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Changes in color, antioxidant, and free radical scavenging enzyme activity of mushrooms under high oxygen modified atmospheres

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ABSTRACT

The effects of high oxygen concentration (80% O_2) on color, antioxidant enzyme and free radical scavenging activity of mushrooms (*Agaricus bisporus*) were investigated. High oxygen modified atmosphere chambers were designed. Mushrooms (*A. bisporus*) were held at 2 °C for 12 d in modified atmosphere chambers, linked by separate lines to continuous flow (1.67 mL s^{-1}) of humidified air (control) and 80% O_2 (balance N_2). Browning of mushroom flesh and surface exposed to 80% O_2 was prevented and the expected increase in membrane permeability and lipid peroxidation was delayed. Compared to the control treatment, high oxygen significantly inhibited the reactive oxygen species (ROS) such as $O_2^{\bullet -}$ and H_2O_2. The corresponding oxygen radical scavenging enzyme activities including SOD, CAT and POD in 80% O_2 were also higher than those in the control ($P < 0.05$). Higher antioxidant activity was found in high oxygen treated mushrooms. The treatment with 80% O_2 could be used in modified atmosphere of mushrooms to avoid browning, which was due to enhanced antioxidant and free radical scavenging enzyme activity.

1. Introduction

The commercial value of mushroom decreases within 2–3 d mainly because they have no cuticle to protect them from physical damage or microbial attack and water loss (Burton and Noble, 1993; Nerya et al., 2006). Browning is the major factor limiting shelf life of mushroom. High oxygen has been proposed as an alternative to low O_2 modified atmosphere in order to inhibit microbial growth and therefore maintain fresh sensory quality (Day, 1996; Amanatidou et al., 1999; Wszelaki and Mitcham, 2000; Jacxsens et al., 2001; Van der Steen et al., 2002). However, exposure to high oxygen concentrations may have very different effects, depending on the commodity. Thus, the effect of high oxygen concentration to control browning needs further investigation.

In previous work, high oxygen concentration was effective at maintaining the quality of mushrooms (Liu et al., 2010). Mushroom slices packaged under 80% O_2/20% N_2 and stored at 8 °C had more than 12-d shelf life (Day, 2001). But elevated O_2 concentrations can cause the production of reactive oxygen species (ROS), which could act as signals and secondary messengers for the activation of stress responses and defense pathways (Desikin et al., 2001; Knight and Knight, 2001). Susceptibility to oxidative stress depends on the overall balance between oxidants and antioxidant. Defense against oxidative stress in plants by preventing or reducing the damage from ROS includes enzymatic ROS scavenging systems and non-enzymatic antioxidant compounds. Enzymatic ROS scavenging systems include superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) (Asada, 1992; Scandalios, 1993). Non-enzymatic antioxidant compounds include reduced glutathione and various types of secondary metabolities mostly consisting of phenolic compounds. The behavior of these non-enzymatic compounds has also been linked to ROS scavenging activity (Tappel, 1972; Siddhuraju et al., 2002). It is still not clear whether high oxygen ameliorates or aggravates the production of ROS and reactive oxygen scavenging enzymes activities. Meanwhile, little information is available on the effect of high oxygen modified atmosphere on browning of mushrooms in relation to ROS metabolism.

The objective of our research was to determine the effects of the application of a high oxygen atmosphere of 80% O_2, balance N_2 on color, antioxidant enzyme and free radical scavenging activity of mushrooms that might be involved in browning control.

2. Materials and methods

2.1. High oxygen modified atmosphere chambers

High oxygen modified atmosphere box chambers were designed. The schematic diagram of the chambers used in the experiment is as shown in Fig. 1. The dynamic control system maintains the concentration of oxygen and carbon dioxide, and

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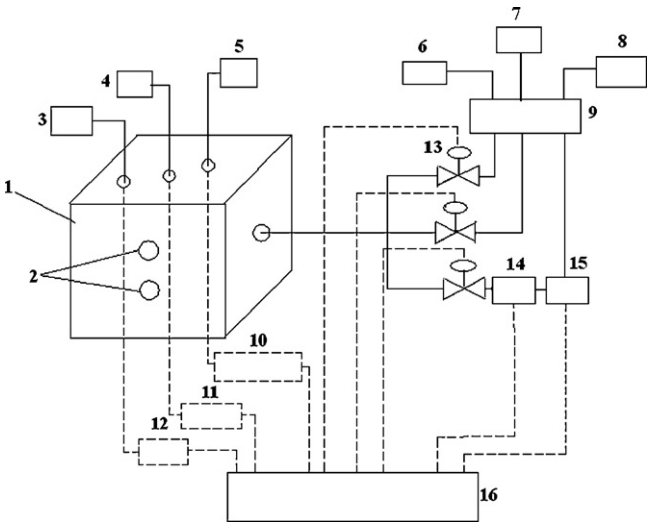

Fig. 1. The structure diagram of high oxygen modified atmosphere chamber (1) experimental chamber; (2) sampling hole; (3) CO_2 sensor; (4) O_2 sensor; (5) temperature and humidity sensor; (6) O_2 bottle; (7) CO_2 bottle; (8) nitrogen gas generator; (9) splitter fitting; (10) temperature and humidity transmitter; (11) O_2 transmitter; (12) CO_2 transmitter; (13) micro-metering valve; (14) solenoid valve; (15) flow meter; and (16) paperless recorder.

determines nitrogen flow, temperature and humidity of each chamber in real-time.

2.2. Sample preparation

Fresh mushrooms (*Agaricus bisporus*) were purchased from a local commercial greenhouse and brought to the laboratory within 1 h after harvest. Mushrooms were sorted to eliminate damaged mushrooms and were selected for uniform color and size. Mushrooms with cap size of 40–50 mm were selected. Three kilograms of mushrooms were placed in each high oxygen modified atmosphere chamber. There were three chambers at high oxygen and three at standard air conditions as controls. The chambers were held at 2 °C and linked by separate lines to continuous flow (1.67 mL s^{-1}) of humidified air (control), 80% O_2 (balanced with N_2). The relative humidity of the chambers remained at approximately 95%. Samples were taken initially and at 3-d intervals during storage.

2.3. Color measurement

Color was measured with a colorimeter (SC-80C, Kangguang Instrument Co., Ltd., Beijing, China). Surface and flesh color of mushrooms were evaluated for each treatment and sampling time. CIE L^* (lightness), a^* (red–green) and b^* (yellow–blue) parameters were measured from reflectance measurements. Color changes were described using a whiteness index (Eq. (1)) (Oms-Oliu et al., 2008).

$$WI = 100 - [(100 - L*)^2 + (a*)^2 + (b*)^2]^{1/2} \quad (1)$$

2.4. Measurement of membrane permeability

Membrane permeability was expressed by tissue electrolyte leakage. Electrolyte leakage was measured following a procedure from Liu et al. (2010).

2.5. Determination of lipid peroxidation

Lipid peroxidation was evaluated by measuring malondialdehyde (MDA) content. Mushroom tissue (1.5 g) was homogenized in 6 mL of 10% trichloroacetic acid (TCA) and centrifuged for 10 min at 4000 × *g*. The supernatant was collected to determine MDA concentration. A 2-mL aliquot of supernatant was mixed with 2 mL of 0.6% TBA and incubated for 15 min in boiling water, then cooled quickly and finally centrifuged for 10 min at 4000 × *g*. Absorbance of the supernatant was measured at 532 nm, 600 nm and 450 nm. MDA concentration was calculated using Eq. (2). Then MDA content was expressed as μmol kg^{-1}.

$$C(\mu mol/L) = 6.45(OD_{532} - OD_{600}) - 0.56OD_{450} \quad (2)$$

2.6. Determination of superoxide radical ($O_2^{\bullet -}$)

Superoxide radical was measured according to the method of Yan et al. (1996) with some modifications. Mushroom tissue (5 g) was homogenized with 20 mL of 50 mM Na-phosphate buffer (pH 7.8). The homogenate was centrifuged at 10,000 × *g* for 15 min. The supernatant was used for measuring the superoxide production rate. A 1-mL aliquot of the supernatant was mixed with 0.9 mL of 50 mM Na-phosphate buffer, pH 7.8 and 0.1 mL of 10 mM hydroxylammonium chloride. After incubation for 20 min at 25 °C, 1 mL of the above reaction mixture was added to 1 mL of 17 mM 4-aminobenzene sulfonic acid and 1 mL of 7 mM α-naphthylamine and mixed, then separated into two layers using ether to remove the interference caused by pigments. The absorbance, of the lower pink water-phase was measured at 530 nm.

2.7. Measurement of hydrogen peroxide (H_2O_2) content

The content of H_2O_2 in mushroom tissue was measured by monitoring the absorbance of the titanium-peroxide complex at 410 nm, following the method of Patterson et al. (1984). The absorbance was calibrated to a standard curve generated using known concentration of H_2O_2.

2.8. Enzyme assays

POD activity, using guaiacol as a substrate, was measured according to the method of Liu et al. (2010). POD activity were expressed as U kg^{-1} of mushroom.

The activity of superoxide dismutase (SOD) was measured according to Giannopolitis and Ries (1977), with slight modifications. SOD was extracted from 5 g of mushroom tissue ground in 4 mL of 50 mM phosphate buffer, pH 7.8, containing 1% PVPP at 4 °C. The supernatant was used to determine SOD activity. The reaction mixture (3 mL) contained 50 mM phosphate buffer (pH 7.8), 130 mM methionine, 100 μM EDTA-Na_2, 20 μM riboflavin, H_2O and 0.05 mL of enzyme extract. The mixtures were illuminated by 30 W light for 30 min and the absorbance was then determined at 560 nm. Identical solutions held in the dark served as blanks. One unit of SOD was defined as the amount of enzyme that caused a 50% decrease of the SOD-inhibitable NBT reduction. The results were expressed as units of activity (U) per kilogram of mushroom.

The activity of catalase (CAT) was assayed according to the method of Bailly et al. (1996), with slight modifications. CAT was extracted from 0.5 g of mushroom tissue in 6 mL of 50 mM phosphate buffer (pH 7.8) at 4 °C and then centrifuged at 10,000 × *g* for 20 min. One unit of CAT activity was defined as the increase in absorbance of 0.01/min under the conditions of the assay. The results were expressed as U kg^{-1} of mushroom.

2.9. Determination of total phenolic

Total phenolic contents in mushrooms were determined by the method of Folin-Ciocalteu reaction (Slinkard and Singleton, 1977) using gallic acid as a standard.

2.10. Analysis of DPPH radical scavenging activity

DPPH radical scavenging activity was assessed according to the method of Larrauri et al. (1998) with some modifications. Briefly, 2 mL of methanol extract was mixed with 2 mL of 0.2 mM DPPH-methanol solution. After the solution was incubated for 30 min at 25 °C in dark, the decrease of the absorbance at 517 nm was measured. The control contained methanol instead of DPPH solution. The scavenging of DPPH radicals by the samples was calculated according to the following equation: DPPH scavenging activity (%) = [1 − (absorbance of sample − absorbance of blank)/absorbance of control] × 100.

2.11. Superoxide radical scavenging activity

Superoxide radical scavenging activity was evaluated according to the method of determining SOD activity above mentioned.

2.12. Statistical analysis

Experiments were performed using a completely randomized design. Data were subject to statistical analysis by ANOVA. Least significant differences (LSDs) were calculated to compare significant effects at the 5% level.

3. Results and discussion

3.1. Color

Mushroom has a very short shelf-life, as it turns brown and loses its quality within only a few days. The browning of flesh and surface is a major postharvest problem for mushroom. As shown in Fig. 2, the whiteness index of mushroom flesh and surface decreased rapidly with storage time. Browning of mushrooms appeared after 3 d of storage and became serious after 9 d under air treatment. However, browning was found in mushrooms under high 80% O_2 on day 9. The mushrooms kept in air had a lower whiteness index, while high oxygen significantly delayed the decrease of the whiteness index. After 12 d of storage, the whiteness index for the control mushroom flesh and surface was respectively 69.67 and 69.65, while high oxygen treated mushroom flesh and surface had a whiteness index of 80.41and 71.94. The results showed that high oxygen concentration was effective at inhibiting discoloration of mushrooms. A similar result was obtained by Day (2003), Limbo and Piergiovanni (2006), who demonstrated the benefit and effectiveness of high oxygen levels (80–85%) to enzymatic browning. Zheng et al. (2000) and Duan et al. (2004, 2011) also found high oxygen treatment reduced browning of loquat and litchi fruit.

Enzymatic browning is related to a loss of membrane integrity, which resulted in the decompartmentalization of enzymes and substrates (Jiang et al., 2004; Liu et al., 1991). The flesh and surface of mushrooms treated with high oxygen showed higher whiteness index (Fig. 2). However, a detrimental effect of high oxygen concentration was also shown on the fruit quality of strawberry (Wszelaki and Mitcham, 2000) and sweet cherry (Jiang et al., 2002). Thus, the effect of high oxygen concentration on browning depended on the commodity, maturity, O_2 concentration and temperature.

3.2. Membrane permeability and lipid peroxidation

Relative leakage rate is generally considered an indirect measure of cell membrane damage. Changes in relative leakage rate of mushrooms were presented in Fig. 3A. In general, relative leakage rate in mushrooms increased with the storage, which was consistent with the decline in whiteness index. The initial relative leakage rate was 21.4%, while it increased respectively to 27.5% and 34.3%

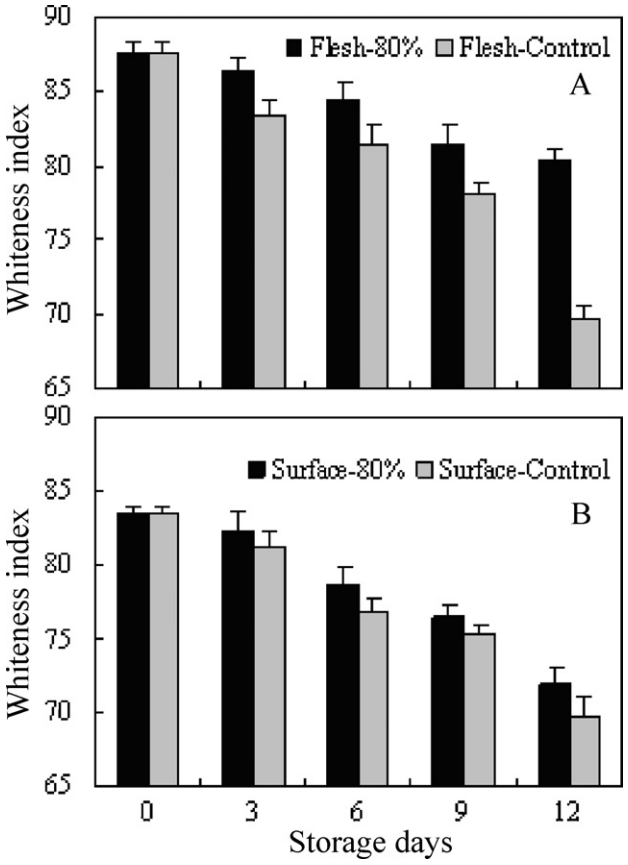

Fig. 2. Whiteness index of mushroom flesh (A) and surface (B) under 80% O_2 and air during storage at 2 °C. Each value was presented as a mean ± standard error (n = 3).

under 80% O_2 and air. Higher relative leakage rate was found under normal air (P < 0.05). Duan et al. (2011) suggested that pure oxygen alleviated the relative leakage rate, which resulted in the retention of compartmentalization of enzymes and substrate. Cantos et al. (2002) also found that membrane stability is potentially a major factor of controlling the browning. Our results showed that the loss of membrane integrity was associated with the browning of mushrooms (Fig. 2).

The level of lipid peroxidation was measured in terms of MDA content (Fig. 3B). During the storage of 12 d, MDA content increased from the initial value (1.75 μmol kg^{-1}) to 3.52 μmol kg^{-1} under control treatment, while 1.75–2.75 μmol kg^{-1} under 80% O_2. Marked increase in MDA content of mushrooms stored in air was found. The difference was significant (P < 0.05). The results indicated that high oxygen treatment could prevent the existence of mushroom oxidative injury to some degree. Our results are in agreement with those of Duan et al. (2011) who found that pure oxygen could significantly inhibit the accumulation of MDA in litchi fruit. Zheng et al. (2008) had also reported that there were higher levels of MDA content in Chinese bayberry under high oxygen. In the study, the decrease of relative leakage rate was correlated with the loss of membrane integrity, which could be partly due to lipid peroxidation.

3.3. Superoxide production rate and H_2O_2 content

Reactive oxygen species (ROS) such as $O_2^{\bullet -}$ and H_2O_2 have a role in lipid peroxidation, membrane damage and consequently in senescence. The effect of high oxygen concentration on $O_2^{\bullet -}$ production rate and H_2O_2 content was shown in Fig. 4. The $O_2^{\bullet -}$ production rate had marked increase during the first 3 d of storage,

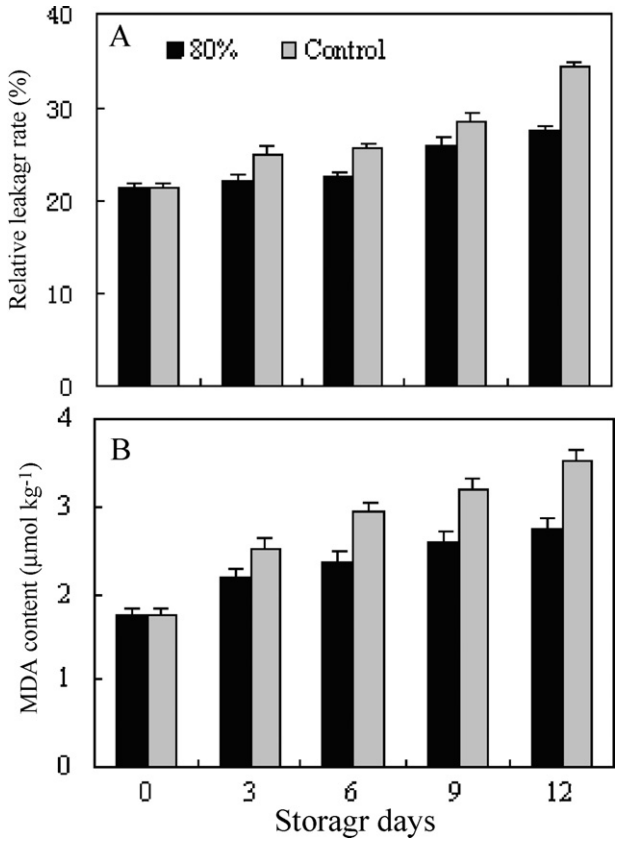

Fig. 3. Relative leakage rate (A) and MDA content (B) under 80% O_2 and air during storage at 2 °C. Each value was presented as a mean ± standard error ($n = 3$).

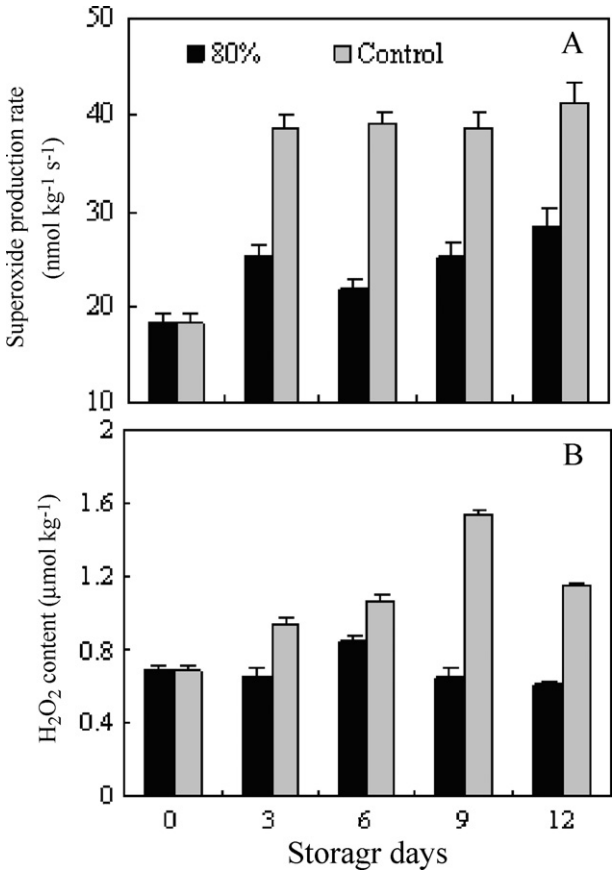

Fig. 4. $O_2^{\bullet -}$ production rate (A) and H_2O_2 content (B) under 80% O_2 and air during storage at 2 °C Each value was presented as a mean ± standard error ($n = 3$).

and was kept at high level at the end of storage (Fig. 4A). A higher level of $O_2^{\bullet -}$ production rate was noticed in mushrooms under the control treatment ($P < 0.05$). The results showed that high oxygen treatment had a significant inhibition on $O_2^{\bullet -}$ production.

The H_2O_2 content in mushrooms under the control and high oxygen treatments continually increased then decreased during storage (Fig. 4B). The contents of H_2O_2 in control mushrooms were 23.7% higher than those in high oxygen treated mushrooms on day 9. Application of high oxygen resulted in significantly lower H_2O_2 content compared with the control ($P < 0.05$).

The overproduction of ROS is an intrinsic feature of senescence and fruit ripening (Buchanan-Wollaston et al., 2003; Jiménez et al., 2002). The accumulation of ROS is one of the processes that contribute to loss of membrane integrity and membrane-bound enzyme activities (Bartoli et al., 1996). It has been reported that the $O_2^{\bullet -}$ formation and H_2O_2 accumulation of tomato fruit enhanced during ripening, as indicated by the increase in lipid peroxidation (Jiménez et al., 2002). Very little information is available on the effects of high oxygen concentration on H_2O_2 and $O_2^{\bullet -}$. High oxygen can be linked to lipid peroxidation and free radical formation (Marangoni et al., 1996). In this experiment, high oxygen concentration was associated with significantly lower levels of H_2O_2 and $O_2^{\bullet -}$ ($P < 0.05$), which might be due to the antioxidant protective system for membrane in response to the oxidative stress.

3.4. Oxygen radical scavenging enzyme activities

SOD, CAT and POD are important active free-radical scavenging enzymes (Lee and Lee, 2000; Scandalios, 1993). The changes of these enzyme activities were shown in Fig. 5. POD activity showed a marked increase during 9 d of storage (Fig. 5A). The significant increase of POD activity was found in high oxygen treated mushrooms ($P < 0.05$). The highest enzyme activity was detected in the mushrooms on day 9. At the end of storage, POD activity decreased. POD is ubiquitous enzymes that have diverse biochemical functions in higher plants. The activity of POD has been found to be higher in pure oxygen treated Chinese Bayberry fruit than air treated fruit (Yang et al., 2005). POD activity increased in high oxygen treated squash and peaked at around day 3–6 before it decreased, while POD activity increased substantially at day 6 in control samples (Zheng et al., 2008).

SOD was mainly responsible for catalyzing the reduction of superoxide radical to O_2 and H_2O_2, and CAT was responsible for eliminating H_2O_2. The mushrooms stored under high oxygen maintained remarkably higher SOD activity during storage (Fig. 5B). CAT activity in both treatments increased to a peak on day 6, and then decreased during the rest of the days (Fig. 5C). CAT activity showed significantly higher levels in the high oxygen treatments compared with the control ($P < 0.05$). A similar change pattern has been reported for litchi fruit stored under pure oxygen, where the activities of SOD and CAT were maintained at higher levels (Duan et al., 2011).

High levels of antioxidant enzymes are involved in alleviating oxidative damage and delaying the senescence process (Lacan and Baccou, 1998). In this work, the increase of POD, SOD and CAT activity has been found in mushrooms under high oxygen. Thus, the decrease of SOD, CAT and POD may contribute to the development of browning in mushrooms. The effectiveness of high oxygen in delaying the occurrence of browning may result from delaying the reduction of antioxidant enzymes during the storage. Some reports have shown that high oxygen induced the activities of SOD and CAT and maintained membrane integrity in peach (Wang et al., 2005) and loquat (Ding et al., 2006). The application of high

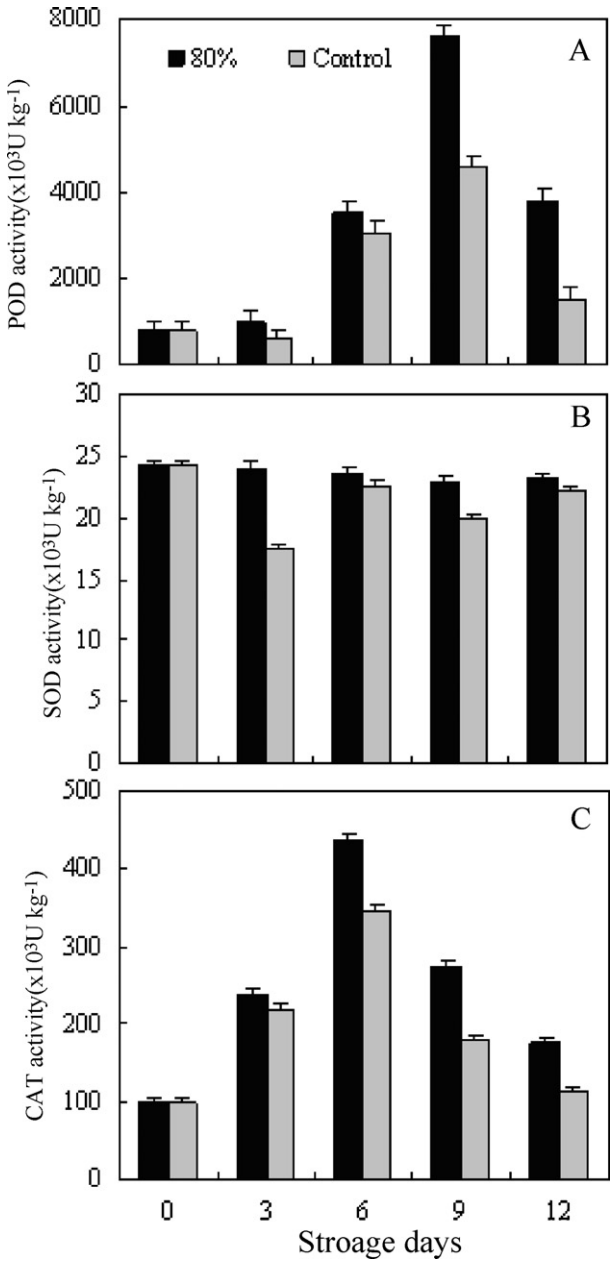

Fig. 5. POD (A), SOD (B), and CAT (C) activity under 80% O_2 and air during storage at 2 °C. Each value was presented as a mean ± standard error (n = 3).

oxygen concentration maintained higher activities of CAT and POD, and delayed the decay of Chinese bayberry (Yang et al., 2009).

3.5. Antioxidant activity

The initial phenolic content was about 1.00 g/kg in mushrooms (Table 1). The total phenolic content in high oxygen treated mushrooms exhibited an increase during the first 9 d, reaching a maximum accumulation about 1.59 g/kg. Thereafter, it decreased gradually. The phenolic content in mushrooms under air was 1.20 g/kg on day 9. There were significantly higher levels of total phenolic content in mushroom tissues under 80% O_2 (P < 0.05). Cocci et al. (2006) demonstrated that the oxygen availability in the package headspace of fresh-cut apples stored under air could lead to a stronger degradation of the functional compounds such as phenolics. It has been proved that the activity of phenylpropanoid pathway increases under stressful conditions and phenolic compounds are synthesized and accumulated (Kang and Saltveit, 2002).

DPPH-radical scavenging activity has been extensively used for screening antioxidant activity in plant extracts (Benjakul et al., 2005). As shown in Table 1, mushrooms exposed to 80% O_2 exhibited higher DPPH-radical scavenging activity after 6 d of storage (P < 0.05). The increase of phenolic content resulted in higher DPPH-radical scavenging activity, which, in turn, possibly accelerated the browning of mushrooms. Cheng et al. (2009) reported that lower DPPH-radical scavenging activity in Longan fruit stored at 60% O_2 might be due to oxidation of phenolic compounds.

Superoxide anion is an important radical that is involved in the formation of other cell-damaging free radicals. The superoxide radical scavenging activity of mushrooms at harvest was around 8% (Table 1). No significant differences were observed between high oxygen and the control in the first 3 d. After 3 d, comparable superoxide radical scavenging activity was found, and 80% O_2 was more efficient in increasing superoxide radical scavenging activity. At the end of storage, superoxide radical scavenging activity decreased in both treatments.

High oxygen induced a higher production of total phenolic and non-enzymatic antioxidant activity compared to the control. Antioxidant activity of fruits and vegetables is known to depend on a wide number of compounds. In our study, the increase in antioxidant activity was probably due to the synthesis of phenolic compounds, which may be related to induced stress metabolism. These results were consistent with those reported by Zheng et al. (2008), who found that significantly higher total phenolic content and DPPH-radical scavenging activity were obtained in high oxygen treated Chinese bayberry from day 6 to the end of storage. Duan et al. (2011) found that pure oxygen delayed the decrease of phenol compounds content and DPPH scavenging activity. According to Martínez-Sánchez et al. (2006), air treatment induced a particularly marked decrease in antioxidant capacity in leaves of wild rocket, which could be due to losses in some antioxidant constituents and total phenolic compounds.

Table 1
Total phenolic content, DPPH-radical scavenging activity and superoxide radical scavenging activity of mushroom under 80% O_2 and air during storage at 2 °C.

	0 d	3 d	6 d	9 d	12 d
Total phenolic content (g/kg)					
Air	1.00 ± 0.02a	1.33 ± 0.02a	0.98 ± 0.01b	1.20 ± 0.02b	0.98 ± 0.01a
80% O_2	1.00 ± 0.02a	1.15 ± 0.02b	1.49 ± 0.02a	1.59 ± 0.02a	1.12 ± 0.01a
DPPH-radical scavenging activity (%)					
Air	80.43 ± 1.51a	98.25 ± 1.80a	63.43 ± 1.32b	94.34 ± 1.57b	87.96 ± 1.02b
80% O_2	80.43 ± 1.51a	85.76 ± 1.73 b	99.67 ± 1.86a	97.49 ± 1.64a	94.73 ± 1.21a
Superoxide radical scavenging activity (%)					
Air	8.00 ± 0.93a	40.00 ± 2.46b	58.73 ± 2.35b	60.00 ± 2.35b	6.50 ± 0.53b
80% O_2	8.00 ± 0.93a	50.00 ± 2.23a	72.04 ± 2.61a	63.86 ± 2.46a	8.82 ± 0.51a

Data were expressed as the mean ± SEM of triplicate assays. Values in the same column with different letters for each day were significantly different at P < 0.05.

4. Conclusion

Postharvest metabolism of mushrooms was deeply modified by the application of high oxygen, which inhibited browning and delayed ripening. Mushrooms exposed to high oxygen concentration (80% O_2) were shown to have a higher whiteness index, and a lower increase in relative electrolyte leakage rate, lipid peroxidation, and ROS ($O_2^{\bullet-}$ and H_2O_2) production indicating lower membrane damage. Higher activities of SOD, POD and CAT and higher non-enzymatic antioxidant activities in mushrooms under high oxygen corresponded to low levels of ROS (H_2O_2 and $O_2^{\bullet-}$) accumulation, lipid peroxidation and relative electrolyte leakage rate. These effects were evidently responsible for reduced browning in mushroom flesh and surface during storage.

Acknowledgments

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