# CLIMATE CHANGE AND AGRICULTURE RESEARCH PAPER
# Effects of elevated CO$_2$ and temperature on seed quality

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## SUMMARY

Successful crop production depends initially on the availability of high-quality seed. By 2050 global climate change will have influenced crop yields, but will these changes affect seed quality? The present review examines the effects of elevated carbon dioxide (CO$_2$) and temperature during seed production on three seed quality components: seed mass, germination and seed vigour.

In response to elevated CO$_2$, seed mass has been reported to both increase and decrease in C$_3$ plants, but not change in C$_4$ plants. Increases are greater in legumes than non-legumes, and there is considerable variation among species. Seed mass increases may result in a decrease of seed nitrogen (N) concentration in non-legumes. Increasing temperature may decrease seed mass because of an accelerated growth rate and reduced seed filling duration, but lower seed mass does not necessarily reduce seed germination or vigour.

Like seed mass, reported seed germination responses to elevated CO$_2$ have been variable. The reported changes in seed C/N ratio can decrease seed protein content which may eventually lead to reduced viability. Conversely, increased ethylene production may stimulate germination in some species. High-temperature stress before developing seeds reach physiological maturity (PM) can reduce germination by inhibiting the ability of the plant to supply the assimilates necessary to synthesize the storage compounds required for germination.

Nothing is known concerning the effects of elevated CO$_2$ on seed vigour. However, seed vigour can be reduced by high-temperature stress both before and after PM. High temperatures induce or increase the physiological deterioration of seeds. Limited evidence suggests that only short periods of high-temperature stress at critical seed development stages are required to reduce seed vigour, but further research is required.

The predicted environmental changes will lead to losses of seed quality, particularly for seed vigour and possibly germination. The seed industry will need to consider management changes to minimize the risk of this occurring.

## INTRODUCTION

With global change, atmospheric carbon dioxide (CO$_2$) concentration is predicted to rise from today's value of *c*. 370–550 ppm by 2050 and could reach between 730 and 1010 ppm by 2100 (Solomon *et al.* 2007). This, combined with other atmospheric changes, is projected to increase global mean temperatures by 1·4–5·8 °C (Houghton *et al.* 2001). Jaggard *et al.* (2010) concluded that CO$_2$ enrichment was likely to allow yield increases of *c*. 13% in most C$_3$ crops, but yields of C$_4$ crops are not expected to change. However, increasing temperatures may negate these increases in C$_3$ crops, particularly if they occur during reproductive growth (Allen & Boote 2000; Wheeler *et al.* 2000). Gornall *et al.* (2010) noted that extreme weather events are more likely to occur in the changed climate of the future, and predicted that over much of the world's crop land, maximum daily temperature highs may be increased by around 3 °C by 2050.

A major challenge ahead for those involved in the seed industry, therefore, is to provide cultivars that can maximize future crop production in a changing

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climate (Ainsworth *et al.* 2008*a*; Bruins 2009; Ceccarelli *et al.* 2010). Ainsworth *et al.* (2008*b*) considered that this will be possible within a decade.

Successful crop production in any environment depends initially on the quality of the seed being sown. The term 'seed quality' is used in practice to describe the overall value of a seed lot for its intended purpose (Hampton 2002), and includes the components of species and cultivar purity, seed mass (size), physical purity, germination, vigour, moisture content and seed health. The present review examines the effects of increased $CO_2$ and increased temperature on three of these seed quality components, seed mass, germination and vigour.

## SEED MASS

Within the seed industry, seed size is commonly denominated by the mean seed weight, often expressed as 'thousand seed weight', the weight of 1000 seeds of the seed lot. However, seed size refers to volume, while seed weight and seed mass refer to density, which are different traits (Castro *et al.* 2006). Seed mass in crop cultivars is considered the least variable of the seed yield components because of plant breeding for increased seed uniformity (Almekinders & Louwaars 1999) and the removal of small seeds during the seed cleaning processes. Factors affecting seed mass, including genetic factors, water availability and nutrient availability were reviewed by Castro *et al.* (2006).

Increased atmospheric $CO_2$ concentrations might be expected to increase seed mass because of increased plant assimilate availability (Jablonski *et al.* 2002), but the reported effects of elevated $CO_2$ are highly variable among species (Miyagi *et al.* 2007; Hikosaka *et al.* 2011). Different studies have reported seed mass to increase (Musgrave *et al.* 1986; Baker *et al.* 1989; Dijkstra *et al.* 1999; Steinger *et al.* 2000; Quaderi & Reid 2005), show no change (Edwards *et al.* 2001; Prasad *et al.* 2002) and decrease (Huxman *et al.* 1998; Smith *et al.* 2000; Wagner *et al.* 2001) in response to elevated $CO_2$. Jablonski *et al.* (2002) conducted a meta-analysis of 184 $CO_2$ enrichment studies from 79 species and found a mean 4% increase in seed mass, with the response being greater in legumes ($+8\%$) than non-legumes ($+3\%$), and absent in $C_4$ plants. Considerable variation in seed mass in response to elevated $CO_2$ was also reported within species. Hikosaka *et al.* (2011) reported the enhancement ratio of seed mass per plant (seed mass in

elevated $CO_2$/seed mass in ambient $CO_2$) ranged from 0·75 to 4·45 in rice (*Oryza sativa* L.), from 0·93 to 1·87 in soybean (*Glycine max* (L.) Merrill), and from 0·88 to 2·07 in wheat (*Triticum aestivum* L.).

Jablonski *et al.* (2002) found a 14% reduction in seed nitrogen (N) in response to elevated $CO_2$ averaged across all 79 species in their analysis, although there was significant variation; seed N was not reduced in legumes, but was reduced in non-legumes. Hikosaka *et al.* (2011) suggested that seed mass could only increase when N became more available at elevated $CO_2$ concentrations. Legumes may use increased carbon (C) gain under elevated $CO_2$ for increased nitrogen fixation (Allen & Boote 2000), and can therefore increase seed mass without decreasing seed N. In non-legumes, seed mass increases may result in a decrease in seed N concentration. In some species, this decreased seed N may be at the expense of seed quality (Fenner 1991; Andalo *et al.* 1996).

Increasing temperature can negate the response to elevated $CO_2$ (Prasad *et al.* 2002) and may reduce seed mass (Spears *et al.* 1997) because of the resulting acceleration in seed growth rate (dry matter accumulation) and reduction in the duration of seed filling (Weigand & Cueller 1981; Young *et al.* 2004). However, a reduction in the rate of seed dry matter accumulation can also occur (Gibson & Paulsen 1999) and seed mass has also been reported not to change, or sometimes increase, in response to temperature increase (Peltonen-Sainio *et al.* 2011). A reduced seed mass for a seed lot does not necessarily mean a loss in other seed quality attributes. Many studies have shown no relationship between seed mass and germination (Castro *et al.* 2006) or seed mass and seed vigour (Powell 1988).

## GERMINATION

For high-quality seed lots, germination (defined as the process that begins with imbibition and which is completed by the production of a normal seedling; ISTA 2011) is desired by the seed industry to be as close to 100% as possible. The germination of a seed lot can be negatively affected by the conditions the seeds are exposed to during harvesting, drying, cleaning and storage, but can also be reduced by unfavourable environmental conditions in the field during seed growth and development (Dornbos 1995), particularly temperature, rainfall and relative humidity (Egli *et al.* 2005).

Table 1. *Effect of temperature during seed development on seed germination and seed vigour of two soybean cultivars (adapted from Spears* et al. *1997)*

| | Temperature regime and duration* | | | | | |
| | 27/22 °C | | 33/28 °C | | 38/33 °C | |
| | R5-PM | R5-R8 | R5-PM | R5-R8 | R5-PM | R5-R8 |
|---|---|---|---|---|---|---|
| Germination (%) | | | | | | |
| McCall† | 100 | 100 | 98 | 100 | 94 | 63 |
| Hutchenson | 100 | 100 | 99 | 98 | 57 | 14 |
| Germination (%) after accelerated ageing*‡ | | | | | | |
| McCall† | 98 | 100 | 73 | 86 | 8 | 7 |
| Hutchenson | 98 | 95 | 43 | 86 | 2 | 1 |
| Conductivity‡ (µS/cm/g) | | | | | | |
| McCall† | 5·5 | 5·4 | 7·0 | 6·3 | 16·1 | 23·9 |
| Hutchenson | 6·5 | 6·2 | 9·1 | 10·6 | 29·8 | 35·9 |

* Day/night temperatures with 10 h at the day temperature; R5 = beginning of seed fill; PM = physiological maturity; R8 = harvest maturity.
† Soybean cultivars; McCall = indeterminate growth habit; Hutchenson = determinate growth habit.
‡ Seed vigour tests.

Seed germination in response to elevated $CO_2$ has been reported to decrease (Farnsworth & Bazazz 1995; Andalo *et al.* 1996; Quaderi & Reid 2005), show no change (Huxman *et al.* 1998; Steinger *et al.* 2000; Thomas *et al.* 2009; Way *et al.* 2010) or increase (Wulf & Alexander 1985; Ziska & Bunce 1993; Edwards *et al.* 2001). The responses vary among species (Ziska & Bunce 1993) and genotypic variation has also been reported (Andalo *et al.* 1996).

Elevated $CO_2$ has been shown to increase the C/N ratio in seeds (Huxman *et al.* 1998; Steinger *et al.* 2000; He *et al.* 2005) and in non-legumes, seed N reduction can occur when seed mass is increased by elevated $CO_2$ (see previous section). High seed N is an advantage for germination rate (Hara & Toriyama 1998), but not germination *per se*. However, a change in C/N ratio can lead to a decrease in seed protein content, resulting in a reduction in the ability of the seed to supply the amino acids required for the *de novo* protein synthesis necessary for embryo growth in the germinating seed. This could reduce seed viability (Andalo *et al.* 1996).

Elevated $CO_2$ also increases ethylene production (Esashi *et al.* 1986) and Ziska & Bunce (1993) suggested that an increased availability of ethylene may have been the reason for the stimulated germination they reported. Ethylene is implicated in the promotion of germination of non-dormant seeds of many species (Leubner-Metzger 2006).

In different plant species, sometimes even small differences in temperature during seed development and maturation can have an influence on germination (Gutterman 2000). High temperatures during seed filling frequently disrupt normal seed development, which increases the proportion of seeds that are shrivelled, abnormal and are of lower quality (Spears *et al.* 1997). However, it has been shown that after removal of these seeds, the germination of the remaining seeds decreases as mean maximum temperature during seed filling increases (Khalil *et al.* 2001, 2010; Egli *et al.* 2005; Thomas *et al.* 2009; Table 1). High-temperature stress before the developing seeds achieve physiological or mass maturity (PM – the end of the seed filling phase) is likely to inhibit the ability of the plant to supply the seeds with the assimilates necessary to synthesize the storage compounds required during the germination process (Dornbos & McDonald 1986), and/or the seeds suffer physiological damage (see McDonald & Nelson 1986; Coolbear 1995; Powell 2006) to the extent that the ability to germinate is lost.

High-temperature stress after PM can also sometimes reduce germination (Green *et al.* 1965; Table 1), but more often reduces seed vigour (see next section).

The relationship between temperature during seed development and subsequent seed germination requires further investigation. For example in soybean, temperatures (32–38 °C) that reduced the germination

Table 2. *Effect of high temperature (30/25 °C) for 4 days at different stages of seed development and maturation in two cultivars of pea (*Pisum sativum *L.) on seed quality components (adapted from Shinohara* et al. *2006b)*

| Stage at treatment* | Mean seed weight (g) | | Germination (percentage) | | Hollow heart (proportion) | | Average conductivity† (µS/cm/g) | |
|---|---|---|---|---|---|---|---|---|
| | Alderman‡ | E. Onward‡ | Alderman | E. Onward | Alderman | E. Onward | Alderman | E. Onward |
| Control | 379 | 350 | 95 | 93 | 0·04 | 0·00 | 220 | 363 |
| S1 | 309 | 289 | 84 | 97 | 0·01 | 0·03 | 315 | 368 |
| S2 | 326 | 262 | 86 | 92 | 0·24 | 0·04 | 367 | 374 |
| S3 | 391 | 345 | 86 | 96 | 0·08 | 0·00 | 339 | 467 |
| S4 | 378 | 362 | 88 | 98 | 0·01 | 0·00 | 371 | 475 |
| S5 | 376 | 337 | 92 | 96 | 0·04 | 0·00 | 424 | 420 |
| S.E.D. (D.F.) | 11 (18) | 9 (18) | 6·7 (18) | 3·9 (18) | 0·054 (18) | 0·020 (18) | 31 (140) | 123 (140) |

\* S1 = beginning of seed filling (810 mg/g SMC); S2 = rapid seed filling (700 mg/g SMC); S3 = PM (630 mg/g SMC); S4 = beginning of desiccation (440 mg/g SMC); S5 = harvest maturity (230 mg/g SMC); SMCs are mean of the two cultivars.
† Data are the average of 25 results in the single seed conductivity vigour test.
‡ Pea cultivars.
S.E.D. (between cultivars) = 10 (mean seed weight), 5·4 (germination), 0·041 (hollow heart) and 71 (average conductivity).

of some cultivars in controlled environments did not vary during seed filling, in contrast to field temperatures which can vary substantially (Egli *et al.* 2005), and the plants were at these temperatures from anthesis until seed harvest. However, there may be critical periods during seed development when seeds are particularly sensitive to temperature (Egli *et al.* 2005; Shinohara *et al.* 2006a). This was investigated for pea (*Pisum sativum* L.) by Shinohara *et al.* (2006a), who showed that when plants were exposed to a day/night temperature of 30/20 °C for 4 days (= 240 °C h above a base temperature (Tb) of 25 °C) at the beginning of seed filling and then returned to the field until seed harvest, germination was significantly reduced in one of two cultivars (Table 2). Exposure to these conditions at later stages of seed development did not affect germination.

SEED VIGOUR

While the term germination has long been used to describe the planting value of a seed lot (ISTA 2011), when conditions in the seed bed are less than optimal the germination test is a poor predictor of field emergence (Dornbos 1995), suggesting that a further physiological aspect to seed quality exists – seed vigour (Powell 2006). Seed vigour is defined by ISTA (2011) as 'the sum of those properties that determine the activity and level of performance of seed lots of acceptable germination in a wide range of

environments', or more simply, the ability of a high germination seed lot to emerge under seed-bed stress.

While there have been reports that elevated $CO_2$ increases or decreases seedling vigour (i.e. growth rate or biomass production) because of the effect on seed mass (Huxman *et al.* 1998; Steinger *et al.* 2000), there have been no reports on the effects of elevated $CO_2$ on seed vigour.

Seed vigour is reduced by high-temperature stress before PM (Spears *et al.* 1997; Egli *et al.* 2005; Shinohara *et al.* 2006a; Table 1) and after PM (TeKrony *et al.* 1979, 1980; Gibson & Mullen 1996; Hampton 2000). Shinohara *et al.* (2008) examined the relationship between vigour test results for 262 garden pea seeds lots produced in New Zealand and climate data in five regions over four consecutive production seasons, and while regional and seasonal variation for vigour occurred, these variations were significantly associated with temperature during seed development – generally the higher the temperature, the lower the seed vigour.

The susceptibility of seeds to loss of vigour following high-temperature stress depends on the stage of development (Shinohara *et al.* 2006a). Using hollow heart, a physiological disorder of germinating pea seeds (Halligan 1986) as a seed vigour indicator (Castillo *et al.* 1993), Shinohara *et al.* (2006a) found in a field study that hourly thermal time (HTT, measured in degree hours, °Ch, Tb = 25 °C) when seeds were at the green-wrinkled pod stage (700–800 mg/g seed

Table 3. *Effect of temperature during seed development and maturation on nucleotide content, mitochondrial respiration rate and adenylate energy charge (AEC) of excised wheat embryos after 4 h imbibition (adapted from Grass & Burris 1995)*

|  | Temperature regime* | | |
|---|---|---|---|
|  | 20/15 °C | 28/21 °C | 36/29 °C |
| Nucleotide content† (nmol/g) | | | |
| AMP | 400 | 370 | 448 |
| ADP | 571 | 518 | 412 |
| ATP | 452 | 393 | 141 |
| Total | 1422 | 1180 | 1001 |
| State 3 mitochondrial respiration rate (nmol $O_2$/min) | 9·7 | 6·9 | 5·3 |
| AEC‡ | 0·52 | 0·51 | 0·35 |

\* Day/night with 8 h day temperature and 16 h night temperature.
† AMP, adenosine monophosphate; ADP, adenosine diphosphate; ATP, adenosine triphosphate.
‡ AEC expressed as the ratio (ATP+0·5ADP/ATP+ADP+AMP)=energy status of the seed (Atkinson 1968).

moisture content (SMC)) was significantly correlated with hollow heart incidence at harvest, and that 100 °Ch were required to induce the condition. There was no such relationship between HTT and hollow heart after PM. While there were cultivar differences, for one cultivar there was a linear increase in hollow heart incidence as the degree hours (°Ch) increased. In a follow-up controlled environment study, Shinohara *et al.* (2006*b*) confirmed this result, by demonstrating that exposure to day/night temperatures of 30 and 25 °C, respectively, for 4 days (240 °Ch, Tb=25 °C) at the green-wrinkled pod stage induced hollow heart, but exposure to the same conditions at the beginning of seed fill (>800 mg/g SMC), PM (550–650 mg/g SMC) or after PM did not (Table 2). Single-seed conductivity (which is an indicator of cell membrane integrity – see Powell 2006) was increased only after exposure of the developing seeds to the high temperature at or after PM, and not before (Table 1).

Seed vigour loss is associated with seed physiological deterioration (Powell 1988; Hampton & Coolbear 1990), and lipid peroxidation is the most frequently cited cause (McDonald 1999). Lipid peroxidation causes cellular degeneration through free radical assault on important cellular molecules and structures (Wilson & McDonald 1986). McDonald (1999), in his model of seed deterioration, proposed four types of cell damage, viz. mitochondrial dysfunction, enzyme

Table 4. *Effect of sowing date at the same field site on HTT (Tb = 25 °C) and the number of hours of exposure to temperature exceeding 25 and 30 °C during the period when SMC was between 700 and 800 mg/g for garden pea cvar Alderman (adapted from Shinohara* et al. *2006*a*).*

| Sowing date | Period† | SMC 700–800 mg/g | | | |
|---|---|---|---|---|---|
|  |  | HTT (°Ch) | No. of hours | | PM* |
|  |  |  | >25 °C | >30 °C |  |
| 26 Sep | 31 Dec–4 Jan | 198 | 45 | 19 | 11 Jan |
| 21 Oct | 8 Jan–13 Jan | 106 | 38 | 8 | 21 Jan |
| 19 Nov | 1 Feb–7 Feb | 21 | 5 | 0 | 18 Feb |

\* Dates when seeds were adjudged to have reached PM.
† Period when SMC was between 700 and 800 mg/g.

inactivation, membrane degradation and genetic damage.

Grass & Burris (1995) reported that high-temperature stress of the parent plant caused mitochondrial degeneration and reduced adenosine triphosphate (ATP) accumulation, energy levels and rates of oxygen uptake in imbibing wheat embryos (Table 3), providing clear evidence for metabolic changes at the mitochondrial level in early seed germination in response to heat stress during seed development and maturation. High temperatures during reproductive growth increase seed cell membrane damage (Nilsen & Orcutt 1996; Shinohara *et al.* 2006*b*) so that electrolyte leakage from seeds is increased (Castillo *et al.* 1994; Spears *et al.* 1997; Shinohara *et al.* 2006*b*). High leachate conductivity in pea has been associated with dead/deteriorating tissue on the abaxial surface of the cotyledons (Powell 1985; Shinohara *et al.* 2006*b*), and on the adaxial cotyledonary surface for hollow heart (Don *et al.* 1984; Shinohara *et al.* 2006*b*). However, temperature stress also results in damage to the shoot apical meristem of the embryonic axis (Fu *et al.* 1988; Senaratna *et al.* 1988). Membrane disorganization would reduce mitochondrial efficiency and may allow the release of peroxidative enzymes capable of causing subsequent cellular damage after imbibition has begun (McDonald 1999).

If heat stress leads to mitochondrial dysfunction and membrane damage, it may also result in reduced enzyme activity (e.g. decreased α-amylase – Shephard *et al.* 1996) and genetic damage (e.g. decreased DNA synthesis – Cruz-Garcia *et al.* 1995). Whether these

and other seed deteriorative changes (see McDonald 1999) occur following heat stress during seed development and maturation is yet to be determined.

## CONCLUSIONS

The environment during seed development and maturation can significantly reduce seed quality (Dornbos 1995; Gusta *et al*. 2004; Egli *et al*. 2005; Shinohara *et al*. 2008), particularly seed vigour. How likely is it that elevated $CO_2$ levels and temperature increases of up to 3 °C by 2050 will further increase this loss of seed quality? To answer this question accurately will require substantially more research in order to determine the critical periods during seed development when seeds are sensitive to environmental stresses, and for temperature, how this interacts with the duration of exposure to elevated temperatures which are deleterious to seed quality. For example, Shinohara *et al*. (2006*b*) found that during the rapid seed filling stage in pea, a temperature of 30/25 °C for 2 days (120 °Ch at Tb = 25 °C) did not induce hollow heart, but 4 days induced hollow heart in one cultivar (see Table 2), and 6 days (360 °Ch) induced the condition in both cultivars used (0·43 in cvar Alderman and 0·23 in cvar Early Onward).

From the information that is available, it can be concluded that predicted environmental changes will lead to the increased occurrence of loss of seed quality, particularly seed vigour and possibly germination. While seed mass will also change, this does not necessarily imply any negative effect on germination or vigour. To minimize the risk of reductions in seed quality the seed industry will therefore have to consider:

(a) Moving seed production to the limits of adaptation either in latitude (northern or southern) or in elevation (highland and mountainous regions) in order to reduce the chances of environmental stress (Egli *et al*. 2005; Shinohara *et al*. 2008).
(b) Changing sowing date so that seed filling occurs at lower temperatures (Castillo *et al*. 1994; Egli *et al*. 2005; Shinohara *et al*. 2006*a*). The latter authors demonstrated that for the pea cultivar Alderman, HTT (Tb = 25 °C) during the rapid seed filling stage was 198, 106 and 21 °Ch for sowings at the same site in September, October and November, respectively, and the number of hours during this stage when temperature exceeded 25 or 30 °C also reduced as sowing date was delayed (Table 4).
(c) Exploring genotypic differences in the ability to acquire and retain good seed quality in stressful environments, firstly among existing cultivars (Spears *et al*. 1997; Shinohara *et al*. 2006*a*), and in the breeding of new cultivars (Ainsworth *et al*. 2008*b*).

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