941 in a 14-acre field, from which the original stand of bindweed had been eradicated in 1921. No bindweed plants had been permitted to fruit during the intervening period.

The plant ecologist, the farmer, and the seed physiologist are interested in these "soil-stored seeds" because of their importance to the long persistence of plant species that are thus scattered in time as well as in space.

The forest floor under stands of mature timber often contains surprising numbers of viable seeds. One study in Maine indicated a total viable seed population of 650 thousand per acre.

A research worker in California found 2,820 thousand viable seeds per acre. Seeds of trees in ecologically climax vegetation are seldom found in abundance in these studies.

Seeds and other plant residues in adobe buildings in the Southwest and sodhouses in the Midwest have been studied to estimate seed longevity and to date the introduction of weeds.

Drastic disturbances to the soil mantle, such as war bombings, often have caused seedlings of plant species to emerge in unexpected places.

The knowledge that some seeds remain viable in soil for decades stimulated several extensive buried-seed experiments. Investigators mixed seeds of known species, age, and condition with sand or soil and packed them in replicated bottles. They buried the bottles, mouth downwards, at one or several depths below the soil surface. They removed one or a set of bottles at planned intervals for testing. The remaining bottles were kept undisturbed.

These buried-seed tests simulate, but do not necessarily duplicate, environmental conditions of seeds naturally stored in the soil. One big advantage of the planned tests is that the age of the seed is known precisely.

Prof. W. J. Beal, of the State University of Michigan, started one of the earliest of these tests. He buried 20 pint bottles of weed seeds mixed with sand in the autumn of 1879. Each bottle contained 50 seeds each of 20 kinds of weedy plants. He buried the 20 bottles, with mouths tilted downward, 18 inches below the soil surface.

After 40 years in the soil, but not after 50 years, seeds of the following five plants were still viable: *Amaranthus retroflexus* (pigweed), *Ambrosia elatior* (ragweed), *Lepidium virginicum* (peppergrass), *Plantago major* (plantain), and *Portulaca oleracea* (purslane).

After 40 and 50 years, but not after 60 years, two additional species grew: *Brassica nigra* (mustard) and *Polygonum hydropiper* (knotweed).

After 40, 50, and 60 years, but not after 70 years, *Silene noctiflora* (catchfly) grew.

And after 70 years, three species were still germinable: *Oenothera biennis* (evening-primrose), *Rumex crispus* (a dock), *Verbascum blattaria* (mullein).

J. W. T. Duvel, of the Department of Agriculture, in 1902 buried multiple sets of seeds of 107 species of wild and cultivated plants near Rosslyn, Va. He packed the seeds in sterile soil in flowerpots covered with porous clay lids and buried the pots in the open at three depths—8, 22, and 42 inches. Sets of seeds were removed periodically and tested for germination.

Of the 107 species buried in 1902, 71 grew after 1 year, 61 after 3 years, 68 after 6 years, 68 after 10 years, 51 after 16 years, 51 after 20 years, 44 after 30 years, and 36 after 39 years. The tests were discontinued with the 39-year-old set of pots dug up in 1941.

W. L. Goss, of the California Department of Agriculture, in 1932 buried samples of seeds of 12 troublesome weeds. Seeds of bindweed (*Convolvulus arvensis*), a nightshade (*Solanum elaeagnifolium*), and Klamathweed (*Hypericum perforatum*) were the only ones viable after 10 years.

From the many experiments and observations on seed longevity, we can now draw some generalizations in terms of seed morphology and chemistry and in terms of plant ecology and taxonomy.

Seeds vary widely in size. The coco de mer, a coconut of Praslin Island, Seychelles group, Indian Ocean, is credited with a maximum fruit weight of 40 to 50 pounds. The air-dry seeds of a small American plant in the figwort family (*Ilysanthes dubia*) are said to run about 137 million per pound. In the Temperate Zone, large, heavy seeds tend to be few and long lived, and small, easily distributed seeds tend to be numerous but short lived.

The number of seeds produced per plant also varies enormously. Relatively few seeds are produced by a coconut palm, but it has been estimated that one plant of *Amaranthus graecizans*, an annual tumbleweed, may produce as many as 6 million seeds.

Seedcoats are important in the longevity of seed. Seedcoats of most long-lived seeds have on or near the outside a palisade, or a Malpighian, layer made up of heavy-walled, tightly packed, radially placed, columnar cells. The cells are hard and horny. Usually they are lignified or cutinized. There are no intercellular spaces.

The palisade layer is mechanically protective and highly impervious to water and to respiratory gases. Morphologically, it is the most important structure in seed longevity; most seeds with exceptional longevity have a well developed palisade layer. This layer is not so all-important to buried seeds or to soil-stored seeds, because the soil habitat apparently provides some of the same or similar protective conditions necessary to longevity.

Little need be said here about seed extraction, cleaning, and storage, except to point out that the least damaged seeds—mechanically and biologically—and the best stored seeds will have the greatest longevity.

Many seeds with marked longevity look much alike. Typically they are larger and heavier than the average. Coats are thick and hard and often have a smooth, polished surface. The seeds commonly will not plump if soaked in cold water.

Some examples of well-known native macrobiotic seeds are: *Gymnocladus dioicus* (Kentucky coffeetree), about 240 seeds to the pound; *Gleditsia triacanthos* (honeylocust), about 2,840 seeds to the pound; *Robinia pseudoacacia* (black locust), about 25 thousand seeds; *Ceanothus cuneatus* (buckbrush), about 55 thousand seeds; and *Lotus americanus* (deervetch), about 110 thousand seeds to the pound.

Seeds of cultivated plants long used in their entirety as food commonly have thinner and weaker coats than closely related wild plants. The food seeds generally are shorter lived.

The chemical composition of many crop seeds, but few others, is well known. Seeds are sometimes classified broadly according to the kind of food reserves they store, as starchy seeds (such as those of the Gramineae, the grass family); proteinaceous seeds (for example, those of the Leguminosae, the legumes); and oily seeds (from

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most tree nuts and many other plants).

The classification is arbitrary, because the food reserves of seeds commonly are mixtures of various carbohydrates, proteins, and fats. I know of no comprehensive English summary of the chemical characteristics of seeds.

The longevity of the oily seeds of sugar pine (*Pinus lambertiana*) is related closely to the kind and amount of unsaturated fatty acids in the seeds. Another suggestion is that rancidity of seed fats in pine and other seeds varies inversely with seed viability.

The degeneration of proteins in food grains roughly parallels reduction of seed viability.

Some biochemical aspects of seed viability are known, but the precise reasons for loss of viability—death of the seed—are not yet clear.

The amazing thing about seeds is not that they degenerate with time but that some deteriorate so slowly.

One theory for the degeneration of long-lived seeds suggests that the various proteins slowly coagulate and denature with time and eventually cannot function in germination.

A related theory—perhaps the most plausible one in the present state of our knowledge—is that loss of viability is due to gradual degeneration, in the nuclei of cells, of the chromatin—the material basis of heredity—and of the delicate mechanism for mitosis, the process by which cells divide and increase in number.

Experiments that support this second theory show that aging, heating, and X-ray treatment of dry seeds all cause similar degeneration—increased mitotic aberrations and chromosome changes and increased plant mutations and abnormalities.

Degrees of aging and of treatment cause more or less proportional increases in extent of abnormalities and mutations until all viability is lost. An extension of this theory is that the mutations resulting from aged seeds is one means by which Nature produces varying races and strains of plants and advances evolution.

Seed longevity in a broad sense is an ecologic characteristic of a plant as well as a morphologic and a biochemical one. Over the great reaches of geologic time, the biology of most plant species and their seeds has come to fit approximately the habitat in which they are characteristically found.

Some plants are primary pioneers. They grow most commonly on ecologically tough sites where soil is scarce or poor.

Other plants are secondary pioneers. They are found commonly in abundance on well-developed soil profiles from which much or all of the previous plant cover has been removed by fire, logging, or clearing. And of course there are other comparable ecologic types of plants.

What about the life history of those secondary pioneers that are killed outright by fire but produce heavy seeds not scattered by wind?

How are these plants able to revegetate a burned area promptly and abundantly, as they so often do? Simply because they have mechanically durable, heat-resistant, and long-lived seeds.

In studies of soil-stored seed under ecologically mature forests, it is common to find more seeds of the pioneer vegetation, largely displaced by ecologic development, than of the climax tree species. There is an obvious and essential ecologic value to pioneer plants from long-lived seeds—that is, from seeds well distributed in time.

A few plants produce two kinds of seeds according to season and physiologic status of the plant. An example is *Halogeton glomeratus*, a serious weed of wildland desert ranges. One kind of seed will germinate immediately upon maturity. The second kind is dormant and will not germinate until some time after maturity. This again is distribution of seeds in time, with seed longevity as one requirement for success of the process.

Plants (particularly woody plants) characteristic of arid climates are believed in general to have longer lived seeds than plants of tropical or of humid-temperate habitats.

Plant taxonomy in relation to seed longevity is another interesting field of inquiry. The taxonomic plant families—for example, the Cruciferae, the Rosaceae, and the Leguminosae—commonly are rather uniform in flower structure, type and arrangement of leaves, and other traits.

Are these plant families also uniform in seed biology, or is seed longevity more a matter of ecology ("fit" to the environment) than of taxonomic relationships?

Species of the Leguminosae, considered here in a broad taxonomic sense to include the Mimosaceae, have turned up very frequently in lists of long-lived seeds, and it seems that this family has a marked tendency to longevity of seeds.

Other plant families that apparently have greater than average proportions of species with exceptionally long-lived seeds include the palms, cannas, waterlilies (lotuses), spurges, soapberries, buckthorns, mallows, and morning-glories. Within a single species, varieties and strains with somewhat differing genetic constitution may vary in germination and longevity.

In conclusion, let us say that we have a great many records—some amazing records—of long-lived seeds. Up to the present time, however, most data on seed longevity, particularly of wild plants, have been considered piecemeal, species by species.

Much more research and analysis must be done before broad generalizations can accurately relate seed longevity to an integrated consideration of seed and plant biochemistry, physiology, morphology, taxonomy, and ecology.

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Until Time and Place Are Suitable

EBEN H. TOOLE AND VIVIAN KEARNS TOOLE

One must keep in mind the place of the seed in the life of the plant if he is to understand the processes of germination.

A seed is essentially a young plant whose life activities are at a minimum. The drying out of the young seed as it ripens on the plant brings about this reduction of activities. The dry seed thus is in a condition to be held, stored, and preserved until time and place are suitable for the start of a new plant.

Many seeds, especially crop seeds, begin to germinate as soon as they are planted under moist conditions and they absorb water. Thus new corn plants appear promptly when corn grains are kept over winter and planted in moist, warm soil.

The germination of other seeds, including seeds of many flowers and weeds, does not begin until special conditions, besides moisture, are provided. Such seeds have a block or blocks to the germination processes. They do not germinate until the blocks are removed.

If a crabgrass seed (*Digitaria*) should germinate when it fell to the ground at maturity in late summer, cold weather would soon kill the young seedlings. Special germination requirements of the freshly ripened crabgrass seed prevent it from germinating until the next season.

Seeds with special germination requirements are called dormant (blocked). The special conditions associated with seed dormancy are considered in the chapter that follows.