

# Genetic Aspects of Seed Longevity

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Seed longevity is the most important trait related to the management of gene banks because it governs the regeneration cycle of seeds. Thus, seed longevity is a quantitative trait. Prior to the discovery of molecular markers, classical genetic studies have been performed to identify the genetic determinants of this trait. Post-2000 saw the use of DNA-based molecular markers and modern biotechnological tools, including RNA sequence (RNA-seq) analysis, to understand the genetic factors determining seed longevity.

seed longevity

genetics

## 1. Introduction

Sustainable agriculture depends on the judicious use of natural resources, including use of crop varieties that are resistant to pests and diseases and do not require pesticide spraying, thus providing environmental benefits in addition to fulfilling the energy requirements of mankind. At present, >7000 plants are cultivated for food, shelter, and other purposes <sup>[1]</sup>, and approximately 50% of human food comes from maize, wheat, and rice. Climate change has posed an extinction threat to 8% of the 250,000 species of flowering plants by 2025. To arrest this calamity, plant genetic resources are stored and regenerated in >1750 gene banks storing >7,000,000 accessions <sup>[2]</sup>. To successfully maintain such an extensive germplasm, a systematic evaluation of seed survival and longevity of the plant material stored is always under progress <sup>[3]</sup>. Because seeds are the prime storage material, research on seed longevity is of particular importance <sup>[4]</sup>.

Seed longevity is defined as the maximum time period during which seeds can germinate <sup>[5][6][7]</sup> and produce viable seedlings capable of developing into healthy plants and bearing seeds for the next generation. In addition to many other features, seed longevity is influenced by pre-storage and storage conditions and the genetic and physiological storage potential of seeds. It is also affected by harsh conditions during or after seed development or damage prior to or during storage <sup>[8]</sup>. The long-term storage of seeds, particularly under unfavorable conditions, leads to the loss of viability, which is variable in nature. Loss of viability is related to various seed properties, including color, weight, and membrane composition, which are often species or, in some cases, even variety specific <sup>[9]</sup>.

Seed quality can be reduced in parental plants owing to adverse environmental conditions, premature germination <sup>[10]</sup> and pathogens <sup>[11]</sup>. Damage to seed quality can be categorized into either short-term deterioration (occurring in the field, such as deterioration of the mother plant) or long-term deterioration (occurring during storage). The latter includes membrane and genetic damage, changes in respiratory activity and enzymes and protein damage <sup>[9][10]</sup>.

All parts of the seed deteriorate with time, the damage from which can be sustained by the chemical constituents of seeds and the way these compounds interact to form biological structures. Integrity of DNA, proteins, and membranes is especially important for maintaining seed viability [12].

Seed deterioration during storage may involve many physical and chemical changes, including disrupted intracellular integrity, decreased enzyme activity, lipid peroxidation, and nonenzymatic reactions [13][14]. Seed viability and vigor are dependent on the integrity of cellular macromolecules and orderly compartmentalization of the cell [13]. Aging is an inexorable trend to disorder. Defense mechanisms innate to the seed's structural and chemical features that are characteristic of a particular species may limit the rate of this decay [15].

Seed deterioration varies between different varieties of the same species. Even within a variety, the storage potential of individual lots varies, and within a seed lot, individual seeds have different storage potentials [9]. Broken, cracked, or bruised seeds deteriorate more rapidly than undamaged seeds [14][16]. Environmental stresses, including deficiency of minerals (including nitrogen, potassium, and calcium) [17], water [18] and temperature extremes [19] during seed development and prior to physiological maturity can also reduce the longevity of seeds.

## 2. Mechanisms of Seed Ageing

A number of mechanisms of seed aging have been identified [20], including lipid peroxidation, which results in membrane damage and generation of toxic byproducts [21], oxidative damage to DNA and proteins [22], and loss of protein function during deterioration as a result of the formation of sugar–protein adducts [23]. In contrast, antioxidants, heat shock proteins (HSPs) and enzymes to repair protein damage are thought to be involved in mitigating the effects of ageing on seed longevity [24][25].

Genetic differences between species are also responsible for differential seed longevity; for example, seeds of *Canna* [26] and *Lotus* [27] are thought to be viable even after 1300 years. *Albizia benth.*, *Cassia* L., *Goodia*, and *Trifolium* L. seeds can germinate after 100 years [28]. Seeds of other species are characteristically short-lived, including lettuce (*Lactuca sativa* L.), onions (*Allium cepa* L.), parsnips (*Pastinaca sativa* L.), and rye (*Secale cereal* L.) [29]. The influence of oil content on longevity under open storage conditions has also been addressed [29]; however, further analysis is required to arrive at a definitive conclusion. Species with similar chemical composition could also have significantly different storability. For example, chewing fescue (*Festuca rubra* subsp. *commutata* Gaudin) and annual ryegrass seeds have similar appearances and chemical compositions. However, ryegrass seeds were stored much better under comparable conditions [30]. Seed longevity can vary by as much as seven-fold depending on the genetic differences among cultivars of the same species [31].

Very little is known about the genetic basis of differences in seed quality because this trait is strongly affected by environmental factors during seed formation, harvest, and storage and is probably controlled by many genes. Therefore, seed longevity is a composite trait because in genetic studies of longevity [32], genetically identical seed lots of seeds, even when grown under identical conditions or derived from a single plant, lose their viability at different intervals after harvest. Seed longevity is a quantitative trait [12] and is strongly affected by the environment

during seed formation, harvest, and storage [33][34] through a variety of mechanisms, whose understanding might enable us to greatly increase the seed longevity of agriculturally important species and varieties and preserve plant genetic resources for generations [35].

### 3. Classical Genetic Studies

Awareness of seed longevity dates back to ~2500 years ago (372 BC–287 BC) when Theophrastus discussed seed deterioration in his botanical writings [14][36]. Similarly, in Fan Sheng-zhi Shu, an agricultural book of China written in the 1st century BC [37], the longevity of wheat and millet seeds is discussed. Their viability was maintained if they were kept as dry as possible, cool, and free from pests. It was also suggested that only large and solid ears of wheat should be chosen for sowing, and they should be dried as thoroughly as possible by the heat of the sun before storage.

Classical genetic studies were first initiated and probably the best characterized in maize (*Zea mays* L.). Maize seeds have been declared more susceptible to aging [38] if they carry homozygous alleles for either the *luteus 2* or *luteus 4* genes, although the physiological basis of this difference remains obscure. Later, two unrelated studies [39][40] demonstrated that the long-lived character of maize appeared to be dominant, although a non-cytoplasmic maternal plant influence was also identified. Thirty-seven years later, Rao et al. [41] transferred the same nuclear genotype used by Haber [40] to genetically different cytoplasmic types and concluded that cytoplasmic factors had a marked influence on seed storability. Later, single-cross hybrids were employed to investigate long- and short-lived lines of maize, which demonstrated the dominant character of the long-lived seeds [42]. After three selection cycles (based on resistance to aging using experimental procedures (42 °C and saturated humidity)), a reduction in sensitivity to aging was reported, which suggested that genetic improvement for storability is achievable [43].

The longevity of spring and winter wheat remains controversial. For example, according to Van der Mey et al. [44], winter wheat stores better than spring wheat over periods of 15–20 years at 5 °C. In contrast, Arif et al. [45] did not find any difference in longevity between spring and winter wheat after experimental aging. Furthermore, [46] reported no association between grain color and longevity in wheat.

In legumes, hard seeds within a particular seed lot retain viability for longer storage periods than their softer companions [47]. Seed color and coat thickness have also been reported to play role in seed longevity in chickpeas. For example, pale-seeded “Kabuli” chickpeas have also been reported to be shorter lived than “Desi” types with thicker, harder and darker coats [48]. Dark-seeded soybeans were also more resistant to storage under high humidity [49]. In *Phaseolus vulgaris*, a diallele cross-analysis was used to demonstrate that superior longevity was dominant in nature [50]. In soybean, reciprocal crosses revealed a strong maternal influence through the characteristics of the seed coat on the longevity of F<sub>1</sub> seeds [51] in addition to a minor influence of the seed's own genotype.

In a study of 55 accessions of barley stored in the Gatersleben gene bank since 1974, intraspecific variability in longevity was addressed [52]. Germination tests after 35 years of storage indicated intraspecific variability in seed longevity within barley owing to genetic determinants. A similar conclusion was drawn for *Brassica napus* L. [53] based on the results of 42 accessions. Hence, genotypic components are involved in determining seed viability. The same phenomenon of intraspecific variability towards longevity has been observed in *Sorghum bicolor* L., *Secale cereale* L., and *Linum usitatissimum* L. [54].

## 4. Future Directions

The most important steps to discover the genetic determinants of seed longevity are population development, genotyping, intensive phenotyping, and computational analysis. All of these steps are expensive. Consequently, scientists, breeders, seed technologists, physiologists, molecular biologists, and genebank curators must exchange the germplasm developed by them in their respective projects to accelerate genetic research on seed longevity. **Table 1** provides some examples of germplasm resources of different plant species that can be exploited to hasten research on seed longevity.

**Table 1.** Germplasm collections with genotype data for future research on seed longevity of various crops.

Sr. No.	Plant Species	Number of Accessions	Genotyping Platform	References
1	Hexaploid wheat ( <i>Triticum aestivum</i> L.)	>2500 accession in SeeDs of Discovery project	7180 genotyping by sequencing (GBS) SNPs	[55][56]
2	Durum wheat ( <i>Triticum durum</i> Desf.)	(i) 6280 RILs (50 interconnected families constituting a nested association mapping population (NAM))	(i) 13,000 SNPs from Infinium 15K Ultra HD chip	(i) [57]
		(ii) 1336 genotypes (from 25 families constituting a NAM)	(ii) 5398 SNPs from Illumina Infinium iSelect HD 9k chip	(ii) [58]
3	Sorghum ( <i>Sorghum bicolor</i> (L.) Moench.)	971 world wide accessions	GBS SNPs	[59]
4	Rice ( <i>Oryza sativa</i> L.)	1568 inbred varieties	700,000 high density rice array SNPs	[60]
5	Tomato ( <i>Solanum lycopersicum</i> L.)	163 accesions, 291 accesions and 402 accesions	5995 SNPs, 9013 SNPs and 2014,488 SNPs, respectively	[61]

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Sr. No.	Plant Species	Number of Accessions	Genotyping Platform	References
6	Pepper ( <i>Capsicum</i> spp.)	10,038 genebank accession	GBS SNPs	[62]
7	Soybean ( <i>Glycine max</i> L.)	(i) 421 accessions	(i) 1536 SNPs	(i) [63]
		(ii) 305 accessions	(ii) 37,573 SNPs	(ii) [64]

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