

Effect of post-anthesis high temperature on seed longevity and vigour in wheat (*Triticum aestivum* L.)

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The effect of post-anthesis high temperature on seed quality was studied in four promising genotypes (T 2003R, R 902, R 958 and R 965) of wheat (*Triticum aestivum* L.) under a controlled environment (30°/25°C day/night temperature from 81 days after sowing to harvest maturity). Seed mass, density, seed membrane development, ability to germinate, subsequent seed longevity and seedling vigour declined in the seeds harvested from high temperature after post-anthesis, resulting in early maturation and poor desiccation tolerance at harvest maturity. Genotype R 965 showed greater resilience to damage compared to the other genotypes.

Keywords: Climate change, high temperature, post-anthesis, seed quality, vigour, wheat.

CONSIDERING changing climate, the impact of short periods of extreme temperature on seed development and quality is relevant for global adoption of crops at present and more so for future climate. A climate model has predicted an increase in global mean surface temperature from 0.4°C to 1.6°C by 2046–65 and from 2.6°C to 4.8°C by 2081–2100, depending on the greenhouse gas emissions scenario considered¹. Moreover, future climates will provide more frequent high-temperature extremes of longer duration². Wheat production primarily depends on the availability of high-quality seeds, which enhances the yield by 15–20% (ref. 3). In India, long-duration rice varieties constrain wheat crops to be grown under late sown conditions (late December to early January), leading to anthesis and seed filling duration coinciding with high temperature, and resulting in low yield with poor quality^{4,5}. Systematic studies have been conducted to assess the effect of high temperature on crop phenology⁶, growth⁷ and yield^{8,9}. However, the effect of high temperature on seed quality has been less understood. Moreover, in previous studies, seed mass, the ability of seeds to germinate and bread-making quality have been used as indicators to assess seed quality deterioration due to high-temperature exposure at post-anthesis and seed-filling in wheat^{10,11}. The differences in seed quality have been attributed to various environmental factors

in both time and space, including temperature¹². Studies have indicated that high temperature during seed development significantly reduces seed vigour and longevity, but not germination and hence have underestimated the role of high-temperature effects on seed quality¹³.

Abiotic stress, including high temperature experienced under field conditions, significantly affects seed production in wheat¹⁴. The hypothesis of the present study is that high-temperature exposure at post-anthesis and seed-filling duration do not affect the subsequent ability of the seeds to germinate, seed vigour and their longevity during storage. The seed quality may be affected by environmental temperature during seed development and consequently decline¹⁵. Hence other factors (moisture, nutrients and pests) were kept optimum, except temperature. Thus, the effect of brief exposure to high temperatures on wheat seed quality was studied exclusively.

Materials and method

The effect of high temperature during seed development on subsequent seed quality was examined in four promising genotypes of wheat (T 2003R, R 902, R 958 and R 965). The plants were grown in a controlled environment (CT) of a glasshouse (photoperiod-controlled, heated and ventilated) of size 20 × 15 m and a growth chamber (HT) with two compartments at the National Phytotron Facility, ICAR-Indian Agricultural Research Institute, New Delhi from 2016 to 2018. Plants were grown in a 250 mm diameter plastic pot (with drain holes). The growing medium consisted of coarse sand, gravel, cocopeat (sterilized) and vermiculites in the ratio 2 : 4 : 4 : 2. Fertilizer (N : P₂O₅ : K₂O) was added with 50 mg pot⁻¹ as basal application. The soil mixed with the pot was presoaked with distilled water and left to drain overnight. Eight seeds of each genotype were sown 3 cm deep in each pot and seedlings were thinned to four plants per pot 28 days after sowing. The pot was rinsed with distilled water (pH 5.5–6.0) manually when required.

Temperature treatment

The daily day/night temperatures were maintained at 15°C/10°C (12 h/12 h, thermal period synchronized with 12 h

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Table 1. Comparison of plant growth, phenology and seed development in four wheat genotypes under two treatments

Genotype	Treatment	Photoperiod and day temperature (h day ⁻¹)	Day/night temperature after anthesis (°C, mean)	Date of sowing	Days to 50% anthesis (DAS)	Harvesting maturity (DAA)	Seed mass (g)	Seed density (gm ⁻³)
T 2003R	CT	12	25/20 (22.5)	12 November 2018	87	59	41.8 ^{ab}	1.13 ^d
	HT	12	30/25 (32.5)		60	50	36.7 ^d	1.10 ^{cd}
R 902	CT	12	25/20 (22.5)		84	56	41.5 ^{ab}	1.27 ^c
	HT	12	30/25 (32.5)		62	53	39.8 ^c	1.11 ^{cd}
R 958	CT	12	25/20 (22.5)		85	59	44.5 ^a	1.40 ^a
	HT	12	30/25 (32.5)		65	53	42.1 ^b	1.32 ^b
R 965	CT	12	25/20 (22.5)		95	57	41.6 ^{ab}	1.42 ^a
	HT	12	30/25 (32.5)		66	46	34.3 ^c	1.40 ^a

DAS, Days after sowing; DAA, Days after anthesis; CT, Control environment; HT, Post-anthesis high temperature; ^{a-c}Significant difference.

day⁻¹ photoperiod) from sowing to 60 DAS (days after sowing), 20°C/15°C (day/night) from 61 to 80 DAS and 25°C/20°C (day/night) from 81 DAS to harvest maturity of plants, considered as the controlled environment of temperature in a glasshouse. High-temperature treatment at post-anthesis and subsequent seed-filling duration in a growth chamber were achieved by maintaining the temperature at 30°C/25°C after anthesis and until harvest maturity, while growth temperature from sowing to 80 DAS was the same as in control (Table 1).

Seed quality assessment

Seed mass and density: Seeds were threshed gently from several hundred spikes after harvest from the glasshouse and growth chamber separately by hand. The moisture content of the seeds was reduced up to 12% level by drying in the shade and dry-stored for six months to avoid dormancy effects. Seed mass (thousand seed weight) was determined using eight replications of 100 seeds of each genotype¹⁶. True seed density (ρ_t) of the seeds was assessed by employing the toluene displacement method using the following equation¹⁷

$$\rho_t = \frac{M}{V_b},$$

where M is the mass of 100 seeds and V_b is the volume displaced by the seeds.

Ability to germinate and seed longevity: The ability of dried seeds to germinate was assessed using a sample of 400 seeds (4 × 100) in moist germination paper towels at 20°C for eight days¹⁶. The percentage of normal seedlings was a criterion to determine germination percentage. Seed longevity period was assessed employing the accelerated ageing (AA) method using 50 seeds with three replicates, aged for 24, 48, 72, 96, 120 and 144 h period with high temperature (42° ± 0.5°C) and high humidity (≥95%) for rapid seed deterioration in the AA chamber. Seed moisture content was adjusted (14%) by placing the weighed seed

samples (in a muslin bag) over water with the help of a mesh wire at 20°C for 2–40 h, with the seed weight monitored¹⁶. Then the seed bags were maintained at 2°–4°C for three days to allow moisture to equilibrate within and between samples. The samples were withdrawn from the ageing chamber at regular intervals for up to 144 h and viability was assessed. Seed survival curves were fitted by probit analysis according to the equation of Ellis and Hong¹⁸

$$V = K_i - \left(\frac{p}{\sigma} \right),$$

where V is the viability (in normal equivalent deviates, NED) of the seed lot after p days in storage, K_i the initial viability (NED) of the seed lot and σ is the time (h) for viability to fall by 1 NED (i.e. the standard deviation of normal distribution of seed deaths over time). The product of K_i and σ is the period of viability to decline to 50% (P_{50}). A General Linear Model (GLM) with binomial error and probit link function was fitted to the survival data with storage period as an explanatory variable.

Seed vigour: This was assessed by examining the membrane integrity of seeds through electrical conductivity (EC) of solute leakage from the imbibed seeds and seed reserve mobilization efficiency (SRME). The EC of pre-soaked seeds (50 × three replicates) in distilled water was measured at 6-h intervals for up to 24 h (ref. 16) with the help of an EC meter (Labman EC meter, model LMCM-20). SRME was assessed for each seed sample by weighing the seeds and seedlings before germination and using the formula of Hasan *et al.*¹⁹.

The amount of seed material lost as respiration (SMLR) was calculated as follows

$$\text{SMLR (mg)} = \text{SDW} - (\text{SHW} + \text{RTW} + \text{RSW}),$$

where SDW is the seed dry weight before germination, SHW the shoot dry weight, RTW the root dry weight and RSW is the remaining seed dry weight.

Table 2. Comparison of germination ability in the four wheat genotypes affected by post-anthesis high temperature

Genotype	CT					HT				
	G%	NS	AS	FUS	D	G%	NS	AS	FUS	D
T2003 R	93 (74.7) ^a	90.5 (72.1) ^a	5.5 (13.5) ^a	2 (7.9) ^a	2.0 (8.1) ^a	87 (68.9) ^a	84.5 (66.8) ^a	8.5 (16.9) ^b	2.5 (9.1) ^a	2.5 (9.1) ^a
R 902	92 (73.6) ^a	90 (71.6) ^a	5.5 (13.5) ^a	2.0 (7.9) ^a	2.5 (9.1) ^a	84 (66.4) ^a	82 (64.9) ^a	11.5 (19.8) ^a	2 (7.9) ^a	4.5 (12.2) ^a
R 958	94 (75.8) ^a	92.5 (74.1) ^a	4.5 (12.2) ^a	1.5 (6.9) ^a	1.0 (5.7) ^a	88 (69.7) ^a	86.5 (68.4) ^a	8.5 (16.9) ^b	1.5 (6.9) ^a	3.5 (10.8) ^a
R 965	95 (77.1) ^a	92 (73.6) ^a	3 (9.8) ^a	2.5 (9.1) ^a	2.5 (9.1) ^a	89 (70.6) ^a	87.5 (69.3) ^a	6.5 (14.8) ^c	1.5 (6.9) ^a	4.5 (12.2) ^a

Figures within brackets represent the corresponding arcsine transformed values.

G%, Germination percentage; NS, Normal seedling; AS, Abnormal seedling; FUS, Freshly ungerminated seeds; D, Dead seeds.

SRME calculated using the following formula

$$\text{SRME (mg mg}^{-1} \text{ seed)} = \frac{\text{SHW} + \text{RTW}}{\text{SMLR}}$$

Seedling vigour: This was assessed using seedling parameters (length, dry weight, and root : shoot ratio) of ten seedlings from each sample after the germination test¹⁶.

Statistical analysis

Analysis of variance (ANOVA) was used to compare seed mass, seed density, germination percentage, SMRE, seedling length, seedling dry weight and root : shoot ratio of the four genotypes. Duncan's multiple range test (DMRT) was used to compare means ($P = 0.05$) among the treatments. The ability to germinate, percentage of abnormal, freshly ungerminated seeds, dead seeds, seedling length, seedling dry weight and root : shoot ratio were transformed to arcsine before using ANOVA.

Results and discussion

High-temperature episodes often occur in the field during the reproductive phase, and subsequent seed development and maturation in wheat²⁰. In the present study, plants were grown inside a glasshouse and growth chamber having a controlled environment. Hence, modifying the temperature environment affected the temporal pattern of seed development and maturation in terms of seed mass, seed density, longevity and seed quality. The effects of high temperature assessed in the present study are relevant to all wheat-production systems exposed to high temperature during the reproductive phase and the subsequent seed development and maturation phase.

Seed mass and density

High-temperature exposure resulted in more rapid seed development and reduced the seed-filling duration, result-

ing in lower seed mass (9.8%) and density (4.8%) in seeds harvested from the growth chamber (Table 1). Seed mass of genotype R965 harvested at maturity (46 DAA) under HT condition had decreased due to stress treatment (17.5%), while genotype R 902 less was affected (4.1%) at maturity (53 DAA). This is a common consequence of high-temperature stress during the reproductive phase in wheat²¹; as observed in the present study when high temperature was applied close to anthesis. Genotype T2003 R was more damaged by high-temperature exposure than the control and produced low-density seeds (1.10 g m⁻³).

Ability to germinate and seed longevity

Despite differences in seed desiccation and the filling period between control and growth chamber, there was a clear effect of high temperature on the ability of seeds to germinate, percentage of abnormal seedlings, as well as dead and freshly ungerminated seeds. The ability to germinate decreased in seeds harvested from the growth chamber by 7%, while the percentage of abnormal seedlings increased by 47 (Table 2). The ability to germinate after six months of dry storage decreased (88%) in seeds harvested from the growth chamber, while it did not affect seeds harvested from the glasshouse, which showed germination close to 100%. Exposing wheat plants to high temperatures during the reproductive phase damaged the subsequent seed quality, but it varied among the genotypes and treatments. Such damage was reflected in the genotypes R 902, R 58, and R 965 (Table 2), but seed quality in genotype T2003 R was more prone to damage from high-temperature stress. These may be the effects of high temperature during seed development and maturation, resulting in poorly filled seeds and underdeveloped embryos, unable to produce healthy seedlings even under conducive environments of germination²².

Subsequent longevity of seeds harvested at maturity decreased during the AA test with increasing AA time (h), in both the growth chamber and glasshouse with respect to the genotypes (Table 3). The longevity (P_{50}) of seeds from the glasshouse was highest compared to the growth chamber,

Table 3. Comparison of subsequent seed longevity in the four wheat genotypes affected by post-anthesis high temperature

Genotype	Growing environment	K_i	SE	σ	SE	r^2	P_{50}
T 2003R	CT	2.40	0.06	49.40	0.90	0.89	119.59
	HT	2.51	0.15	26.95	1.65	0.97	69.31
R 902	CT	1.94	0.01	90.85	4.35	0.62	175.85
	HT	1.84	0.01	28.75	3.15	0.96	52.69
R 958	CT	2.32	0.01	69.65	4.45	0.96	161.05
	HT	1.44	0.02	29.70	0.10	0.97	42.37
R 965	CT	2.44	0.01	42.00	2.40	0.92	102.34
	HT	2.14	0.01	37.20	1.60	0.93	79.47

Genotype and seed lot source (growing environment) have been included as factors. K_i , Initial viability (normal equivalent deviates (NED)) of the seed lot; σ , Time (h) for viability to decrease by 1 NED; P_{50} , Time (h) for viability to decrease to 50%.

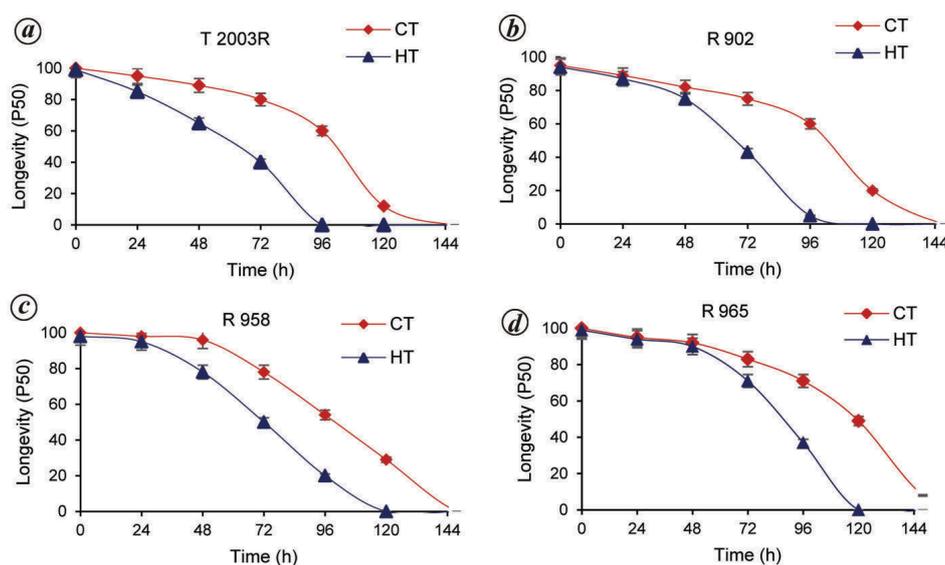


Figure 1. Survival curve of seeds aged for 144 h from two treatments for four wheat genotypes, viz. (a) T 2003R, (b) R 902, (c) R 958, (d) R 965. CT, Seeds harvested from the glasshouse; HT, Seeds harvested from the growth chamber. Bar represents \pm SE of mean.

indicating high-temperature treatment deteriorate the seed longevity (Figure 1 a–d). The differences in initial viability (k_i) and death time (σ) were significant ($P < 0.05$) for all the genotypes. Hence, the time taken for longevity to fall to 50% showed a difference (Table 3). Differences in the pattern of decrease in subsequent longevity in HT were observed earlier than in control (CT), as a consequence of poor histo-differentiation, short seed-filling phase and earlier seed desiccation, despite less effect on the ability to germinate. The major events and regulatory pathways during seed development, especially in the late phase, affect its subsequent ability to germinate, desiccation tolerance ability, and longevity, including chlorophyll degradation and accumulation of raffinose family oligosaccharides, LEA proteins, RNA and heat shock proteins²³. These results are also in broad agreement with those where damage by high temperature at post-anthesis and seed development resulted in short seed longevity in bean²⁴ and rice²⁵. High temperature-mediated physiological and molecular imbal-

ances in these pathways during seed development may damage seed quality and subsequent longevity in seeds harvested from the growth chamber.

Seed and seedling vigour

High temperatures after anthesis and seed development can increase seed cell membrane damage²⁶ and thus increase electrolyte leakage from seeds. In the present study, EC of water-soluble leachates of imbibed seeds increased rapidly with increasing time (0–24 h) in all the seeds harvested from the glasshouse and growth chamber at maturity (Figure 2). However, seeds harvested from the growth chamber had high solute leakage during the imbibition period, reflected in the high EC ($34.5 \mu\text{S cm}^{-1} \text{g}^{-1}$ seed), regardless of genotype and imbibition period (h). The seeds of genotype R902 harvested from the growth chamber showed the lowest seed membrane integrity and highest EC ($37.3 \mu\text{S cm}^{-1} \text{g}^{-1}$ seed) compared to the other genotypes.

Table 4. Comparison of subsequent seed and seedling vigour in the four wheat genotypes affected by post-anthesis high temperature

Genotype	CT				HT			
	SRME	SL	SDW	R : S ratio	SMRE	SL	SDW	R : S ratio
T 2003R	1.18 ^c	26.6 ^a	0.87 ^a	1.66 ^a	0.62 ^c	15.8 ^a	0.63 ^a	1.30 ^a
R 902	1.94 ^b	26.9 ^a	0.91 ^a	1.60 ^a	0.88 ^b	17.2 ^a	0.69 ^a	0.91 ^b
R 958	0.81 ^d	23.9 ^a	0.87 ^a	1.36 ^a	0.44 ^{bc}	16.2 ^a	0.78 ^a	1.06 ^b
R 965	2.23 ^a	25.1 ^a	0.81 ^a	1.49 ^a	2.03 ^a	17.8 ^a	0.79 ^a	0.86 ^b

SRME, Seed mobilization reserve efficiency; SL, Seedling length; SDW, Seedling dry weight; R : S ratio, Root-to-shoot ratio.

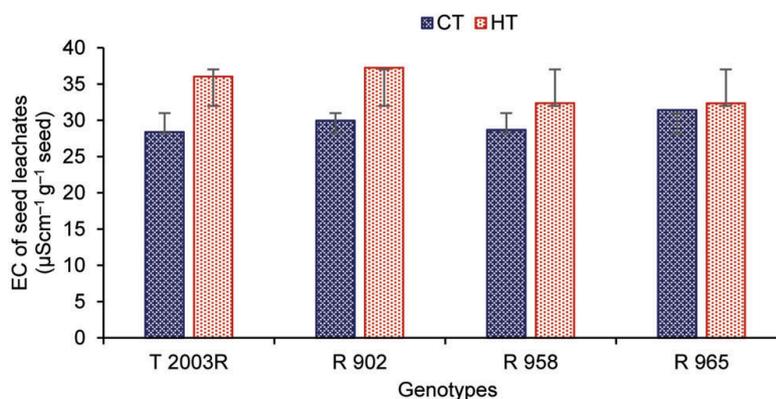


Figure 2. Seed coat membrane integrity in the four wheat genotypes (T 2003R, R 902, R 958 and R 965) from two treatments through electrical conductivity of seed leachates solution. \pm SD from mean.

SRME was significantly influenced by temperature after anthesis and seed development. A decrease in SRME in seeds by high-temperature exposure could be due to their poor vigour (Table 4), having failed to accumulate the respiratory product into a seedling, despite the increased rate of respiration²⁷. Reserve mobilization efficiency of dried seeds harvested from the glasshouse was higher ($1.54 \text{ mg}^{-1} \text{ seed}$) compared to that from the growth chamber and varied significantly in genotypes ($P < 0.001$). These results agree with other studies that have revealed that the respiratory pathway does not link with an accumulation of respiratory products as root and shoot biomass and could have led to thermal dissipation of respiratory energy by altering the oxidase pathway or cyanide-resistant pathway at high temperature¹⁹.

High-temperature exposure during seed development affected the subsequent seedling vigour in all the seeds harvested from the growth chamber ($P < 0.05$). However, there was no significant variability among the genotypes ($P > 0.05$) (Table 4). The seedling length produced by seeds from the glasshouse was more (25.6 cm) than that from the growth chamber (16.8 cm). This decrease in seedling length has been attributed to poor seed vigour achieved by low seed-filling duration and early post-anthesis desiccation at high temperature^{6,19}. There was a significant interaction of temperature for the seedling dry weight ($P < 0.05$), but not for the genotypes. Seeds developing and attaining maturity at high temperatures may have

low vigour due to an increased rate of drying and rapid desiccation, resulting in improper seed maturation and reserve accumulation in wheat¹¹. The root-to-shoot ratio is an indicator of balanced seedling development and high seed vigour. The root : shoot ratio of seedlings produced from seeds was also significantly affected by temperature treatment ($P < 0.05$), though genotypic interaction was nonsignificant. Genotype R 965 failed to provide a balanced root : shoot ratio which was low in comparison to mean of four genotypes (0.86). Decreased root : shoot ratio was also found in previous studies in other genotypes of wheat due to poor seed vigour⁶.

Conclusion

The present study focuses on the seed quality of wheat damaged by high-temperature exposure at post-anthesis, and subsequent seed development and maturation. Germination potential is not the only indicator of seed quality damage, but the subsequent seed longevity is also vulnerable to high-temperature exposure during seed development, which is a major concern for the seed industry and policymakers in India. Seed-quality damage due to extreme environmental conditions, coincides with temporal phenology of wheat crop needs to be assessed for better adaption in near future.

Conflict of interest: None.

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