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Development of ability to germinate and of longevity in air-dry storage in wheat seed crops subjected to rain shelter or simulated supplementary rainfall

Running title. Rain, shelter and wheat seed quality development

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Keywords: development, germination, longevity, rain, *Triticum aestivum* L., viability, wheat

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Abstract

Climate change will alter rainfall patterns. The effect of rainfall during seed development and maturation on wheat (*Triticum aestivum* L.) seed quality (ability to germinate normally; air-dry longevity in hermetic storage at 40^{o}C with c. 15% moisture content) was investigated in field experiments (2011, 2012) by providing rain shelter or simulating additional rainfall. High ability to germinate was detected from mid seed filling until after harvest maturity. Subsequent longevity was more sensitive to stage of development. It increased progressively reaching maximum values during maturation drying at 53-56 DAA, 5-11 (2011) or 8-14 (2012) days beyond mass maturity; maximal values were maintained thereafter in 2011; longevity declined with further delay to harvest in 2012. Post-anthesis protection from rain had no major effect: in later harvests longevity was slightly greater than the control in each year, but in 2011 wetting treatments were also superior to the control. Wetting ears at all stages of development reduced longevity immediately, but considerable recovery in subsequent longevity occurred when seeds re-dried *in planta* for several days. The greatest damage to longevity from ear wetting occurred with treatments at about 56 DAA, with poorest recovery at 70 DAA (i.e. around harvest maturity) in absolute terms but at 56-70 DAA relative to gross damage. Hence, seed quality in highly-dormant wheat varieties was resilient to rain. Net damage was greatest from rain late in maturation. The phase of seed quality improvement *in planta* was dynamic with deterioration also occurring then, but with net improvement overall.

Keywords: development, germination, longevity, rain, *Triticum aestivum* L., viability, wheat

Introduction

Climate change will increase mean global temperature, but will also affect future rainfall patterns with more intense and more frequent extreme precipitation events (Intergovernmental Panel on Climate Change, 2014). Indeed, during the 20th century precipitation increased by some 10–40% across northern Europe (Klein Tank *et al*., 2002). Seed quality is influenced by environment during seed development and maturation (Gusta *et al*., 2004; Hampton *et al*., 2013). Rainfall and temperature are the main environmental factors affecting crop yield and quality of wheat (*Triticum aestivum* L.) in the periods preceding harvest (Smith and Gooding, 1999; Landau *et al*., 2000; Yadav and Ellis, 2016).

Warmer temperatures in the UK improve wheat seed quality development (Sanhewe *et al*., 1996), whereas rainfall incident upon developing seed crops in cool, wet summers has long been reported to be deleterious to UK wheat seed quality (MacKay, 1972). At the extreme, heavy or prolonged rainfall to wheat varieties with low dormancy results in visible sprouting (Flintham, 2000) - and so poor seed quality.

Simulated rainfall to developing wheat seed crops in the UK reduced the subsequent air-dry longevity of seeds harvested soon afterwards (Ellis and Yadav, 2016). That study showed that damage to longevity could be detected from a single rainfall event insufficient to promote sprouting, but also that this immediate damage was reversed *in planta* when harvest was delayed and seeds re-dried.

Post-harvest wetting of mature seed can benefit seed survival (Villiers and Edgecumbe, 1975). Seed hardening (a wetting and drying cycle) has long been applied by farmers in advance of sowing, but the effects of such wetting treatments (e.g. priming) have

been reported to both reduce (e.g. Argerich *et al.*, 1989; Tarquis and Bradford, 1992) and improve longevity (e.g. Georghiou *et al.*, 1987; Probert *et al.*, 1991). Priming post-harvest has also been shown to improve subsequent longevity when applied to immature seed but to reduce longevity in seeds closer to maturity (Demir and Ellis, 1992a). Hence the effect of rainfall on longevity may vary with stage of seed development.

We report here the effect of either rain shelter or additional simulated rainfall on seed quality, assessed by ability to germinate normally with or without desiccation and by longevity in air-dry storage, on seed crops of wheat in two years. The null hypotheses of (a) no effect of rainfall on subsequent seed quality assessed by both ability to germinate normally and by subsequent air-dry seed storage longevity, where the latter is the more sensitive to discriminate amongst high–quality seed lots in seed development studies (Pieta-Filho and Ellis, 1991), and (b) no interaction with developmental stage were tested. Accordingly, treatments were applied at different stages of, and for different durations during, seed development and maturation. Wheat seed quality improves throughout seed development and maturation reaching maximum values at or approaching harvest maturity (Ellis and Pieta Filho, 1992), where harvest maturity is typically 15% seed moisture content (but can vary from 12-20% depending upon ambient relative humidity). Hence, the response to treatments was assessed against those developmental changes within control crops.

Materials and methods

Crops of wheat (*Triticum aestivum* L.) cv. Tybalt were grown from March to August 2011 and similarly in 2012 in the field at the University of Reading, Crop Research Unit (CRU), Sonning (51°30' N, 00 °54' W), in split-plot designs. The main plots (each 7.5 m x 2.5 m)

were the open, sheltered (protection from rainfall), or wetted (additional simulated rainfall) treatments allocated at random within each block, with serial seed harvest dates as subplots. Full details of agronomy, weather, rain shelter construction, dynamics of seed filling and desiccation, and resultant crop quality are provided by Yadav and Ellis (2016). Rain shelter was provided by polythene covers (2m x 5m, 1.5m tall) - twice the height of the crop and open at the sides to aid air circulation and reduce the possibility of temperature build-up above the crop canopy. Simulated rainfall treatments were provided to an area of 1.5m x 4m marked by bamboo canes at the centre of those plots. The developing ears were wetted with (tap) water equivalent to 2.5 cm rainfall on each occasion in two halves with a 30 minutes gap, as described by Ellis and Yadav (2016).

The 2011 investigation comprised 22 main plots (11 treatments in each of two blocks). One treatment was untreated and always open to rainfall (C1O; open control) and one covered by full rain shelter from 50% anthesis until the last harvest (C2S; sheltered control). Four treatments were provided with rain shelter for 14 day periods at 0-14 days after 50% anthesis (DAA) (S1), 14-28 DAA (S2), 28-42 DAA (S3), or 42-56 DAA (S4). A further five treatments were provided with simulated rain: four were ear wetting treatments at 7 DAA (W1), 21 DAA (W2), 35 DAA (W3), or 49 DAA (W4); the fifth was wetted four times, i.e. at 7, 21, 35 and 49 DAA (W5; wetting control). Samples from treatments subjected to ear wetting that day were drawn 30 min after treatments ended.

Samples of seeds from each treatment were harvested serially by cutting 100 ears from about 0.5 m^2 with scissors at about 1-2 cm below the spikes on up to nine occasions (depending upon when a treatment began) during seed development and maturation, from 14 DAA on 23 June and then 25, 32, 39, 46, 53, 60, 67 and finally 74 DAA. The first two

harvests (14 and 25 DAA) comprised six treatments, those on 32 and 39 DAA nine, and thereafter all 11 treatments from each block.

In 2012, there were 20 main plots (ten treatments in each of two blocks). One treatment was always open to rainfall (C1O; open control) and one covered by full rain shelter from 50% anthesis until the last harvest (C2S; sheltered control). The three temporary rain shelter treatments were applied later in development than in 2011 and also differed in duration: S1 (42-70 DAA), S2 (42-56 DAA) and S3 (56-70 DAA). The five ear wetting treatments were also applied later than in 2011: at 42 DAA (W1), 49 DAA (W2), 56 DAA (W3), 63 DAA (W4), or 70 DAA (W5). Samples of seeds from each treatment were harvested serially on up to ten occasions during seed development and maturation: the first four harvests (14, 21, 28 and 35 DAA) comprised two treatments, those on 42, 49, 56, 63 and 70 DAA 5, 6, 8, 9 and 10 treatments, respectively, and an additional sample was drawn 30 min after wetting treatments ended from each block. In the case of W5, the last wetting treatment, a sample was also taken at 77 DAA in order to provide a sample 7 days after wetting for this treament also. In 2012, samples were taken shortly before each wetting as well as 30 min after treatments ended. The results for ability to germinate and subsequent longevity for samples harvested 30 min after wetting treatments ended are designated W (af) to distinguish these treatments' immediate effect from results immediately before wetting.

Samples were harvested between 7 and 9 a.m. and seeds threshed from ears by hand. Throughout the study, seeds from the same treatment but from different blocks were analysed separately. With the exception of samples drawn to determine the moisture content [results reported previously by Yadav and Ellis (2016)] and ability to germinate of freshly-harvested

seed, samples were dried to 10-14% moisture content (wet basis) in a drying cabinet maintained at 15-17°C with 12-15% relative humidity. Decline in seed sample weight was monitored as a proxy for moisture content during drying. Drying period varied between extremes of 2 to 21 days amongst samples, depending upon stage of development and hence initial seed moisture content. Samples were then drawn to determine seed moisture content and ability to germinate after drying. The remainder of each sample was sealed in a laminated-aluminium-foil bag (Retort laminate, Moore and Buckle Ltd, St Helens, UK) and stored temporarily at -20^{o}C.

Ability to germinate was tested for two replicates of 50 seeds each between moist rolled paper towels (Kimberley Clark Professional 6803 HOSTESS, Natural, 24 x 35 cm, Greenham Sales, UK) in an incubator at 10°C. Tests were monitored for germination at 7 day intervals up to 28 days. Seedlings were evaluated as normal, abnormal or dead seeds according to the ISTA rules (International Seed Testing Association, 2011). Seeds that had not germinated after 28 days were pricked in order to break any possible dormancy and tests continued until all seeds had either germinated or were no longer fresh (i.e. dead).

Seed moisture content was determined using the two-stage or the single-stage high-constant-temperature-oven method (International Seed Testing Association, 2011), depending upon expected moisture content; two 100 seed replicates were used in place of two 4-5 g samples due to limited seed supply.

Seed storage longevity was determined in a constant hermetic environment of 40^{o}C with c. 15% moisture content. Seed packets were withdrawn from storage at -20^{o} C about

four months after harvest. They were first exposed to laboratory temperature within the sealed packets for 24 hours to avoid moisture condensing on seed surfaces. Seed moisture content was then estimated indirectly using a non-destructive equilibrium relative humidity (erh) water activity meter (65% relative humidity at 20°C being the common target for all the seed samples). In order to adjust seed moisture content to 15% (±0.5%), samples were weighed and either placed in a muslin bag to dry at 15°C, 15% relative humidity, or humidified at 20°C above deionised water, depending upon estimated initial moisture content. This adjustment was controlled by weighing repeatedly and determining erh until the desired weight/erh was reached. To enable moisture to equilibrate within and amongst samples, the separate muslin bags were placed together for 15 days in a sealed container at 2-4^{o}C.

The moisture content of each seed sample was then determined using the high-constant-temperature-oven method (ISTA, 2011). Estimates ranged between extremes of 14.1 and 15.7% in 2011 (mean 15.0%) and 14.2 and 15.6% in 2012 (mean 14.7%). Ten subsamples of 100 seeds from each sample were sealed in separate laminated-aluminium-foil packets and stored in an incubator maintained at 40°C. One sample from each treatment was withdrawn from storage after different periods (0 - 49 days) of experimental storage and tested for ability to germinate. Seed survival curves in hermetic storage at 40^{o}C with 15% moisture content were fitted by probit analysis for each sample in accordance with the seed viability equation (Ellis and Roberts, 1980):

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

where v is probit percentage viability after p days in storage in a constant environment, K_i is a constant specific to seed lot (equivalent to initial probit viability), and σ is the standard deviation of the frequency distribution of seed deaths in time (days) using Genstat (13th Edition, VSN International Ltd., UK). The product of K_i and σ is the period for viability to decline to 50% (p_{50}). The ability of a seed to produce a normal seedling was the criterion of survival. Genstat was also applied to compare seed survival curves.

Results

Fifty per cent anthesis occurred on 8 June 2011 (84 days after sowing) or 18 June 2012 (95 days after sowing), when the first rain shelters were installed (e.g. C2S). Sheltered plots provided mean temperatures 0.8 to 0.9 ^{o}C warmer than control plots in both years, with 90.2% direct light and 84.6 % photosynthetically-active radiation. Both years provided post-anthesis environments wetter and cooler than long-term site means, with 2011 cooler and wetter than 2012 on average.

The treatments affected seed filling duration in 2011, only, and towards harvest maturity in both years (Table 1). In 2011, seed filling durations were reduced by rain shelter throughout (C2S) or late within this period (S3). Durations from anthesis to (almost) harvest maturity were reduced by shelter throughout (C2S in 2011 and 2012) or during late maturation drying (S1, S3 in 2012) but only increased by multiple simulated rainfall events (2011, W5). Seed moisture contents were 2-5% greater 30 min after ear wetting, the only exception being a 10% increase in W5, 2011 at 21 DAA, with control values regained in subsequent harvests (Yadav and Ellis, 2016).

Ability to germinate

No pre-harvest sprouting was detected in any treatment. Ability to germinate normally improved greatly amongst early harvests, when it also benefited from post-harvest drying (Figs 1, 2). From 32-74 DAA in 2011, all treatments provided 100% normal germination for dried seed samples (Figs 1c, d). Ability to germinate without post-harvest drying was slightly lower during this period, but also more variable; a marked decline (P<0.001) occurred from 39-53 DAA with subsequent reversal from 53-67 DAA in 2011 (Figs 1a, b). This contrasted with 100% normal germination throughout for dried seeds (Figs 1c, d). Ability to germinate normally was also greater with post-harvest drying in 2012 from 35-70 DAA (Fig. 2), but in this case slightly more variation was apparent amongst treatments with lower values during S3 shelter (56-70 DAA; Fig. 2c) and 30 min after ear wetting ended in W2 (49 DAA) and W3 (56 DAA) (Fig. 2d).

Longevity

The seed survival curves were sigmoidal, conformed to negative cumulative normal distributions, and described well by Equation (1). In each year, seed survival curve comparisons showed significant differences in K_i (P <0.001) and σ (P <0.001). The major differences in longevity (p_{50}) resulted from differences in estimates of K_i. There was a clear main effect of harvest date on longevity (P <0.001). This main effect provided a somewhat erratic pattern of considerable improvement in longevity until 53 DAA, but with a plateau between 32 and 46 DAA, in 2011 (Fig. 3) or 56 DAA in 2012 (Fig. 4). A further difference amongst years occurred after maximum longevity was first attained: longevity declined after 56 DAA in 2012, but was stable between 53 and 74 DAA in 2011.

The treatments had comparatively little effect on the development of longevity in 2011, other than that shelter throughout (C2S) may have been in advance of the control (C1O) early on, with close agreement amongst treatments at 53 DAA when maximum longevity was first attained (Figs 3a, b). It is also noteworthy that longevity 21 days later at 74 DAA after all five wetting treatments (W1-W5) was not only slightly greater than the control (C1O) but also similar to shelter throughout (C2S).

Longevity for shelter throughout (C2S) improved in advance of the control (C1O) at 28 and 35 DAA in 2012 (Fig. 4a). Moreover, from 56 to 70 DAA longevity was greater from all shelter treatments than the control. Wetting reduced longevity immediately, as shown by comparisons between W (af) and C1O (Fig. 4b). However, W(af) is not one treatment *per se* but a compilation of all wetting treatments' results 30 min after the treatments ended; after a further 7 or more days *in planta* all wetting treatments completed by then provided similar longevity at 56 DAA to the control, and only two subsequent wetting treatment observations were below control values (W2 at 63 DAA; W3 at 70 DAA).

To investigate the effect of the timing of ear wetting more closely, Figure 5 provides a compilation of the 2012 results for longevity immediately before and 30 min after ear wetting treatments ended, and after a further 7 days *in planta* for treatments applied up to 28 days apart late in maturation. Subsequent air-dry longevity was reduced 30 min after wetting in each of the five wetting treatments, to a similar extent in W2-W5 but to about half this extent in the earliest treatment W1 (42 DAA), but 7 days *in planta* thereafter resulted in improvement to longevity in every treatment. These reductions and subsequent improvements in p_{50} resulted from changes in the estimates of K_i and to a lesser extent σ. For each ear

wetting treatment, the difference between the first and second samples (vertical broken line in Fig. 5) provides an estimate of the immediate (gross) damage to seed quality (as assessed by longevity) from simulated rainfall, whilst that between the second and third samples (solid line in Fig. 5) the reversal of that damage over 7 days. The difference between the first and third samples provides an estimate of net damage from simulated rainfall, therefore. The magnitude of the initial damage to longevity from simulated rainfall and the subsequent improvement (difference between second and third samples), in (a) absolute terms and (b) relative to the gross (immediate) damage from wetting, showed clear patterns over developmental time amongst treatments about a fulcrum at 56 DAA (when longevity reached maximum values, Fig.4). Gross damage showed a consistent pattern where W1 < W2 < W3 = W4 >W5; for the subsequent improvement in absolute terms, least in W1 and W5, greatest in W2, and about a quarter of W2 in both W3 and W4. In relative terms, the improvement was similar to initial (gross) damage in W1, more than twice as great in W2, but just under half of the gross damage in W3 - W5.

Discussion

The general temporal pattern of development in the ability of seeds to germinate during seed development and maturation was similar in the two years, and largely as expected in wheat (Ellis and Pieta Filho, 1992). Onset of ability to germinate and of desiccation tolerance was apparent from the first harvest (14 DAA) early in the seed-filling phase (Figs 1, 2), at which time seeds were only about 10% filled (Ellis and Yadav, 2016), with full or close to full ability to germinate achieved 70-80% through the seed-filling phase – and so well before mass maturity [end of the seed-filling phase (Ellis and Pieta-Filho, 1992)]. Post-harvest drying early in seed development promoted ability to germinate. Such improvements from

drying immature seeds are well known (Dasgupta *et al.*, 1982; Bewley and Black, 1994). The effect was equivalent to several days of further development *in planta*, which drying *ex planta* mimics to a certain extent. No decline in ability to germinate normally of the dried seeds was detected amongst harvests later in development and maturation in either year, despite sampling until 74 DAA (extremes of 32 days after mass maturity, or 13 days after seeds dried to 20% moisture content; Table 1).

Testing ability to germinate at 10 ^{o}C combined with pricking minimized dormancy limiting germination, as expected in temperate cereals (Ellis *et al*., 1987). Nevertheless, the results for freshly-harvested seeds harvested between 39 and 67 DAA in 2011 showed first a decline and then an increase in ability to germinate, whereas seeds first dried showed 100% throughout this period (Fig. 1). This represents late induction and subsequent loss in wheat seed dormancy (Mitchell *et al.*, 1980; Gooding *et al.*, 2012). In sorghum (*Sorghum bicolor* L.), Fenner (1991) noted that plant water status during seed filling affected dormancy. No consistent effect on dormancy induction and loss pattern was detected here, however, with the extreme opposite treatments of shelter (S1, S2) or wetting (W1, W2, W3) during seed filling both providing greater dormancy than the control (Fig. 1).

Seed longevity can be a more sensitive indicator of differences in seed quality than ability to germinate amongst high quality seed lots (Ellis and Roberts, 1981). This was the case here with substantial differences in seed longevity identified (Figs 3, 4) amongst the high-viability samples (Figs 1, 2) harvested from 25 (2011) or 35 DAA (2012) onwards. Prior to this, both approaches provided a consistent increase in seed quality but whereas ability to germinate then reached maximum values longevity showed continued improvement thereafter, albeit not linear, with further development. Subsequent longevity first reached

maximum values during the maturation drying phase at 53-56 DAA (Figs 3, 4), some 5-11 (2011) or 8-14 (2012) days after mass maturity and 9-23 (2011) or 1-18 days before seed moisture content declined *in planta* to 20% (Table 1). This confirms earlier studies in barley (*Hordeum vulgare* L.) and wheat in which subsequent longevity continued to improve, and considerably so, beyond the end of the seed-filling phase (Pieta Filho and Ellis, 1991; Ellis and Pieta Filho, 1992; Sanhewe *et al*., 1996; Ellis and Yadav, 2016).

Longevity remained high, possibly improving a little, from 53 DAA until the last harvest at 74 DAA in 2011 (Fig. 3) but declined, more or less linearly and consistently, between 56 and 70 DAA in 2012 (Fig. 4). A somewhat similar difference between years was reported in a study with barley: longevity declined immediately after improvement ended in 1988, whereas in the warmer, drier 1989 longevity was maintained at high values for around 14 days, before then declining (Pieta Filho and Ellis, 1991). Decline in longevity after attaining maximum values was detected in wheat in both 2008 and 2009 and was steeper in the wetter and marginally (only 0.1 ^{o}C) cooler 2008 than in 2009 (Ellis and Yadav, 2016). However, the potential assumption that warmer, drier conditions reduce decline in longevity with delay to harvest is not borne out by the current results, because August 2011 was appreciably wetter and cooler than August 2012 (Yadav and Ellis, 2016). Hence, the assumption that seeds deteriorate post peak-longevity more rapidly the wetter the environment is not supported consistently by these inter-annual comparisons.

A similar lack of clarity for the effect of rainfall is provided by comparison within years between shelter and ear wetting treatments amongst later harvests. In 2011, longevity in the ear wetting treatments (at 7 - 49 DAA) from 54 DAA onwards was similar to or perhaps

greater than the control (Fig. 3b), but this was also the case for the rain shelter treatments (Fig. 3a). In 2012, the later harvests (56 DAA onwards) provided consistently greater longevity with shelter than the control (Fig. 4a) and while longevity 30 min after wetting (at 42 - 70 DAA, and so applied later than 2011) was reduced, thereafter most wetting treatments provided longevity similar to the control (Fig. 4b). Differences in longevity amongst treatments were slightly greater in 2012 (Fig. 4) than in 2011 (Fig. 3), perhaps because the majority of treatments were applied later, deliberately, during seed development and maturation in 2012. The greater effect of treatments applied later tallies with differences detected amongst previous years (Ellis and Yadav, 2016), but that comparison was confounded with that between field and protected environments.

Generally, therefore, it would appear that rainfall events result in gross damage to subsequent longevity at all stages of development and maturation, but that the damage is reversed *in planta* in whole or in part thereafter such that there is often little or no net damage. Net damage may be detected from rainfall in the period approaching harvest maturity and thereafter (W3-W5, Fig. 5), however, especially if it is repeated rainfall (Ellis and Yadav, 2016). Moreover, there is a clear trend with respect to developmental stage: simulated rainfall early-mid development is less damaging initially and is more likely to be entirely reversed thereafter *in planta*, than from late maturation drying onwards. Hence, net damage to seed quality from rainfall is more likely in the period approaching harvest maturity and thereafter than earlier in seed development. The comparatively limited net damage from ear wetting may help to explain the absence of any consistent effect of rain shelter versus wetting and control treatments amongst the final samples harvested between the years. It also agrees with 2008 and 2009 field results in which simulated rainfall early in development delayed the pattern of seed quality improvement but only by a few days, and the more

dramatic damage but largely reversible from treatment at close to harvest maturity in a tunnel house in 2010 (Ellis and Yadav, 2016).

We suggested previously that damage to longevity from rainfall at harvest maturity and subsequent reversal *in planta* might be associated with changes to the glassy state – which may affect air-dry seed survival (Buitink and Leprince, 2004; Walters, 2015), because seeds were at 14-19 % moisture content, the gross damage occurred rapidly, and subsequent recovery was within 24 h (Ellis and Yadav, 2016). Whilst we continue to support that argument for rainfall events close to harvest maturity in very dry seeds, the damage and reversal detected here over a longer period of 7 days and, moreover, earlier in seed development and maturation (W1-W2, Fig. 5) coincides with periods when both oligosaccharides and low molecular weight heat-stable proteins are accumulating, albeit with oligosaccharide accumulation more prevalent during development and heat-stable protein accumulation more during maturation drying (Sinniah *et al*., 1998), and both benefit subsequent air-dry seed survival (e.g., Crowe *et al*., 1984; Galau et al., 1986; Leopold, 1990). A recent network analysis of the co-expression of a considerable number of regulatory genes, associated with seed longevity, during seed development and maturation in *Medicago truncatula* L. confirms there is a substantial temporal pattern of expression of different genes, but that gene expression can be detected quite late when moisture content is only c. 20% (Righetti *et al*., 2015). Hence, it is possible that the drivers of both the damage to longevity from rainfall and its subsequent reversal may differ depending upon when during seed development and maturation the rainfall event occurs. If so, that might explain the differences in the magnitude of the gross and net responses at different stages of seed development.

This research, particularly Fig. 5 here in combination with Fig. 4 of Ellis and Yadav (2016), confirms a long-held suspicion: during the period of seed quality development from the beginning of seed filling until close to harvest maturity, the improvement in seed quality detected is net improvement whereby both improvement and deterioration occur, but the former is (usually) by far the greater. Similarly, once maximum seed quality has been attained, it is net loss in quality that is detected with, again, improvement and deterioration possible, but in this case the latter is (usually) the greater. Hence, the difference between years during late maturation drying of no appreciable change in seed quality between 53 and 74 DAA in 2011 (Fig. 3) but consistent decline from 56 to 70 DAA in 2012 (Fig. 4): in the latter deterioration was greater than improvement, whereas in the former they were almost equal, presumably, cancelling each other out. Certain earlier observations in rice (*Oryza sativa* L.) and tomato (*Lycopersicon esculentum* Mill.) may also be compatible with this interpretation. Longevity of a *japonica* rice at 32/24 ^{o}C plateaued from mass maturity onwards during the maturation drying phase, whereas longevity continued to improve over this period at 28/20 ^{o}C and in other (*indica*) cultivars in both regimes (Fig. 4a, Ellis *et al.*, 1993). We suggest that the former represents no net change, because deterioration and improvement were in balance, whereas in the latter improvement exceeded deterioration. Similarly, tomato seed survival periods were stable over a 40-day period *in planta*, within fleshy fruits, from 55 DAA, 13 d after mass maturity, to 95 DAA (Fig. 3c, Demir and Ellis, 1992b) – again representing a possible close match between rates of seed deterioration and improvement.

Greater tolerance to heat and drought stress are priorities for the genetic improvement of wheat in order to maintain future yield by adapting to climate change (Semenov *et al.*, 2014). In the UK at least, warmer summer temperatures from anticipated climate change will

benefit wheat seed quality (Sanhewe *et a1*., 1996). Wheat has long been reported to produce poor quality seed in cool, wet UK summers (MacKay, 1972) and similarly poor quality grain for bread-making purposes in wet UK summers (Smith and Gooding, 1999) as a result of germination (visible and so pre-harvest sprouting, or *sensu strictu*). The bread-making quality wheat cultivar selected for this study shows strong dormancy, in order to maintain grain quality in wet UK summers (Yadav and Ellis, 2016). Clearly, such high dormancy also provides resilience in terms of high seed quality following rainfall events in wet summers. Hence, high seed dormancy is an important character to include in breeding programmes to provide new feed, as well as quality, cultivars adapted to future NW Europe climates, in order to safeguard high quality wheat seed supplies.

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Table 1. Effect of rain shelter or ear wetting on durations to mass maturity and 20% moisture content (i.e. approaching harvest maturity) in wheat cv. Tybalt in 2011 and 2012. From Yadav and Ellis (2016).

Treatment	Duration to mass maturity (DAA)	Duration to 20% moisture content (DAA)
2011		
Control (C1O) [1]	46.3	70.0
C2S (Shelter 0-56 DAA)	41.8	62.0
S1 (Shelter 0-14 DAA)	46.1	72.5
S2 (Shelter 14-28 DAA)	46.7	72.0
S3 (Shelter 28-42 DAA)	43.6	71.0
S4 (Shelter 42-56 DAA)	46.3	69.0
W1 (Wetting 7 DAA)	45.8	72.5
W2 (Wetting 21 DAA)	48.3	71.5
W3 (Wetting 35 DAA)	48.3	70.5
W4 (Wetting 49 DAA)	46.6	71.5
W5(Wetting 7-49 DAA)	46.8	76.0
$LSD_{0.05}$	2.17	4.61
P	*0.002*	*0.007*
2012		
Control (C1O) [1]	42.8	74.0
C2S (Shelter 0-70 DAA)	45.6	56.5
S1 (Shelter 42-70 DAA)	42.8	58.0
S2 (Shelter 42-56 DAA)	48.5	74.0

S3 (Shelter 56-70 DAA)	45.3	59.0
W1 (Wetting 42 DAA)	41.8	74.0
W2 (Wetting 49 DAA)	42.3	74.0
W3 (Wetting 56 DAA)	44.6	74.0
W4 (Wetting 63 DAA)	42.3	74.0
W5 (Wetting 70 DAA)	44.6	74.0
W (30 mins after wetting)	47.1	74.0
$LSD_{0.05}$	4.92	1.49
P	*0.155*	*0.001*

[1] Open control: neither rain shelter nor ear wetting provided.

Captions to Figures

Figure 1. Ability of fresh (a, b) or dried (c, d) seeds of wheat cv. Tybalt to germinate normally when tested at 10^{o}C after harvesting at different times during seed development when grown (a, c) under rain shelter (C2S, S1, S2, S3, S4) or (b, d) with ear wetting (W1, W2, W3, W4, W5) compared with a control (C1O; no shelter or ear wetting) in 2011. C2S is the equivalent shelter control, with rain shelter provided from 50% anthesis until the last harvest.

Figure 2. Ability of fresh (a, b) or dried (c, d) seeds of wheat cv. Tybalt to germinate normally when tested at 10^{o}C after harvesting at different times during seed development when grown (a, c) under rain shelter (C2S, S1, S2, S3) or (b, d) with ear wetting (W1, W2, W3, W4, W5, Waf) compared with a control (C1O; no shelter or ear wetting) in 2012. C2S is the equivalent shelter control, with rain shelter provided from 50% anthesis until the last harvest. Note that Waf is not a separate treatment: it represents the results of samples harvested 30 min after ear wetting, once, on the day shown (to distinguish it from that treatment's harvest just before wetting that day).

Figure 3. Improvement in subsequent air-dry seed storage longevity (p_{50}, days, provided by probit analysis), in hermetic storage at 40°C with c. 15% moisture content, during seed development in wheat cv. Tybalt in 2011 comparing amongst rain shelter (a) or ear wetting treatments (b)**.** Standard errors of estimates shown (but largely similar to or smaller than symbols). Control treatment results (C10) are shown in both a and b. Further details as Figure 1.

Figure 4. Improvement, and later decline, in subsequent air-dry seed storage longevity (p_{50}, days, provided by probit analysis), in hermetic storage at 40°C with c. 15% moisture content, during seed development in wheat cv. Tybalt in 2012 comparing amongst rain shelter (a) or ear wetting treatments (b)**.** Standard errors of estimates shown (but largely similar to or smaller than symbols). Control treatment results (C10) are shown in both a and b. The negative values for p_{50} in the first two harvests are because initial viability was <50% (see Fig. 2). Further details as Figure 2.

Figure 5. Damage from ear wetting to subsequent seed storage longevity (p_{50}) of wheat cv. Tybalt (— — —) 30 min after wetting and subsequent improvement with 7 days' natural re-drying *in planta* (——) from treatments at different times during seed development: W1 (■), W2 (□), W3 (▲), W4 (△),W5 (◆). Data repeated from Figure 4.

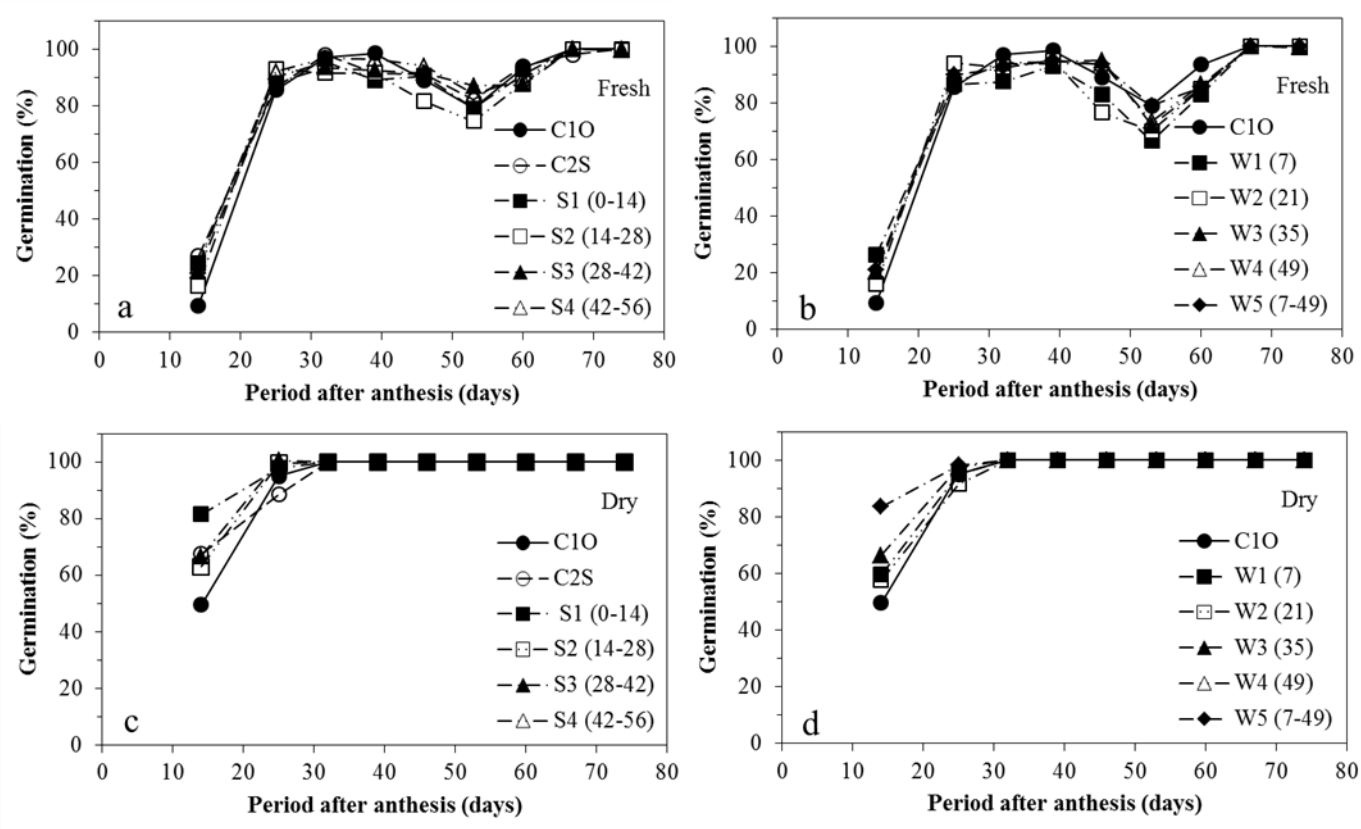

a
Fresh
C1O
C2S
S1 (0-14)
S2 (14-28)
S3 (28-42)
S4 (42-56)
Germination (%)
Period after anthesis (days)
b
Fresh
C1O
W1 (7)
W2 (21)
W3 (35)
W4 (49)
W5 (7-49)
Germination (%)
Period after anthesis (days)
c
Dry
C1O
C2S
S1 (0-14)
S2 (14-28)
S3 (28-42)
S4 (42-56)
Germination (%)
Period after anthesis (days)
d
Dry
C1O
W1 (7)
W2 (21)
W3 (35)
W4 (49)
W5 (7-49)
Germination (%)
Period after anthesis (days)

Fig 1

Fig 2

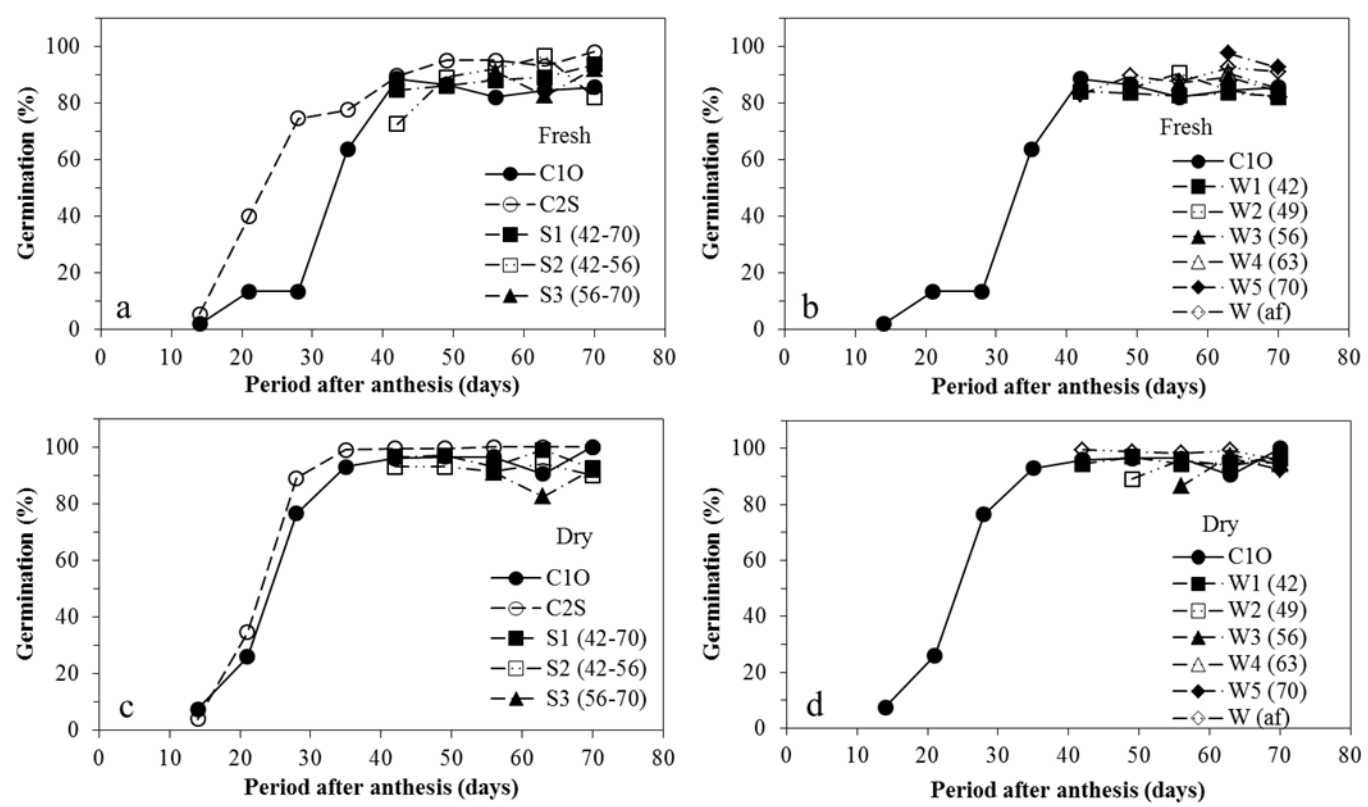

a
Fresh
C1O
C2S
S1 (42-70)
S2 (42-56)
S3 (56-70)
b
Fresh
C1O
W1 (42)
W2 (49)
W3 (56)
W4 (63)
W5 (70)
W (af)
c
Dry
C1O
C2S
S1 (42-70)
S2 (42-56)
S3 (56-70)
d
Dry
C1O
W1 (42)
W2 (49)
W3 (56)
W4 (63)
W5 (70)
W (af)
Germination (%)
Period after anthesis (days)

Fig 3

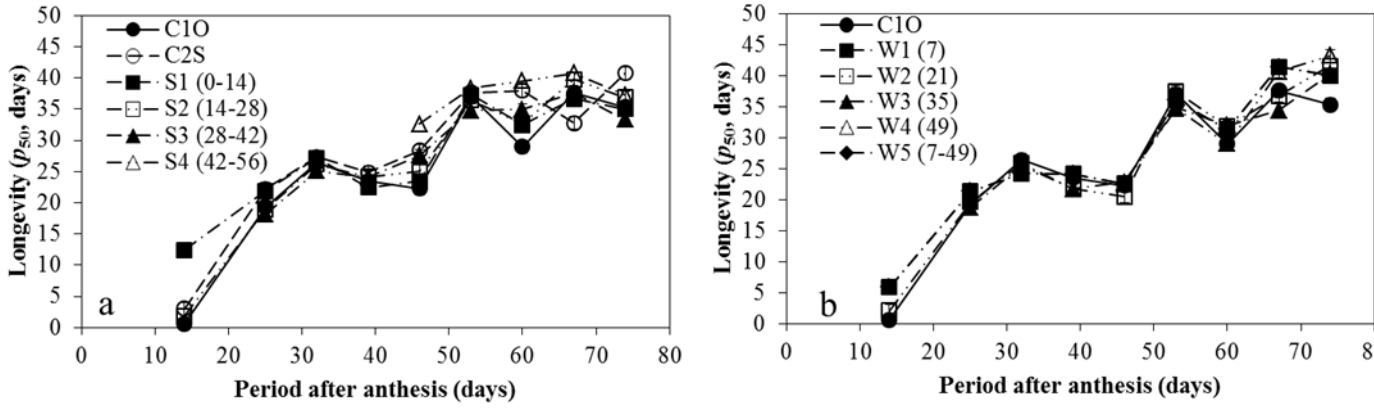

C1O
C2S
S1 (0-14)
S2 (14-28)
S3 (28-42)
S4 (42-56)
Longevity (p_{50}, days)
Period after anthesis (days)
a
C1O
W1 (7)
W2 (21)
W3 (35)
W4 (49)
W5 (7-49)
Longevity (p_{50}, days)
Period after anthesis (days)
b

Fig 4

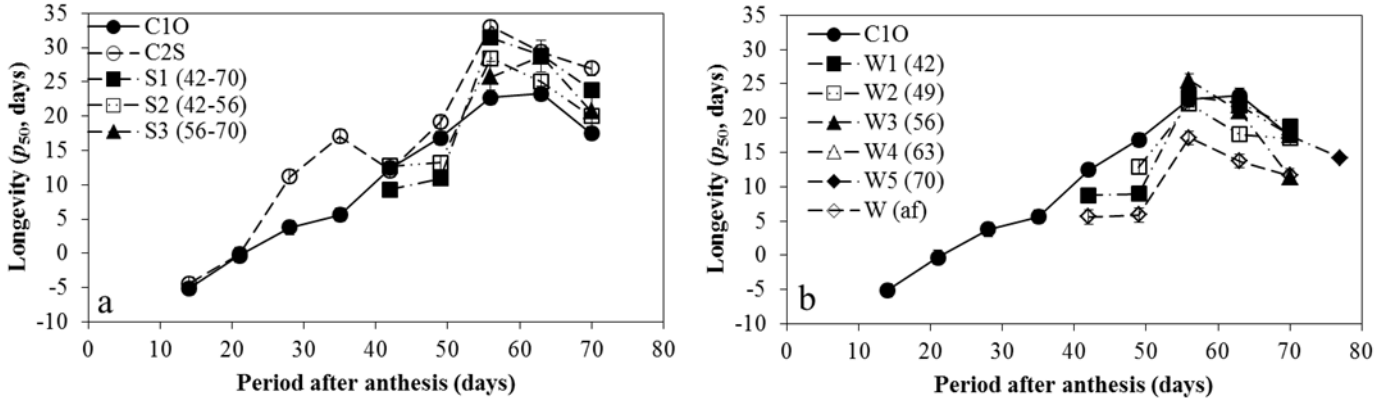
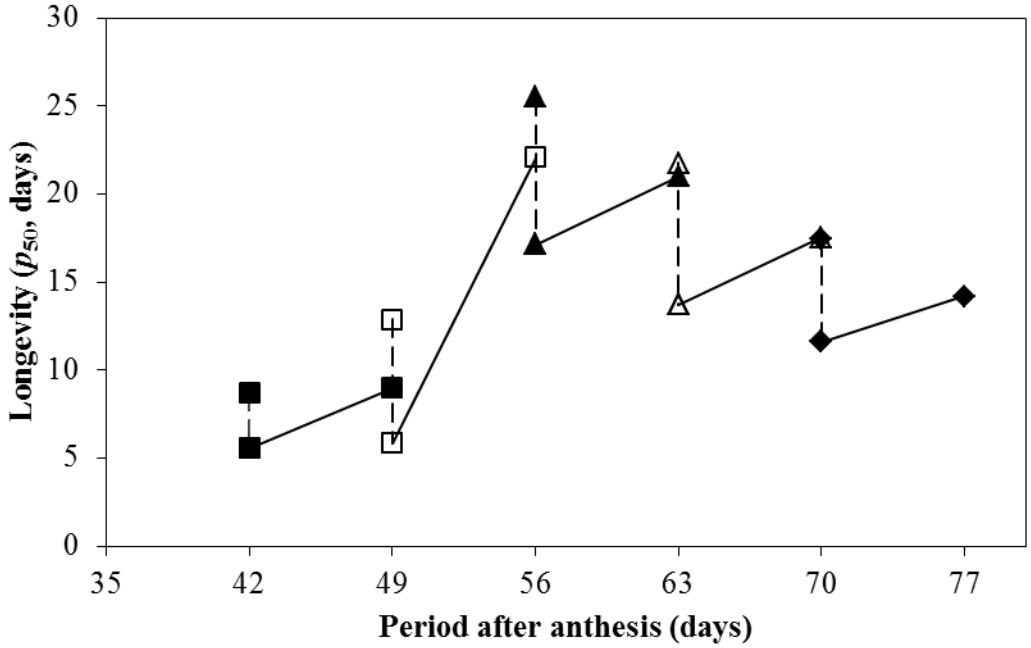

C1O
C2S
S1 (42-70)
S2 (42-56)
S3 (56-70)
Longevity (p_{50}, days)
Period after anthesis (days)
a
C1O
W1 (42)
W2 (49)
W3 (56)
W4 (63)
W5 (70)
W (af)
Longevity (p_{50}, days)
Period after anthesis (days)
b

Fig 5


30
25
20
15
10
5
0
Longevity (p_{50}, days)
35
42
49
56
63
70
77
Period after anthesis (days)