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REVIEW

Markers of seed quality: from present to future

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Abstract

Methods of evaluation of seed quality providing accurate prediction of seed performance under field conditions are needed by the seed industry. Various physiological tests, i.e. germination tests in suboptimal conditions of temperature, oxygenation and water potential of the medium, or accelerated ageing and controlled deterioration allow sensitive differentiation between seed lots. A better understanding of the biochemical, cellular and molecular mechanisms involved in the acquisition of seed vigour during seed development, in the germination process and in seed deterioration during ageing could suggest various markers of seed quality. Among these markers, electrolyte leakage and ethylene production during imbibition, cell-cycle markers (DNA replication, β-tubulin), soluble sugar metabolism (in particular, changes in the raffinose family of oligosaccharides), proteins (11S globulin B-subunit, late embryogenesis abundant protein, heat-shock protein) and the efficiency of reactive oxygen species scavenging through antioxidant defence systems (e.g. catalase activity) have potential for the evaluation of the state of seed maturity, seed performance and effectiveness of seed priming treatments. Use of global approaches such as transcriptomic, proteomic or metabolomic analysis could also result in the identification of new markers.

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Introduction

Seed germination is subjected to very precise regulation, the complexity of which originates both in the action of various external factors (temperature, oxygen, light, water potential of the medium) and in characteristics within the seeds themselves (Bewley and Black, 1994; Bewley, 1997). Germination of a seed lot results from the functioning of the genome, but is also largely dependent on numerous factors which intervene throughout the seed life, from its development on the parent plant up until sowing, including storage conditions (Priestley, 1986; Bewley and Black, 1994). A seed population is therefore heterogeneous, which leads to a lack of uniform performance, especially when environmental conditions at sowing are not optimal. Seed quality includes genetic purity, health quality and seed germination and vigour (McDonald, 1998).

Successful stand establishment requires high-quality seeds, i.e. seeds that: (1) germinate completely; (2) germinate quickly and simultaneously; (3) produce normal and vigorous seedlings; and (4) have germination which shows little sensitivity to external factors, enabling them to germinate in a wide range of agro-climatic conditions (Corbineau and Côme, 2006). To these criteria, storability of the seeds can be added. For seed companies a major challenge toward improving crop yield is a better control of seed vigour. Therefore methods of evaluation of seed quality, providing accurate prediction of seed performance under field conditions, must be developed. Such methods are also

required for assessing the effectiveness of technologies used to enhance seed performance, such as priming or seed health treatments. The objective of this short review is to demonstrate that a better understanding of the cellular, molecular and biochemical mechanisms involved in the acquisition of seed vigour during seed development, in the germination process and in seed deterioration during ageing, could yield new markers of seed quality, besides the classical physiological tests.

Overview of acquisition, loss and improvement of seed vigour

Seed dehydration is the normal terminal event in the development of 'orthodox' seeds (Vertucci and Farrant, 1995) that ensures the switch from a developmental mode to a germination one (Kermode, 1997). The involvement of the maturation-drying phase in the acquisition of seed vigour is subject to discussion. Some authors have claimed that seeds attain maximum germinability at the end of seed-filling phase and therefore age (TeKrony and Egli, 1997), others found that storability, which can be considered as an indicator of vigour, improves during maturation drying (Sanhewe and Ellis, 1996; Kermode, 1997; Bailly *et al.*, 2001). Numerous cellular and biochemical events appear to be associated with seed maturation and, consequently, acquisition of desiccation tolerance; these include modification of ultrastructural characteristics such as cellular vacuolization, synthesis of late embryogenesis abundant (LEA) proteins or heat-shock proteins (HSP), accumulation of the raffinose family oligosaccharides and activation of antioxidant defence systems (Vertucci and Farrant, 1995; Kermode, 1997; Bailly, 2004; Buitink and Leprince, 2008; Leprince and Buitink, 2010).

Loss of seed vigour, and subsequently of seed viability, is highly dependent on temperature and seed moisture content (Priestley, 1986). Free radicals and lipid peroxidation are widely considered to be major contributors to seed deterioration, including loss of membrane integrity, reduced energy metabolism, impairment of RNA and protein synthesis, and DNA degradation (Priestley, 1986; Hendry, 1993; Bailly *et al.*, 1996; McDonald, 1999; Bailly, 2004). Proteomic analyses revealed that the loss in seed vigour resulted in changes in proteins in the dry seeds and in the inability of the low vigour seeds to display a normal proteome during germination (Job *et al.*, 2005; Oracz *et al.*, 2007; Bailly *et al.*, 2008; Rajjou and Debeaujon, 2008; Rajjou *et al.*, 2008). Antioxidant metabolites and enzymatic detoxifying mechanisms (catalase, glutathione reductase, superoxide dismutase) limit lipid oxidation and oxidative damage to proteins and nucleic acids (McDonald, 1999; Bailly, 2004; Bailly *et al.*, 2008; Rajjou and Debeaujon, 2008). Besides these mechanisms, repair of protein damage through the activity of L-isoaspartyl methyltransferase might also play an important role in seed longevity and vigour (Ogé *et al.*, 2008).

Seed germination has been characterized by a triphasic curve of water uptake, with a rapid imbibition (phase I) followed by a plateau phase when moisture content exceeds 40–50% [fresh weight (FW) basis] (phase II), and a further increase in water uptake associated with radicle elongation (phase III) (Bewley and Black, 1994; Bewley, 1997). Phase I results in a gradual resumption of cellular metabolism (respiratory activity, RNA and protein synthesis, initiation of reserve degradation, etc.); phase II is associated with various events, including an accumulation of osmotic solutes, activation of H^+ ATPase in the plasmalemma and weakening of the surrounding tissues; whereas phase III corresponds to radicle growth. Recent proteomic and transcriptomic analysis of seeds has led to the identification of specific proteins which might contribute to seed vigour (Gallardo *et al.*, 2001; Rajjou *et al.*, 2004; Job *et al.*, 2005; Catusse *et al.*, 2008a, b). Using sugar-beet seed as a model, Catusse *et al.* (2008b) have been able to reconstruct the metabolic pathways involved in germination and vigour, and to demonstrate that the germination vigour is built up during seed maturation on the parent plant.

Seed priming is widely used for enhancing seed performance by improving the rate of germination and decreasing the seed sensitivity to external factors. This technique is based on the progress of germination, and the objective of priming is to allow a controlled water uptake by the seeds up to the end of phase II, before the radicle protrudes from the seed coat (Corbineau and Côme, 2006). Priming improves germination in a wider range of temperatures and in hypoxia, and also restores the germination of aged seeds (Bailly *et al.*, 1998). Modulating vigour by ageing and priming allows seed batches of various vigour to be obtained, the proteomic and transcriptomic analysis of which may result in the identification of new markers of quality (Gallardo *et al.*, 2001; Rajjou *et al.*, 2006; Catusse *et al.*, 2008a, b).

Which germination tests for the assessment of seed vigour?

Official germination testing is performed using rules produced by the International Seed Testing Association (ISTA) or the Association of Official Seed Analysts (AOSA), prescribing substrate (paper, sand), moisture (quantity of water to moist the germination substrate, quality of water), light, temperature

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(constant or alternating temperatures) and dormancy-breaking techniques when required. These tests are usually carried out under near-optimal conditions for germination (ISTA, 2006), and therefore give information about the viability of the seed population, but do not predict its field performance when the sowing conditions are generally not optimal.

Measurements of seedling dry weight (soybean, maize) or shoot elongation (barley, wheat, oat, maize, ryegrass and fescue grass) have also been developed to evaluate growth potential. The topographical tetrazolium test (TTZ) allows seed viability to be determined, measuring the red staining of living tissues after reducing the colourless tetrazolium salt to a red, non-diffusible dye, formazan, catalysed by dehydrogenase activity (Moore, 1973). This test is very suitable when seed germination is difficult or in the presence of dormancy.

Besides the ISTA tests, various germination tests are used in order to predict the behaviour of a seed lot at sowing. They are based on the kinetic criteria of germination under suboptimal conditions (too low or too high temperatures, low water potential of the medium, hypoxia, high salinity, etc.). Germination rates, expressed as mean germination time (MGT) or the time to attain 50% germination, are often used to evaluate seed vigour. Physiological tests based on the sensitivity/tolerance of seeds to stress during germination are also often performed to evaluate seed vigour or to discriminate among different batches. In the cold test, for example, seeds are imbibed for 4–7 d at low temperature (usually 10°C) and then germinated at 20–25°C for the assessment of normal seedlings. This is widely used for maize and vegetable sweet corn (Van Waes, 1995; McDonald, 1999; Nijenstein and Kruse, 2000); similar tests can be used for soybean.

The responsiveness of seeds to ageing is considered to be a vigour test and is used for numerous species. The accelerated ageing test consists of placing seeds at high relative humidity (75–100%) and warm temperature (35–45°C) (Delouche and Baskin, 1973; TeKrony, 1993; TeKrony and Egli, 1997). The controlled deterioration test differs from accelerated ageing by imbibing seeds to a precise water content (generally between 19 and 24% FW) before the warm temperature treatment (Powell and Matthews, 1981; Powell, 1995; TeKrony and Egli, 1997). It provides information about the tolerance of seeds to stress and on their storability potential (Priestley, 1986).

Which biological, biochemical and cellular markers for seed vigour?

Understanding the mechanisms involved in the acquisition of quality during seed development, loss of quality during seed ageing and in the germination process, may allow the identification of three main groups of markers for the assessment of seed vigour: (1) indicators of cell deterioration [membrane damage, accumulation of reactive oxygen species (ROS), protein carbonylation, RNA oxidation, etc.]; (2) indicators of the protective/defence system effectiveness (soluble sugars, specific proteins, antioxidant contents, antioxidant defence enzymes, such as catalase, etc.); and (3) indicators of the germination process (respiratory activity, cell-cycle induction, hydrolytic activity, etc.).

Indicators of membrane properties

Leakage of low molecular weight solutes (sugars, amino acids, ions, etc.) occurs during seed imbibition and is associated with the phase transition of membranes from the dry gel state to a liquid crystalline state. The degree of leakage correlates with the time taken to complete this phase transition and increases with seed deterioration. It is then used as an indicator of the effectiveness of membranes as barriers to solute diffusion, and consequently of seed vigour (Powell, 1986; Hampton, 1995). Low seed quality is generally associated with high leakage during the imbibition phase. However, this test cannot be used for all crops, in particular because of the presence of high sugar contents (sweet corn), a semipermeable membrane (McDonald, 1999) or phenolic compounds in the seed coat. Such a test is recommended by ISTA for large-seeded legumes (Hampton and TeKrony, 1995).

In higher plants, ethylene is mainly synthesized through the pathway from S-adenosyl methionine (SAM) to 1-aminocyclopropane 1-carboxylic acid (ACC), the latter being converted to ethylene through ACC oxidase activity (Yang and Hoffmann, 1984). ACC-dependent ethylene production is a good indicator of membrane deterioration, since the *in vivo* activity of ACC oxidase depends on membrane integrity or properties (Odawara *et al.*, 1977; Porter *et al.*, 1986). Decrease in ACC conversion to ethylene is one of the early indicators of cell membrane damage during dehydration of recalcitrant *Araucaria angustifolia* embryos (Salmen Espindola *et al.*, 1994) and developing pea seeds (Corbineau *et al.*, 2000) or during cold temperature exposure of chilling-sensitive tissues (Chen and Patterson, 1985; Corbineau *et al.*, 1990, 1999). A close relationship between ACC-dependent ethylene production and seed vigour has been reported in various species (Samimy and Taylor, 1983; Gorecki *et al.*, 1991; Khan, 1994; Chojnowski *et al.*, 1997). A curvilinear relationship of germination parameters to ethylene production seems to be fitted by second-degree polynomial and

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logarithmic equations, as suggested by Khan (1994) and a sub-linear relationship exists between ethylene production during the first 20 h of imbibition and the vigour of carrot seeds primed for different durations, as assessed by germination rate (T_{50}) at 20°C (Corbineau, unpublished data).

Indicators of the efficacy of protective systems

In terms of seed germinability, carbohydrate metabolism, specific proteins such as LEA proteins and HSPs, as well as the capacity of seed tissues to protect cellular structures against activated forms of oxygen, are of particular interest (Horbowicz and Obendorf, 1994; Vertucci and Farrant, 1995; Buitink and Leprince, 2008; Leprince and Buitink, 2010). The possibility of repairing injury upon rehydration may also be very important in seed quality.

Oligosaccharides, mainly those of the raffinose family of oligosaccharides (RFO) which accumulate during seed maturation on the parent plant, are considered to contribute to the stabilization of intracellular glasses by increasing cytoplasmic viscosity and the glass-to-liquid transition temperature, which are likely to slow down ageing-related modifications (Bernal-Lugo and Leopold, 1995; Sun, 1997). However, Buitink *et al.* (2000) demonstrated that oligosaccharides are not involved in the stabilization of the glassy state in *Impatiens* and bell pepper seeds that had been osmoprimed. Also, accumulation of soluble sugars during seed maturation depends on the rate of seed dehydration (Blackman *et al.*, 1992; Black *et al.*, 1999; Corbineau *et al.*, 2000) and might be used as indicator of drying conditions. In pea, a clear relationship exists between electrolyte leakage and RFO/sucrose ratio in the cotyledons (Corbineau *et al.*, 2000). Moreover, numerous data (Bernal-Lugo and Leopold, 1992, 1995; Horbowicz and Obendorf, 1994; Lin and Huang, 1994; Sun and Leopold, 1994; Steadman *et al.*, 1996; Sun, 1997; Sinniah *et al.*, 1998) have suggested that seed sugar content, particularly the ratio of oligosaccharides to sucrose, might be used as an indicator of seed storability. Besides sugars, proteins might play an important role in the formation of intracellular glass during dehydration (Sun and Leopold, 1994; Sinniah *et al.*, 1998; Wolkers *et al.*, 2001; Boudet *et al.*, 2006; Tunnacliffe and Wise, 2007). In *Brassica campestris*, Sinniah *et al.* (1998) demonstrated a relationship between potential longevity and both the oligosaccharide/total sugar ratio and the 58 kDa heat-stable protein content. A strong correlation also exists between longevity in *Medicago truncatula* and the level of sucrose and stachyose, as well as some LEA polypeptides (Chatelain, 2011).

The ability of seeds to withstand desiccation during maturation and their tolerance to ageing, i.e. acquisition and loss of seed quality during seed life, might be related, at least partly, to their ability to scavenge ROS to avoid deleterious events (Vertucci and Farrant, 1995). The main detoxifying systems involve enzymes, mainly superoxide dismutase (SOD), catalase (CAT) and enzymes of the ascorbate–glutathione cycle, and antioxidant compounds such as reduced glutathione and ascorbate, and α-tocopherol (Scandalios, 1997; Bailly, 2004). The efficacy of ROS scavenging through antioxidant enzyme activities has been shown to increase during seed development in bean (Bailly *et al.*, 2001) and sunflower (Bailly *et al.*, 2004), and CAT activity is linearly correlated with seed moisture content in sunflower (Bailly *et al.*, 2004). In sunflower seeds, reinvigoration of aged seeds by osmopriming is associated with the restoration of the cell detoxifying defence mechanisms, resulting from the recovery of SOD, CAT and glutathione reductase (GR), and a relationship exists between the germination rate, assessed by T_{50} at 15°C, and antioxidant enzyme activity (Bailly *et al.*, 1997, 1998). There is also a linear relationship between T_{50} at 10°C and CAT activity in seeds of *Brassica napus* aged for different durations (Corbineau, unpublished data). However, it is difficult to establish a clear relationship between antioxidant system activity at harvest and seed quality in wheat (Lehner *et al.*, 2006), sugar-beet and carrot seeds (Corbineau, unpublished data).

Events occurring during the germination process

The rate of oxygen uptake during seed imbibition, before radicle protrusion, is often correlated with seed vigour, as assessed by subsequent rates of germination and seedling growth in pea, *Zea mays, Capsicum annuum* and *Brassica* seeds (Woodstock and Grabe, 1967; Carver and Matthews, 1975, Halpin-Ingham and Sundstrom, 1992; Bettey and Finch-Savage, 1996), but is not a good indicator of the germination of other species (Côme and Corbineau, 1989). In *Brassica*, activities of glucose 6-phosphate dehydrogenase and pyrophosphate:fructose 6-phosphate 1-phosphotransferase were correlated with T_{50} (Bettey and Finch-Savage, 1996). Imbalances in metabolism in aged or low-quality seeds may also result in accumulation of acetaldehyde and ethanol (Priestley, 1986). In canola seed, both compounds appeared to be promising for assessment of seed vigour (Buckley and Buckley, 2009), and 24-h assays for seed deterioration have been developed by Agriculture and Agri-Food Canada.

Identification of biochemical and molecular events associated with germination has emphasized the importance of cell repair (mitochondria, DNA, proteins, etc.), protein synthesis from stored mRNA, initial mobilization of reserves and activation of the cell cycle (Bewley, 1997; Boubriak *et al.*, 1997;

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Ogé *et al.*, 2008; Rajjou and Debeaujon, 2008). The beneficial effects of priming are associated with various metabolic, biochemical, cellular and molecular events, including synthesis of proteins and RNA, degradation of LEA and heat-stable proteins, mobilization of reserves (decrease in oligosaccharides, increase in soluble 11-S globulin B-subunit, etc.), and induction of cell-cycle processes (β-tubulin accumulation, percentage of 4C DNA nuclei). In sugar-beet, pepper and tomato seeds, a positive correlation was found between the induction of DNA replication, measured by the increase in 4C nuclei or the 4C/2C ratio, and the efficacy of the priming treatment (Lanteri *et al.*, 1994; Özbingöl *et al.*, 1999; Sliwinska *et al.*, 1999). However, in tomato, there were some limits to this relationship, in particular when priming was performed at too low or too high a temperature (Özbingöl *et al.*, 1999). There is also a sub-linear relationship between sucrose and oligosaccharide contents, and sucrose/oligosaccharide ratio and the T_{50} at 10°C in carrot seeds (Corbineau and Côme, 2006). A linear relationship was found between the extent of 11S globulin B-subunit and the advancement of priming in sugar-beet seeds (Job *et al.*, 1997), whereas accumulation of endo-β-mannanase is also a good indicator of the priming effect in tomato (Still *et al.*, 1997). However, for the same effectiveness of priming, the accumulation of soluble B-subunit per seed depended on the priming technique used (Capron *et al.*, 2000). In addition, Bailly *et al.* (1997) demonstrated that catalase activity is sub-linearly correlated with the germination rate of primed sunflower seeds.

Conclusion

A better understanding of the biochemical, cellular and molecular mechanisms involved in the acquisition of seed vigour, in the germination process and in seed deterioration would allow various markers to be proposed for assessing seed quality. Some of these markers seem to be promising for evaluating seed maturity, seed performance in suboptimal conditions or/and priming efficiency. However, a single marker is often not enough for a good evaluation of seed quality and, very often, a marker cannot be applied to different species or even to different batches of the same species. For seed companies, the determination of the marker must also be fast and easy to perform in routine.

Seed quality depends on the conditions of seed development and seed storage, and it can be modulated through treatments such as priming. However, it is important to distinguish between markers of advancement of germination (i.e. priming) and those of seed vigour at harvest. Seed quality studies would also benefit from non-invasive techniques for assessing seed viability and vigour. For example, X-ray radiography, a non-destructive method, providing information on mechanically damaged, empty and filled seeds in a batch (Halmer, 2000); chlorophyll fluorescence (Jalink *et al.*, 1998); and infrared thermography, which can be used to predict seed viability in various species (Kranner *et al.*, 2010). Biophysical techniques, such as differential scanning calorimetry, can also be used to detect changes in thermal properties of lipids, which occur during loss of seed vigour or after priming treatment (Walters *et al.*, 2005).

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References

Bailly, C. (2004) Active oxygen species and antioxidants in seed biology. *Seed Science Research* **14**, 93–107.

Bailly, C., Benamar, A., Corbineau, F. and Côme, D. (1996) Changes in malondialdehyde content and in superoxide dismutase, catalase and glutathione reductase in sunflower seeds as related to deterioration during accelerated aging. *Physiologia Plantarum* **104**, 646–652.

Bailly, C., Benamar, A., Corbineau, F. and Côme, D. (1997) Changes in superoxide dismutase, catalase and glutathione reductase activities in sunflower seeds during ageing and subsequent priming. pp. 665–672 *in* Ellis, R.H.; Black, M.; Murdoch, A.J.; Hong, T.D. (Eds) *Basic and applied aspects of seed biology.* Dordrecht, Kluwer Academic Publishers.

Bailly, C., Benamar, A., Corbineau, F. and Côme, D. (1998) Free radical scavenging as affected by accelerated ageing and subsequent priming in sunflower seeds. *Physiologia Plantarum* **104**, 646–652.

Bailly, C., Audigier, C., Ladonne, F., Wagner, M.H., Coste, F., Corbineau, F. and Côme, D. (2001) Changes in oligosaccharide content and antioxidant enzyme activities in developing bean seeds as related to acquisition of drying tolerance and seed quality. *Journal of Experimental Botany* **52**, 701–708.

Bailly, C., Leymarie, J., Lehner, A., Rousseau, S., Côme, D. and Corbineau, F. (2004) Catalase activity and expression in developing sunflower seeds as related to drying. *Journal of Experimental Botany* **55**, 475–483.

Bailly, C., El-Maarouf-Bouteau, H. and Corbineau, F. (2008) From intracellular signaling networks to cell death: the

dual role of reactive oxygen species in seed physiology. *Comptes Rendus Biologies* **331**, 806–814.

Bernal-Lugo, I. and Leopold, A.C. (1992) Changes in soluble carbohydrates during seed storage. *Plant Physiology* **98**, 1207–1210.

Bernal-Lugo, I. and Leopold, A.C. (1995) Seed stability during storage: raffinose content and seed glassy state. *Seed Science Research* **5**, 75–80.

Bettey, M. and Finch-Savage, W.E. (1996) Respiratory enzyme activities during germination in *Brassica* seed lots of differing vigour. *Seed Science Research* **6**, 165–173.

Bewley, J.D. (1997) Seed germination and dormancy. *Plant Cell* **9**, 1055–1066.

Bewley, J.D. and Black, M. (1994) *Seeds: Physiology of development and germination*. New York, Plenum Press.

Black, M., Corbineau, F., Gee, H., Guy, P. and Côme, D. (1999) Water content, raffinose, and dehydrins in the induction of desiccation tolerance in immature wheat embryos. *Plant Physiology* **120**, 463–471.

Blackman, S.A., Obendorf, R.L. and Leopold, A.C. (1992) Maturation proteins and sugars in desiccation tolerance of developing soybean seeds. *Plant Physiology* **100**, 225–230.

Boubriak, I., Kargiolaki, H., Lyne, L. and Osborne, D.J. (1997) The requirement for DNA repair in desiccation tolerance of germinating embryos. *Seed Science Research* **7**, 97–105.

Boudet, J., Buitink, J., Hoekstra, F.A., Rogniaux, H., Larre, C., Satour, P. and Leprince, O. (2006) Comparative analysis of the heat stable proteome of radicles of *Medicago truncatula* seeds during germination identifies late embryogenesis abundant proteins associated with desiccation tolerance. *Plant Physiology* **140**, 1418–1436.

Buckley, W.T. and Buckley, K.E. (2009) Low-molecular-weight volatile indicators of canola seed deterioration. *Seed Science and Technology* **37**, 676–690.

Buitink, J. and Leprince, O. (2008) Intracellular glasses and seed survival in the dry state. *Comptes Rendus Biologies* **331**, 788–795.

Buitink, J., Hemminga, M.A. and Hoekstra, F.A. (2000) Is there a role for oligosaccharides in seed longevity? An assessment of intracellular glass stability. *Plant Physiology* **122**, 1217–1224.

Capron, I., Corbineau, F., Dacher, F., Job, C., Côme, D. and Job, D. (2000) Sugarbeet seed priming: effects of priming conditions on germination, solubilization of 11-S globulin and accumulation of LEA proteins. *Seed Science Research* **10**, 243–254.

Carver, M.F.F. and Matthews, S. (1975) Respiratory measurements as indicators of field emergence ability in peas. *Seed Science and Technology* **3**, 871–879.

Catusse, J., Job, C. and Job, D. (2008a) Transcriptome- and proteome-wide analyses of seed germination. *Comptes Rendus Biologies* **331**, 815–822.

Catusse, J., Strub, J.-M., Job, C., Van Dorsselaer, A. and Job, D. (2008b) Proteome-wide characterization of sugarbeet seed vigour and its tissue specific expression. *Proceedings of the National Academy of Sciences, USA* **105**, 10262–10267.

Chatelain E. (2011) Contribution à la caractérisation des phases tardives de la maturation des graines de *Medicago truncatula*: une etude physiologique et biochimique pour comprendre la longévité. Doctoral thesis, Université d'Angers.

Chen, Y.Z. and Patterson, B.D. (1985) Ethylene and 1-aminocyclopropane-1-carboxylic acid as indicators of chilling sensitivity in various plant species. *Australian Journal of Plant Physiology* **12**, 377–385.

Chojnowski, M., Corbineau, F. and Côme, D. (1997) Physiological and biochemical changes induced in sunflower seeds by osmopriming and subsequent drying, storage and aging. *Seed Science Research* **7**, 323–331.

Côme, D. and Corbineau, F. (1989) Some aspects of metabolic regulation of seed germination and dormancy. pp. 165–179 *in* Taylorson, R.B. (Ed.) *Recent advances in the development and germination of seeds*. New York, Plenum Press.

Corbineau, F. and Côme, D. (2006) Priming: a technique for improving seed quality. *Seed Testing International* **132**, 38–40.

Corbineau, F., Engelman, F. and Côme, D. (1990) Ethylene production as an indicator of chilling injury in oil palm (*Elaeis guineensis* Jacq.) somatic embryos. *Plant Science* **71**, 29–34.

Corbineau, F., Bogatek, R., Picard, M.A. and Côme, D. (1999) Chilling injury in *Vigna radiata* seedlings and its evaluation by ethylene biosynthesis. pp. 241–248 *in* Sanchez-Diaz, M.; Irigoyen, J.J.; Aguirreolea, J.; Pithan, K. (Eds) *Crop development for cool and wet climate of Europe*. Luxembourg, Office for publications of the European Communities.

Corbineau, F., Picard, M.A., Fougereux, J.-A., Ladonne, F. and Côme, D. (2000) Effects of dehydration conditions on desiccation tolerance of developing pea seeds as related to oligosaccharide content and cell membrane properties. *Seed Science Research* **10**, 329–339.

Delouche, J.C. and Baskin, C.C. (1973) Accelerated aging techniques for predicting the relative storability of seed lots. *Seed Science and Technology* **1**, 427–452.

Gallardo, K., Job, C., Groot, S.P.C., Puype, M., Demol, H., Vandekerckhove, J. and Job, D. (2001) Proteomic analysis of Arabidopsis seed germination and priming. *Plant Physiology* **126**, 835–848.

Gorecki, R.J., Ashino, H., Satoh, S. and Esashi, Y. (1991) Ethylene production in pea and cocklebur seeds of differing vigour. *Journal of Experimental Botany* **42**, 407–414.

Halmer, P. (2000) Commercial seed treatment technology. pp. 257–286 *in* Black, M.; Bewley, J.D. (Eds) *Seed technology and its biological basis*. Boca Raton, CRC Press.

Halpin-Ingham, B. and Sundstrom, F.J. (1992) Pepper seed water content, germination response and respiration following priming treatments. *Seed Science and Technology* **20**, 589–596.

Hampton, J.G. (1995) Conductivity test. pp. 10–28 *in* van de Venter, H.A. (Ed.) *Seed vigour testing seminar*. Zurich, International Seed Testing Association.

Hampton, J.G. and TeKrony, D.M. (1995) *Handbook of vigour test methods*. Zurich, International Seed Testing Association.

Hendry, G.A.F. (1993) Oxygen, free radical processes and seed longevity. *Seed Science Research* **3**, 141–153.

Horbowicz, M. and Obendorf, R.L. (1994) Seed desiccation tolerance and storability: dependence on flatulence-producing oligosaccharides and cyclitols – review and survey. *Seed Science Research* **4**, 385–405.

ISTA (2006) *International rules for seed testing* (Edition 2006). Zurich, International Seed Testing Association.

Jalink, H., van der Schoor, R., Frandas, A., van Pijlen, J.G. and Bino, R.J. (1998) Chlorophyll fluorescence of *Brassica oleracea* seeds as a non-destructive marker for seed maturity and seed performance. *Seed Science Research* **8**, 437–443.

Job, C., Kersulec, A., Ravasio, L., Chareyre, S., Pépin, R. and Job, D. (1997) The solubilization of the basic subunit of sugar beet seed 11S globulin during priming and early germination. *Seed Science Research* **7**, 225–243.

Job, C., Rajjou, L., Lovigny, Y., Belghazi, M. and Job, D. (2005) Patterns of protein oxidation in Arabidopsis seeds and during germination. *Plant Physiology* **138**, 790–802.

Kermode, A.R. (1997) Approaches to elucidate the basis of desiccation-tolerance in seeds. *Seed Science Research* **7**, 75–95.

Khan, A.A. (1994) ACC-derived ethylene production, a sensitive test for seed vigour. *Journal of the American Society for Horticultural Science* **119**, 1083–1090.

Kranner, I., Kastberger, G., Hartbauer, M. and Pritchard, H.W. (2010) Non-invasive diagnosis of seed viability using infrared thermography. *Proceedings of the National Academy of Sciences, USA* **107**, 3912–3917.

Lanteri, S., Saracco, F., Kraak, H.L. and Bino, R.J. (1994) The effects of priming on nuclear replication activity and germination of pepper (*Capsicum annuum*) and tomato (*Lycopersicon esculentum*) seeds. *Seed Science Research* **4**, 81–87.

Lehner, A., Bailly, C., Flechel, B., Poels, P., Côme, D. and Corbineau, F. (2006) Changes in wheat seed germination ability, soluble carbohydrate and anti-oxidant enzyme activities in the embryo during the desiccation phase of maturation. *Journal of Cereal Science* **43**, 175–182.

Leprince, O. and Buitink, J. (2010) Desiccation tolerance: From genomics to the field. *Plant Science* **179**, 554–564.

Lin, T.P. and Huang, N.H. (1994) The relationship between carbohydrate composition of some tree seeds and their longevity. *Journal of Experimental Botany* **45**, 1289–1294.

McDonald, M.B. (1998) Seed quality assessment. *Seed Science Research* **8**, 265–275.

McDonald, M.B. (1999) Seed deterioration: physiology, repair and assessment. *Seed Science and Technology* **27**, 177–237.

Moore, R.P. (1973) Tetrazolium staining for assessing seed quality. pp. 347–366 *in* Heydecker, W. (Ed.) *Seed Ecology*. London, Butterworths.

Nijenstein, J.H. and Kruse, M. (2000) The potential for standardization in cold testing of maize (*Zea mays* L.). *Seed Science and Technology* **28**, 837–851.

Odawara, S., Watanabe, A. and Imaseki, H. (1977) Involvement of cellular membrane in regulation of ethylene production. *Plant and Cell Physiology* **18**, 569–575.

Ogé, L., Bourdais, G., Bove, J., Collet, B., Godin, B., Granier, F., Boutin, J.-P., Job, D., Jullien, M. and Grappin, P. (2008) Protein repair L-isoaspartyl methyltransferase 1 is involved in both seed longevity and germination vigour in Arabidopsis. *Plant Cell* **20**, 3022–3037.

Oracz, K., El-Maarouf-Bouteau, H., Farrant, J., Cooper, K., Belgazhi, M., Job, C., Job, D., Corbineau, F. and Bailly, C. (2007) ROS production and protein oxidation as novel mechanism of seed dormancy alleviation. *Plant Journal* **50**, 452–465.

Özbingöl, N., Corbineau, F., Groot, S.P.C., Bino, R.J. and Côme, D. (1999) Activation of the cell cycle in tomato (*Lycopersicon esculentum* Mill.) seeds during osmoconditioning as related to temperature and oxygen. *Annals of Botany* **84**, 245–251.

Porter, A.J.R., Borlakoglu, J.T. and John, P. (1986) Activity of the ethylene-forming enzyme in relation to plant cell structure and organization. *Journal of Plant Physiology* **125**, 207–216.

Powell, A.A. (1986) Cell membranes and seed leachate conductivity in relation to the quality of seed for soaking. *Journal of Seed Technology* **10**, 81–100.

Powell, A.A. (1995) The controlled deterioration test. pp. 73–87 *in* van de Venter, H.A. (Ed.) *Seed vigour testing seminar*. Zurich, International Seed Testing Association.

Powell, A.A. and Matthews, S. (1981) Evaluation of controlled deterioration, a new vigour test for small seeded vegetables. *Seed Science and Technology* **9**, 633–640.

Priestley, D.A. (1986) *Seed aging. Implications of seed storage and persistence in the soil*. Ithaca, NY, Cornell University Press.

Rajjou, L. and Debeaujon, I. (2008) Seed longevity: survival and maintenance of high germination ability of dry seeds. *Comptes Rendus Biologies* **331**, 796–805.

Rajjou, L., Gallardo, K., Debeaujon, I., Vandekerckhove, C., Job, C. and Job, D. (2004) The effect of α-amanitin on the Arabidopsis seed proteome highlights the distinct roles of stored and neosynthesized mRNAs during germination. *Plant Physiology* **134**, 1598–1613.

Rajjou, L., Huguet, R., Robin, C., Belghazi, M., Job, C. and Job, D. (2006) Proteomic investigation of the effect of salicylic acid on Arabidopsis seed germination and establishment of early defense mechanisms. *Plant Physiology* **141**, 910–923.

Rajjou, L., Lovigny, Y., Groot, S.P.C., Belghazi, M., Job, C. and Job, D. (2008) Proteome-wide characterization of seed aging in *Arabidopsis*: A comparison between artificial and natural aging protocols. *Plant Physiology* **148**, 620–641.

Salmen Espindola, L., Noin, M., Corbineau, F. and Côme, D. (1994) Cellular and metabolic damage induced by desiccation in recalcitrant *Araucaria angustifolia* embryos. *Seed Science Research* **4**, 193–201.

Samimy, C. and Taylor, A.G. (1983) Influence of seed quality on ethylene production of germinating snap bean seeds. *Journal of the American Society for Horticultural Science* **108**, 767–769.

Sanhewe, A.J. and Ellis, R.H. (1996) Seed development and maturation in *Phaseolus vulgaris*. I. Ability to germinate and to tolerate desiccation. *Journal of Experimental Botany* **47**, 949–958.

Scandalios, J.G. (1997) *Oxidative stress and the molecular biology of antioxidant defences*. New York, Cold Spring Harbor Laboratory Press.

Sinniah, U.R., Ellis, R.H. and John, P. (1998) Irrigation and seed quality development in seed rapid-cycling brassica: soluble carbohydrates and heat-stable proteins. *Annals of Botany* **82**, 647–655.

Sliwinska, E., Jing, H.-C., Job, C., Job, D., Bergervoet, J.H.W., Bino, R.J. and Groot, S.P.C. (1999) Effect of harvest time and soaking treatment on cell cycle activity in sugarbeet seeds. *Seed Science Research* **9**, 91–99.

Steadman, K.J., Pritchard, H.W. and Dey, P.M. (1996) Tissue-specific soluble sugars in seeds as indicators of storage category. *Annals of Botany* **77**, 667–674.

Still, D.W., Dahal, P. and Bradford, K.J. (1997) A single-seed assay for endo β-mannanase activity from tomato endosperm and radicle tissues. *Plant Physiology* **113**, 13–20.

Sun, W.Q. (1997) Glassy state and seed storage stability: the WLF kinetics of seed viability loss at T-Tg and the plasticization effect of water on storage stability. *Annals of Botany* **79**, 291–297.

Sun, W.Q. and Leopold, A.C. (1994) Glassy state and seed storage stability: a viability equation analysis. *Annals of Botany* **74**, 291–297.

TeKrony, D.M. (1993) Accelerated aging test. *Journal of Seed Technology* **17**, 110–121.

TeKrony, D.M. and Egli, D.B. (1997) Relationship between standard germination, accelerated ageing germination and field emergence in soyabean. pp. 593–600 *in* Ellis, R.H.; Black, M.; Murdoch, A.J.; Hong, T.D. (Eds) *Basic and applied aspects of seed biology.* Boston, Kluwer Academic Publisher.

Tunnacliffe, A. and Wise, M.J. (2007) The continuing conundrum of the LEA proteins. *Naturwissenschaften* **94**, 791–812.

Van Waes, J. (1995) The use of a cold-test to predict field emergence of maize in official variety trials in Belgium. *Seed Science and Technology* **23**, 211–224.

Vertucci, C.W. and Farrant, J.M. (1995) Acquisition and loss of desiccation tolerance. pp. 237–271 *in* Kigel, J.; Galili, G. (Eds) *Seed development and germination*. New York, Marcel Dekker.

Walters, C., Landré, P., Hill, L., Corbineau, F. and Bailly, C. (2005) Organization of lipid reserves in cotyledons of primed and aged sunflower seeds. *Planta* **222**, 397–407.

Wolkers, W.F., McCready, S., Brandt, W., Lindsey, G.G. and Hoekstra, F.A. (2001) Isolation and characterization of a D-7 LEA protein from pollen that stabilizes glasses *in vitro*. *Biochimica et Biophysica Acta* **1544**, 196–206.

Woodstock, L.W. and Grabe, D.F. (1967) Relationships between seed respiration during imbibition and subsequent seedling growth in *Zea mays* L. *Plant Physiology* **42**, 1071–1076.

Yang, S.F. and Hoffmann, N.E. (1984) Ethylene biosynthesis and its regulation in higher plants. *Annual Review of Plant Physiology* **34**, 155–189.