Available online at http://www.ijabbr.com

International journal of Advanced Biological and Biomedical Research

Volume 1, Issue 8, 2013: 885-898

Biochemical aspects of protein changes in seed physiology and germination

Morad Shaban

Young researchers club, Boroujed branch, Islamic Azad University, Boroujerd, Iran

ABSTRACT

Seed storage proteins are synthesized as sources of carbon, nitrogen and sulfur for the next generation of plants. Reactive oxygen species serve as second messengers for signal transduction; however, molecular targets of oxidant signaling have not been defined. Here, many researchers showes that ligand–receptor mediated signaling promotes reactive oxygen species– dependent protein carbonylation. Carbonylation of the majority of proteins occurred transiently. Protein carbonylation in response to ligand–receptor interactions represents a novel mechanism in redox signaling. The role of protein oxidation in dormancy alleviation could be discussed in relation to the nature of the carbonylated proteins. Carbonylation of storage proteins has previously been reported in dry mature Arabidopsis seeds, and it was suggested that carbonylation of these proteins facilitates their mobilization during germination. Also, in sunflower seeds, breaking of dormancy in the dry state may be associated with preparation for storage protein mobilization. Hence, ROS accumulation appears to be a key signal governing cell activity during after-ripening. The role of specific proteins in maintenance of seed viability or longevity has been well documented However, quality and hardiness in seeds determined by protein contrnt.

Key words: Protein, seed germination and seed physiology

INTRODUCTION

In higher plants, seed storage proteins are synthesized during seed development as nutritional sources of sulfur and nitrogen to be utilized during germination, and their accumulation varies according to the availability of nutrients in the soil (Tabe et al., 2002). Protein carbonylation is a type of protein oxidation that can be promoted by reactive oxygen species. It usually refers to a process that forms reactive ketones or aldehydes that can be reacted by 2,4-dinitrophenylhydrazine (DNPH) to form hydrazones (Yuichiro, et al, 2010). Direct oxidation of side chains of lysine, arginine, proline, and threonine residues, among other amino acids, in the ‘‘primary protein carbonylation’’ reaction produces DNPH detectable protein products (Stadtmanet al, 2000; Levine, 2002 and Butterfield and Stadtman, 1997). DNPH derivatizable protein products can also be formed in the ‘‘secondary protein carbonylation’’ reaction via the addition of aldehydes such as those generated from lipid peroxidation processes (Grimsrud et al, 2008 and Sayre et al, 2006) Although the biology of oxidative protein modifications is complex and remains incompletely

Corresponding Author E-mail: Shaban.morad@yahoo.com

defined, protein carbonylation and chemistry of the reactions that give rise to carbonyl groups have been well characterized (Stadtman and Levine, 2006). More recently, these methods contributed to a rapid progress in proteomic analyses of carbonylated proteins using two-dimensional gel electrophoresis, followed by immunoblotting and mass spectrometry. This redox proteomics approach allowed for the identification of carbonylated proteins in various diseases in humans, animals models, and cell models, and has provided important information to biologists by describing the effects of modifications by carbonyl species on protein function, as well as the consequences of such modifications at the cellular level (Yuichiro, et al, 2010). Reactive oxygen species (ROS) have been proposed to serve as second messengers for signal transduction processes. Numerous studies demonstrated that (1) ligand–receptor interactions produce ROS; (2) antioxidants block signal transduction; and (3) ROS can stimulate signaling events. ROS signaling is thought to play important roles in various diseases, including cancer, neurological disorders, immune diseases, and cardiovascular diseases. Although mechanisms of ROS actions during oxidant signaling have not been defined, protein thiols being the oxidation targets have been a popular concept (Chi Ming Wong, 2007). Recently, Lee and Helmann (2006) described a regulatory mechanism for the Bacillus subtilis PerR transcription factor by metal-catalyzed oxidation. Thus, other types of protein oxidation such as metalcatalyzed protein carbonylation may also be important for cell signaling. Seed dormancy, defined as the failure of viable mature seeds to germinate under favorable conditions, is assumed to be an important adaptive trait in nature, enabling seeds to remain quiescent until the conditions for germination and seedling establishment become favorable (Bewley, 1997; Bewley and Black, 1994; Finch-Savage and Leubner-Metzger, 2006). This trait can have an embryo and/or a coat component, hence the terms ‘embryo’ and ‘coat’ dormancy to distinguish between these two mechanisms. Under natural conditions, release of dormancy generally occurs during after-ripening (storage in dry conditions) or during stratification (imbibition at low temperature), which result in widening of the conditions allowing seed germination (Baskin and Baskin, 1998; Bewley, 1997; Bewley and Black, 1994; Donohue et al., 2005; Finch-Savage and Leubner-Metzger, 2006; Koornneef et al., 2002). After-ripening is an intriguing phenomenon as it occurs at low seed moisture contents. Under these extreme conditions, water is generally not available for biochemical reactions, and very little is known about the cellular and molecular mechanisms involved in this process. However, changes in gene expression and/or protein synthesis during after-ripening have been shown to occur in seeds (Leubner-Metzger, 2005; Bove et al., 2005; Cadman et al., 2006; Chibani et al., 2006), which presumably reflects the existence of hydrated pockets within cells or tissues of the mature seeds (Leubner-Metzger, 2005). Non-enzymatic reactions are also likely to occur during dry storage of seeds, such as lipid peroxidation (McDonald, 1999; Priestley, 1986; Wilson and McDonald, 1986) or the Amadori and Maillard reactions associated with free radical production and oxidation processes (Esashi et al., 1993; Murthy and Sun, 2000; Murthy et al., 2003; Sun and Leopold, 1995). Furthermore, several studies have documented the production of reactive oxygen species (ROS) during seed storage in the dry state (Bucharov and Gantcheff, 1984; Hendry, 1993; McDonald, 1999; Pukacka and Ratajczak, 2005). ROS can react with virtually all biological molecules including lipids, DNA and proteins. Because proteins have numerous biological functions, their oxidation may result in modification of their enzymatic and binding properties and lead to diverse functional changes. Oxidation of proteins can occur through a number of different mechanisms, such as the formation of disulfide cross-links and glycoxidation adducts, nitration of tyrosine residues, and carbonylation of specific amino acid residues (Davies, 2005). Recent studies have indicated that protein oxidation is not necessarily a deleterious phenomenon in plants (Job et al., 2005; Johansson et al., 2004). Moreover, cellular ROS may show some selectivity with respect to their targets. For example, H2O2, which is an oxidant, can react with specific molecules at specific sites (Davies, 2005; Halliwell and Gutteridge, 1999). Importantly, ROS have been invoked to play a role in cellular signaling (Bailly, 2004), raising the hypothesis that these compounds can facilitate the shift from a

dormant to a non-dormant status in seeds. Molecular chaperones are known to be targets of carbonylation in yeast and bacteria challenged by oxidative stress (Cabiscol et al., 2000; Tamarit et al., 1998). Increased cellular levels of reactive oxygen species are known to occur during seed development and germination, but the consequences in terms of protein degradation are poorly characterized.

Different Studies on seed physiology

Many studies has been performed on seed germination for protein changes. In animals, protein carbonylation has been widely used as a measurement of oxidative damage, and it has been shown to increase in aging tissues (Dalle-Donne et al., 2003; Ding et al., 2006; Nystro¨ m, 2005) but, in the plants such as sunflower seed system, protein carbonylation may result from an accumulation of ROS themselves, and from accumulated lipid peroxidation products such as malondialdehyde, which is known to react with lysine residues to form carbonyl derivatives (Burcham and Kuhan, 1996; Liu and Wang, 2005). Also, carbonylation of numerous proteins also occurs during Arabidopsis seed germination, although the germinated seeds gave rise to vigorous plantlets (Job et al., 2005). Moreover, it has also been suggested that ROS might play a key role in hormone signaling pathways (Kwak et al., 2006). A complex network of plant hormones, including abscisic acid (ABA), GAs, ethylene, auxin, brassinosteroids, and jasmonates, controls seed dormancy and germination (Finkelstein et al., 2008), but the cross talk between ROS and hormones is still poorly understood. Interestingly, in dormant sunflower (*Helianthus annuus*) seeds, whose dormancy is released by ethylene (Corbineau et al., 1990), cyanide triggered the expression of the transcription factor Ethylene Response Factor1 (ERF1), thus suggesting a cross talk between ethylene and cyanide pathways (Oracz et al., 2008). However, it has not been investigated so far whether ROS signal transduction might be involved in this cross talk. Sunflower (*Helianthus annuus* L.) seeds provide an excellent system for studying dormancy because they are deeply dormant at harvest, but this dormancy is progressively lost during dry storage (Corbineau et al., 1990). Their dormancy results from both seed coat- and embryo-imposed dormancy, the latter being involved in the failure to germinate at 10-15°C. However, the molecular mechanisms of embryo dormancy and of its release during after-ripening are still largely unknown. Krystyna Oracz, et al, (2007) To determine whether ROS production during after-ripening could be associated with protein oxidation (carbonylation), one-dimensional (1D) and two-dimensional (2D) PAGE of seed protein extracts were performed, and the presence of carbonyl groups was detected by Western blotting using the 2,4-dinitrophenylhydrazine (DNPH) immunoassay. They proposed that Dormancy is a characteristic feature of sunflower seeds at their harvest. This dormancy exhibits both seed coat and embryo components, and progressively appears during seed development on the mother plant (Corbineau et al., 1990). The seed-coat-imposed dormancy acts through the effects of phenolics on oxygen availability for the embryo, and is therefore expressed to a greater extent at temperatures, while the embryo-imposed dormancy is likely to be involved in the restriction of germination at temperatures below 15°C (Corbineau et al., 1990; Gay et al., 1991). After-ripening is associated with an accumulation of superoxide anions and hydrogen peroxide in the embryonic axes (Krystyna Oracz, et al, 2007). They also, proposed that by storing the seeds at various RH, it was possible to modulate the extent of dormancy release. This suggests that the water status within the embryo cell is likely to play a critical role in the process of after-ripening, and shows that hydrogen peroxide accumulation is tightly associated with the breaking of embryo dormancy as this compound only accumulated under conditions associated with dormancy release. Thus a causal link between ROS production, or at least H_2O_2 accumulation, and after-ripening is likely to exist, and this process is not just related to seed storage. This demonstrates that, in sunflower seeds, ROS production in the dry state is initiated after harvest, and that, in agreement with previous proposals that ROS can act as cell messengers (Bailly, 2004), these molecules could therefore act as a signal to allow dormancy release and favor

subsequent seed germination. However, it is also likely that prolonged storage of seeds in the dry state would be associated with a sustained production of ROS, which would lead to oxidative stress and to the related deteriorative events known to occur during seed aging (Bailly, 2004). In plants, and more especially in seeds, ROS may originate from the mitochondrial respiratory chain or be produced through the action of enzymes such as NADPH oxidase (Bailly, 2004). However, in dry tissues, such as in mature orthodox seeds, respiration is prevented and enzymes are presumably not active, which suggests the occurrence of other mechanisms for ROS production. At low moisture content, non-enzymatic reactions are known to occur, such as the Amadori and Maillard reactions (Priestley, 1986; Sun and Leopold, 1995) and lipid peroxidation (McDonald, 1999). Using model systems, such as those based on oil encapsulation in a glassy matrix, it has been demonstrated that glasses do not prevent oxygen diffusion, thus allowing autoxidation reactions of lipids (Andersen and Skibsted, 2002; Andersen et al., 2000; Nelson and Labuza, 1992). Howevwr, protein carbonyla tion results from oxidative attack on Arg, Lys, Pro or Thr residues of proteins, which can affect enzyme activities or alter susceptibility of the modified proteins to proteolysis (Berlett and Stadtman, 1997; Davies, 2005; Dunlop et al., 2002). Experimental data Krystyna Oracz, et al, (2007) clearly indicate that the occurrence of carbonylation of specific embryonic proteins during afterripening of sunflower seeds. They also suggested that An alternative possibility to account for our results could be a redistribution of carbonylated proteins in the various protein fractions (i.e. soluble and non-soluble proteins) because of cell structural changes occurring during after-ripening that would render the carbonylated proteins more soluble from the non-dormant axes than from the corresponding dormant ones. However, the fact that no marked ultrastructural changes occurred during after-ripening and that the soluble proteomes revealed by silver nitrate staining were very similar for the dormant and non-dormant axes does not favor this idea They suggested that, in the sunflower seed system, protein carbonylation may result from an accumulation of ROS themselves, and from accumulated lipid peroxidation products which is known to react with lysine residues to form carbonyl derivatives (Burcham and Kuhan, 1996; Liu and Wang, 2005). Thus, in sunflower seeds, breaking of dormancy in the dry state may be associated with preparation for storage protein mobilization. In animals, protein carbonylation has been widely used as a measurement of oxidative damage, and it has been shown to increase in aging tissues (Dalle-Donne et al., 2003; Ding et al., 2006; Nystro¨ m, 2005). In marked contrast, protein carbonylation may not be an inevitable consequence of tissue aging in plants. Also, in Arabidopsis, patterns of protein carbonylation vary widely during progression of the life cycle, and the extent of protein carbonylation drops abruptly prior to the vegetative to reproductive transition (Johansson et al., 2004). Carbonylation of numerous proteins also occurs during Arabidopsis seed germination, although the germinated seeds gave rise to vigorous plantlets (Job et al., 2005). The role of protein oxidation in dormancy alleviation could be discussed in relation to the nature of the carbonylated proteins(Krystyna Oracz, et al, 2007). Carbonylation of storage proteins has previously been reported in dry mature Arabidopsis seeds, and it was suggested that carbonylation of these proteins facilitates their mobilization during germination (Job et al., 2005).

Seed viability

During storage, aging causes deaths of a variable number of seeds, and dead seed provides valuable information on the maintenance of seed viability and the effects of aging (Revilla et al. 2009). Seed viability is a complicated trait controlled by genetic, developmental, and environmental factors (Bettey et al. 2000; Pukacka and Ratajczak 2007). One important factor governing the rate of viability loss is lipid peroxidation in consequence of an increased amount of free oxygen radicals (McDonald 1999). Lipid peroxidation has been demonstrated to be involved in seed aging in a variety of seeds (Linn and Pearce 1990).As a novel tool for protein identification and gene function analysis, proteomics become widely

applicable in seed research field (Gallardo et al. 2001; Job et al. 2005; Rajjou et al. 2006, 2008). Proteomic analysis revealed that the viability loss of Arabidopsis seed is related to protein changes in dry seeds and an inability of low-viability seeds to produce a normal proteome during germination (Rajjou et al. 2008). However, In sugarbeet, several metabolic pathways are found to contribute to seed viability (Catusse et al. 2008). The role of specific proteins in maintenance of seed viability or longevity has been well documented. For example, L-isoaspartyl methyltransferase1 is involved in both seed longevity and germination vigor in Arabidopsis and its reduced accumulation results in heightened sensitivity to controlled deterioration treatment (CDT) and loss of seed viability (Oge´ et al. 2008). Rice aldehyde dehydrogenase7 plays an important role in maintaining seed viability by detoxifying aldehydes generated by lipid peroxidation (Shin et al. 2009). By controlled deterioration test and proteomic analysis, group 2 late embryogenesis abundant (LEA) proteins (the dehydrin/RAB group) was shown to contribute to Arabidopsis seed viability (Rajjou et al.
2008).

LEA proteins

Late embryogenesis abundant proteins are characterized by high hydrophilicity and accumulate to high levels during the last stage of seed maturation (Dure et al. 1989; Espelund et al. 1992). They are classified into distinctive families, based on the sequence similarities and motifs conserved across species (Dure et al. 1989; Battaglia et al. 2008). Although the roles of LEA proteins remain speculative, there is evidence supporting their participation in acclimation and/or in the adaptive response to dehydration, low temperature, salinity, or exogenous ABA treatment stress (Ramanjulu and Bartels 2002; Fujita et al. 2005; Boudet et al. 2006; Battaglia et al. 2008). Their overexpression enhances tolerance to salt, drought, and osmotic stresses in transgenic plants (Brini et al. 2007). A recent study showed that the larger proteins (group 2 LEA proteins, the dehydrin/RAB group) seem to contribute to seed viability of Arabidopsis (Rajjou et al. 2008). However, A function assignment of two group 1 LEA proteins from mung bean implies a possible DNA/RNA binding function (Rajesh and Manickam 2006). Manfre et al. (2006) found that a group 1 LEA protein (ATEM6) is required for normal seed development in Arabidopsis.

HSP proteins

In plants, small heat shock proteins (sHSPs) are a numerous and diverse protein group. Changes in sHSPs expression are similar to those in LEA proteins at the time of dehydration and crucial developmental stages (Zur Nieden et al. 1995). Their expression in seeds responds to discrete development signals and may play a general protective role in desiccation tolerance. Arabidopsis mutants sensitive to desiccation contain smaller amounts of HSP17.4 during maturation (Wehmeyer and Vierling 2000). Different HSPs may have different functional properties but common to all of them is their capacity to interact with other proteins and to act as molecular chaperones (Feder and Hofmann 1999). However, HSP17.2 is found to be up-regulated in response to fungal infection in maize embryos (Mittler 2002).

Proteins, seed hardness and seed quality

Numerous parameters like milling, chemical, baking and rheological dough properties influence the wheat quality. Seed quality is a produce of overall contribution of seed stock, effects of soil, climate, and kernel components. It may also be defined in terms of its suitability for a particular purpose or use (Finney et al., 1987). Factors that persuade seed quality have been broadly classified into two groups: physical and chemical characteristics. Grain vitreousness, color, weight shape and hardness are some

essential physical characteristics, which influence wheat grain quality (Gaines et al., 1996) while chemical characteristics include protein content, SDS-sedimentation value and gluten strength, etc. The major determinants of softness and hardness are particle size index (Osborne et al., 2001), energy required for grinding a selected weight of sample (Kosmolak, 1978), pearling value (Kramer and Albrecht, 1948) and near infrared reflectance (Manely et al., 1996). For example in wheat the interaction between carbohydrates and proteins strongly influence the processing quality of flour and is closely related with the hardness of endosperm (Preston, 1998). There are two main types of protein fraction which are associated tightly with starch granules, storage proteins and starch granule-associated proteins. Proteins which remain adsorbed to the starch granules surface even after extraction of starch are glutenins and gliadins, also called grain storage protein. As the starch granule-associated proteins (SGAPs) are tightly bound to the surface or integral starch component, so these proteins are biologically different from plant storage proteins (Baldwin, 2001). The SGAPs have been divided into two groups on the basis of molecular weights: low molecular weight proteins which are termed as 'surface' SGAPs; and proteins with higher molecular weight which are called 'internal' granule-associated starch proteins (Baldwin, 2001). The proteins of more interest for scientists are the 15 kDa 'group of polypeptides' in which the major sub-group is puroindoline and is also termed as friabilin. It has been indicated by the SDS-PAGE that the friabilin band is prominent in soft wheat varieties; wheat of hard character; has a faint band, while it is totally lacking in durum wheat (Schofield and Greenwell, 1987). The discovery of friabilin, a starch granule protein, which linked with the texture and quality of wheat grain, formed the biochemical basis for assessment of kernel texture. The protein complex friabilin regulates adhesion degree of starch granules to the protein matrix and this factor is of great importance as it tells about the hardness (Beecher et al., 2002). Two main components are present in friabilin: Pin a and Pin b puroindoline (Wanjugi et al., 2007). The puroindolines have five disulfide bonds with tryptophan-rich domains, hence these proteins were named owing to the unique tryptophan-rich region, which has an indole ring (puros means wheat and indoline from indole ring of tryptophan) (Dubreil et al., 1997). The puroindolines are categorized as lipid-binding proteins and grain softness is controlled by these proteins having various transgenic changes (Giroux and Morris, 1998). Grain hardness is normally influenced by various environmental, physical and chemical factors like kernel protein, vitreousness of grain, kernel size, water-soluble pentosans, moisture content and lipid content (Turnbull and Rahman,2002). For example, in wheat high protein content tends to be hard, have strong gluten and produce good quality bread. Wheat of low protein content tends to be soft, have weak gluten and produce small loaves of inferior crumb structure (Tipples et al., 1994), but produce better quality cookies. The higher protein content and density are exhibited only by vitreous kernels than that of those kernels which are starchy or mealy, as air pockets account for low density. The total protein content showed nonsignificant correlation with kernel hardness (Miller et al., 1984), while in some individual varieties no correlation was found (Pomeranz et al., 1985). Environmental factors are able to affect composition of grain protein but this protein composition and concentration are genetically controlled parameters (Zhu and Khan, 2001).

CONCLUSION

The role of protein oxidation in dormancy alleviation could be discussed in relation to the nature of the carbonylated proteins. Carbonylation of storage proteins has previously been reported in dry mature Arabidopsis seeds, and it was suggested that carbonylation of these proteins facilitates their mobilization during germination. Also, in sunflower seeds, breaking of dormancy in the dry state may be associated with preparation for storage protein mobilization. This mechanism involves a change in proteome oxidation, resulting from an accumulation of ROS during after-ripening. Hence, ROS accumulation appears to be a key signal governing cell activity during after-ripening. The role of specific proteins in

maintenance of seed viability or longevity has been well documented However, quality and hardiness in seeds determined by protein content.

REFERENCES

Andersen, A.B., Risbo, J., Andersen, M.L. and Skibsted, L.H. (2000) Oxygen permeation through an oil-encapsulating glassy food matrix studied by ESR line broadening using a nitroxyl spin probe. Food Chem. 70, 499–508.

Andersen, M.L. and Skibsted, L.H. (2002) Detection of early events in lipid oxidation by electron spin resonance spectroscopy. Eur. J. Lipid Sci. Technol. 104, 65–68.

Baldwin P.M. (2001). Starch granule-associated proteins and polypeptides: a review. Starch/Sta¨rke 53: 475_503.

Boudet J, Buitink J, Hoekstra FA, Rogniaux H, Larre C, Satour P et al (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 Physiol 140:1418–1436

Battaglia M, Olvera-carrillo Y, Garciarrubio A, Campos F, Covarrubias AA (2008) The enigmatic LEA proteins and other hydrophilins. Plant Physiol 148:6–24

Butterfield DA, and Stadtman ER. Protein oxidation processes in aging brain. In: Advances in Cell Aging and Gerontology Volume 2, edited by Timiras PS and Bittar EE.

Greenwich, CT: JAI Press, 1997, pp. 161–191.

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, 2nd edn. New York: Plenum Press.

Finch-Savage, W.E and Leubner-Metzger, G. (2006) Seed dormancy and the control of germination. New Phytol. 171, 501–523.

Baskin, J.M. and Baskin, C.C. (1998) Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination. San Diego, CA: Academic Press.

Donohue, K., Dorn, L., Griffith, C., Kim, E., Aguilera, A., Polisetty, C.R. and Schmitt, J. (2005) Niche construction through germination cueing: life-history responses to timing of germination in Arabidopsis thaliana. Evolution 59, 771–785.

Davies, M.J. (2005) The oxidative environment and protein damage. Biochim. Biophys. Acta, 1703, 93–109.

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

Johansson, E., Olsson, O. and Nystro¨m, T. (2004) Progression and specificity of protein oxidation in the life cycle of Arabidopsis thaliana. J. Biol. Chem. 279, 22204–22208.

Halliwell, B. and Gutteridge, J.M.C. (1999) Free Radicals in Biology and Medicine, 3rd edn. New York: Oxford University Press.

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

Cabiscol, E., Piulats, E., Echave, P., Herrero, E. and Ros, J. (2000) Oxidative stress promotes specific protein damage in Saccharomyces cerevisiae. J. Biol. Chem. 275, 27393–27398.

Tamarit, J., Cabiscol, E. and Ros, J. (1998) Identification of the major oxidatively damaged proteins in Escherichia coli cells exposed to oxidative stress. J. Biol. Chem. 273, 3027–3032.

Corbineau, F., Bagniol, S. and Coˆ me, D. (1990) Sunflower (Helianthus annuus L.) seed dormancy and its regulation by ethylene. Isr. J. Bot. 39, 313–325.

Gay, C., Corbineau, F. and Coˆ me, D. (1991) Effects of temperature and oxygen on seed germination and seedling growth in sunflower (Helianthus annuus L.). Environ. Exp. Bot. 31, 193–200.

Stadtman ER and Levine RL. Protein oxidation. Ann NY Acad Sci 899: 191–208, 2000.

Levine RL. Carbonyl modified proteins in cellular regulation, aging, and disease. Free Radic Biol Med 32: 790–796, 2002.

. Krystyna Oracz, Hayat El-Maarouf Bouteau, Jill M. Farrant, Keren Cooper, Maya Belghazi, Claudette Job, Dominique Job, Franc¸oise Corbineau and Christophe Bailly. 2007. ROS production and protein oxidation as a novel mechanism for seed dormancy alleviation. The Plant Journal. 10. 1-14.

Grimsrud PA, Xie H, Griffin TJ, and Bernlohr DA. Oxidative stress and covalent modification of protein with bioactive aldehydes. J Biol Chem 283: 21837–21841, 2008.

Sayre LM, Lin D, Yuan Q, Zhu X, and Tang X. Protein adducts generated from products of lipid oxidation: focus on HNE and one. Drug Metab Rev 38: 651–675, 2006.

Stadtman ER and Levine RL. Chemical modification of proteins by reactive oxygen species. In: Redox Proteomics: From Protein Modifications to Cellular Dysfunction and Diseases, edited by Dalle–Donne I, Scaloni A, and Butterfield DA. Hoboken NJ: John Wiley & Sons, 2006, pp. 3–23.

Burcham, P.C. and Kuhan, Y.T. (1996) Introduction of Carbonyl groups into proteins by the lipid peroxidation product, malondialdehyde. Biochem. Biophys. Res. Commun 220,

996–1001.

Corbineau F, Bagniol S, Coˆme D (1990) Sunflower (Helianthus annuus) seed dormancy and its regulation by ethylene. Isr J Bot 39: 313–325

Kwak JM, Nguyen V, Schoeder JI (2006) The role of reactive oxygen species in hormonal responses. Plant Physiol 141: 323–329

Finkelstein R, ReevesW, Ariizumi T, Steber C (2008) Molecular aspects of seed dormancy. Annu Rev Plant Biol 59: 387–415

Oracz K, El-Maarouf-Bouteau H, Bogatek R, Corbineau F, Bailly C (2008) Release of sunflower seed dormancy by cyanide: cross-talk with ethylene signalling pathway. J Exp Bot 59: 2241–2251

Dalle-Donne, I., Giustarini, D., Colombo, R., Rossi, R. and Milzani, A. (2003) Protein carbonylation in human diseases. Trends Mol. Med. 9, 169–176.

Ding, Q., Dimayuga, E. and Keller, J.N. (2006) Proteasome regulation of oxidative stress in aging and age-related diseases of the CNS. Antioxid. Redox Signal. 8, 163–172.

Nystro¨m, T. (2005) Role of oxidative carbonylation in protein quality control and senescence. EMBO J. 24, 1311–1317.

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

Liu, W. and Wang, J.Y. (2005) Modification of protein by polyunsaturated fatty acid ester peroxidation products. Biochim. Biophys. Acta. 1752, 93–98.

Tabe, L., Hagan, N. and Higgins, T.J. (2002) Plasticity of seed protein composition in response to nitrogen and sulfur availability. Curr. Opin. Plant Biol. 5, 212–217.

Preston K.R. (1998). Protein-carbohydrate interactions. In: Hamer R.J. and Hoseney R.C. (eds), Interactions: The Keys to Cereal Quality, St. Paul, MN: AACCI, pp. 83_91.

Finney K.F., Yamazaki W.T., Youngs V.L. and Rubenthaler G.L. (1987). Quality of hard, soft and durum wheats. In: Geyne E.G. (ed.), Wheat and Wheat Improvement, 2nd edn. Medison, WI: Agronomy Monograph No. 13, pp. 667_748.

Gaines C.S., Finney P.F., Fleege L.M. and Andrews L.C. (1996). Predicting a hardness measurement using the single-kernel characterization system. Cereal Chemistry 73: 278_283.

Osborne B.G., Turnbull K.M., Anderssen R.S., Rahman S., Sharp P.J. and Appels R. (2001). The hardness locus of Australian wheat lines. Australian Journal of Agricultural Research 52: 1275_1286.

Kosmolak F.G. (1978). Grinding time-A screening test for kernel hardness in wheat. Canadian Journal of Plant Science 58:

415_420.

Kramer H.H. and Albrecht H.R. (1948). The adaptation to small samples of the pearling test for kernel hardness in wheat. Journal of the American Society of Agronomy 20: 422_431.

Manely M., McGill A.E.J. and Osborne B.G. (1996). Whole wheat grain hardness measurement by near infrared spectroscopy. In: Davis A.M.C. and Williams P. (eds), Near Infrared Spectroscopy: The Future Waves. Chichester, UK: NIR Publications, pp. 466_470.

Wanjugi H.W., Hogg A.C., Martin J.M. and Giroux M.J. (2007). The role of puroindoline A and B individually and in combination on grain hardness and starch association. Crop Science 47: 67_76.

Dubreil L., Compoint J.P. and Marion D. (1997). Interaction of puroindolines with wheat flour polar lipids determines their foaming properties. Journal of Agricultural and Food Chemistry 45: 108_116.

Giroux M.J. and Morris C.F. (1998). Wheat grain hardness results from highly conserved mutations in the friabilin components puroindoline a and b. The Proceedings of the National Academy of Sciences, USA 95: 6262_6266.

Turnbull K.M. and Rahman S. (2002). Endosperm texture in wheat. Journal of Cereal Science 36: 327_337.

Pomeranz Y., Peterson C.J. and Mattern P.J. (1985). Hardness of winter wheats grown under widely different climatic conditions. Cereal Chemistry 62: 463_467.

Zhu J. and Khan K. (2001). Effects of genotype and environment on glutenin polymers and bread making quality. Cereal Chemistry 78: 125_130.

Miller B.S., Pomeranz Y. and Afework S. (1984). Hardness (texture) of hard red winter wheat grown in a soft area and of soft red winter wheat grown in a hard wheat area. Cereal Chemistry 61: 201_203.

Tipples K.H., Kilborn R.H. and Preston K.R. (1994). Bread-wheat quality defined. In: Bushuk W. and Rasper V.F. (eds), Wheat: Production, Properties and Quality, Glasgow: Chapman and Hall, pp. 25_35.

Beecher B., Bettge A., Smidansky E. and Giroux M.J. (2002). Expression of wild type pin B sequence in transgenic wheat complements a hard phenotype. Theoretical and Applied Genetics 105: 870_877.

Schofield J.D. and Greenwell P. (1987). Wheat starch granule proteins and their technological significance. In: Morton I.D. (ed.), Cereals in a European Context. Chichester: Ellis Horwood, pp. 407_420.

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7:405–410

Feder ME, Hofmann GE (1999) Heat-shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. Ann Rev Physiol 61:243–282

Wehmeyer N, Vierling E (2000) The expression of small heat shock proteins in seeds responds to discrete development signals and suggests a general protective role in desiccation tolerance. Plant Physiol 122:1099–1108

Zur Nieden U, Neumann D, Bucka A, Neumann D (1995) Tissuespecific localization of heat-stress proteins during embryo development. Planta 196:530–538

Manfre AJ, Lanni LM, Marcotte WR (2006) The Arabidopsis group 1 late embryogenesis abundant protein ATEM6 is required for normal seed development. Plant Physiol 140:140–149

Rajesh S, Manickam A (2006) Prediction of functions for two LEA proteins from mung bean. Bioinformation 1:133–138

Brini F, Hanin M, Lumbreras V, Amara I, Khoudi H, Hassairi A et al (2007) Overexpression of wheat dehydrin DHN-5 enhances tolerance to salt and osmotic stress in Arabidopsis thaliana. Plant Cell Rep 26:2017–2026

Ramanjulu S, Bartels D (2002) Drought- and desiccation-induced modulation of gene expression in plants. Plant Cell Environ 25:141–151

Fujita Y, Fujita M, Satoh R, Maruyama K, Parvez MM, Seki M et al (2005) AREB1 is a transcription activator of novel ABREdependent ABA signaling that enhances drought stress tolerance in Arabidopsis. Plant Cell 17:3470–3488

Battaglia M, Olvera-carrillo Y, Garciarrubio A, Campos F, Covarrubias AA (2008) The enigmatic LEA proteins and other hydrophilins. Plant Physiol 148:6–24

Espelund M, Saeboe-Larssen S, Hughes DW, Galau GA, Larsen F, Jakobsen KS (1992) Late embryogenesis-abundant genes encoding proteins with different numbers of hydrophilic repeats are regulated differentially by abscisic acid and osmotic stress. Plant J 2:241–25

Dure L, Crouch M, Harada JJ, Ho THD, Mundy J, Quatrano R et al (1989) Common amino acid sequence domains among the LEA proteins of higher plants. Plant Mol Biol 12:475–486

Revilla R, Butro´n A, Rodrı´guez VM, Malvar RA, Orda´s A (2009) Identification of genes related to germination in aged maize seed by screening natural variability. J Exp Bot 60:4151–4157

Bettey M, Finch-Savage WE, King GJ, Campos F, Covarrubias AA (2000) Quantitative genetic analysis of seed viability and preemergence seedling growth traits in Brassica oleracea. New Phytol 148:277–286

Pukacka S, Ratajczak E (2007) Age-related biochemical changes during storage of beech (Fagus sylvatica L.) seeds. Seed Sci Res 17:45–53

McDonald MB (1999) Seed deterioration: physiology, repair and assessment. Seed Sci Technol 27:177–237

Linn SS, Pearce RS (1990) Changes in lipids in bean seeds (Phaseolus vulgaris) and corn caryopses (Zea mays) aged in contrasting environments. Ann Bot 65:452–456

Job CL, Lovigny Y, Belghazi M, Belghazi M, Job D (2005) Patterns of protein oxidation in Arabidopsis seeds and during germination. Plant Physiol 138:790–802

Gallardo K, Job C, Groot SPC, Puype M, Demol H, Vandekerckhove J et al (2001) Proteomic analysis of Arabidopsis seed germination and priming. Plant Physiol 126:835–848

Rajjou L, Belghazi M, Huguet R, Robin C, Moreau A, Job C et al (2006) Proteomic investigation of the effect of salicylic acid on Arabidopsis seed germination and establishment of early defense mechanisms. Plant Physiol 141:910–923

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

Catusse J, Strub JM, Job C, Van Dorsselaer A, Job D (2008) Proteome-wide characterization of sugar beet seed viability and its tissue specific expression. Proc Natl Acad Sci USA 105:10262–10267

Oge´ L, Bourdais G, Bove J, Collet B, Godin B, Granier F et al (2008) Protein repair L-isoaspartyl methyltransferase 1 is involved in both seed longevity and germination viability in Arabidopsis. Plant Cell 20:3022–3037

Shin JH, KimSR, AnG (2009) Rice aldehyde dehydrogenase7 is needed for seed maturation and viability. Plant Physiol 149:905–915

Nelson, K.A. and Labuza, T.P. (1992) Relationship between water and lipid oxidation rates: water activity and glass transition theory. In Lipid Oxidation in Foods (St Angelo, A.J., ed). Washington, DC: American Chemical Society, pp. 93–103.

Berlett, B.S. and Stadtman, E.R. (1997) Protein oxidation in aging, disease and oxidative stress. J. Biol. Chem. 272, 20313–20316.

Dunlop, R.A., Rodgers, K.J. and Dean, R.T. (2002) Recent development in the intracellular degradation of oxidized proteins. Free Radic. Biol. Med. 33, 894–906.

Burcham, P.C. and Kuhan, Y.T. (1996) Introduction of Carbonyl groups into proteins by the lipid peroxidation product, malondialdehyde. Biochem. Biophys. Res. Commun 220, 996–1001.

Liu, W. and Wang, J.Y. (2005) Modification of protein by polyunsaturated fatty acid ester peroxidation products. Biochim. Biophys. Acta. 1752, 93–98.

Ding, Q., Dimayuga, E. and Keller, J.N. (2006) Proteasome regulation of oxidative stress in aging and age-related diseases of the CNS. Antioxid. Redox Signal. 8, 163–172.

Dalle-Donne, I., Giustarini, D., Colombo, R., Rossi, R. and Milzani, A. (2003) Protein carbonylation in human diseases. Trends Mol. Med. 9, 169–176.

Nystro¨m, T. (2005) Role of oxidative carbonylation in protein quality control and senescence. EMBO J. 24, 1311–1317.

Koornneef, M., Bentsink, L. and Hilhorst, H. (2002) Seed dormancy and germination. Curr. Opin. Plant Biol. 5, 33–36.

Leubner-Metzger, G. (2005) Beta-1,3-glucanase gene expression in low-hydrated seeds as a mechanism for dormancy release during tobacco after-ripening. Plant J. 41, 133–145.

Bove, J., Lucas, P., Godin, B., Oge, L., Jullien, M. and Grappin, P. (2005) Gene expression analysis by cDNA-AFLP highlights a set of new signaling networks and translational control during seed dormancy breaking in Nicotiana plumbaginifolia. Plant Mol. Biol. 57, 593–612.

Cadman, C.S.C., Toorop, P.E., Hilhorst, H.W.M. and Finch-Savage, W.E. (2006) Gene expression profiles of Arabidopsis Cvi seeds during dormancy cycling indicate a common underlying dormancy control mechanism. Plant J. 46, 805–822.

Chibani, K., Ali-Rachedi, S., Job, C., Job, D., Jullien, M. and Grappin, P. (2006) Proteomic analysis of seed dormancy in Arabidopsis. Plant Physiol. 142, 1493–1510.

McDonald, M.B. (1999) Seed deterioration: physiology, repair and assessment. Seed Sci. Technol. 27, 177–237.

Priestley, D.A. (1986) Seed Aging. Implications for Seed Storage and Persistence in the Soil. Ithaca, NY: Cornell University Press.

Wilson, D.O. and McDonald, M.B. (1986) The lipid peroxidation model of seed aging. Seed Sci. Technol. 14, 269–300.

Murthy, U.M.N. and Sun, W.Q. (2000) Protein modification by Amadori and Maillard reactions during seed storage: roles of sugar hydrolysis and lipid peroxidation. J. Exp. Bot. 51, 1221– 1228.

Esashi, Y., Ogasawara, M., Go´ recki, R. and Leopold, A.C. (1993) Possible mechanisms of afterripening in Xanthium seeds. Physiol. Plant. 87, 359–364

Murthy, U.M.N., Kumar, P.P. and Sun, W.Q. (2003) Mechanisms of seed ageing under different storage conditions for Vigna radiate (L.) Wilczek: lipid peroxidation, sugar hydrolysis, Maillard reactions and their relationship to glass state transition. J. Exp. Bot. 54, 1057–1067.

Sun, W.Q. and Leopold, A.C. (1995) The Maillard reaction and oxidative stress during aging of soybean seeds. Physiol. Plant. 94, 94–104.

Bucharov, P. and Gantcheff, T. (1984) Influence of accelerated and natural aging on free radical levels in soybean seeds. Physiol. Plant. 60, 53–56.

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

Pukacka, S. and Ratajczak, E. (2005) Production and scavenging of reactive oxygen species in Fagus sylvatica seeds during storage at varied temperature and humidity. J. Plant Physiol. 162, 873– 885.

Lee JW, Helmann JD. 2006. The PerR transcription factor senses H_2O_2 by metal-catalysed histidine oxidation. *Nature*.;440:363–367.

Chi Ming Wong, Amrita K. Cheema, Lihua Zhang and Yuichiro J. Suzuki. 2007. Protein Carbonylation as a Novel Mechanism in Redox Signaling. *Circulation Research* is published by the American Heart Association. 102:310-318

Yuichiro J. Suzuki, Marina Carini, and D. Allan Butterfield. 2010. Protein Carbonylation. ANTIOXIDANTS & REDOX SIGNALING Volume 12, Number 3. 323-325.