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Seed collection and processing practices affect subsequent seed storage longevity in durum wheat and wild relatives

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Abstract

Potential seed storage longevity is influenced by environment during seed development and maturation but post-harvest processing may also affect longevity, particularly in accessions with variable maturity or seed shedding. The impact of sequential harvesting and post-harvest processing was examined in durum wheat (*Triticum turgidum* subsp. *durum*) and its wild relatives, *Triticum turgidum* subsp. *dicoccoides* and *T. monococcum* subsp. *boeoticum*. Spikes were collected in sequential harvests as they matured and either processed immediately (fumigated, threshed, cleaned, dried) or delayed (remaining in the field until all plots were harvested). A separate study with durum wheat assessed seed quality throughout development and maturation and the effects of initial post-harvest drying temperatures. Delayed processing resulted in equal or greater seed longevity than immediate processing across all accessions. In durum wheat, longevity improved considerably between 21 and 41 days after heading but declined thereafter. Initial seed drying temperature affected longevity: 30°C was optimal for the earliest harvests, whereas 15°C was superior at harvest maturity and beyond. These findings demonstrate that immature seeds can continue to develop in quality *ex planta* under warm, dry conditions, challenging conventional recommendations for immediate post-harvest processing and suggesting a potential role for delayed processing in optimising seed longevity.

Keywords: drying, genebanks, germination, harvest, seed development, seed longevity, seed storage

Introduction

High-quality seeds are vital to global seed supplies. Seed development, drying and post-harvest storage have all been studied to better understand how to produce high-quality seeds and reduce post-harvest deterioration, but harvesting practices have received less attention, partly because harvesting takes place in dynamic field circumstances making controlled investigation more difficult. Many cereal and other large-scale, field-grown seed crops are typically combine-harvested when mature and seeds processed immediately in a sequence of drying (if needed to reduce seed moisture content), cleaning (to remove debris, especially weed seeds and broken crop seeds) and then placed into storage. Seeds harvested by hand from small plots, for example to regenerate a genebank accession, are similarly processed as soon as possible after collection, and placed in storage. Genebanks are recommended to transfer seeds as soon as possible after harvest to a controlled drying environment, typically a dedicated drying room at 15-20°C and 10-20% RH (Cromarty *et al*., 1982; FAO/IPGRI, 1994; Rao *et al*., 2006; FAO, 2014).

Well-managed genebanks play a key role in long-term crop genetic resources conservation (FAO, 2014; Ebert and Engels, 2020). Seed quality is important for the long-term conservation of germplasm as it affects seed storage longevity in genebanks (Hay and Smith, 2003). Seed longevity, the period of storage seeds remain alive in a specific environment, can be affected by pre- and post-harvest environment and practices (Hay *et al*., 2006; Probert *et al*., 2007; Khatun *et al*., 2009). High potential seed longevity is an important objective for *ex situ* biodiversity conservation as it has direct implications on genebank core activities and costs; it reduces the regeneration workload and conserves the genetic integrity of accessions (Ellis *et al*., 1985; Rao *et al*., 2006; FAO, 2014).

The International Center for Agricultural Research in the Dry Areas (ICARDA) holds in trust more than 150,000 accessions of cultivated cereals and their wild relatives, as well as food, forage and range legumes in its genebank in Lebanon. Typically, the seed accessions are dried to equilibrium at 15°C with 15% RH before being processed (cleaning and packaging) and then entering the medium-term (2-4°C) and long-term (-20°C) stores. ICARDA has developed a seed-harvesting protocol to manage accessions prone to seed shattering and/or variable maturity, particularly common in wild relatives of cereals and legumes, and sometimes in cultivated accessions. This protocol involves sequential harvesting which can result in long delays between harvest and subsequent processing: each plot is checked daily and mature pods or spikes are collected by hand and placed in a cloth bag fixed to a peg at the edge of the plot, which remains in the field (or plastic or screen house), with the newly matured and harvested pods or spikes added each day, until the harvest is complete. Harvesting can span a period from a few days to several weeks, during which time the seeds within these cloth bags are subjected to fluctuations in temperature and relative humidity (as are the later-maturing seeds that remain *in planta*). Once harvesting is completed for all accessions, the collected samples are dried *in situ* for 1-2 weeks, then transferred to a fumigation chamber for three days, to eliminate insects, before being threshed and transferred to the drying room.

This delay to seed processing has the potential to damage seeds and thereby reduce subsequent seed storage longevity, but damage from delay may not be inevitable. While delays in seed processing may negatively affect seed longevity, the extent of damage remains unclear and may depend on species, environmental conditions and seed development stage (Ellis, 2019). Moreover, previous research suggests that brief periods of high temperature or high moisture may not necessarily be damaging to maturing seeds: for example, in bread wheat (*Triticum aestivum* L.) high temperatures in late seed maturation benefitted subsequent seed longevity (Nasehzadeh and Ellis, 2017) and the damage to longevity from rain on the maturing seed crop was reversed during subsequent drying *in* *planta* (Ellis and Yadav, 2016; Yadav and Ellis, 2016). In addition, brief high temperature treatment to dry seeds of rice (*Oryza sativa* L.) harvested at high seed moisture content improved subsequent seed longevity (Whitehouse *et al*., 2015).

The objective of our research was to determine whether the ICARDA seed harvest protocol, described above, maximises subsequent seed storage longevity in durum wheat (*Triticum turgidum* subsp. *durum* (Desf.) Husn.) and its wild relatives or whether immediate processing as recommended in the Genebank Standards (FAO, 2014) is preferable. Three investigations were undertaken at the same experimental site in Lebanon where the ICARDA Genebank regenerates accessions. Two were of similar design and compared different harvesting protocols for accessions of cultivated durum wheat and wild relatives in 2017-18 and in 2018-19 to determine the effect of delayed processing on subsequent seed storage longevity. The third examined seed development and seed quality development patterns, and the effect of seed drying temperature on subsequent seed storage longevity, in one cultivated durum wheat accession in 2018-19. We tested three null hypotheses: (1) seed longevity of *Triticum* spp. accessions is not affected by delays to seed processing (storing harvested seeds in bags in the field); (2) harvest date has no effect on subsequent seed longevity; and (3) post-harvest drying temperature does not influence seed longevity.

Materials and methods

The accessions were grown at the experimental field station of AREC (Advancing Research Enabling Communities, American University of Beirut) in Lebanon's Beqaa valley (33.924783° N; 36.075792° E) at an altitude of 1000 m a.s.l. The soil is primarily limestone and clay. Post-harvest work was undertaken at the ICARDA Genebank in Terbol-Zahle, Lebanon, located 25 km south of the field site.

The first experiment was sown on 7 December 2017 with two accessions (table 1): one plot (sowing 1) of a cultivated durum wheat (*Triticum turgidum* subsp. *durum* (Desf.) Husn.), IG 89263, and three plots (sowings 1-3) of its wild relative *Triticum turgidum* subsp. *dicoccoides* (Korn. ex Asch. & Graebn.) Thell, IG 46508. Three replicate plots of the latter were included to assess the repeatability of results. The second experiment was sown on 21 November 2018 with three accessions (table 2): one plot of the same cultivated durum wheat as before (sowing 2), two plots of the wild relative *T. turgidum* subsp. *dicoccoides* (sowings 4 and 5) and one plot of *Triticum monococcum* subsp. *boeoticum* (Boiss.) Hayek, IG 44857 (sowing 1). The third experiment was also sown on 21 November 2018 with seeds of the same accession of cultivated durum wheat (IG 89263, sowing 3). All seeds were drawn from ICARDA's active collection and had been harvested in 2016, dried to equilibrium at approximately 15°C and 15% RH, and then stored hermetically at 2-4°C.

Seeds of cultivated durum wheat and the wild wheat accessions were sown in 18 or 22 rows, respectively, each 30 mm apart and 2.5 m long with 125 seeds/row. Triticale (× *Triticosecale*) was sown between plots to separate them and avoid contamination. Agronomic practices and plant protection measures followed ICARDA's Standard Operating Protocol, with weeds removed by hand.

Table 1. Information on the accessions and seeds of durum wheat (*Triticum turgidum* subsp. *durum*) and wild wheat (*T. turgidum* subsp. *dicoccoides*) sown in December 2017 (Experiment 1) and the seed samples produced. The weight shown is total weight of seeds provided by each treatment. IMD = immediate and Delay = delayed processing treatments and the subsequent numeral is the harvest number.

Accession (IG number*) – sowing number	Taxon name	Origin	Treatment	DHE**	Harvest date (2018)	Weight (g) ***	Germination (%) ***	MC (%) ***	eRH (%) ***
89263-S1	*Triticum turgidum* subsp. *durum*	Turkey	IMD 1	143	31 May	289.2	66	3.7	31.0
			IMD 2		4 June	173.7	54	4.2	71.1
			IMD 3		8 June	172.1	77	4.9	46.2
			IMD 4		11 June	217.4	85	2.8	47.9
			Delay 1		31 May	263.9	96	7.1	37.8
			Delay 2		4 June	268.2	83	6.4	20.3
			Delay 3		8 June	174.1	92	6.8	19.4
			Delay 4		11 June	210.1	88	4.4	23.7
			Current ICARDA		31 May – 11 June	1039.1	85	7.8	22.2
46508-S1	*Triticum turgidum* subsp. *dicoccoides*	Lebanon	IMD 1	145	31 May	367.3	96	3.7	28.8
			IMD 2		4 June	114.3	83	4.7	34.3
			IMD 3		8 June	94.1	75	8.9	42.4
			Delay 1		31 May	466.6	93	8.7	34.7
			Delay 2		4 June	225.9	75	7.8	16.6
			Delay 3		8 June	124.3	79	3.8	20
			Ground		8 June	119.1	95	6.6	42.3
			Current ICARDA		31 May – 11 June	522.6	90	6.1	32.6
46508-S2	*Triticum turgidum* subsp. *dicoccoides*	Lebanon	IMD 1	147	31 May	283.4	94	3.9	27.5
			IMD 2		4 June	142.1	80	2.8	35.9
			IMD 3		8 June	133.2	80	8	42.2
			Delay 1		31 May	391.8	92	3.1	31.5
			Delay 2		4 June	94.2	83	4.7	16.2
			Delay 3		8 June	112.9	80	7	16.8
			Ground		8 June	241.5	100	8.2	41.5
			Current ICARDA		31 May – 11 June	325.3	70	5.3	27.3

* IG ICARDA Genebank unique number; ** DHE = days from sowing to heading; *** after threshing, cleaning and fumigation.

Table 1. *cont'd*

Table 1. *Continued.*

Accession (IG number*) – sowing number	Taxon name	Origin	Treatment	DHE**	Harvest date (2018)	Weight (g) ***	Germination (%) ***	MC (%) ***	eRH (%) ***
46508-S3	*Triticum turgidum* subsp. *dicoccoides*	Lebanon	IMD 1	147	31 May	310.2	97	5.3	28.3
			IMD 2		4 June	185.2	98	2.7	33
			IMD 3		8 June	114.5	96	8.7	42
			Delay 1		31 May	425.9	99	7.8	32.4
			Delay 2		4 June	89.5	76	5.7	16.1
			Delay 3		8 June	110.2	96	8.4	17.3
			Ground		8 June	90.1	75	8.8	41.7
			Current ICARDA		31 May –11 June	298.1	96	6.6	31.9

* IG ICARDA Genebank unique number; ** DHE = days from sowing to heading; *** after threshing, cleaning and fumigation.

Table 2. Information on the accessions of durum wheat (*Triticum turgidum* subsp. *durum*) and wild wheat (*T. turgidum* subsp. *dicoccoides* and *T. monococcum* subsp. *boeoticum*) and seeds sown in November 2018 (Experiment 2) and the seed samples produced. The weight shown is total weight of seeds provided by each treatment. IMD = immediate and Delay = delayed processing treatments and the subsequent numeral is the harvest number.

Accession (IG number*) – sowing number	Taxon name	Origin	Treatment	DHE**	Harvest date (2019)	Weight (g) ***	Germination (%) ***	MC (%) ***	eRH (%) ***
89263-S2	*Triticum turgidum* subsp. *durum*	Turkey	IMD 1	145	7 June	128.9	100	13.9	66.9
			IMD 2		13 June	197.6	95	9	55.2
			IMD 3		17 June	209	85	8.9	55.8
			IMD 4		20 June	383.2	95	8.6	53.5
			Delay 1		7 June	55.8	99	6.4	44.8
			Delay 2		13 June	169.6	98	6.4	44.5
			Delay 3		17 June	184.2	100	6.1	43.9
			Delay 4		20 June	419.3	99	6	48.7
			Current ICARDA		7 June – 4 July	522.3	100	6.2	56.2

* IG ICARDA Genebank unique number; ** DHE = days from sowing to heading; *** after threshing, cleaning and fumigation.

Table 2. *cont’d*

Table 2. *Continued.*

Accession (IG number*) – sowing number	Taxon name	Origin	Treatment	DHE**	Harvest date (2019)	Weight (g) ***	Germination (%) ***	MC (%) ***	eRH (%) ***
			IMD 1		7 June	151.5	68	9	65.9
			IMD 2		13 June	254.2	72	9.2	63.5
			IMD 3		17 June	192.6	61	9.3	53.9
			IMD 4		20 June	509.5	65	9.5	57.3
46508-S4		Lebanon	Delay 1	150	7 June	210	99	6.4	58.8
			Delay 2		13 June	180.7	93	6.4	58.7
			Delay 3		17 June	217.3	85	6.1	51.5
			Delay 4		20 June	229.4	82	6	51.9
			Current ICARDA		7 June – 4 July	386.2	96	6.2	57.8
			IMD 1		7 June	153.7	46	9.3	68.2
			IMD 2		13 June	186.2	72	8.6	60
			IMD 3		17 June	147.3	61	9.9	59.3
			IMD 4		20 June	1160.2	62	8.5	56.5
46508-S5	*Triticum turgidum* subsp. *dicoccoides*	Lebanon	Delay 1	148	7 June	195.4	91	6.9	54.2
			Delay 2		13 June	215	82	6.8	53.8
			Delay 3		17 June	174.9	88	6.7	54
			Delay 4		20 June	474.4	90	6.2	50.4
			Current ICARDA		7 June – 4 July	459.2	92	6.9	55.5
			IMD 1		20 June	87.8	56	9	64
			IMD 2		24 June	51.1	78	7.6	63.5
			IMD 3		27 June	162	90	7.5	55.8
44857-S1	*Triticum monococcum* subsp. *boeoticum*	Bulgaria	Delay 1	172	20 June	60.3	73	6.6	58.7
			Delay 2		24 June	25.6	77	7.3	57
			Delay 3		27 June	54.1	73	7.7	54.2
			Current ICARDA		20 June – 4 July	122.3	85	7.3	55.2

* IG ICARDA Genebank unique number; ** DHE = days from sowing to heading; *** after threshing, cleaning and fumigation.

Seed harvests and post-harvest processing, Experiments 1 and 2

Experienced field workers inspected each plot in Experiments 1 and 2 every 3-4 days during the harvest period and collected those spikes they deemed mature (changes in spike colour used as indicator) and/or at risk of shedding. There were four harvest dates for durum wheat and three for the wild relative in Experiment 1. Very heavy rain, exceptional for this site, occurred towards the end of the harvest period and caused large numbers of seeds of the wild relative to shatter and shed to the ground. These seeds were then collected from the ground to create an additional "Ground" treatment which was subjected to the Immediate processing treatment (see below). In Experiment 2 there were four harvest dates for durum wheat and *T. turgidum* subsp. *dicoccoides*, and three for *T. monococcum* subsp. *boeoticum*.

The spikes maturing on any one harvest date were collected by hand from each plot and divided at random into three samples which were then subjected to one of the following treatments.

1) *Immediate ('IMD') processing*
   Spikes were taken from the field and transferred the same day into the fumigation chamber at ICARDA for three days, then threshed, cleaned and dried.
2) *Delayed ('Delay') processing*
   Spikes harvested when mature were placed in a separate cloth bag (i.e., one bag per collection date per plot) fixed to a peg at the edge of the plot. Each bag remained in the field until the final harvest of the investigation and only then transferred from the field to be fumigated, threshed, cleaned and dried.
3) *Current ICARDA practice*
   Spikes harvested when mature were placed in a cloth bag, one for each plot. This was a cumulative sample with seeds from successive dates of harvest added to the bag. When the final harvest of the investigation had been added, the contents were then transferred from the plot and fumigated, threshed, cleaned, and dried.

The temperature and RH inside and outside the cloth bags were logged (data logger, precision hygrometer model: HT-3027SD) hourly during the seed harvest periods in both years and minimum, maximum and mean values recorded each day.

Fumigation was carried out in an insulated chamber at 17-30°C, 55 m^3 volume, with 4-6 g of Phostoxin (active ingredient aluminum phosphide, 55%, D & D Holdings, Weyers Cave, VA 24486 USA) per m^3 for three days. The spikes of the wild relatives of wheat were threshed using a de-awner (Kimseed Australia, Pty. Ltd., Buckingham, Western Australia), while durum wheat seeds were threshed using a mechanical thresher (LD350, Wintersteiger AG, Austria). Seed samples were then cleaned in an air-column blower (Kimseed vacuum separator with Venturi flow attachment, Kimseed Australia Pty. Ltd., Buckingham, Western Australia) to remove debris. All equipment was cleaned between samples to avoid mixing. Total seed fresh weight and the moisture content of samples from each treatment combination were determined after threshing and blowing.

The remainder of the seed samples were transferred into labelled paper envelopes and placed in the drying room (15°C, 15% RH) for 4-6 weeks to dry seeds to about 6% moisture content. After drying, equilibrium relative humidity (eRH) was assessed and subsamples drawn to test germination and moisture content of the dried seeds. The remaining seeds were packed and sealed into labelled laminated aluminium foil bags (Moore and Buckle, Sutton Fold, Saint Helens WA9 3GL, UK) and stored at 2-4°C until the laboratory experiments to determine seed storage survival began.

Seed harvests and post-harvest treatments, Experiment 3

Seven serial harvests of spikes were taken by hand on different dates from 17 May (four days after heading, one day after flowering) until 1 July 2019, i.e., from early seed filling until after harvest maturity. Nine spikes were taken for the first three harvest dates (4, 10 and 17 days after heading), but around 80 spikes from each later harvest. On each date, spikes were selected at random from the middle third and each end of the plot, pooled, and seeds extracted by hand. Seed moisture content, dry weight and eRH at harvest were determined on samples drawn from all seven harvests. Total seed fresh weight was also recorded.

The remaining seeds from the fourth to the final harvest were each divided at random into three, each sub-sample placed in a cloth bag inside a plastic container filled with silica gel and, on the same day as harvest, subjected to one of the following drying regimes for three days: (i) incubator at 30°C; (ii) drying room (15°C; 15% RH); (iii) laboratory bench (23-27°C). After drying as above, the sub-samples were removed from the plastic containers, samples drawn at random to estimate germination and moisture content, and the remainder moved to the drying room (15°C; 15% RH) for 4-6 weeks. Contrary to normal ICARDA practice, these samples were not fumigated.

After drying, seed eRH was assessed and subsamples drawn at random to estimate germination and moisture content. The remaining seeds were packed and sealed into labelled laminated aluminium foil bags (as above) and stored at 2-4°C until the laboratory experiments to determine seed storage survival began.

Equilibrium relative humidity and moisture content

To estimate eRH, seeds were placed inside a 3.2 ml sample holder in the measuring chamber of a water activity meter (Hygrolab C1, Rotronic Instruments (UK) Ltd, Crawley, West Sussex). Seed moisture content (fresh weight basis) was determined for all harvests using the low-constant-temperature-oven method (whole seeds, 103°C for 17 hours; ISTA 2020) on two sub-samples, each of 100 seeds, from each treatment combination. For the wild relatives, the glumes were first removed from the 100-seed samples by hand. The samples were weighed before being placed in a mechanical convection oven (model 52412-90; Cole-Parmer Instrument Company Ltd, UK) at 103°C for 17 hours. The samples removed from the oven after drying were then placed in a desiccator over silica gel for one hour to cool before reweighing.

Germination

Ability to germinate was estimated on 100 seed samples. Two replicates of 50 seeds were sown in 90 mm diameter Petri dishes on top of Whatman No. 1 filter paper wetted with distilled water, incubated at 21°C (12/12 hours light/dark cycle), and germination was recorded at 4, 7, 10, 14 and 21 days. Seeds were considered germinated when the radicle had emerged by at least 2 mm. A cut-test was performed of non-germinated seeds at 21 days to determine if dormant or dead. Seeds were sliced lengthwise and examined visually; those with firm and healthy-looking embryos were classed as dormant, and those with soft, shrivelled or decomposing embryos were classed as dead.

Experimental seed storage

The aluminium foil bags containing seeds were removed from cold storage and allowed to equilibrate to room temperature before opening. Up to 12 subsamples (eight samples for germination tests and four to determine moisture content) of 100 seeds each for treatment combination were sampled at random from each bulk and prepared for experimental storage.

Seed moisture content was first raised by placing subsamples of seeds in 50 mm × 15 mm glass Petri dishes over a non-saturated lithium chloride (LiCl) solution at 60% RH in a sealed 300 mm × 600 mm × 132 mm (L × W × H) electrical enclosure box at 21°C. The LiCl solution was checked and adjusted regularly, by adding distilled water and stirring and rechecked. Seed eRH was assessed (as above). When seeds were equilibrated to the target value of 60% RH, three subsamples for each treatment combination were used to estimate initial germination and moisture content before experimental storage.

The remaining seeds were sealed into individual laminated aluminium foil packets and placed in an incubator (GR-66L; Percival Scientific, 505 Research Dr, Perry, IA 50220, USA) at 45°C. Subsamples were removed after different intervals of storage and tested for ability to germinate after up to 67 (wild wheats) or 90 days (durum wheat). Mid-way through experimental storage, two subsamples were removed from the incubator and seed moisture content estimated.

Analyses

The germination data from the seed storage experiments were subjected to probit analysis using the FITNONLINEAR directive in Genstat 21st Edition (VSN International Ltd., Hemel Hempstead, UK) and the seed viability equation fitted:

$$g = 100 \times \Phi(v) = 100 \times \Phi(K_i - p/\sigma) \quad [1]$$

in which, g is percentage germination, Φ is the cumulative normal distribution function, v is viability (ability to germinate) in normal equivalent deviates (NED) after p days in experimental storage, K_i is the fitted initial viability in NED, and σ (days) is the period taken for viability to decline by 1 NED (Ellis and Roberts, 1980; Hay *et al*., 2014). In some treatment combinations, the ability to germinate increased during early storage (indicating loss in dormancy) before loss in viability was detected. In such cases the following equation was used to quantify the combined effects of dormancy being broken and loss of viability occurring during experimental storage:

$$g = 100 \times \Phi(nd) \times \Phi(v) = 100 \times \Phi(K_{nd} + p/\sigma_{nd}) \times \Phi(K_i - p/\sigma) \quad [2]$$

in which, g, v, p, K_i and σ are as in eqn. 1; nd is non-dormant seeds in NED, K_{nd} is the fitted initial germination (non-dormant fraction of seeds in the sample) in NED and σ_{nd} is the period of time (days) for germination to increase due to release of dormancy by 1 NED

(Kebreab and Murdoch, 1999). In some treatment combinations there appeared to be some loss in dormancy in early storage, but the data were insufficient to fit Equation 2. In these cases, Equation 1 was fitted but results in early storage were omitted from analysis, with fitted survival curves commencing from the start of the observations analysed.

The CALC directive in Genstat was used to calculate the F-statistic to compare models with different combinations of parameter constraints for different treatments (and so whether or not longevity differed among treatments). This directive was also used to estimate p_{50} (days) from the fitted parameter values, where p_{50} is the product of K_i and σ (i.e., the period from the start of storage to when viability has declined to 50% [and when v = 0 NED]).

Results

Experiment 1

The objective of this experiment was to compare different harvest protocols for one accession of cultivated wheat and one accession (three replicate plots) of a wheat wild relative. The wild wheat plots flowered 2-4 days later than durum wheat (table 1). The harvested fresh seed sample weights ranged from 89.5 to 1039.1 g, with the first harvests yielding more than later harvests. Ability to germinate after fumigation and cleaning varied between 54 and 100%, and seed moisture contents ranged from 2.8 to 8.9%. The samples of the wild accession (IG 46508) collected from the ground after heavy rain had a higher moisture content than those harvested from plants that day but ability to germinate was similar.

Seed storage moisture content ranged from 8.8 to 10.4% among the seed lots with a mean of 9.6% (appendix 1). Ability to germinate ultimately declined over time in all cases (figures 1-4), but in the wild wheat plots germination initially increased before eventual decline (figures 2-4). Seed survival curves were quantified by Equation 1 where only loss in viability was observed (e.g., all durum wheat treatments) and Equation 2 where loss in both dormancy and viability were detected (in some wild wheat treatments).

In durum wheat, the immediate processing treatment of harvest 1 showed the poorest ability to germinate at the start of storage and thereafter, compared to all eight other samples (figure 1). Delayed processing (i.e., seed left in bags in field) provided greater initial germination and greater longevity for the first and greater longevity for the second harvests, but later harvests provided similar survival curves for immediate and delayed processing. Delayed processing of harvest 3 seeds provided the greatest longevity (p_{50} = 67 days), but the ICARDA protocol of delayed processing of seeds from the other three collection dates provided almost as great estimates of longevity (p_{50} = 57-62 days) (appendix 2).

The survival curves for the seeds from the three plots of the wild wheat accession showed increase in ability to germinate in early storage before evidence of decline emerged (figures 2-4). Differences among the 24 seed survival curves from the several harvest dates and processing methods among the three plots of the wild wheat accession showed some similarities but differed in other respects. The similarities were as follows. The ICARDA protocol resulted in the highest or equally highest longevity in each plot.

Seeds collected from the ground after heavy rain exhibited good longevity, though slightly lower than those from the ICARDA protocol. Within the same harvest date, delayed processing generally resulted in greater or equal longevity compared to samples processed immediately, and the greatest improvement in longevity from delaying processing was provided by the third harvest, which harvest date also provided superior longevity to the first and second. The major difference among the three replicate plots of the wild wheat accession was that consistent patterns of loss and dormancy were detected most often in the first plot (46508-S1, figure 2) and less so in the second and third (46508-S2, figure 3; 46508-S3, figure 4).

Experiment 2

In this experiment, we further explored the relative effects of harvesting protocol on subsequent seed longevity, including an additional accession of a different wheat wild relative. The two plots of *Triticum turgidum* subsp. *dicoccoides* flowered 3-5 days later than durum wheat, whereas *Triticum monococcum* subsp. *boeoticum* flowered 27 days later (table 2). Ability to germinate after fumigation and cleaning varied from 46 to 100% among all treatment combinations, and moisture content from 6.0 to 13.9%.

Seed storage moisture content ranged between 8.3 and 10.6% among all seed lots with a mean of 9.6% (appendix 3); seeds of *Triticum monococcum* subsp. *boeoticum* were slightly moister (mean 10.4%). The seed survival curves for durum wheat were sigmoidal with similar slopes and were described well by Equation 1 provided observations over the initial 40 days or so in storage were excluded from analysis (figure 5). Delayed processing resulted in greater longevity than immediate processing across all four harvests (figure 5, appendix 4). Seed storage longevity showed a slight but consistent increase from the first to the fourth harvest. The ICARDA protocol and delayed processing of harvest 4 seeds provided the greatest, and similar, longevity.

As in Experiment 1, observations for ability to germinate of samples withdrawn from storage showed much greater evidence for loss in dormancy in early storage in the wild wheats (figures 6-8). These results were modelled using Equation 2, where possible, or if not then Equation 1 but omitting observations over the first 15-30 days of storage. The seed survival curves of *Triticum turgidum* subsp. *dicoccoides* differed among treatments but were broadly similar between the two plots (figures 6 and 7). Some loss in dormancy was evident during early seed storage in all treatments: it was least for delayed processing of harvest 1 and greatest for both treatments of harvest 4 in both plots. In the latter, and also harvest 3 of both plots, the timing of processing affected neither the pattern of loss in dormancy nor that of viability whereas longevity was greater with delayed processing of harvests 1 and 2. In 46508-S4, longevity was greatest, and similar, for the ICARDA protocol and delayed processing of harvests 1 and 2 (figure 6). In 46508-S5 these three treatments also provided greater longevity than the remaining treatments, but in this plot delayed processing of harvest 2 provided the greatest longevity followed by delayed processing of harvest 1 and then the ICARDA protocol (figure 7).

There was some indication of loss in dormancy in early storage for *Triticum monococcum* subsp. *boeoticum* (figure 8), though it was less obvious than in *Triticum turgidum* subsp. *dicoccoides* (figures 6 and 7) and insufficient to fit Equation 2. Delayed seed processing resulted in considerably greater longevity than immediate processing for all three harvests of *Triticum monococcum* subsp. *boeoticum* (figure 8). Within each processing treatment the three harvest dates provided similar longevity, with harvest 2 marginally but consistently the greatest. Overall, the ICARDA protocol provided the greatest longevity of the seven treatments, albeit only slightly more than delayed processing of harvest 2.

Experiment 3

For this experiment, the objective was to understand the role of the degree of seed maturity at harvest in the response to different post-harvest protocols, focusing on the cultivated wheat accession. Mean seed weight increased until approximately 35 days after heading, moisture content declined from 74.9% at the first harvest to 7.3% 48 days after heading, whilst ability to germinate at harvest declined between 21 and 35 days after heading but increased to over 90% in later harvests (figure 9). A similar pattern was observed for seeds tested after drying, whilst drying increased ability to germinate in seeds harvested 35 days after heading (appendix 5). All drying treatments reduced the moisture content of seeds to between 5.3 and 5.7% after 28 days (appendix 5).

The mean moisture content of seeds during experimental storage was 10.2% (varying from 10.0 to 10.7%). The seed survival curves were quantified well by Equation 1 (figure 10). Initial germination values were considerably below 100% for seeds harvested 35 days after heading. This harvest provided the shallowest and poorest fitting seed survival curves which did not differ among the three drying treatments. In contrast, the fitted survival curves differed significantly ($P < 0.05$) among drying treatments within each of the three later harvest dates. Within each of the latter, the seed survival curves could be explained by common slope or by common intercept models; common slope models were selected for presentation within each of these harvests (figure 10, appendix 6).

Averaged across drying treatments, seeds harvested 41 days after heading showed the greatest subsequent seed longevity with a progressive increase in longevity between 21 and 41 days and a slight decline between 41 and 48 days (figure 10). The optimal drying treatment for seed storage longevity varied by harvest dates. Seeds harvested 21 days after heading showed greater longevity when initially dried in either the incubator (30°C) or laboratory (23-27°C) than the drying room (15°C). No difference was observed in seeds harvested at 35 days. For seeds harvested at 41 days, initial drying in the drying room or laboratory resulted in greater longevity than the incubator. Seeds harvested 48 days after heading showed the greatest longevity when initially dried in the drying room, followed by the incubator, and lastly the laboratory. Overall, the drying room throughout provided better or no worse subsequent longevity than initial drying at warmer temperatures initially for seed harvested 35-48 days after heading, but those harvested earlier at 21 days after heading showed much greater longevity from initial drying at the two warmer temperatures than in the drying room throughout.

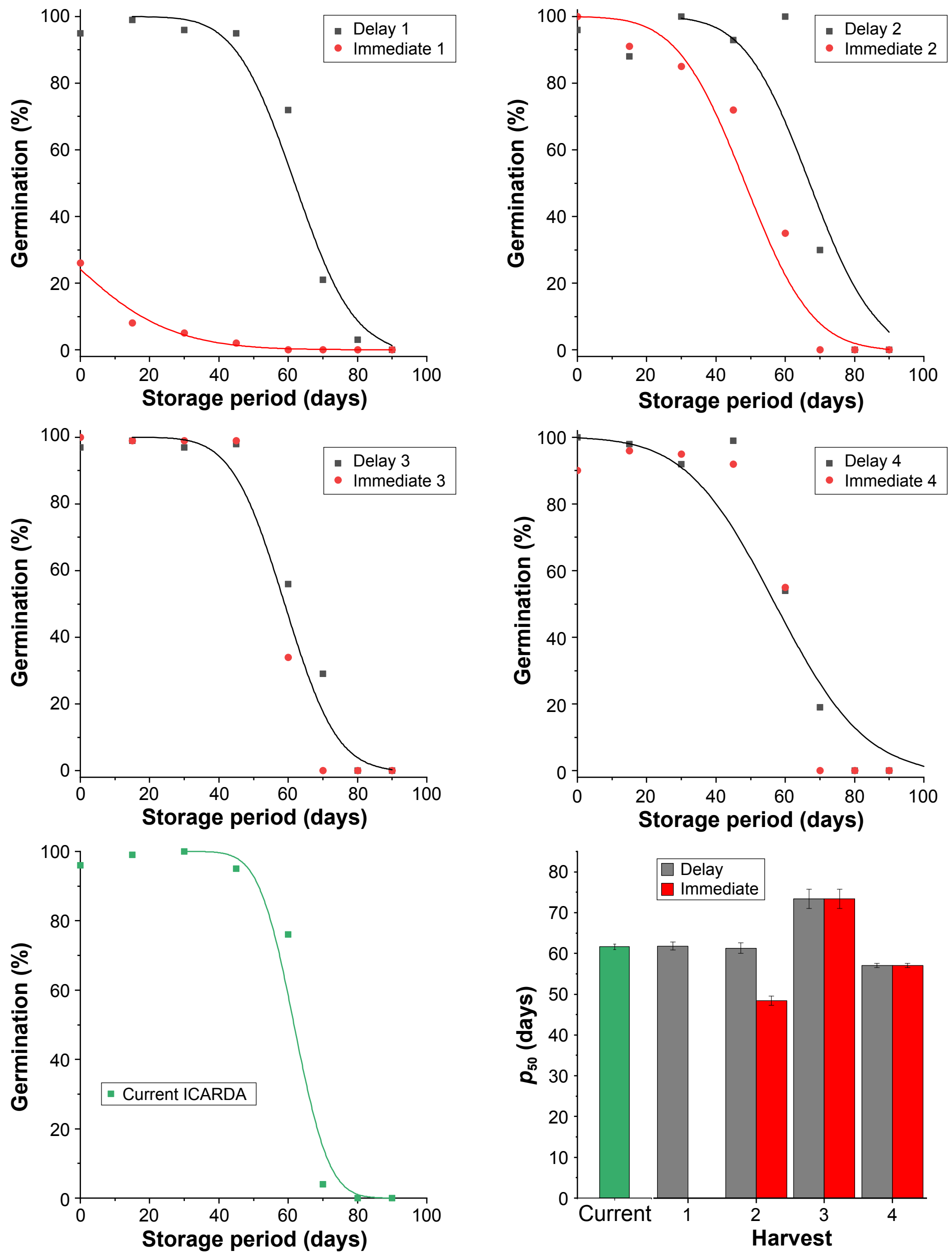

Figure 1. Seed survival curves (criterion of germination, radicle emergence) for durum wheat *Triticum turgidum* subsp. *durum* (89263-S1) in Experiment 1 harvested on four dates between 31 May 2018 and 11 June 2018 and subsequently stored hermetically at 45°C after equilibration of seed moisture content over non-saturated LiCl solution at 60% RH, 21°C; seed storage moisture contents are provided in appendix 1. Estimates (± SE) of longevity (p_{50}) are shown in the bar graph. 'Delay' = seeds harvested when mature and placed in bag and left in field until the last harvest of all wheat accessions; 'Immediate' = seeds removed from field when mature and processed immediately; 'Current ICARDA' = seeds harvested when mature and placed in a common bag, left in field, and all subsequent harvests added to this bag until the last harvest of all wheat accessions, then processed. The fitted curves are quantified in appendix 2.

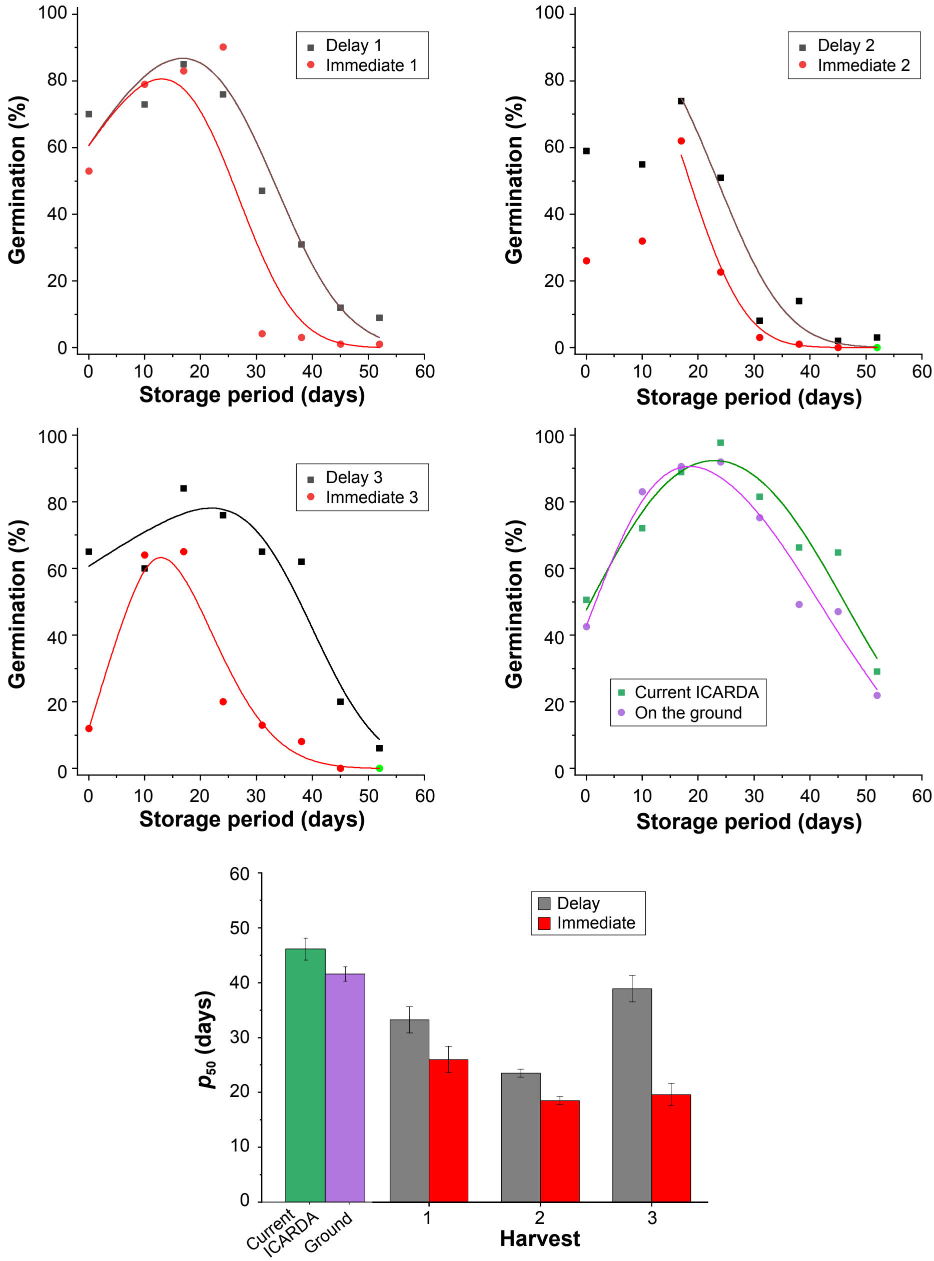

Figure 2. Seed survival curves (criterion for germination, radicle emergence) for the wild wheat *Triticum turgidum* subsp. *dicoccoides* (46508-S1) in Experiment 1 harvested on three dates between 31 May 2018 and 4 June 2018 and subsequently stored hermetically at 45°C after equilibration over non-saturated LiCl solution at 60% RH, 21°C; seed storage moisture contents are provided in appendix 1. Estimates (± SE) of longevity (p_{50}) are compared amongst treatments by the bar graph. 'Delay' = seeds harvested when mature and placed in bag and left in field until the last harvest of all wheat accessions; 'Immediate' = seeds removed from field when mature and processed immediately; 'Current ICARDA' = seeds harvested when mature and placed in a common bag, left in field, and all subsequent harvests added to this bag until the last harvest of all wheat accessions, then processed; 'Ground' = seeds that shattered due to rain, collected from the ground then processed immediately. The fitted curves are quantified in appendix 2.

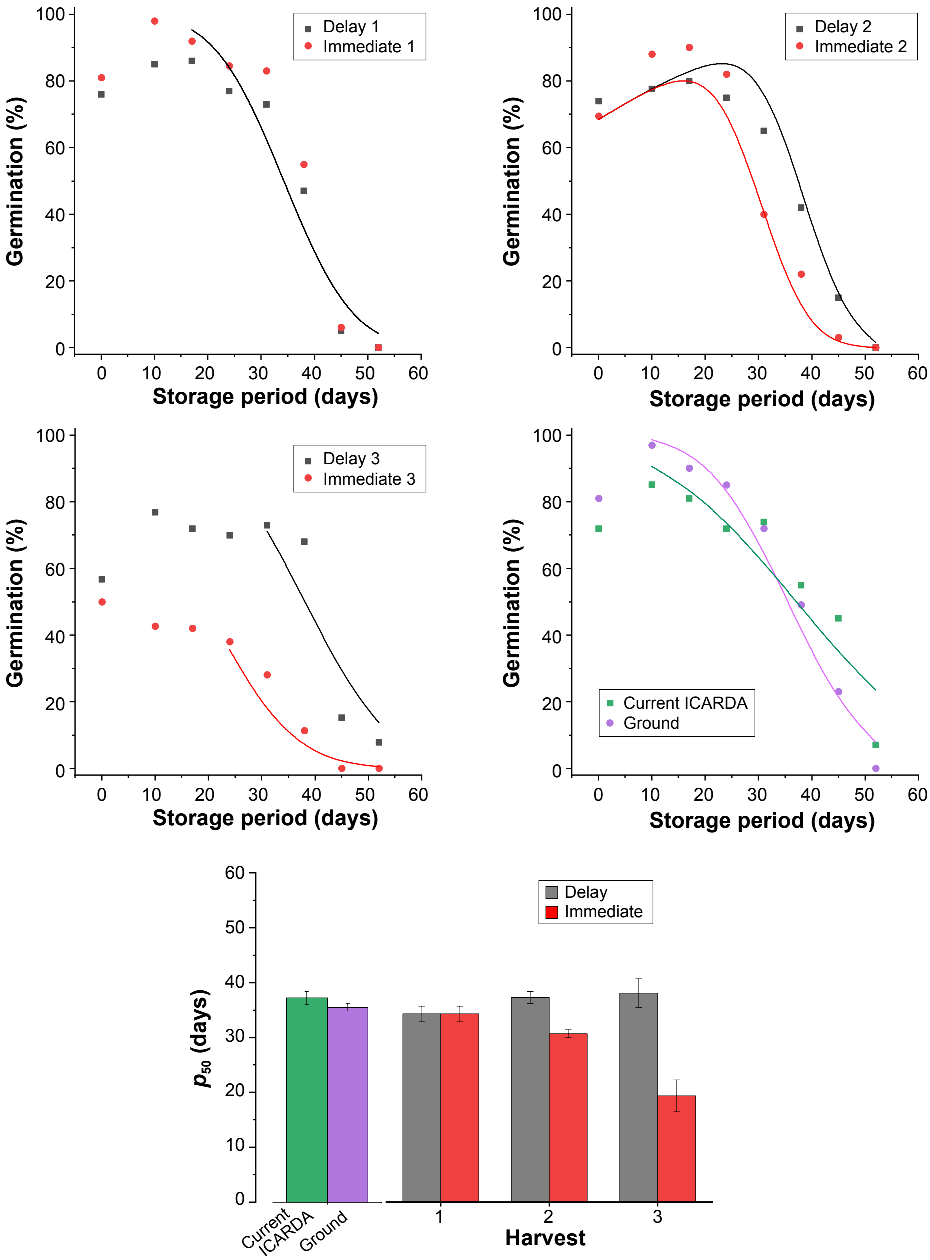

Figure 3. Seed survival curves (criterion for germination, radicle emergence) for the wild wheat *Triticum turgidum* subsp. *dicoccoides* (46508-S2) in Experiment 1 harvested on three dates between 31 May 2018 and 4 June 2018 and subsequently stored hermetically at 45°C after equilibration of seed moisture content over non-saturated LiCl solution at 60% RH, 21°C; seed storage moisture contents are provided in appendix 1. Estimates (± SE) of Longevity (p_{50}) are compared amongst treatments by the bar graphs. 'Delay' = seeds harvested when mature and placed in bag and left in field until the last harvest of all wheat accessions; 'Immediate' = seeds removed from field when mature and processed immediately; 'Current ICARDA' = seeds harvested when mature and placed in a common bag, left in field, and all subsequent harvests added to this bag until the final harvest of all wheat accessions, then processed; 'Ground' = seeds that shattered due to rain, collected from the ground then processed immediately. The fitted curves are quantified in appendix 2.

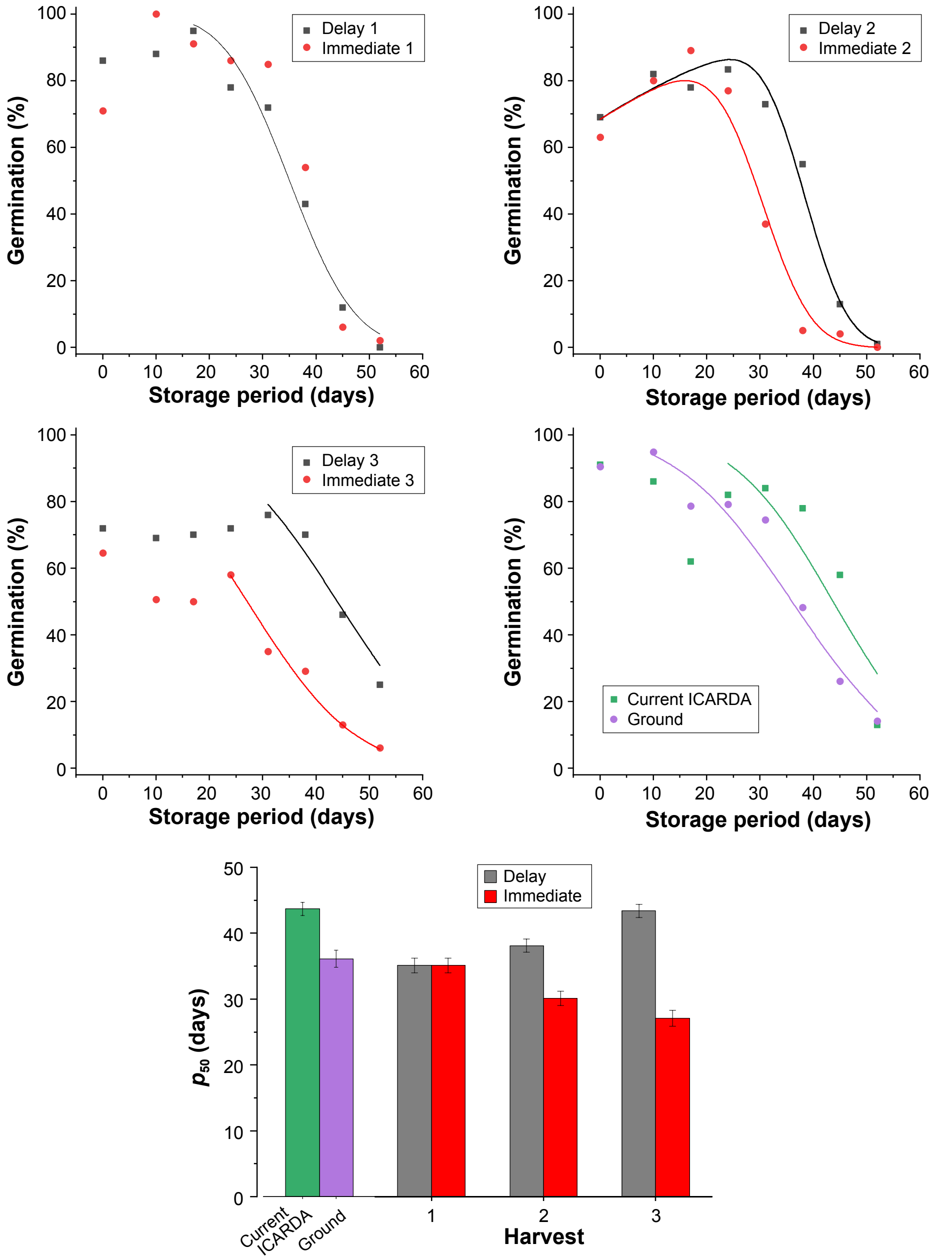

Figure 4. Seed survival curves (criterion of germination, radicle emergence) for the wild wheat *Triticum turgidum* subsp. *dicoccoides* (46508-S3) in Experiment 1 harvested on three dates between 31 May 2018 and 4 June 2018 and subsequently stored hermetically at 45°C after equilibration of seed moisture content over non-saturated LiCl solution at 60% RH, 21°C; seed storage moisture contents are provided in appendix 1. Estimates (± SE) of longevity (p_{50}) are compared amongst treatments by the bar graph. 'Delay' = seeds harvested when mature and placed in bag and left in field until the last harvest of all wheat accessions; 'Immediate' = seeds removed from field when mature and processed immediately; 'Current ICARDA' = seeds harvested when mature and placed in a common bag, left in field, and all subsequent harvests added to this bag until the last harvest of all wheat accessions, then processed; 'Ground' = seeds that shattered due to rain, collected from the ground then processed immediately. The fitted curves are quantified in appendix 2.

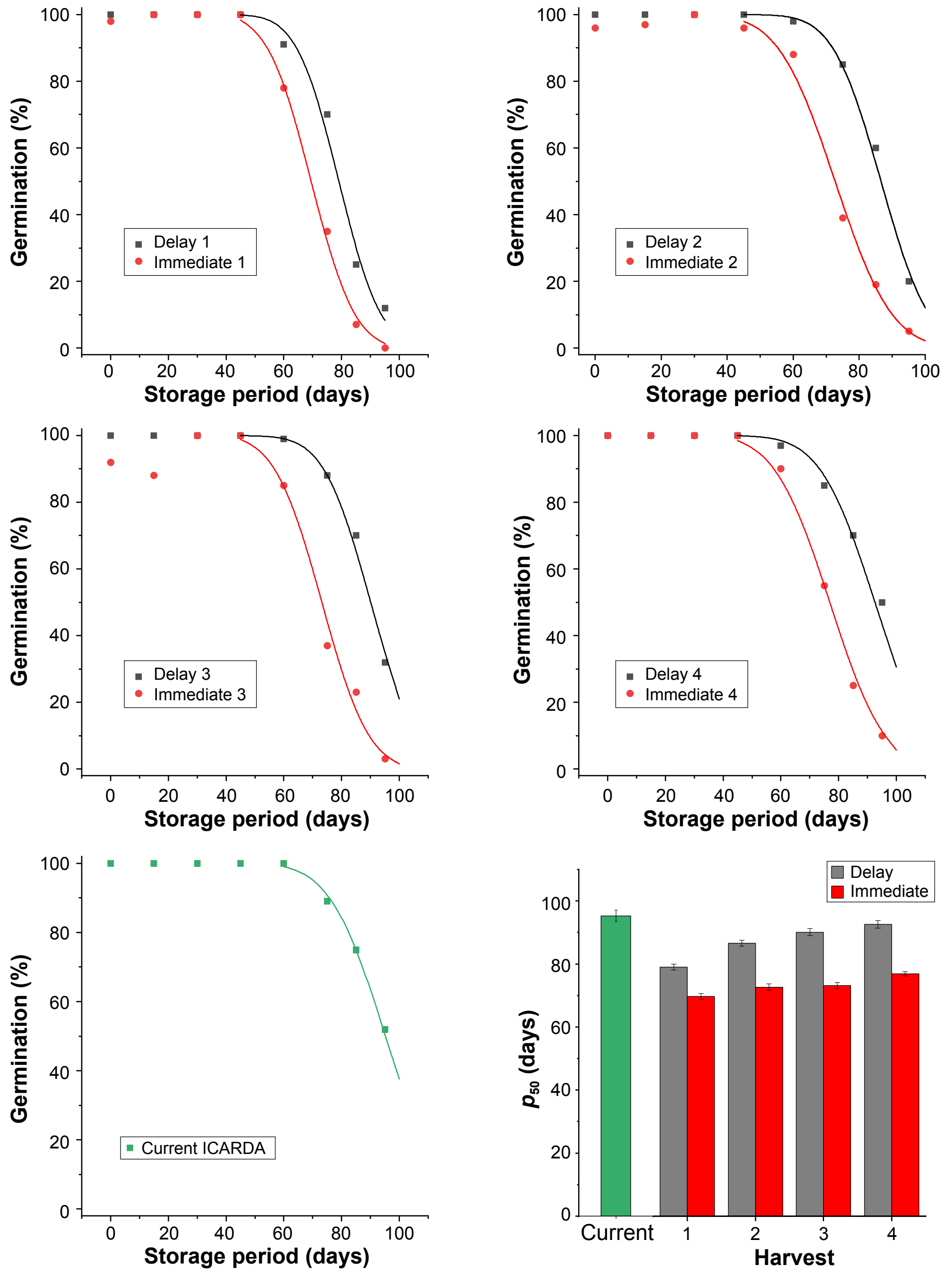

Figure 5. Seed survival curves (criterion of germination, radicle emergence) for durum wheat *Triticum turgidum* subsp. *durum* (89263-S2) in Experiment 2 harvested on four dates between 7 June and 20 June 2019, and subsequently stored hermetically at 45°C after equilibration of seed moisture content over non-saturated LiCl solution at 60% RH, 21°C; seed storage moisture contents are provided in appendix 3. Estimates (± SE) of longevity (p_{50}) are compared amongst treatments by the bar graph. 'Delay' = seeds harvested when mature and placed in bag and left in field until the last harvest of all wheat accessions; 'Immediate' = seeds removed from field when mature and processed immediately; 'Current ICARDA' = seeds harvested when mature and placed in a common bag, left in field, and all subsequent harvests added to this bag until the last harvest of all wheat accessions, then processed. The fitted curves are quantified in appendix 4.

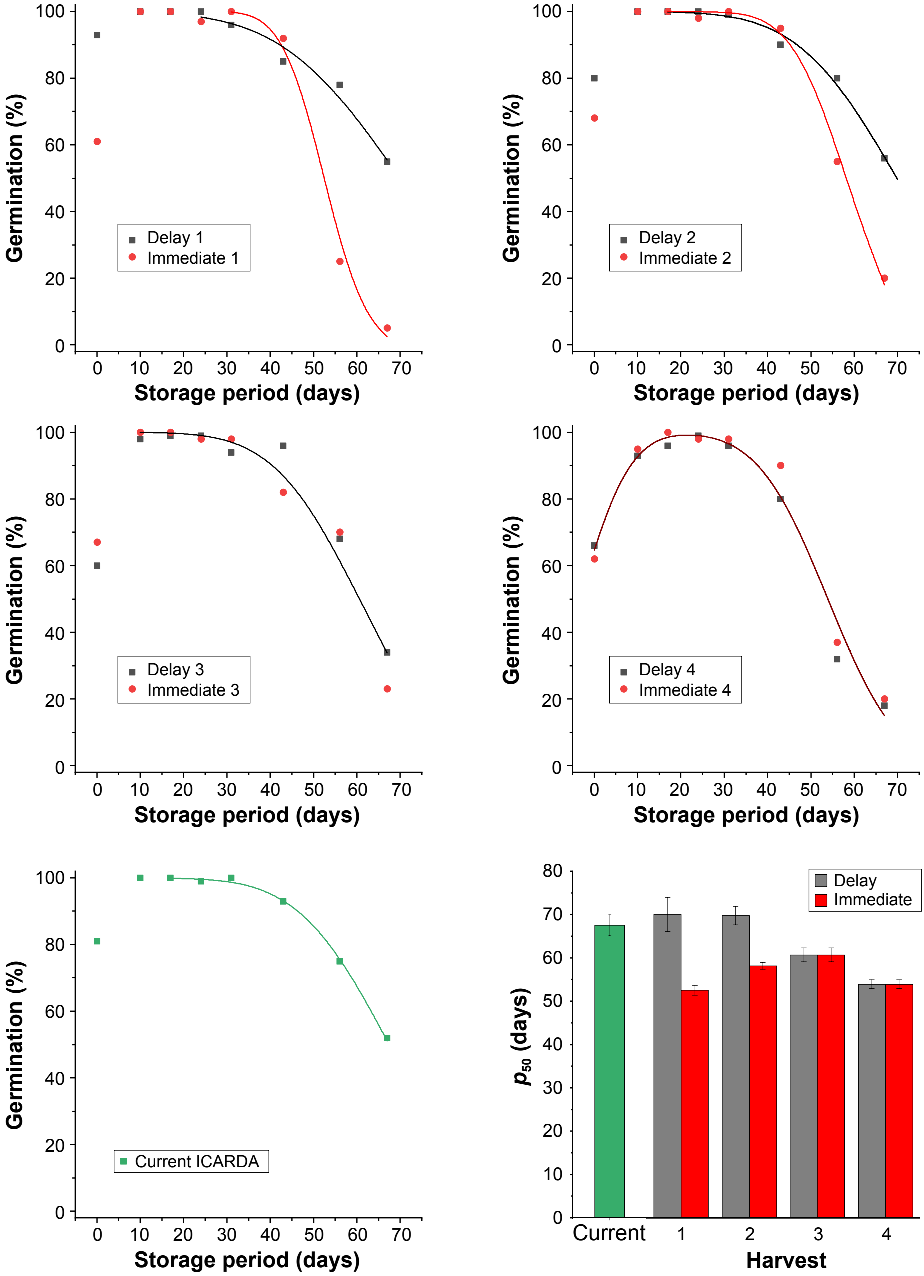

Figure 6. Seed survival curves (criterion of germination, radicle emergence) for the wild wheat *Triticum turgidum* subsp. *dicoccoides* (46508-S4) in Experiment 2 harvested on four dates between 7 June and 20 June 2019 and subsequently stored hermetically at 45°C after equilibration of seed moisture content over non-saturated LiCl solution at 60% RH, 21°C; seed storage moisture contents are provided in appendix 3. Estimates (± SE) of longevity (p_{50}) are compared amongst treatments by the bar graph. 'Delay' = seeds harvested when mature and placed in bag and left in field until the last harvest of all wheat accessions; 'Immediate' = seeds removed from field when mature and processed immediately; 'Current ICARDA' = seeds harvested when mature and placed in a common bag, left in field, and all subsequent harvests added to this bag until the last harvest of all wheat accessions, then processed. The fitted curves are quantified in appendix 4.

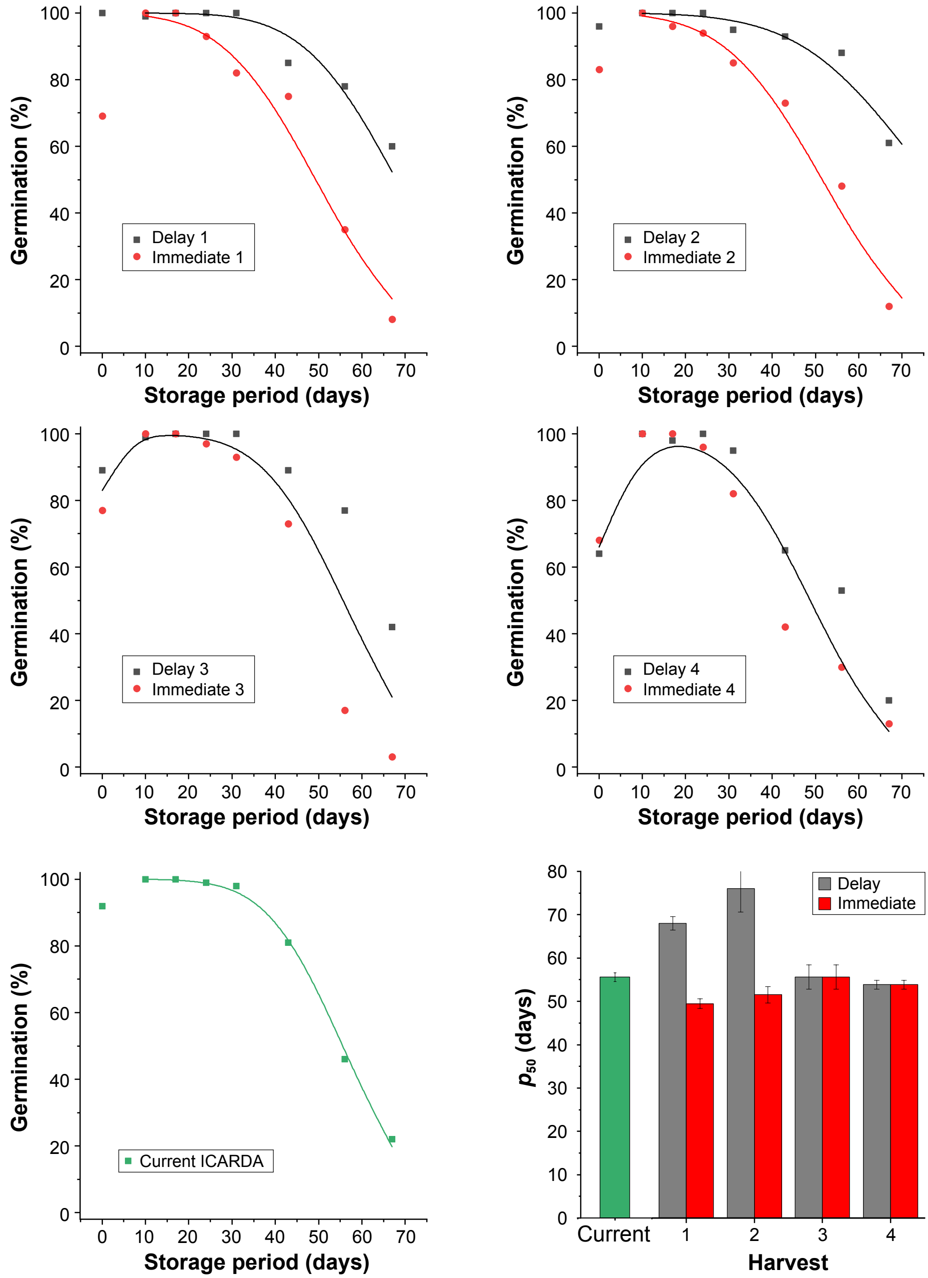

Figure 7. Seed survival curves (criterion of germination, radicle emergence) for the wild wheat *Triticum turgidum* subsp. *dicoccoides* (46508-S5) in Experiment 2 harvested on four dates between 7 June and 20 June 2019 and subsequently stored hermetically at 45°C after equilibration of seed moisture content over non-saturated LiCl solution at 60% RH, 21°C; seed storage moisture contents are provided in appendix 3. Estimates (± SE) of longevity (p_{50}) are compared amongst treatments by the bar graphs. 'Delay' = seeds harvested when mature and placed in bag and left in field until the last harvest of all wheat accessions; 'Immediate' = seeds removed from field when mature and processed immediately; 'Current ICARDA' = seeds harvested when mature and placed in a common bag, left in field, and all subsequent harvests added to this bag until the last harvest of all wheat accessions, then processed. The fitted curves are quantified in appendix 4.

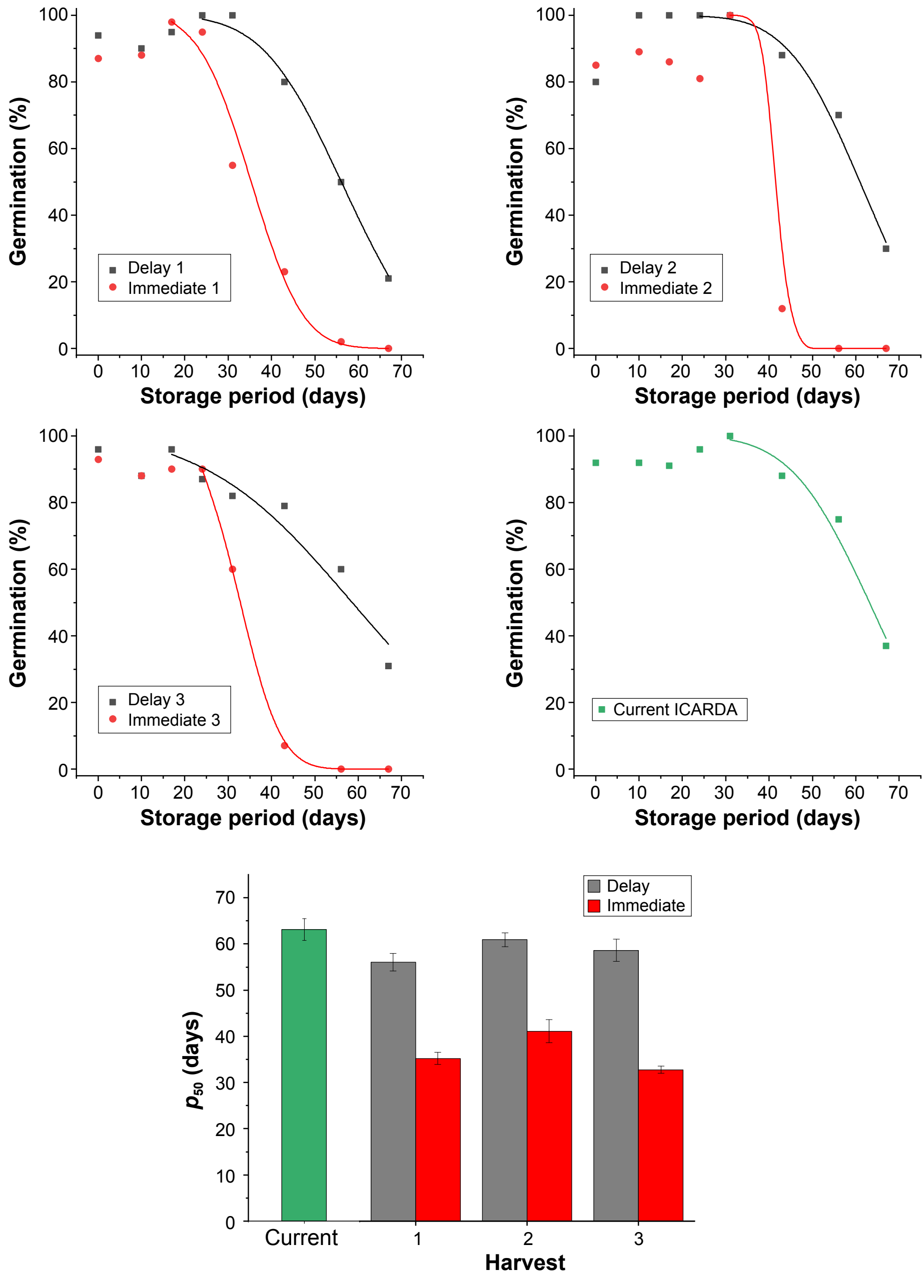

Figure 8. Seed survival curves (criterion for germination, radicle emergence) for the wild wheat *Triticum monococcum* subsp. *boeoticum* (44857-S1) in Experiment 2 harvested on three dates between 20 June and 4 July 2019 and subsequently stored hermetically at 45°C after equilibration of seed moisture content over non-saturated LiCl solution at 60% RH, 21°C; seed storage moisture contents are provided in appendix 3. Estimates (± SE) of longevity (p_{50}) are compared amongst treatments by the bar graph. 'Delay' = seeds harvested when mature and placed in bag and left in field until the last harvest of all wheat accessions; 'Immediate' = seeds removed from field when mature and processed immediately; 'Current ICARDA' = seeds harvested when mature and placed in a common bag, left in field, and all subsequent harvests added to this bag until the last harvest of all wheat accessions, then processed. The fitted curves are quantified in appendix 4.

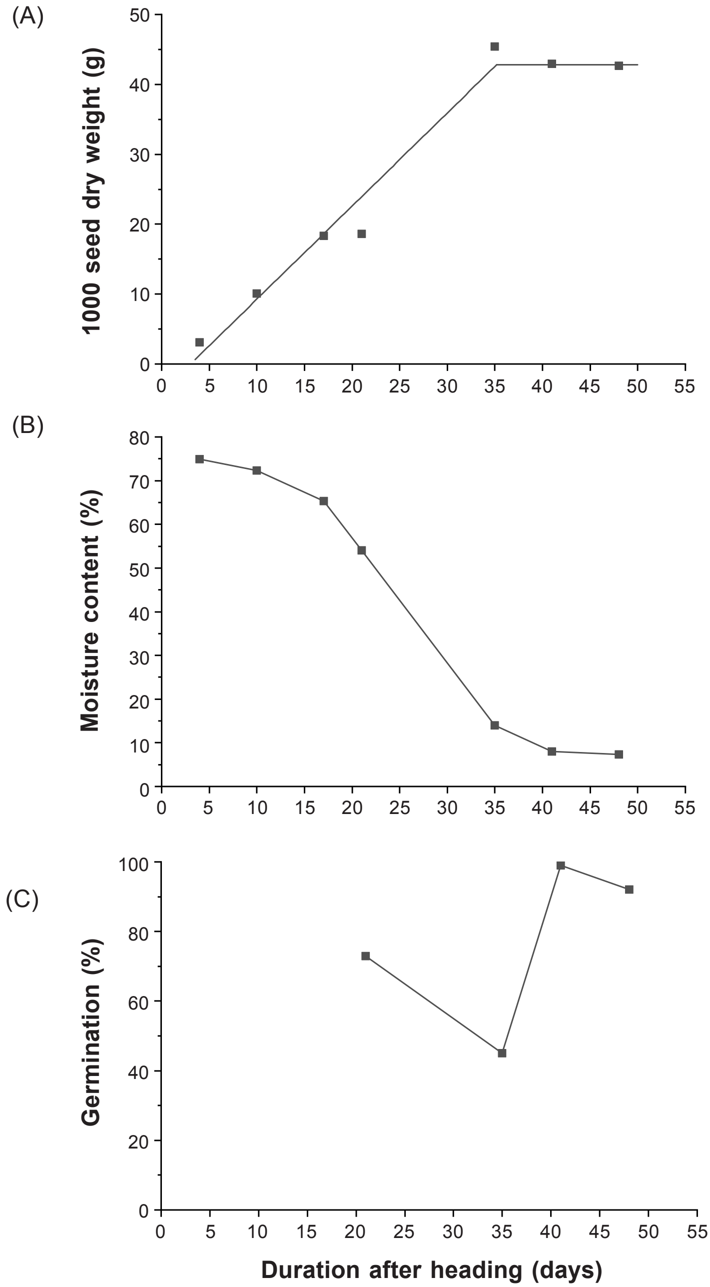

Figure 9. Seed development and maturation in durum wheat (Experiment 3; 89263-S3) showing changes in (**A**) seed dry weight fitted with a broken stick model with maximum dry weight achieved at ca. 35 days after heading; (**B**) moisture content; and (**C**) ability to germinate of freshly-harvested seeds.

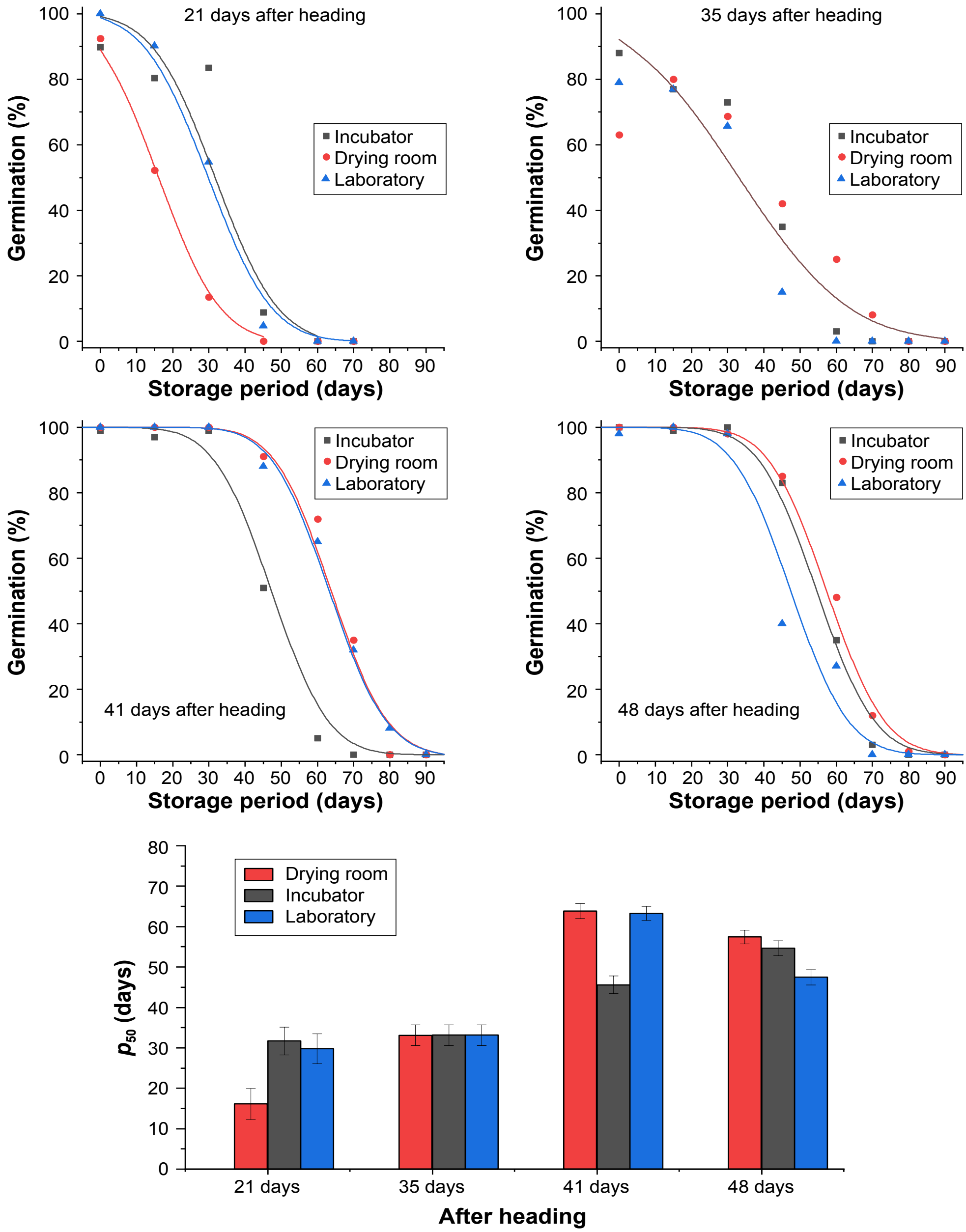

Figure 10. Seed survival curves (criterion for germination, radicle emergence) for cultivated wheat durum wheat *Triticum turgidum* subsp. *durum* in Experiment 3 (89263-S3) harvested on four dates between 3 June and 1 July 2019, dried initially for three days in a drying room (15°C, 15% RH), an incubator at 30°C, or in the laboratory (22-25°C), then for a further 28 days in the drying room, and subsequently stored hermetically at 45°C after equilibration of seed moisture content over non-saturated LiCl solution at 60% RH, 21°C (seed storage moisture contents ranged from 10.0 to 10.7%). Estimates (± SE) of longevity (p_{50}) are compared amongst treatments by the bar graph. The fitted curves are quantified in appendix 6.

Discussion

The ICARDA seed harvest protocol for accessions with variable maturity and/or seeds that may shed involves sequentially collecting mature spikes or pods and storing them in a bag within the plot which remains in the field until all spikes from all accessions are collected; only then does threshing and drying take place. This procedure reduces the risk of misidentification during regeneration or multiplication, but contrasts with standard genebank advice to dry seeds as soon as possible after harvest in a controlled environment. The objective of our research was to evaluate how delayed processing might affect subsequent seed storage longevity. This was tested directly, with seed quality development and drying temperature effects also studied in a contemporaneous experiment.

The null hypothesis that delaying post-harvest seed transfer to the ICARDA genebank has no effect on seed longevity can now be rejected. Contrary to expectations that this delay might be damaging to the seeds, at this field site in Lebanon, the ICARDA protocol either provided similar subsequent seed storage longevity to immediate seed processing or, quite often, greater longevity (figures 1-8). Similarly, comparisons within harvests (where the sequential harvests were not bulked) confirmed that delayed processing either resulted in comparable or improved longevity. In durum wheat in Experiment 2, delayed processing provided greater longevity than immediate processing at all four harvests (figure 5), and similarly for all three harvests of *Triticum turgidum* subsp. *dicoccoides* plot 1 (figure 2) in Experiment 1 and all three harvests of *Triticum monococcum* subsp. *boeoticum* in Experiment 2 (figure 8). In the remaining five plots across the two years, delayed processing provided greater longevity than immediate processing at two of the three or four harvests with no difference at others (figures 1, 3, 4, 6, 7). The greatest benefit to longevity from delayed processing was seen in harvest 1 of durum wheat in Experiment 1 where ability to germinate at the start of storage was especially poor (figure 1).

At first glance, these findings run counter to a report in barley (*Hordeum distichum* L.) of no difference in post-harvest longevity between immature (seeds still green) and mature seeds (Ellis and Roberts, 1981a). In that study, however, spikes on the straw were harvested by hand and allowed to dry in a well-aerated room for three weeks before threshing. Hence, the immature samples had considerable time to mature *ex planta* before threshing and drying. The two studies are, thus, consistent in that both show immature seeds can achieve good longevity given sufficient time to mature *ex planta* before processing. Interestingly, before the advent of the combine harvester, commercial cereal seed crops were harvested by binder or scythe and placed upright in stooks to dry in the field for several days before threshing; that traditional practice would have provided time for immature seeds to progress to maturity after harvest.

The decision on when to harvest maturing spikes was made by field staff on site. Although subjective to some extent, it was based on their collective experience and the imperative to avoid seeds being shed before harvest. The latter not only reduces the number of seeds available for conservation but also contributes to the soil seed bank and thereby weed problems in later seasons and the risk of contamination to subsequent regenerations. This seed collection strategy introduces the possibility of seeds being collected before fully mature. This was likely the case for the first harvest of durum wheat processed immediately in Experiment 1: ability to germinate after drying and short-term storage in the cold room was much reduced compared to that after harvest, threshing and cleaning (table 1), with no evidence of loss in dormancy in early storage (figure 1).

The risk that plants may shed seeds before harvest was realised in the case of the wild relative in Experiment 1 following heavy rain before the final harvest. The opportunistic additional seed sample collected from the ground and processed immediately provided slightly poorer longevity than the best samples for each of these three plots but not the worst (figures 2-4). Rainfall *in planta* can damage subsequent seed longevity in bread wheat, but the damage can be repaired by a further period of desiccation *in planta* (Yadav and Ellis, 2016). The immediate processing of the samples from the ground in the current study allowed some time for redrying in the field *ex planta* between the end of rainfall and seed collection but did not allow the possibility of benefit from a further period of desiccation in the field to be tested. Nonetheless, the findings show that collecting and conserving shed seeds can be a viable strategy when valuable material is being regenerated or multiplied.

As orthodox seeds develop, they acquire the ability to germinate and to survive desiccation. When fresh seeds are removed from the mother plant, they are capable of germinating once they have reached their maximum dry weight and started to lose water (Dasgupta *et al*., 1982; Greenwood and Bewley, 1982; Kermode and Bewley, 1985; Kermode *et al*., 1986), or earlier if first dried (King, 1976; Rosenberg and Rinne, 1986; Kermode and Bewley, 1986; Kermode, 1990). This was confirmed in Experiment 3 for durum wheat seeds harvested 21 days after heading when only partially filled; these seeds were not only able to germinate (figure 9C), but also to survive desiccation to low moisture content (appendix 5).

Abscisic acid regulates dormancy and peaks as the seed filling phase ends and declines thereafter (Taiz and Zeiger, 1991). Development and decline in dormancy around the end of seed filling was evident in this study. Durum wheat seeds harvested 35 days after heading showed poorer germination than earlier or later harvests (figure 9C). In addition, ability to germinate in this sample was increased by both drying (appendix 5) and by a brief period of experimental storage (figure 10) providing evidence of after-ripening. Observations of similar short periods of greater dormancy at this stage of seed development and maturation has been reported previously for bread wheat (*Triticum aestivum* L.) (Mitchell *et al*., 1980; Ellis and Pieta-Filho, 1992; Nasehzadeh and Ellis, 2017). In Experiments 1 and 2, seed dormancy at harvest was greater in the two wild species, greater in *Triticum turgidum* subsp. *dicoccoides* than *Triticum monococcum* subsp. *boeoticum*, and greater in earlier than later harvests (figures 1-8). Despite the longer time in the field, the Delay and ICARDA protocol treatments often showed similar dormancy to seeds processed immediately (e.g., figure 2).

In all three experiments, the longevity of all samples was assessed in hermetic storage at 45°C with approximately 9% moisture content, suggesting a similar estimate of σ (equation 1) across samples within each species should apply (Ellis and Roberts, 1980, 1981a, b). In practice, both seed storage moisture content and estimates of σ varied amongst samples (appendices 1-4; appendix 6). The greatest fitted value for σ of 29.1 days was for durum wheat in Experiment 1; these seeds were probably immature as most were not able to germinate after harvest and desiccation (figure 1). The second greatest value of 23.3 days was for seeds of durum wheat in Experiment 3 which were also harvested early at 35 days after heading (figure 10). In both these samples, Equation 2 could not be fitted, and it is probable that loss of dormancy (after ripening) and loss in viability were confounded during storage; hence the estimate of σ would be greater than for loss in viability alone. The range in the estimates of σ for the remaining samples was 6.9 to 21.5 days. Seed longevity predictions for durum wheat are unavailable, but the viability constants for bread wheat provided by Ellis and Hong (2007) suggest σ values of 48.4 and 14.2 days at 45°C with 8.3 and 10.7% moisture content, respectively. Whilst this range overlaps that for the current study, it seems probable that bread wheat shows greater longevity than durum wheat or the two wild relatives studied here.

As durum wheat seeds dried naturally between 21 and 41 days after heading (figure 9B), their longevity increased considerably whereas delaying harvest further to 48 days resulted in a slight decline in longevity on average (figure 10). Hence, whilst the developing seeds were capable of high germination and were desiccation tolerant at 21 days after heading (appendix 5), seed quality in durum wheat reached its maximum at this site in Lebanon some 20 days later, at 41 days after heading, when seeds had dried naturally to 8.0% moisture content (figure 9B) and about six days beyond the end of the seed-filling phase (figure 9A). This aligns with results in bread wheat grown in the UK in which seeds attained maximum longevity between 3 and 21 days after the end of the seed-filling phase when seed moisture contents had declined naturally to 16-28% in that cool temperate environment (Ellis and Pieta-Filho, 1992). Similarly, Chatelain *et al*. (2012) proposed that seeds collected at a low moisture content have progressed further through the desiccation phase of seed development, a process associated with seed quality improvement and increased longevity, and so seeds may live longer due to this further maturation.

The harvests in Experiment 3 were made over the same period and environment as those of durum wheat in Experiment 2, where 21 and 41 days after heading in the former (figure 10) were 3 days before the first and 4 days after the last harvest, respectively, in the latter (figure 5). Whilst the harvesting protocols differed (random spikes in Experiment 3, cf. spikes judged mature in Experiment 2), the observation that subsequent seed storage longevity from all four harvests in Experiment 2 benefitted from a further period in the field *ex planta* before processing (figure 5) is compatible with the conclusion from Experiment 3 that subsequent seed storage longevity continued to develop *in planta* to a maximum at 41 days after heading (figure 10), since this was 4 days after the last harvest in Experiment 2. Hence, seeds that were not fully mature were able to continue to develop both *ex planta* within the plot (Experient 2) and in *planta* (Experiment 3) at this site.

Seed drying temperature affected subsequent seed longevity. The best seed drying regime depended upon the extent of seed development and maturation when harvested: at 21 days after heading subsequent longevity was poorer with initial drying at 15°C than at 23-27°C or 30°C; at 35 days there were no differences among drying temperatures; the 41-day sample provided greater longevity at 15°C and 23-27°C than 30°C; and the final sample at 48 days showed greatest longevity with drying at 15°C (figure 10).

Thus, the warmest initial drying temperature (30°C) was most effective for the least mature seeds harvested at 21 days whereas the coolest drying temperature (15°C) was optimal for mature (41 days) and over-mature (48 days) seeds. Similarly in rice (*Oryza sativa* L.), seeds harvested early at moisture contents above 16.5% showed greater subsequent longevity if dried initially at 45°C compared to a drying room at 15°C, but this advantage diminished when seeds were harvested at lower moisture contents (Whitehouse *et al*., 2015, 2018). So called "safe" seed drying temperatures in heated-air driers have been recommended to farmers for around a century in Europe, but the maximum temperatures (not to be exceeded) cited for bread wheat differ considerably among countries: from 30°C in France, to 45°C in Germany, to yet warmer in the UK (Nellist, 1980). The warmest temperature applied here (30°C) corresponded to the most conservative of these recommendations.

Mean temperatures in the field and within the seed bags during the harvest period in 2019 were 30.2 and 32.0°C (appendix 7), respectively, and so similar to the warmest drying temperature in Experiment 3. The results from harvests between 21 and 41 days after heading and warmer temperature drying in Experiment 3, and those from delayed processing in Experiment 2, confirm that exposure of nearly mature durum wheat seeds to a period at warm temperatures, whether *in planta* or *ex planta*, improves subsequent seed storage longevity. This is compatible with advice for rice where seeds harvested at low moisture contents are likely to have already acquired high initial seed quality and so are recommended to be dried immediately at 15°C and 15% RH, whereas the quality of immature seeds may be improved by drying at warmer temperatures (Whitehouse *et al*., 2015).

The similar benefits to seed storage longevity from delayed processing of seed maturing *ex planta* in warm dry conditions (figures 1-8) and from warmer temperature drying of not quite mature seeds (figure 10) is compatible with the suggested protective role in seeds of heat-stable, low molecular weight proteins. These are involved in coping with stress and damage (Bray, 1997), and include late embryogenesis-abundant proteins (i.e., as seeds mature) and heat-shock proteins (e.g. in response to warmer temperature drying). Late-embryogenesis-abundant proteins have been associated with the ability of seeds to tolerate desiccation (Galau *et al*., 1986) and the accumulation of heat-stable, low molecular weight, proteins in seeds during late maturation is positively correlated with subsequent longevity (Sinniah *et al*., 1998).

Conclusions

Previous advice to process and dry seeds as soon as possible after harvest remains valid when seeds are fully mature (or over- mature). However, this study has demonstrated that seeds harvested before full maturity can continue to improve in quality - specifically, their potential seed storage longevity - both *ex planta* as well as *in planta* under suitable environmental conditions. Similarly, the standard recommendation to dry seeds in a cool, dry environment (typically 15-17°C and 10-20% RH) to the low moisture contents required for long-term storage in genebanks remains appropriate for seeds that are fully or over-mature or have already undergone partial drying *ex planta*. However, if seeds of *Triticum* spp. are harvested before fully mature then initial drying at warmer temperatures (e.g., 30°C in this study) is preferable. Hence, the delay in seed processing inherent in the ICARDA seed collection protocol not only reduces the risks of seed shedding before harvest but also maximises the potential longevity of the seed accessions entering long-term storage. However, in regions where the environment at harvest time is less suitable or unreliable for seed maturation (e.g., if cool and wet), leaving seeds in cloth bags in the field may be inadvisable. In such cases warmer temperature drying may provide an alternative method to improve seed quality post-harvest for seed not fully mature at harvest.

Acknowledgements

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Appendix 1. Mean seed moisture content (%, wet basis) of samples of durum and wild wheats in experimental storage (Experiment 1). Mean values with the same letter are not significantly different ($P > 0.05$). See table 1 for accession and treatment codes.

Treatment	Accession (IG number) – sowing number			
	89263-S1	**46508-S1**	**46508-S2**	**46508-S3**
Current ICARDA	9.8 b,c	9.3 a	9.7 a	9.2 b
Ground	-	9.6 b	10.0 b,c	9.3 b
Delay 1	9.7 b	9.7 b	9.8 a,b	8.8 a
Immediate 1	9.9 d,e	10.2 c	9.9 a,b,c	9.7 c
Delay 2	9.7 b,c	9.7 b	9.5 a,b,c	8.7 a
Immediate 2	10.4 e	10.2 c	10.1 c	9.7 c
Delay 3	9.1 a	9.6 b	9.8 a,b	8.5 a
Immediate 3	9.8 c,d	10.2 c	10.0 b,c	9.8 c
Delay 4	9.9 d	-	-	-
Immediate 4	9.8 b,c	-	-	-
Overall mean	**9.8**	**9.8**	**9.9**	**9.2**

Appendix 2. Estimates of seed longevity and dormancy loss (where appropriate) parameters (Equations 1 and 2) for seeds of durum (89263-S1) and a wild (46508-S1, -S2, -S3) wheat in Experiment 1. The 'accepted model' is the model with the fewest parameters that could be accepted without a significant increase in residual deviance.

Accession (IG number) – sowing number	Harvest	Accepted model	Treatment	K_d ± s.e. (NED)	$1/\sigma_d$ ± s.e. (days^{-1})	K_i ± s.e. (NED)	$1/\sigma$ ± s.e. (days^{-1})	p_{50} ± s.e. (days)
89263-S1	Current ICARDA practice			-	-	8.82 ± 0.85	0.1430 ± 0.0134	61.6 ± 0.7
	1	Best fit	Delay	-	-	4.93 ± 0.72	0.0797 ± 0.0114	61.8 ± 2.1
			Immediate	-	-	-0.70 ± 0.77	0.0343 ± 0.0174	-20.5 ± 14.5
	2	Common slope	Delay	-	-	4.71 ± 1.23	0.0703 ± 0.0181	67.0 ± 5.6
			Immediate	-	-	3.40 ± 0.63	0.0703 ± 0.0181	48.4 ± 5.0
	3	One line	Delay	-	-	5.40 ± 1.01	0.0916 ± 0.0168	59.0 ± 2.2
			Immediate	-	-	5.40 ± 1.01	0.0916 ± 0.0168	59.0 ± 2.2
	4	One line	Delay	-	-	2.97 ± 0.64	0.0520 ± 0.0117	57.0 ± 4.7
			Immediate	-	-	2.97 ± 0.64	0.0520 ± 0.0117	57.0 ± 4.7

Appendix 2. *cont'd*

Appendix 2. *Continued.*

Accession (IG number) – sowing number	Harvest	Accepted model	Treatment	K_d ± s.e. (NED)	1/σ_d ± s.e. (days^{-1})	K_i ± s.e. (NED)	1/σ ± s.e. (days^{-1})	p_{50} ± s.e. (days)
46508-S1	Current ICARDA practice			-0.06 ± 0.25	0.0806 ± 0.0260	3.46 ± 0.78	0.0750 ± 0.0179	46.1 ± 2.0
	1	Common intercept	Delay	0.27 ± 0.28	0.0658 ± 0.0410	3.29 ± 0.84	0.0992 ± 0.0219	33.2 ± 2.4
			Immediate	0.27 ± 0.28	0.0658 ± 0.0410	3.29 ± 0.84	0.1265 ± 0.0117	26.0 ± 2.4
	2	Common intercept	Delay	-	-	2.42 ± 0.20	0.1030 ± 0.0072	23.5 ± 0.7
			Immediate	-	-	2.42 ± 0.20	0.1309 ± 0.0051	18.5 ± 0.7
	3	Common slope	Delay	0.27 ± 0.5	0.0284 ± 0.0198	3.99 ± 0.86	0.1025 ± 0.0185	38.9 ± 2.4
			Immediate	-1.17 ± 0.43	0.1930 ± 0.0602	2.01 ± 0.45	0.1025 ± 0.0185	19.6 ± 2.0
	Ground			-0.18 ± 0.16	0.1150 ± 0.0227	2.86 ± 0.36	0.0688 ± 0.0089	41.6 ± 1.3
46508-S2	Current ICARDA practice			-	-	1.80 ± 0.14	0.0485 ± 0.0040	37.2 ± 1.2
	1	One line	Delay	-	-	3.33 ± 0.47	0.0972 ± 0.0138	34.3 ± 1.4
			Immediate	-	-	3.33 ± 0.47	0.0972 ± 0.0138	34.3 ± 1.4
	2	Best fit	Delay	0.60 ± 0.10	0.0114 ± 0.0083	4.94 ± 0.51	0.1325 ± 0.0114	37.3 ± 1.1
			Immediate	0.60 ± 0.10	0.0566 ± 0.0142	4.07 ± 0.19	0.1325 ± 0.0114	30.7 ± 0.7
	3	Common slope	Delay	-	-	3.00 ± 0.76	0.0787 ± 0.0185	38.1 ± 2.6
			Immediate	-	-	1.52 ± 0.38	0.0787 ± 0.0185	19.4 ± 2.9
	Ground			-	-	3.04 ± 0.20	0.0856 ± 0.0054	35.5 ± 0.7
46508-S3	Current ICARDA practice			-	-	3.03 ± 0.28	0.0693 ± 0.0068	43.7 ± 1.0
	1	One line	Delay	-	-	3.62 ± 0.41	0.1033 ± 0.0118	35.1 ± 1.1
			Immediate	-	-	3.62 ± 0.41	0.1033 ± 0.0118	35.1 ± 1.1
	2	Common slope	Delay	0.48 ± 0.13	0.0282 ± 0.0106	5.88 ± 0.75	0.1543 ± 0.0177	38.1 ± 1.0
			Immediate	0.48 ± 0.13	0.0282 ± 0.0106	4.64 ± 0.23	0.1543 ± 0.0177	30.1 ± 1.1
	3	Common slope	Delay	-	-	2.75 ± 0.23	0.0635 ± 0.0052	43.4 ± 1.0
			Immediate	-	-	1.72 ± 0.23	0.0635 ± 0.0052	27.1 ± 1.2
	Ground			-	-	2.15 ± 0.21	0.0597 ± 0.0058	36.1 ± 1.3

Appendix 3. Mean seed moisture content (%, wet basis) of samples of durum and wild wheats in experimental storage (Experiment 2). Mean values with the same letter are not significantly different ($P > 0.05$). See table 2 for accession and treatment codes.

Treatment	T1S2	T2S4	T2S5	T3S1
Current ICARDA protocol	8.8 b	9.4 c,d,e	9.7 d	10.4 b
Delay 1	9.1 c	8.8 a	9.3 a	10.4 b
Immediate 1	10.2 f	9.6 e	9.8 e	9.6 a
Delay 2	8.3 a	9.5 d,e	9.5 c	10.4 b,c
Immediate 2	9.4 d,e	9.4 c,d	9.9 e	10.6 c,d
Delay 3	8.4 a	9.2 b	9.4 b	10.6 d
Immediate 3	9.7 e	9.8 f	9.8 e	10.6 d
Delay 4	8.4 a	9.4 b,c	9.7 d	-
Immediate 4	9.3 c,d	9.6 e	9.7 d	-
Overall Mean	**9.1**	**9.4**	**9.6**	**10.4**

Appendix 4. Estimates of seed longevity and dormancy breaking (where appropriate) parameters (Equations 1 and 2) for seeds of *Triticum turgidum* subsp. *durum* (89263-S2); *T. turgidum* subsp. *dicoccoides* (46508-S4 and -S5) and *T. monococcum* subsp. *boeoticum* (44857-S1) (Experiment 2). The 'accepted model' is the model with the fewest parameters that could be accepted without a significant increase in residual deviance.

Accession (IG number) – sowing number	Harvest	Accepted model	Treatment	K_d ± s.e. (NED)	$1/\sigma_d$ ± s.e. (days^{-1})	K_i ± s.e. (NED)	$1/\sigma$ ± s.e. (days^{-1})	p_{50} ± s.e. (days)
89263-S2	Current ICARDA practice			-	-	6.35 ± 0.74	0.0666 ± 0.0085	95.3 ± 1.8
	1	Common slope	Delay	-	-	6.90 ± 0.59	0.0872 ± 0.0072	79.1 ± 1.3
			Immediate	-	-	6.06 ± 0.17	0.0872 ± 0.0072	69.5 ± 1.4
	2	Common slope	Delay	-	-	6.78 ± 0.39	0.0780 ± 0.0046	86.9 ± 1.1
			Immediate	-	-	5.67 ± 0.12	0.0780 ± 0.0046	72.8 ± 1.0
	3	Common slope	Delay	-	-	7.31 ± 0.48	0.0812 ± 0.0055	90.1 ± 1.1
			Immediate	-	-	5.94 ± 0.13	0.0812 ± 0.0055	73.1 ± 1.0
	4	Common intercept	Delay	-	-	5.65 ± 0.27	0.0602 ± 0.0033	93.8 ± 1.1
			Immediate	-	-	5.65 ± 0.27	0.0735 ± 0.0010	76.8 ± 0.7

Appendix 4. *cont'd*

Appendix 4. *Continued.*

Accession (IG number) – sowing number	Harvest	Accepted model	Treatment	K_d ± s.e. (NED)	1/σ_d ± s.e. (days^{-1})	K_i ± s.e. (NED)	1/σ ± s.e. (days^{-1})	p_{50} ± s.e. (days)
46508-S4	Current ICARDA practice			-	-	4.18 ± 0.53	0.0619 ± 0.0092	67.5 ± 2.4
	1	Best fit	Delay	-	-	3.25 ± 0.47	0.0465 ± 0.0086	70.0 ± 3.9
			Immediate	-	-	7.09 ± 1.04	0.1353 ± 0.0191	52.5 ± 1.1
	2	Best fit	Delay	-	-	3.89 ± 0.38	0.0557 ± 0.0066	69.7 ± 2.1
			Immediate	-	-	6.04 ± 0.66	0.1038 ± 0.0115	58.1 ± 0.8
	3	One line	Delay	-	-	3.97 ± 0.40	0.0655 ± 0.0069	60.7 ± 1.6
			Immediate	-	-	3.97 ± 0.40	0.0655 ± 0.0069	60.7 ± 1.6
	4	One line	Delay	0.38 ± 0.13	0.1084 ± 0.0179	4.28 ± 0.33	0.0793 ± 0.0062	53.9 ± 1.0
			Immediate	0.38 ± 0.13	0.1084 ± 0.0179	4.28 ± 0.33	0.0793 ± 0.0062	53.9 ± 1.0
46508-S5	Current ICARDA practice			-	-	4.14 ± 0.31	0.0744 ± 0.0058	55.6 ± 1.0
	1	Common slope	Delay	-	-	4.12 ± 0.22	0.0606 ± 0.0037	68.0 ± 1.5
			Immediate	-	-	2.99 ± 0.11	0.0606 ± 0.0037	49.5 ± 1.1
	2	Best fit	Delay	-	-	3.40 ± 0.54	0.0447 ± 0.0096	76.0 ± 5.4
			Immediate	-	-	2.96 ± 0.61	0.0575 ± 0.0113	51.5 ± 1.9
	3	One line	Delay	0.954 ± 0.384	0.168 ± 0.156	3.83 ± 0.21	0.0690 ± 0.0040	55.6 ± 2.8
			Immediate	0.954 ± 0.384	0.168 ± 0.156	3.83 ± 0.21	0.0690 ± 0.00399	55.63 ± 2.84
	4	One line	Delay	0.413 ± 0.33	0.1084 ± 0.0179	3.30 ± 0.16	0.06768 ± 0.00333	53.85±1.0119
			Immediate	0.413 ± 0.33	0.1084 ± 0.0179	3.30 ± 0.16	0.06768 ± 0.00333	53.85±1.0119
44857-S1	Current ICARDA practice			-	-	4.48 ± 0.44	0.0709 ± 0.0076	63.1 ± 1.4
	1	Common intercept	Delay	-	-	4.01 ± 0.40	0.0715 ± 0.0076	56.0 ± 1.9
			Immediate	-	-	4.01 ± 0.40	0.1136 ± 0.0060	35.3 ± 1.2
	2	Best fit	Delay	-	-	4.74 ± 0.61	0.0778 ± 0.0106	60.9 ± 1.5
			Immediate	-	-	25 ± 3306	0.6 ± 76.9	41.1
	3	Best fit	Delay	-	-	2.24 ± 0.20	0.0382 ± 0.0043	58.6 ± 2.4
			Immediate	-	-	4.77 ± 0.55	0.1456 ± 0.0163	32.8 ± 0.7

Appendix 5. Ability to germinate and moisture content of *Triticum turgidum* subsp. *durum* seeds from successive harvests after initial drying and after a further 28 days in the drying room (DR, 15°C, 15% RH) (Experiment 3).

Harvest (days after heading)	Germination (%)	Moisture content (%)	Initial drying regime	Moisture content (%)		Germination (%)	
	At Harvest			after 3 days	after 28 days	after 3 days	after 28 days
21	73	54	DR (15°C)	39.6	5.7	93	80
			LAB (23-27°C)	42.5	5.3	83	100
			Incubator (30°C)	36.8	5.5	81	73
35	45	14	DR (15°C)	8.6	5.7	42	66
			LAB (23-27°C)	8.6	5.4	40	72
			Incubator (30°C)	7.3	5.4	45	69
41	99	8	DR (15°C)	6.6	5.4	96	94
			LAB (23-27°C)	6.1	5.7	96	98
			Incubator (30°C)	5.8	5.4	92	99
48	92	7	DR (15°C)	6.2	5.4	95	99
			LAB (23-27°C)	5.9	5.6	94	98
			Incubator (30°C)	5.3	5.3	93	95

Appendix 6. Estimates of seed longevity parameters of the seed viability equation for seeds of *Triticum turgidum* subsp. *durum* (89263-S3) from successive harvests after initial drying in different regimes (Experiment 3). The 'accepted model' is the model with the fewest parameters that could be accepted without a significant increase in residual deviance. Where the common slope and common intercept models were both acceptable, the former was selected.

Harvest (days after heading)	Accepted model	Treatment	K_i ± s.e. (NED)	1/σ ± s.e. (days^{-1})	p_{50} ± s.e. (days)
21	Common slope	Incubator	2.41 ± 0.41	0.0761 ± 0.0121	31.7 ± 3.4
		Drying room	1.23 ± 0.34	0.0761 ± 0.0121	16.1 ± 3.8
		Laboratory	2.27 ± 0.44	0.0761 ± 0.0121	29.8 ± 3.7
35	One line	Incubator	1.42 ± 0.21	0.0429 ± 0.0054	33.1 ± 2.6
		Drying room	1.42 ± 0.21	0.0429 ± 0.0054	33.1 ± 2.6
		Laboratory	1.42 ± 0.21	0.0429 ± 0.0054	33.1 ± 2.6
41	Common slope	Incubator	4.43 ± 0.93	0.0936 ± 0.0095	45.6 ± 2.2
		Drying room	5.97 ± 0.62	0.0936 ± 0.0095	63.8 ± 1.8
		Laboratory	5.92 ± 0.07	0.0936 ± 0.0095	63.3 ± 1.7
48	Common slope	Incubator	5.03 ± 0.23	0.0920 ± 0.0084	54.6 ± 1.9
		Drying room	5.28 ± 0.51	0.0920 ± 0.0084	57.4 ± 1.7
		Laboratory	4.37 ± 0.25	0.0920 ± 0.0084	47.5 ± 1.9

Appendix 7. Relative humidity (%) in the field from data loggers outside (Ambient) and inside the cloth bag during the harvesting period for Experiments 1 (2017-2018) and 2 (2018-2019)

Date	Ambient (outside cloth bag)				Inside cloth bag			
	Mean	Max	Min	(Max)-(Min)	Mean	Max	Min	(Max)-(Min)
Experiment 1								
31/5/2018	35	39	26	13	44	82	14	68
1/6/2018	46	82	27	55	66	89	28	61
2/6/2018	57	100	14	86	59	91	15	76
3/6/2018	53	100	16	84	55	86	12	74
4/6/2018	62	99	15	84	55	83	9	74
5/6/2018	49	99	13	86	50	90	7	83
6/6/2018	47	88	16	72	63	99	6	93
7/6/2018	22	45	17	28	60	99	16	83
8/6/2018	30	54	13	41	56	100	20	80
9/6/2018	32	52	15	37	55	95	22	73
10/6/2018	44	47	17	30	57	94	21	73
11/6/2018	54	44	20	24	61	100	21	79
Mean	**44**	**71**	**17**	**53**	**57**	**92**	**16**	**76**
Experiment 2								
7/6/2019	33	62	8	54	37	70	17	53
8/6/2019	37	61	12	49	40	72	20	52
9/6/2019	44	71	16	55	47	83	23	60
10/6/2019	54	88	17	71	60	90	22	68
11/6/2019	47	63	19	44	54	72	25	47
12/6/2019	56	83	11	72	53	77	21	56
13/6/2019	46	77	12	65	55	80	19	61
14/6/2019	43	73	15	58	52	77	21	56
15/6/2019	50	81	13	68	55	84	17	67
16/6/2019	47	78	14	64	53	88	21	67
17/6/2019	45	88	15	73	55	93	18	75
18/6/2019	28	43	8	35	39	64	15	49
19/6/2019	31	46	10	36	40	52	17	35
20/6/2019	32	45	17	28	43	50	20	30
21/6/2019	38	56	20	36	40	53	25	28
22/6/2019	38	56	22	34	43	65	25	40
23/6/2019	37	54	19	35	40	68	23	45
24/6/2019	32	51	11	40	37	55	16	39
25/6/2019	33	51	9	42	45	64	13	51
26/6/2019	35	48	12	36	47	55	16	39
27/6/2019	32	50	15	35	45	61	21	40
28/6/2019	38	43	17	26	43	58	19	39
29/6/2019	37	45	20	25	44	55	22	33
30/6/2019	33	40	19	21	37	53	20	33
1/7/2019	38	43	18	25	42	57	22	35
2/7/2019	34	40	16	24	40	51	20	31
3/7/2019	37	42	18	24	39	47	21	26
4/7/2019	32	37	15	22	37	53	18	35
Mean	**39**	**58**	**15**	**43**	**45**	**66**	**20**	**46**