Shango, Mosha, N’Danikou, Ramadhani, Kamala, Sumaye,
Venkataramana, Mtui, Philipo, Kusolwa and van Zonneveld (2026).
Seed Science and Technology, **54**, 2, 161-177.
https://doi.org/10.15258/sst.2026.54.2.01

Derivation of seed viability constants (C_{W}, K_{E}) and predicting seed longevity for jute mallow (*Corchorus capsularis* and *C. olitorius*)

Abdul Jafari Shango[1,2]*, Emmanuel Willium Mosha[3], Sognigbé N’Danikou[1,4], Shebati Ramadhani[1], Moses Kamala[1], Saphina Sumaye[1], Pavithravani Venkataramana[2], Hosea Dunstan Mtui[3], Mashamba Philipo[2], Paul Kusolwa[3] and Maarten van Zonneveld[5]

[1] World Vegetable Center, Eastern and Southern Africa, P.O. Box 10, Duluti, Arusha, Tanzania
[2] School of Life Sciences and Bioengineering, The Nelson Mandela African Institution of Science and Technology, P.O. Box 447, Arusha, Tanzania
[3] Department of Crop Science and Horticulture, Sokoine University of Agriculture, P.O. Box 3005, Chuo Kikuu, Morogoro, Tanzania
[4] Ecole d’Horticulture et d’Aménagement des Espaces Verts, Université Nationale d’Agriculture, BP 43 Kétou, Kétou, Bénin
[5] World Vegetable Center, Shanhua 74151, Taiwan
* Author for correspondence (E-mail: abdulshango@gmail.com)

(Submitted September 2025; Accepted February 2026; Published online May 2026)

Abstract

Genebanks support long-term germplasm conservation and ensure availability of viable seeds to users. The improved seed viability equation enables prediction of longevity by combining species-specific moisture content constants (C_{W}, K_{E}) with universal temperature constants ($C_{\mathrm{H}} = 0.0329$; $C_{\mathrm{Q}} = 0.000478$). While the number of genebank collections of jute mallow (*Corchorus capsularis* and *C. olitorius*) has significantly increased in recent years, such constants are lacking to support management. To derive C_{W} and K_{E} and predict longevity, seeds of both species were equilibrated to five moisture content levels (7.5-12.2%) and subjected to experimental storage at 60°C for 25 or 35 days for *C. olitorius* and *C. capsularis*, respectively. The viability constants were then estimated as $C_{\mathrm{W}} = 6.80$ and $K_{\mathrm{E}} = 10.78$ for *C. capsularis* and $C_{\mathrm{W}} = 6.21$ and $K_{\mathrm{E}} = 10.06$ for *C. olitorius*. The validation of the derived constants indicated good agreement between predicted and observed viability at high viability levels in both species, with increasing divergence as seeds deteriorated. The predicted seed longevity under genebank conditions indicated that *C. capsularis* seeds live longer than *C. olitorius*. The derived constants provide a practical tool for genebanks to optimise germplasm regeneration cycles and minimise the risk of genetic erosion.

Keywords: genebank management, opportunity crops, probit model, seed ageing, seed moisture content, survival curves, traditional African vegetables, viability equations

---

Introduction

Jute mallow (*Corchorus* spp.) is known for its ability to grow in resource-limited areas and multipurpose use, including for food, fibre and medicine. Jute mallow is among the priority crops that are strategically positioned to support food security and climate-resilient production systems in Sub-Saharan Africa (van Zonneveld *et al*., 2021; N'Danikou *et al*., 2024a). Jute mallow confers a diverse array of traits, especially in the face of ever-increasing global warming (Sileshi *et al*., 2025). It is a versatile crop with the potential to address malnutrition in limited-resource settings and harsh environments as compared with conventional vegetable crops (N'Danikou *et al*., 2024a).

Collectively, the World Vegetable Center (WorldVeg) genebanks hold 606 jute mallow accessions that are publicly accessible through Genesys (https://www.genesys-pgr.org/). Despite the crop's importance and ongoing efforts to conserve its genetic resources, knowledge of seed longevity in genebank dry storage conditions remains largely unknown, limiting evidence-based management of the growing jute mallow collections. This lack of information poses challenges for the proper planning of seed regeneration cycles (Volk *et al*., 2023; N'Danikou *et al*., 2024a). The longevity of orthodox seeds in a particular storage condition can be mathematically quantified using the improved seed viability equation proposed by Ellis and Roberts (1980a):

$$v = K_{\mathrm{i}} - p / 10^{K_{\mathrm{E}} - C_{\mathrm{W}} \log_{10} m - C_{\mathrm{H}} t - C_{\mathrm{Q}} t^2} \tag{1}$$

where v is final viability in NEDs or probits after p days of storage, m is % moisture content (fresh weight basis), t is storage temperature (°C), K_{i} is the initial viability of the seed lot at $p = 0$ days (seed lot constant), C_{H} and C_{Q} are temperature constants, C_{W} is the species-specific moisture content constant and K_{E} is the theoretical viability (in probits) at 1% moisture content and 0°C.

Since the effect of temperature is the same for all species, C_{W} and K_{E} are exceptionally important parameters in storage as they may vary both within and between species (Hay *et al*., 2022; Nadarajan *et al*., 2023). We hypothesise that the seeds of *Corchorus capsularis* and *C. olitorius* are orthodox in nature, tolerating drying and low-temperature storage, and that the seed viability equation can be used to predict seed longevity of these species. Although the seed viability equation has been widely applied to predict seed longevity of several crops to date (Ellis and Roberts, 1980a; N'Danikou *et al*., 2024a,b; Kaweya *et al*., 2026), this knowledge was lacking for cultivated jute mallow species (*C. capsularis* and *C. olitorius*). The objective of this study was therefore to estimate species-specific seed viability constants (C_{W} and K_{E}) for these jute mallow species and predict seed longevity under genebank dry storage conditions.

Materials and methods

Seed materials

Seed samples of three accessions of *Corchorus capsularis* and four accessions of *C. olitorius* were sourced from WorldVeg's Africa Vegetable Genebank in Arusha, Tanzania (table 1). Prior to the accelerated ageing experiment, all seeds had been stored at 5°C (medium-term storage condition) and were confirmed to have 100% viability at the time of the experiment.

Estimation of initial seed moisture content

The initial seed moisture status of the sampled seeds was measured using a water activity meter at 22.5°C by filling the 3.2 ml sample holder with intact seeds. The holders were placed in the measuring chamber of an AW-D10 water activity station used in conjunction with a HygroLab 3 display unit (Rotronic AG, Bassersdorf, Switzerland). Once stabilised, the displayed water activity was multiplied by 100 to give the equilibrium relative humidity (eRH). This was used together with the temperature to estimate the seed moisture content based on oil contents for *C. capsularis* (13.2%) and *C. olitorius* (12.7%) (Earle and Jones, 1962), using the Seed Information Database (SER/INSR/RBGK, 2025).

Adjusting seed moisture content

The seeds of *C. capsularis* accession TOT 6278 and *C. olitorius* accession ES were each divided into five samples which were equilibrated to five different moisture content (MC) levels: 7.5, 8.5, 10.2, 11.2 and 12.2% on a fresh weight basis (f. wt.) (Whitehouse and Norton, 2022). Seeds were placed in glass crucibles without lids and humidified in a desiccator over non-saturated lithium chloride (LiCl) solution until the target MCs of 10.2, 11.2 and 12.2% were reached (Hay *et al.*, 2008; Gómez Barreiro *et al.*, 2025). The lower MCs of 7.5 and 8.5% were achieved using non-indicating silica gel in a desiccator. The MCs were checked every two days by weighing the samples until the targeted equilibrium was reached, using the following formula (Hay *et al.*, 2023):

$$Seed\ weight\ at\ desired\ MC = initial\ seed\ weight \times \frac{(100 - initial\ MC)}{(100 - desired\ MC)} \tag{2}$$

Experimental storage

The equilibrated seeds were sealed into 7 or 8 (depending upon species) laminated aluminium foil packets, one for each sampling interval, at each seed MC. They were then stored for up to 25 or 35 days, respectively, in an oven (Thermo Fisher Scientific, Heratherm OGH180, Germany) at 60°C.

Germination tests

Seeds were sampled from the ageing chamber at intervals of 0, 1, 3, 6, 9, 15, 25 and 35 days (depending on species) for germination testing. The sampled seeds were placed in Petri dishes (top-of-paper) in four replicates of 25 seeds at 20°C in a germination chamber (Model: Memmert IPP750 Plus, Memmert GmbH + Co. KG, Schwabach, Germany) with an alternate 8-hour light and 16-hour dark cycle for 14 days. About 6 ml of distilled water was added to moisten the two-layer tissue paper in each Petri dish. Germination was scored at 14 days when the radicle had emerged by at least 2 mm, to determine the percentage germination (ISTA, 2024).

Modelling seed viability loss and determination of C_W *and* K_E

Seed survival data, i.e. the ability to germinate (seed germination percentage) upon removal from the experimental storage regime were fitted by probit viability analysis using R statistical software v.4.5.1 (R Core Team, 2025; Wolkis *et al*., 2025), thereby fitting the seed viability equation when temperature is constant (3):

$$\log \sigma = K_t - C_W \log m \tag{3}$$

where σ is the standard deviation of the frequency distribution of seed deaths in time (days). The model simultaneously estimated K_i, K_t and C_w, with K_i (eqn. 1) constrained within each accession × MC level. Approximate *F*-tests were used to confirm that the survival curves could be constrained to a common estimate of K_i within each accession × MC level. The universal values for the temperature constants, C_H and C_Q (0.0329 and 0.000478, respectively) (Dickie *et al*., 1990), as well as K_t were then used to determine K_E:

$$K_E = K_t + C_H t + C_Q t^2 \tag{4}$$

where, t is temperature (°C), thereby solving all the parameters of the full viability equation (equation 1; Ellis and Roberts, 1980a; Ellis, 2022).

Estimates of the time (days) for viability to fall to 50% (p_{50}) were also computed using the '*MASS*' package v.7.3-65 (Venables and Ripley, 2002). Tables were rendered with '*knitr*' package v.1.50 (Xie, 2015, 2025). Package '*msm*' v.1.8.2 (Jackson, 2011) was used in delta-method standard error estimation for derived longevity parameters. The packages tidyverse v.2.0.0, '*ggplot2*' v.4.0.0 and '*dplyr*' v.1.1.4 (Wickham *et al*., 2019, 2025; Wickham, 2025) were used for data wrangling and visualisation.

Model validation

Seeds of three *C. capsularis* accessions and three *C. olitorius* accessions (table 1), were used for validating the newly derived seed viability constants. The seeds were artificially aged at 50°C and 12.2% MC for 35 days. The ability of the aged seeds to germinate (observed germination) was measured at intervals of 0, 1, 3, 6, 9, 15, 25 and 35 days.

Table 1. List of *Corchorus capsularis* and *C. olitorius* accessions used in the study.

Species	Accession name	Accession number	Regeneration year	Country of origin
C. capsularis	TOT 6278*	RVI002609	2016	Vietnam
C. capsularis	TOT 6278**	RVI002609	2017	Vietnam
C. capsularis	ALV MN 059	RVI002659	2011	Unknown
C. capsularis	TOT 4157	RVI009704	2016	Vietnam
C. olitorius	ES*	RVI000642	2016	Tanzania
C. olitorius	MIX	RVI000644	2015	Bangladesh
C. olitorius	TOT 4541	RVI009710	2015	Bangladesh
C. olitorius	SUD 4	RVI000675	2015	Sudan

* was used to determine viability constant; ** was used during validation; RVI = Regional Genebank Vegetable Introduction Number.

The pattern of observed viability loss over storage time was analysed following the hierarchical modelling framework described by Wolkis *et al*. (2025). Generalized linear models (GLMs) were fitted to evaluate four nested model assumptions: (i) an independent model, allowing each accession to have its own intercept (K_i) and slope ($-1/\sigma$); (ii) a common-intercept model; (iii) a common-slope model; and (iv) a one-line model with both parameters shared across accessions. Model fitting and hypothesis testing (residual deviance tests, Akaike Information Criterion (AIC) comparisons and *F*-tests were implemented (Wolkis *et al*., 2025). Data handling and plotting were performed as above.

The newly derived C_W and K_E for both species and the initial viability of the selected seed lots (K_i), obtained from the genebank, were used to predict the germination when seeds were stored for the same storage intervals. This was done via the online Seed Information Database (SER/INSR/RBGK, 2025). The observed and predicted values were then compared using a scatter plot. Observed versus predicted values were plotted for each species and accession, and deviations from the 1:1 relationship were used to evaluate the accuracy of the predictions across the full range of viability levels. Data handling and visualisation were performed in R using the '*tidyverse*' package v.2.0.0 (Wickham *et al*., 2019).

Seed longevity prediction at 5°C and −18°C dry storage in genebanks

The newly derived viability equation constants, C_W and K_E, were used to predict the expected time for *C. capsularis* and *C. olitorius* accessions, with a starting viability of 99% (7.33 probits or 2.33 NED) to reach 85% viability (p_{85} in years) under genebank storage conditions. MCs examined were 4 and 7%, the estimated MC when seeds are equilibrated at 15% RH and 15°C (drying conditions) as per FAO's genebank standards (FAO, 2022), and 10.5% the initial estimated MC of the seed lots. Storage conditions examined were −18°C for the base collection (long-term) and 5°C for the active collection (medium-term) (FAO, 2022). Seed longevity prediction was achieved with the aid of the Seed Information Database (SER/INSR/RBGK, 2025).

Results

Jute mallow seed survival and derived viability constants

The one-step fitting of the viability equation revealed clear species-level differences in the estimated constants governing seed longevity (table 2). The *C. olitorius* seed lot exhibited a higher K_i value (2.52 ± 0.18 probits) than the *C. capsularis* seed lot (0.78 ± 0.08 probits), indicating a higher fitted theoretical initial viability. For *C. capsularis*, constraining K_i to a common value across moisture contents did not significantly increase residual deviance ($F_{4,15} = 0.34$, $p = 0.846$), indicating that a single intercept adequately described initial viability across moisture levels. In contrast, for *C. olitorius*, allowing K_i to vary among moisture levels significantly improved model fit ($F_{4,18} = 9.78$, $p < 0.001$), indicating heterogeneity in intercept estimates across moisture treatments. However, because K_i represents the seed-lot intercept in the viability framework, it was retained as a constant parameter across moisture contents for consistency with the model assumption.

Table 2. One-step estimation of the viability equation parameters (s.e. in parentheses) for two *Corchorus* species, using the universal temperature constants (C_H, C_Q) values to estimate K_E.

Species	K_i	K_t	C_W	K_E	C_H	C_Q
C. capsularis	0.78 (0.08)	7.09 (0.28)	6.80 (0.28)	10.78	0.0329	0.000478
C. olitorius	2.52 (0.18)	6.36 (0.21)	6.21 (0.20)	10.06	0.0329	0.000478

Parameters K_i = the intercept which is the fitted or theoretical initial viability of the seed lot in probits; K_t = intercept or theoretical value that is constant for one seed lot at a given temperature. K_E = a species-specific constant for inherent seed longevity; C_W = effect of change in moisture content on longevity.

C. capsularis showed a larger K_t (7.09 ± 0.28) than *C. olitorius* (6.36 ± 0.21), reflecting a slightly slower baseline rate of deterioration at the reference temperature (60°C). Estimates of C_W were 6.80 ± 0.28 for *C. capsularis* and 6.21 ± 0.18 for *C. olitorius*, while the K_E values were 10.78 and 10.06 for *C. capsularis* and *C. olitorius*, respectively.

Seed longevity (p_{50}) declined sharply with increasing moisture content in both species (table 3), but *C. capsularis* consistently maintained higher σ but lower p_{50} values across all MC levels. In *C. capsularis* (accession 'TOT 6278') seeds, σ decreased from 13.57 days at 7.5% MC to 0.50 days at 12.2% MC, with corresponding p_{50} values falling from 10.53 days to 0.38 days. *C. olitorius* (accession 'ES') seeds showed the same moisture-dependent decline but with smaller σ values 8.49 days to 0.41 days and longer p_{50} estimates of 21.36 days to 1.04 days. These trends are visually reflected in the less steeper survival curves and lower moisture sensitivity of *C. capsularis* compared with *C. olitorius* (figure 1A, B). The fitted $\log_{10}(\sigma)$ vs. $\log_{10}(m)$ relationship in both species further illustrates the predictable decline in longevity with increasing MC, while the higher σ and p_{50} values of *C. capsularis* across all moisture levels emphasise its greater inherent storability.

Table 3. Estimated seed longevity parameters derived from the one-step fitting of the seed viability equation describing changes in the germination of *Corchorus capsularis* and *C. olitorius* seeds during storage at 60°C with different moisture content (MC).

MC (% f.wt.)	Sigma (estimate ± s.e.; days)	p_{50} (estimate ± s.e.; days)
C. capsularis (accession 'TOT 6278')		
7.5	13.57 ± 1.21	10.53 ± 2.10
8.5	5.79 ± 0.31	4.49 ± 0.73
10.2	1.68 ± 0.00	1.30 ± 0.14
11.2	0.89 ± 0.02	0.69 ± 0.06
12.2	0.50 ± 0.02	0.38 ± 0.02
C. olitorius (accession 'ES')		
7.5	8.49 ± 0.71	21.36 ± 3.31
8.5	3.9 ± 0.23	9.82 ± 1.27
10.2	1.26 ± 0.03	3.16 ± 0.29
11.2	0.7 ± 0.00	1.77 ± 0.13
12.2	0.41 ± 0.01	1.04 ± 0.06

s.e. = standard error.

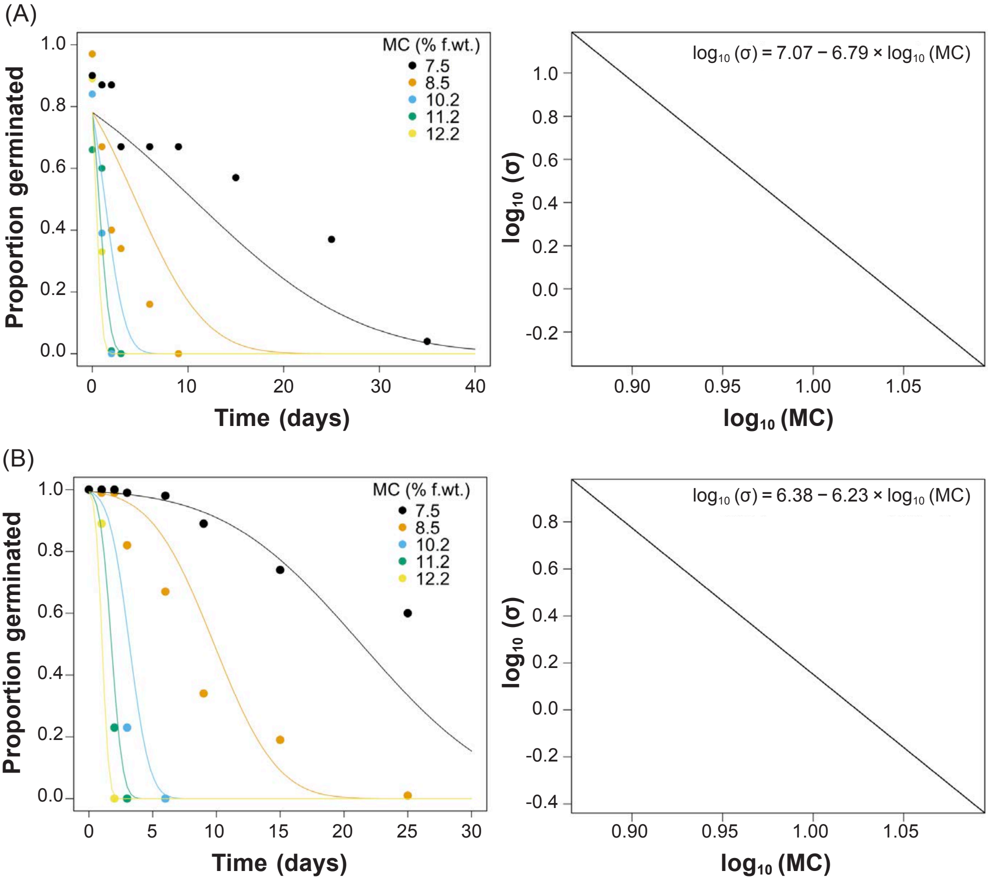

Figure 1. Seed survival curves and moisture–longevity relationships for (**A**) *Corchorus capsularis* (accession 'TOT 6278') and (**B**) *C. olitorius* (accession 'ES'), derived from the general nonlinear one-step model fitting of the seed viability equation. For each species, the left panel shows the observed proportions of seeds remaining viable (points) and the fitted probit survival curves (lines) during storage at 60°C with different moisture contents (MC). The right panel illustrates the negative logarithmic relation between seed longevity (σ) and seed storage moisture content (m) in hermetic storage at 60°C.

Fitting multiple survival curves and hypothesis testing for multiple seed lots

Using the observed viability data for three accessions per species from the validation experiment, multiple survival curves were fitted using hierarchical probit models to assess accession-level differences in initial viability and ageing rate during storage at 50°C and 12.2% MC. For *C. capsularis*, the independent model provided the best overall fit (figure 2A, table 4). Parameter estimates from the independent model revealed significant ($p < 0.001$) accession-level differences among the *C. capsularis* seed lots, with ALV MN 059 (1.28 ± 0.20; -0.406 ± 0.060), TOT 4157 (1.79 ± 0.21; -0.224 ± 0.029), and TOT 6278 (2.79 ± 0.32; -0.178 ± 0.023) exhibiting distinct intercepts and slopes, respectively, indicating variation in both initial seed quality and the rate of viability loss. For *C. olitorius*, both the independent and common-slope models fitted the observed data well, while the common-intercept and one-line models showed substantially poorer fit (table 5). Parameter estimates from the common-slope model (figure 2B) showed that K_i ranged between 2.00 ± 0.18 (TOT 4541) and 3.32 ± 0.29 (SUD 4).

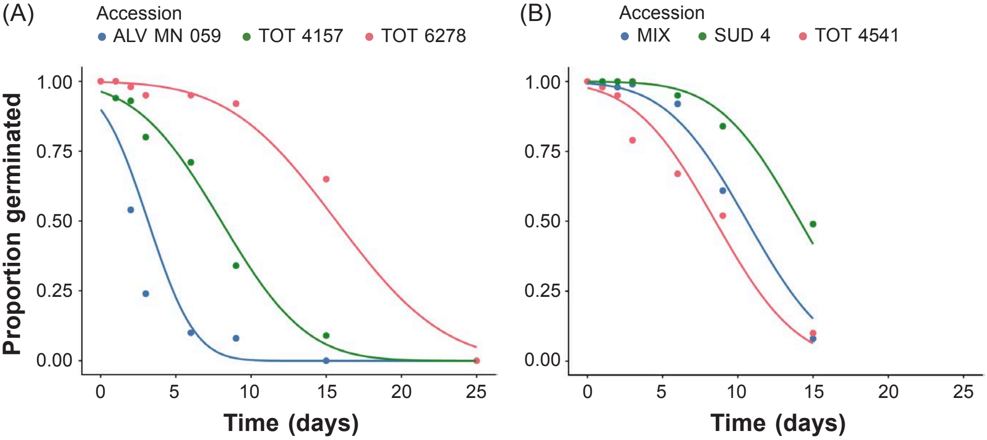

Figure 2. Probit model fitting for observed viability loss of seed lots stored at 50°C and 12% moisture content, showing the relationship between storage time and proportion of seeds germinated. (**A**) Independent model with separate slopes and intercepts for each accession for *Corchorus capsularis* accessions and (**B**) common-slope model for *C. olitorius*. Points represent observed germination, and curves represent predicted viability decline.

Table 4. Model fit statistics and hypothesis tests for hierarchical probit models describing seed viability decline in *Corchorus capsularis* during storage at 50°C and 12.2% MC

Model / comparison	Deviance	df	AIC	DF change	*F* statistic	*p*-value
Model fit						
Independent model	42.381	18	96.46			
Common-intercept model	61.447	20	109.842			
Common-slope model	58.48	20	110.012			
One-line model	221.078	22	268.748			
Model comparisons (*F*-tests)						
Common-intercept vs. Independent				2	4.049	0.035
Common-slope vs. Independent				2	3.419	0.055
One-line vs. Common-intercept				2	25.979	<0.001
One-line vs. Common-slope				2	27.804	<0.001

Table 5. Model fit statistics and hypothesis tests for hierarchical probit models describing seed viability decline in *Corchorus olitorius* during storage at 50°C and 12.2% MC

Model / comparison	Deviance	df	AIC	DF change	*F* statistic	*p*-value
Model fit						
Independent model	7.244	15	56.883			
Common-intercept model	17.585	17	63.078			
Common-slope model	10.486	17	55.621			
One-line model	46.539	19	89.054			
Model comparisons (*F*-tests)						
Common-intercept vs. Independent				2	10.706	0.0013
Common-slope vs. Independent				2	3.356	0.0624
One-line vs. Common-intercept				2	13.995	0.0003
One-line vs. Common-slope				2	29.226	<0.0001

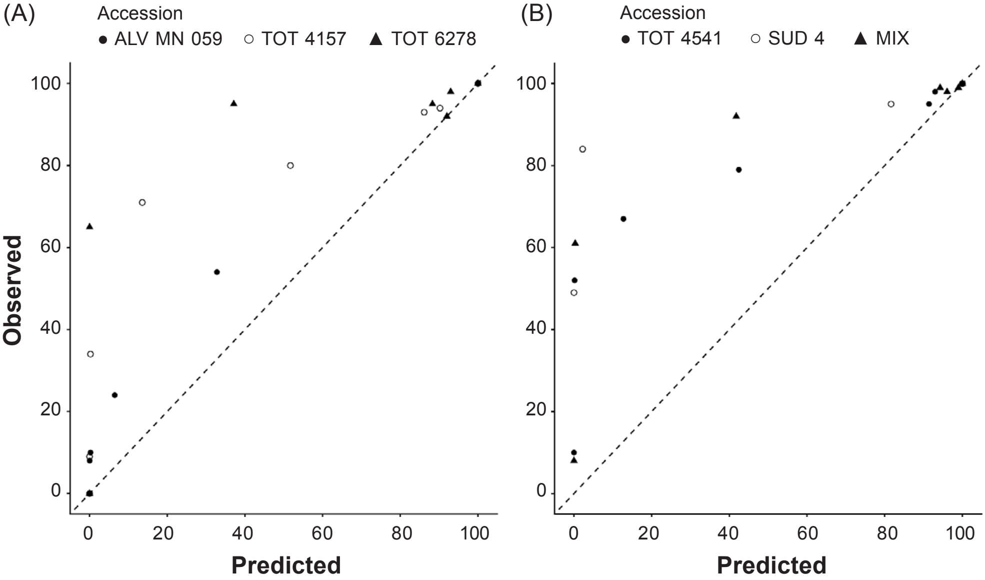

Figure 3. Relationship between observed and predicted seed viability for (**A**) *Corchorus capsularis* and (**B**) *C. olitorius*. Each point represents an individual observation across storage times for a given accession. The dashed line represents the observed = predicted values.

Validation of derived constants (C_W *and* K_E)

Observed and predicted seed viability showed close agreement at high viability levels for both species, with most observations clustering near the 1:1 relationship (figure 3). However, clear species-level differences emerged at low predicted viability. In *C. capsularis* (figure 3A), deviations from the 1:1 line were more pronounced and variable, indicating greater overestimation of viability loss as seeds deteriorated. In contrast, *C. olitorius* (figure 3B) showed a more consistent pattern, with observed viability remaining systematically higher than predicted values but with reduced scatter. These results suggest that prediction accuracy declines during advanced deterioration in both species, although the magnitude and variability of divergence differ between them.

Discussion

A comprehensive understanding of differences in seed ageing rate is vital for effective management of seed collections conserved in ex-situ genebanks, including those of jute mallow. In our study, the survival curves for *Corchorus capsularis* and *C. olitorius* exhibited typical patterns of orthodox seeds, where germination declined progressively over time, especially under elevated seed moisture content and temperature conditions. With one-step fitting, intercept values (K_i) of the seed survival curves is estimated at the seed lot level; therefore, variation in K_i primarily reflect variation in initial seed quality among lots rather than intrinsic species differences (Daniel *et al*., 2013; N'Danikou *et al*., 2024b). The traditional two-step method for modelling seed longevity first fits separate survival curves for each moisture content–temperature combination using probit analysis and then regresses the resulting σ values against moisture and/or temperature to estimate the species constants (K_E, C_W, C_H, C_Q). However, this approach has key limitations: (i) it ignores the binomial error inherent in the original germination data; (ii) it requires a strict factorial storage design with fixed moisture contents and temperatures; and (iii) it treats moisture and temperature as exact fixed values, even though they may vary slightly between samples (Hay *et al*., 2014). Advances in statistical modelling allow direct fitting of the full viability equation in one-step, incorporating all sources of error, including sampling error. The one-step approach also accommodates variable moisture contents and/or temperatures without requiring perfectly balanced treatment combinations (Hay *et al*., 2003). Hence, A one-step fitting method was adopted to provide more accurate, statistically robust and design-flexible estimates of the seed longevity parameters.

Storage conditions, particularly seed moisture content and temperature, have a strong influence on the rate of seed deterioration, which is reflected in the shape and slope of the survival curves. Jute mallow seeds stored at lower moisture contents exhibited greater longevity (higher p_{50} values), demonstrating a slower rate of deterioration. Higher seed moisture content accelerates oxidative and degenerative metabolic processes such as lipid peroxidation, Amadori-Maillard reactions and protein carbonylation (Veselova *et al*., 2015). The moisture content of the seeds dictates the type of chemical reactions that can occur, while the storage temperature influences the rate at which these reactions proceed. It is therefore essential to dry orthodox seeds like jute mallow to lower MC levels (i.e., between 4 to 7%) before storage in genebanks. However, further drying beyond a certain critical seed moisture threshold may not confer additional benefits and can even be detrimental to seed longevity (Demir *et al*., 2009). Seed moisture content in this study was estimated indirectly using a water activity meter and estimates of species oil content using Cromarty's equation (IBPGR, 1990; Hay *et al*., 2022) in the Seed Information Database (SER/INSR/RBGK, 2025). However, the lower moisture limit (threshold) at which drying ceases to be beneficial or becomes harmful in jute mallow species were not assessed in this study, suggesting an area for future research. A negative relationship between seed moisture content and longevity was observed in *C. capsularis* and *C. olitorius*, confirming that reduced moisture content enhances seed longevity. This relationship provided the basis for deriving the C_W and K_E constants in both species.

The derived moisture-sensitivity constant (C_W) for *C. capsularis* (6.80) and *C. olitorius* (6.21) in our study fall well within the range of those for other orthodox crop species and are comparable to those of *Delphinium elatum* (6.54) (Kwong *et al*., 2001), *Eragrostis tef* (6.01) (Ellis *et al*., 1988), *Eucalyptus grandis* (6.47) (Fantinatti and Usberti, 2007), *Sorghum bicolor* (6.31) (Kuo *et al*., 1990), *Vigna radiata* (6.27) (Ellis *et al*., 1988) and *Zea mays* (6.37) (Ellis and Hong, 2007). They also lie within the broader moisture–longevity sensitivity spectrum documented for species such as *Salvia splendens* (6.67–6.68) (Kwong *et al*., 2001) and *Euphorbia* spp. (*E. heterochroma*, *E. pseudoburuana*, *E. quinquecostata*) (6.89–8.09) (Muthoka *et al*., 2009). Among the species documented to date, the lowest C_W was reported for *Dioscorea dumetorum* (−3.06) (Daniel *et al*., 2003), while the highest was observed in *E. quinquecostata* (8.09) (Muthoka *et al*., 2009). All these species have seed oil content ≤ 5% (Jones and Earle, 1966; Eckey, 1954), unlike *C. capsularis* (13.2%) and *C. olitorius* (12.7%) (Earle and Jones, 1962). The hydrophobic nature of lipids in oil-rich seeds limits moisture uptake at a given relative humidity, enabling them to maintain lower equilibrium moisture content, an attribute often linked to improved longevity (Jones and Earle, 1966). However, this advantage may be offset by increased susceptibility to oxidative damage, particularly in seeds rich in unsaturated fatty acids, under suboptimal storage conditions (Nickas *et al*., 2025; Sileshi *et al*., 2025). While oil content influences seed longevity through its relations with moisture, it does not act in isolation. Seed longevity is also influenced by factors such as genetic background, seed coat characteristics, dormancy status and the presence of protective molecules like late embryogenesis abundant (LEA) proteins, which help stabilise cellular structures during desiccation, and antioxidants that mitigate oxidative stress (Demir *et al*., 2011; Whitehouse and Norton, 2022; Nickas *et al*., 2025). These interacting factors also influence C_W, which quantifies the sensitivity of seed viability to changes in moisture content. Although C_W values are largely species-specific and generally consistent among seed lots within a species, variation can still occur between species or accessions due to differences in oil content, seed structure, and biochemical composition (Demir *et al*., 2009, 2011; Kartika *et al*., 2012; Whitehouse and Norton, 2022). Taken together, these observations underscore the importance of viewing seed longevity as a multifactorial trait, shaped not only by physical seed properties but also by underlying genetic and biochemical defenses.

The derived K_E values for *C. capsularis* (10.78) and *C. olitorius* (10.06) align closely with those reported for various crop species, including *Eragrostis tef* (10.098) (Ellis *et al.*, 1988), *Euphorbia pseudoburuana* and *E. quinquecostata* (10.10–10.20) (Muthoka *et al.*, 2009), *S. bicolor* (10.588) (Kuo *et al.*, 1990), *Vigna radiata* (10.858) (Ellis *et al.*, 1988) and *Zea mays* (10.562) (Ellis and Hong, 2007). Among the species documented to date, the lowest K_E was reported for *S. bicolor* (2.49) (Ali, 2014; Tabatabaei, 2014), while the highest was observed in *Tagetes patula* (12.22) (Simões *et al.*, 2008). Inherent seed longevity is said to vary with factors such as seed maturity, ecotypic differences (genetic variations among populations of the same species adapted to distinct environmental conditions), genetic mutation, and even between subspecies within the same species (Hay *et al.*, 2003; Lyall *et al.*, 2003; Demir *et al.*, 2009). Longevity differences have also been observed between seed lots of the same cultivar, suggesting the influence of environmental and management factors during seed development and post-harvest handling (Whitehouse and Norton, 2022). Nevertheless, the estimated C_W and K_E values fell within the range reported for other orthodox species, indicating that they retain broad species-level relevance. Consistent with the framework proposed by Ellis and Roberts (1980a,b), the present findings suggest that C_W and K_E are largely species-dependent parameters, but their practical application should be interpreted with caution, particularly where prediction accuracy is reduced by seed lot heterogeneity or other unmodelled influences on longevity.

Prediction of seed longevity using the viability equation requires consideration of potential intraspecific variation, as there is a risk of overextrapolation when applying constants beyond the tested seed lots. To ensure reliability, it is essential to validate whether the derived viability constants (C_W and K_E) apply consistently across different seed lots within the same species. The validation results indicate that the derived constants can be applied to approximate seed longevity of independent seed lots within the two Corchorus species using the seed viability equation (Ellis and Roberts, 1980a). However, the poor relationship between predicted and actual longevity suggests that fitted parameters did not fully account for the variability in seed survival in *C. capsularis* and *C. olitorius*. This deviation likely reflects sources of variation in seed survival beyond those captured by the fitted viability parameters.

Seed longevity is generally improved at subfreezing temperatures, provided that the moisture content stays below 14%, which prevents the formation of damaging ice crystals. At a seed moisture content of 4%, improving storage temperature from 5°C to −18°C markedly increases predicted seed longevity in *C. capsularis* (from 11,423.8 to 46,944.9 years), and *C. olitorius* (from 4,932.0 to 20,267.7 years) when the initial germination is close to 100% (table 6). These predictions underscore the substantial differences in inherent seed longevity between the two species, with *C. capsularis* predicted to be markedly longer-lived. Predictions at 5°C and −18°C are extrapolated from data at 60°C and should be interpreted cautiously, as temperature effects on ageing may not remain linear across such a wide range.

The derived seed viability constants offer a practical tool for predicting the longevity of the seed collections of two commonly cultivated jute mallow species. Using these constants can improve the management of seeds stored in both genebank and commercial stores (Daniel *et al.*, 2012). In genebanks, this information can be used to optimise

Table 6. Predicted seed longevity (p_{85} years) of *Corchorus capsularis* and *C. olitorius* under dry-cold storage conditions at 5°C and −18°C using the constants derived from a one-step fitting of viability equation (table 2) and seed MC.

Species	Accession	Initial viability (%) before storage	Moisture content (%)	p_{85} (years)
		Storage temperature 5°C		
C. capsularis	TOT 4157	99	4	11,423.8
			7	254.2
			9.92	23.7
C. olitorius	MIX	99	4	4,932.0
			7	152.7
			10.5	12.3
		Storage temperature −18°C		
C. capsularis	TOT 4157	99	4	46,944.9
			7	1,044.6
			9.92	97.6
C. olitorius	MIX	99	4	20,267.7
			7	627.4
			10.5	50.6

p_{85} = the time taken for viability to fall to 85%; genebanks often use this as a signal for when to begin regeneration of a particular seed lot.

regeneration cycles and reduce the risk of genetic erosion by ensuring timely regeneration of jute mallow seed collections in line with established standard operating procedures (FAO, 2022). Seed traders and farmers can also benefit by adjusting storage conditions to maintain seed viability, forecasting shelf-life, and improving inventory planning. This supports quality assurance throughout the supply chain and helps ensure timely seed availability for distribution and planting.

Conclusion and recommendation

This study provides additional knowledge and understanding of the seed longevity of the two commonly cultivated jute mallow species (*Corchorus capsularis* and *C. olitorius*). The derived species-specific seed viability constants for moisture sensitivity (C_W and K_E) can support evidence-based management of jute mallow seed collections in genebanks and commercial stores. Looking into the future, having determined these species-specific seed viability constants (C_W and K_E), it would be interesting to delve into historical genebank viability monitoring data and to see whether real-time jute mallow viability data could provide further information on the relative longevity of jute mallow seeds in long-term genebank storage conditions. There is still a need to extend similar research to crop wild relatives (CWRs) of jute mallow and other traditional African vegetables, for which this knowledge is critical to the effective management of their seed collections conserved in ex-situ genebanks. Further investigation into the genetic and physiobiochemical factors influencing seed longevity, including their response to a broader range of moisture contents and temperature conditions, is recommended.

Data availability

The datasets used and/or analysed in the current study are available from the corresponding author upon reasonable request.

Contributions

Conceptualization, AS., S.N., E.W.M.; methodology, AS., E.W.M., S.N.; validation, S.N., P.V., M.P., H.M., P.K.; resources, S.N., M.Z., data collection, E.W.M., AS., M.K., S.R., S.S.; data curation, E.W.M., A.S; formal analysis, A.S., E.W.M.; writing-original draft, E.W.M., A.S.; writing-review and editing, E.W.M., A.S., S.N., P.V., M.P., H.M., P.K., M.K., S.R., S.S.; supervision, S.N., P.V., M.P., H.M., P.K; project administration, S.N.; funding acquisition, S.N., M.Z. All authors have read and agreed to the published version of the manuscript.

Competing interests

The authors declare no competing interests.

Financial support

This research was financially supported by the "Taiwan-Africa Vegetable Initiative (TAVI)" project; the Norwegian Agency for Development Cooperation (NORAD) through the FAO ITPGRFA grant to support WorldVeg genebank in Tanzania (Ref: LoA/TF/019-MUL/Baby 5/2024); and the Genebank Long-Term Grant from the Global Crop Diversity Trust (Crop Trust). Funding for Africa's Vegetable Genebank is provided by strategic long-term donors to the WorldVeg: Republic of China (Taiwan), UK aid from the UK government, Australian Center for International Agricultural Research (ACIAR), Germany, Thailand, Philippines, Korea, and Japan.

Additional information

The seed samples used in this experiment were acquired by WorldVeg's genebank, following national and international guidelines and legislation. The study was conducted under Africa's Vegetable Genebank, maintained by WorldVeg in Arusha, Tanzania.

References

Ali, T.S. (2014). Determination of seed viability constants in sorghum under various storage conditions. *Iranian Journal of Field Crop Science (Iranian Journal of Agricultural Sciences)*, **45**, 377-387.

Daniel, I.O., Ng, N.Q., Tayo, T.O. and Togun, A.O. (2003). Storage of West African yam (*Dioscorea* spp.) seeds: modelling seed survival under controlled storage environments. *Seed Science and Technology*, **31**, 139-147. <https://doi.org/10.15258/sst.2003.31.1.14>

Daniel, I.O., Kruse, M. and Borner, A. (2012). Predicting longevity of *Celosia argentea* L. seeds during storage. *Acta Horticulturae*, **953**, 319-324. <https://doi.org/10.17660/ActaHortic.2012.953.44>

Daniel, I.O., Kruse, M. and Börner, A. (2013). Controlled deterioration and predicting viability of okra seed in storage. *International Journal of Vegetable Science*, **19**, 324-333. <https://doi.org/10.1080/19315260.2012.729261>

Demir, I., Kenanoglu, B.B., Hay, F., Mavi, K. and Celikkol, T. (2011). Determination of seed moisture constants (K_E, C_W) for the viability equation for watermelon, melon, and cucumber seeds. *Seed Science and Technology*, **39**, 527-532. <https://doi.org/10.15258/sst.2011.39.2.23>

Demir, I., Kenanoglu, B.B., Mavi, K., Celikkol, T., Hay, F. and Sariyildiz, Z. (2009). Derivation of constants (K_E, C_W) for the viability equation for pepper seeds and the subsequent test of its applicability. *HortScience*, **44**, 1679–1682. https://doi.org/10.21273/HORTSCI.44.6.1679

Dickie, J.B., Ellis, R.H., Kraak, H.L., Ryder, K. and Tompsett, P.B. (1990). Temperature and seed Storage Longevity. *Annals of Botany*, **65**, 197-204. <https://doi.org/10.1093/oxfordjournals.aob.a087924>

Earle, F.R. and Jones, Q. (1962). Analyses of seed samples from 113 plant families. *Economic Botany*, **16**, 221-250.

Eckey, E. (1954). Vegetable fats and oils. In *American Chemical Society Monograph*, Series No. 123, Reinhold Publishing Corporation.

Ellis, R.H. (2022). Seed ageing, survival and the improved seed viability equation; forty years on. *Seed Science and Technology*, **50**, 1-20. <https://doi.org/10.15258/sst.2022.50.1.s.01>

Ellis, R.H. and Hong, T.D. (2007). Quantitative response of the longevity of seed of twelve crops to temperature and moisture in hermetic storage. *Seed Science and Technology*, **35**, 432-444.

Ellis, R.H. and Roberts, E.H. (1980a). Improved equations for the prediction of seed longevity. *Annals of Botany*, **45**, 13-30. <https://doi.org/10.1093/oxfordjournals.aob.a085797>

Ellis, R.H. and Roberts, E.H. (1980b). The influence of temperature and moisture on seed viability period in barley (*Hordeum distichum* L.). *Annals of Botany*, **45**, 31-37. <https://doi.org/10.1093/oxfordjournals.aob.a085798>

Ellis, R.H., Hong, T.D. and Roberts, E.H. (1988). A low moisture content limit to logarithmic relations between seed moisture content and longevity. *Annals of Botany*, **61**, 405-408.

Fantinatti, J.B. and Usberti, R. (2007). Seed viability constants for *Eucalyptus grandis*. *Pesquisa Agropecuaria Brasileira*, **42**, 111-117.

FAO (2022). *Practical Guide for the Application of the Genebank Standards for Plant Genetic Resources for Food and Agriculture: Conservation of Orthodox Seeds in Seed Genebanks*, Food and Agriculture Organization of the United Nations, Rome.

Gómez Barreiro, P., Hudson, A.R., Hay, F.R. and Adams, J. (2025). *LiCl Calc*: Tools to use lithium chloride solutions to control relative humidity in seed experiments. *Seed Science and Technology*, **53**, 233-238. <https://doi.org/10.15258/sst.2025.53.2.08>

Hay, F.R., Mead, A., Manger, K. and Wilson, F.J. (2003). One-step analysis of seed storage data and the longevity of *Arabidopsis thaliana* seeds. *Journal of Experimental Botany*, **54**, 993-1011. <https://doi.org/10.1093/jxb/erg103>

Hay, F.R., Adams, J., Manger, K. and Probert, R. (2008). The use of non-saturated lithium chloride solutions for experimental control of seed water content. *Seed Science and Technology*, **36**, 737-746. <https://doi.org/10.15258/sst.2008.36.3.23>

Hay, F.R., Mead, A. and Bloomberg, M. (2014). Modelling seed germination in response to continuous variables: use and limitations of probit analysis and alternative approaches. *Seed Science Research*, **24**, 165-186.

Hay, F.R., Rezaei, S. and Buitink, J. (2022). Seed moisture isotherms, sorption models, and longevity. *Frontiers in Plant Science*, **13**, article 891913. <https://doi.org/10.3389/fpls.2022.891913>

Hay, F.R., Rezaei, S., Wolkis, D. and McGill, C. (2023). Determination and control of seed moisture. *Seed Science and Technology*, **51**, 267-285. <https://doi.org/10.15258/sst.2023.51.2.11>

IBPGR (1990). *Design of Seed Storage Facilities for Genetic Conservation*, Revised 1985 and 1990, International Board for Plant Genetic Resources, Rome.

ISTA (2024). *International Rules for Seed Testing*, International Seed Testing Association, Bassersdorf, Switzerland.

Jackson, C.H. (2011). Multi-state models for panel data: the *msm* package for R. *Journal of Statistical Software*, **38**, 1-29.

Jones, Q. and Earle, F.R. (1966). Chemical analyses of seeds II: Oil and protein content of 759 species. *Economic Botany*, **20**, 127-155. <https://doi.org/10.1007/BF02904010>

Kartika, I.A., Yuliani, S., Kailaku, S.I. and Rigal, L. (2012). Moisture sorption behaviour of jatropha seed (*Jatropha curcas*) as a source of vegetable oil for biodiesel production. *Biomass and Bioenergy*, **36**, 226-233. <https://doi.org/10.1016/j.biombioe.2011.10.026>

Kaweya, B.S., N'Danikou, S., Shango, A.J., Sanga, H.G., Kabululu, M.S., Hamisy, W., Tryphone, G.M. and van Zonneveld, M. (2026). Derivation of seed viability constants (K_E and C_W) and prediction of seed longevity for spider plant (*Cleome gynandra*). *Seed Science and Technology*, **54**, 19-30. <https://doi.org/10.15258/sst.2026.54.1.03>

Kuo, W.H.J., Shan, M.L. and Tseng, M.T. (1990). Effects of temperature and seed moisture content on the longevity of sorghum seeds. *Journal of the Agriculture Association of China*, **149**, 32-41.

Kwong, F., Stodolski, L., Mari, J., Gurusinghe, S.H. and Bradford, K.J. (2001). Viability constants for *Delphinium* and *Salvia* seeds. *Seed Technology*, **23**, 113-125.

Lyall, T.W., Ellis, R.H., John, P., Hedley, C.L. and Wang, T.L. (2003). Mutant alleles at the rugosus loci in pea affect seed moisture sorption isotherms and the relations between seed longevity and moisture content. *Journal of Experimental Botany*, **54**, 445-450. <https://doi.org/10.1093/jxb/erg059>

Muthoka, P.N., Hay, F.R., Dida, M.M., Nyabundi, J.O. and Probert, R.J. (2009). Moisture content and the longevity of seeds of six *Euphorbia* species in open storage. *Seed Science and Technology*, **37**, 383-397. <https://doi.org/10.15258/sst.2009.37.2.12>

Nadarajan, J., Walters, C., Pritchard, H.W., Ballesteros, D. and Colville, L. (2023). Seed longevity—the evolution of knowledge and a conceptual framework. *Plants*, **12**, article 471. <https://doi.org/10.3390/plants12030471>

N'Danikou, S., Ayenan, M.A.T., Sigalla, J.P., Shango, A.J. and Zonneveld, M.V. (2024a). Storage behaviour and seed longevity of traditional African vegetables: A review. *Seed Science and Technology*, **52**, 177-192. <https://doi.org/10.15258/sst.2024.52.2.04>

N'Danikou, S., Nickas, J., Shango, A.J. and Kilasi, N. (2024b). Derivation of seed viability constants (K_E and C_W) and prediction of longevity of *Solanum aethiopicum* seeds. *Seed Science and Technology*, **52**, 193-203. <https://doi.org/10.15258/sst.2024.52.2.05>

Nickas, J., N'Danikou, S., Shango, A.J. and Kilasi, N. (2025). Physio-biochemical response of vegetable seeds to ageing: A systematic review. *Plant Physiology and Biochemistry*, **228**, article 110223. <https://doi.org/10.1016/j.plaphy.2025.110223>

R Core Team (2025). *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria. Available from: <https://www.R-project.org> (Accessed 20 June 2025).

SER/INSR/RBGK (2025). *Seed Information Database (SID)*, Society for Ecological Restoration, International Network for Seed-Based Restoration, Royal Botanic Gardens Kew. Available from: <https://ser-sid.org/> (Accessed 25 June 2025).

Sileshi, G.W., Borgemeister, C., Kuyah, S., Nath, A.J. and Arshad, S. (2025). About Neglected and underutilized crops for agroecological transition of food systems. *CABI Agriculture and Bioscience*, **6**, article 47. <https://doi.org/10.1079/ab.2025.0047>

Simões, F.C., Usberti, R. and Paiva, P.D.O. (2008). Controlled seed deterioration in *Tagetes patula* L. cultivars. *Seed Science and Technology*, **36**, 524-533. <https://doi.org/10.15258/sst.2008.36.3.02>

Tabatabaei, S.A. (2014). Determination of seed viability constants in sorghum under various storage conditions. *Iranian Journal of Field Crop Science*, **45**, 377-387.

van Zonneveld, M., Kindt, R., Solberg, S.Ø., N'Danikou, S. and Dawson, I.K. (2021). Diversity and conservation of traditional African vegetables: Priorities for action. *Diversity and Distributions*, **27**, 216-232. https://doi.org/10.1111/ddi.13188>

Venables, W. N. and Ripley, B. D. (2002). *Modern Applied Statistics with S* (4th Edition). Springer.

Veselova, T.V., Veselovsky, V.A. and Obroucheva, N.V. (2015). Deterioration mechanisms in air-dry pea seeds during early aging. *Plant Physiology and Biochemistry*, **87**, 133-139. <https://doi.org/10.1016/j.plaphy.2014.12.019>

Volk, G.M., Carver, D., Irish, B.M., Marek, L., Frances, A., Greene, S., Khoury, C.K., Bamberg, J., Del Rio, A., Warburton, M.L. and Bretting, P.K. (2023). Safeguarding plant genetic resources in the United States during global climate change. *Crop Science*, **63**, 2274-2296. <https://doi.org/10.1002/csc2.21003>

Whitehouse, K.J. and Norton, S.L. (2022). Estimation of seed viability constants (K_E, C_W) for lentils (*Lens culinaris*). *Seed Science and Technology*, **50**, 103-115. <https://doi.org/10.15258/sst.2022.50.1.09>

Wickham, H. (2025). *ggplot2: Elegant Graphics for Data Analysis*, Springer-Verlag, New York. <https://ggplot2.tidyverse.org>

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K. and Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, **4**, article 1686. <https://doi.org/10.21105/joss.01686>

Wickham, H., François, R., Henry, L., Müller, K. and Vaughan, D. (2025). *dplyr: A Grammar of Data Manipulation*, R package version 1.1.4, <https://dplyr.tidyverse.org>

Wolkis, D., Carta, A., Rezaei, S. and Hay, F.R. (2025). Seed longevity: analysing post-storage germination data in R to fit the viability equation. *Seed Science Research*, **35**, 33-40. <https://doi.org/10.1017/S0960258524000291>

Xie, Y. (2015). *Dynamic Documents with R and knitr* (2nd Edition), Chapman and Hall/CRC.

Xie, Y. (2025). *knitr: A General-Purpose Package for Dynamic Report Generation in R* (Version 1.50).