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# Research Note

## Longevity of 285 seed lots of wheat in hermetic storage compared with independent estimates from the seed viability equation

**Gajender Yadav[1,2] and Richard H. Ellis[1*]**

[1] School of Agriculture, Policy and Development, University of Reading, Earley Gate, PO Box 237, Reading RG6 6AR, UK (E-mail: r.h.ellis@reading.ac.uk)
[2] Present address: Division of Soil and Crop Management, ICAR Central Soil Salinity Research Institute, Zarifa Farm, Kachhwa Road, Karnal-132001, India
* Author for correspondence

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### Abstract

The longevity in hermetic storage at 40°C with 14.1-15.7% moisture content of 285 seed lots of wheat (*Triticum aestivum* cv. Tybalt), harvested at or before maturity from control or modified environments under rain shelter or after simulated rainfall in three consecutive years (2010-12), was compared with independent estimates from the seed viability equation and previously-published viability constant values for wheat. Around half of the observations provided good agreement with these independent estimates of longevity, but some of the seed lots harvested close to maturity in 2012, or before the end of the seed-filling phase in 2011, survived longer in storage than prior estimates.

**Keywords:** longevity, moisture content, seed storage, temperature, *Triticum aestivum* L., viability equation, wheat

### Experimental and discussion

The seed viability equation (Ellis and Roberts, 1980) quantifies the effect of storage temperature ($t$, °C) and moisture content ($m$, % fresh weight) in constant, hermetic environments on seed longevity.

The equation comprises two components. The first:

$$v = K_i - p/\sigma \quad (1)$$

estimates $v$ (probit percentage viability) after $p$ days in storage, where $K_i$ is a constant specific to the seed lot (equivalent to initial probit viability) and $\sigma$ is the standard deviation of the frequency distribution of seed deaths in time (days). That is, equation 1 defines a point on the transformed seed survival curve of intercept $K_i$ and slope $1/\sigma$. The second equation:

$$\log_{10}\sigma = K_E - C_W\log_{10}m - C_Ht - C_Qt^2 \quad (2)$$

quantifies the exponential relation between seed longevity ($\sigma$) and (constant, hermetic) seed storage environment where $K_E$, $C_W$, $C_H$ and $C_Q$ are species constants (Ellis and Roberts, 1980). The value $\sigma$ is a particular period of longevity which links the two equations.

The suggestion that $K_E$, $C_W$, $C_H$ and $C_Q$ are invariant within a species, and hence that, in any one identical environment, $\sigma$ is the same for different seed lots, was well founded at the time (Ellis and Roberts, 1980, 1981a), as well as subsequently (e.g. Ellis and Hong, 2007). The approach has also been applied successfully to estimate the survival of different seed lots in hermetic storage (e.g. Ellis and Roberts, 1981b), or, moderately so, in open storage (e.g. Fabrizius *et al.*, 1999). On the other hand, variation in $\sigma$ in one environment or in $K_E$ has been reported, for example, amongst some cultivars (Zewdie and Ellis, 1991; Zanakis *et al.*, 1993), ecotypes (Hay *et al.*, 2003), mutants (Lyall *et al.*, 2003) or sub-species (Ellis *et al.*, 1992) within a species, or during seed development (Hay *et al.*, 1997).

Here we compare estimates of $\sigma$ derived from probit analysis in accordance with eqn (1) reported previously (Ellis and Yadav, 2016; Yadav and Ellis, 2016), for 285 seed lots of wheat (*Triticum aestivum* L.) cv. Tybalt produced in 2010-2012, with independent estimates of $\sigma$. The latter were calculated from eqn (2) and previously-published values of $K_E$, $C_W$, $C_H$ and $C_Q$ derived from studies over a wide range of different, constant storage environments with cvs. Highbury, Hobbit, Sportsman and Mardler (Ellis and Hong, 2007).

Ellis and Yadav (2016) and Yadav and Ellis (2016) have described in detail the seed production conditions and subsequent determination of seed storage longevity for these 285 seed lots. Briefly, seeds were produced in a plastic tunnel house (2010) or in the field (2011, 2012) and harvested by hand at or close to harvest maturity (2010, 2011, 2012) or throughout seed development and maturation (2011, 2012), with treatments to alter the exposure of the developing and maturing seeds to natural (protected from rainfall, or not) or simulated rainfall (ears wetted, or not) (table 1). Seed survival in hermetic storage at 40°C with about 15% moisture content was then determined. The moisture content of storage was determined for each seed lot using the high-constant-temperature-oven method (ISTA, 2011), but with two replicates of only 100 seeds as the number of seeds per lot was limited: individual estimates varied amongst the 285 seed lots from 14.1 to 15.7% moisture content (fresh weight basis).

Independent estimates of $\sigma$ were calculated at 39, 40 and 41°C in combination with the above range of moisture contents using eqn (2) with the viability constants for wheat (Ellis and Hong, 2007). Equation (2) describes a logarithmic, negative relation between

Table 1. Summary of wheat seed lot data analysed, treatments *in planta*, harvest date (days after anthesis; DAA) and source of observations.

| Year | Environment | Treatment | Seed harvest date (DAA) | Number of seed lots | Source |
|---|---|---|---|---|---|
| 2010 | Tunnel House | Control | 55, 56, 62 | 3 | Ellis and Yadav (2016) |
| | | Ears sprayed, water[1], 55 and 56 DAA; WA1-4 | 55[2], 56, 56[2], 63 | 4 | |
| | | Ears sprayed, water[1], 56 DAA; WB | 56[2], 63 | 2 | |
| 2011 | Field[3] | Control (Open); C1O | 14, 25, 32, 39, 46, 53, 60, 67, 74 | 9+9 | Yadav and Ellis (2016) |
| | | Control (Rain shelter; 0-74 DAA); C2S | 14, 25, 32, 39, 46, 53, 60, 67, 74 | 9+9 | |
| | | Rain shelter 0-14 DAA; S1 | 14, 32, 39, 46, 53, 60, 67, 74 | 8+8 | |
| | | Rain shelter 14-28 DAA; S2 | 14, 25, 32, 39, 46, 53, 60, 67, 74 | 9+9 | |
| | | Rain shelter 28-42 DAA; S3 | 25, 32, 39, 46, 53, 60, 67, 74 | 8+8 | |
| | | Rain shelter 42-56 DAA; S4 | 46, 53, 60, 67, 74 | 5+5 | |
| | | Ears sprayed, water[1], 7 DAA; W1 | 14, 32, 39, 46, 53, 60, 67, 74 | 8+8 | |
| | | Ears sprayed, water[1], 21 DAA; W2 | 14, 25, 32, 39, 46, 53, 60, 67, 74 | 9+9 | |
| | | Ears sprayed, water[1], 35 DAA; W3 | 32, 39, 46, 53, 60, 67, 74 | 8+8 | |
| | | Ears sprayed, water[1], 49 DAA; W4 | 46, 53, 60, 67, 74 | 5+5 | |
| | | Ears sprayed, water[1], 7, 21, 35, 49 DAA; W5 | 14, 32, 39, 46, 53, 60, 67, 74 | 8+8 | |
| 2012 | Field[3] | Control (Open); C1O | 14, 21, 28, 35, 42, 49, 56, 63, 70 | 9+9 | Yadav and Ellis (2016) |
| | | Control (Rain shelter; 0-70 DAA); C2S | 14, 21, 28, 35, 42, 49, 56, 63, 70 | 9+9 | |
| | | Rain shelter, 42-70 DAA; S1 | 42, 49, 56, 63, 70 | 5+5 | |

[1] To simulate 25 mm rainfall.
[2] Samples harvested 30 minutes after simulated rainfall ended.
[3] Field investigations comprised two blocks; 9+9, for example, is 18 seed lots from nine harvest dates from each of two blocks.

Table 1. *cont'd*

Table 1. *Continued.*

| Year | Environment | Treatment | Seed harvest date (DAA) | Number of seed lots | Source |
|---|---|---|---|---|---|
| 2012 | Field[3] | Rain shelter, 42-56 DAA; S2 | 42, 49, 56, 63, 70 | 5+5 | Yadav and Ellis (2016) |
| | | Rain shelter, 56-70 DAA; S3 | 56, 63, 70 | 3+3 | |
| | | Ears sprayed, water[1], 42 DAA; W1 | 42, 49, 56, 63, 70 | 5+5 | |
| | | Ears sprayed, water[1], 49 DAA; W2 | 49, 56, 63, 70 | 4+4 | |
| | | Ears sprayed, water[1], 56 DAA; W3 | 56, 63, 70 | 3+3 | |
| | | Ears sprayed, water[1], 63 DAA; W4 | 63, 70 | 2+2 | |
| | | Ears sprayed, water[1], 70 DAA; W5 | 70, 77 | 2+2 | |
| | | Ears sprayed, water[1], Waf[2] | 42[2], 49[2], 56[2], 63[2], 70[2] | 5+5 | |

[1] To simulate 25 mm rainfall.
[2] Samples harvested 30 minutes after simulated rainfall ended.
[3] Field investigations comprised two blocks; 9+9, for example, is 18 seed lots from nine harvest dates from each of two blocks.

seed longevity and seed storage moisture content. That format was used here to compare the observed values of $\sigma$ with those estimated independently by the viability equation (figure 1). Seed lots comprising immature seeds harvested before mass maturity (end of the seed-filling phase; Ellis and Pieta-Filho, 1992) are identified by solid symbols in figure 1; those after mass maturity by open symbols.

In our earlier studies, $\sigma$ varied amongst seed lots in each year (Ellis and Yadav, 2016; Yadav and Ellis, 2016). Those 285 seed lots were in similar but not identical storage environments (figure 1). However, comparison at any single moisture content in figure 1 also shows variation in the observations for $\sigma$.

Seed longevity is very sensitive to the environment, eqn (2). It varies exponentially from minutes to, possibly, thousands of years over wide ranges of storage temperature and moisture content (Ellis and Roberts, 1980). For example, the experimental results analysed to provide the seed viability constants applied here varied up to around a thousand-fold in longevity (Ellis and Hong, 2007). Accordingly, the independent estimates of $\sigma$ from the viability equation are shown as three parallel lines at 39, 40 or 41°C from 14.1 to 15.7% moisture content in figure 1. The sensitivity of predictions and observations to small errors in moisture content and/or temperature is shown by this triplet of lines at 39-41°C against the x-axis. Tolerances for seed moisture content differences between replicates is ± 0.2% for crop seeds (ISTA, 2011) and ± 0.5% for small tree seeds (Bonner, 1984); however, repeatability and reproducibility of seed moisture content measurements are poorer than this. Temperatures within well-regulated incubators vary spatially and also over time (the sensor on/off range) by 0.5-1.0°C.

The steeper, thicker line in figure 1 is that fitted directly to all 285 observations. That analysis confirmed that seed moisture content affected longevity ($P < 0.0001$). However, the estimate of the slope (i.e. $C_W$), and its standard error, calculated across the narrow range of 14.1-15.7% moisture content (11.383, s.e. 0.564), was much greater than that of 4.836 (s.e. 0.366) provided by Ellis and Hong (2007) from observations between 6 and 25% moisture content. Similarly, it was much greater than that of 5.896 (s.e. 0.248), determined for barley (*Hordeum vulgare* L.) between 8 and 25% moisture content (Ellis and Roberts, 1980).

Whilst the range of observations straddled the independent estimates at low and high moisture contents, more of the observations showed greater estimates for $\sigma$ than predicted at lower moisture contents. The fitted line crossed the (shallower) predicted lines between 14.8 and 15.7% moisture content at 39-41°C such that, on average, the predictions underestimated $\sigma$ below 14.8% moisture content (figure 1). The fitted regression lines for each year varied: 2012 and 2011 were just above and below the 2010-2012 fitted line, respectively, whereas that for 2010 was below 2011 and 2012 and also below the predicted line.

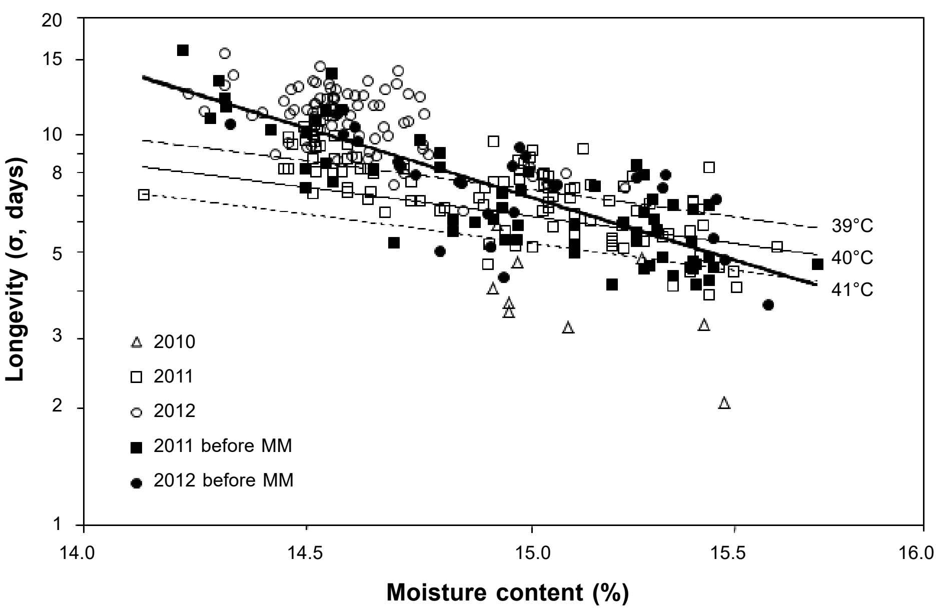


Figure 1. Comparison of the longevity ($\sigma$, days) of 285 seed lots of wheat cv. Tybalt harvested during seed development and maturation in 2010 (△), 2011 (□, ■), or 2012 (○, ●) in hermetic storage at 40°C at the moisture contents shown with the logarithmic, negative, relations between $\sigma$ and moisture content (%) at 39, 40, or 41°C (three parallel lines of shallower slope) derived independently from the seed viability equation (Ellis and Roberts, 1980) and species constants for wheat (Ellis and Hong, 2007); MM is mass maturity (see text). The negative logarithmic relation of steeper slope is that fitted to the 285 observations from harvests in all three years ($\log_{10}\sigma = 14.239$ (s.e. 0.661) – 11.383 (s.e. 0.564) × $\log_{10} m$; $R^2 = 0.591$, $P < 0.0001$).

Given that longevity varies exponentially with storage environment (Ellis and Roberts, 1980) and the crossover of the fitted and predicted lines, the independent estimates of longevity provided a reasonable prediction of many, but not all, of the 285 observations with which they are compared in this study (figure 1). Observations differed in the extent of their variation about estimated longevity, but around half provided good agreement with the independent estimates and straddled the lines at 39 to 41°C evenly above 14.8% moisture content. Whilst some observations at lower moisture contents also matched the independent estimates, for example those harvested at maturity in 2011, most seed lots at moisture contents below 14.8% survived longer than expected. Prominent amongst them were seed lots harvested close to maturity in 2012, or seeds harvested early in development during the seed-filling phase in 2011. In the latter case, the most extreme deviation from the independent estimates was provided by seeds harvested only 14 days after anthesis. Most of those seeds were too immature to be able to germinate without initial drying *ex planta* (Yadav and Ellis, 2016). Whilst that would support a conclusion of variation in $\sigma$ during seed development (Hay *et al*., 1997), the systematic discrepancy from the independent estimates was not seen above 14.8% moisture content in these seed lots (figure 1). Moreover, estimates of $\sigma$ during seed development and maturation were invariant in barley (Pieta Filho and Ellis, 1991) and *Phaseolus vulgaris* L. (Sanhewe and Ellis, 1996), for example.

The physical sciences are founded upon a high degree of mathematical predictability and precision. That is essential to their application in, for example, engineering. Predicting absolute outcomes quantitatively in the biological sciences has long proved far more challenging, particularly for population responses – such as is the case for survival within a seed lot. Farmers, gardeners, commercial traders, plant breeders and genebank managers assume (implicitly if not explicitly) some predictability in relations amongst seed survival, storage environment and duration of storage each time they dry and/or store seeds. The current comparison (figure 1) illustrates the degree to which the seed viability equation (Ellis and Roberts, 1980) combined with the species constants for wheat (Ellis and Hong, 2007) is able to satisfy the desire for predictability in seed storage (in this case for cv. Tybalt using constants from four different cultivars). No model is perfect, as shown here (figure 1). One source of the variation in observations about the model response will have been due to errors in the model: see Ellis and Hong (2007) for the errors associated with the estimation of the values of each of the species constants. The other sources of error will have derived from the observations themselves, estimates of $\sigma$ being subject to error; the standard errors of those estimates are small, however, in relation to the variation about either the predicted or fitted lines here. Finally, there are also errors in defining the precise storage environment, particularly determining seed moisture content.

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