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Abstract

The potential longevity of *japonica* rice (*Oryza sativa* L. subsp. *japonica*) seed is particularly sensitive to high temperature – and thus climate change – during development and maturation. Cultivar Taipei 309 was grown at 28/20°C (12 h/12 h) and then from 19 DAA (days after 50% anthesis), when seeds were just over half filled, at 28/20°C, 30/22°C, 32/24°C or 34/26°C (12 h/12 h). Whereas ability to germinate *ex planta* had been achieved in almost all seeds by 24 DAA, only half the population were desiccation tolerant. Desiccation tolerance continued to increase over the subsequent 28 d, similarly at all four temperatures. Subsequent longevity, assessed by p_{50} (period in days to reduce viability to 50% in hermetic storage at 40°C with *c*. 15% moisture content), increased progressively at 28/20°C until 38 DAA, and remained constant until the final harvest (52 DAA). The three warmer temperature regimes provided similar longevity to 28/20°C at any one harvest, except at 38 DAA where the warmest (34/26°C) was poorer. That temperature regime also provided greater seed-to-seed variability within each survival curve. The results confirm that appreciable improvement in seed quality occurs during seed development and also subsequent maturation in *japonica* rice, but that increase in temperature from 28/20°C to 34/26°C during late seed filling onwards has comparatively little effect thereon. Comparison with previous investigations suggests that seed quality development may be less sensitive to high temperatures during late development and maturation than during the early seed development that precedes it.

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Introduction

Determining seed survival period *ex planta* in air-dry, hermetic storage (a sensitive indicator of seed quality) has shown that seed quality continues to improve during seed development and maturation for some considerable time after seed filling ends in cereals (e.g. Pieta Filho and Ellis, 1991; Rao *et al.*, 1991; Ellis and Pieta Filho, 1992), other crops (e.g. Demir and Ellis, 1992a, b, 1993; Sanhewe and Ellis, 1996) and wild species (e.g. Hay and Probert, 1995).

In rice (*Oryza sativa* L.), similar conclusions have been drawn (Ellis *et al.*, 1993). That study discovered that seed quality development in a *japonica* rice (cv. Taipei 309) was much more sensitive to high temperature than in *javanica* and *indica* rices. Seed filling and the pattern of loss in moisture were almost identical for the *japonica* rice in the two production regimes investigated (imposed from sowing onwards). However, whereas at 28/20°C (12 h/12 h) potential longevity (seed survival period if harvested) continued to increase throughout seed development and maturation until 32 DAA (days after anthesis), in the warmer regime of 32/24°C (12 h/12 h) no further improvement occurred beyond 22 DAA (2–3 d after seed filling ended), such that seed quality was very much poorer in the warmer regime at the normal time for harvest (Ellis *et al.*, 1993). Moreover, this difference in potential longevity was maintained with no change in either regime for a further 20 d if harvest was delayed. A parallel investigation showed that the ability to tolerate considerable desiccation to very low moisture contents was similarly poorer in the warmer regime during later stages of seed development and maturation (Ellis and Hong, 1994). Subsequent independent investigations in the field confirmed that *japonica* seeds produce longer-lived seeds in cooler than warmer regimes (Rao and Jackson, 1996, 1997).

The divergence in *japonica* rice seed quality development between the two temperature regimes was first detected close to mass maturity (Ellis *et al.*, 1993; Ellis and Hong, 1994), this being the end of the seed-filling phase (Ellis and Pieta Filho, 1992).

The current study investigated the effect of different temperatures on seed quality development when imposed only from late seed filling onwards. The objective was to determine whether or not, and if so the extent to which, modifying the temperature regime during this late period, rather than throughout development and maturation, affected seed quality.

Materials and methods

Production of seed material

Seeds (caryopses enclosed by paleas and lemmas throughout this paper) of the *japonica* rice cv. Taipei 309, provided by the International Rice Research Institute (IRRI), were graded by eye to remove extremely large or small seeds and sown 4–5 per 18-cm-diameter pot into a soil-less medium on 8 June 2007. The latter comprised steam-sterilized sand and gravel mixed with peat compost and vermiculite (2:4:1:4 by volume, respectively). The filled pots were soaked with tap water and allowed to drain for 24 h before sowing and were arranged on four mobile trolleys (each 2.85 m × 0.96 m, 15 rows of 6 pots). The position of each pot on each trolley was recorded. Plants were grown at the Plant Environment Laboratory, University of Reading, UK (51°27′N, 00°56′W), initially in a controlled-environment, naturally lit, glasshouse with day and light-proof night compartments. The automated mobile trolleys were drawn out from and into night compartments (3.57 m × 1.74 m) each morning and evening to provide a short, inductive photoperiod of 11 h d^{-1}. Temperature (logged continuously at several points) in the greenhouse was maintained at 28/20°C day/night (12 h/12 h) through a combination of heating and venting during the day, and heating at night. In general, set temperatures were maintained to within 0.5°C (but see below).

The first seedlings emerged 6 DAS (days after sowing) and the majority by 11 DAS. At this time, pots with fewer than three strong seedlings were moved to provide the guard rows on the trolleys, and all pots provided with an automatic drip-feed irrigation system. The number of seedlings was reduced to three per pot at 14 DAS and subsequently thinned to one per pot at the three-leaf stage. The complete nutrient solution contained 100 mg l^{-1} inorganic nitrogen, acidified to pH 4.8 to avoid iron deficiency. Plants were also sprayed with a foliar feed (Miracle-Gro®, The Scotts Company UK Ltd, Godalming, Surrey, UK) at 3.75 g l^{-1} 68, 83 and 101 DAS and with Torque (50% w/w fenbutatin oxide) at 0.5 g l^{-1} of water to control red spider mites at 61 DAS. Biological control (*Phytoseiulus persimilis*) of the latter was also applied at 75 and 97 DAS. Aphids detected at 143 DAS were controlled by an application of Savona (an insecticidal soap containing 50% w/w potassium salts of fatty acids).

As panicles reached first anthesis each day they were tagged: 50% anthesis was reached on 28 September 2007 (112 DAS). Anthesis was protracted across the plant population. To limit this source of variation, only panicles that anthesed 108–114 DAS were used.

The plan had been to move plants to growth cabinets towards the end of the seed-filling phase. However, 2007 was a poor summer and ambient light levels and external temperature in early autumn declined such that plants were moved to four modified Saxil growth cabinets, internal dimensions 1.4 × 1.4 × 1.5 m, slightly earlier than planned, on 4 or 5 October [118 or 119 DAS; 6 or 7 DAA, days after (50%) anthesis]: plants were staked before moving. All cabinets provided the same regime as the glasshouse (28/20°C), initially.

On 17 October (131 DAS; 19 DAA), each growth cabinet was altered to one of the following regimes: 28/20°C, 30/22°C, 32/24°C, 34/26°C (12 h/12 h). On the day before, plants were re-randomized amongst the four cabinets. The carbon dioxide concentration in the cabinets was maintained at 385 μmol mol^{-1} of air. Relative humidity was maintained at 60 ± 5% by day and 80 ± 5% at night. A combination of cool white fluorescent tubes and incandescent lamps provided a photosynthetic photon flux density (measured at base of cabinet) of 650 μmol m^{-2} s^{-1}. Irrigation continued until 1 November 2007 (146 DAS; 34 DAA).

Panicles were harvested serially 11 (9 October 2007), 13, 17, 19, 24, 31, 38, 45 and 52 DAA (19 November 2007) throughout seed development and maturation. Each harvest comprised about 30 panicles from 4–8 pots per temperature regime.

Seeds were threshed gently by hand, and empty seeds removed. Samples of 100 seeds plus 1 g each were withdrawn to determine germination and moisture content, respectively. The remaining seeds were dried in a drying cabinet maintained at 15–17°C with 12–15% relative humidity to 15% moisture content (one sample for a germination test) or further to 10–14% moisture content , respectively (wet basis). One subsample was then dried further, over regularly regenerated silica gel at 20°C, to 4.5% moisture content and tested for ability to germinate. The remainder was stored hermetically at 3–5°C initially, then at −20°C once moisture content was confirmed to be at or below 14%. Seed moisture contents were determined using the high-constant-temperature-oven method (International Seed Testing Association, 2005), except that 2 × 100 seed samples were used in place of 2 × 4–5 g samples in each case. The two-stage method (International Seed Testing Association, 2005) was used for moist seeds.

Seed germination and storage

Samples of seeds (100; two replicates of 50) were tested for germination between moist rolled paper towels in the alternating regime of 34/11°C (16 h/8 h) recommended by Ellis *et al.* (1983) to break dormancy 'safely', for 28 d initially. Non-germinated seeds that were not soft at this time were then pricked with a needle to promote further loss of dormancy and tests continued until all had germinated (often within a further 7 d, but the most dormant required a much longer duration, sometimes combined with further surgical treatment).

The determination of potential longevity, i.e. seed survival during post-harvest experimental storage, began on 3 March 2008. Seeds were withdrawn from storage at -20°C and held overnight at 20°C before opening the packets. Each sample was adjusted to *c.* 15% moisture content by humidification above water at 20°C for 2–36 h (depending on initial value) using a target of 75% equilibrium relative humidity (since this could be assessed repeatedly and non-destructively). The seeds were then stored hermetically at 3–5°C for 3 d for moisture to equilibrate. For each combination of harvest date and temperature regime, 10–14 samples (depending upon number available) of 100 seeds were sealed in separate laminated aluminium-foil bags. These were stored in an incubator maintained at 40 ± 0.5°C and samples removed for germination tests (as above) at regular intervals for up to 49 d. Mean seed storage moisture content, determined for samples withdrawn from hermetic storage at the end of experimental storage, was 14.6% (range 14.2–14.9%). Seed survival curves were fitted to the data by probit analysis using GENSTAT (Release 10.1, VSN International Ltd, Hemel Hempstead, Herts, UK) in accordance with

$$v = K_i - p/\sigma \tag{1}$$

where v is viability (normal equivalent deviate) after p days' storage in a constant environment, K_i is the intercept, and σ is the standard deviation of the distribution of seed deaths in time (days) (Ellis and Roberts, 1980): the criterion of survival was visible germination.

Results

The pattern of seed moisture content decline (Fig. 1) was similar to that noted earlier (Ellis *et al.*, 1993), with a tendency for seeds in warmer environments to be slightly drier (from 24 DAA onwards). Seed filling followed the expected linear trend between 11 and 24 DAA (0.83 mg d^{-1}, SE 0.08) and continued until around 30 DAA: the gradient was much reduced beyond 24 DAA, making it difficult to define mass maturity precisely. Mature seed dry weight was 18.9 mg (SE 0.27), with no effect of temperature regime on this value ($P > 0.05$). Hence, treatments in the four different temperature treatments began about two-thirds through the period between anthesis and the end of seed filling when seeds were just over half their ultimate dry weight.

Ability to germinate *ex planta* developed progressively within the population between 11 and 24 DAA (Fig. 2A). Ability to germinate following enforced desiccation to 15% (Fig. 2B) or 4.5% moisture content
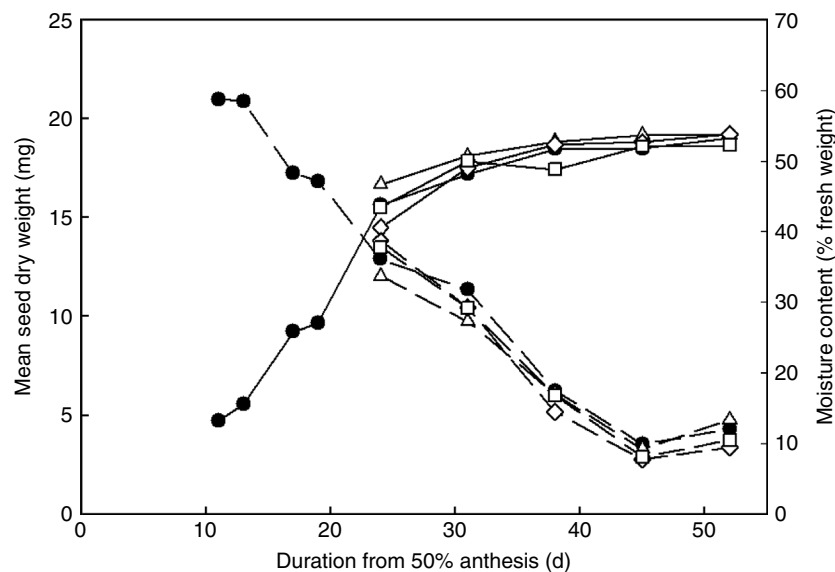

Figure 1. Increase in mean dry weight (solid lines) and decline in moisture content (broken lines) of seeds of *japonica* rice cv. Taipei 309 harvested serially during their development and maturation from plants grown in controlled environments of 28/20°C (●) throughout, or at 28/20°C until 19 DAA and then 30/22°C (△), 32/24°C (◇) or 34/26°C (□) thereafter.
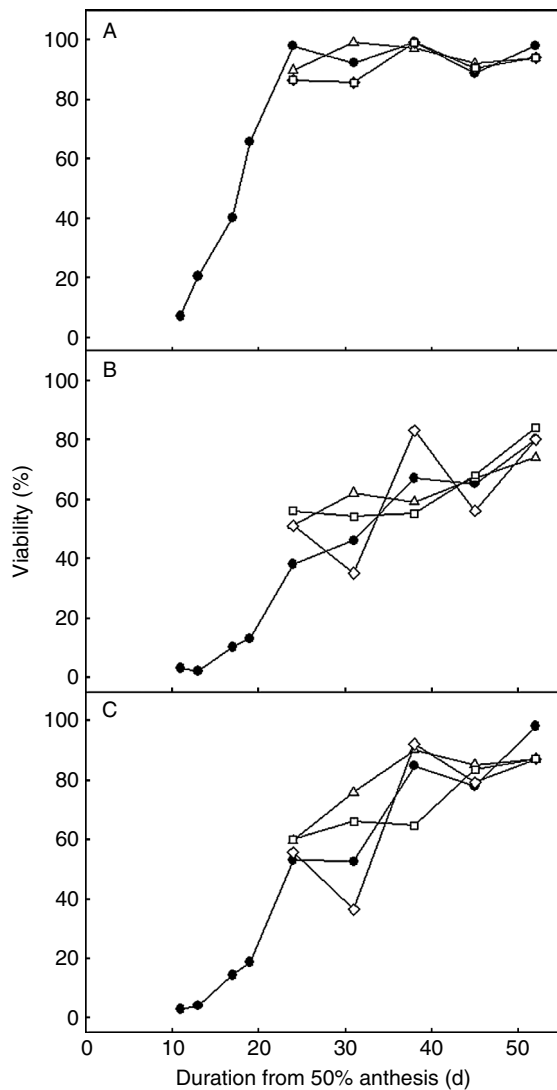
Negative sigmoidal seed survival curves were obtained in hermetic air-dry storage for each harvest in the four different temperature regimes, as the examples for 38 and 52 DAA (Fig. 3) show. The lower initial viability of dry seeds prepared for experimental storage in early harvests (as in Fig. 2B) resulted in shorter survival periods – whereby longevity increased during seed development and maturation (Fig. 4). In the final harvest (52 DAA), almost all seeds were viable and desiccation tolerant before experimental storage began (Fig. 3B).

Each harvest provided seed survival curve shapes compatible with those of Ellis *et al.* (1993). Whereas the mode of the distribution of seed deaths in time (i.e. the pattern of loss in viability from around 80 to 20% with storage period) was broadly similar amongst the three cooler temperatures, Fig. 3 shows that the warmest regime (34/26°C) tended to show a shallower curve (i.e. more variation in individual seed lifespans within the population) until around 20–40% viability, with the remainder of the curve (i.e. the longest-lived seeds within the population) differing less from the cooler temperatures. Accordingly, the seed survival curves,

Figure 2. Changes in viability (ability to geminate *ex planta* in standard tests at 34/11°C) for seeds of *japonica* rice cv. Taipei 309 freshly-harvested (A), or dried to 15% moisture content (B) or to 4.5% moisture content (C), when harvested serially during their development and maturation, from plants grown in controlled environments of 28/20°C (●) throughout, or at 28/20°C until 19 DAA and then 30/22°C (△), 32/24°C (◇) or 34/26°C (□) thereafter. Seed filling ended close to 30 DAA (Fig. 1).

(Fig. 2C) developed less rapidly, but nevertheless progressively and consistently throughout the population(s) from 13 to 52 DAA. The three different warmer temperature regimes, imposed when most seeds were able to germinate *ex planta* but only about one-fifth were desiccation tolerant (Fig. 2), provided somewhat more variable results than 28/20°C, but there was no evidence of any consistent effect of temperature on the trend of improving desiccation tolerance throughout seed maturation. Similarly, there was no evidence that further desiccation from 15% (Fig. 2B) to 4.5% moisture content (Fig. 2C) reduced viability.

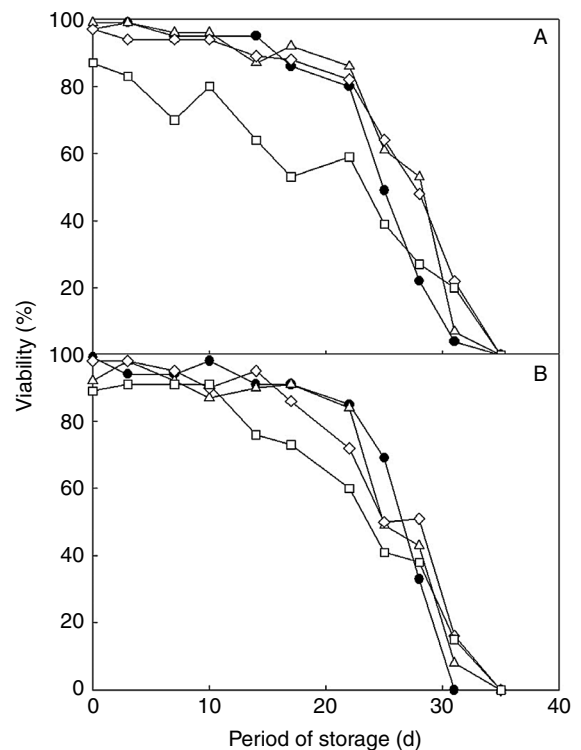**Figure 3.** Seed survival curves (viability, estimated by ability to germinate, plotted against period of experimental hermetic storage at 40°C with 14.2–14.9% moisture content) for the *japonica* rice cv. Taipei 309 for seeds harvested 38 DAA (A) or 52 DAA (B) from plants grown in controlled environments of 28/20°C (●) throughout, or at 28/20°C until 19 DAA and then 30/22°C (△), 32/24°C (◇) or 34/26°C (□) thereafter.

Figure 4. Changes in the longevity (p_{50}, period of experimental hermetic storage at 40°C with 14.2–14.9% moisture content until viability reduced to 50%; estimates provided by probit analysis) of seeds of *japonica* rice cv. Taipei 309 harvested serially during their development and maturation from plants grown in controlled environments of 28/20°C (●) throughout, or at 28/20°C until 19 DAA and the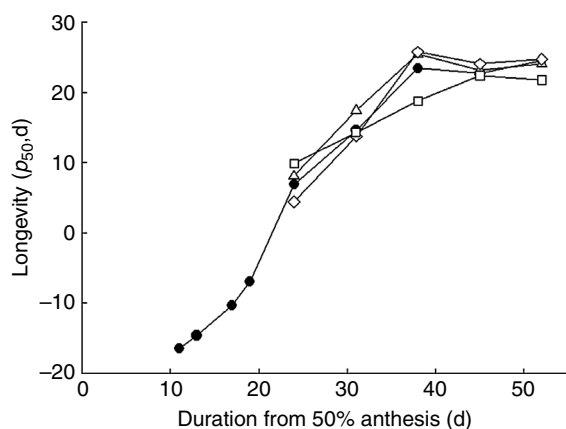n 30/22°C (△), 32/24°C (◇) or 34/26°C (□) thereafter. Seed filling ended close to 30 DAA (Fig. 1). The standard errors of the estimates of p_{50} between 24 and 52 DAA were smaller than the symbols shown, varying only from 0.33 (24 DAA, 28/20°C) to 0.72 d (24 DAA, 32/24°C). Estimates of p_{50} for 11–19 DAA (note the negative values) are based on limited data since few dried seeds were viable (e.g. see Fig. 2B) and represent back extrapolation using the common value of σ (9.5 d) from 24 seed lots (i.e. all treatment combinations).

and so estimates of K_i and σ (equation 1), varied substantially amongst seed lots ($P < 0.005$). Thus p_{50} (storage period in days to reduce viability to 50%, the product of K_i and σ) was estimated separately for each lot in order to determine changes in air-dry seed storage potential during seed development and maturation, and to compare the four temperature regimes.

At 28/20°C, seed longevity increased consistently and progressively throughout seed development and maturation until 38 DAA (when moisture content had first declined naturally to below 20%) and then remained constant over the remainder of the investigation (Fig. 4). The three warmer temperature regimes provided a similar trend and also similar estimates of p_{50} at any one date during seed development and maturation, except at 38 DAA when the warmest regime (34/26°C) provided a shorter viability period than the cooler regimes (Fig. 4).

Discussion

Seed filling continued for longer than previously (Ellis *et al.*, 1993; Ellis and Hong, 1994). Then, high ambient

temperatures had resulted in the nominal 28/20°C being exceeded on occasion. In contrast, here it was difficult to warm to 28°C in the glasshouse after anthesis, even with supplemental heating. Hence, plants may have been disrupted during seed filling by this, the transfer to growth cabinets being implemented earlier than planned, and the lower light levels in the cabinets. The longer duration of seed filling also resulted in the different temperature regimes being imposed well before seed filling ended (seeds only 53% filled). Despite these differences amongst the studies (including light levels in growth cabinets being lower than ambient), mature seed dry weights were almost identical [18.9 mg compared with 17.5–17.6 mg (Ellis *et al.*, 1993) and 19.0–20.3 mg (Ellis and Hong, 1994)], with no effect of temperature regime on mature seed dry weight within any of the three investigations.

The detection, magnitude and sign of any effects of temperature on seed quality development depend on the temperature(s) imposed, duration, species and cultivar. In wheat (*Triticum aestivum* L.), for example, there was good evidence of a positive effect of increase in temperature on the rate of improvement in potential seed longevity during seed development and maturation, but that study was at comparatively cool temperatures (Sanhewe *et al.*, 1996). At slightly warmer temperatures in *Phaseolus vulgaris* L., on the other hand, increase in seed production temperature resulted in poorer subsequent seed longevity (Sanhewe and Ellis, 1996).

Seed quality, i.e. both desiccation tolerance and subsequent seed storage survival period, in this *japonica* rice increased considerably after mass maturity in all temperature regimes. The 2–6°C increase in mean temperature above 24°C was not imposed until late seed filling – and not until after the development of ability to germinate (Fig. 2A). The temperature treatments had no effect on the subsequent development of desiccation tolerance (Fig. 2). Neither did temperature affect the improvement in seed storage potential (p_{50}) save perhaps for the warmest regime at 38–52 DAA (Fig. 4). However, that regime (34/26°C) did reduce the survival period of the shortest-lived seeds in each population, i.e. the first 60–80% to die (Fig. 3). This fraction of each population coincides approximately with that fraction (*c.* 80%) which had not achieved desiccation tolerance by the time when the different temperatures were imposed (Fig. 2). Hence, there is some evidence that seed quality in certain seeds (possibly the last to develop) was damaged by the warmest regime.

Comparison of seed quality development between 28/20°C and 32/24°C when provided to this *japonica* rice *throughout* crop and seed development showed an abrupt change from mass maturity onwards (Ellis *et al.*, 1993; Ellis and Hong, 1994): results for storage

potential were similar until that point in development, but then diverged greatly with little or no further improvement at 32/34°C and considerable further improvement at 28/20°C for the next 12 days or so. The consequence was a 55% reduction in storage potential by harvest maturity (Ellis *et al.*, 1993). The current study indicates that delaying the imposition of temperatures warmer than 28/20°C (within the range investigated) until two-thirds through the seed-filling phase results in comparatively little (34/26°C) or no (30/22°C, 32/24°C) damage to the storage potential of the mature seed (Fig. 4).

Three further comparisons are apposite. First, seed storage potential improved substantially post-mass maturity at all temperatures (Fig. 4), but only in the cooler regime previously (Ellis *et al.*, 1993). Second, potential longevity at the warmer and cooler temperatures plateaued from 22 and 32 DAA, respectively, previously (Ellis *et al.*, 1993), but from 38 or 45 DAA in the three coolest and the warmest regimes, respectively, here (Fig. 4). Third, extreme desiccation tolerance diverged from mass maturity onwards with difference in temperature when imposed throughout seed development and maturation (Ellis and Hong, 1994), but not when provided only late in development and maturation (Fig. 2C). All of which tends to suggest that, while previously the consequences were not manifest until after mass maturity, providing warmer temperature throughout seed development and maturation was more damaging to subsequent seed quality in this *japonica* rice than when it was not imposed until seeds were already half filled.

The hypothesis that the damaging effect of high temperature to seed quality development is reduced the later during seed development and maturation it is imposed – together with one (not mutually exclusive) that duration of high temperature is also a factor – is worthy of further investigation in rice, and other species. There is evidence in other aspects of reproductive biology of greater sensitivity to temperature at specific developmental stages. In particular, pollination, and so seed set, are particularly sensitive to brief exposure to high temperature, e.g. in rice (Yoshida *et al.*, 1981; Prasad *et al.*, 2006; Jagadish *et al.*, 2010), groundnut (*Arachis hypogaea* L.) (Craufurd *et al.*, 2003) and wheat (Wheeler *et al.*, 1996; Ferris *et al.*, 1998).

Anthropogenic greenhouse gas emissions are now considered very likely to have caused most of the global warming observed in the second half of the 20th century and may result in further warming of 1.3–1.8°C by around the middle of this century, with heat waves very likely to become more frequent, intense and longer (Solomon *et al.*, 2007). The regimes of 28/20°C and 32/24°C represent major rice production areas and seasons in Japan and the Philippines, respectively (Ellis *et al.*, 1993). Accordingly, the results

to date imply that such an increase in mean temperature during seed development rather than during seed maturation in the former may hinder future production of quality seed (and so affect subsequent crop production) in *japonica* rices. Moreover, the absence of any impact on mean seed weight (at constant plant densities) suggests no effect on yield and thus that seed quality might be a more sensitive indicator than yield in order to monitor climate change impacts on crops in real time. More generally, seed quality in other rices in other regions might also be affected by climate change, as might other crops. Attempts to quantify the full impacts of climate change (and post-anthesis stress in particular) on crop production, therefore, may need to include the consequences for crop seed supply – quantity and quality – for subsequent seasons as well as the direct (within-season) impacts on crop production. Such considerations are likely to be particularly pertinent in regions where crop production is already marginal due to high temperature. If such impacts are to be understood and modelled, then it will be necessary to determine the extent to which the sensitivity of seed quality development to temperature might vary, depending upon precisely when during seed development and maturation high (or indeed cool) temperature episodes occur.

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