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# Negative Association between Seed Dormancy and Seed Longevity in Bread Wheat

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## Abstract

Many organisms have dormant stages with an extension of their life span to increase longevity, and deeper dormancy is usually related to greater longevity. In cereal crops, seed dormancy is significantly associated with pre-harvest sprouting tolerance during seed development, as seed longevity is a valuable trait for seed banks and providing reliable crop seeds to farmers. In this study, we evaluated both seed dormancy and longevity in bread wheat based on germination and artificial aging tests. According to phenotypic clustering analysis, relative germination rate/potential and relative seedling vigor index were more effective to indicate seed longevity than relative electrical conductivity in wheat, while all the four investigated phenotypes of relative germination potential, relative germination rate, germination index and degree of seed dormancy fit well as a reflex of wheat seed dormancy. In the correlation analysis, the germination level of newly harvested grain negatively reflected its degree of seed dormancy, while the germination ability of grain after artificial aging reflected its seed longevity. However, in contrast to the current opinion in plant, seed dormancy was significantly negatively correlated to seed longevity in our study, and it was not an accidental phenomenon, for that the majority of accessions with high degree of seed dormancy had short seed longevity. To our knowledge, this is the first to report the negative association between seed dormancy and longevity in cereal crops. It would lead to further concerns about how to breed wheat with both prolonged seed longevity and deep dormancy to avoid pre-harvest sprouting.

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**Keywords**

Wheat Seed, Germination Test, Artificial Aging, Longevity and Dormancy, Negative Relationship

## 1. Introduction

Dormancy is described as a condition of apparent metabolic arrest with life activities reduced or brought to a halt. Many organisms have dormant stages, which have been related to an extension of their life span to increase longevity [1]. Cereal crops such wheat [2], rice [3] [4] and maize [5] [6] [7] usually produce dormant seeds at maturity stage, which is called as seed (innate) dormancy and described as the temporary failure of an intact viable seed to complete germination under favorable conditions [8]. In bread wheat, seed dormancy often shows negative association with pre-harvest sprouting (PHS) [9]-[15], which is usually induced by wet conditions after maturity or before harvest and can severely reduce grain end-use quality, and even grain yield. PHS resistance enhancement is often used interchangeably with deep seed dormancy.

Seed longevity is defined as seed viability after dry storage, which is valuable for seed banks and provides reliable crop seeds to farmers. Seed longevity is often negatively correlated with the advancement of germination [16]. It is a complex trait influenced by two most important environmental factors: 1) relative humidity, which is related to seed moisture content; 2) temperature, which affects the rate of biochemical processes in seeds [17] [18]. In the case of wheat seed longevity has negative relation with temperature and moisture [19], and it also shows their diversification in different varieties [20].

In plant, seed dormancy and longevity have been described as two separate traits. And the commonly held view is that dormancy may be positively related to longevity in plant seeds [21] [22] [23] [24], and most of these works have been based on environmental-stress-induced or mutant dormancy genotypes. However, Nguyen *et al.* (2012) firstly reported a negative relationship between seed dormancy and longevity in natural variations of *Arabidopsis* [25]. In cereal seeds, Roberts (1963) investigated the seed dormancy of 6 rice cultivars with the same seed longevity, and found remarkable differences among their seed dormancy [26], indicating the independence between innate dormancy and longevity [3]. Rehman Arif *et al.* (2012) conducted germination tests for both seed dormancy and longevity in wheat without any description for relationship between them, and no obvious relationship was found between them from a genetic sight [27]. In this study, both seed dormancy and longevity were evaluated for the accessions from Core Wheat Germplasm Panel (CIMCOG) of Mexico International Maize and Wheat Improvement Center (CIMMYT), and a significantly negative relationship between seed dormancy and longevity was observed, which was in contrast to the current opinion in plant and discussed in the context. And this dramatic association between them raised new advantages or

challenges for breeding wheat cultivars with both long longevity and deep dormancy against pre-harvest sprouting.

## 2. Materials and Methods

### 2.1. Plant Materials and Field Trial

A total of 60 elite accessions from CIMCOG panel provided by CIMMYT were planted in the greenhouse of Sichuan Academy of Agricultural Sciences (SAAS) in the growing season of 2012-2013. Two replicates per trial were performed for each accession. Each plot consisted of two 1.5 m rows spaced 0.5 m apart, and 10 plants were evenly spaced in each row to minimize border effects.

The seeds of each accession were harvested near the end of its dough stage, air-dried to 10% - 12% moisture content, and then stored at a condition of −20˚C and moisture content less than 12% to maintain dormancy until all 60 accessions were collected, in consideration of their different maturation times. After 2-day's air-drying, these seeds with <12% moisture content were treated with aluminum phosphide for 5 days and then transferred into an airtight container at a room temperature. Among 60 accessions, 58 of them were *Triticum aestivum*, including 13 accessions derived from the crosses between *T. aestivum* and synthetic hexaploid wheat, and the remaining two were durum cultivars. And most of them (52 accessions) obtained white seed coat color.

### 2.2. Seed Longevity Measurement

#### 2.2.1. Artificial Aging

Artificial aging (AA) test was conducted to stimulate biochemical and hence allow for the evaluation of seed longevity. In this study, 50 seeds of uniform size were selected for artificial aging tests with eight replicates for each accession after 6-month storage for eliminating the possible influence of seed dormancy, and these seeds were dispersedly placed in a stainless metal cage sealed inside a required container adding 2 cm of deionized and sterilized water to its bottom. The container was covered and held at 43˚C ± 0.5˚C for 72 h and more than 90% relative humidity [28]. Then these treated seeds were air-dried and stored at 4˚C.

#### 2.2.2. Germination and Seedling Vigor Test

Four replicates of 50 seeds each for AA tests with three replicate for control were subjected to a standard ISTA germination test, in which the seeds were placed on the wet filter papers, formed into rolls and stood on a Jacobsen apparatus at 25˚C ± 1˚C during the day and 23˚C ± 1˚C during the night [29]. The seed germination potential and rate were recorded on the $4^{th}$ and $8^{th}$ day, respectively [28]. Apart from the absolute germination (in both non-treated and treated seed lots), a relative germination potential and rate was determined by dividing the rates obtained after AA treatment by that of the non-treated control.

For the seedling vigor, 10 seedlings for each 50-seed plot were randomly selected from the germinated seedlings without any injury or defect in the $8^{th}$ day simultaneously, to measure average seedling length. The seedling vigor index

and relative seedling vigor index were calculated following the formula described as Abdul-Baki and Anderson (1973): vigor index = seed germination rate × seedling length, relative vigor index (%) = [(vigor index of AA treatment)/(vigor index of control)] × 100% [30].

#### 2.2.3. Electrical Conductivity Test

The remaining four AA-treated replicates and three control replicates of 50 air-dried seeds for each accession were used to estimate the membrane integrity after AA treatment, as measured by electrical conductivity, which is suggested as an indicator of seed aging during storage at room temperature. And higher value of electrical conductivity caused by damaged cell membranes of deteriorated seeds is often positively related to the degree of seed aging [31] [32] [33].

The average weight of 50 AA-treated seeds of each accession ranged from 0.961 g to 1.667 g and the control was from 1.016 g to 1.721 g. After weighed, all the seeds were soaked in plastic cups (200 mL) containing 75 mL deionized water for 24 hours at 25˚C. After soaking, the value of absolute electrical conductivity was determined in a conductivity meter (Analyzer 600) with an electrode with constant 1. Deionized water without any seeds soaked was conducted as a control of background level. And the absolute electrical conductivity of each lot (50 seeds) was calculated following the formula: absolute electrical conductivity ($\mu Scm^{-1}g^{-1}$) = (absolute electrical conductivity for seed soak water-absolute electrical conductivity for background-level control)/ the weight of each lot. In this study, the electrical conductivity of each AA-treated accession was represented by relative electrical conductivity (%) = [(absolute electrical conductivity for AA-treated seed)/ (absolute electrical conductivity for seed without AA-treatment)] × 100%.

### 2.3. Seed Dormancy Measurement

After harvested and threshed by hand with sterile PE disposable gloves, the air-dried seeds of each accession were immediately transferred to −20˚C to maintain their dormancy as described in the section of "*Plant materials and field trial*". Once all accessions were collected from the field, those seeds were used for dormancy measurement. Fifty kernels for each accession were surface-sterilized with 25% bleach, placed on a sterilized wet filter paper in a Petri dish, and incubated in a temperature-controlled growth room with temperature control as described in the section of "*Germination and seedling vigor test*". Germinated kernels were counted daily and removed after counting. The seed germination potential and rate for dormancy measurement were recorded on the $4^{th}$ and $8^{th}$ day, respectively [28]. A weighted germination index [34], relative germination potential and rate were used to measure seed dormancy based on the following formula in this study:

Germination index = $100 \times [(x \times n_1 + (x-1) \times n_2 + \ldots + 1 \times n_i)/N \times x]$, relative germination potential = (germination potential for seed dormancy)/(germination potential of seeds after 6-month storage), relative germination rate = (germination rate for seed dormancy)/(germination rate of seeds after

6-month storage), and the degree of seed dormancy = Ln[1/(relative germination rate × germination index)].

Where $x$ is the total number of days between seed planting and the end of the experiment, $N$ is total number of grains, and $n_1$, $n_2$, … $n_x$ are the numbers of kernels that germinated on a specific day $i$, $i$ is number of days after seed planting ranging from 1 to $x$.

### 2.4. Statistical Analysis

Pearson correlation analysis and Duncan's multiple range test for all phenotypes were made in IBM SPSS Statistics Version 22 package (IBM Corp., Chicago, IL). Population distribution of phenotypic data was performed in MS Excel 2003 and SPSS.

Cluster analysis was carried out using NTSYS pc Version 2.10e [35]. After linear transformation with "Standardization" program, the selected phenotypic data matrix was transformed to a similarity matrix using Euclidian distance (EUCLID). The EUCLID similarity matrix of all accessions was analyzed using un-weighted pair group method with arithmetic average (UPGMA) algorithm in sequential agglomerative hierarchical nested (SAHN) routines, and the results were used to construct a dendrogram. The goodness of fit of the phenotypes to a specific cluster in the UPGMA cluster analysis was determined by the Mantel matrix correspondence test [36].

## 3. Results

### 3.1. Seed Dormancy and Longevity Related Traits

The germination rates of the air-dried seeds after 6 months storage in an airtight container at a room temperature that was used for control set ranged from 45.8% to 100.0%. And these seeds were used for AA test and as control for dormancy measurement. Among the 60 accessions, 58 accessions remained > 80% germination rate, and only No. 9 and 40 accessions' germination rate (54.3%, 45.8%) was less than 80%.

For the measurement of seed dormancy, 4 germination related indexes including, relative germination potential, relative germination rate, germination index and degree of seed dormancy were used for indicating seed dormancy. A total of 4 indexes were calculated for the measurement of seed longevity, as relative germination potential, relative germination rate, relative vigor index and relative electrical conductivity after artificial aging. In AA test, greater germinating ability and lower relative electrical conductivity often reflect higher seed longevity. The frequency distribution, median, mean and phenotypic standard deviation of seed dormancy and longevity related traits in CIMCOG panel are showed in **Figure 1**. For seed dormancy, the relative germination potential, germination index and degree of seed dormancy have larger means than their medians in the panel. For seed longevity, the medians of relative germination potential, relative germination rate, relative vigor index are more than their means in the population, and the median of relative electrical conductivity are

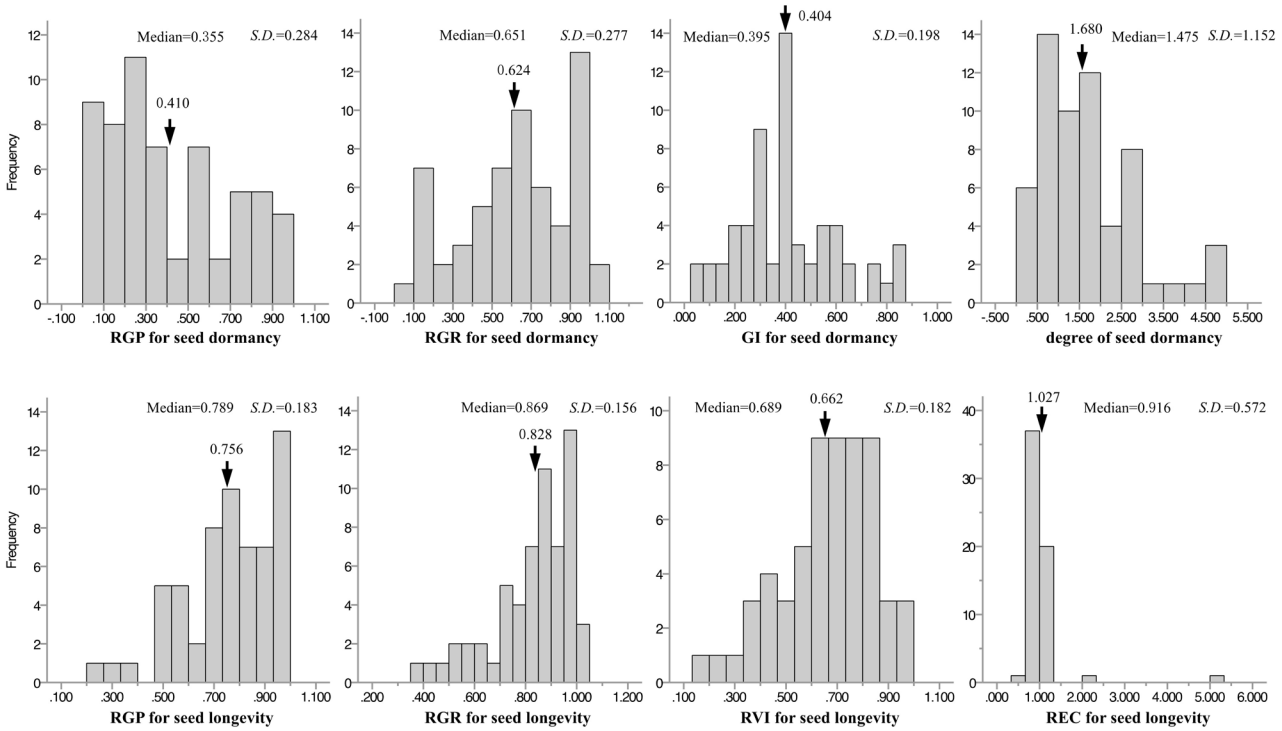


**Figure 1.** Frequency distribution of seed dormancy and longevity related traits in CIMCOG panel. The position pointed by black arrow in X-axis represents phenotypic mean for the population. "Median" means the middle value of the population. "S.D." means its phenotypic standard deviation. RGP, relative germination potential; RGR, relative germination rate; GI, germination index; DSD, degree of seed dormancy; RVI, relative vigor index; REC, relative electrical conductivity.

less than its mean. The means of degree of seed dormancy and relative electrical conductivity for seed longevity and are over 10% larger than the medians, indicating their significant right-skewed distribution.

For the morphological diversity of seed dormancy related traits, the correlation coefficient $r$ between the data matrix for the dendrogram (cophenetic matrix) and the Euclidian distance matrix for similarity coefficients (original matrix) was 0.69 when $t$ value for Mantel $t$-test was 20.31 and $p$ value for Prob. ($Z_{random} < |Z_{obs.}|$) was 1.00 (**Figure 3(a)**). All the 60 accessions, with Euclidian distance ranging from 0.15 to 3.28, were also grouped into 3 clusters (**Figure 2(a)**). The first group $I_{SD}$ with 22 accessions had low degree of seed dormancy, the 2nd group $II_{SD}$ contained 6 accessions with high degree of seed dormancy, and the rest of accessions belong to the 3rd group $III_{SD}$ with intermediate level of seed dormancy (**Table 1**). Significant difference among groups on relative germination potential, relative germination rate, germination index and degree of seed dormancy indicated that all the four investigated phenotypes fit well as a reflex of dormancy degree (**Table 1**). Four traits related to seed longevity were selected for the clustering analysis of the 60 CIMCOG accessions (**Figure 2(b)**). The cophenetic coefficient $r$ computed against the original data matrix was 0.86 ($t$ = 9.22; $p$ = 1.00) (**Figure 3(b)**), indicating that the cophenetic matrix for the dendrogram and the Euclidian distance matrix for the similarity coefficients (original matrix) were in very close agreement. Fifty-seven out of 60 accessions, with

Euclidian distance ranging from 0.15 to 7.80, were grouped into 3 clusters (Figure 2(b)). Duncan's multiple range test showed significant difference ($\alpha$ = 0.01 level) between each group on relative germination rate and relative vigor index (Table 2), and their phenotypic scores could reflect the seed longevity of these accessions.

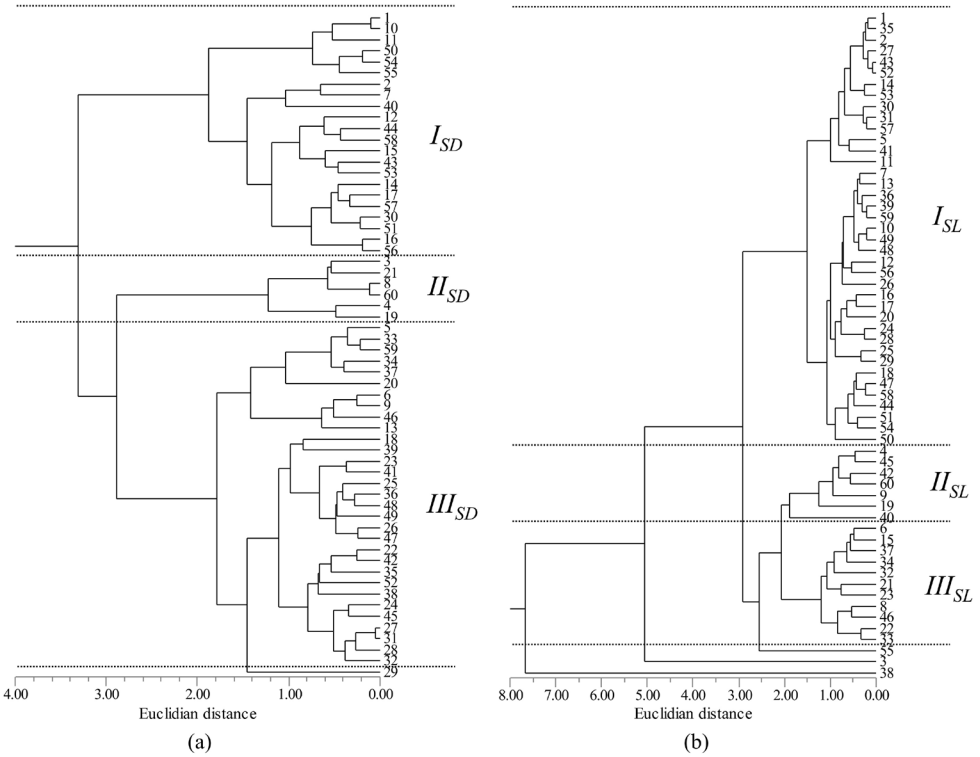


**Figure 2.** Cluster analysis of CIMCOG accessions based upon (a) seed dormancy and (b) longevity related phenotypic scores.

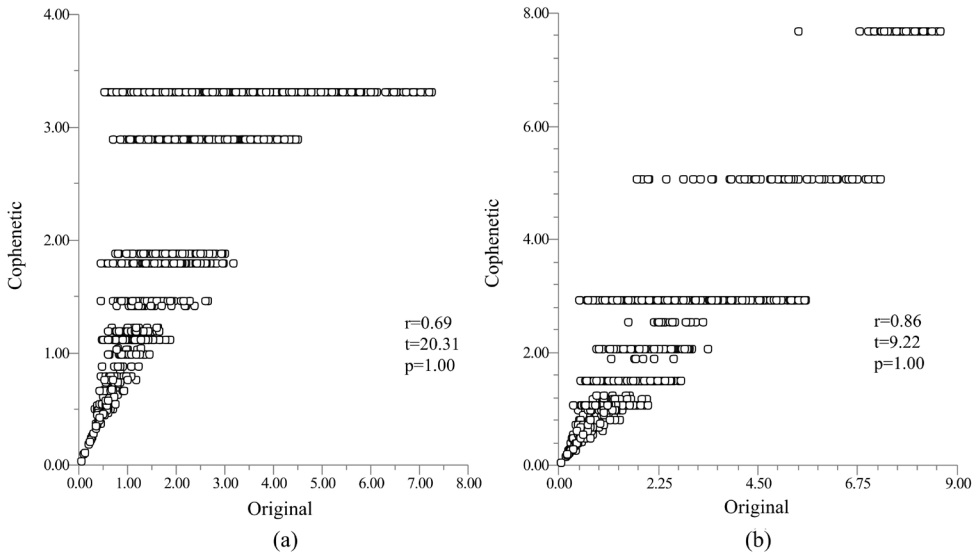


**Figure 3.** Mantel matrix correspondence tests between cophenetic matrix and Euclidian distance matrix of (a) seed dormancy and (b) longevity related traits.

**Table 1.** Multiple comparison of seed dormancy related traits between different clustering groups¶.

| Cluster | No. | RGP | RGR | GI | DSD |
|---|---|---|---|---|---|
| $I_{SD}$ | 22 | 0.72 (c, C) | 0.90 (c, C) | 0.59 (c, C) | 0.66 (c, C) |
| $II_{SD}$ | 6 | 0.06 (a, A) | 0.15 (a, A) | 0.11 (a, A) | 4.26 (a, A) |
| $III_{SD}$ | 32 | 0.26 (b, B) | 0.52 (b, B) | 0.33 (b, B) | 1.90 (b, B) |

¶Lower case and capital letters represent Duncan's multiple range test at $\alpha = 0.05$ and 0.01 level, respectively. RGP, relative germination potential; GRG, relative germination rate; GI, germination index; DSD, degree of seed dormancy.

**Table 2.** Multiple comparison of seed longevity related traits between different clustering groups¶.

| Cluster | No. | RGP | RGR | RVI | REC |
|---|---|---|---|---|---|
| $I_{SL}$ | 39 | 0.86 (a, A) | 0.92 (a, A) | 0.77 (a, A) | 0.95 (a, A) |
| $II_{SL}$ | 7 | 0.51 (c, B) | 0.53 (c, C) | 0.37 (b, C) | 0.91 (a, A) |
| $III_{SL}$ | 11 | 0.61 (b, B) | 0.75 (b, B) | 0.56 (c, B) | 0.92 (a, A) |

¶Lower case and capital letters represent Duncan's multiple range test at $\alpha = 0.05$ and 0.01 level, respectively. RGP, relative germination potential; GRG, relative germination rate; RVI, relative vigor index; REC, relative electrical conductivity.

### 3.2. Correlations between Seed Dormancy and Longevity Related Traits

In this study, 6-month storage was set up to let the harvest seeds finish their physiological after-ripening completely, and these dormancy-released seeds were used as control for measuring seed dormancy. Correlations among investigated traits for seed dormancy, longevity and seed coat color (white = 0, red = 1) are presented in Table 3. For the seed longevity, significant positive correlations were detected among (relative) germination potential, (relative) germination rate and (relative) seedling vigor index. However, electrical conductivity had no significant relationship with seed germination related traits (Table 3). For seed dormancy, significantly positive relationships were also observed among these seed germination related traits such (relative) germination potential, (relative) germination rate and germination index. However, more seeds that sprouted as soon as being harvested usually means the lower degree of seed dormancy, which was negatively related to germination related traits in this study (Table 3). Moreover, seed coat color was significantly negatively related to (relative) germination rate with the absolute value of coefficients more than 0.50 but positively to degree of seed dormancy (Table 3), suggesting that the seed dormancy of red wheat accessions was higher than the white ones.

The germination potential, germination rate and seeding vigor index of the control group were positively related to the germination potential (rate) and seeding vigor index of AA-treated group for seed longevity with their coefficients more than 0.50, respectively. However, the relative germination potential

of AA-treated group for seed longevity was not significantly correlated with germination potential of the control group. The correlation coefficient between relative germination rate of AA-treated group for seed longevity and germination rate of the control group was 0.33 at P = 0.05 level, which was much less than 0.77 between germination rates of AA-treated and control groups. The relative seeding vigor index for seed longevity were weakly correlated with seeding vigor index of the control group with correlation coefficient only 0.28 (Table 3). And these indicated that relative germination potential (rate) and relative seeding vigor index could almost evaluate the influence caused by AA-treatment totally. This similar situation also happened to seed dormancy related traits, and the relative germination potential/rate for seed dormancy was not significantly related to germination potential/rate of the control, respectively.

**Table 3.** Correlation coefficients between seed dormancy, seed longevity related traits and seed coat color[¶].

| | | SL | | | | | | | Control | | | | SD | | | | | | SCC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RGP | GR | RGR | VI | RVI | AEC | REC | GP | GR | VI | AEC | GP | RGP | GR | RGR | GI | DSD | |
| SL | GP | 0.85** | 0.94** | 0.84** | 0.93** | 0.82** | −0.15 | −0.13 | 0.68** | 0.66** | 0.64** | −0.02 | 0.61** | 0.45** | 0.69** | 0.55** | 0.50** | −0.62** | −0.40** |
| | RGP | | 0.76** | 0.86** | 0.77** | 0.84** | −0.06 | −0.14 | 0.19 | 0.20 | 0.27* | 0.20 | 0.58** | 0.57** | 0.66** | 0.66** | 0.47** | −0.66** | −0.45** |
| | GR | | | 0.92** | 0.90** | 0.87** | −0.22 | −0.15 | 0.70** | 0.72** | 0.59** | −0.18 | 0.58** | 0.39** | 0.65** | 0.49** | 0.47** | −0.55** | −0.43** |
| | RGR | | | | 0.81** | 0.93** | −0.17 | −0.16 | 0.31* | 0.33* | 0.32* | −0.03 | 0.53** | 0.42** | 0.62** | 0.54** | 0.43** | −0.56** | −0.47** |
| | VI | | | | | 0.85** | −0.20 | −0.13 | 0.64** | 0.64** | 0.71** | −0.13 | 0.45** | 0.29* | 0.54** | 0.40** | 0.35** | −0.48** | −0.33** |
| | RVI | | | | | | −0.19 | −0.14 | 0.37** | 0.39** | 0.28* | −0.08 | 0.50** | 0.38** | 0.58** | 0.51** | 0.40** | −0.53** | −0.41** |
| | AEC | | | | | | | 0.92** | −0.18 | −0.21 | −0.13 | 0.25 | 0.04 | 0.09 | 0.09 | 0.15 | 0.15 | −0.20 | −0.16 |
| | REC | | | | | | | | −0.04 | −0.05 | −0.04 | −0.13 | 0.00 | 0.00 | 0.04 | 0.06 | 0.10 | −0.11 | −0.11 |
| Control | GP | | | | | | | | | 0.98** | 0.81** | −0.34** | 0.33** | 0.05 | 0.38** | 0.14 | 0.27* | −0.25 | −0.19 |
| | GR | | | | | | | | | | 0.81** | −0.42** | 0.35** | 0.08 | 0.38** | 0.13 | 0.28* | −0.24 | −0.21 |
| | VI | | | | | | | | | | | −0.23 | 0.20 | −0.01 | 0.25 | 0.06 | 0.12 | −0.18 | −0.16 |
| | AEC | | | | | | | | | | | | 0.03 | 0.14 | 0.10 | 0.21 | 0.09 | −0.21 | −0.16 |
| SD | GP | | | | | | | | | | | | | 0.93** | 0.90** | 0.85** | 0.80** | −0.80** | −0.42** |
| | RGP | | | | | | | | | | | | | | 0.84** | 0.89** | 0.74** | −0.79** | −0.44** |
| | GR | | | | | | | | | | | | | | | 0.96** | 0.77** | −0.91** | −0.55** |
| | RGR | | | | | | | | | | | | | | | | 0.72** | −0.91** | −0.57** |
| | GI | | | | | | | | | | | | | | | | | −0.85** | −0.31* |
| | DSD | | | | | | | | | | | | | | | | | | 0.53** |

[¶]SL, seed longevity; SD, seed dormancy; GP, germination potential; RGP, relative germination potential; GR, germination rate; RGR, relative germination rate; VI, vigor index; RVI, relative vigor index; AEC, absolute electrical conductivity; REC, relative electrical conductivity; GI, germination index; DSD, degree of seed dormancy; SCC, seed coat color; * and ** indicate significance at the P = 0.05 and 0.01 levels, respectively; Shaded cell represents the absolute value of correlation coefficient more than 0.50.

### 3.3. Negative Association between Seed Dormancy and Longevity

Interestingly, the seed dormancy related traits germination potential and (relative) germination rate that negatively reflecting the degree of seed dormancy were significantly positively correlated with the seed longevity related traits such relative germination potential (rate) and relative seeding vigor index with their coefficients more than 0.50 (Table 3). Contrary to controls, the degree of seed dormancy was significantly negatively correlated with relative germination potential (rate) and relative seeding vigor index for seed longevity (Table 3), where greater germination potential (rate) and relative seeding vigor index expressed higher seed longevity.

This negative relationship was not caused by their initial germination ability statistically, for the germination ability of control group was independent of seed longevity related traits (Table 3). In the cluster analysis, the groups $II_{SD}$ and $II_{SL}$ were composed of accessions with the deepest seed dormancy and shortest longevity (Table 1 and Table 2), respectively. A total of 10 accessions were involved in these two groups (Figure 2, Table 4). Among accessions No. 3, 4, 8, 19, 21 and 60 of $II_{SD}$, No. 4, 19 and 60 were clustered to $II_{SL}$, No. 8 and 21 were clustered to $III_{SL}$, whose seed longevity related traits (RGP, RGR and RVI) were smaller than the means of the CIMCOG panel (Table 2, Figure 1 and Figure 2). Among the 7 accessions of $II_{SL}$, 6 were clustered to the groups $II_{SD}$ and $III_{SD}$ with deeper seed dormancy and 1 belonged to $I_{SD}$ with non-deep seed dormancy (Table 1, Figure 1 and Figure 2). The degrees of seed dormancy of all involved accessions except for No. 40 were more than the mean in the panel, while their seed longevity traits were less than the mean in the panel (Table 4), and there was also huge difference in means between the two groups and the whole CIMCOG panel (Table 4). These suggested a significant negative correlation between seed dormancy and longevity, deep seed dormancy correlating with short seed longevity and vice versa.

**Table 4.** Degree of seed dormancy and longevity related traits of $II_{SD}$ and $II_{SL}$ accessions.

| Accession | Cluster | GR[a] (%) | DSD (1.68)[b] | SL | | |
|---|---|---|---|---|---|---|
| | | | | RGP (0.76) | RGR (0.83) | RVI (0.66) |
| 3 | $II_{SD}$ | 94.0 | 4.28 | 0.21 | 0.38 | 0.20 |
| 4 | $II_{SD}$, $II_{SL}$ | 94.5 | 3.25 | 0.50 | 0.57 | 0.43 |
| 8 | $II_{SD}$, $III_{SL}$ | 100.0 | 4.89 | 0.53 | 0.71 | 0.48 |
| 9 | $III_{SD}$, $II_{SL}$ | **54.3** | 2.91 | 0.55 | 0.46 | 0.32 |
| 19 | $II_{SD}$, $II_{SL}$ | 80.0 | 3.63 | 0.33 | 0.60 | 0.37 |
| 21 | $II_{SD}$, $III_{SL}$ | 90.0 | 4.67 | 0.56 | 0.82 | 0.62 |
| 40 | $I_{SD}$, $II_{SL}$ | **45.8** | 1.22 | 0.75 | 0.44 | 0.26 |
| 42 | $III_{SD}$, $II_{SL}$ | 93.9 | 1.69 | 0.48 | 0.53 | 0.37 |
| 45 | $III_{SD}$, $II_{SL}$ | 98.0 | 2.05 | 0.58 | 0.59 | 0.46 |
| 60 | $II_{SD}$, $II_{SL}$ | 95.0 | 4.85 | 0.40 | 0.54 | 0.36 |
| Mean | | | 3.35 | 0.49 | 0.56 | 0.39 |

[a]germination rate of control indicating seed quality; [b]Trait average mean in the CIMCOG panel.

## 4. Discussion

Except for elative germination potential, relative germination rate and relative vigor index, relative electrical conductivity were also investigated for seed longevity in this study, and electrical conductivity is valid to assess longevity of dicotyledon seeds such pea [37] and soybean [31] when these seeds are stored in room temperature condition [33] [38]. However, relative electrical conductivity was independent of other three indexes in both correlation (**Table 2**) and cluster analysis (**Table 3**), which challenged the electrical conductivity of seed-steep water to be a good indicator for the deterioration of AA-treated wheat seeds stored at a room temperature. Except for seed stored temperature, the efficiency of electrical conductivity test for seed longevity or viability is also variable according to different genotypes [39] [40] [41], seed imbibition leakage [42] and proportion of endosperm in seed. Those wheat genotypes with heat resistance often enhance their cell membrane stability [43], and their membrane repair or reorganization in AA-treated condition may reduce the correlation between electrical conductivity and seed deterioration in the germplasm panel of wheat. Electrical conductivity is less sensitiveness to declines viability or longevity of seeds that comprise a large proportion of endosperm, such as corn seed [38] [44] and wheat seed [45], and most of the seed imbibition leakage for electrical conductivity test is from the deteriorated endosperm, which reduces the efficiency of electrical conductivity test for the embryo. For this, electrical conductivity tests tend to be more helpful in grain legumes without endosperm. Moreover, seeds with different longevity often needed different AA-treated times to reach the max value of their relative electrical conductivity, when all the seed imbibition leakage from both endosperm and embryo (without any seed vigor). Seeds with long longevity need more AA-treated time to reach the max values of their relative electrical conductivity. In this study, the seeds of accession No.57, 6 and 9 needed the AA-treated times of 11 d, 7 d and 5 d to obtain their largest relative electrical conductivity, respectively (**Figure 4**). Thus, it is difficult to choose one unified AA-treated time for a germplasm panel with different cultivars and compare their seed longevity using electrical conductivity. And it also seems that the max value of relative electrical conductivity had no significant relationship with seed longevity (**Figure 4**). We suggested that the AA-treated time of reaching max values of electrical conductivity could be a good indicator for evaluating seed longevity.

In this study, correlation analysis showed that the seed dormancy of red wheat accessions was higher than the white ones, and this has been accepted in wheat. Because dormancy genes are thought to be tightly linked or pleiotropic with seed coat color determined by R alleles on chromosome 3A, 3B, and 3D (in durum wheat [46]; in common wheat [47]; in synthetic wheat [48]). And dormancy is often thought to be positively related to longevity in plant seeds [21] [22] [23] [24]. A dormant stage may be related to an extension of their life span to increase longevity [1]; however, the dormant stage of wheat seeds is often only

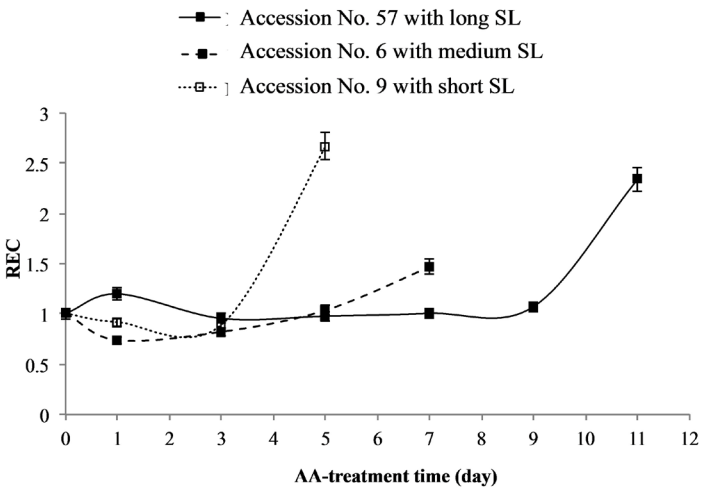


**Figure 4.** Effect of AA-treatment time on relative electrical conductivity.

several weeks/months, and it is difficult for wheats to expand their seed longevity significantly by dormancy, while the longevity of wheat seed under commercial storage conditions is often up to years with half-viability. The germination rate of wheat seed remained >85% after 3-year storage under ambient conditions of room temperature and 50% relative humidity [49]. In our study, there is a strong negative relationship between seed dormancy and longevity in the CIMCOG wheat panel, and the correlation coefficients between degree of seed dormancy and seed longevity related indexes were more than 0.50 with significant level at 0.01. This result was based on the natural variation from germplasm pool, while most of the reported investigations about their positive relationship were under inducement of environmental stress or based on dormancy-mutant genotypes. Nguyen *et al.* (2012) reported a negative correlation between seed dormancy and longevity in the natural variation of Arabidopsis, and their molecular basis for seed dormancy and longevity were also dissected in the populations, which was the first report in seed plants [25].

Long seed longevity is beneficial to preserving seeds for germplasm banks and providing reliable crop seeds to farmers, while deep seed dormancy is associated with the resistance to pre-harvest sprouting in wheat. In the CIMCOG panel, most of accessions with degree of seed dormancy more than 3.00 had short seed longevity, and their average relative germination rate for seed longevity was only 0.60, suggesting a negative association between seed dormancy and longevity. However, further investigation was needed to understand the molecular and physiological basis of these extreme accessions, in order to create breeding wheat lines with both long seed longevity and deep dormancy against pre-harvest sprouting.

## 5. Conclusion

We evaluated the seed longevity of 60 wheat accessions after artificial aging and

their seed dormancy, and analyzed the relationship between them seed dormancy and longevity. The data revealed a negative correlation, in contrast to commonly held view, as high longevity with shallow seed dormancy, and low storability correlated with deep seed dormancy.

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## Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

## References

[1] Lubzens, E. and Cerda, J. (2010) Dormancy and Resistance in Harsh Environments. Springer, Berlin. https://doi.org/10.1007/978-3-642-12422-8

[2] Mares, D.J. and Mrva, K. (2001) Mapping Quantitative Trait Loci Associated with Variation in Grain Dormancy in Australian Wheat. *Australian Journal of Agricultural Research*, **52**, 1257-1265. https://doi.org/10.1071/AR01049

[3] Roberts, E.H. (1972) Dormancy: A Factor Affecting Seed Survival in the Soil. In: Roberts, E.H., Ed., *Viability of Seeds*, Chapman and Hall, London, 324-327. https://doi.org/10.1007/978-94-009-5685-8_11

[4] Gu, X.Y., Chen, Z.X. and Foley, M.E. (2003) Inheritance of Seed Dormancy in Weedy Rice. *Crop Science*, **43**, 835-843. https://doi.org/10.2135/cropsci2003.8350

[5] Mangelsdorf, P.C. (1930) The Inheritance of Dormancy and Premature Germination in Maize. *Genetics*, **15**, 462-494. https://doi.org/10.1093/genetics/15.5.462

[6] Lan, H., Li, X.H., Wang, F.G., Gao, S.B., Cao, M.J., Tang, Q.L., Pan, G.T., Zhao, J.R. and Rong, T.Z. (2007) QTL Mapping of Seed Dormancy in Maize (*Zea mays* L.). *Acta Agronomica Sinica*, **33**, 1474-1478.

[7] Lopez, A.N.A., Gonzalez, J.J.S., Corral, J.A.R., Larios, L.C., Santacruz-Ruvalcaba, F., Hernandez, C.V.S. and Holland, J.B. (2011) Seed Dormancy in Mexican *Teosinte*. *Crop Science*, **51**, 2056-2066. https://doi.org/10.2135/cropsci2010.09.0538

[8] Bewley, J.D. (1997) Seed Germination and Dormancy. *Plant Cell*, **9**, 1055-1066. https://doi.org/10.1105/tpc.9.7.1055

[9] Chang, S.C. (1943) Length of Dormancy in Cereal Crops and Its Relationship to After-Harvest Sprouting. *Agronomy Journal*, **35**, 482-490. https://doi.org/10.2134/agronj1943.00021962003500060003x

[10] Derera, N.F. amd Bhatt, G.M. (1980) Germination Inhibition of the Bracts in Relation to Pre-Harvest Sprouting Tolerance in Wheat. *Cereal Research Communications*, **8**, 199-201.

[11] Roy, J.K., Prasad, M., Varshney, R.K., Balyan, H.S., Blake, T.K., Dhaliwal, H.S., Singh, H., Edwards, K.J. and Gupta, P.K. (1999) Identification of a Microsatellite on Chromosomes 6B and a STS on 7D of Bread Wheat Showing an Association with Pre-Harvest Sprouting Tolerance. *Theoretical and Applied Genetics*, **99**, 336-340.

https://doi.org/10.1007/s001220051241

[12] Rodríguez, M.V., Mendiondo, G.M., Cantoro, R., Auge, G.A., Luna, V., Masciarelli, O., and Benech-Arnold, R.L. (2012) Expression of Seed Dormancy in Grain Sorghum Lines with Contrasting Pre-Harvest Sprouting Behavior Involves Differential Regulation of Gibberellin Metabolism Genes. *Plant and Cell Physiology*, **53**, 64-80. https://doi.org/10.1093/pcp/pcr154

[13] Rodriguez, M.V., Barrero, J.M., Corbineau, F., Gubler, F. and Benech-Arnold, R.L. (2015) Dormancy in Cereals (Not Too Much, Not So Little): About the Mechanisms behind This Trait. *Seed Science Research*, **25**, 99-119. https://doi.org/10.1017/S0960258515000021

[14] Shorinola, O., Bird, N., Simmonds, J., Berry, S., Henriksson, T., Jack, P., Werner, P., Gerjets, T., Scholefield, D., Balcárková, B., Valárik, M., Holdsworth, M.J., Flintham, J. and Uauy, C. (2016) The Wheat *Phs-A*1 Pre-Harvest Sprouting Resistance Locus Delays the Rate of Seed Dormancy Loss and Maps 0.3 cm Distal to the *PM*19 Genes in UK Germplasm. *Journal of Experimental Botany*, **67**, 4169-4178. https://doi.org/10.1093/jxb/erw194

[15] Zhang, Y., Xia, X. and He, Z. (2017) The Seed Dormancy Allele *TaSdr-A*1*a* Associated with Pre-Harvest Sprouting Tolerance Is Mainly Present in Chinese Wheat Landraces. *Theoretical and Applied Genetics*, **130**, 81-89. https://doi.org/10.1007/s00122-016-2793-0

[16] Liu, Y., Bino, R.J., van der Burg, W.J., Groot, S.P.C. and Hilhorst, H.W.M. (1996) Effects of Osmotic Priming on Dormancy and Storability of Tomato (*Lycopersicon esculentum* Mill.) Seeds. *Seed Science Research*, **6**, 49-55. https://doi.org/10.1017/S0960258500003020

[17] Harrington, J.F. (1972) Seed Storage and Longevity. In: Kozlowski, T.T., Ed., *Seed Biology*, *Insects*, *and Seed Collection*, *Storage*, *Testing and Certification*, Academic Press, New York, 145-245. https://doi.org/10.1016/B978-0-12-395605-7.50009-0

[18] Copeland, L.C. and McDonald, M.B. (2001) Principles of Seed Science and Technology. 4th Edition, Kluwer Academic Publishers, Norwell. https://doi.org/10.1007/978-1-4615-1619-4

[19] Roberts, E.H. (1972) Storage Environment and the Control of Viability. In: Roberts, E.H., Ed., *Viability of Seeds*, Chapman and Hall, London, 14-58. https://doi.org/10.1007/978-94-009-5685-8_2

[20] Wu, S.Y. and Zhou, G.Y. (2011) Comparison of Aging Characteristics and Longevity of Wheat Seeds in Vacuum and Non-Vacuum Packages Storage in Mid-Term Low-Temperature Genebank. *Acta Agronomica Sinica*, **37**, 1109-1115. https://doi.org/10.3724/SP.J.1006.2011.01109

[21] Sahadevan, P.C. (1953) Studies on the Loss of Viability of Rice Seeds in Storage. *Madras Agricultural Journal*, **40**,133-143.

[22] Bewley, J.D. and Black, M. (1982) Life-Span of Seeds Buried in Soil, In: Bewley, J.D. and Black, M., Eds., *Physiology and Biochemistry of Seeds in Relation to Germination Volume* 2: *Viability*, *Dormancy*, *and Environmental Control*, Springer-Verlag, Berlin Heidelberg, 3-7.

[23] Debeaujon, I., Léon-Kloosterziel, K.M. and Koornneef, M. (2000) Influence of the Test on Seed Dormancy, Germination, and Longevity in Arabidopsis. *Plant Physiology*, **122**, 403-413. https://doi.org/10.1104/pp.122.2.403

[24] Giorgi, J., Piskurewicz, U., Loubery, S., Utz-Pugin, A., Bailly, C., Mène-Saffrané, L. and Lopez-Molina, L. (2015) An Endosperm-Associated Cuticle Is Required for Arabidopsis Seed Viability, Dormancy and Early Control of Germination. *PLOS*

*Genetics*, **11**, e1005708. https://doi.org/10.1371/journal.pgen.1005708

[25] Nguyen, T., Keizer, P., Van Eeuwijk, F., Smeekens, S. and Bentsink, L., (2012) Natural Variation for Seed Longevity and Seed Dormancy Are Negatively Correlated in Arabidopsis. *Plant Physiology*, **160**, 2083-2092. https://doi.org/10.1104/pp.112.206649

[26] Roberts, E.H. (1963) An Investigation of Inter-Varietal Differences in Dormancy and Viability of Rice Seed. *Annals of Botany*, **27**, 365-369. https://doi.org/10.1093/oxfordjournals.aob.a083853

[27] Rehman Arif, M.A., Nagel, M., Neumann, K., Kobiljski, B., Lohwasser, U. and Börner, A. (2012) Genetic Studies of Seed Longevity in Hexaploid Wheat Using Segregation and Association Mapping Approaches. *Euphytica*, **186**, 1-13. https://doi.org/10.1007/s10681-011-0471-5

[28] ISTA (2014) International Rules for Seed Testing. International Seed Testing Association, Bassersdorf.

[29] Agacka-Mołdoch, M., Rehman Arif, M.A., Lohwasser, U., Doroszewska, T., Qualset, C.O. and Börner, A. (2016) The Inheritance of Wheat Grain Longevity: A Comparison between Induced and Natural Ageing. *Journal of Applied Genetics*, **57**, 477-481. https://doi.org/10.1007/s13353-016-0348-3

[30] Abdul-Baki, A.A. and Anderson, J.D. (1973) Vigor Determination in Soybean Seed by Multiple Criteria. *Crop Science*, **13**, 630-633. https://doi.org/10.2135/cropsci1973.0011183X001300060013x

[31] Vieira, R.D., Tekrony, D.M., Egli, D.B. and Rucker, M. (2001) Electrical Conductivity of Soybean Seeds after Storage in Several Environments. *Seed Science and Technology*, **29**, 599-608.

[32] Fessel, S.A., Vieira, R.D., Cruz, M.C.P., Paula, R.C. and Panobianco, M. (2006) Electrical Conductivity Testing of Corn Seeds as Influenced by Temperature and Period of Storage. *Pesquisa Agropecuária Brasileira*, **41**, 1551-1559. https://doi.org/10.1590/S0100-204X2006001000013

[33] Panobianco, M., Vieira, R.D. and Perecin, D. (2007) Electrical Conductivity as an Indicator of Pea Seed Aging of Stored at Different Temperatures. *Scientia Agricola* (*Piracicaba*, *Bra.*), **64**, 119-124. https://doi.org/10.1590/S0103-90162007000200003

[34] Walker-Simmonds, M.K. (1987) ABA Levels and Sensitivity in Developing Embryos of Sprouting Resistant and Susceptible Cultivars. *Plant Physiology*, **84**, 61-66. https://doi.org/10.1104/pp.84.1.61

[35] Rohlf, F.J. (2000) NTSYS-pc V2.10e: Numerical Taxonomy and Multivariate Analysis System. Exeter Software, New York.

[36] Mantel, N.A. (1967) The Detection of Disease Clustering and a Generalized Regression Approach. *Cancer Research*, **27**, 209-220.

[37] Machado, C.G., Martins, C.C., de Santana, D.G., Cruz, S.C.S. and de Oliveira, S.S.C. (2011) Suitability of Electrical Conductivity Test for Seeds of *Pisum sativum* subsp. Arvense. *Ciência Rural* (*Santa Maria*), **41**, 988-995. https://doi.org/10.1590/S0103-84782011005000062

[38] Fessel, S.A., Panobianco, M., de Souza, C.R. and Vieira, R.D. (2010) Electrical Conductivity Test of Soybean Seeds Stored under Different Temperatures. *Bragantia*, **69**, 207-214. https://doi.org/10.1590/S0006-87052010000100026

[39] Short, G.E. and Lacy, M.L. (1976) Carbohydrate Exudation from Pea Seeds: Effect of Cultivar, Seed Age, Seed Color, and Temperature. *Phytopathology*, **66**, 182-187. https://doi.org/10.1094/Phyto-66-182

[40] Panobianco, M. and Vieira, R.D. (1996) Electrical Conductivity of Soybean Soaked Seeds. I. Effect of Genotype. *Pesquisa Agropecuária Brasileira*, **31**, 621-627.

[41] S.S., Silva, R.D., Vieira, C.R.S., Grzybowski, T.C., Carvalho, M. and Panobianco (2013) Electrical Conductivity of Different Common Bean Seeds Genotypes. *Journal of Seed Science*, **35**, 216-224. https://doi.org/10.1590/S2317-15372013000200011

[42] Hill, H.J., Taylor, A.G. and Huang, X.L. (1988) Seed Viability Determinations in Cabbage Utilizing Sinapine Leakage and Electrical Conductivity Measurements. *Journal of Experimental Botany*, **39**, 1439-1447. https://doi.org/10.1093/jxb/39.10.1439

[43] Blum, A. and Ebercon, A. (1981) Cell Membrane Stability as a Measure of Drought and Heat Tolerance in Wheat. *Crop Science*, **21**, 43-47. https://doi.org/10.2135/cropsci1981.0011183X002100010013x

[44] Sivritepe, H.O., Senturk, B. and Teoman, S. (2015) Electrical Conductivity Tests in Maize Seeds. *Advances in Plants & Agriculture Research*, **2**, 296-297. https://doi.org/10.15406/apar.2015.02.00075

[45] Khan, A.Z., Khalil, S.K., Shah, P., Muhammad, F. and Amanullah (2007) Vigor Tests Used to Rank Seed Lot Quality and Predict Field Emergence in Wheat. *American Journal of Plant Physiology*, **42**, 3147-3155. https://doi.org/10.3923/ajpp.2007.311.317

[46] Watanabe, N. and Ikebata, N. (2000) The Effects of Homoeologous Group 3 Chromosomes on Grain Colour Dependent Seed Dormancy and Brittle Rachis in Tetraploid Wheat. *Euphytica*, **115**, 215-220. https://doi.org/10.1023/A:1004066416900

[47] Himi, E., Mares, D., Yanagisawa, A. and Noda, K. (2002) Effect of Grain Colour Gene (R) on Grain Dormancy and Sensitivity of the Embryo to Abscisic Acid (ABA) in Wheat. *Journal of Experimental Botany*, **53**, 1569-1574. https://doi.org/10.1093/jxb/erf005

[48] Imtiaz, M., Ogbonnaya, F.C., Oman, J. and Van Ginkel, M. (2008) Characterization of Quantitative Trait Loci Controlling Genetic Variation for Preharvest Sprouting in Synthetic Backcross-Derived Wheat Lines. *Genetics*, **178**, 1725-1736. https://doi.org/10.1534/genetics.107.084939

[49] Nagel, M. and Börner, A. (2010) The Longevity of Crop Seeds Stored under Ambient Conditions. *Seed Science Research*, **20**, 1-12. https://doi.org/10.1017/S0960258509990213

## Supplementary Material

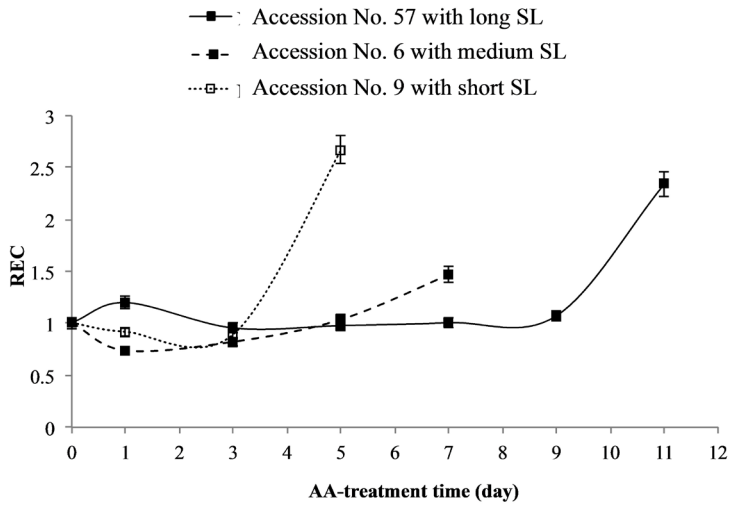


**Figure S1.** Effect of AA-treatment time on relative electrical conductivity. SL, seed longevity.

**Table S1.** The pedigrees of the 60 accessions from CIMCOG panel and their seed coat color (SCC).

| No. | Pedigree | SCC |
|---|---|---|
| 1 | ATTILA | White (W) |
| 2 | ATTILA*2/PBW65 | W |
| 3 | ATTILA*2/PBW65*2/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES | Red (R) |
| 4 | ATTILA//PGO/SERI/3/PASTOR | R |
| 5 | BABAX/LR42//BABAX/3/ER2000 | W |
| 6 | BABAX/LR42//BABAX/3/VORB | R |
| 7 | BACANORA T 88 | W |
| 8 | BAVIACORA M 92 | W |
| 9 | BCN/RIALTO | R |
| 10 | BCN/WBLL1 | W |
| 11 | BECARD | W |
| 12 | BECARD/KACHU | W |
| 13 | BRBT1*2/KIRITATI | R |
| 14 | C80.1/3*BATAVIA//2*WBLL1/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES | W |
| 15 | SAUAL/4/CROC_1/AE.SQUARROSA (205)//KAUZ/3/ATTILA/5/SAUAL | W |
| 16 | SAUAL/WHEAR//SAUAL | W |
| 17 | CHIR3/4/SIREN//ALTAR 84/AE.SQUARROSA (205)/3/3*BUC/5/PFAU/WEAVER | W |
| 18 | CHWL86/6/FILIN/IRENA/5/CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER | W |
| 19 | CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6/RIALTO | R |
| 20 | CIRNO C 2008 | W |
| 21 | CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/OCI/5/PASTOR/6/TEMPORALERA M 87/ROMO96 | W |
| 22 | CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER/5/2*KAUZ | W |
| 23 | CNO79//PF70354/MUS/3/PASTOR/4/BAV92*2/5/FH6-1-7 | W |

**Continued**

| | | |
|---|---|---|
| 24 | CROC_1/AE.SQUARROSA (205)//BORL95/3/PRL/SARA//TSI/VEE#5/4/FRET2 | W |
| 25 | GK ARON/AG SECO 7846//2180/4/2*MILAN/KAUZ//PRINIA/3/BAV92 | W |
| 26 | KINGBIRD #1//INQALAB 91*2/TUKURU | W |
| 27 | KFA/3/PFAU/WEAVER//BRAMBLING/4/PFAU/WEAVER*2//BRAMBLING | R |
| 28 | MEX94.27.1.20/3/SOKOLL//ATTILA/3*BCN | W |
| 29 | MILAN/KAUZ//PRINIA/3/BAV92 | W |
| 30 | MUNAL #1 | W |
| 31 | ATTILA/PASTOR | W |
| 32 | OASIS/5*BORL95/5/CNDO/R143//ENTE/MEXI75/3/AE.SQ/4/2*OCI | W |
| 33 | MISR 1 | W |
| 34 | OASIS/SKAUZ//4*BCN/3/2*PASTOR/5/FRET2*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/6/SAUAL #1 | W |
| 35 | PANDORA//WBLL1*2/BRAMBLING | W |
| 36 | PASTOR/3/URES/JUN//KAUZ/4/WBLL1 | W |
| 37 | PAVON F 76 | W |
| 38 | PBW343*2/KUKUNA*2//FRTL/PIFED | W |
| 39 | PFAU/SERI.1B//AMAD/3/WAXWING | W |
| 40 | ARMENT//2*SOOTY_9/RASCON_37/4/CNDO/PRIMADUR//HAI-OU_17/3/SNITAN | W |
| 41 | QUAIU #3//MILAN/AMSEL | W |
| 42 | RL6043/4*NAC//2*PASTOR | W |
| 43 | ROLF07*2/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES | W |
| 44 | SERI M 82 | W |
| 45 | SIETE CERROS T66 | W |
| 46 | SOKOLL*2/3/BABAX/LR42//BABAX | W |
| 47 | SOKOLL//PBW343*2/KUKUNA/3/ATTILA/PASTOR | W |
| 48 | TACUPETO F2001/SAUAL/4/BABAX/LR42//BABAX*2/3/KURUKU | W |
| 49 | TACUPETO F2001/BRAMBLING*2//KACHU | W |
| 50 | TC870344/GUI//TEMPORALERA M 87/AGR/3/2*WBLL1 | W |
| 51 | TRAP#1/BOW/3/VEE/PJN//2*TUI/4/BAV92/RAYON/5/KACHU #1 | W |
| 52 | TRCH/SRTU//KACHU | W |
| 53 | UP2338*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/5/MILAN/KAUZ//CHIL/CHUM18/6/UP2338*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ | W |
| 54 | W15.92/4/PASTOR//HXL7573/2*BAU/3/WBLL1 | W |
| 55 | BECARD | W |
| 56 | WBLL1*2/4/BABAX/LR42//BABAX/3/BABAX/LR42//BABAX | W |
| 57 | WBLL1*2/KURUKU*2/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES | W |
| 58 | WBLL1*2/TUKURU*2/4/CROC_1/AE.SQUARROSA (205)//BORL95/3/2*MILAN | W |
| 59 | WHEAR/SOKOLL | W |
| 60 | YAV_3/SCO//JO69/CRA/3/YAV79/4/AE.SQUARROSA(498)/5/LINE1073/6/KAUZ*2/4/CAR//KAL/BB/3/NAC/5/KAUZ/7/KRONSTAD F2004/8/KAUZ/PASTOR//PBW343 | R |

**Table S2.** Correlation analysis between kernel weight and seed dormancy and longevity related traits[¶].

| | KW | | KW | | KW |
|---|---|---|---|---|---|
| RGP for SL | 0.36** | GP for control | 0.22 | RGP for SD | 0.18 |
| RGR for SL | 0.42** | GR for control | 0.22 | RGR for SD | 0.19 |
| RVI for SL | 0.38** | VI for control | 0.15 | GI for SD | 0.27* |
| REC for SL | −0.15 | EC for control | −0.10 | DSD | −0.18 |

[¶]KW, kernel weight; GR, germination rate; RGR, relative germination rate; GP, germination potential; RGP, relative germination potential; SL, seed longevity; SD, seed dormancy; DSD, degree of seed dormancy.