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Full Length Research Paper

Biochemical Signature of Ultra-Long-Term Storage in Alfalfa (*Medicago sativa L.)* Seeds

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This study was carried out to evaluate the effect of long-term natural aging on germination capability and several biochemical characteristics regarding antioxidative response of both the dry seeds and the during germination of alfalfa (*Medicago sativa* L.) seeds stored for 42 years. Percent germination ratio of the seeds was monitored for 7 days. The activities of catalase, peoroxidase and superoxide dismutase, lipid peroxidation level, and the contents of phenolic matter and H_2O_2 were tested in both dry seeds and germinating seeds on 1st, 3rd and 7th days of germination. On the final day of seed germination, the percent germination was 35% in the 42-years old seeds while %96 in the control seeds (non-aged). In addition, the long-term aging caused an important increase in lipid peroxidation and total phenolic content in the aged dry seeds. Long-term aged seeds showed low H_2O_2 content and the activities of catalase, peroxidase and superoxide dismutase. Decreased germination ability of the aged legume seeds were well correlated with the increase in lipid peroxidation levels and the decrease in the activities of enzymatic antioxidants studied. However, during germination, the differences in biochemical parameters studied were not statistically significant in the aged seeds in comparison to their controls.

Keywords: Aging, alfalfa, antioxidant response, germination.

INTRODUCTION

All seeds undergo aging process during long-term storage which leads to deterioration in seed quality, especially in the humid tropical regions. However, the rate of seed deterioration can vary among various plant species (Merritt et al., 2003). Aged seeds show decreased vigour and produce weak seedlings that are unable to survive once reintroduced into a habitat (Atıcı et al., 2007). Many of the processes implicated in seed aging during storage appear to be free-radical mediated, and lipid peroxidation is suggested to be a primary cause of deterioration in stored seeds (Wilson and McDonald, 1986; McDonald, 1999). However, seeds are known to contain numerous antioxidant compounds, both enzymatic and non-enzymatic, which act to prevent oxidative damage by scavenging free radicals before they attack membranes or other seed components (Leprince et al., 1993; McDonald, 1999; Merritt et al., 2003). Some protective mechanisms involving free radical and peroxide scavenging enzymes, such as catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD) have been evaluated within the mechanism of seed aging (Hsu et al., 2003; Goel et al., 2003; Pukacka and Ratajczak, 2007).

Biochemical and physiological deterioration during seed aging has been studied mostly under accelerated aging conditions using high temperature and high seed water content (McDonald, 1999; Hsu et al., 2003). Under such storage conditions, seeds typically lose their viability within a few days or weeks. Although these studies allowed important progress towards the understanding of seed aging mechanisms, a major question has been raised whether mechanisms of seed aging are similar under conditions of accelerated aging and natural aging. According to some research, lipid peroxidation and the degradation of membrane phospholipids are major causes of seed aging under accelerated aging conditions (Wilson and McDonald, 1986; Walters, 1998; McDonald, 1999). Some studies regarding long-term seed storage

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also showed little or no lipid peroxidation and loss of phospholipids from seeds of rice (Matsuda and Hirayama, 1973), peanuts (Pearce and Abdel-Samad, 1980), soybean (Priestley and Leopold, 1983), and wheat (Petruzzelli and Taranto, 1984). We hypothesise that the studies on biochemical mechanisms in long-term stored seeds can supply an important contribution to the understanding of natural aging process in seeds.

The present study, therefore, focused on some biochemical mechanisms in the natural aged seeds of *Medicago sativa* which have been stored for 42 years. For this aim, we determined percent germination, lipid peroxidation degrees, activity levels of enzymatic antioxidants (CAT, POX and SOD) and phenolic matter and H_2O_2 contents in both aged and non-aged seeds of dry and germinating ones.

MATERIALS AND METHODS

Plant materials and growth conditions

Non-aged seeds (harvested on fall 2009) and 42-year-old seeds of Medicago sativa L. were obtained from Agricultural Faculty of Ataturk University, Erzurum, Turkey. The aged seeds have been stored since 1967 in a warehouse (tightly sealed polyethylene containers, dry and dark conditions) under cool temperature (15-20 °C). The seeds were surface sterilized with 1% sodium hypochloride for 5 min and thoroughly rinsed with distilled water. The seeds then were placed to germinate on Petri dishes containing double sterile filter papers and 6 ml distilled water. Germination was evaluated in the dark at 22 °C for 7 days. The percent germination of the seeds were monitored for 7 days and the samples obtained from the seeds or seedlings on 0, 1st , 3rd and 7th days were first frozen in liquid N_2 and then stored at -80 °C. Unless stated otherwise, frozen tissues were grinded in a mortar by means of a pestle for the assays.

Determination of total phenolic content

Total phenolics were determined spectrophotometrically (Shimadzu UV-1700, Japan) using the Folin-Ciocalteu reagent method. Samples (500 mg) were homogenized and extracted in 10 ml of acidified methanol (79 : 20 : 1, methanol : water : HCl (v/v)) at 80 °C. The extracts were clarified by centrifugation (15 000 x *g*) for 15 min at 4 °C (Mikro 22 R Hettich, Germany). The aliquots of supernatant were diluted to 5 ml and mixed with 0.5 ml of Folin- Ciocalteu solution (50 %); 5 min later, 1 ml of saturated sodium carbonate (Na_2CO_3) solution was added, and the mixture was made up to 7 ml. The reaction was left in a dark for 1 h, and then the absorbance of the mixture was measured at 725 nm. The total phenolic content of the extracts were determined as gallic acid equivalent using the standard curve prepared at different concentrations of gallic acid (100-1000 µg/ml) and reported as µg gallic acid equivalent /g tissue (Pukacka and Ratajczak 2007).

Determination of the malonyldialdehyde (MDA) content

The thiobarbituric acid (TBA) test, which determines MDA as an end product of lipid peroxidation, was used to measure lipid peroxidation in dry and germinating seeds. The protocol suggested by Velikova et al. (2000) was used with some modificactions. Tissue material (500 mg) was grinded by means of a pestle in 5 ml 0.1% (w/v) trichloroacetic acid (TCA) solution with sand in a mortar. The homogenate was centrifuged at 10 000 x *g* for 20 min and 1 ml of supernatant was divided into two eppendorph tubes as 0.5 ml per tube. Then; 1 ml 0.5% (w/v) TBA in 20% TCA, or 1 ml 20% TCA solution was added into these aliquots and they were incubated at 95°C for 30 min. The reaction was stopped by placing the reaction tubes in an ice bath for 5 min. and then centrifuged at 10 000 x *g* for 5 min. The absorbance of the supernatants was monitored at 532 and 600 nm. The value for non-specific absorption at 600 nm was subtracted. The amount of MDA-TBA complex was calculated from the extinction coefficient, 155 mM^{-1} cm^{-1}.

Determination of antioxidant enzyme activities

Tissue material (500 mg) was grinded in 5 ml of 10 mM potassium phosphate buffer (pH 7.0) containing 4% (w/v) polyvinylpyrrolidon (Av. M.W. = 25000). The homogenate was centrifuged at 12 000 x *g* for 30 min at 4 °C and supernatant obtained was used as enzyme extract. Catalase (EC 1.11.1.6) activity was measured by monitoring the decrease in absorbance at 240 nm in 50 mM phosphate buffer (pH 7.5) containing 20 mM H_2O_2. One unit of CAT activity was defined as the amount of enzyme that used 1 µmol H_2O_2 per min (Upadhyaya *et al.* 1985). Peroxidase (EC 1.11.1.7) activity was measured by monitoring the increase in absorbance at 470 nm in 50 mM phosphate buffer (pH 7.0) containing 1 mM guaiacol and 0.5 mM H_2O_2. One unit of POX activity was defined as the amount of enzyme that caused an increase in absorbance of 0.01 per min (Upadhyaya *et al.* 1985). The activity of superoxide dismutase (EC 1.15.1.1) was calculated by recording the decrease in absorbance of nitro-blue tetrazolium dye by the enzyme (Dhindsa *et al.* 1981). The reaction mixture contained 2 µM riboflavine, 13 mM methionine, 75 µM nitroblue tetrazolium chloride (NBT), 0.1 mM EDTA, 50 mM phosphate buffer (pH 7.8), 50 mM sodium carbonate and 0.1 ml of the enzyme fraction. Reaction was started by adding 0.06 ml 100 µM riboflavine solution and placing the tubes under two 30 W fluorescent lamps for 15 min. A complete reaction mixture without enzyme, which gave the maximal colour, served as control. Reaction was stopped by switching off the light. A non- irradiated complete reaction mixture served as a blank. The absorbance was recorded at 560 nm, and one unit of enzyme activity was taken as that amount of enzyme, which reduced the absorbance reading to 50% in comparison with tubes lacking enzyme (Dhindsa et al. 1981).

Determination of H_2O_2 content

Tissue material (500 mg) was grinded in 5 ml 0.1% (w/v) TCA with sand in a mortar on ice bath. The homogenate was centrifuged at 12000 x *g* for 15 min. 0.5 ml of the supernatant was mixed with the equal volume of 10 mM potassium phosphate buffer (pH 7.0) and 1 ml 1 M KI. The absorbance of the mixture was monitored at 390 nm. The content of H_2O_2 was calculated by using a standard curve (Velikova et al., 2000).

Statistical analysis

All experiments were performed 6 times. Data were analyzed by two-way analysis of variance (ANOVA) and means were compared by Duncan's multiple range test ($P<0.01$) using SPSS 15.0 for Microsoft Windows.

RESULTS AND DISCUSSION

We describe the effect of natural aging on the activites of radical-scavenging enzymes such as CAT, POX and SOD in both the dry (non-germinated) and germinating

seeds of the aged alfalfa seeds. In addition, lipid peroxidation degree, H_2O_2 and total phenolics contents were determined. All results were compared with respective non-aged controls. Alfalfa seeds used in the present study have been stored since 1967 in a warehouse under the warehouse conditions. In general, seed viability remains high over the storage period for all species stored under 23°C, and it is not possible to determine the optimum water content. However, detrimental effects of storage at -18°C were also evident for some seeds (Ellis, 1998; Merritt et al*.,* 2003). In our study, the long-term (42 years) storage significantly ($P<0.01$) reduced the percent germination of the aged alfalfa seeds, compared to their controls (non-aged seeds). On the final day of germination, the percent germination was 35% (data not shown). The germination speed of the same seeds was also importantly delayed by the natural aging. These results re-confirmed our previously research findings in which was indicated that the aging in the same seeds decreased both germination capacity and seedling growth (Atıcı et al*.,* 2007, Cakmak et al., 2009). Some researches also showed that germination capability could be negatively affected by both natural and accelerated aging (Walters, 1998; Rice and Dyer, 2001; Merritt et al*.,* 2003).See figure 1 and 2

High correlation between seed viability and total phenolic content has indicated their important role in the prevention of seed aging processes (Pukacka and Ratajczak, 2007). Phenolic compounds have ideal structural chemistry for free radical-scavenging activities, and it has been shown that they are more effective antioxidants in vitro than some antioxidant vitamins or enzymes (Rice-Evans et al., 1997) and they can be abundantly present in dry seeds (Shirley, 1998). In our study, phenolic matter (PM) content was insignificantly ($P<0.01$) high in the aged dry seeds of alfalfa as compared with control seeds (Fig. 1A). However, during germination, PM content in the aged seeds was higher on only 1st day of germination, but on the other days, there were no important change determined between the aged seeds and control seeds (Fig. 1A). Sredojevic et al. (2004) also reported that maize seeds, during first five days of accelerated aging, showed changes neither in germination nor in concentration of phenolics. After that period, an important decrease in germination and increase in total phenolic content was reported to be observed. It is seen that this result obtained from the aged maize in agreement with the result obtained from our study. The results can manifest that both in accelerating aging and in natural aging, the germination capacity of seeds decrease, which causes an increase in phenolic compounds in aged seeds.

On the other hand, the level of MDA, a product of the lipid peroxidation, was significantly ($P<0.01$) high in the aged dry seeds, compared to controls (Fig. 1B). High lipid peroxidation and oxidative stress have been observed during storage of various seeds and have been widely proposed as the major cause of deterioration during seed aging (Wilson and McDonald, 1986; McDonald, 1999; Pukacka and Ratajczak, 2005, 2007). Accelerated seed aging also resulted in increased lipid peroxidation (Kumar and Knowles, 1993, 1996; Chiu et al., 1995; Hsu et al., 2003). Our results show that high lipid peroxidation is one of the major results of the natural aging of the long-term stored alfalfa seeds. However, the degree of lipid peroxidation was not higher during the germination of the aged seeds than that of control seeds, even on 1st day of germination, MDA level of control seeds was found more than those of the 42-year-old seeds studied (Fig. 1B). May be it is because metabolism of the old-seeds are low due to their week germination capability, while metabolism velocites are fairly high in germinating control seeds, especially at the beginning of germination. Therefore, the lipid peroxidation degree can be stable between the germinating aged seeds and control seeds (non-aged). It has been known that the reactive oxygen species (ROS) ,major cause of lipid peroxidation in cell membranes, can be generated not only in metabolism during stress and aging, but also in metabolism of a plant under normal conditions (Kumar and Knowles 1993, 1996).

Previous data obtained from various species, such as sunflower (Bailly *et al.,* 1996), bean (Velikova et al*.,* 2000) and beech (Pukacka and Ratajczak, 2007), have demonstrated that an accumulation of MDA during seed aging is related to the accumulation of increased H_2O_2. Intriguingly, our results showed that H_2O_2 contents were low in the aged dry seeds of alfalfa (Fig. 1C). Furthermore, during germination, no important statistical difference could be observed between the aged and non- aged seeds (Fig. 1C). Similarly, Girard and Le Meste (1992) did not observe any correlation between free radical content and the viability of wheat seeds. Recently, Lehner et al. (2008) determined that loss of seed viability at 45 ºC and 100% RH (accelerated aging) was associated with an accumulation of H_2O_2 which was concomitant with a progressive decrease in CAT and SOD activities. In return, aging of the same seeds at 30 ºC and 75% RH was not associated either with changes in CAT and SOD or with an accumulation of H_2O_2. Although the loss of seed viability leads to cellular damage, different mechanisms might also be involved in mortality depending on aging conditions, mainly on water content (Kibinza et al*.,* 2006), temperature and the term of storage (Goel et al*.,* 2003), which might explain why H_2O_2 contents in the aged dry seeds studied here were low.

CAT activity was low significantly ($P<0.01$) in the aged dry seeds of alfalfa as compared to non-aged ones (Fig. 2A). This diversity between the aged and non-aged seeds (control) was also observed during germination for 7 days (Fig. 2A). It has been proposed that the activity of CAT usually decreases during accelerating seed aging (Chiu et al., 1995; Goel et al., 2003). Both POX and SOD

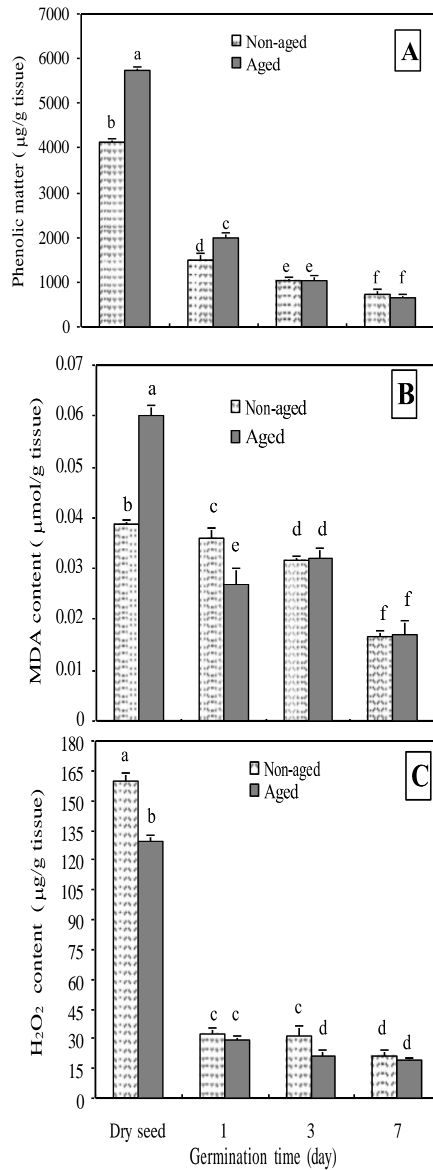

Figure 1. The effect of natural aging on the contents of phenolic matter, MDA and H_2O_2 in the dry and the germinating seeds of *Medicago sativa* seeds stored for 42 years. Different letters are significantly different (P<0.01) according to Duncan's multiple range test. Vertical bars represent standard errors.

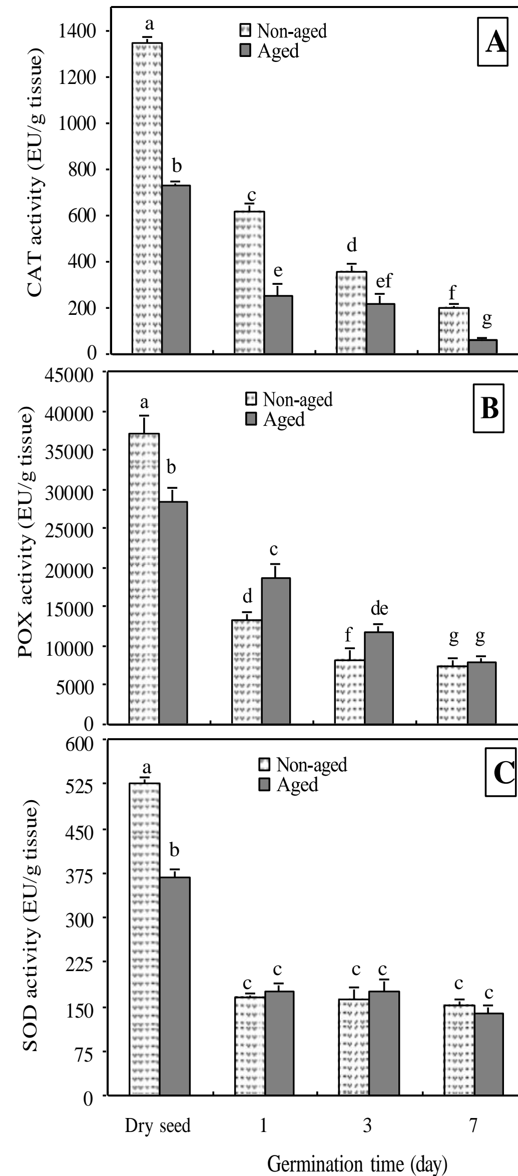

Figure 2. The effect of natural aging on the activities of antioxidant enzymes in the dry and the germinating seeds of *Medicago sativa* seeds stored for 42 years. Different letters are significantly different (P<0.01) according to Duncan's multiple range test. Vertical bars represent standard errors.

and SOD activities (Sung and Jeng, 1994; Chiu et al., 1995; Bailly et al., 1996; Goel et al., 2003). During germination, however, POX activity increased in the aged seeds on only 3rd and 7th days of germination (Fig. 2B). Enhanced peroxidase activity in germinating aged seeds was reported as an efficient growth signature (Gaspar et al., 1985), since they are involved in the control of cell

activities were significantly low in the aged dry seeds, compared to respective controls (Fig. 2B, C). Accelerated aging was reported to result in decreased level of POX elongation (Cooper and Varner, 1984) and related signalling processes, as well as seedling development (Puntarulo et al., 1991). We also observed a higher activity of POX in the germinating aged alfalfa seeds. The

result may show that POX activity can be low in naturally aged dry seeds, but its activity may be regulated during germination. However, it was shown that the contribution of biochemical reactions in mechanism of seed aging can also vary under different storage conditions (Murthy et al., 2003). During germination, SOD activity did not show any significant differences between the aged and non-aged seeds (Fig. 2C). Some studies showed that the activity of SOD decrease during artificial aging of some aged seeds such as beech (Pukacka and Ratajczak, 2005; 2007), cotton (Goel et al*.,* 2003) and soybean (Sung, 1996), on the other hand Spychalla and Desborough (1990) reported that there were not significant changes in free radical-scavenging enzymes such as SOD in older potato tubers.

In conclusion, the long term storage (42 years) reduced the germination capability, and caused a delay in the germination speed the of alfalfa *(M. sativa)* seeds. In addition, from antioxidant enzymes, CAT, POX, and SOD activities were also low in the aged dry seeds. However, total phenolic matter content and lipid peroxidation were high while H_2O_2 content was low. The decrease in germination capability of the aged dry seeds of alfalfa was well correlated with the increased levels of lipid peroxidation and phenolic content, and the decreased activities of POX, CAT and SOD. However, the most noticeable result was high POX and low CAT activity in long-term stored alfalfa seeds during the germination. Other biochemical parameters were not significantly different between the germinating aged and non-aged alfalfa seeds.

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